



Understanding spatial patterns of diversity and productivity in alpine plant communities: application of high-resolution imagery in the French Alps

Bradley Carlson

► To cite this version:

Bradley Carlson. Understanding spatial patterns of diversity and productivity in alpine plant communities: application of high-resolution imagery in the French Alps. Vegetal Biology. Université Grenoble Alpes, 2016. English. NNT: 2016GREAV057 . tel-01686736

HAL Id: tel-01686736

<https://theses.hal.science/tel-01686736>

Submitted on 17 Jan 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THÈSE

Pour obtenir le grade de

DOCTEUR DE LA COMMUNAUTE UNIVERSITE GRENOBLE ALPES

Spécialité : **Biodiversité Ecologie et Environnement**

Arrêté ministériel : 7 août 2006

Présentée par

Bradley Zeller CARLSON

Thèse dirigée par **Philippe CHOLER** et
Co-encadrée par **Wilfried THUILLER**

préparée au sein du **Laboratoire d'Ecologie Alpine (LECA)**
dans l'**École Doctorale de Chimie et des Science du Vivant**

Understanding spatial patterns of diversity and productivity in alpine plant communities: application of high-resolution imagery in the French Alps

Thèse soutenue publiquement le **14 novembre 2016**,
devant le jury composé de :

M. Niklaus ZIMMERMANN

Senior Scientist, WSL (Zurich), Rapporteur

Mme Isla MYERS-SMITH

Chancellor's Fellow, Univ. of Edinburgh, Rapporteur

Mme Sonja WIPF

Research Associate, WSL (Davos), Examineur

M. Björn REINEKING

Directeur de Recherche, IRSTEA (Grenoble), Président du jury

Mme Marie DUMONT

Chargée de Recherche, Météo France (Grenoble), Invitée

M. Cyrille VIOLLE

Chargé de Recherche, CNRS (Montpellier), Invité

M. Philippe CHOLER

Chargé de Recherche, CNRS (Grenoble), Directeur de thèse

M. Wilfried THUILLER

Directeur de Recherche, CNRS (Grenoble), Co-directeur de thèse



Abstract

Remote sensing is a promising means of quantifying spatial turnover in both environmental conditions and plant communities in the context of heterogeneous alpine landscapes. With the aim of contributing to understanding of responses of alpine plant communities to climate change in the context of the French Alps, I investigated the importance of quantifying snow cover duration at high-spatial resolution for predicting patterns of alpine plant community diversity, habitat and productivity. Using an observational approach in the Ecrins National Park, I also tested for long-term changes in the productivity of high-elevation plant communities in the context of land-use pressure and recent climate change. In Chapter I, I found that accounting for snow cover duration significantly improves predictions of taxonomic and functional diversity relative to standard topo-climatic predictors. In Chapter II, I demonstrate that satellite imagery shows strong agreement with ground-based measures of snow melt-out timing, and further show how metrics of snow cover duration and peak productivity can be used to differentiate habitat for dominant alpine plant communities at the regional scale. In the last chapter, I provide evidence from multiple satellite platforms pointing to recent “greening” of alpine vegetation in the Ecrins National Park. I propose that a decrease in snow cover duration and pronounced warming occurring in the 1980s likely contributed to increased canopy productivity in high alpine contexts, and are driving long-term greening independently of domestic grazing pressure. Taken collectively, my work emphasizes the need to quantify snow cover dynamics in order to understand responses of alpine plant communities to climate change, and highlights the complementarity between remote sensing and field-based approaches for addressing questions in alpine ecology.

Résumé

La télédétection représente un outil prometteur pour quantifier la variabilité spatiale à la fois des conditions environnementales et des communautés végétales dans le contexte des paysages alpins. Afin de mieux comprendre la réponse des plantes alpines au changement climatique dans les Alpes françaises, j’ai testé l’intérêt de quantifier la durée d’enneigement à haute résolution spatiale pour caractériser la diversité, l’habitat et la productivité au niveau des communautés végétales. Dans un contexte de réchauffement récent et de différentes pratiques pastorales, j’ai voulu également voir s’il y a eu des changements dans la productivité de la végétation d’altitude dans le Parc National des Ecrins pendant les dernières décennies. Dans le premier chapitre, je démontre que la prise en compte de l’enneigement améliore de manière significative les prédictions de la diversité taxonomique et fonctionnelle par rapport aux prédicteurs topo-climatiques classiques. Dans le deuxième chapitre, je trouve une forte relation entre la durée d’enneigement estimée par des capteurs au sol et par des images satellitaires, et j’applique cette information pour différencier l’habitat des communautés alpines en fonction de l’enneigement et leur productivité maximale. Je montre dans le dernier chapitre une tendance de « verdissement » de la végétation alpine dans le Parc National des Ecrins, que je confirme avec les satellites MODIS et Landsat. Je propose qu’une réduction dans la durée d’enneigement et un réchauffement marqué depuis la fin des années 1980s ont probablement contribué à une hausse de la productivité des canopées dans des contextes alpin et nival de haute altitude, et cela indépendamment de la pression pastorale. Pris ensemble, ce travail souligne l’importance de quantifier la dynamique nivale pour comprendre la réponse des plantes alpines au changement climatique, et met en évidence la complémentarité entre la télédétection et les suivis de terrain pour répondre aux questions fondamentales dans l’écologie alpine.

Acknowledgements

First thanks are due to my teachers and mentors growing up in Vermont – Jeff Munroe who introduced me to research, Marielle Aunave, Mike Martin and Annie Claude Roullet who taught me to speak French, and Justin Chapman, Joanne Moore and Anne Knowles who pushed me to write. And that's only to name a few of the wonderful teachers I have had along the way, all of whom gave me the ingredients to dive into whatever came next.

Five years ago I worked up the courage to ask Philippe to take me on as an intern at the end of an introductory course in R programming, during which I was completely lost. I found the subject and objectives of the course to be fascinating, however, and quickly understood that if I wanted to do remote sensing work on alpine plants this was my opportunity. Philippe accepted, and has since guided me on an extended intellectual adventure all over the French Alps. From co-writing our first paper in front of a projector, to teaching me the fundamentals of alpine ecology at the Col du Lautaret, to continually putting fresh ideas and rigor into my work, Philippe has been an outstanding advisor for me during these past years.

I am grateful to Wilfried, who believed in my abilities from the start and who readily welcomed me into the TEEMBIO group. Despite my stubbornness as a geographer, Wilfried has never given up and has continued to push me scientifically by introducing me to new ideas, people and opportunities during my time at the LECA. Beyond research-related goals, as a director I think that at the end of the day Wilfried truly has our best interest and wellbeing in mind, and I am thankful for this support.

I would also like to thank my unofficial advisors, who have always kept the big picture in mind: Seb, for making the Vermont-Grenoble connection and for encouraging me to do the master's program in the first place; Anne, for being patient with the twists and turns of my project and for always keeping a light on in Chamonix; and Cédric, for teaching me the basics of alpine botany and for encouraging me to pursue old dreams in the mountains.

Special thanks are due to Julien, Damien and Maya, the LECA engineers, without whom my work would never have gotten off the ground. In addition to helping me get the job done with good humor and style, these three have taught me most all of the skills I have learned over the last five years.

I am grateful to the LECA family for good times and support – Thibaut first and foremost, Monica et le bureau 313, Flo Maz, Loïc, Marc, Giovanni, Marta C., Ceres, Joao, Steph C., Matt, Laura, Hannah, Tamara, Flo and Laure, Steph Bec, Laure Z., Marti, Cristina, Jan, Flo A., Marta D., Amélie, Irène, Rolland, Thierry, and Florence...

And finally thanks to Hillary, who has been my companion throughout this adventure, and to my parents, who have supported my projects in France from the beginning.

Table of Contents

Introduction.....	1
i) General context.....	1
ii) Hierarchical drivers of plant distribution, diversity and growth in alpine landscapes.....	3
iii) Questions and aims.....	17
iv) Study area context in the French Alps.....	19
v) Remote sensing and alpine ecology: a combined approach.....	23
 Chapter I. Snow cover as a predictor of alpine plant diversity and productivity: a case study in the Vallon de Roche Noire.....	 39
Introduction.....	40
IA. Modeling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities (<i>Annals of Botany 2015</i>)	42
IIB. Contributions of solar energy availability and vegetation properties to high resolution gross primary productivity in an alpine watershed (<i>Unpublished</i>)	55
Discussion.....	78
 Chapter II. Quantifying alpine plant community habitat and growth responses: application of satellite imagery.....	 85
Introduction.....	86
IIA. On the importance of high-resolution time series of optical imagery for quantifying effects of snow cover duration on alpine plant habitat (<i>Remote Sensing 2016</i>)	88
IIB. Habitat mapping of alpine snowbed and wind-blown alpine meadows using multi-temporal satellite imagery (<i>Unpublished</i>)	110

IIC. Linking functional diversity to productivity responses of alpine plant communities for three contrasting growing seasons (<i>Unpublished</i>)	119
--	-----

Discussion.....	131
-----------------	-----

Chapter III. Long-term monitoring of vegetation changes in the French

Alps	134
-------------------	-----

Introduction.....	135
-------------------	-----

IIIA. Long-term modeling of the forest-grassland ecotone in the French Alps: implications for land management and conservation (<i>Ecological Applications 2014</i>)	137
--	-----

IIIB. Observed long-term greening of alpine vegetation in a protected area of the French Alps (<i>In prep.</i>)	151
---	-----

Discussion.....	175
-----------------	-----

Conclusion and perspectives	178
--	-----

Supplementary material	198
-------------------------------------	-----

S1. Working towards integrated models of alpine plant distribution (<i>Alpine Botany 2013</i>)	199
--	-----

S2. Accounting for treeline shift, glacier retreat and primary succession in mountain plant distribution models (<i>Diversity and Distributions 2014</i>)	213
---	-----

Introduction

I) General context

Monitoring and quantifying responses of natural systems to climate change has become a central objective for ecologists seeking to improve fundamental understanding of ecosystem dynamics and communicate key findings to the scientific community, policy makers and the general public. Earth surface temperatures have increased on average by 0.85 °C between 1880 to 2012, and the 1983 to 2012 period is very likely to have been the warmest 30-year period in the last 800 years in the Northern Hemisphere (IPCC 2014). Global-scale analyses indicate widespread “fingerprints” of recent climate change in all terrestrial biomes, expressed as directional shifts in species’ distributions and the timing of biological events, i.e. phenology (Parmesan and Yohe 2003; Thackeray *et al.* 2016).

Within the broader context of global change research, alpine ecosystems are considered to be especially sensitive to climate change and have received a substantial amount of targeted attention. Mountains contain exceptionally high biodiversity relative to their surface area and compared to other terrestrial environments (Körner 2004), and this unique flora and fauna represents a priority for conservation efforts. Distribution patterns of biota in mountainous areas are tightly linked to extreme variation in environmental gradients over short distances, particularly in the case of plants. Steep environmental gradients render alpine landscapes susceptible to abrupt shifts in plant distribution and abundance over brief time scales (Frei *et al.* 2010; Gottfried *et al.* 2012), and allow scientists to conduct “natural experiments” aimed at testing theories concerning the ecology and evolution of alpine biodiversity (Körner *et al.* 2011). Furthermore, mountainous areas provide a number of important ecosystem services to human populations. Plant cover influences both water runoff and erosion processes, which affect fresh water supply as well as exposure to slope-related risks such as rock fall, landslides and avalanches. Although alpine tundra ecosystems represent only a small proportion of biomass production relative to forest and non-mountainous grassland ecosystems (Knapp and Smith 2001), plant productivity in high-elevation areas determines pasture resource for domestic grazing that in many areas of the world constitutes a traditional form of subsistence agriculture.

Lastly, in addition to scientific and pragmatic arguments in support of the study of alpine vegetation, there is an undeniable subjective dimension that has appealed to generations of ecologists and which has motivated me during my studies, and that is simply the striking beauty of high places. Landscapes such as the one shown in Figure 1 inspire one to understand how this complex ecological system works and also how these “islands in the sky” might respond to ongoing climate change during the coming decades. The remainder of the introduction will (i) present state-of-the-art knowledge concerning drivers affecting alpine vegetation in a global change context, (ii) present the main scientific objectives and questions addressed in this thesis, (ii) introduce the study area context in the French Alps and (iv) present fundamental methodology applied throughout this work.

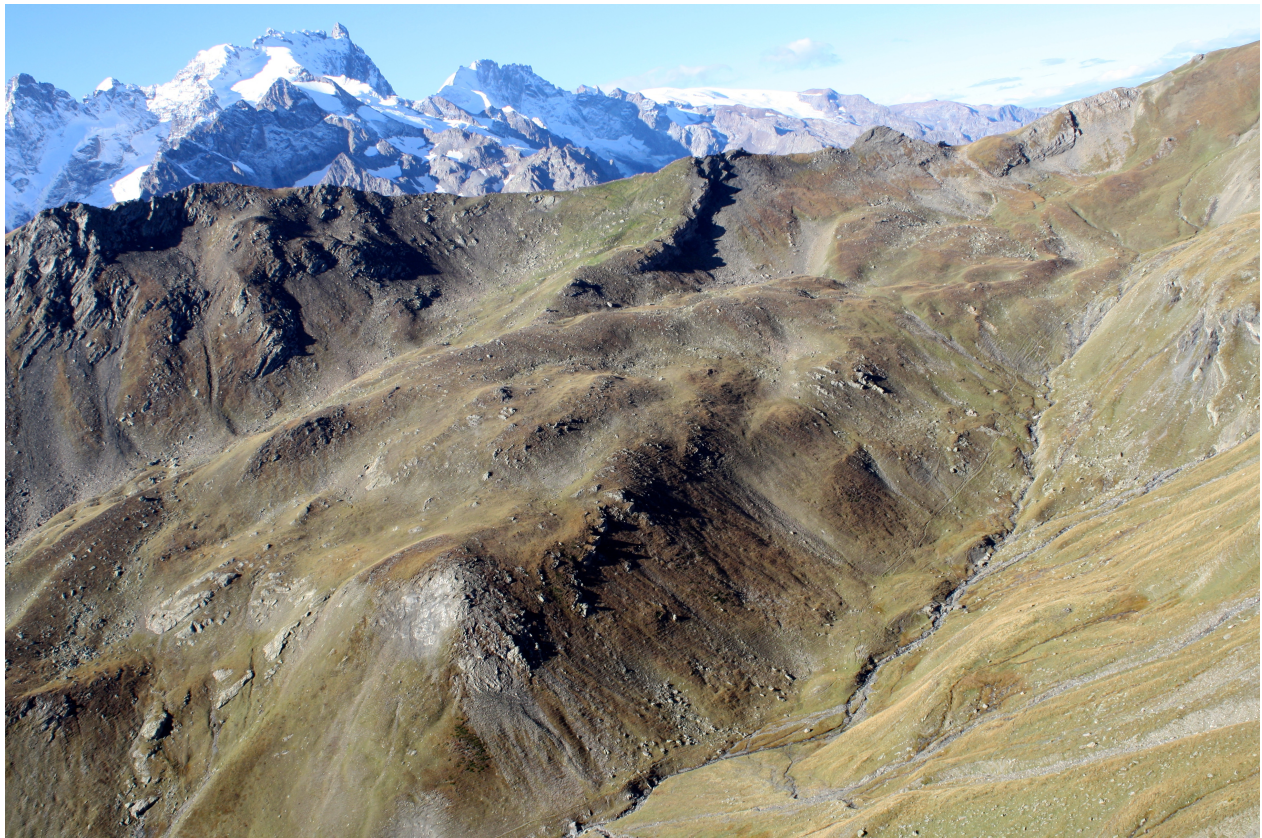


Figure 1. The northeast flank of the Vallon de Roche Noire situated above the Col du Lautaret (2057 m a.s.l.) in the French Alps, with the Grand Pic de la Meije (3984 m a.s.l.) and other summits of the Ecrins National Park in view. The Vallon de Roche Noire defines the study area for Chapter I, and is included in regional-scale analyses in Chapters II and III.

II) Hierarchical drivers of plant distribution, diversity and growth in alpine landscapes

Interactions between long-term climate change and geological processes define the landscapes and environmental conditions available to plants. Inferring when, where and how certain plants dispersed to mountainous areas or evolved key traits following mountain uplift or climate change is a challenging and fascinating area of investigation in alpine biogeography (e.g. Boucher *et al.* 2012), and one that is rendered all the more difficult by patchy historical evidence (Molnar and England 1990). In my work, while acknowledging the importance and scientific

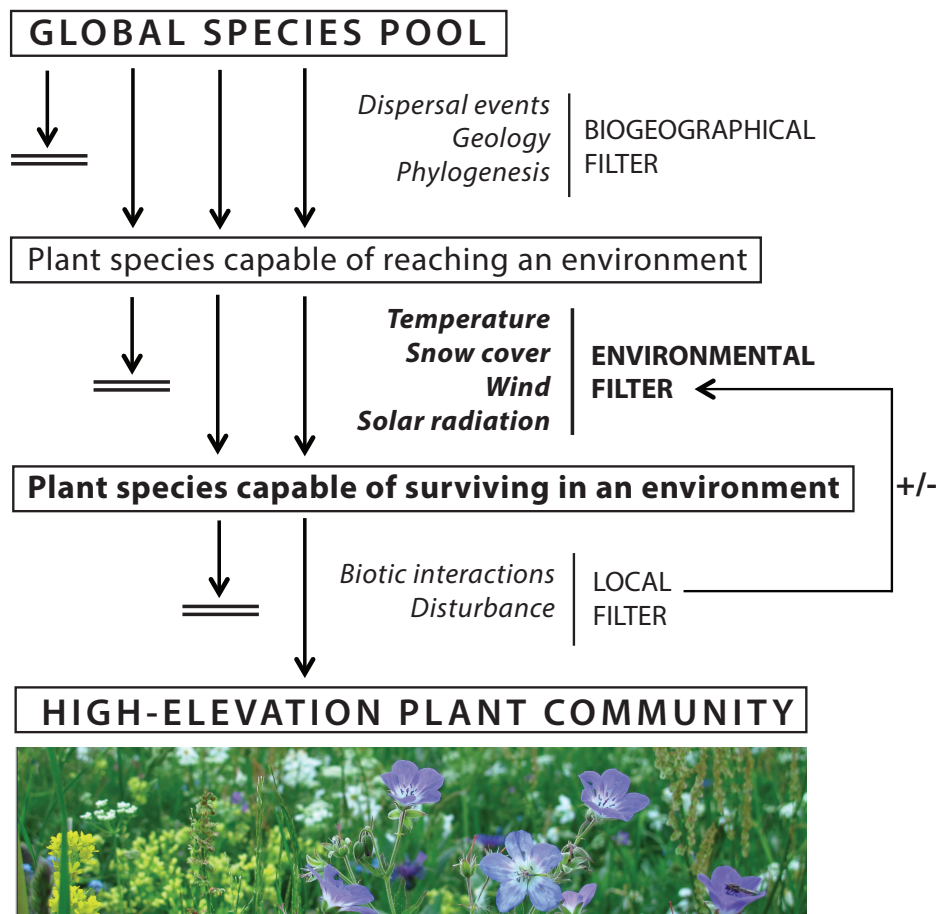


Figure 2. Successive filters structuring high-elevation plant communities observed in the field, based on a figure proposed in Lortie *et al.* (2004). My work is focused on the environmental filter, which is highlighted in bold.

interest of the long-term biogeographical filter underlying and shaping the composition of regional floras (Figure 2), I will not account for or directly study these processes. Instead, my work will focus on the environmental filter and its role in structuring plant communities within context of the current regional flora of the French Alps. While spatial heterogeneity in bedrock remains an important factor, for example sorting calcicole and calcifuge floras, most of my work will be carried out on relatively homogenous geologic contexts (either all sedimentary at the local scale or mostly crystalline at the regional scale). Lastly, although I will discuss the importance of certain local-scale, non-environmental drivers affecting alpine plant distribution at the end of this section, analysis conducted in this work will not extend to community assembly processes operating at local scales (Figure 2).

Much of this introduction is based on ideas published in a review paper at the beginning of my thesis (Carlson *et al.* 2013; Supplementary Material - S1) articulating ways in which plant distribution models could be improved in the context of alpine environments. Although in the end I did not maintain a strong focus on modeling during the rest of my project, the ideas presented in this paper remain highly pertinent for structuring the various drivers and interaction effects acting on alpine plant communities, and provide the backbone of the writing presented here. The remainder of this section will be dedicated to discussing drivers of ecotone position in high-elevation landscapes, as well as various environmental filters affecting plant distribution patterns within the alpine zone.

Sub-alpine and nival ecotone distribution

First, it seems important to specify the boundaries of the alpine zone and to describe some of the main factors affecting the spatial position of these transitional zones, i.e. ecotones. The alpine zone is defined at its lower boundary by the limit of tree life (hereafter referred to as treeline, Körner and Paulsen 2004; Körner *et al.* 2011) as well as the upper limit of sub-alpine shrubs (Körner 2003), and at its upper boundary by the presence of permanent snowfields, glaciers and steep rock formations characteristic of the alpine-nival ecotone (Gottfried *et al.* 1998). During recent decades, both the upper treeline (Harsch *et al.* 2009) and the shrub upper margin (Kullman 2002), as well as the lower limit of permanent snowfields and glaciers (Paul *et al.* 2007) have moved upward in elevation in response to climate change. In heterogeneous high mountain landscapes, sub-alpine and nival boundaries are best defined as transitional zones rather

than spatially precise shifts (Körner 2007). In the Vallon de Roche Noire, for example, the sub-alpine ecotone is not a single boundary, as favorable topo-climatic contexts allow for isolated outposts of sub-alpine vegetation interspersed with alpine plant communities. The nival ecotone can be viewed from the same perspective, as locally favorable micro-sites allow for dense patches of alpine vegetation in an otherwise mineral or nival habitat matrix. I propose that the framework of Körner (2007), used to explain spatial variation in the location of the alpine treeline ecotone, is equally applicable to both shrub and nival ecotone boundaries. In this framework, temperature (or elevation) define the upper potential limits of species of plant life forms, and subsequently non-elevation specific drivers locally modify ecotone position throughout the landscape (Figure 3).

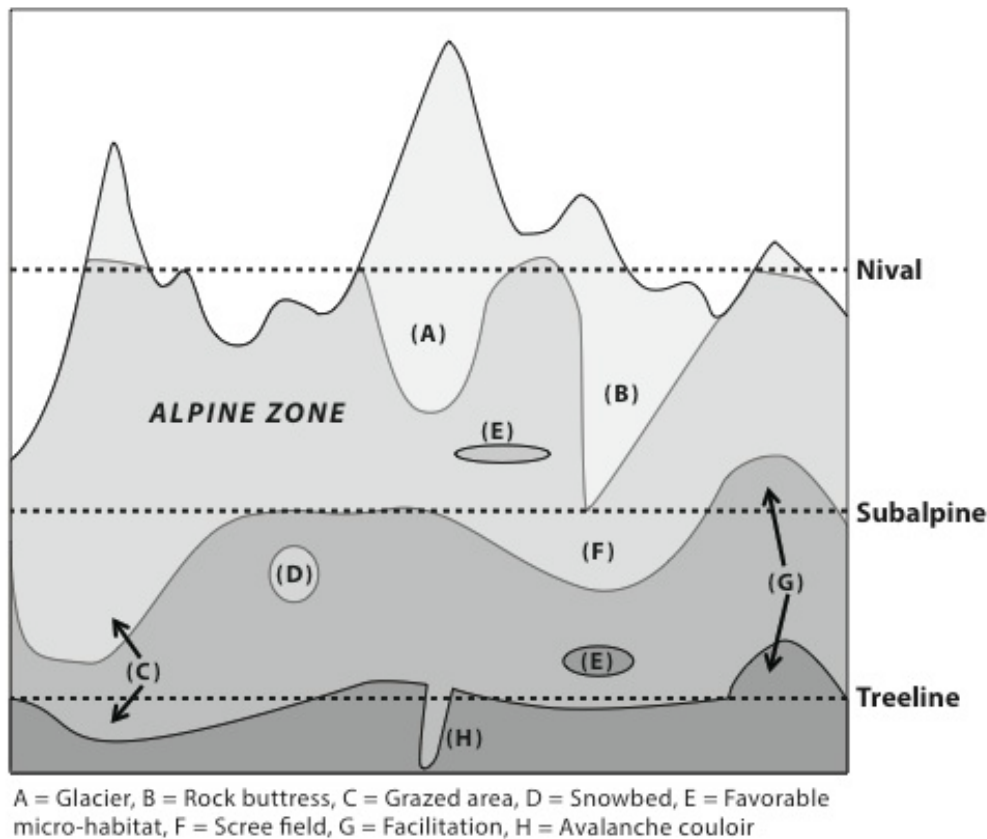


Figure 3. Conceptual illustration of elevation-dependent and elevation-independent drivers affecting high-elevation ecotones, based on the framework described in Körner (2007). Dashed horizontal lines represent elevation-dependent climatic limits of ecotone position. Elevation-independent drivers (A-H) represent phenomena locally modifying ecotone position.

The position of the sub-alpine ecotone is known to be affected by both temperature and land-use drivers, although disentangling the effects of these two factors on observed vegetation dynamics is not an easy task (Gehrig-Fasel *et al.* 2007). On a global scale, the position of treeline has been shown to correspond with mean annual growing season temperatures of $6.7 \pm 0.8^{\circ}\text{C}$ (Körner 2004). This definition was later refined to include a minimum growing season length of 94 days (constrained by the first and last transition of a weekly average of daily mean air temperature of 0.9°C) and a mean air temperature during that period of at least 6.4°C (Körner *et al.* 2011). At the global scale, 52% of alpine treelines have manifested an upward shift in response to rising measured air temperatures (Harsch *et al.* 2009), and continued warming is expected to favor treeline rise at the expense of alpine and subalpine grassland communities. In addition to temperate limits, non-elevation specific drivers such as alpine land-use (especially domestic grazing), geomorphic disturbance and substrate can locally modify ecotone location and suppress tree distributions below physiological limits (Körner 2007; Macias-Fauria and Johnson 2013; Figure 3).

The sub-alpine ecotone is rarely a sharp transition between forest and grassland, and is generally shaped by the intermediate presence of shrubs. The shrub-tundra ecotone has received increasing attention during recent years in arctic and alpine environments, owing to i) strong observed dynamics of shrub expansion both in the Pan-Arctic (Tape *et al.* 2006) and in European mountains (Anthelme *et al.* 2007; Hallinger *et al.* 2010), and ii) strong implications of shrub expansion for ecosystem functioning, especially in permafrost environments (Sturm *et al.* 2005). Increases in shrub biomass, abundance and cover have been linked to warming air temperatures (Hallinger *et al.* 2010; Tape *et al.* 2006), and to land-use abandonment in the Alps (Anthelme *et al.* 2007). Among the numerous drivers influencing shrub dynamics, Myers-Smith *et al.* (2011) identify temperature, soil disturbance and herbivory as the main processes influencing shrub habitat suitability. Biotic interactions between pioneer trees and shrubs are also an important process to consider in subalpine ecotone dynamics, considering that ‘nurse shrubs’ can facilitate tree installation by providing safe-sites for seed germination in harsh environments (Batllori *et al.* 2009; Castro *et al.* 2004). In addition to lowering species richness and influencing plant-plant interactions through shading (Anthelme *et al.* 2007), increases in shrub cover have the potential initiate positive feedback loops by influencing snow accumulation and hydrologic dynamics, soil temperature, nutrient exchange, net carbon balance and surface albedo (Hallinger *et al.* 2010).

Improved understanding of i) the mechanisms affecting shrub recruitment and growth ii) effects of shrub growth on soil temperature regimes and snowpack, and iii) shrub dynamics at the landscape scale represent ongoing research priorities (Myers-Smith *et al.* 2011).

Perhaps due to its less striking appearance and the reduced amount of associated plant biomass, the upper limit of the alpine zone has received a fraction of the attention dedicated to the lower alpine treeline ecotone (but see Gottfried *et al.* 1998). As for the subalpine ecotone, the primary elevation-dependent driver affecting nival ecotone position is climate, however this boundary is even more difficult to visually identify in a landscape. The alpine zone ends and nival vegetation begins when consistent plant cover is no longer possible and consists of isolated plant occurrences in a dominant matrix of rock, scree, gravel, snow or ice. In addition to geomorphic disturbance, glaciers represent an important non-elevation dependent driver locally precluding the presence of alpine vegetation. The spatial distribution of alpine glaciers is affected by climate (temperature and snow fall), the extent and elevation of the upper accumulation zone, ice flow dynamics and topography (Haeberli and Beniston 1998). Climate-induced glacier retreat can cause the nival ecotone to shift upward and enable plant succession dynamics to occur in un-colonized glacier forelands. In the case of low-elevation valley glaciers, such as the Mer de Glace in the French Alps (Carlson *et al.* 2014; Supplementary Material S2) or Glacier Bay in coastal Alaska (Chapin *et al.* 1994), plant colonization following glacier retreat may not represent a shift in the nival ecotone but simply a redeployment of adjacent tree and shrub vegetation. In Glacier Bay, Alaska, *Dryas* shrubs are documented within thirty years of glacial retreat, followed by alder shrubs within 50 years and spruce within 100 years (Chapin *et al.* 1994). In addition to climate severity and the presence of glaciers and permanent snow, the transition from alpine to nival vegetation is also influenced by summit morphology and a shift to steep and sustained rock faces.

Alpine environmental gradients

Within the alpine zone, the prevailing importance of climate and topography in determining plant distribution is well established (Bliss 1962; Billings 1973). Abiotic conditions are considered to be especially strong drivers of alpine plant distribution due to the tight coupling between plant physiology and the harsh climatic conditions found in alpine environments. In alpine landscapes where human disturbance is minimal, physiological responses to abiotic stress

gradients primarily shape the fundamental limits of species' niches and determine the upper elevational limit of plant distributions (Normand *et al.* 2009). At broad scales, turnover in plant community composition and species richness can be largely explained by differences in elevation responsible for change in air temperature and growing season length (Bello *et al.* 2013; Körner *et al.* 2011). Within broad-scale habitat templates defined by elevation and geologic substrate, complex mountain topography leads to micro-scale heterogeneity in plant-level abiotic conditions as well as the presence of micro-refugia known to buffer plant species from long-term changes in regional climate (Dobrowski 2010). As defined by Billings (1973), mesotopographic gradients refer to elevation-independent variation in topographic context, i.e. slope, aspect and form, and this heterogeneity is known to have strong effects on local environmental conditions experienced by alpine plants (Choler 2005). Contrasting the effects of elevation and mesotopographic gradients on alpine plant communities will be a strong theme throughout this work.

Soil temperature regimes at 0 to 25 cm depth are tightly linked to both growing season length and exposure to frost stress for alpine plants, and are known to vary substantially along both elevation and mesotopographic gradients (Choler *unpublished data*). For example, winter soil temperatures are generally maintained close to 0° C under deep snowpack in topographic concavities typical of snowbed vegetation (Björk and Molau 2007), while soil temperatures at the same elevation on ridge crests might be well below zero due to a thin snowpack and stronger coupling between soil and air temperatures. Exposure to frost stress has been linked to conservative plant growth strategies and the presence of plant species with high leaf dry matter content and low leaf area (Choler 2005). Conversely, plant communities not exposed to freezing soil temperatures, either due to warmer air temperatures or persistent snow cover, tend to have high leaf area and a higher proportion of fresh biomass. In addition to frost stress, the number of days with above-zero soil temperatures determines growing season length and has strong implications for potential plant productivity. The significance of soil temperature as a predictor of plant distribution and functioning highlights the importance of distinguishing between meteorological temperature (air temperatures >2 m above ground) and experienced temperature from a plant perspective (soil and air temperatures within 20 cm of the ground surface). Measuring soil temperature at micro-scales is especially critical in an alpine setting where plants are decoupled from atmospheric conditions and a distance of 2 m can cause greater temperature fluctuations than the most extreme IPCC climate scenario (Scherrer and Körner 2011). Recent

work suggests that climate-induced extinction of alpine flora could be buffered by the presence of micro-refugia, where locally favorable conditions are conserved by nuances in aspect and slope angle (Dobrowski 2010).

In addition to temperature, spatial heterogeneity in soil moisture and nutrient levels has strong effects on patterns of plant distribution and biomass. Understanding responses of alpine vegetation to interactions between climate and nutrient availability is particularly important in the context of increasing atmospheric nitrogen deposition, which has recently been identified as one of the major drivers of global change (Galloway *et al.* 2008). An experimental study found that biomass production in dry alpine meadows was limited by nitrogen availability, while productivity in wet meadows was limited by both nitrogen and phosphorus (Bowman *et al.* 1993). Evidence from sites distributed across mountainous areas in North America demonstrated that for a given growing season length, soil moisture regulates productivity in alpine meadows by enhancing water and nitrogen availability (Berdanier and Klein 2011). Snowpack dynamics also contribute inorganic nitrogen to underlying vegetation, providing a “pulse” of water and nutrients during the snowmelt period that has been associated with accelerated plant growth (Williams and Melack 1991).

Incoming solar radiation, as mediated by topography and snow cover, is a key environmental parameter in alpine environments affecting air and soil temperature, humidity, soil moisture and plant photosynthesis (Bliss 1962). The intensity of incident radiation generally increases with elevation, although changes in slope orientation and angle lead to highly contrasting energy budgets over short distances. Measurements of carbon dioxide uptake in a *Carex curvula* alpine sedge community showed that the number of hours with high radiation is a more direct driver of productivity than temperature, at least for this cold-adapted species (Körner 1982). In addition to fueling photosynthesis, the intensity of ultraviolet rays at high elevation can cause damage to leaf tissues and can become a source of stress for alpine plants (Billings and Mooney 1968). As is the case generally for plants, incident photosynthetically active radiation combined with suitable temperature, moisture and nutrient availability determines carbon uptake in alpine plant canopies. The unique challenge posed by alpine environments consists of quantifying the fine spatial and temporal variation in the aforementioned abiotic conditions, and in assessing their relative importance for plant distribution and productivity.

Topography influences exposure of alpine vegetation to wind, which is a complex and ubiquitous meteorological feature of alpine environments. Wind affects alpine plant habitat in multiple ways, including i) increasing differences in water vapor pressure between plant leaves and the air, ii) causing heat loss through convection and iii) leading to mechanical damage to leaf and stem tissues either due to wind-blown snow and ice or direct battering of plant tissues (Bliss 1962; Tranquillini 1980). Wind also interacts with topography to re-distribute snow, especially when it is cold and has a low moisture content, and this process increases environmental heterogeneity along mesotopographic gradients of frost exposure and growing season length. Wind thus acts as both a form of abiotic stress and disturbance, and plays an important role in the physiology and morphology of alpine plants.

Snow cover dynamics and alpine plant habitat and growth

Patterns of seasonal snowmelt in alpine landscapes are found to occur with remarkable consistency from one year to the next (Figure 4; Walsh et al. 1994), and are known to mediate the afore-mentioned abiotic constraints acting upon plant distribution (Bliss 1962; Choler 2005). Alpine plant phenology, including start of growth, timing of flowering, peak productivity and senescence are all tightly linked to the timing of snow melt-out (Inouye 2008). As previously evoked, the height of mid-winter and spring snow pack has direct effects on i) energy availability, as persistence of snow cover regulates the amount of received photosynthetically active radiation, especially for short-stature alpine plants, ii) frost exposure, given that snow serves as an insulator from frigid air temperatures, iii) protection from wind, and iv) water and nutrient availability. Snow cover duration also affects biotic interactions within plant communities, as early snow melting sites represent stressful conditions where facilitation among species has been shown to predominate (Choler *et al.* 2001). Although snow cover duration generally increases with elevation, differences of up to one month in the timing of snow melt-out are common for plant communities situated at similar elevations but in contrasting mesotopographic contexts. Accordingly, snow cover duration in mountainous terrain represents a complex and hierarchical environmental gradient that is a partially elevation-dependent and partially elevation-independent driver, *sensu* Figure 2. In summary, quantifying a single environmental variable, i.e. the date of snow melt-out, has the potential to account for substantial variation in a number of important abiotic parameters and processes affecting alpine plant community habitat and community

structure (Figure 5). In my work, I focused in particular on the impacts of snow cover duration on environmental gradients as experienced by alpine plant communities, including energy availability and frost exposure.



Figure 4. Photo of spring snowmelt near the Col du Lautaret, showing characteristic spatial heterogeneity in snow cover duration and the differential timing of plant green-up. Photo courtesy of P. Choler/Station Alpine Joseph-Fourier.

One of the key current questions in alpine plant ecology consists of understanding the implications of a longer growing season, i.e. shorter snow cover duration, for the growth, survival and distribution of alpine plants. Experimental studies demonstrate that prolongation of the growing season through snow removal did not lead to enhanced growth among most dwarf shrubs because of increased vulnerability to freezing air temperatures (Wipf *et al.* 2009; Wheeler *et al.* 2014). Furthermore, snowbed plant communities, characteristic of late-meting sites, did not produce more biomass in response to experimental lengthening of the snow-free period (Baptist *et al.* 2010). Transplant and common garden studies have been carried out in order to better

understand to what degree growth responses of alpine plants are genetically pre-determined as opposed to plastic in response to environmental conditions (Sedlacek *et al.* 2015). While a growing body of experimental evidence documents the negative effects of a longer snow free period, a study of inter-annual variability in aboveground gross primary productivity (GPP) conducted with satellite imagery found a tight overall relationship between length of snow free period and increased plant productivity (Choler 2015). Teasing apart the positive effects of a longer snow-free growing season, i.e. more available energy, from the detrimental effects of early snowmelt, i.e. freezing stress, exposure to wind, less moisture and nutrients, is an ongoing challenge that is key to understand potential responses of alpine plant communities to climate change.

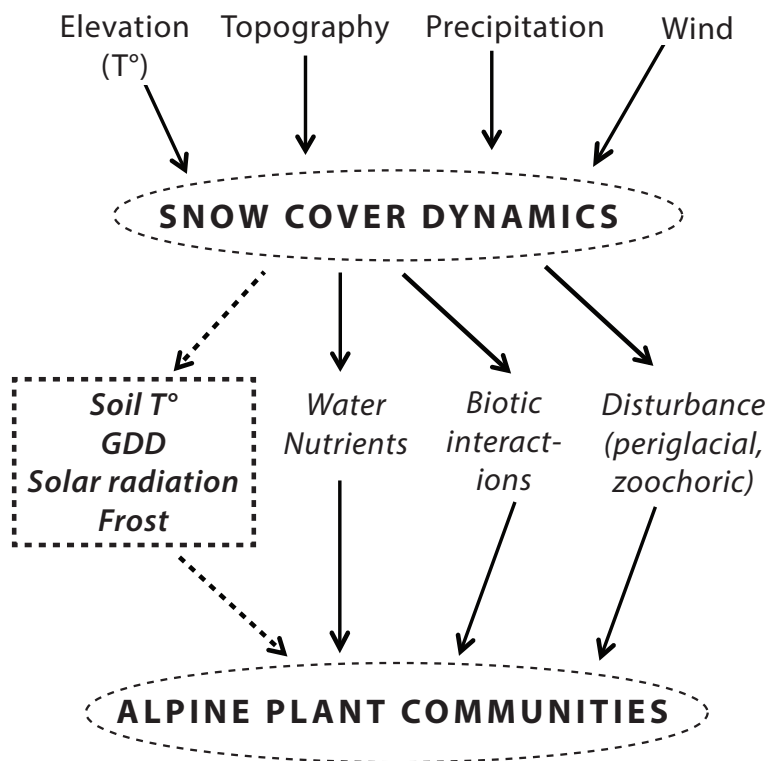


Figure 5. Conceptual diagram showing how snow cover dynamics mediate drivers affecting alpine plant communities. Dashed lines indicate the relationships that I focused on during my work. Specifically, I quantified snow cover dynamics and how snow affects temperature and radiation, and tested the effects of snow-integrated energy gradients on alpine plant community distribution and functioning.

Local processes: biotic interactions, disturbance and dispersal

While the focus on snow cover and environmental gradients has been clearly stated, this section will describe various local processes affecting alpine plant community assembly, which although not directly studied will be evoked later in discussion sections throughout this work. Returning to the concept of successive filters shaping observed plant communities (Figure 2), if plant species can reach a particular region and can adapt to local environmental conditions, a number of local-scale processes may still intervene to structure observed plant communities. Some of these processes are applicable to plant communities in general, while others are more specific to an alpine context. This section will be dedicated to describing the effects of biotic interactions, geomorphic and land-use related forms of disturbance and patch-scale dispersal.

Field ecologists have traditionally reported strong co-occurrence patterns among alpine plants, attributing turnover in plant communities to environmental heterogeneity (Bliss 1963). While abiotic factors are still considered to be the predominant driver of alpine plant assemblages (Körner 2003), experimental studies conducted along gradients have demonstrated that in stressful contexts, positive interactions enable plants to occur in environments that would be too severe in the absence of neighbors (Choler *et al.* 2001). High levels of competition in less stressful environments prevented high-elevation species from moving down the gradient, however facilitation enabled certain species to move up the gradient beyond their distribution optima, which highlighted the importance of biotic interactions in shaping observed alpine plant assemblages. In a modeling study conducted in northern Norway, the authors found that the presence of a shrub, *Empetrum nigrum*, was a significant predictor of the presence of non-focal species in addition to environmental variables (Pellissier *et al.* 2010). Although experimental evidence was lacking, it was concluded that the presence of this dwarf shrub excluded certain grasses and forbs by means of more efficient resource uptake and shading. In a high-alpine and nival environments, a substantial amount of research attention has been dedicated to alpine cushion plants, which have been identified as engineer species altering micro-site conditions by locally increasing temperature, nutrient availability and water availability (Körner 2003). The cushion plant *Silene acaulis* has been associated with local increases in plant (Badano and Cavieres 2006) and arthropod (Molina-Montenegro *et al.* 2006) diversity, signaling strong examples of facilitation in the harshest high-elevation contexts. A recent study found that *Silene acaulis* cushions altered micro-habitat conditions and the composition of bacterial and fungal

communities by found buffering soil pH and enhancing soil nutrients (Roy *et al.* 2013). Collectively, this evidence highlights the signature of biotic interactions in addition to environmental forcing in shaping observed alpine plant assemblages.

Alpine environments are subject to a number of disturbance processes that are particular to this system, and which affect vegetation distribution at varying spatial and temporal scales. First, human land-use and associated agro-pastoral practices constitute an important form of disturbance in many alpine environments, especially in densely populated mountain ranges such as the European Alps (Gehrig-Fasel *et al.* 2007). Second, disturbance from wild animals including the action of herbivores and burrowing mammals has the potential to modify soil properties and the composition of plant communities (Olofsson *et al.* 2004). Third, slope and freezing temperatures engender a host of mechanical disturbance processes in periglacial environments that affect vegetation distribution, including solifluction, cryoturbation, avalanches and rockslides.

Disturbance processes linked to human land-use and mountain agriculture represent an important non-elevation specific driver of alpine vegetation distribution. Land-abandonment has the potential to affect plant communities by i) reducing domestic grazing pressure and ii) ceasing tree and shrub removal aimed at maintaining open fields. Domestic herbivores, i.e. sheep and cattle, are known to modify plant community structure in alpine environments by i) altering the relative abundance of species within the community through selective grazing, ii) modifying competitive interactions between plants, iii) dispersing seeds, iv) removing biomass and v) modifying local nitrogen availability. In Europe, mountain areas have been inhabited and subject to anthropogenic deforestation and agro-pastoral practices for multiple centuries, and the long-term presence of traditional mountain agricultural in sub-alpine and alpine valleys has typically lead to the persistence of diverse and stable plant communities. Since the mid-20th century, land abandonment in mountain areas has become a widespread phenomenon throughout Europe and much of the world, as large-scale agriculture has oriented cultivation toward less steep and more productive slopes. Recent studies in the Pyrenees and Swiss Alps have made direct links between declining human agricultural activity and rapid forest densification and encroachment into grassland communities over the past fifty years (Gehrig-Fasel *et al.* 2007; Améztegui *et al.* 2010). In densely populated mountain ranges, shifts in land-use have been found to be a more direct driver of vegetation change than climate change (Gehrig-Fasel *et al.* 2007).

Although wild herbivores affect plant communities through the same mechanisms as identified for domestic herbivores, their actions deserve mention as a separate driver given that the timing, duration and intensity of wild grazing pressure cannot be directly controlled by human land management. In an experimental study carried out in the Swedish Scandes, in addition to transient grazing from caribou, locally intense herbivory from small burrowing mammals was identified as a strong disturbance affecting plant communities (Olofsson *et al.* 2004). Winter herbivore strategies of either large ungulates accessing plants from above the snow pack or from small mammals burrowing beneath the snow pack are especially important for vegetation dynamics in seasonally snow covered landscapes (Jefferies *et al.* 1994). In addition to herbivory, small mammals influence plant microhabitats through “residential” mechanisms such as burrowing, trampling and defecation. Black-capped marmots in Northern Siberia were found to modify micro-relief and soil properties, which facilitated the presence of certain forb and grassland species and altered plant community structure (Semenov *et al.* 2001). In Colorado, soils disturbed by gophers were characterized by increased nitrogen and higher rates of erosion, further demonstrating that disturbance from small mammals increases micro-scale ecosystem heterogeneity in alpine tundra (Sherrod and Seastedt 2001).

In addition to land-use and various forms of zoochoric disturbance, patterns of sub-alpine and alpine vegetation distribution are also structured by geomorphic processes. For example, the location of treeline can be locally suppressed by avalanche and rock fall couloirs, and constrained by mass-wasting events (Körner 2003). Opportunist, non-dominant species are able to persist in sub-alpine and alpine communities by means of disturbance events that remove competitors and create temporarily favorable conditions. For example, shade-intolerant *Larix decidua* is able to remain present in sub-alpine landscapes dominated by shade-tolerant *Abies alba* due to frequent disturbance events in the form of snow avalanches and landslides that create gaps (Bebi *et al.* 2009). A modeling study conducted in the Canadian Rockies found that the observed upper limits of tree species rarely corresponded to spatial expectations based on temperature alone, and showed that geomorphic context, i.e. bedrock, sediment type, avalanche couloir, fan, etc., was an equally important explanatory variable (Macias-Fauria and Johnson 2013). Geomorphic disturbance thus affects species distributions by precluding plant growth in certain areas and by enabling resilient species to persist in disturbed sites that would otherwise be occupied by more competitive species.

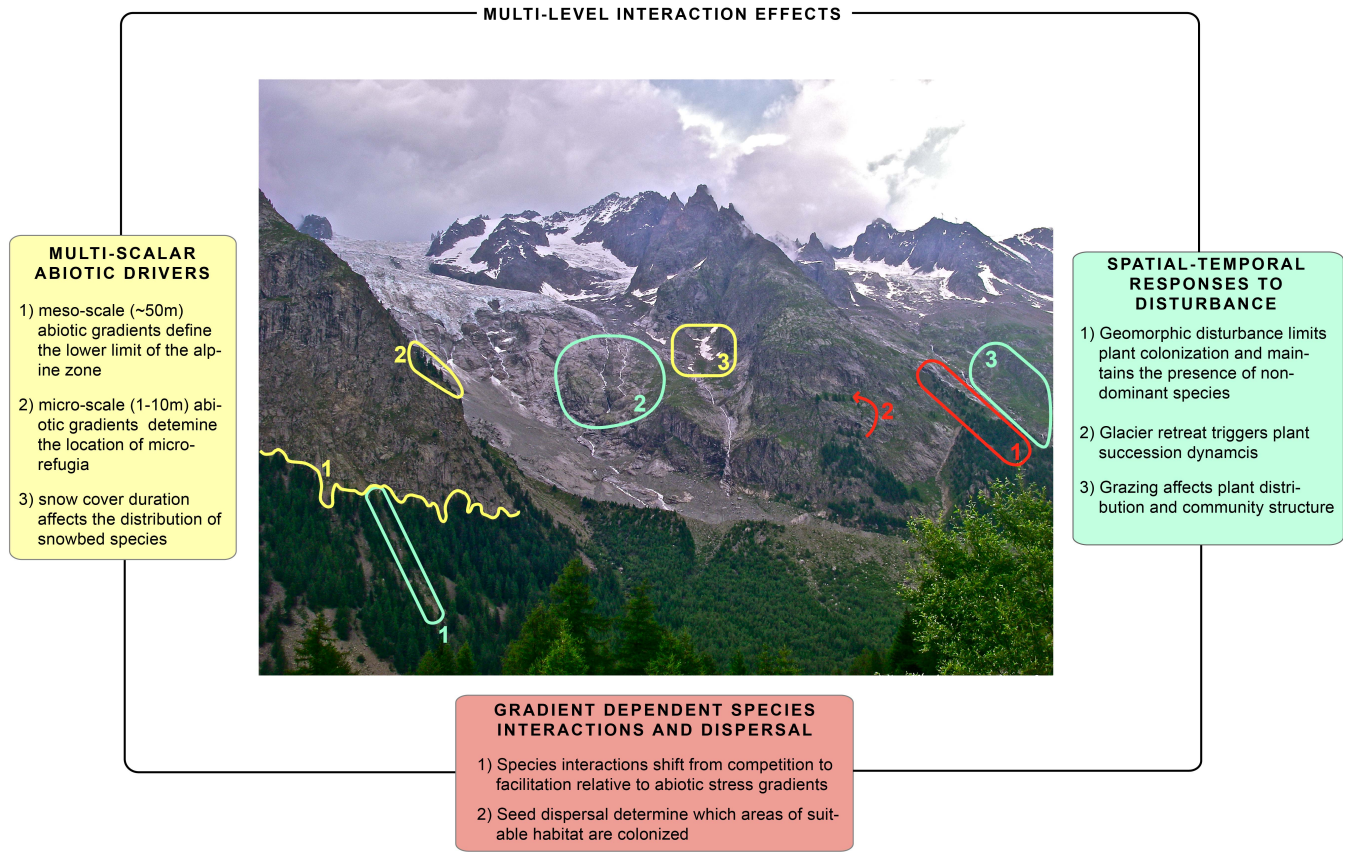


Figure 6. Key drivers and processes affecting alpine plant distribution in a typical high mountain landscape (Carlson *et al.* 2013; S1).

Recent work emphasizes the importance of patch configuration, seed dispersal and site availability as drivers of alpine plant distribution (Dullinger *et al.* 2011). An experimental study manipulated alpine snowbed plants to investigate whether species were limited primarily by abiotic conditions or by dispersal (Dullinger and Hülber 2011). Successful establishment of transplanted individuals underpinned the importance of seed dispersal and patch connectivity as drivers of distribution in a meta-population system of specialized alpine species (Dullinger and Hülber 2011). Such findings suggest that post-Little Ice Age re-colonization dynamics may be at the origin of the observed phenomenon of increasing species richness within the alpine zone, and that dispersal capacity in addition to abiotic conditions is likely to be an important factor limiting species distribution (Kammer *et al.* 2007). Additionally, detection of a lag time between climate warming and observed demographic response suggests that dispersal limitation leads to the accumulation of extinction debt within alpine plant populations (Dullinger *et al.* 2012).

Reconstructing colonization patterns and distinguishing between short-term (adjacent colonization over the span of a century) vs. long-term (evolutionary scale patterns linked to long-term climate change and species migration) dispersal constitutes an on-going challenge in the field of alpine biogeography (Schönswetter *et al.* 2005).

III) Questions and aims

Bearing in mind the multitude of drivers affecting the distribution of alpine plant communities in a global change context (Figure 6), I chose to focus my work on links between snow cover duration and alpine plant habitat, diversity and functioning. On the one hand, alpine ecologists unanimously acknowledge the importance of snow as a driver of plant distribution in high-elevation environments, and snow-vegetation interactions have long been studied in this context (Walker *et al.* 1993). On the other hand, quantifying snow cover duration at the landscape scale and at a spatial resolution pertinent to questions in alpine plant ecology has been seldom attempted in the literature, particularly using a remote sensing approach. Addressing the effects of snow cover dynamics on alpine plant communities is a necessary step for improving our understanding of how high-elevation ecosystems might respond to ongoing climate change, in particular to changes in both air temperature and snow cover regimes. The decision to focus on snow-vegetation interactions was further supported by my fieldwork experience in the Ecrins and Mont Blanc massifs, as well as reading and re-reading of classic papers in alpine ecology, whose authors contributed key insights based on field observations and yet who lacked the means to quantify certain patterns they intuitively understood.

The central aim of this thesis is to contribute to current understanding of environmental drivers of plant distribution, diversity and productivity as well as of recent changes in vegetation structure in a temperate alpine context, the French Alps. Chapter I investigates the ecological and statistical relevance of snow cover duration as a predictor of plant diversity and productivity at the scale of an alpine watershed. Chapter II intersects plot-level plant diversity with snow cover and plant phenology at the regional-scale, with two objectives: 1) improving habitat mapping in the context of complex mosaics of alpine vegetation; and 2) investigating to what degree plant

Chapter I	A)* <i>"Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities"</i>	What is the importance of quantifying snow cover duration for predicting patterns of alpine plant diversity?	Snow cover as a predictor of alpine plant diversity and productivity: A case study in the Vallon de Roche Noire
	B) <i>"Contributions of solar energy availability and vegetation properties to high resolution gross primary productivity in an alpine watershed"</i>	To what degree does canopy productivity vary for a given level of energy availability, as mediated by snow cover duration?	
Chapter II	A)* <i>"On the Importance of High-Resolution Time Series of Optical Imagery for Quantifying the Effects of Snow Cover Duration on Alpine Plant Habitat"</i>	Do satellite derived estimates of snow melt-out match growing season conditions experienced by alpine plant communities?	Quantifying alpine plant community habitat and growth responses: application of satellite imagery
	B) <i>"Habitat mapping of alpine plant communities using multi-temporal remote sensing"</i>	Is it possible to differentiate habitat for dominant plant communities based on snow cover duration and peak productivity derived from satellite imagery?	
	C) <i>"Productivity responses of alpine plant communities to contrasting growing season lengths (2013-2015) in the southwestern French Alps"</i>	Does plant functional diversity mediate productivity responses to inter-annual variation in snow cover duration?	
Chapter III	A)* <i>"Long-term modeling of the forest – grassland ecotone in the French Alps : implications for land management and conservation"</i>	How has the forest-grassland ecotone responded to recent climate and land-use change in a protected mountain reserve?	Long-term monitoring of vegetation changes in the French Alps
	B)° <i>"Observed long-term greening of alpine vegetation in a protected area of the French Alps "</i>	Are there long-term trends in peak NDVI in a high-mountain French national park and what are possible drivers and mechanisms?	

Table 1. Outline of Chapters I-III including proposed questions and themes. * Indicates a published paper, ° indicates a submitted manuscript and no symbol indicates an unpublished manuscript.

functional diversity mediates productivity responses to inter-annual variation in snow cover duration. Between Chapters II and III there is a shift in approach from quantifying snow cover as a driver of alpine plant community properties to observing long-term, i.e. decadal scale, changes in vegetation cover, without explicitly accounting for the drivers of this change. While providing observational data of ecosystem dynamics is worthwhile in its own right, the shift in methodology was forced by lack of sufficient historical and spatially explicit data on snow cover duration, temperature and land-use practices, rather than scientific preference. In this context, in

Chapter III I investigate long-term trends in forest cover and peak productivity in two different protected areas, a natural reserve in the limestone Vercors massif situated in the French Pre-Alps and an interior and mostly crystalline massif, the Oisans in the Ecrins National Park. Rather than pursuing a single overarching question, my project consists of a series of inter-related questions (summarized in Table 1) within the broader aim of improving our understanding of the responses of alpine plant communities to global change.

IV) Study area context in the French Alps

This project is centered on the southwestern French Alps near the city of Grenoble, France (Figures 7-8). The study region is a high mountain area, where 50% of the territory is located at elevations above 2000 m a.s.l., including both ski resorts and glaciers. Land cover above inhabited valleys is a combination of forest (mainly spruce, beech, larch and fir) interspersed with grasslands and subalpine heathlands, transitioning to alpine meadows, and finally rock, snowfield and glacier at the highest elevations. The lowest points in the study area consist of broad, glacier-carved valleys with elevations between 200 and 300 m a.s.l.. The Chartreuse, Vercors and Dévoluy massifs to the south and west of Grenoble are part of the French “Pre-Alps” and are composed of limestone bedrock, with maximum elevations between 2000 and 2600 m a.s.l.. The massifs of the French Interior Alps are located to the east of Grenoble, and include the Vanoise and Ecrins national parks. Geologic substrate in the Ecrins National Park is predominantly crystalline and composed of gneiss and granite, although numerous pockets of sedimentary rock can be found in peripheral areas of the park, which is the case for the Vallon de Roche Noire study area indicated in Figure 6. The Barre des Ecrins (4102 m a.s.l.) is the highest point in the Ecrins National Park and the Ecrins massif, which constitutes a vast alpine area stretching across nearly 1000 km² with over 150 summits above 3000 m a.s.l.. Two protected areas within this study region have been designated as part of the Long Term Ecological Research Network (LTER) “Zone Atelier Alpes”: the Ecrins National Park and the Vercors Regional Park, which includes the High Plateau Natural Reserve (Figure 8).



Figure 7. Map of the French Alps providing regional context. The red rectangle indicates the study area that is the focus of this work. Source: J. Renaud (LECA)

Climate and human activities have shaped vegetation structure in the French Alps for centuries. Evidence from lake sediment DNA in the northern French Alps demonstrates a peak in the intensity of cattle and sheep grazing during the Roman era, which was associated with decreased *Pinus* sp. and *Alnus* sp. cover and increased sediment erosion (Giguet-Covex *et al.* 2014). Following fluctuations in climate over past centuries, i.e. the Medieval Warming Period (~900-1300) and the Little Ice Age (~1300-1850), recent decades have been marked by important

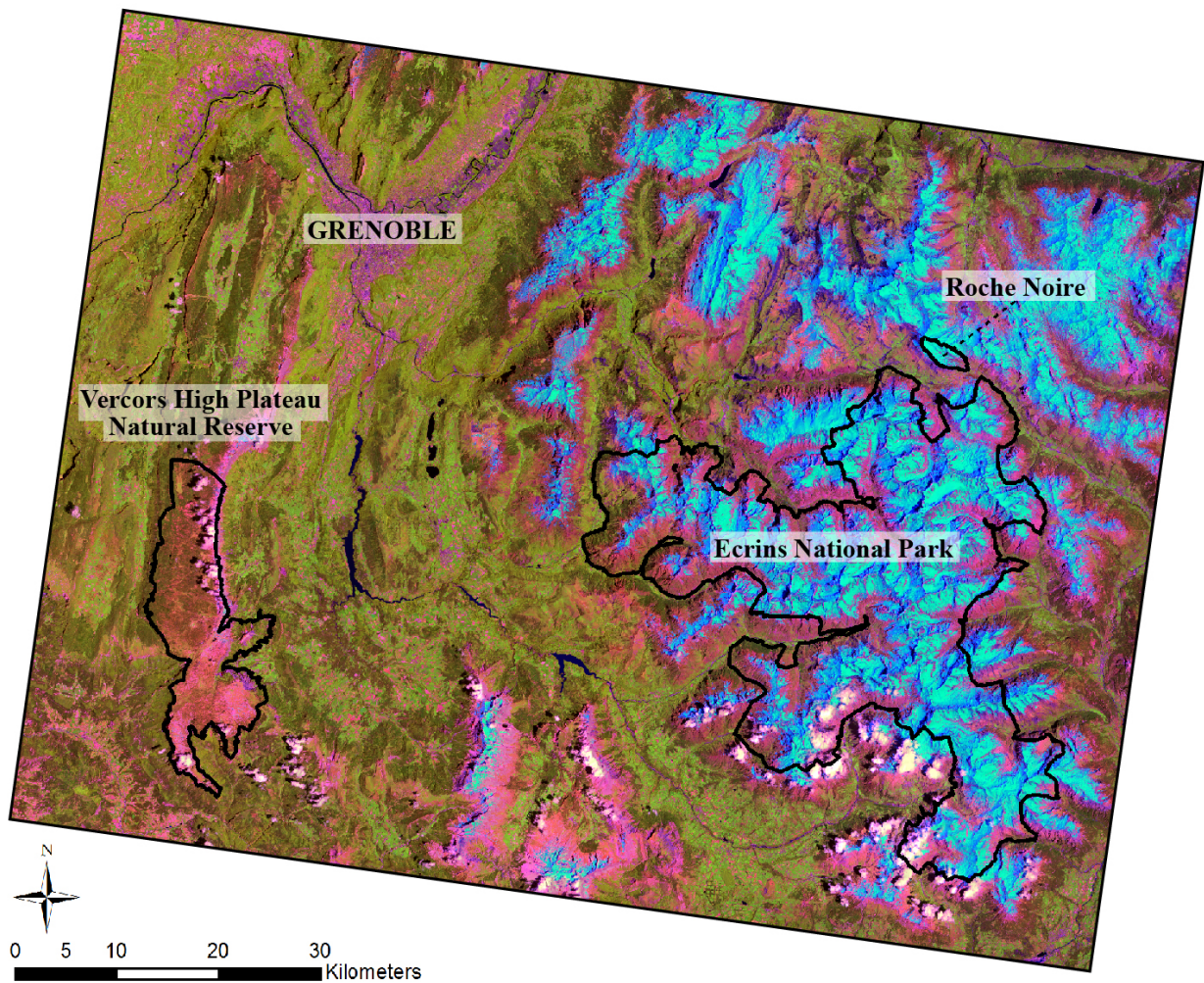


Figure 8. Color composite SPOT-4 image acquired on June 13, 2013, showing the location of Grenoble and the different study areas of this work. It is important to note that the Vercors High Plateau Natural Reserve is part of the greater Vercors Natural Regional Park, and the boundary shown for the Ecrins National Park represents the “core area” of the park. Snow cover is shown in blue.

observed changes in climate in the French Alps with strong implications for vegetation cover. Since the 1950s, average air temperature in the French Alps has increased by 1°C, with the bulk of the warming occurring between 1980 and 1990 (Durand *et al.* 2009a). While precipitation regimes have been highly variable during this period, a significant decrease in snow cover duration since the 1980s has also been observed throughout the French Alps (Durand *et al.*

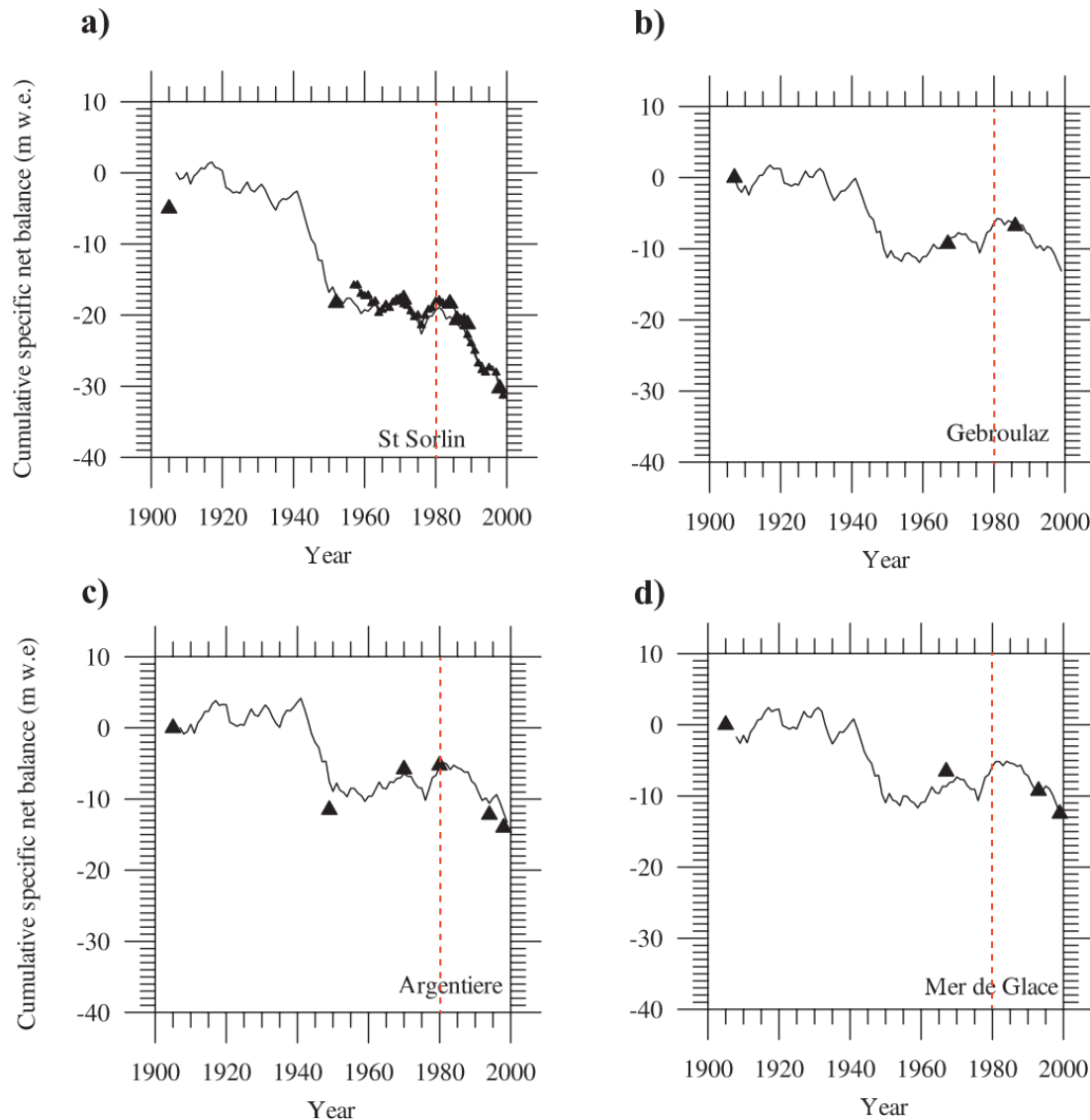


Figure 9. Figure from Vincent (2002) showing modeled (solid line) and measured (triangles) of mass balance for four glaciers in the French Alps during the 20th century. Dashed red lines were added to indicate the sharp decline in mass balance between 1980 and 2000.

2009b). Measured warming during the 1980s corresponded with a pronounced decline in the mass balance of glaciers in the French Alps during the same period (Figure 9). Since the late 1960s, the surface area of glaciers in the Ecrins National Park has decreased by 33% (Gardent *et al.* 2014). Alongside changes in climate, patterns of land-use have also fluctuated in the French Alps during recent decades. Sheep grazing is still a widespread activity in high-elevation pastures of both the interior and pre-alpine massifs, and assessing the effects of recent spatial and temporal shifts in grazing pressure on high-elevation grasslands remains an open area of investigation. Numerous and ongoing long-term monitoring programs have been put in place by the Ecrins National Park in cooperation with research institutions and non-academic partners, with the goal of assessing recent impacts of climate and land-use change on multiple facets of mountain ecosystems (Bonet *et al.* 2016).

V) Remote sensing and alpine ecology: a combined approach





A brief history

Alpine ecologists have long commented on the striking visual patterns formed by alpine landscapes, resulting from complex topography and abrupt turnover in plant communities (Bliss 1960). Remote sensing emerges as a potential means of quantifying this heterogeneity, and there is a long-standing if modest tradition in the literature of alpine ecologists including remote sensing data in their analyses. One of the earliest examples I could find was a vegetation mapping study conducted at the Niwot Ridge site in Colorado, in which the authors utilized aerial photographs and a digital elevation model to classify dominant plant communities (Frank and Isard 1986). Another pioneering Niwot Ridge study differentiated plant communities based on field measures of snowpack height and mid-summer values of the normalized difference vegetation as measured by the Landsat-5 satellite (Walker *et al.* 1993). More recently, the majority of alpine vegetation studies incorporating remote sensing data have focused on phenology trends, relying on vegetation indices (VIs) such as the normalized difference vegetation index (NDVI). Fontana *et al.* (2007) assessed the ability of three low to medium resolution satellites (AVHRR, SPOT VEG. and MODIS) to quantify snow melt-out as well as the start and end of plant growth, and found that time series of 500 m to 1 km images correlated

strongly with ground-based phenology measures. Along a broad latitudinal gradient in the Rocky Mountains, Dunn and de Beurs (2011) demonstrated that spatial variability in the start of the growing season, as measured by MODIS, could be well captured using climate, latitude and topography as predictors. While broad-scale phenology studies provide valuable insight into the functioning of alpine ecosystems, application of 500 m resolution satellite imagery to diversity-related questions is nonetheless limited when intra-pixel variability in both environmental conditions and plant communities is known to be high. Broadly speaking, there thus appears to be an opportunity to utilize satellite imagery at higher spatial resolution to carry out phenology studies closer to the scale of turnover in alpine plant communities.

Mapping alpine plant phenology and snow cover dynamics

Concerning vegetation, I used three types of imagery, including i) publically available historical aerial photographs from the French National Institute of Geographic Information (IGN), ii) airborne hyperspectral imagery from a project-based flight over the Vallon de Roche Noire and iii) multi-spectral satellite imagery acquired from the National Aeronautics and Space Administration (NASA), the United States Geological Survey (USGS) and the Centre National d'Etudes Spatiales (CNES). Contrasting spatial, temporal and spectral properties of acquired

	SENSOR	Spatial		Temporal		Spectral
		RES.	EXTENT	RES.	EXTENT	RES.
	Aerial photos*	~50 cm	~25 km ² , or mosaic	Annual campaigns	1930-present	RGB
	Hyperspectral	~80 cm	3-10 km ²	Project-based	Project-based	400-2450nm (350 bands)
	Landsat 7/8	30 m	~22500 km ²	16-day	Landsat 7 (1999-2003) Landsat 8 (2013-present)	400-2300nm (9 bands)
	SPOT 4/5*	10-20 m	~150000 km ²	26-day	SPOT 4 (1998-2013) SPOT 5 (2002-present)	500-1750nm (4 bands)
	MODIS*	250 - 1000 m	10° x 10°	Daily	1999-present	400-1450nm (36 bands)

**Publically available data*

Table 2. Summary of imagery used in this project with associated spatial, temporal and spectral resolutions details for each sensor.

imagery enabled a variety of different image processing and analysis techniques, which were suited to an equally wide range of topics and ecological questions (Table 2). Historical aerial photos containing only grey-scale pixel values were combined with underlying topographic information to carry out object-based image segmentation (Pappas 1992) of multi-date forest cover at high spatial resolution (5 m), which was used to investigate long-term land-cover change. The wealth of spectral information contained in hyperspectral imagery was used to estimate biophysical canopy properties such as leaf area index and leaf chlorophyll content during peak vegetation productivity (Haboudane *et al.* 2002), which was appropriate for exploring variation in canopy properties along snow cover gradients. Stacks of multi-spectral satellite images, including Landsat, SPOT and MODIS imagery, were analyzed to quantify spatial and temporal variation in NDVI at the landscape scale and for high-elevation plant communities. NDVI was calculated as follows:

$$NDVI = \frac{\rho \text{ NIR} - \rho \text{ Red}}{\rho \text{ NIR} + \rho \text{ Red}}$$

where $\rho \text{ Red}$ is reflectance in the red band and $\rho \text{ NIR}$ is reflectance in the near infrared band. NDVI has been extensively validated and applied since its introduction by Rouse *et al.* (1974) as an optical proxy of plant photosynthetic activity, owing to high absorption of photosynthetically active radiation (PAR) captured by the red band, combined with low absorption of low-energy infrared radiation, which can lead to overheating and cause damage in plant tissues. Considering the overwhelming complexity of studying growth responses of individual plant species to snow cover duration at the landscape scale, combining approaches from remote sensing and functional ecology emerges as a promising avenue to improve understanding of community-level vegetation responses to changing environmental conditions (Violle *et al.* 2014).

Use of optical satellite imagery to quantify the physical properties of snow and ice on the Earth's surface constitutes a field of study in its own right, with clear implications for i) global circulation models (Henderson-Sellers and Wilson 1983) and broad-scale energy fluxes (Dumont *et al.* 2014), ii) for validating and improving regional-scale snowpack models (Charrois *et al.* 2016), hydrological forecasting in mountainous areas (Sirguey *et al.* 2009) and iv) for observation of glacier dynamics (Rabatel *et al.* 2013), to name a few. In the context of my project, I sought to apply well established and long-standing methods for mapping snow cover

using multi-spectral satellite imagery, using two different. First, the panchromatic band of Landsat-7 and 8 images, which has a ground resolution of 15 as opposed to 30 m, was classified into binary snow maps using the same image segmentation techniques applied to map forest cover based on aerial photographs. Although the higher ground resolution of exported maps was a considerable gain in precision, this method nonetheless presented a number of drawbacks, including i) time-consuming manual training of objects for each acquired image, ii) no automated method for dealing with cloud cover, iii) necessitated expensive software and iv) did not make use of information contained in multiple spectral bands and was based solely on the panchromatic band. Second, I applied a classic method proposed by Dozier (1989) to differentiate snow covered pixels from non-snow covered pixels in alpine environments, which consists of applying a threshold to the normalized difference snow index (NDSI), calculated as follows:

$$NDSI = \frac{\rho_{\text{Green}} - \rho_{\text{SWIR}}}{\rho_{\text{Green}} + \rho_{\text{SWIR}}}$$

where ρ_{Green} is reflectance in the red band and ρ_{SWIR} is reflectance in the shortwave infrared band. Based on a similar rationale to NDVI, NDSI relies on the high absorption of shortwave infrared and high emissivity in the green band. Cloud masks were either provided by the USGS in the case of Landsat-8 or by THEIA/CNES for SPOT imagery, or were derived by applying thresholds to the blue and thermal infrared bands in the case of Landsat-7 imagery. This approach had the advantage of being entirely automated, and accordingly was well suited to efficiently analyze stacks of images for multiple years. Optimal use of satellite imagery in the context of mountainous study areas required correcting reflectance values for differences in illumination caused by topographic heterogeneity, as discussed by Shepherd and Dymond (2003). Overall, my goal for this portion the project was to produce snow cover maps based on time series of optical imagery, i.e. first snow free day, length of the snow free period, using straightforward methods that could be readily replicated by non-specialist plant ecologists in the context of their own questions and research aims. A further objective was to validate satellite-based estimates of snow cover duration using ground observations of soil temperature, in order to test agreement between optical signal and environmental conditions experienced by alpine plant communities.

Measuring plant distribution and diversity

The goal of this section is to broadly define how plant communities were observed and quantified in the context of this thesis. It should be noted that all field data utilized during my project were provided by botanists associated with either the Centre de Botanique National Alpin (CBNA) or the Parc National des Ecrins (PNE), whose personnel have spent decades collecting field observations of plant communities in the French Alps. This wealth of information, which consists of thousands of geolocalized and dated surveys of plant communities, is an undeniable asset for ecologists working in this study region (Mauz and Granjou 2013). “Phytosociological relevés”, which throughout the rest of this work will be referred to as vegetation plots, were collected using the Braun-Blanquet method (Braun-Blanquet 1957), which consists of estimating the relative cover of vascular plant species as well as proportions of bare ground, lichen and moss, herbaceous, and shrub and tree cover for several height classes, typically for 10x10 meter plots. This method has been criticized due to the non-random selection of sample point locations and the potential bias of botanists seeking to document “representative” plant communities (Botta-Dukát *et al.* 2007). However, while it is worth bearing these sources of bias in mind, data generated by years of work on the part of field botanists remains an invaluable source of information for plant ecologists that goes far beyond what would be possible in the context of a three-year PhD project.

Knowledge of the percent cover of all vascular plants within a 100 m² plot allows for quantifying plant diversity in myriad different ways. The most straightforward metric of taxonomic diversity consists of converting abundance measures to a binary indicator of species presence or absence, which provides the basis for species distribution models linking plant presence to suitable environmental conditions (SDMs; Guisan and Thuiller 2005). Community-level taxonomic diversity may also be summarized in terms of alpha diversity, including species richness, i.e. the number of species present in a given plot, or using abundance-based measures of evenness, i.e. Simpson or Shannon indices. Gamma-diversity can be derived by summing species richness for multiple vegetation plots at the scale of study region. Beta-diversity, or spatial turnover in species composition between vegetation plots, can be quantified using a variety of dissimilarity metrics based on i) which species are present in plot A, ii) which species are present in plot B, and iii) which species are found in both (Koleff *et al.* 2003). Multi-dimensional ordination techniques, such as weighted principal co-ordinates analysis (PCoA) or nonmetric

multidimensional scaling (NMDS), can be applied to pairwise measures of dissimilarity in order to further quantify differences in species composition across multiple vegetation plots (Faith *et al.* 1987).

In addition to taxonomic measures, plant diversity can be quantified on the basis of functional traits, which in the case of plants are defined as measured morphological, phenological and physiological features affecting plant performance. Examples of plant morphological traits include vegetative plant height, specific leaf area (ratio of leaf area to leaf mass), seed mass, leaf dry matter content and leaf nitrogen content. I am especially interested in relationships between functional traits and vegetation indices, considering that traits linked to canopy properties can be expected to contribute to remotely sensed estimates of aboveground productivity. This approach, which will be explored in Chapter IIC, represents a promising means of testing biodiversity-ecosystem functioning hypotheses along environmental gradients.

Typically plant functional traits are measured in the field for a small number of individuals of a target species, and trait values are stored in databases, i.e. TRY (<https://try-db.org/>). Two shortcomings of this approach include i) that intra-specific trait variability is ignored when species are assigned a single or mean trait value and ii) field measures stored in databases are typically not *in situ* and may not be representative of plant phenotypes in a particular study area, especially for species distributed across large gradients of elevation or latitude. Recent work in plant functional ecology emphasizes the strong signal of intraspecific trait variability in observed biodiversity patterns and in underlying ecological processes (Albert *et al.* 2012). Additional work has shown that intra-specific variability is less of a confounding factor for analysis of regional-scale patterns of functional diversity along strong abiotic gradients, given that turnover in species composition and associated inter-specific trait variability is the dominant observed pattern (Chalmandrier *et al.* 2016).

A variety of approaches exist for calculating community-level functional diversity, i.e. values estimated at the scale of a vegetation plot. The most prevalent metric is the community weighted mean (CWM), which accords more weight to the trait values of dominant species by taking the sum of abundances multiplied by trait values for all species present in a community (Garnier *et al.* 2004). CWM trait values are calculated using the following equation:

$$CWM = \sum_{i=1}^S p_i \times t_i$$

where S corresponds to each species in the community, p_i is the relative abundance of each species and t_i is the trait value for a given species. The purpose of the CWM metric is to represent the mean trait value for a plant community as defined by the biomass-ratio hypothesis (Grime 1998). Additionally, ecologists are often interested in the divergence or variance in trait values within a community, which led to the development of the community weighted variance (CWV) metric, which is calculated as follows:

$$CWV = \sum_{i=1}^S p_i \times (t_i - CWM)^2$$

where S corresponds to each species in the community, p_i is the relative abundance of each species, t_i is the trait value for a given species and CWM is the community weighted mean trait value of the vegetation plot.

Functional diversity can also be estimated on the basis of multiple traits by calculating pairwise distances between communities based on any number of measured traits (Mouchet *et al.* 2010). Often-used metrics of multi-trait functional diversity include mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), which are presented in Webb *et al.* (2002). Standard methodology involves calculating functional diversity for a given vegetation plot, and subsequently comparing observed functional diversity to a null-distribution of values in order to test for significant patterns of either functional divergence (higher diversity of trait values than expected) or functional convergence (lower diversity of trait values than expected). Resulting patterns of functional diversity along environmental gradients can be used to infer community assembly processes, including the relative importance of abiotic filtering and biotic interactions (Spasojevic *et al.* 2012). Care must be taken if multiple traits are used in functional distance estimates, as contrasting responses for single traits, i.e. a significant positive relationship for one trait and a significant negative relationship for another along a stress gradient, could result in a misleading overall flat relationship in multi-trait functional diversity along the gradient. Also it is important to select traits with a testable hypothesis in mind, as it is possible to simply miss the “right traits” playing a role in community assembly processes (Kraft *et al.* 2015). A further

methodological consideration consists of how much weight should be given to dominant vs. rare species within a community, which has been shown to have strong effects on estimated diversity patterns and should be tailored to research questions and aims (Chalmandrier *et al.* 2015). Lastly, the same community-level diversity metrics can be calculated using phylogenetic distance between communities in order to infer evolutionary processes contributing to community assembly (Webb *et al.* 2002). I did not analyze phylogenetic data in my project, preferring to test hypotheses related to morphological functional traits due to the stronger potential articulation with optical measures plant canopy properties.

Climate data

Climate data used in this work were provided by Météo France and the Centre d'Etudes de la Neige in Grenoble. Air temperature data were generated by the SAFRAN model, which is a physical model of atmospheric processes developed specifically for avalanche and hydrological forecasting in the French Alps (Durand *et al.* 2009a). The model is fed by a network of meteorological stations distributed throughout the study region. SAFRAN is not a spatially distributed model, and provides numerical simulations of air temperature, solar radiation and wind, nebulosity and precipitation by mountain massif and by 300 m elevation classes, slope aspect (cardinal directions) and angle (flat, 20° or 40° and above) at a one-hour time step. Simulations are available from 1959 onward, constituting a rich historical climate record for the French Alps. Although it is possible to map SAFRAN values by assigning values to topographic classes, one can readily imagine that raw spatial outputs would be too coarse to explain fine-scale turnover in alpine plant communities. Accordingly, I smoothed temperature values using a digital elevation model, and in certain cases added further spatial heterogeneity by including information on snow cover duration derived from remote sensing. It is important to mention that the SAFRAN model provides the meteorological forcing for a snowpack model called CROCUS (Durand *et al.* 2009b), which simulates snow height and moisture content for the same topographic classes. Although I did not attempt to downscale snow height values, and decided not to use these data as a driver of observed vegetation patterns, I did include a re-analysis of snow melt-out timing in the Oisans massif from the 1980s to present as a contextual element providing a point of discussion in relation to observed changes in alpine vegetation.

Overall approach

Throughout my work, I address research questions by intersecting measures of plant diversity with remote sensing and climate data. In Chapter I, I use multi-temporal satellite imagery to calibrate an empirical model of snow cover distribution, which I combine with temperature and solar radiation data to predict patterns of plot-level diversity and hyperspectral-derived vegetation indices. In Chapter II I switch from a local to regional scale, and combine time series of snow and vegetation indices from satellite imagery with metrics of taxonomic and functional diversity. Finally, in Chapter III I quantify change in forest cover and peak NDVI over time and in relation to available land cover and land-use data in order to assess long-term shifts in vegetation structure. From a methodological standpoint, the main contribution of this thesis is to propose a number of novel applications of remote sensing products, including aerial photographs, airborne hyperspectral, LIDAR and multi-spectral satellite imagery for addressing fundamental questions in alpine plant ecology.

References

- Albert, C. H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S., & Thuiller, W. (2012). On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, 121(1), 116-126.
- Améztegui, A., Brotons, L., & Coll, L. (2010). Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecology and Biogeography*, 19(5), 632-641.
- Anthelme, F., Villaret, J. C., & Brun, J. J. (2007). Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale. *Journal of Vegetation Science*, 18(3), 355-362.
- Badano, E. I., & Cavieres, L. A. (2006). Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Diversity and Distributions*, 12(4), 388-396.
- Baptist, F., Flahaut, C., Streb, P., & Choler, P. (2010). No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biology*, 12(5), 755-764.
- Batlloori, E., Camarero, J. J., Ninot, J. M., & Gutiérrez, E. (2009). Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography*, 18(4), 460-472.

- Bebi, P., Kulakowski, D., & Rixen, C. (2009). Snow avalanche disturbances in forest ecosystems—state of research and implications for management. *Forest ecology and Management*, 257(9), 1883-1892.
- Bello, F. D., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013). Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography*, 36(3), 393-402.
- Berdanier, A. B., & Klein, J. A. (2011). Growing season length and soil moisture interactively constrain high elevation aboveground net primary production. *Ecosystems*, 14(6), 963-974.
- Billings, W. D. (1973). Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience*, 23(12), 697-704.
- Billings, W. D., & Mooney, H. A. (1968). The ecology of arctic and alpine plants. *Biological Reviews*, 43(4), 481-529.
- Björk, R. G., & Molau, U. (2007). Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research*, 39(1), 34-43.
- Bliss, L. C. (1962). Adaptations of arctic and alpine plants to environmental conditions. *Arctic*, 15(2), 117-144.
- Bonet, R., Arnaud, F., Bodin, X., Bouche, M., Boulangeat, I., Bourdeau, P., ... & Dentant, C. (2016). Indicators of climate: Ecrins National Park participates in long-term monitoring to help determine the effects of climate change. *Ecomont - Journal on Protected Mountain Areas Research*, 8, 44-52.
- Botta-Dukát, Z., Kovács-Láng, E., Rédei, T., Kertész, M., & Garadnai, J. (2007). Statistical and biological consequences of preferential sampling in phytosociology: theoretical considerations and a case study. *Folia Geobotanica*, 42(2), 141-152.
- Boucher, F. C., Thuiller, W., Roquet, C., Douzet, R., Aubert, S., Alvarez, N., & Lavergne, S. (2012). Reconstructing the origins of high-alpine niches and cushion life form in the genus *Androsace* s.l. (Primulaceae). *Evolution*, 66(4), 1255-1268.
- Bowman, W. D., Theodose, T. A., Schardt, J. C., & Conant, R. T. (1993). Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, 74(7), 2085-2097.
- Braun-Blanquet, J. (1957). Ein Jahrhundert Florenwandel am Piz Linard (3414 m). *Bulletin du Jardin botanique de l'Etat, Bruxelles/Bulletin van den Rijksplantentuin, Brussel*, 221-232.
- Carlson, B. Z., Georges, D., Rabatel, A., Randin, C. F., Renaud, J., Delestrade, A., Choler, P. & Thuiller, W. (2014). Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models. *Diversity and Distributions*, 20(12), 1379-1391.
- Carlson, B. Z., Randin, C. F., Boulangeat, I., Lavergne, S., Thuiller, W., & Choler, P. (2013). Working toward integrated models of alpine plant distribution. *Alpine Botany*, 123(2), 41-53.
- Castro, J., Zamora, R., Hódar, J. A., Gómez, J. M., & Gómez-Aparicio, L. (2004). Benefits of Using Shrubs as Nurse Plants for Reforestation in Mediterranean Mountains: A 4-Year Study. *Restoration Ecology*, 12(3), 352-358.

- Chalmandrier, L., Münkemüller, T., Lavergne, S., & Thuiller, W. (2015). Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. *Ecology*, 96(1), 143-153.
- Chalmandrier, L., Munkemüller, T., Collace, M.P., Renaud, J., Aubert, S., Carlson, B.Z., Clément, J.C., Legay, N., Pellet, G., Saillard, A. & Thuiller, W. Spatial Scale and intraspecific variability mediate trait-environment relationships in alpine grasslands. *Ecology*, in press.
- Charrois, L., Cosme, E., Dumont, M., Lafaysse, M., Morin, S., Libois, Q., & Picard, G. (2016). On the assimilation of optical reflectances and snow depth observations into a detailed snowpack model. *The Cryosphere*, 10(3), 1021-1038.
- Chapin, F. S., Walker, L. R., Fastie, C. L., & Sharman, L. C. (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, 64(2), 149-175.
- Choler, P. (2015). Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. *Biogeosciences*, 12(12), 3885-3897.
- Choler, P., Michalet, R., & Callaway, R. M. (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82(12), 3295-3308.
- Choler, P. (2005). Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research*, 37(4), 444-453.
- Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, 17(2), 1022-1035.
- Dozier, J. (1989). Spectral signature of alpine snow cover from the Landsat Thematic Mapper. *Remote Sensing of Environment*, 28, 9-22.
- Dullinger, S., and Hülber, K. (2011). Experimental evaluation of seed limitation in alpine snowbed plants. *PloS One*, 6(6), e21537.
- Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., ... & Caccianiga, M. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2(8), 619-622.
- Dullinger, S., Mang, T., Dirnböck, T., Ertl, S., Gattringer, A., Grabherr, G., ... & Hülber, K. (2011). Patch configuration affects alpine plant distribution. *Ecography*, 34(4), 576-587.
- Dumont, M., Brun, E., Picard, G., Michou, M., Libois, Q., Petit, J. R., ... & Josse, B. (2014). Contribution of light-absorbing impurities in snow to Greenland's darkening since 2009. *Nature Geoscience*, 7(7), 509-512.
- Dunn, A. H., & de Beurs, K. M. (2011). Land surface phenology of North American mountain environments using moderate resolution imaging spectroradiometer data. *Remote Sensing of Environment*, 115(5), 1220-1233.
- Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B., & Mérindol, L. (2009a). Reanalysis of 44 Yr of climate in the French Alps (1958-2002): methodology, model validation, climatology, and trends for air temperature and precipitation. *Journal of Applied Meteorology and Climatology*, 48(3), 429-449.

- Durand, Y., Giraud, G., Laternser, M., Etchevers, P., Mérindol, L., & Lesaffre, B. (2009b). Reanalysis of 47 years of climate in the French Alps (1958-2005): Climatology and trends for snow cover. *Journal of Applied Meteorology and Climatology*, 48(12), 2487-2512.
- Faith, D. P., Minchin, P. R., & Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69(1-3), 57-68.
- Frank, T. D., & Isard, S. A. (1986). Alpine vegetation classification using high-resolution aerial imagery and topoclimatic index values. *Photogrammetric Engineering and Remote Sensing*, 52(3), 381-388.
- Fontana, F., Rixen, C., Jonas, T., Aberegg, G., & Wunderle, S. (2008). Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series—a comparison with in situ measurements. *Sensors*, 8(4), 2833-2853.
- Frei, E., Bodin, J., & Walther, G. R. (2010). Plant species' range shifts in mountainous areas—all uphill from here? *Botanica Helvetica*, 120(2), 117-128.
- Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., ... & Sutton, M. A. (2008). Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, 320(5878), 889-892.
- Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., ... & Neill, C. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9), 2630-2637.
- Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment?. *Journal of Vegetation Science*, 18(4), 571-582.
- Giguet-Covex, C., Pansu, J., Arnaud, F., Rey, P. J., Griggo, C., Gielly, L., ... & Poulenard, J. (2014). Long livestock farming history and human landscape shaping revealed by lake sediment DNA. *Nature Communications*, 5.
- Gottfried, M., Pauli, H., & Grabherr, G. (1998). Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research*, 207-221.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J. L. B., ... & Krajčič, J. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), 111-115.
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86(6), 902-910.
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9), 993-1009.
- Haeberli, W., & Beniston, M. (1998). Climate change and its impacts on glaciers and permafrost in the Alps. *Ambio*, 258-265.
- Haboudane, D., Miller, J. R., Tremblay, N., Zarco-Tejada, P. J., & Dextraze, L. (2002). Integrated narrow-band vegetation indices for prediction of crop chlorophyll content for application to precision agriculture. *Remote Sensing of Environment*, 81(2), 416-426.

- Hallinger, M., Manthey, M., & Wilmking, M. (2010). Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist*, 186(4), 890-899.
- Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12(10), 1040-1049.
- Henderson-Sellers, A., & Wilson, M. F. (1983). Surface albedo data for climatic modeling. *Reviews of Geophysics*, 21(8), 1743-1778.
- Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89(2), 353-362.
- IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Jefferies, R. L., Klein, D. R., & Shaver, G. R. (1994). Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos*, 193-206.
- Kammer, P. M., Schöb, C., & Choler, P. (2007). Increasing species richness on mountain summits: Upward migration due to anthropogenic climate change or re-colonisation?. *Journal of Vegetation Science*, 18(2), 301-306.
- Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. *Science*, 291(5503), 481-484.
- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72(3), 367-382.
- Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems; with 47 tables*. Springer Science & Business Media.
- Körner, C. (2004). Mountain biodiversity, its causes and function. *Ambio*, 11-17.
- Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31(5), 713-732.
- Körner, C. (2007). Climatic treelines: conventions, global patterns, causes (Klimatische Baumgrenzen: Konventionen, globale Muster, Ursachen). *Erdkunde*, 316-324.
- Körner, C. (1982). CO₂ exchange in the alpine sedge *Carex curvula* as influenced by canopy structure, light and temperature. *Oecologia*, 53(1), 98-104.
- Körner, C., Paulsen, J., & Spehn, E. M. (2011). A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany*, 121(2), 73-78.
- Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29(5), 592-599.

- Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of ecology*, 90(1), 68-77.
- Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I., & Callaway, R. M. (2004). Rethinking plant community theory. *Oikos*, 107(2), 433-438.
- Macias-Fauria, M., & Johnson, E. A. (2013). Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proceedings of the National Academy of Sciences*, 110(20), 8117-8122.
- Mauz, I., & Granjou, C. (2013). A new border zone in science. Collaboration and tensions between modelling ecologists and field naturalists. *Science as Culture*, 22(3), 314-343.
- Molina-Montenegro, M. A., Badano, E. I., & Cavieres, L. A. (2006). Cushion plants as microclimatic shelters for two ladybird beetles species in alpine zone of central Chile. *Arctic, Antarctic, and Alpine Research*, 38(2), 224-227.
- Molnar, P., & England, P. (1990). Late Cenozoic uplift of mountain ranges and global climate change: chicken or egg?. *Nature*, 346(6279), 29-34.
- Mouchet, M. A., Villeger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4), 867-876.
- Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., ... & Ropars, P. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509.
- Normand, S., Treier, U. A., Randin, C., Vittoz, P., Guisan, A., & Svenning, J. C. (2009). Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, 18(4), 437-449.
- Olofsson, J., Hulme, P., Oksanen, L., & Suominen, O. (2004). Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, 106(2), 324-334.
- Pappas, T. N. (1992). An adaptive clustering algorithm for image segmentation. *IEEE Transactions on signal processing*, 40(4), 901-914.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42.
- Pellissier, L., Anne Bråthen, K., Pottier, J., Randin, C. F., Vittoz, P., Dubuis, A., ... & Guisan, A. (2010). Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography*, 33(6), 1004-1014.
- Puşcaş, M., Choler, P., Tribsch, A., Gielly, L., Rioux, D., Gaudeul, M., & Taberlet, P. (2008). Post-glacial history of the dominant alpine sedge *Carex curvula* in the European Alpine System inferred from nuclear and chloroplast markers. *Molecular Ecology*, 17(10), 2417-2429.

- Rabatel, A., Letréguilly, A., Dedieu, J. P., & Eckert, N. (2013). Changes in glacier equilibrium-line altitude in the western Alps from 1984 to 2010: evaluation by remote sensing and modeling of the morpho-topographic and climate controls. *Cryosphere*, 7(5), p-1455.
- Rouse Jr, J., Haas, R. H., Schell, J. A., & Deering, D. W. (1974). Monitoring vegetation systems in the Great Plains with ERTS. *NASA Special Publication*, 351, 309.
- Roy, J., Albert, C. H., Choler, P., Clément, J. C., Ibanez, S., Lavergne, S., ... & Geremia, R. A. (2013). Microbes on the cliff: alpine cushion plants structure bacterial and fungal communities. *Frontiers in Microbiology*, 4, 64.
- Schönschwetter, P., Stehlik, I., Holderegger, R., & Tribsch, A. (2005). Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology*, 14(11), 3547-3555.
- Sedlacek, J., Wheeler, J. A., Cortés, A. J., Bossdorf, O., Hoch, G., Lexer, C., ... & Rixen, C. (2015). The response of the alpine dwarf shrub *Salix herbacea* to altered snowmelt timing: lessons from a multi-site transplant experiment. *PloS One*, 10(4), e0122395.
- Semenov, Y., Ramousse, R., Le Berre, M., & Tutukarov, Y. (2001). Impact of the black-capped marmot (*Marmota camtschatica bungei*) on floristic diversity of arctic tundra in Northern Siberia. *Arctic, Antarctic, and Alpine Research*, 204-210.
- Shepherd, J. D., & Dymond, J. R. (2003). Correcting satellite imagery for the variance of reflectance and illumination with topography. *International Journal of Remote Sensing*, 24(17), 3503-3514.
- Sherrod, S. K., & Seastedt, T. R. (2001). Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry*, 55(2), 195-218.
- Sirguey, P., Mathieu, R., Arnaud, Y., & Fitzharris, B. B. (2009, July). Seven years of snow cover monitoring with MODIS to model catchment discharge in New Zealand. In *2009 IEEE International Geoscience and Remote Sensing Symposium* (Vol. 2, pp. II-863). IEEE.
- Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology*, 100(3), 652-661.
- Sturm, M., Douglas, T., Racine, C., & Liston, G. E. (2005). Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research: Biogeosciences*, 110(G1).
- Tape, K. E. N., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686-702.
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., ... & Mackay, E. B. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241-245.
- Tranquillini, W. Winter desiccation as the cause for alpine timberline Ed. by U. Benecke and MR Davis Mountain Environments and Subalpine Tree Growth 1980. *Forest Research Institute, Technical Paper*, 70, 263-267.
- Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, 111(38), 13690-13696.

- Walker, D. A., Halfpenny, J. C., Walker, M. D., & Wessman, C. A. (1993). Long-term studies of snow-vegetation interactions. *BioScience*, 43(5), 287-301.
- Walsh, S. J., Butler, D. R., Allen, T. R., & Malanson, G. P. (1994). Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science*, 5(5), 657-672.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 475-505.
- Wheeler, J. A., Hoch, G., Cortés, A. J., Sedlacek, J., Wipf, S., & Rixen, C. (2014). Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia*, 175(1), 219-229.
- Williams, M. W., & Melack, J. M. (1991). Solute chemistry of snowmelt and runoff in an alpine basin, Sierra Nevada. *Water Resources Research*, 27(7), 1575-1588.d
- Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic change*, 94(1-2), 105-121.

Chapter I

*Snow cover duration as a predictor of
alpine plant community diversity and
productivity: a case study in the Vallon
de Roche Noire*

Chapter I Introduction

Despite strong observational evidence for the ecological importance of snow cover duration in shaping mosaics of alpine plant communities, relatively few modeling studies in plant ecology account for snow when quantifying high-elevation environmental gradients. Often used macro-climatic variables, such as Worldclim, are based on interpolations of temperature and precipitation measured at weather stations typically located in large cities, which tends to increase uncertainty in mountainous regions (Hijmans *et al.* 2005). Furthermore, growing season-related energy gradients such as growing degree days and received solar radiation are often estimated assuming a snow-free landscape, which is particularly problematic in temperate alpine areas that are snow covered during the majority of the year. Temperature data-loggers, often buried just below the soil surface, represent an alternative approach to estimating climate variables in topographically complex study areas, and allow for estimation of snow cover duration and temperatures experienced by plant communities (Ford *et al.* 2013). It is difficult to extrapolate point-based measures from data-loggers over space, however, which is a major limitation given the importance of aligning climate variables with other layers in a GIS and of being able to extrapolate model predictions over space.

In this context, remote sensing emerges as a promising tool for estimating spatial heterogeneity in snow cover duration, especially in alpine landscapes where low-stature vegetation becomes entirely covered by snow and the spectral signal of snow is minimally affected by plant canopies. Satellite imagery has been routinely used for snow cover mapping in mountainous areas (Dozier 1989), however examples of applications of snow cover maps based on satellite imagery in alpine ecology studies are rare (but see Kivinen *et al.* 2012). Limitations of remote sensing to map snow cover include i) the ability of the sensor to distinguish snow from other objects such as clouds, rock and vegetation, ii) ground resolution, i.e. pixel size, iii) spatial extent, i.e. scene size and iv) temporal resolution, which determines the time interval between acquired scenes. Additionally, remote sensing-derived environmental variables are not easily transferable to prediction periods in future decades, which is undoubtedly one of the reasons why snow cover has been neglected in many modeling studies predicting responses of alpine plants to climate change (e.g. Engler *et al.* 2011). Process-based models of snowpack dynamics are necessary in order to forecast changes in snow cover duration and enable transferability of snow

cover variables to future decades (Randin *et al.* 2014). Predicting snow height, snow water equivalent and snow distribution at spatial resolutions pertinent to mesotopographic variation in an alpine context (<50 m) constitutes an ongoing challenge in the realm of mechanistic climate and hydrological modeling (Vionnet *et al.*, 2014), however, and for the time being remote sensing observations remain the best option for mapping fine-scale patterns of snow cover duration.

The aim of this first chapter is to explore the relevance of snow-mediated energy gradients, i.e. temperature and solar radiation, for predicting patterns of plant diversity and productivity in a high-elevation watershed. The novelty of our approach lies in developing an empirical snow distribution model based on multi-temporal satellite imagery that can be applied to add information to estimated environmental gradients. We expect that taking the time to quantify spatial heterogeneity in snow cover duration, and filtering air temperature and solar radiation by the presence of snow, will bring us closer to the environmental constraints experienced by plant communities and will improve our ability to predict both turnover in species composition and traits as well as biomass produced over the course of the growing season. Generally speaking, the goal is to find an intermediate approach between: i) a field naturalist approach, where an expert repeatedly observes particular assemblages of species in certain topoclimatic contexts, and is satisfied by the qualitative conclusion that snow cover regulates distribution patterns of alpine plant communities and ii) a purely model-based approach, where environmental variables are selected based on availability and universal applicability, and the value of the model is assessed on the basis of statistical performance alone. Essentially, are our strong expectations concerning the impacts of snow cover duration on alpine plant diversity and productivity stemming from field observations supported in a quantitative modeling framework? The first part of the chapter will assess the statistical and ecological relevance of accounting for snow cover duration when predicting community-level functional and taxonomic diversity. The second part of the chapter will explore variation in NDVI and canopy chlorophyll content relative to energy availability as determined by snow cover duration, and attempt to infer contrasting growth strategies of alpine plant communities within this context.

Chapter IA

*Modeling snow cover duration improves predictions
of functional and taxonomic diversity for alpine
plant communities^{*}*

^{*} **Carlson, B. Z.**, Choler, P., Renaud, J., Dedieu, J. P., & Thuiller, W. (2015).
Modelling snow cover duration improves predictions of functional and taxonomic
diversity for alpine plant communities. *Annals of Botany*, mcv041.

PART OF A SPECIAL ISSUE ON PLANTS AND CLIMATE CHANGE

Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities

Bradley Z. Carlson^{1,2,*}, Philippe Choler^{1–5}, Julien Renaud^{1,2}, Jean-Pierre Dedieu^{6–8} and Wilfried Thuiller^{1,2}

¹Université Grenoble Alpes, LECA, F-38000 Grenoble, France, ²CNRS, LECA, F-38000 Grenoble, France, ³Université Grenoble Alpes, SAJF, F-38000 Grenoble, France, ⁴CNRS, SAJF, F-38000 Grenoble, France, ⁵LTER 'Zone Atelier Alpes', F-38000 Grenoble, France, ⁶Université Grenoble Alpes, LTHE, F-38000 Grenoble, France, ⁷CNRS, LTHE, F-38000 Grenoble, France and ⁸IRD, LTHE, F-38000 Grenoble, France

* For correspondence. E-mail brad.z.carlson@gmail.com

Received: 7 December 2014 Returned for revision: 26 February 2015 Accepted: 3 March 2015

• **Background and Aims** Quantifying relationships between snow cover duration and plant community properties remains an important challenge in alpine ecology. This study develops a method to estimate spatial variation in energy availability in the context of a topographically complex, high-elevation watershed, which was used to test the explanatory power of environmental gradients both with and without snow cover in relation to taxonomic and functional plant diversity.

• **Methods** Snow cover in the French Alps was mapped at 15-m resolution using Landsat imagery for five recent years, and a generalized additive model (GAM) was fitted for each year linking snow to time and topography. Predicted snow cover maps were combined with air temperature and solar radiation data at daily resolution, summed for each year and averaged across years. Equivalent growing season energy gradients were also estimated without accounting for snow cover duration. Relationships were tested between environmental gradients and diversity metrics measured for 100 plots, including species richness, community-weighted mean traits, functional diversity and hyperspectral estimates of canopy chlorophyll content.

• **Key Results** Accounting for snow cover in environmental variables consistently led to improved predictive power as well as more ecologically meaningful characterizations of plant diversity. Model parameters differed significantly when fitted with and without snow cover. Filtering solar radiation with snow as compared without led to an average gain in R^2 of 0.26 and reversed slope direction to more intuitive relationships for several diversity metrics.

• **Conclusions** The results show that in alpine environments high-resolution data on snow cover duration are pivotal for capturing the spatial heterogeneity of both taxonomic and functional diversity. The use of climate variables without consideration of snow cover can lead to erroneous predictions of plant diversity. The results further indicate that studies seeking to predict the response of alpine plant communities to climate change need to consider shifts in both temperature and nival regimes.

Key words: Alpine grassland, climate change, French Alps, GAM, generalized additive model, growing season length, Landsat, mesotopography, plant community structure, remote sensing, snow cover.

INTRODUCTION

In alpine landscapes, variation in snow cover duration along elevation and mesotopographic gradients has long been recognized as a key environmental filter structuring patterns of plant distribution and community composition (Billings, 1973; Evans *et al.*, 1989). Snowpack affects the functioning of alpine ecosystems by exerting strong regulatory control on near-surface soil temperature (Edwards and Cresser, 1992), water and nutrient availability (Freppaz *et al.*, 2007; Weingartner *et al.*, 2007), plant growth and phenology (Kudo and Hirao, 2006; Wipf *et al.*, 2009), growing season length and gross primary production (Baptist and Choler, 2008). Snowmelt timing has also been related to consistent shifts in alpine plant functional traits (Choler, 2005; Venn *et al.*, 2011). Certain late-melting sites, for example, while limited by a short growing season, benefit from decreased exposure to frigid air temperatures in the winter and

spring as well as increased water and nitrogen availability at the time of snow melt (Björk and Molau, 2007), and are identified as taxonomically distinct snowbed communities with particular functional traits, including low stature, high nitrogen leaf content per unit of mass and high specific leaf area (Choler, 2005). In the Alps, altered snow cover regimes in the form of earlier melt dates and rising snow lines have been observed during recent decades, and are anticipated to be an important ongoing consequence of climate change in alpine environments (Beniston, 2012). Collectively, this evidence highlights the importance of better understanding the linkages between snow cover regimes and plant diversity in order to improve models of alpine biodiversity in response to climate change.

Recognizing the importance of snow in alpine systems and building upon a naturalist tradition of field observations and

descriptive studies (e.g. Walker *et al.*, 1993), several authors have incorporated snow as an explanatory variable with the goal of improving species distribution models (Heegaard, 2002; Odland and Munkejord, 2008; Randin *et al.*, 2009; Schöb *et al.*, 2009). Previous studies connecting plant occurrence or traits to snow-melt gradients have quantified snow cover duration by snowmelt rank (e.g. Heegaard, 2002), or by the first snow-free Julian day (e.g. Choler, 2005). Additionally, species distribution modelling studies focused on alpine plants have routinely estimated growing season length-related energy variables (e.g. solar radiation and growing degree days), without considering the mediating effect of snow cover duration on incoming solar radiation or near-surface air temperature (e.g. Zimmermann and Kienast, 1999; Randin *et al.*, 2009; Carlson *et al.*, 2014), which may lead to unrealistic estimates of energy availability for plants (Scherrer and Körner, 2011; Ford *et al.*, 2013).

One consistent difficulty shared by plant ecologists seeking to take snow into account involves mapping and quantifying snow cover duration at sufficiently fine grain to represent mesotopographic heterogeneity (<50 m). Approaches used thus far have been based on manual field surveys (Heegaard, 2002; Choler, 2005; Odland and Munkejord, 2008; Schöb *et al.*, 2009), *in situ* repeat photography (Scherrer and Körner, 2011) and at least one application of a mechanistic model of snow redistribution by wind (Randin *et al.*, 2009). Process-based models accounting for meteorological forcing, topography and land cover have been developed and applied to forecast the effect of anticipated climate change on water budgets in mountainous environments (Liston and Elder, 2006; Viviroli *et al.*, 2009; Vionnet *et al.*, 2014). Validation of snow cover maps generated by two state-of-the-art hydrological models (Liston and Elder, 2006; Viviroli *et al.*, 2009) relative to classified high-resolution imagery, however, showed fairly weak spatial agreement of snow-covered pixels during the snowmelt period (Randin *et al.*, 2014; Table E.1), which is of critical interest to plant ecologists. Classification routines applied to Landsat imagery have long existed as tools for generating high-resolution snow cover maps at the regional scale (Dozier, 1989; Rosenthal and Dozier, 1996). Landsat images are freely available and have the added advantage of providing multiple scenes during the spring and summer months.

Here we implement a remote sensing-based framework for high-resolution mapping of snow cover duration that can be applied to larger extents than would be feasible with a field-mapping approach. While acknowledging the merits of a physical model of snow distribution (Randin *et al.*, 2009), we present our approach as an empirical alternative for snow distribution modelling at the mesotopographic scale. In this study, our goal was to investigate the importance of snow cover duration for predicting multiple facets of plant community structure, including both trait-based and taxonomic diversity. At the scale of a 6.7-km² alpine basin, we mapped snow cover at 15-m resolution for five snowmelt cycles using Landsat imagery, modelled daily snow melt relative to time and mesotopography and combined snow cover maps with air temperature and solar radiation maps at a daily time step and for all five years. Assuming that the presence of snow cancelled incoming solar radiation and maintained near surface air temperature at 0 °C, we averaged the sum of snow-free growing season days, frost days and solar radiation across years. Comparable energy

budgets were also estimated without taking snow cover into account. We then analysed the statistical and ecological implications of snow for predicting taxonomic and functional diversity metrics for 100 vegetation plots, including species richness, Simpson index, species composition as measured by non-metric multidimensional scaling (NMDS) dissimilarity (Faith *et al.*, 1987), community-weighted mean plant height, specific leaf area (SLA), hyperspectral-derived estimates of leaf chlorophyll content and functional diversity. While we focus here on predicting current patterns of alpine plant community structure, a secondary aim is to elucidate which predictive variable(s) may be the most ecologically meaningful for forecasting the response of alpine plant communities to climate change.

MATERIALS AND METHODS

Study area and floristic data

The study area consists of a 6.7-km² watershed, spanning an elevation range from 1980 to 3114 m a.s.l., situated in the Grand Galibier Massif of the south-western French Alps (Fig. 1). This area, referred to as the Vallon de Roche Noire, is located in the commune of Le Monétier-les-Bains within the Ecrins National Park. Vegetation consists of a mosaic of heath, sub-alpine and alpine forb and graminoid communities. Summer grazing is limited to sheep and cattle from late July to mid-September. Comprehensive botanical relevés, including visual estimates of species' relative abundance (Braun-Blanquet, 1957), were carried out for 90 plots of radius 2–5 m in July 2007. Ten additional relevés were completed in July 2011, making a total of 100 plots available for this analysis (Fig. 1).

Measuring alpine plant community diversity

For each plot, species richness and Simpson diversity were quantified based on the community relevé. We used NMDS (Kruskal, 1964) to estimate turnover in species composition across plots. Bray–Curtis dissimilarity was calculated between plots and the resulting dissimilarity matrix was used as an input for NMDS ordination (stress = 0.2). Twenty-five per cent quantiles of scores from the first axis were used to class plots into four distinct groups, based on their taxonomic dissimilarity.

Morphological plant functional traits, including plant height, SLA, leaf dry matter content and leaf nitrogen content were collected from several field campaigns carried out in the study area (Choler, 2005; Chalmandrier *et al.*, 2014). To reduce the pervasive effects of intraspecific trait variability on diversity estimates (Albert *et al.*, 2012), we only used trait measurements sampled above 1800 m a.s.l. Community-weighted mean (CWM; Garnier *et al.*, 2007) trait values for each plot were calculated for SLA and plant height by summing species-level trait values weighted by the abundance of species in the community. Plots for which we lacked trait data for ≥20 % of relative community composition were excluded from the analysis, as recommended by Pakeman and Queded (2007), resulting in the exclusion of 31 plots. For each of the 69 remaining plots, functional diversity was estimated by (1) calculating Gower's distance between all species relative to plant height, SLA, leaf dry matter content and leaf nitrogen content and (2) calculating

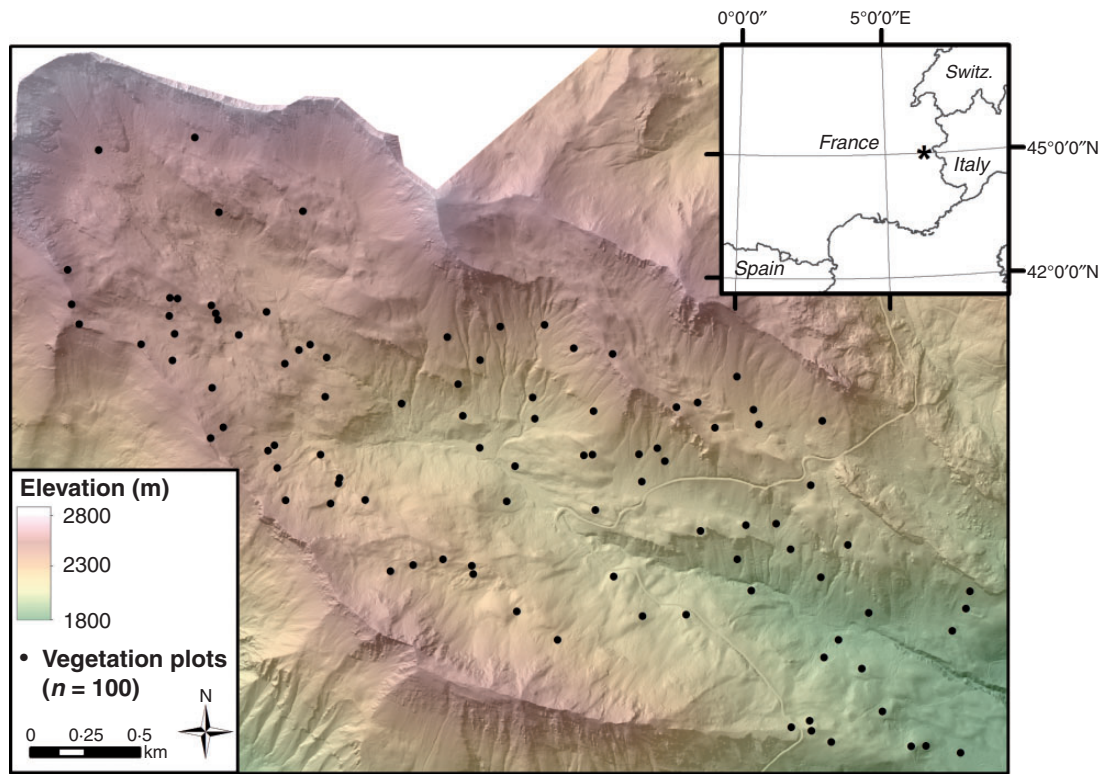


FIG. 1. Locator map for the study area displaying elevation and the location of vegetation plots. *Location of the study area in the inset map.

the abundance-weighted mean pairwise distance between all species in each plot using the *mpd* function in the *picante* R-package. Lastly, a community reshuffling routine that randomized species composition within plots while maintaining species richness was used to test whether convergence of functional diversity differed significantly from a null distribution following 1000 repetitions.

To complement field-based measures of plant diversity, leaf chlorophyll content ($a + b$; $\mu\text{g cm}^{-2}$) was extracted from a hyperspectral image (AISA; Specim Ltd., Finland) obtained for the study area in 2008. Leaf chlorophyll content estimated from reflectance values of hyperspectral imagery has been shown to be a reliable proxy for leaf nitrogen content (Haboudane *et al.*, 2002). Details concerning image acquisition and processing can be found in Pottier *et al.* (2014). The initial 0.8-m resolution image was resampled to 5 m using a mean function and values were extracted for each of the 100 vegetation plots.

Quantifying energy gradients

Daily solar radiation values for 2013 were calculated with the area solar radiation tool in ArcGIS (version 10.2, 2013; Redlands, CA, USA) using a 2-m LiDAR digital elevation model and the clear sky model set to a sky size of 2800 pixels. Output solar radiation maps (W m^{-2}) for 2013 were used for corresponding calendar days in all other years, given that the underlying model did not account for inter-annual variation caused by nebulousity.

One-minute interval air temperature data for the Grand Galibier Massif was obtained by 300-m elevation class from

the SAFRAN–Crocus–MEPRA model chain developed by Météo France. Details of data description, methodology and validation of this regional climate model for the French Alps are provided in Durand *et al.* (2009). Time series of air temperature for the years 2000–14 were aggregated to daily minimum (T_{\min}) and mean (T_{mean}) values. Daily T_{mean} values averaged across years were used to assess the potential length of the growing season, which was defined by the number of consecutive days with a mean temperature above 0°C . The threshold of 0°C was selected based on the minimum required temperature for alpine plant growth, as in Zimmermann and Kienast (1999). To add spatial grain, temperature values associated with a given elevation class (e.g. 2100–2400 m a.s.l.) were assigned to the median elevation (e.g. 2250 m a.s.l.) and elevation-dependent linear regression was used to downscale temperature values across the study area. Daily T_{mean} and T_{\min} rasters were reclassified into binary maps, in which growing season days were defined as grid cells above 0°C and frost days were defined as grid cells less than 0°C . For each day falling within the potential estimated growing season and for five years (2000, 2001, 2002, 2013 and 2014), daily frost and growing season day maps were exported for the study area at 2-m resolution.

Snow cover mapping and modelling

Landsat 7 (ETM+ sensor) imagery was obtained for five dates in 2000, five dates in 2001 and four dates in 2002. Landsat 8 (OLI sensor) was obtained for six dates in 2013 (Supplementary Data Fig. S1) and four dates in 2014.

All retained images had <30 % cloud cover and were acquired between late March and mid-August. Adequate imagery between 2003 and the commissioning of the Landsat 8 satellite in April 2013 was unavailable due to irreparable sensor damage to the Landsat 7 satellite occurring in the spring of 2003 (<http://landsat.usgs.gov/>). The panchromatic band 8 at 15-m resolution was selected for this analysis in order to maximize the resolution of snow cover maps. Scenes were re-projected to Lambert 93 and cropped to the study area prior to classification in eCognition Developer (version 8-0, 2012; Munich, Germany). Binary snow cover maps were generated first by segmenting the greyscale image according to the spectral values of the pixels and second by applying an object-based classification to the segmented image based on a nearest neighbour algorithm. Assignment of objects to snow or no snow classes took into account spectral signal values, as well as topographic context (slope and aspect). Given that available Landsat scenes did not always cover the end of the snow-melt cycle, a snow cover map derived from a 50-cm aerial photograph obtained on 6 August 2003 was aggregated to 15-m resolution using the majority parameter in ArcGIS and subsequently added to each annual Landsat time series. This additional step ensured that late summer snow patches, which occur in consistent locations in the study area from one year to the next (P. Choler, personal observation), were consistently documented.

Following data exploration, for each Landsat year a binomial generalized additive model (GAM; Wood, 2006) in the mgcv R package was used to relate the presence/absence of snow cover to temporal and topographic variables at 15-m resolution ($n = 654\,858$ grid cells). Restricted maximum likelihood was used to estimate penalized regression splines without a fixed number of degrees of freedom. Explanatory variables included: (1) calendar day; (2) solar radiation (estimated by calendar day); (3) normalized topographic position index (TPI; Wilson and Gallant, 2000) multiplied by slope for a 45-m moving window; (4) normalized TPI multiplied by slope for a 225-m moving window; and (5) mean annual temperature. Solar radiation was calculated using the same approach detailed above with a 15-m digital elevation model (DEM) as the input. We calculated TPI as a proxy for convexity and concavity relative to a neighbourhood of surrounding cells. Normalizing TPI values between 0 and 1 and multiplying this term by slope angle was intended to account for the expected increased likelihood of snow accumulation and persistence in low-angle, convex areas (Supplementary Data Fig. S2). The use of two different window sizes is supported by previous work (e.g. Revuelto *et al.*, 2014) and was intended to quantify local topographic heterogeneity both in a local 3×3 (45 m^2) grid cell neighbourhood and at the scale of a slope in a 15×15 (225 m^2) neighbourhood. Mean annual temperature was estimated across the study area by (1) calculating mean annual temperature by elevation class from 2000 to 2013, (2) averaging mean annual temperature across years, and (3) applying elevation-dependent regression in order to provide continuous temperature predictions. In the GAM, mean annual temperature values were grouped by slope orientation category (N, NE, E, SE, S, SW, W and NW) and a response curve was fitted for each aspect class.

Fitted GAMs for each year were used to generate daily snow cover maps for five Landsat years (2000, 2001, 2002, 2013 and 2014). Although topographic variables remained constant, date

and corresponding solar radiation varied by time step. Continuous probability of snow cover maps were converted to binary snow cover maps using the optimal threshold as determined by the true skill statistic (TSS) calculated between probability maps and observed snow cover maps (Allouche *et al.*, 2006; Thuiller *et al.*, 2009). Daily snow cover maps were exported for the five years at 15-m resolution.

Snow cover model validation

SPOT 4 images were obtained for four additional dates in 2013 (www.cnes.fr). After correcting reflectance values for topography (Shepherd and Dymond, 2003), snow cover maps were generated at 20-m resolution by applying a threshold to the normalized difference snow index (NDSI; Dozier, 1989). SPOT 4 and Landsat-derived snow cover maps were resampled to a common 15-m resolution and compared with predicted GAM snow cover maps both (1) non-spatially, i.e. comparing estimates of percentage snow cover for the study area and (2) spatially, by applying the TSS (Allouche *et al.*, 2006).

Combining snow cover with energy gradients

For the length of the estimated growing season and for the five years considered, snow cover maps were combined with daily maps of air temperature and solar radiation. Snow cover maps were disaggregated to 2-m resolution to align with high-resolution maps and applied as a mask; e.g. if a grid cell contained snow, frost days, solar radiation and growing season days were set to zero. Temperature and solar radiation rasters were not upsampled to 15 m (the resolution of snow cover maps) in order to preserve variation in energy variables linked to finer topographic heterogeneity. Snow-free growing season days, frost days and solar radiation were summed for each grid cell and for each year, averaged across years and exported as 2-m raster layers. The sum of snow-free growing season days will be referred to from now on as growing season length (GSL). In addition to calculating average GSL across years, the variability in GSL was also estimated by extracting the range (maximum–minimum) of GSL from all five years and for each grid cell. This metric will be referred to as GSL variability. Solar radiation (for one year) and growing season length (for all five years, and then averaged) were also calculated by summing daily radiation and growing season day maps in the absence of snow cover.

Relating energy gradients to community properties

Values for GSL and solar radiation with and without snow, GSL variability and snow-free frost days were extracted for each of the 100 vegetation plots and integrated into a common data table. Additionally, the percentage of bare ground at 5-m resolution was derived from a high-resolution aerial photograph using image segmentation and this information was extracted for each vegetation plot. We considered the percentage of bare ground to be a proxy for geomorphic disturbance related to slope and possible cryoturbation (Le Roux *et al.*, 2013) and

also for biotic disturbance linked primarily to alpine marmot (*Marmota marmota*) activity (Choler, 2005).

To simplify parameter comparison across models, ordinary least squares linear regression was used to relate GSL and solar radiation with and without snow to taxonomic and functional diversity metrics. Model performance was measured by adjusted R^2 and mean absolute error (MAE). In the case of GSL and solar radiation filtered by snow cover, GSL variability, frost days and the percentage of bare ground were tested as explanatory variables against linear model residuals. Predictors explaining a significant portion of model residuals were retained and the best multivariate model (taking into account possible interaction effects) was fitted to each of the seven biodiversity metrics tested (species richness, Simpson index, NMDS dissimilarity, CWM plant height, CWM SLA, functional diversity and hyperspectral-based leaf chlorophyll content). Finally, to test for spatial patterns in diversity metrics not explained by selected input variables, Moran's I was systematically used to test for spatial autocorrelation among residuals of the best-fitting model.

RESULTS

Snow cover model validation

Model performance for snow cover GAMs was consistent across years, with adjusted R^2 varying from 0.75 to 0.81 and explained deviance varying from 71 to 81 %. Comparison of estimates of relative snow cover area across the study site for seven dates in 2013 showed strong agreement between observed snow cover maps derived from Landsat 8 and SPOT imagery with GAM model outputs (MAE = 6.02 %, R^2 = 0.94, P < 0.001; Supplementary Data Fig. S3A, B). Agreement estimated by TSS between observed and predicted snow cover maps was especially elevated up to mid-July (>0.50), followed by a decline in agreement after this date (mean TSS = 0.54; Fig. S3C). Sensitivity exhibited a similar pattern, with close to 100 % of true positives detected up to July 15 followed by decreasing precision during the second half of the snowmelt period (mean sensitivity = 0.68).

Quantifying energy gradients

The maximum length of the potential alpine growing season based on inter-annual daily mean air temperatures was found to occur from 22 April to 7 November (Supplementary Data Fig. S4). Here we summed growing degree days and solar radiation from 22 April to 15 August as the length of the initial period of growth has been shown to be a primary factor driving plant phenology and growth in alpine systems (Wipf *et al.*, 2009). Growing season length in this case is defined by relative differences in snowmelt timing prior to 15 August and therefore does not represent total energy received during the potential summer growing season.

Median differences in GSL and in the sum of solar radiation with and without snow cover duration were significant (P < 0.001). When GSL was plotted against elevation, the standard error was substantially higher when snow cover was integrated (2.12 days compared with 0.38 days without snow),

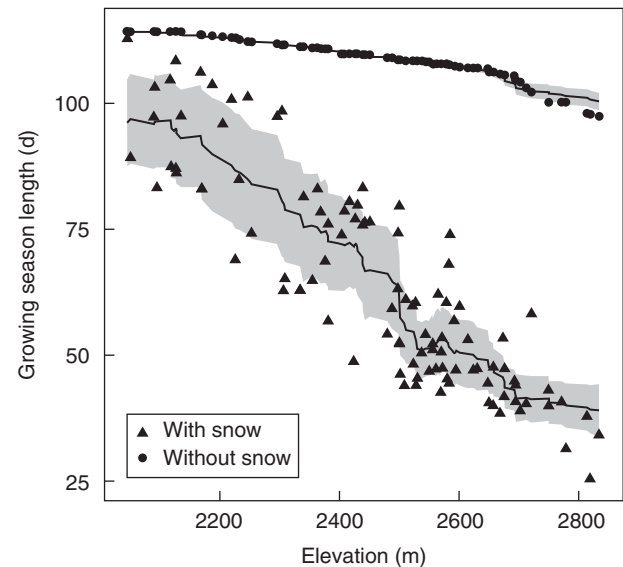


FIG. 2. Variation in growing season length relative to elevation estimated with and without snow cover (as indicated in key). Trend lines represent the running mean ($k = 20$), while the shaded ribbon represents the running mean \pm the running mean absolute error ($k = 20$).

which was also the case for solar radiation ($14\,173\text{ W m}^{-2}$ with snow compared with 6569 W m^{-2} without). For a given elevation, the range of GSL with snow varied by up to 40 d, whereas without snow fluctuation in GSL relative to elevation was almost non-existent and could be attributed to inter-annual variability in daily air temperatures (Fig. 2). The Supplementary Data include a video file illustrating the combination of daily snow cover and solar radiation maps for 2013.

Relating energy gradients to community properties

Due to strong co-linearity between solar radiation and GSL estimated with snow cover (Pearson's $r = 0.96$), energy gradients were analysed separately in relation to plant community properties. Pearson's r estimated between GSL and solar radiation without snow was substantially weaker ($r = -0.32$). For GSL estimated with snow cover, adjusted R^2 increased and mean absolute error decreased for all taxonomic and functional diversity metrics, with the exception of leaf chlorophyll content (Table 1). While average gain in explanatory power when snow cover was taken into account was 3–4 %, increase in R^2 was particularly pronounced for community-weighted mean plant height (+0.20) and for functional diversity (+0.10; Table 1). Slope estimates were consistently lower and intercept values were consistently higher for GSL with snow cover compared with the absence of snow cover (Table 1; Fig. 3). For the seven diversity metrics considered, 95 % confidence intervals for parameter estimates (slope and intercept) did not overlap across models fitted to gradients with and without snow cover (Table 1).

For solar radiation, pronounced shifts in both explanatory power and the direction of relationships occurred. Whereas solar radiation exhibited no significant relationship with the

TABLE 1. Linear model parameters, including 95 % confidence intervals and performance measures (adjusted R^2 and MAE) for gradients estimated with (S) and without (NS) snow

		Taxonomic ($n = 100$)		Functional				
		Richness	Simpson index	NMDS	Height ($n = 98$)	SLA ($n = 95$)	Functional diversity ($n = 67$)	Chlorophyll ($n = 74$)
GSL (S)	Intercept, estimated	10.933	0.760	0.507	-1.933	11.712	0.052	17.952
	Intercept, lower	5.529	0.730	0.429	-4.373	10.169	0.040	4.562
	Intercept, upper	16.337	0.791	0.585	0.507	13.255	0.065	31.342
	Slope, estimated	0.288	0.001	-7.78×10^{-3}	0.196	0.035	7.56×10^{-4}	0.296
	Slope, lower	0.208	0.001	-8.94×10^{-3}	0.160	0.012	5.70×10^{-4}	0.113
	Slope, upper	0.368	0.002	-6.62×10^{-3}	0.231	0.057	9.43×10^{-4}	0.478
	MAE	6.673	0.035	0.096	2.804	1.784	0.012	11.008
	R^2 (adjusted)	0.334***	0.292***	0.641***	0.543***	0.080**	0.495***	0.114**
GSL (NS)	Intercept, estimated	-128.947	-0.056	4.523	-84.062	-4.082	-0.335	-36.700
	Intercept, lower	-178.584	-0.316	3.804	-110.305	-17.904	-0.467	-472.083
	Intercept, upper	-79.311	0.205	5.243	-57.820	9.741	-0.202	-201.309
	Slope, estimated	1.147	8.37×10^{-3}	-0.042	0.871	0.166	4.0×10^{-3}	3.410
	Slope, lower	1.000	5.97×10^{-3}	-0.048	0.630	0.039	2.79×10^{-3}	2.181
	Slope, upper	1.913	10.8×10^{-3}	-0.035	1.112	0.293	5.22×10^{-3}	4.640
	MAE	7.787	0.035	0.096	3.530	1.801	0.013	9.914
	R^2 (adjusted)	0.283***	0.324***	0.609***	0.342***	0.057*	0.390***	0.288***
Solar (S)	Intercept, estimated	13.549	0.771	0.438	-0.763	11.137	0.056	25.270
	Intercept lower	8.174	0.741	0.353	-3.164	9.731	0.044	12.040
	Intercept upper	18.924	0.800	0.523	1.639	12.543	0.068	38.500
	Slope, estimated	3.88×10^{-5}	2.03×10^{-7}	-1.05×10^{-6}	2.79×10^{-5}	6.817×10^{-6}	1.073×10^{-7}	3.00×10^{-5}
	Slope lower	2.63×10^{-5}	1.35×10^{-7}	-1.25×10^{-6}	2.23×10^{-5}	3.596×10^{-6}	7.96×10^{-8}	1.848×10^{-6}
	Slope upper	5.13×10^{-5}	2.71×10^{-7}	-8.57×10^{-7}	3.41×10^{-5}	1.004×10^{-5}	1.35×10^{-7}	5.810×10^{-5}
	MAE	6.953	0.036	0.107	2.941	1.705	0.012	10.894
	R^2 (adjusted)	0.273***	0.257***	0.531***	0.505***	0.151***	0.471***	0.046*
Solar (NS)	Intercept, estimated	60.842	0.941	-0.617	13.897	2.696	0.099	113.500
	Intercept, lower	38.285	0.816	-1.059	1.357	-2.328	0.025	69.508
	Intercept, upper	83.399	1.066	-0.174	26.438	7.721	0.174	157.568
	Slope, estimated	-4.28×10^{-5}	-1.19×10^{-7}	8.50×10^{-7}	-4.37×10^{-6}	1.531×10^{-5}	1.62×10^{-9}	-1.02×10^{-4}
	Slope, lower	-7.33×10^{-5}	-2.88×10^{-7}	2.51×10^{-7}	-4.37×10^{-6}	8.504×10^{-6}	-9.80×10^{-8}	-1.61×10^{-4}
	Slope, upper	-1.22×10^{-5}	5.066×10^{-8}	1.45×10^{-7}	-4.37×10^{-6}	2.211×10^{-5}	1.01×10^{-7}	-4.19×10^{-6}
	MAE	7.745	0.041	0.160	4.132	1.572	0.018	10.418
	R^2 (adjusted)	0.064**	0.009	0.065**	-0.008	0.168***	-0.015	0.126**

P values: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

NMDS, scores from the first axis of NMDS ordination; SLA, community-weighted mean specific leaf area.

Simpson index, plant height or functional diversity, these relationships became highly significant when snow cover was added (Table 1; Fig. 4C, D). Although the direction of relationships remained positive both with and without snow, substantial gains in R^2 occurred when snow was included with respect to species richness (+0.21) and relative to first-axis NMDS scores (+0.51). Shifts in R^2 corresponded with changes of similar magnitude in mean absolute error (Table 1). Negative slope values estimated without snow for species richness, Simpson index, plant height and leaf chlorophyll content switched to being positive with snow, whereas the relationship between solar radiation and NMDS taxonomic dissimilarity changed from being positive to negative when snow was taken into account (Table 1; Fig. 4C, F). Explanatory power was slightly higher for SLA without snow (+0.02); however, mean absolute error was the same for both models. Within the 95 % quantile of SLA, snow bed plots expected to receive low solar radiation and exhibit high SLA were differentiated with snow (Fig. 4A), while these plots were scattered and poorly characterized when solar radiation was summed without snow cover (Fig. 4B). As was the case for GSL, 95 % confidence intervals for slope and

intercept estimates for models with and without snow cover did not overlap (Table 1).

Analysis of residuals

Overall, model residuals for solar and GSL responded in an equivalent manner with respect to other estimated environmental gradients (physical disturbance, frost stress and inter-annual variability in GSL), although R^2 was slightly higher for predictors applied to solar radiation residuals (Table 2). Accordingly, results for the two will be reported simultaneously. Physical disturbance explained a significant portion of residual variation for all taxonomic diversity metrics (Table 2). To a lesser degree, physical disturbance also captured variation in residuals for SLA and leaf chlorophyll content, but not for height or functional diversity. The estimated number of snow-free frost days was not a significant predictor of residual error for diversity metrics, with the exception of a weak relationship with plant height residuals in the case of solar radiation. Inter-annual variability in GSL was a significant predictor of model residuals in

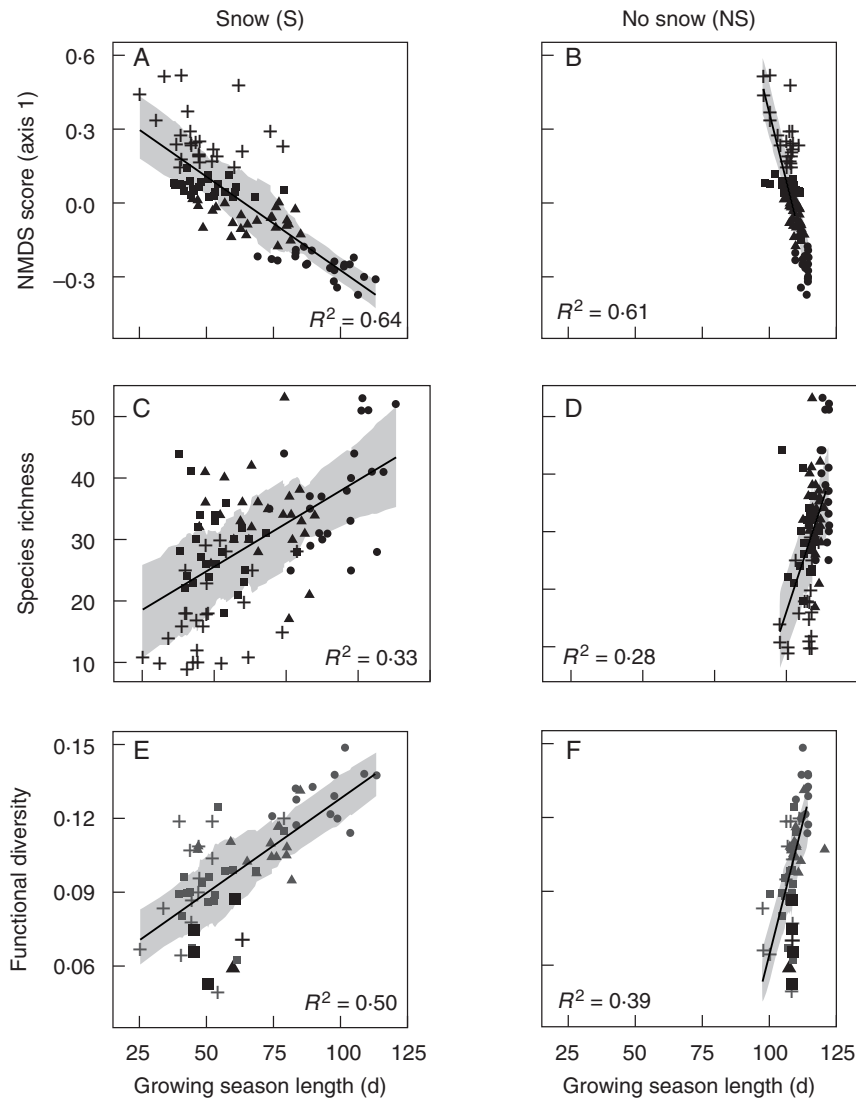


FIG. 3. First-axis NMDS score (A, B), species richness (C, D) and functional diversity (E, F) plotted relative to growing season length estimated with (left) and without (right) snow cover. Point symbols correspond to quartiles of the NMDS score. Black points in (E) and (F) represent significant functional convergence. Shaded ribbons correspond to the linear model \pm the running mean absolute error ($k = 25$).

the case of species richness, NMDS dissimilarity, plant height, SLA and leaf chlorophyll content, but not for Simpson index or functional diversity (Table 2). GSL variability was greatest for high-elevation, south-facing scree communities, characterized by *Ranunculus glacialis* and *Oxyria digyna*.

Model residuals were not found to be spatially autocorrelated for gradients estimated with snow cover (Table 2). When snow cover was not taken into account, however, residuals were spatially autocorrelated for both GSL and solar radiation in the case of NMDS dissimilarity and plant height (results not shown), even when other predictors were incorporated in the model (bare ground and GSL variability). The lack of spatial autocorrelation when snow was included indicates that remaining unexplained variance in diversity metrics was due to local heterogeneity not accounted for in the model rather than systematic error in the estimation of energy availability. Finally, adjusted R^2 for the best-fitting multivariate model was

equivalent or slightly higher in the case of GSL compared with solar radiation, with the exception of SLA, for which the solar radiation model captured 4 % more variation (Table 2). Averaging R^2 across diversity metrics, the multivariate GSL model was able to explain 56 % of variation in taxonomic diversity and 38 % of variation in functional diversity. In comparison, the solar radiation model captured slightly less (51 %) of the variation in taxonomic diversity and an equivalent amount (37 %) of the variation in functional diversity.

DISCUSSION

Although previous studies have examined relationships between snow cover and alpine plant distribution patterns (Heegaard, 2002; Odland and Munkejord, 2008; Randin *et al.*, 2009; Schöb *et al.*, 2009) and functional traits (Choler, 2005;

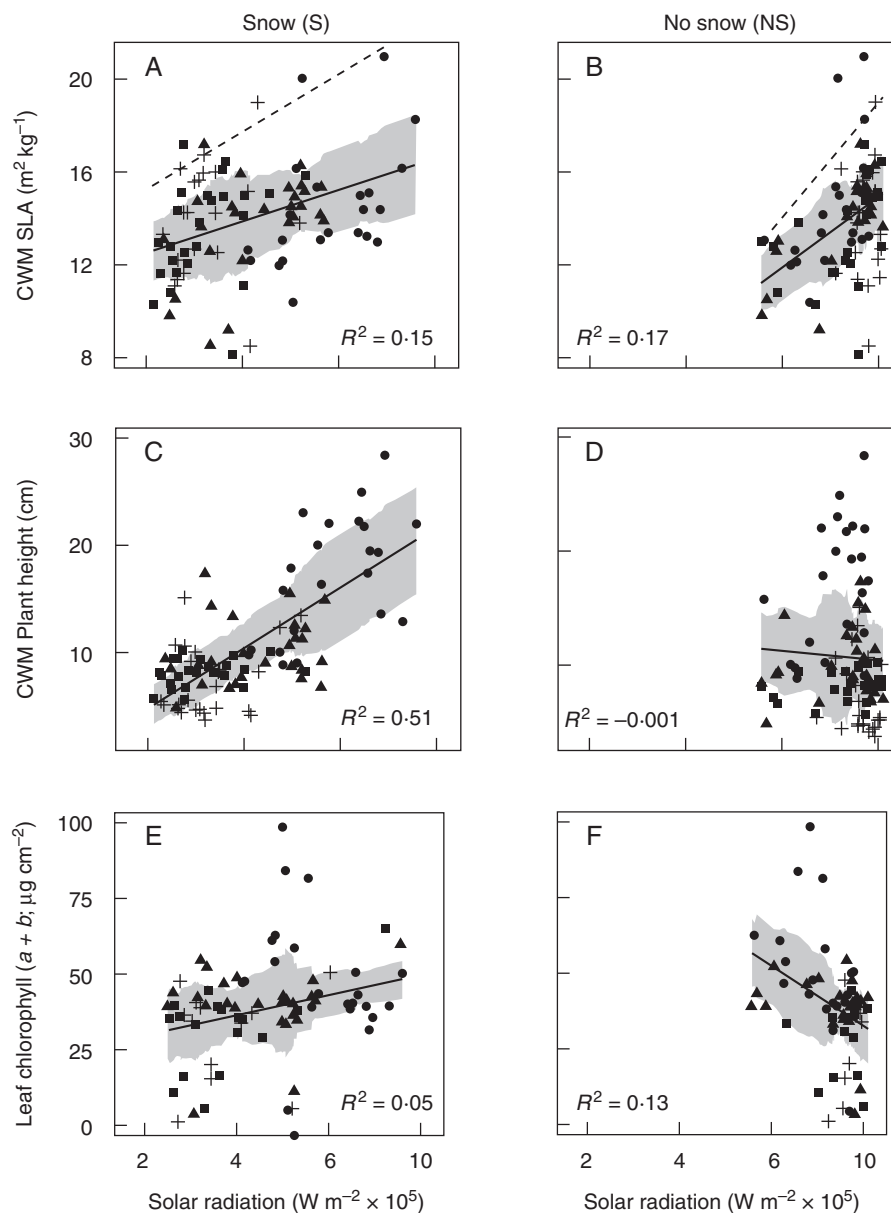


FIG. 4. CWM SLA ($\text{m}^2 \text{kg}^{-1}$; A, B), CWM plant height (C, D) and percentage leaf chlorophyll content ($\text{W m}^{-2} \times 10^5$; E, F) plotted relative to the sum of solar radiation (W m^{-2}) estimated with (S) and without (NS) snow cover. Point symbols correspond to quartiles of the NMDS score. Shaded ribbons correspond to the linear model \pm the running mean absolute error ($k=25$). In (A) and (B), dashed lines represent the best fit regression applied to the 95 % quantile of CWM SLA values.

Venn *et al.*, 2011), to the best of our knowledge this study is the first to quantitatively assess the importance of snow cover duration for predicting multiple facets of alpine plant diversity and structure along environmental gradients at the community level. Methodologically, we used a combination of high-resolution remote sensing products, a digital elevation model and coarse-resolution gridded climate data to implement an empirical snow distribution model (see Appendix for further discussion of our method relative to other approaches). Conceptually, we show the enhanced ecological relevance and statistical predictive power of bioclimatic variables that combine energy inputs (temperature and solar radiation) with snow cover duration. Our findings furthermore indicate that, in

addition to energy gradients, inter-annual variability in growing season length, as well as physical disturbance, have strong effects on alpine plant community properties. Despite the small extent ($\sim 7 \text{ km}^2$) of our study area, given the ubiquitous nature of snow cover throughout high-elevation systems (Billings, 1973), we are confident that our findings are applicable to alpine areas in other geographic contexts.

Ecological and statistical contributions of integrating snow cover

High variability in estimated growing season length for plots located at similar elevations but within contrasting

TABLE 2. Residual variance explained (adjusted R^2) by disturbance (% bare ground), frost (number of snow-free frost days) and inter-annual growing season length (GSL) variation. Model performance (adjusted R^2) and results from Moran's I test are reported for the best model. Significant predictors of model residuals were included in the best model

		Taxonomic		Functional				
		Richness	Simpson	NMDS	Height	SLA	Functional diversity	Chlorophyll
GSL	Residual R^2 (disturbance)	0.098***	0.211***	0.240***	−0.002	0.055*	0.005	0.054*
	Residual R^2 (frost)	−0.01	0.009	−0.001	0.024	−0.002	−0.015	0.026
	Residual R^2 (variation)	0.079**	−0.009	0.069*	0.079*	0.060**	−0.013	0.041*
	Moran's I (P value)	0.305	0.901	0.116	0.725	0.359	0.121	0.95
	R^2 (best model)	0.434***	0.467***	0.768***	0.534***	0.291*** (x)	0.495***	0.213***
Solar	Residual R^2 (disturbance)	0.123***	0.236***	0.257***	−0.008	0.047*	0.009	0.065*
	Residual R^2 (frost)	−0.004	0.002	−0.009	0.030*	−0.011	−0.014	−0.005
	Residual R^2 (variation)	0.158***	0.008	0.197***	0.037*	0.053*	0.012	0.086**
	Moran's I (P value)	0.333	0.917	0.131	0.462	0.453	0.131	0.709
	R^2 (best model)	0.434***	0.456***	0.744***	0.525***	0.332*** (x)	0.471***	0.195***

P values: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

(x) denotes an interaction effect between solar/GSL and GSL variation (all other multivariate combinations are additive).

NMDS, scores from the first axis of NMDS ordination; SLA, community-weighted mean SLA.

mesotopographic contexts (Fig. 2) is in agreement with previous studies applying field-mapping techniques to differentiate environmental conditions for alpine plant communities (Walker *et al.*, 1993; Choler, 2005). Our remote-sensing approach thus provides a spatially continuous method for estimating energy availability, which field measurements have shown is a strong driver of both community type and of aboveground phytomass production (Walker *et al.*, 1994). Ideally, our estimate of growing season days would have been conducted using plot-level measures from *in situ* soil data loggers in order to better approximate thermal conditions found in microhabitats (Scherrer and Körner, 2011; Slavich *et al.*, 2014). These data were not available for all Landsat years, however. Furthermore, and particularly given the remote-sensing approach used here, we argue that it is worthwhile to test the utility of variables that are widely available and that can be applied more readily at broader spatial scales, such as regional or, in this case, massif-scale air temperature. The local meteorological model we used (Durand *et al.*, 2009) is based on continuous measurements from multiple local weather stations, and the outputs by 300-m elevation class that we downscaled are finer than standard macroclimatic variables, such as WorldClim (Hijmans *et al.*, 2005). In the case of solar radiation, simulating daily clear sky gain in a GIS appears to be the best approach, given the difficulty and cost of instrumentation and the impracticality of interpolating point measurements. In summary, we consider that both GSL and solar radiation filtered by snow cover duration represent good proxies of energy availability, providing a more realistic estimate of conditions experienced by plant communities compared with thermal gradients estimated independently of snow cover duration. Furthermore, our selection of environmental variables based on ecological significance, e.g. plants only receiving radiation in the absence of snow, represents an important change in approach relative to modelling studies that frequently select predictors strictly on a statistical basis.

The comparatively strong statistical performance of GSL estimated without snow can be attributed to the underlying elevation gradient resulting from temperature downscaling.

Despite the modest gain in explanatory power conferred by estimating GSL with snow cover (+3–4 %), the shift in model parameters (slope and intercept) emphasizes that snow cover had a strong effect on model fit. Furthermore, the more substantial 20 % gain in R^2 in the case of plant height suggests that energy availability estimated with snow better captures the environmental filter controlling variation in community-weighted mean plant height. By extension, the 10 % increase in R^2 relative to functional diversity is a strong indicator that functional convergence around an optimal trait in stressful conditions is better predicted when snow cover is taken into account (Table 1; Fig. 3E, F). As found in another study measuring leaf chlorophyll in the North American Rockies, we observed a decrease in leaf chlorophyll content with elevation (Spasojevic and Suding, 2012). However, high measured chlorophyll values for both *Vaccinium* sp.-dominated and *Festuca paniculata*-dominated communities, which are found at similar elevations but in opposite mesotopographic contexts, led to a decrease in R^2 for GSL with snow compared with the absence of snow (Table 1). This finding indicates that there may be a broad range of community-aggregated leaf trait values for a given level of snow cover duration.

Our findings strongly caution against the use of incident solar radiation summed without consideration of snow cover duration as a predictive variable for modelling studies in alpine environments. We found summer solar radiation estimated without snow to be a weak and at times misleading predictor of both functional and taxonomic diversity. The pronounced rise in R^2 for species richness, Simpson index, taxonomic dissimilarity (NMDS), plant height and functional diversity when snow was taken into account highlights the statistical gain afforded by summing snow-free incoming radiation during the growing season. Additionally, we found solar radiation summed without snow cover to be a significant *negative* predictor of species richness and leaf chlorophyll content. The switch to a more intuitive positive relationship between energy availability, photosynthetic activity and species richness points to the enhanced ecological significance gained by summing snow-free solar radiation.

While it has been demonstrated that community-weighted mean SLA declines with elevation (Bello *et al.*, 2013) and that SLA increases in late-melting sites along a mesotopographic gradient (Choler, 2005), a third study shows that variation in community-weighted mean SLA measured in the context of a combined mesotopographic and elevation gradient exhibits no clear trend (Spasojevic and Suding, 2012). Although we found a significant relationship between SLA and solar radiation with and without snow (Table 1; Fig. 4A, B), consistently elevated mean absolute error points to the high range of SLA values for a given value of radiation throughout the gradient. We do not consider the R^2 value to be particularly meaningful in the case of SLA, given that previous studies have documented a wide range of community-weighted mean SLA values at high elevation in relation to snow cover duration (Choler, 2005). Diverging functional strategies, linked to fellfield and snowbed communities, are apparent at upper elevations when solar radiation is filtered by snow cover; however, this variation in the cold portion of the gradient is absent when received solar radiation is calculated in the absence of snow (Fig. 4A, B).

Despite the documented importance of frost events as a stress factor affecting the growth and survival of alpine plants (Körner, 2003; Wipf *et al.*, 2006, 2009), our approach to summing snow-free frost days during the growing season did not constitute a significant predictor of model residuals (Table 2). We attribute this absence of explanatory power largely to a lack of measurement of sub-surface soil temperature not only during the winter months but also in spring, when plants are the most sensitive to snow-free frost damage (Bannister *et al.*, 2005). Significant residual variance explained by physical disturbance, particularly in the case of taxonomic diversity (Table 1), however, confirms that the percentage of bare ground estimated from high-resolution imagery is a meaningful proxy for biotic and geomorphic disturbances affecting community composition.

Finally, while it is difficult to classify inter-annual variability in snow cover duration and air temperature as stress or disturbance (Grime, 1977), the amplitude of variation in GSL was a significant predictor of model residuals for the majority of diversity metrics considered (Table 2). A study conducted in Japan documents highly variable phenology of snowbed species relative to inter-annual variation in snow melt, whereas fellfield species initiated flowering and seed-set at consistent times regardless of melt date (Kudo *et al.*, 2006). In addition to phenology, our findings support the conclusion that the taxonomic and functional characteristics of alpine grasslands are sensitive to the inter-annual consistency of snow cover duration, which has implications for ecosystem functioning (Baptist and Choler, 2008). Evidence from long-term monitoring of alpine plant communities' response to environmental change in the Colorado Rockies furthermore indicates that directional shifts in plant diversity are accompanied by fine-scale oscillations in community composition linked to inter-annual variability in environmental conditions, including snow cover duration (Spasojevic *et al.*, 2013).

Implications for predicting community responses to climate change

Our study, while focused on current patterns of alpine plant community properties, has strong implications for forecasting

the response of alpine plants to global change. We view the shift in model parameters with and without snow as being of equivalent importance to the gain in explanatory power conferred by taking snow cover duration into account. More specifically, slope values were consistently higher when GSL was estimated without snow, which could lead to potentially extreme predictions of community responses to incremental climate change if snow cover is not taken into account.

As a next step emerging from this work, geared to linking energy availability to alpine plant diversity and functioning (phenology and productivity), we recommend summing received snow-free solar radiation when air temperature is above a physiologically meaningful threshold, such as 0 °C. Ecologically, this metric of energy availability would aim to quantify the amount of incoming solar radiation available for photosynthesis, as mediated by snow cover duration. Statistically, it would be possible to integrate available air temperature scenarios for the coming decades in order to define the potential growing season length (IPCC, 2007), even if clear-sky solar radiation remained constant for the prediction period. An ongoing challenge involves the procuring of future, climate-driven snow cover maps at appropriate spatial and temporal scales. Despite difficulties predicting persistent snow patches, recent studies demonstrate that forecasting the response of snow regimes to climate change is becoming increasingly feasible due to advances in hydrological modelling in mountainous study areas (Kobierska *et al.*, 2013; Randin *et al.*, 2014).

Conclusions

While other studies have examined current patterns in order to infer the relevance of snow cover for predicting responses of alpine plants to global change (Bannister *et al.*, 2005; Wipf *et al.*, 2009; Venn *et al.*, 2011), to the best of our knowledge ours is the first to demonstrate the utility of high-resolution imagery for mapping snow cover patterns in complex alpine terrain, and furthermore to provide a methodological framework for quantifying relationships between snow-mediated energy budgets and the multiple facets of taxonomic and functional diversity. The findings reported here underscore the importance of considering spatial heterogeneity in both thermal and nival regimes in order to link alpine plant community properties to environmental gradients, both for the present and in the context of global change.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Figure S1: Landsat 8 scenes from 2013 cropped to the study area. Figure S2: combined slope and topographic position index maps derived for a 45-m moving window and for a 225-m moving window. Figure S3: observed and predicted snow cover area for 2013 Landsat and SPOT acquisition dates, and for the nine image acquisition dates. Agreement between observed and predicted snow cover area maps, and proportion of observed snow-covered pixels detected by the GAM model. Figure S4: daily mean air temperatures for the 2000–13 period. Video: animation of daily snow melt combined with daily maps of solar radiation (growing

season day 1 = 22 April 2013; growing season day 110 = 10 August 2013.

ACKNOWLEDGEMENTS

We thank D. Georges, F. Mazel, L. Chalmandrier and C. Dentant for technical assistance and helpful discussions. Thanks are also due to T. Cavallo, who contributed results from the SPOT 4 – TAKE 5 Program. This research was conducted within the Long-Term Ecosystem Research (LTER) Zone Atelier Alpes, a member of the ILTER-Europe network. Data were provided in the context of the SPOT4-TAKE5 Program, initiated by the Centre d'Etudes Spatiales de la Biosphère (CESBIO) and which received additional funding from the Zone Atelier Alpes. The research leading to this paper received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO).

LITERATURE CITED

- Albert CH, de Bello F, Boulangeat I, Pellet G, Lavorel S, Thuiller W. 2012. On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* **121**: 116–126.
- Allouche O, Tsoar A, Kadmon R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**: 1223–1232.
- Bannister P, Maegli T, Dickinson KJ, et al. 2005. Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? *Oecologia* **144**: 245–256.
- Baptist F, Choler P. 2008. A simulation of the importance of length of growing season and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Annals of Botany* **101**: 549–559.
- Bello FD, Lavorel S, Lavergne S, et al. 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography* **36**: 393–402.
- Beniston M. 2012. Is snow in the Alps receding or disappearing? *Wiley Interdisciplinary Reviews: Climate Change* **3**: 349–358.
- Billings WD. 1973. Arctic and Alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience* **23**: 697–704.
- Björk RG, Molau U. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research* **39**: 34–43.
- Braun-Blanquet J. 1957. Ein Jahrhundert Florenwandel am Piz Linard (3414 m). *Bulletin du Jardin Botanique de l'Etat a Bruxelles*, Volume Jubilaire Walter Robyns: 221–232.
- Carlson BZ, Georges D, Rabatel A, et al. 2014. Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models. *Diversity and Distributions* **20**: 1379–1391.
- Chalmandrier L, Münkemüller T, Lavergne S, Thuiller W. 2014. Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. *Ecology* **96**: 143–153.
- Choler P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research* **37**: 444–453.
- Dozier J. 1989. Spectral signature of alpine snow cover from the Landsat Thematic Mapper. *Remote Sensing of Environment* **28**: 9–22.
- Durand Y, Laternser M, Giraud G, Etchevers P, Lesaffre B, Merindol L. 2009. Reanalysis of 44 yr of climate in the French Alps (1958–2002): methodology, model validation, climatology, and trends for air temperature and precipitation. *Journal of Applied Meteorology and Climatology* **48**: 429–449.
- Edwards AC, Cresser MS. 1992. Freezing and its effect on chemical and biological properties of soil. *Advances in Soil Science* **18**: 59–79.
- Evans BM, Walker DA, Benson CS, Nordstrand EA, Petersen GW. 1989. Spatial interrelationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska. *Ecography* **12**: 270–278.
- Faith DP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**: 57–68.
- Ford KR, Ettinger AK, Lundquist JD, Raleigh MS, Lambers JHR. 2013. Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-snow mountain landscape. *PLoS One* **8**: e65008.
- Freppaz M, Williams BL, Edwards AC, Scalenghe R, Zanini E. 2007. Simulating soil freeze/thaw cycles typical of winter alpine conditions: implications for N and P availability. *Applied Soil Ecology* **35**: 247–255.
- Garnier E, Lavorel S, Ansquer P, et al. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* **99**: 967–985.
- Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**: 1169–1194.
- Haboudane D, Miller JR, Tremblay N, Zarco-Tejada PJ, Dextraze L. 2002. Integrated narrow-band vegetation indices for prediction of crop chlorophyll content for application to precision agriculture. *Remote Sensing of Environment* **81**: 416–426.
- Heegaard E. 2002. A model of alpine species distribution in relation to snow-melt time and altitude. *Journal of Vegetation Science* **13**: 493–504.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- IPCC. 2007. *Climate change (2007): The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Kobierska F, Jonas T, Zappa M, Bavay M, Magnusson J, Bernasconi SM. 2013. Future runoff from a partly glacierized watershed in central Switzerland: a 2 model approach. *Advances in Water Resources* **55**: 204–214.
- Körner C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems*. Heidelberg: Springer.
- Kruskal JB. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115–129.
- Kudo G, Hirao AS. 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Population Ecology* **48**: 49–58.
- Liston GE, Elder K. 2006. A distributed snow-evolution modeling system (SnowModel). *Journal of Hydrometeorology* **7**: 1259–1276.
- Odland, A, Munkejord HK. 2008. Plants as indicators of snow layer duration in southern Norwegian mountains. *Ecological Indicators* **8**: 57–68.
- Pakeman RJ, Quested HM. 2007. Sampling plant functional traits: what proportion of the species need to be measured? *Applied Vegetation Science* **10**: 91–96.
- Pottier J, Malenovsky Z, Psomas A, et al. 2014. Modelling plant species distribution in alpine grasslands using airborne imaging spectroscopy. *Biology Letters* **10**: 20140347.
- Randin CF, Vuissoz G, Liston GE, Vittoz P, Guisan A. 2009. Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the Western Swiss Alps. *Arctic, Antarctic, and Alpine Research* **41**: 347–361.
- Randin CF, Dedieu JP, Zappa M, Long L, and Dullinger S. 2014. Validation of and comparison between a semidistributed rainfall-runoff hydrological model (PREVAH) and a spatially distributed snow-evolution model (SnowModel) for snow cover prediction in mountain ecosystems. *Ecohydrology* in press. doi:10.1002/eco.1570.
- Revuelto J, López-Moreno JI, Azorín-Molina C, Vicente Serrano SM. 2014. Topographic control of snowpack distribution in a small catchment in the central Spanish Pyrenees: intra- and inter-annual persistence. *Cryosphere* **8**: 1989–2006.
- Rosenthal W, Dozier J. 1996. Automated mapping of montane snow cover at subpixel resolution from the Landsat Thematic Mapper. *Water Resources Research* **32**: 115–130.
- Le Roux PC, Virtanen R, Luoto M. 2013. Geomorphological disturbance is necessary for predicting fine scale species distributions. *Ecography* **36**: 800–808.
- Scherrer D, Körner C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* **38**: 406–416.
- Schöb C, Kammer PM, Choler P, Veit H. 2009. Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Plant Ecology* **200**: 91–104.
- Shepherd JD, Dymond JR. 2003. Correcting satellite imagery for the variance of reflectance and illumination with topography. *International Journal of Remote Sensing* **24**: 3503–3514.

- Slavich E, Warton DI, Ashcroft MB, Gollan JR, Ramp D. 2014. Topoclimate versus macroclimate: how does climate mapping methodology affect species distribution models and climate change projections? *Diversity and Distributions* **20**: 952–963.
- Spasojevic MJ, Suding KN. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* **100**: 652–661.
- Spasojevic MJ, Bowman WD, Humphries HC, Seastedt TR, Suding KN. 2013. Changes in alpine vegetation over 21 years: are patterns across a heterogeneous landscape consistent with predictions? *Ecosphere* **4**: art117. doi.org/10.1890/ES13-00133.1.
- Thuiller W, Lafourcade B, Engler R, Araujo MB. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* **32**: 369–373.
- Venn SE, Green K, Pickering CM, Morgan JW. 2011. Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecology* **212**: 1491–1499.
- Vionnet, V, Martin E, Masson V, et al. 2014. Simulation of wind-induced snow transport and sublimation in alpine terrain using a fully coupled snowpack/atmosphere model. *Cryosphere* **8**: 395–415.
- Viviroli D, Zappa M, Gurtz J, Weingartner R. 2009. An introduction to the hydrological modelling system PREVAH and its pre-and post-processing-tools. *Environmental Modelling & Software* **24**: 1209–1222.
- Walker DA, Halfpenny JC, Walker MD, Wessman CA. 1993. Long-term studies of snow-vegetation interactions. *BioScience* **43**: 287–301.
- Walker MD, Webber PJ, Arnold EH, Ebert-May D. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology* **75**: 393–408.
- Weingartner R, Viviroli D, Schaedler B. 2007. Water resources in mountain regions: a methodological approach to assess the water balance in a highland–lowland system. *Hydrological Processes* **21**: 578–585.
- Wilson JP, Gallant JC. 2000. *Terrain analysis: principles and applications*. New York: John Wiley & Sons.
- Wipf S, Rixen C, Mulder CP. 2006. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Global Change Biology* **12**: 1496–1506.
- Wipf S, Stoeckli V, Bebi P. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change* **94**: 105–121.
- Wood SP. 2006. *Generalized additive models: an introduction with R*. Boca Raton, FL: CRC Press.
- Zimmermann NE, Kienast F. 1999. Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science* **10**: 469–482.

APPENDIX. STRENGTHS AND LIMITATIONS OF THE SNOW DISTRIBUTION MODEL

Predicting snow height, snow water equivalent and snow distribution at spatial resolutions pertinent to mesotopographic variation in an alpine context (<50 m) constitutes an ongoing challenge in the realm of process-based climate and hydrological modelling (Vionnet *et al.*, 2014). Mechanistic models have been developed for this purpose, taking into account meteorological forcing, land cover and topography [PREVAH (Viviroli *et al.*, 2009)] and also snow redistribution by wind [SnowModel (Liston and Elder, 2006); Crocus (Vionnet *et al.*, 2014)]. Such models are well suited to forecasting the effect of climate change on snow cover regimes (Kobierska *et al.*, 2013), and have already been applied successfully to improve predictive variables in a species distribution modelling context (Randin *et al.*, 2009). For the time being and from the standpoint of plant ecologists, however, we are not convinced that existing process-based models are superior to a remote sensing-based approach at <20-m resolution, particularly when the critical period of interest is the snow-melt cycle. A recent study comparing snow cover maps at 20-m resolution generated by SnowModel and PREVAH in the Austrian Alps to observed snow cover maps classified from SPOT imagery found low agreement during the melting period [5.4 % of true positives were detected in the case of PREVAH, and 10.1 % for SnowModel (Randin *et al.*, 2014)]. Comparison of predicted snow cover maps with 2013 Landsat and SPOT imagery in this study, in contrast, yielded an average detection of 68 % of true positives during the melting period, although this rate did fall below 50 % after 15 July (Supplementary Data Fig. S3D). In short, while a process-based approach to snow modelling is ultimately the most desirable, we argue that the approach used here is viable for two principal reasons: (1)

the spatial patchwork generated by snowmelt patterns is well captured by high-resolution imagery (Supplementary Data Fig. S1), allowing for simple modelling of a complex phenomenon; and (2) our approach is applicable by ecologists with access to high-resolution digital elevation data and Landsat imagery.

Despite a number of advantages, we are aware that our empirical approach to snow modelling is inadequate for precisely predicting end-of-season snow patches persisting until early August. Late-melting sites largely independent of elevation caused by snow accumulation due to avalanches, for example, were not captured by our model. While model performance remained high for the majority of the melt period from the end of April to mid-July (Supplementary Data Fig. S3A, B), the decline in spatial agreement at the end of summer compared with observed snow cover maps can be attributed to increasing relative importance of mesotopographic context and decreasing relative importance of date and elevation over the course of the melt cycle. Failure to account for this tendency in the model explains, at least in part, why the predicted ranking of snow melt by site differed for certain high-elevation plots from field observations. Although late July snow patches can affect the growing season length for certain nival species, such as *Doronicum grandiflorum* and *Geum reptans*, the first snow-free day for snow bed communities dominated by *Salix herbacea*, *Alchemilla pentaphylla* and *Carex foetida* typically occurs before the beginning of July within the study area (Choler, 2005). The strong spatial agreement between observed and predicted snow cover maps up to 15 July therefore justifies the approach adopted here for modelling snowmelt patterns (Supplementary Data Fig. S3), and suggests that our method can be expected to perform well in the context of other alpine environments.

Chapter IB

*Contributions of solar energy availability and vegetation properties to high resolution gross primary productivity in an alpine watershed**

* **Carlson, B. Z.**, Choler, P., Renaud, J., Malenovský, Z. & Thuiller, W. Contributions of solar energy availability and vegetation properties to high resolution gross primary productivity in an alpine watershed. (**Unpublished manuscript**).

Introduction

Understanding relationships between plant diversity and ecosystem functioning is an ongoing priority in ecological research (Isbell *et al.*, 2011), and this task is particularly challenging in the context of alpine landscapes characterized by high turnover in plant species composition and functional traits over short distances (Bliss 1966). Alpine ecologists have long been interested in links between environmental conditions, plant composition and primary productivity, and field studies have demonstrated that the date of snowmelt is a key driver of both plant diversity and biomass production in high-elevation, temperate grasslands (Scott & Billings, 1964, Walker *et al.*, 1994). Moving beyond isolated point measurements and generating spatial models of primary productivity in the context heterogeneous mountain landscapes, however, constitutes both a methodological challenge and an important task, given that temperate mountain grasslands sequester large amounts of carbon and are sensitive to global change (Ernakovich *et al.*, 2014).

Snow cover duration directly influences the ecosystem properties of high-elevation plant communities by determining growing season length, and thus solar energy availability, in the form of growing degree days and the amount of received photosynthetically active radiation (PAR; Keller, Goyette & Beniston, 2005). The height of the snowpack in midwinter and spring also influences soil temperature regimes (Edwards *et al.*, 2008), exposure to frost stress (Wipf, Stoeckli, & Bebi, 2009), and nitrogen availability (Clément *et al.*, 2012), leading to more favorable conditions in late-melting, concave habitats characterized by snow bed vegetation (Björk & Molau, 2007). Spatial heterogeneity in snow cover duration has further been identified as a strong driver of plant taxonomic and functional diversity patterns in topographically complex alpine environments (Walker *et al.*, 1993; Choler, 2005). However, recent work suggests that certain leaf traits, in particular community weighted mean specific leaf area (SLA), can vary strongly for a given length of snow free period (Spasojevic and Sudding, 2012; Carlson *et al.*, 2015). Thus, in order to estimate primary productivity at the scale of turnover in plant diversity in alpine environments, it seems necessary to account for both spatial variation in both plant canopies and solar energy availability.

Plot level studies have utilized field measurements (Kudo, Nordenhäll and Molau, 1999) and also simulation approaches (Baptist and Choler, 2008) to differentiate strategies of alpine

plant growth with respect to growing season length and leaf traits. Their findings demonstrated that, despite a shorter snow-free period, snowbed communities were able to produce more biomass per unit of time than adjacent meadow communities due to a combination of more favorable environmental conditions during the growing season and higher specific leaf area. Although at least one study has extrapolated plot-level relationships between environmental drivers and alpine plant growth and phenology to generate gridded maps (Rammig *et al.*, 2009), this approach can be problematic owing to high heterogeneity in alpine landscapes and turnover in plant community composition between measured points.

Spatially explicit remote sensing approaches have, therefore, been used as a means of quantifying the primary productivity of mountain grasslands at various spatial and temporal scales, while accounting for meteorological forcing and the functional properties of plant canopies (Li *et al.*, 2007; Choler, 2015). The conceptual basis for converting the remotely sensed normalized difference vegetation index (NDVI) measurements to estimates of primary productivity relies on a framework introduced by Monteith and Moss (1977). Their study demonstrated that GPP for a given time interval can be defined as the product of available photosynthetically active radiation, the fraction of PAR absorbed by plant canopies (fAPAR) and a light use efficiency term (LUE), which can be influenced by leaf tissue, water availability and ambient temperature (Veroustraete, Sabbe & Eerens, 2002). For instance, satellite data acquired with the Moderate Resolution Imaging Spectroradiometer (MODIS; <http://modis.gsfc.nasa.gov/>) provide global maps of GPP (gC.m^{-2}) at 8-day intervals and at 250 m spatial resolution from 1999 to the present (Running *et al.*, 2004). The application of MODIS in the context of heterogeneous alpine environments is limited, however, because multiple plant communities typically occur within a grid cell of 250 x 250 m (Fontana *et al.*, 2008), and the snow cover product is too coarse (500 m pixel size) to capture topography-induced local differences in snowmelt timing.

Airborne imaging spectroscopy (AIS) can generate data of exceptionally high spectral and spatial resolution, allowing for the estimation of certain vegetation canopy properties (e.g. leaf chlorophyll content and leaf area index) that are irretrievable from standard multispectral imagery (Zimmermann *et al.*, 2007; Malenovský *et al.*, 2015). AIS maps have been exploited in the context of agro-ecology (Haboudane 2002) and more recently for identification of plant functional types based on remotely sensed optical traits (Ustin *et al.*, 2010). Specifically,

aggregation of leaf traits within a grid cell, such as chlorophyll $a+b$ per unit of leaf area (Malenovsky *et al.*, 2013), can provide the canopy-level equivalent of a community weighted mean trait value (Homolová *et al.*, 2013). AIS thus represents a unique opportunity to incorporate spatially continuous variation in leaf canopy properties into models of ecosystem functioning at spatial scales that are representative of turnover in high-elevation plant communities.

In this study, we applied the Monteith light-use efficiency model to estimate GPP at a very high spatial resolution (2 m) from snowmelt to peak standing biomass in the context of a high-elevation watershed in the southwestern French Alps. Our primary aim was to quantify variability in GPP for a given quantity of available PAR (as mediated by snow cover duration), and subsequently to determine which canopy properties contribute most directly to the energy use efficiency of biomass production (GPP efficiency). A further goal of this work was to test for a consistent relationship between PAR availability and observed $fAPAR_{max}$, which determined GPP efficiency in our model, for canopies organized along a snowmelt gradient. An array of high resolution remote sensing products was used for this analysis, including (1) AIS data to estimate spatial variation in plant canopy properties, namely NDVI, leaf chlorophyll content, leaf area index and canopy chlorophyll content; (2) a digital elevation model derived from airborne light detection and ranging (LIDAR) data, to quantify local topographic variations and (3) Landsat multispectral imagery to retrieve snow cover duration within the study area. Information on daily air temperature and solar radiation was obtained from a regional meteorological model. Finally, 67 vegetation plots within the study area were used to infer growth strategies for dominant plant communities relative to solar energy availability, canopy properties and estimated GPP.

Materials and methods

Study area and floristic data

The study area is a topographically complex 6.7 km² watershed situated in the Grand Galibier Massif of the French Alps (study area center: lat. 45°3'10", long. 6° 23'23") spanning an elevation range from 1980 to 3114 m a.s.l. Vegetation cover is a mosaic of heath, sub-alpine and alpine forb and graminoid communities. Sixty-seven vegetation plots (2-5 m radius), including

visual estimates of species' relative abundances (Braun-Blanquet, 1957), were established within the study area in July, 2007. Vegetation plots were subsequently grouped into 13 community types based on dominant species composition and expert knowledge (Table 1). The resulting typology represents spatial turnover in plant diversity across the study area, and also corresponds to the major community types generally found in the high elevation grasslands of the southwestern Alps (Choler & Michalet, 2002).

Deriving canopy traits from airborne imaging spectroscopy data

Airborne imaging spectroscopy (AIS) data covering the study area were acquired on July 23, 2008, with the Airborne Imaging Spectroradiometer for Applications (AISA; Specim Ltd., Finland) in a dual sensor configuration, i.e. the visible and near infrared (VNIR) AISA Eagle sensor coupled with the short wave infrared (SWIR) AISA Hawk sensor. Raw image data contained 359 spectral bands within the wavelength interval of 401 – 2453 nm, with a bandwidth of 4.3 – 4.8 nm for AISA Eagle and 6.3 nm for AISA Hawk, respectively, and a spatial resolution of 0.8 m. AISA images were converted to the radiance unit, atmospherically corrected, mosaicked, geo-referenced and noise filtered. Following image corrections and orthorectification (see Pottier *et al.*, 2014 S1 for further details), spectral reflectance values were used to calculate four canopy properties: (1) the normalized difference vegetation index (NDVI); (2) leaf chlorophyll *a+b* content (LCC; $\mu\text{g}\cdot\text{cm}^{-2}$ of leaf projection area); (3) leaf area index (LAI; $\text{m}^2\cdot\text{m}^{-2}$); and (4) canopy chlorophyll content (CCC; $\mu\text{g}\cdot\text{cm}^{-2}$), which is the product of LAI x LCC and represents the quantity of chlorophyll contained in leaf tissue per unit of ground area (Verrelst *et al.*, 2015). LCC was estimated from the ratio of two optical vegetation indices, the Transformed Chlorophyll Absorption in Reflectance Index and the Optimized Soil-Adjusted Vegetation Index (TCARI/OSAVI; Haboudane *et al.*, 2002), which has been shown to be sensitive to leaf chlorophyll content variations but insensitive to variations in LAI and solar zenith angle. LCC was computed using non-linear logarithmic function:

$$(1) \quad \text{LCC} = -30.194 \ln(x) - 18.363$$

where *x* is TCARI/OSAVI (Haboudane *et al.*, 2002). Green LAI was determined using the Modified Triangular Vegetation Index 2 (MTVI2; Haboudane *et al.*, 2004), which, contrary to

TCARI/OSAVI, suppresses influence of varying chlorophyll content. The LAI of grasslands was estimated using an exponential relationship:

$$(2) \quad \text{LAI} = 0.223 \exp(3.657x)$$

where x represents MTVI2 (Haboudane *et al.*, 2004). Maps of the computed canopy properties were resampled from 0.8 to 2 m spatial resolution using a mean function. In order to exclude areas of bare ground, only areas with chlorophyll content $> 0 \mu\text{g}\cdot\text{cm}^{-2}$ were retained for analysis. Additionally, isolated values of LAI above 7 and LCC above $100 \mu\text{g}\cdot\text{cm}^{-2}$ were considered as outliers, originating likely from sensor or image processing errors, and were removed from the analysis. This data filtering resulted in 773,925 non-bare ground grid cells at a spatial resolution of 2 m (Fig. S1).

Climate and snow cover data

Daily values of incoming global (i.e. direct and diffuse) short-wave solar radiation and air temperature for the Grand Galibier massif were obtained for 300 m elevation and slope aspect classes from the SAFRAN-Crocus-MEPRA meteorological model, developed for the French Alps by Météo-France. Further details on input data, methodology, and validation of this model can be found in Durand *et al.* (2009). Given that above 0°C temperatures for elevations within the study area did not occur prior to April 22, 2008, this date was used as the beginning of the potential growing season. Daily values of mean air temperature and incoming solar radiation were assigned to a median elevation value (e.g. 2250 m a.s.l. for the class 2100-2400 m a.s.l.) and subsequently downscaled using spatially continuous aspect and elevation values derived from a 2 m digital elevation model. Daily rasters for air temperature and solar radiation were computed for the period from April 22 to July 23, 2008, which corresponded to the date of AIS data acquisition and to the approximate peak standing biomass for vegetation within the study area.

The Enhanced Thematic Mapper Plus (ETM+) Landsat 7 and 8 multispectral images from five years (2000, 2001, 2002, 2013 and 2014) were obtained from the Landsat data archive (<http://earthexplorer.usgs.gov>). Landsat images were employed in mapping and modelling snow cover duration at a spatial resolution of 15 m based on the approach described in Carlson *et al.* (2015), using date and local topography as inputs. Unfortunately, Landsat imagery between 2003

and 2012 was unavailable due to irreparable damage to the ETM+ sensor that occurred in spring 2003. Thus, daily probability maps of snow presence were averaged for the five available years and converted to binary snow cover maps using a threshold of 0.5, which optimized the true skill statistic across all analysed years. Snow cover maps were disaggregated from 15 to 2 m resolution, in order to align with high-resolution AIS layers. Resulting daily snow cover maps for the period from April 22 to July 23 are expected to represent the average snowmelt trajectory for a typical growing season during the past decade, as opposed to quantifying the single snowmelt cycle specific to 2008. Mapping snow cover duration allowed us to estimate spatial variation in the amount of incident PAR available for plant growth.

Estimating GPP

The following formula, introduced by Monteith and Moss (1977), was applied to estimate the gross primary productivity (GPP) of alpine and sub-alpine vegetation at a daily time interval:

$$(3) \quad GPP = fAPAR \times PAR \times LUE$$

where fAPAR is the fraction of absorbed photosynthetically active radiation, PAR is the quantity of photosynthetically active radiation (MJ.m^{-2}), and LUE is a coefficient for light use efficiency. LUE was fixed at 1.1 for grasslands as in Veroustraete, Sabbe & Eerens (2002) and following the assumption that NDVI (and derived fAPAR) captures essential LUE variations among canopies. To derive fAPAR, we linearly rescaled positive NDVI values between zero and one based on Myneni's generalized NDVI/fAPAR relationship (Myneni & Williams, 1994). Our use of NDVI to derive fAPAR from snowmelt to peak standing biomass is supported by a recent study conducted in a grassland system demonstrating a stable relationship between NDVI, field measurements of fAPAR and the fractional light absorption efficiency of canopy chlorophyll from the beginning of the growing season to peak photosynthetic activity (Flanagan *et al.*, 2015). For each 2 m grid cell, we assumed a linear increase of fAPAR from zero at the time of snowmelt to the fAPAR value measured on July 23 in order to estimate a time-integrated value of GPP over the growing season. Daily PAR was estimated by extracting grid cells from daily solar radiation rasters that were snow free and above 0° C. Water availability was not taken into account, as previous work in the study area has shown that soil humidity levels are similar across community

types (Baptist & Choler, 2008). Daily GPP for each grid cell was calculated by multiplying PAR, fAPAR and the LUE constant, and growing season GPP was determined by summing daily GPP values from April 22 to July 23. For purposes of comparison, we also estimated GPP using PAR and NDVI dynamics quantified without consideration of snow cover. In order to validate estimates of primary productivity, we used linear ordinary least squares regression to test relationships between GPP and community weighted mean plant height calculated for the 67 vegetation plots as well as between GPP and green aboveground biomass measured for twenty-one plots in July, 2007.

Quantifying canopy efficiency

The efficiency of plant canopies can be quantified by the ratio of GPP/PAR (Monteith & Moss, 1977). We utilized a fixed value of GPP/PAR of 0.5 as a reference point in order to quantify the relative energy use efficiency of biomass production for plant canopies (GPP efficiency; $\Delta \text{ gC.m}^{-2}$). Accordingly, a grid cell for which $\text{GPP/PAR} > 0.5$ would thus have a positive value of GPP efficiency, whereas a value of $\text{GPP/PAR} < 0.5$ would result in a negative value of GPP efficiency. This relative index of GPP efficiency was calculated for each grid cell within the study area. We tested relationships, once again using linear ordinary least squares regression, between GPP efficiency, canopy properties as measured by AIS and PAR integrated from snowmelt to July 23. Finally, for each of the 13 community types, we extracted mean values of elevation, topographic position index (Wilson & Gallant, 2000) calculated for a 150 x 150 m window, normalized between zero and one and multiplied by slope angle (see Carlson *et al.*, 2015 for further details), time integrated PAR, fAPAR and canopy chlorophyll content measured on July 23, GPP and GPP efficiency.

Results

Quantifying GPP and GPP efficiency

Estimated gross primary productivity (GPP) from time of snowmelt to July 23 varied between 15 and 1208 gC.m^{-2} , which represents a range of values comparable to GPP results

reported by other studies conducted in temperate mountain grasslands using remote sensing approaches (Heinsch *et al.*, 2006; Rossini *et al.*, 2012). Comparison of absolute GPP estimates in this case has limited relevance, however, given differences in both study area context and in integration periods (annual GPP versus GPP estimated from snow melt to peak productivity in this case). Validating estimated GPP with green biomass measurements for twenty-one plots showed weak agreement ($r^2 = 0.16$; Fig. S2A) when snow cover was included, and no agreement when GPP was estimated without accounting for snow cover duration (Fig. S2C). Strong agreement was found between GPP estimated with snow cover and plot-level community-weighted mean plant height (Fig. S2B; $r^2 = 0.58$). There was no relationship between GPP and plant height, however, when snow cover was not taken into account (Fig. S2D). Overall, we consider that our approach is valid for quantifying relative differences in productivity within our study area, however absolute values of estimated GPP should be considered with caution.

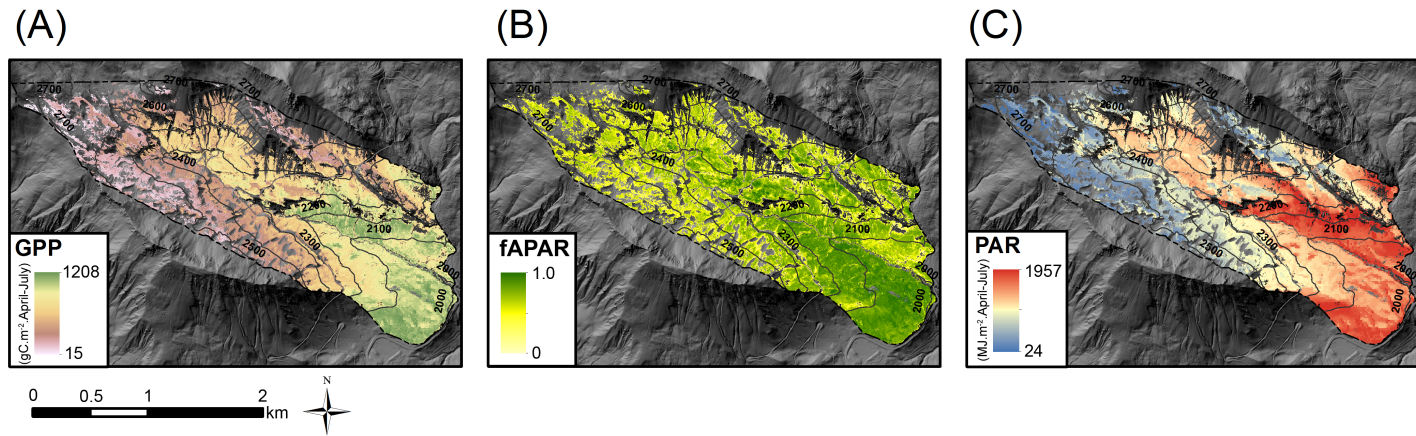


Figure 1. (A) Estimated gross primary productivity (GPP; gC.m^{-2}) for the period from April 22 to July 23, 2008. (B) Fraction of absorbed photosynthetically active radiation (fAPAR), obtained from NDVI, measured on July 23, 2008. (C) Photosynthetically active radiation (PAR; MJ.m^{-2}) integrated between April 22 and July 23, 2008. Spatial resolution of all maps is equal to 2 m.

Spatial variation in estimated GPP was highly structured by photosynthetically active radiation (PAR), which exhibited a strong pattern relative to northeast and southwest facing slopes (Fig. 1A; 1C). Variation in PAR in the context of slopes sharing the same overall aspect was due to contrasting snowmelt dates induced by mesotopographic heterogeneity. A gradient of increasing PAR and the fraction of absorbed PAR measured on July 23 (fAPAR) at lower

elevations was also apparent, regardless of slope orientation (Fig. 1B; Fig. 1C). Similar values of fAPAR occurred across areas with highly contrasting growing season lengths and accumulated PAR (Fig. 1B; 1C).

We found a strong positive relationship between time integrated PAR and estimated GPP ($r^2=0.83$), demonstrating that primary productivity in this context is fundamentally limited by energy availability (Fig. 2). Differences in GPP for a given level of PAR were determined by variation in fAPAR trajectories from snowmelt to peak productivity, expressed as different ratios of GPP/PAR (Fig. 2). The least efficient canopies corresponded to a GPP/PAR ratio of 0.3 while the most efficient canopies corresponded to a ratio of 0.6 (Fig. 2). Notably, the highest ratios of GPP/PAR occurred in an upper envelope of canopies receiving more than 1100 MJ/m² (Fig. 2).

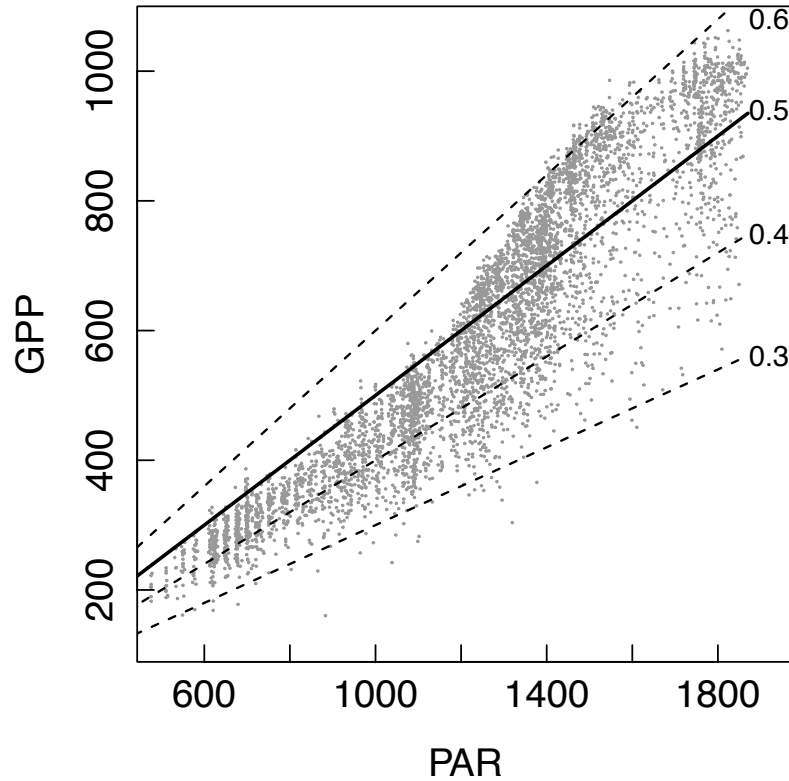


Figure 2. Gross primary productivity (GPP; gC.m⁻²) from April 22 to July 23, 2008, relative to the sum of received photosynthetically active radiation (PAR; MJ.m⁻²) integrated for the same period. Points ($n=5000$) represent a random subset of 2 m grid cells. In accordance with the Monteith framework ($GPP = fAPAR \times LUE \times PAR$), lines represent different ratios of GPP/PAR. GPP efficiency (Δ gC.m⁻²) represents the y-axis distance from the GPP/PAR isoline equal to 0.5.

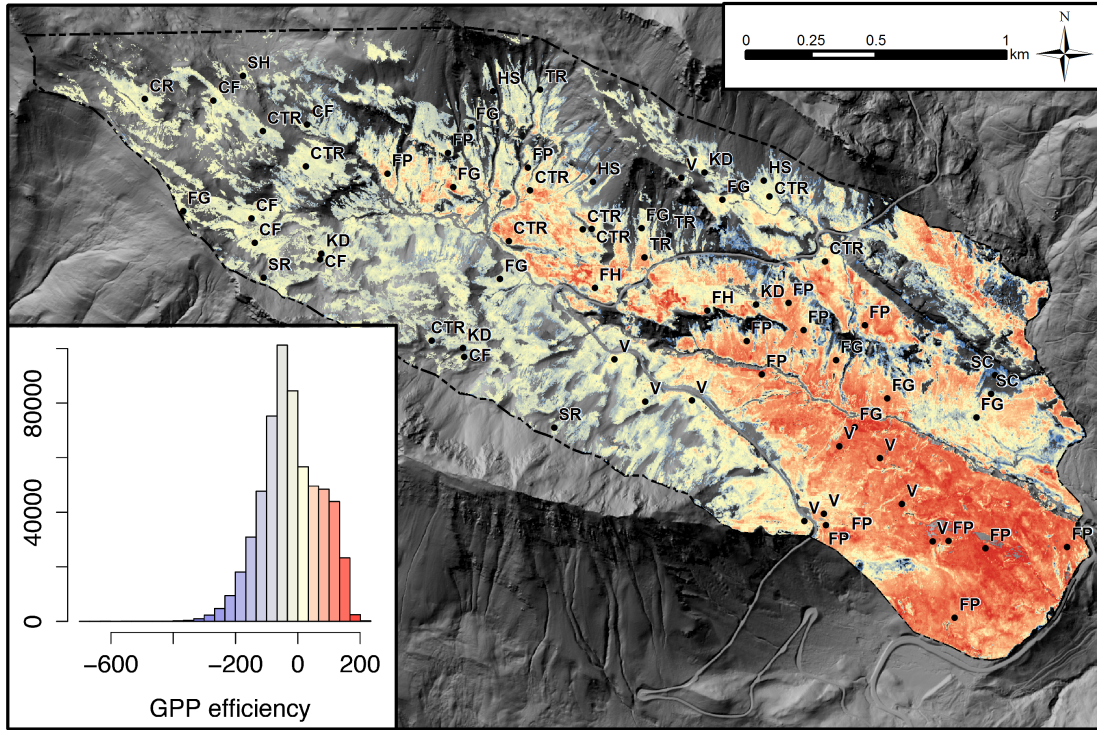


Figure 3. Spatial distribution of GPP efficiency ($\Delta \text{gC.m}^{-2}$). Points indicate vegetation plots ($n = 67$), which are labelled according to dominant species listed in Table 1. The frequency histogram shows the number of analyzed pixels belonging to different GPP efficiency classes.

Patterns of GPP efficiency were highly spatially structured, showing an overall decrease in GPP efficiency with elevation ($r^2=0.37$; Fig. 3). The most efficient canopies were located in the southeast corner of the study area, at low elevation ($<2300 \text{ m a.s.l.}$) with vegetation characterized by *Vaccinium* sp. and *Festuca paniculata* (Fig. 3; Fig. 4). Consistently, the least efficient canopies, receiving high amounts of PAR but producing little biomass, were located on exposed, south-facing slopes at elevations between 2200 and 2500 m a.s.l., with vegetation primarily composed of *Helictotrichon sedenense* at higher elevations and *Sesleria caerulea* at lower elevations (Fig. 3; Fig. 4; Table 1). Certain canopies located on south facing slopes receiving high amounts of PAR and situated well below ridge crests maintained high levels of GPP efficiency at elevations up to 2500 m a.s.l.. Vegetation in these contexts was characterized by *Carex sempervirens*, *Trifolium alpinum* and isolated occurrences of *Festuca paniculata*. Higher elevation alpine communities reflected less variation in GPP efficiency, with values fluctuating between 0 and $-200 (\Delta \text{gC/m}^{-2})$ (Fig. 3; Fig. 4). Communities located in topographic depressions with low values of TPI x slope and characterized by *Carex foetida* and *Salix herbacea* expressed

higher GPP efficiency than adjacent meadow communities dominated by *Kobresia myosuroides* situated in areas with higher values of TPI x slope (Fig. 3; Table 1). In the case of both alpine and subalpine canopies, the lowest values of GPP efficiency corresponded to canopies located in areas of high disturbance in close proximity to exposed crests or micro-scale convexities, as evidenced by elevated values of the TPI x slope index (Table 1).

Community	Dominant species	N plots	Elevation	TPI x slope	PAR	fAPAR	CCC	GPP	GPP efficiency
SH	<i>Salix herbacea</i>	1	2624	0.04	708	0.68	32	300	-54
CF	<i>Carex foetida</i> , <i>Alchemilla pentaphyllea</i> , <i>Salix herbacea</i>	6	2558	0.06	743	0.78	96	350	-21
CR	<i>Carex curvula</i> subsp. <i>rosae</i>	1	2677	0.04	768	0.69	40	322	-62
SR	<i>Salix reticulata</i>	2	2548	0.20	805	0.68	45	328	-75
KD	<i>Kobresia myosuroides</i> , <i>Dryas octopetala</i>	4	2474	0.12	928	0.67	20	374	-90
CTR	<i>Carex sempirvirens</i> , <i>Trifolium alpinum</i>	9	2469	0.09	1236	0.80	119	634	16
FG	<i>Festuca violacea</i> , <i>Geum montanum</i>	10	2344	0.13	1243	0.80	91	634	13
HS	<i>Helictrotrichon sedenense</i>	3	2533	0.17	1262	0.69	60	545	-86
V	<i>Vaccinium uliginosum</i> , <i>Vaccinium myrtillus</i>	10	2256	0.15	1303	0.84	153	708	56
FH	<i>Festuca halleri</i>	2	2358	0.11	1358	0.71	61	638	-42
TR	<i>Trifolium pratense</i> , <i>Geranium sylvaticum</i>	3	2461	0.16	1368	0.76	130	681	-3
FP	<i>Festuca paniculata</i>	14	2232	0.15	1578	0.82	174	867	78
SC	<i>Sesleria caerulea</i>	2	2148	0.18	1933	0.61	41	773	-194

Table 1. Plant community types listed with dominant species along with mean environmental gradients and canopy properties: elevation (m a.s.l.), normalized topographic position index multiplied by slope angle (TPI x slope, see Methods section), photosynthetically active radiation (PAR, MJ.m⁻²) integrated between April 22 and July 23, 2008, fraction of absorbed photosynthetically active radiation (fAPAR) and canopy chlorophyll content (CCC, µg.cm⁻²) measured on July 23, 2008, gross primary productivity (GPP, gC.m⁻²) estimated between April 22 and July 23, 2008, and GPP efficiency (Δ gC.m⁻²). Low values of TPI x slope correspond to concave areas and topographic depressions, whereas high values are indicative of convexities and ridge crests.

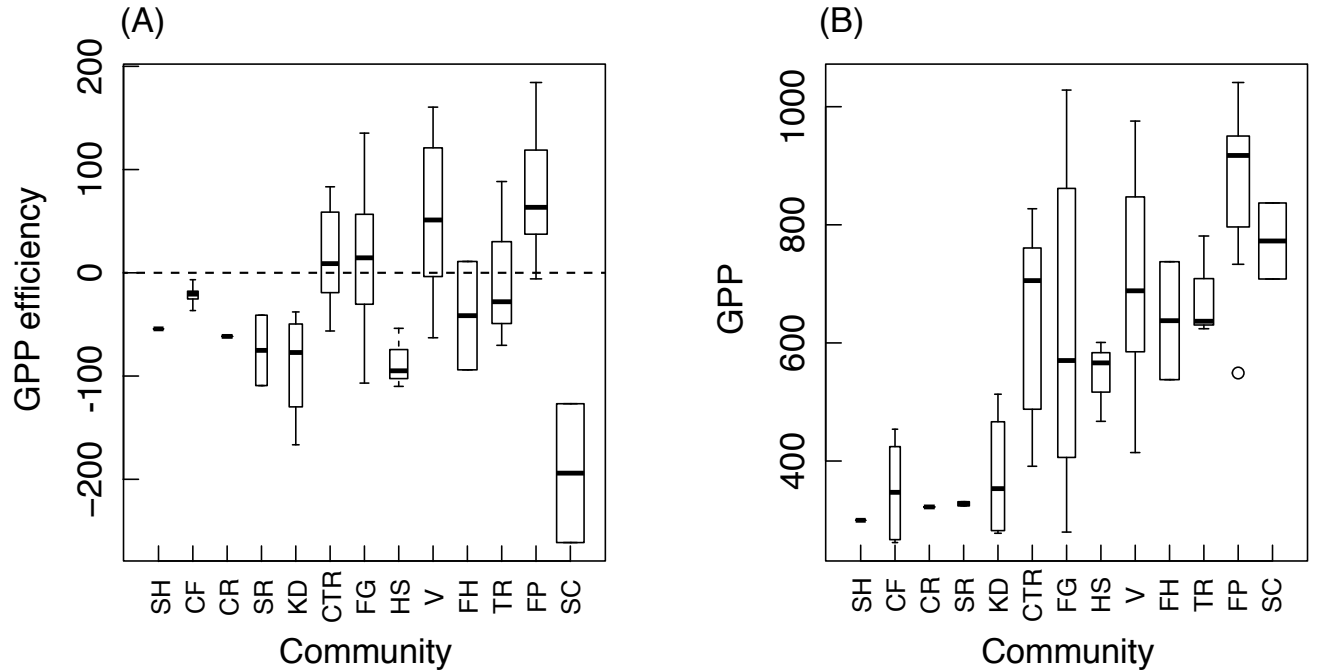


Figure 4. (A) Boxplots of GPP efficiency ($\Delta \text{gC.m}^{-2}$) relative to community type (a list of dominant species per community type is provided in Table 1). Communities are ordered from the shortest to the longest snow free period. Boxplot width is proportional to received photosynthetically active radiation (PAR, MJ.m^{-2}) integrated for the snow free period between April 22 and July 23, 2008. (B) Boxplots of GPP (gC.m^{-2}) between April 22 and July 23, 2008, relative to community type.

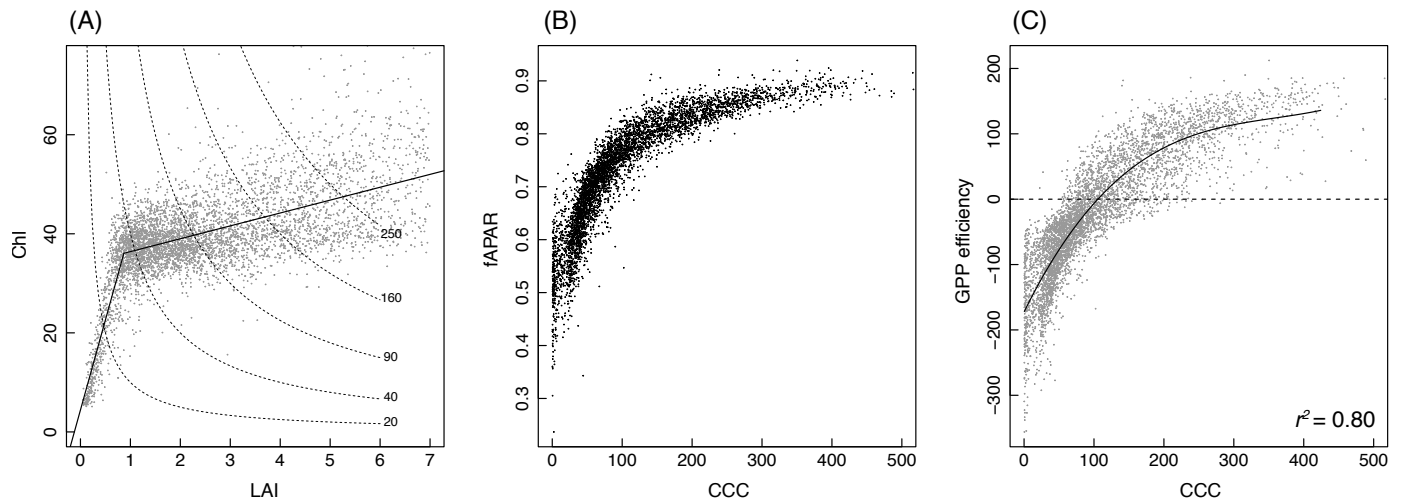


Figure 5. (A) Leaf chlorophyll content (LCC, $\mu\text{g.cm}^{-2}$) relative to leaf area index (LAI; $\text{m}^2.\text{m}^{-2}$), with dashed isolines representing fixed levels of the product of LCC and LAI, referred to as canopy chlorophyll content (CCC, $\mu\text{g.cm}^{-2}$). Solid lines are the result of ordinary least squares

linear regression models applied to LAI and LCC for LAI values >1 , respectively. (B) fAPAR plotted relative to CCC, as measured on July 23, 2008. (C) GPP efficiency ($\Delta \text{gC.m}^{-2}$) relative to CCC measured on July 23, 2008. The line of best fit is the result of a third order polynomial linear regression.

Canopy properties and GPP efficiency

The apparent contributions of both leaf area index (LAI) and leaf canopy chlorophyll (LCC) to the total amount of canopy chlorophyll, as well as the biological relevance of combining these two optical properties, supported the use of canopy chlorophyll content (CCC) as the most pertinent canopy trait for explaining variation in the energy use efficiency of plant canopies (Fig. 5). For LAI values less than one, LAI and LCC showed a strong positive relationship ($r^2 = 0.75$, slope=36.35; Fig. 5A). The strength of the relationship between LAI and LCC declined, however, for LAI values greater than one ($r^2 = 0.30$, slope=2.60; Fig. 5A). For the majority of canopies with LAI values between 1 and 7, LCC was restricted to a range of values between 30 and 45 ($\mu\text{g.cm}^{-2}$). The distribution of observations relative to isolines representing fixed quantities of CCC indicated that varying proportions of LCC and LAI contributed to the same overall value of CCC (Fig. 5A). CCC and fAPAR exhibited a strong, positive relationship, with a non-linear form similar to the relationship between LAI and NDVI demonstrated by Myneni *et al.* (1997; Fig. 5B). CCC was a strong predictor of fAPAR-derived GPP efficiency, with increasing CCC corresponding with greater GPP efficiency ($r^2 = 0.80$; Fig. 5C).

Conversely, PAR was a fairly weak predictor of GPP efficiency ($r^2 = 0.14$), owing in particular to a wide range of possible values of GPP efficiency for high levels of PAR (Fig. 6A). This variation in GPP efficiency for a given level of PAR was mediated by different quantities of CCC (Fig. 6A). Furthermore, variation in GPP efficiency for community vegetation plots was consistently linked to aggregated levels of CCC (Table 1). For example, despite receiving less PAR than communities dominated by *Kobresia myosuroides*, snowbed communities characterized by *Carex foetida* produced an equivalent amount of biomass in less time (in terms of the number of snow free days) owing to higher amounts of CCC and greater canopy efficiency (Table 1; Fig. 4). Finally, Fig. 6B demonstrates the positive relationship ($r^2=0.77$) between PAR and the range of values of GPP efficiency, suggesting the existence of a wide array of possible

plant strategies relative to energy use efficiency for canopies benefitting from a longer growing season.

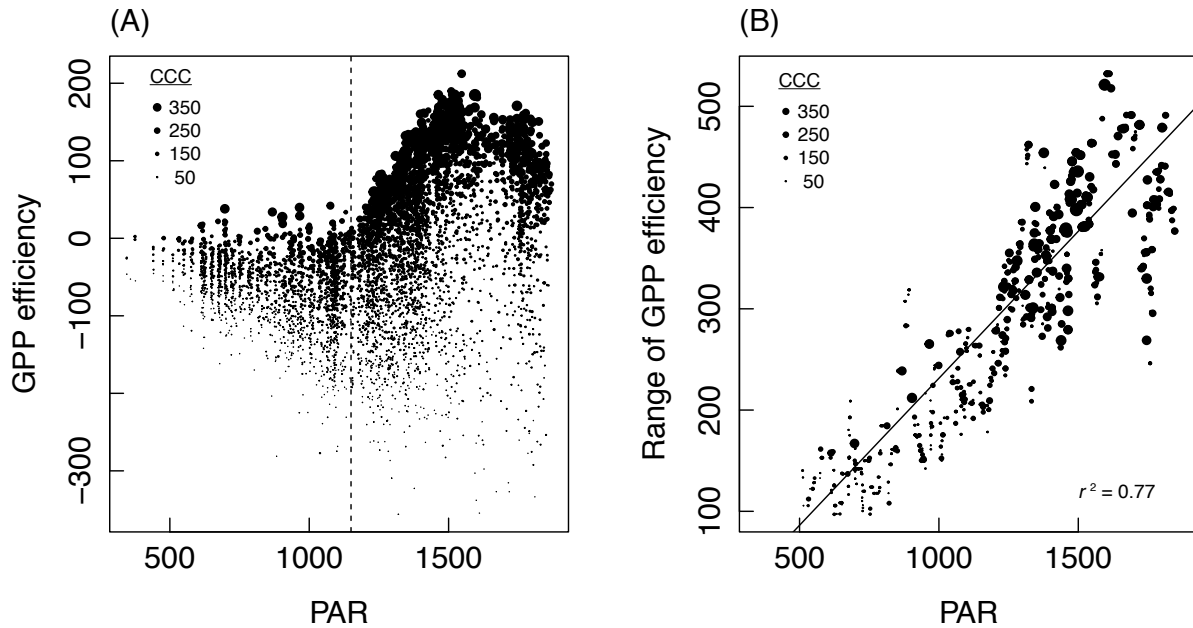


Figure 6. (A) GPP efficiency ($\Delta \text{gC/m}^2$) relative to seasonal photosynthetically active radiation (PAR, MJ.m^{-2}) integrated from April 22 to July 23, 2008. (B) Range of GPP efficiency relative to PAR. Range of GPP efficiency was calculated by ordering observations according to PAR and subsequently extracting the minimum and maximum value of GPP efficiency with a moving window ($k = 50$). Point size for both (A) and (B) is proportional to canopy chlorophyll content (CCC, $\mu\text{g.cm}^{-2}$) measured on July 23, 2008.

Discussion

The presented remote sensing-based approach enabled us to link optical vegetation properties with meteorological forcing relevant to alpine environments and the aboveground gross primary productivity (GPP) of temperate mountain grasslands. We found that canopy efficiency is, in the context of a high-elevation watershed, highly variable for a given level of energy availability, and that spatial heterogeneity in both the length of the growing season and in biophysical canopy properties contribute to high spatial resolution patterns of primary productivity. Specifically, we showed that the most efficient high elevation plant canopies

maximize canopy chlorophyll content for a given amount of energy availability, and that a prolonged snow free period does not necessarily translate into high productivity for plant canopies situated in areas of high stress and disturbance. While multiple studies have shown that snow cover maps of high spatial resolution are pivotal for understanding patterns of alpine plant diversity (Walker *et al.*, 1993; Venn *et al.*, 2011; Carlson *et al.*, 2015), to the best of our best knowledge this is the first landscape-scale study conducted at high spatial resolution to show that snow cover duration correlates with biophysical canopy properties and ecosystem functioning in the context of an alpine watershed.

Contributions of PAR availability and canopy efficiency to GPP

In agreement with other remote sensing studies conducted in temperate grasslands in the Alps at the plot level (Jonas *et al.*, 2008) and at the regional scale (Choler 2015), we demonstrated that the length of the snow free period, which conditions the amount of received photosynthetically active solar radiation (PAR), is the primary driver affecting the productivity of alpine temperate grasslands (Fig. 1 and 2). Substantial variation in GPP for a given level of PAR, however, underscored the functional importance of canopy properties in mediating the efficiency and magnitude of primary productivity. In particular, local differences in the fraction of absorbed photosynthetically active radiation (fAPAR) allowed plant canopies receiving less PAR to produce equivalent or greater amounts of GPP relative to plant canopies benefitting from a longer growing season (Fig. 2). We considered differences in fAPAR among canopies receiving the same amount of seasonal PAR to be the result of local influences of stress, disturbance and water and nutrient availability on plant canopies. This interpretation is supported by a recent study demonstrating that micro-scale (1 m^{-2}) patterns of biomass in arctic-alpine tundra are shaped by micro-topography induced differences in soil temperature, moisture and geomorphological processes, including percent bare ground, solifluction and cryoturbation (Suvanto, Le Roux & Luoto, 2014).

Previous studies have noted that fAPAR, when derived from NDVI, is a “catch-all” property in which it is impossible to assess the contribution of particular traits to canopy efficiency (Myneni & Williams, 1994; Running, 2004). In this context, AIS-derived quantitative canopy traits (LAI, LCC and CCC) constituted a useful means of quantifying relationships between specific canopy properties and simulated GPP efficiency based on NDVI. Similar to

results from field measurements of arctic plant communities (Van Wijk, Williams, & Shaver 2005), we found a tight coupling between LAI and LCC, in our case measured by airborne imaging spectroscopy, for levels of LAI less than one. The more variable relationship between LAI and LCC for higher values of LAI highlights the importance of quantifying both properties in dense canopies, as different proportions of LAI and LCC can result in the same overall amount of CCC (Fig. 5A). Our findings indicate that CCC is a key canopy trait influencing the GPP efficiency of high-elevation plant canopies (Figure 5C).

Identifying functional strategies of plant canopies

Arguing in favour of the use of remote sensing as a tool for assessing “plant functional optical types”, Ustin and Gamon (2010) described plants as “solar energy factories with their canopies structured to optimize the capture of light within existing resource constraints”. In addition to nutrient availability in alpine environments, we would consider as additional constraints slope-related geomorphic disturbance and frost stress, which force more conservative plant strategies for a given level of PAR availability. Previous research has demonstrated that a prolonged snow free period can have a detrimental effect on the growth of high-elevation plant communities (Baptist *et al.*, 2010; Wipf, Stoeckli & Bebi, 2009), due to a combination of limited phenotypic plasticity and increased exposure to spring frost events. Additionally, vegetation located in high-elevation, early melting sites has been shown to have low specific leaf area and high leaf dry matter content indicative of a stress-tolerant growth strategy (Choler, 2005). Our findings contribute to field observations by demonstrating that increased PAR availability does not consistently lead to more efficient primary productivity in an alpine context, as a longer snow free period can be associated with low levels of fAPAR and canopy chlorophyll content.

Plant communities located at the highest elevations, i.e. receiving less than 1100 MJ.m⁻² of seasonal PAR, grow at a minimum level of GPP efficiency that allows them to persist despite the brief growing season imposed by a late snowmelt date (Fig. 6A). The high GPP efficiency of *Carex foetida* snowbed communities, which can produce a high quantity of CCC within a short snow free period (Table 1), could be attributed to the more favourable conditions found in late-melting sites, including reduced exposure to frost stress, low slope angle and high nutrient availability (Björk and Molau, 2007). According to our results, a short snow free period combined with a faster green-up of these snowbed communities resulted in a higher and more

efficient PAR uptake. Contrary to this, the lower CCC of *Kobresia myosuroides* and *Helictotrichon sedenense* meadow communities was indicative of a more conservative growth strategy, which led to the production of smaller amounts of biomass over the course of a longer potential growing season (Table 1; Fig. 4). Despite these differences, the range of GPP efficiency of these low-PAR communities remained significantly smaller as compared to lower-elevation canopies receiving more than 1100 MJ.m⁻² of PAR per season (Fig. 6B). It is important to point out that our analysis of canopy properties did not include sparsely vegetated areas of the nival belt, for which it was not possible to define optical canopy traits.

The range of GPP efficiency exhibited by high-PAR subalpine plant communities (Fig. 6B) points to the existence of a broader range of possible plant growth strategies in energy-rich contexts (Fig. 6). Benefitting from a longer growing season, these canopies can afford to be less energy efficient and still persist in marginal topo-climatic conditions. The least efficient subalpine communities characterized by *Sesleria caurulea* (Table 1) occurred in areas of high biotic and physical perturbation (field observations), and also are also situated on upper slopes associated with increased exposure to freezing events (Table 1; Fig. 3). It is also likely that the productivity of these south-facing, exposed canopies is limited by moisture stress, which has been shown to be an important factor affecting aboveground net primary productivity in mountain grasslands (Berdanier & Klein, 2011). Despite receiving less PAR, canopies dominated by *Vaccinium* sp. heath and *Festuca paniculata* produced far more biomass than plots characterized by *Sesleria caurulea*, owing to high canopy efficiency combined with comparatively low inferred levels of stress and disturbance (Table 1; Fig. 3). Overall, the range of possible plant growth strategies increased with available PAR, as evidenced by consistently high GPP efficiency for canopies experiencing a short growing season and diverging levels of GPP efficiency as growing season length increased.

Conclusion

The Monteith modelling framework, used routinely to estimate GPP of vegetation at global and regional scales (e.g. MODIS; Li *et al.*, 2007; Running *et al.*, 2004), was adopted in this study to assess primary productivity in a high elevation watershed at a spatial scale representative of turnover of plant species composition and ecosystem properties. The introduced research approach allowed us to link biophysical canopy properties, driven by specific taxonomic

compositions and environmental gradients, with aboveground GPP, and to map this key component of ecosystem functioning at a very high spatial resolution of 2 m. Interpretation of our results indicates that while the primary productivity of high-elevation plant communities is fundamentally limited by PAR availability, the efficiency of this productivity is mediated by local variations in plant canopy traits, and in particular canopy chlorophyll content. With the growing availability of high spatial and temporal resolution imaging spectroscopy data provided by airborne systems, including unmanned aircraft (Lucieer *et al.*, 2014), we anticipate increasing complementarity between optical measures of vegetation properties and field-based observations of plant taxonomic and functional diversity.

Acknowledgements

This research was conducted on the Long-Term Ecosystem Research (LTER) Zone Atelier Alpes, which is a member of the ILTER-Europe network. Acquisition and processing of airborne imaging spectroscopy data was supported by the European ECOCHANGE project (GOCE-CT-2007-03866). Acquisition of the high resolution digital elevation model and aerial photographs were funded by SAFJ in the framework of the ReNSEE and the AnaEE-France network of Stations d'Ecologie Expérimentale (CNRS). All authors except ZM are part of Labex OSUG@2020 (ANR10LABX56). The research leading to this paper received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO).

References

- Baptist, F. & Choler, P. (2008) A simulation of the importance of length of growing season and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Annals of Botany*, 101, 549-559.
- Baptist, F., Flahaut, C., Streb, P., & Choler, P. (2010) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biology*, 12, 755-764.
- Berdanier, A. B., & Klein, J. A. (2011) Growing season length and soil moisture interactively constrain high elevation aboveground net primary production. *Ecosystems*, 14, 963-974.
- Bliss, L. C. (1966) Plant productivity in alpine microenvironments on Mt. Washington, New Hampshire. *Ecological Monographs*, 125-155.
- Björk, R.G. & Molau, U. (2007) Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research*, 39, 34-43.
- Braun-Blanquet, J. (1957) Ein Jahrhundert Florenwandel am Piz Linard (3414 m). *Bulletin du Jardin Botanique de l'Etat à Bruxelles*, Volume Jubilaire Walter Robyns, 221-232.
- Carlson, B.Z., Choler, P., Renaud, J., Dedieu, J.P. & Thuiller, W. (2015) Modelling snow cover duration improves predictions of taxonomix and functional diversity for alpine plant communities. *Annals of Botany*, DOI: 10.1093/aob/mcv041.
- Choler, P. (2005) Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research*, 37, 444-453.
- Choler, P. & Michalet, R. (2002) Niche differentiation and distribution of *Carex curvula* along a bioclimatic gradient in the southwestern alps. *Journal of Vegetation Science*, 13, 851-858.
- Choler, P. (2015) Growth response of temperate mountain grasslands to inter-annual variations of snow cover duration. *Biogeosciences*, 12, 3885-3897.
- Clément, J. C., Robson, T. M., Guillemin, R., Saccone, P., Lochet, J., Aubert, S., & Lavorel, S. (2012) The effects of snow-N deposition and snowmelt dynamics on soil-N cycling in marginal terraced grasslands in the French Alps. *Biogeochemistry*, 108, 297-315.
- Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B. & Merindol, L. (2009) Reanalysis of 44 Yr of Climate in the French Alps (1958-2002): Methodology, Model Validation, Climatology, and Trends for Air Temperature and Precipitation. *Journal of Applied Meteorology and Climatology*, 48, 429-449.
- Edwards, A. C., Scalenghe, R., & Freppaz, M. (2007) Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quaternary international*, 162, 172-181.
- Ernakovich, J.G., Hopping, K.A., Berdanier, A.B., Simpson, R.T., Kachergis, E.J., Steltzer, H. *et al.* (2014) Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*, 20, 3256-3269.

- Flanagan, L. B., Sharp, E. J., & Gamon, J. A. (2015) Application of the photosynthetic light-use efficiency model in a northern Great Plains grassland. *Remote Sensing of Environment*, 168, 239-251.
- Fontana, F., Rixen, C., Jonas, T., Aberegg, G., & Wunderle, S. (2008). Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series - a comparison with in situ measurements. *Sensors*, 8, 2833-2853.
- Haboudane, D., Miller, J. R., Tremblay, N., Zarco-Tejada, P. J., & Dextraze, L. (2002) Integrated narrow-band vegetation indices for prediction of crop chlorophyll content for application to precision agriculture. *Remote Sensing of Environment*, 81, 416-426.
- Haboudane, D., Miller, J.R., Pattey, E., Zarco-Tejada, P.J. & Strachan, I.B. (2004) Hyperspectral vegetation indices and novel algorithms for predicting green LAI of crop canopies: Modeling and validation in the context of precision agriculture. *Remote Sensing of Environment*, 90, 337-357.
- Heinsch, F. A., Zhao, M., Running, S. W., Kimball, J. S., Nemani, R. R., Davis, K. J., ... & Flanagan, L. B. (2006) Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations. *Geoscience and Remote Sensing*, 44, 1908-1925.
- Homolova, L., Malenovský, Z., Clevers, J. G., Garcia-Santos, G., & Schaepman, M. E. (2013) Review of optical-based remote sensing for plant trait mapping. *Ecological Complexity*, 15, 1-16.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., ... & Loreau, M. (2011) High plant diversity is needed to maintain ecosystem services. *Nature*, 477, 199-202.
- Jonas, T., Rixen, C., Sturm, M. & Stoeckli, V. (2008) How alpine plant growth is linked to snow cover and climate variability. *Journal of Geophysical Research: Biogeosciences*, 113, G03013.
- Keller, F., Goyette, S., & Beniston, M. (2005) Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Climatic Change*, 7, 299-319.
- Kudo, G., Nordenhäll, U. & Molau, U. (1999) Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. *Ecoscience*, 6, 439-450.
- Li, Z., Yu, G., Xiao, X., Li, Y., Zhao, X., Ren, C., ... & Fu, Y. (2007) Modeling gross primary production of alpine ecosystems in the Tibetan Plateau using MODIS images and climate data. *Remote Sensing of Environment*, 107, 510-519.
- Lucieer, A., Malenovský, Z., Veness, T., Wallace, L. (2014) HyperUAS - Imaging spectroscopy from a multi-rotor unmanned aircraft system, *Journal of Field Robotics*, 31, 571-590.
- Malenovský, Z., Homolová, L., Zurita-Milla, R., Lukeš, P., Kaplan, V., Hanuš, J., Gastellu-Etchegorry, J-P., Schaepman, M.E. (2013) Retrieval of spruce leaf chlorophyll content from airborne image data using continuum removal and radiative transfer, *Remote Sensing of Environment*, 131, 85-102.
- Malenovský, Z., Turnbull, J., Lucieer, A., Robinson, S.A. (2015) Antarctic moss stress assessment based on chlorophyll, water content, and leaf density retrieved from imaging spectroscopy data. *New Phytologist*, in press, <http://dx.doi.org/10.1111/nph.13524>.

- Monteith, J. L. & Moss, C. J. (1977) Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 281, 277-294.
- Myneni, R. B., Ramakrishna, R., Nemani, R., & Running, S. W. (1997) Estimation of global leaf area index and absorbed PAR using radiative transfer models. *Geoscience and Remote Sensing, IEEE Transactions on*, 35, 1380-1393.
- Myneni, R. B. & Williams, D. L. (1994) On the relationship between FAPAR and NDVI. *Remote Sensing of Environment*, 49, 200-211.
- Pottier, J., Malenovský, Z., Psomas, A., Homolová, L., Schaepman, M.E., Choler, P., Thuiller, W., Guisan, A. & Zimmermann, N.E. (2014) Modelling plant species distribution in alpine grasslands using airborne imaging spectroscopy. *Biology Letters*, 10, 20140347.
- Rammig, A., Jonas, T., Zimmermann, N. E., & Rixen, C. (2010) Changes in alpine plant growth under future climate conditions. *Biogeosciences*, 7, 2013-2024.
- Rossini, M., Cogliati, S., Meroni, M., Migliavacca, M., Galvagno, M., Busetto, L., ... & Colombo, R. (2012) Remote sensing-based estimation of gross primary production in a subalpine grassland. *Biogeosciences*, 9, 2565-2584.
- Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004) A continuous satellite-derived measure of global terrestrial primary production. *Bioscience*, 54, 547-560.
- Scott, D., & Billings, W. D. (1964) Effects of environmental factors on standing crop and productivity of an alpine tundra. *Ecological Monographs*, 243-270.
- Suvanto, S., Le Roux, P. C., & Luoto, M. (2014) Arctic and alpine vegetation biomass is driven by fine scale abiotic heterogeneity. *Geografiska Annaler: Series A, Physical Geography*, 96, 549-560.
- Spasojevic, M.J. & Suding, K.N. (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology*, 100, 652-661.
- Ustin, S. L., & Gamon, J. A. (2010) Remote sensing of plant functional types. *New Phytologist*, 186, 795-816.
- Venn, S.E., Green, K., Pickering, C.M. & Morgan, J.W. (2011) Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecology*, 212, 1491-1499.
- Verrelst, J., Camps-Valls, G., Muñoz-Marí, J., Rivera, J. P., Veroustraete, F., Clevers, J. G., & Moreno, J. (2015) Optical remote sensing and the retrieval of terrestrial vegetation bio-geophysical properties—A review. *ISPRS Journal of Photogrammetry and Remote Sensing*.
- Veroustraete, F., Sabbe, H., & Eerens, H. (2002) Estimation of carbon mass fluxes over Europe using the C-Fix model and Euroflux data. *Remote Sensing of Environment*, 83, 376-399.
- Van Wijk, M. T., Williams, M., & Shaver, G. R. (2005) Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia*, 142, 421-427.

Walker, D. A., Halfpenny, J. C., Walker, M. D., & Wessman, C. A. (1993) Long-term studies of snow-vegetation interactions. *BioScience*, 43, 287-301.

Walker, M. D., Webber, P. J., Arnold, E. H. & Ebert-May, D. (1994) Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology*, 2, 393-408.

Wipf, S., Stoeckli, V. & Bebi, P. (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, 94, 105-121.

Wilson, J.P. & Gallant, J.C. (2000) *Terrain analysis: principles and applications*. John Wiley & Sons.

Zimmermann, N. E., Washington-Allen, R. A., Ramsey, R. D., Schaepman, M. E., Mathys, L., Kötz, B., ... & Edwards, T. C. (2007) Modern remote sensing for environmental monitoring of landscape states and trajectories. In *A Changing World* (pp. 65-91). Springer Netherlands.

Chapter I Discussion

The Vallon de Roche Noire proved to be an invaluable test-site for the beginning of my project, allowing me to explore relationships between bioclimatic variables and alpine plant communities with the advantage of being familiar with the study area and having strong mental images of the environment and the plant communities I sought to quantify. This was not a case of “big-data” where I could get lost in the noise and lose track of initial hypotheses. For example, if I predicted higher amounts of received photosynthetically active radiation for alpine fellfield communities than for snowbed communities, then the underlying snow cover duration model probably required revisiting (fortunately, this did not actually occur). Framed in a more positive manner, the small scale, personal familiarity and the wealth of previous work conducted in the Vallon de Roche Noire enabled regular affirmation that the patterns I was finding and allowed me to readily interpret and evaluate my results. In terms of my scientific maturity and analysis experience at the beginning of my project, I think this was an ideal situation as I do not think I was ready to tackle a large dataset with the inevitable associated noise, uncertainty and abstraction.

Scientifically, this largely methodological chapter led to at least two worthwhile findings from my point of view. The first was to demonstrate that building snow cover duration into energy gradients improved statistical and ecological characterization of taxonomic and functional diversity patterns, explaining roughly 50% of variation in diversity when combined with percent bare ground as a proxy of disturbance. This finding encouraged ongoing effort to map snow cover duration at broader spatial scale and to work to improve estimates of frost events and received photosynthetically active radiation. The second piece of information that would help guide me later in my work was to learn that growing season length (or PAR), at least as estimated with the empirical snow cover model, is a fairly weak predictor of NDVI at fine spatial scales. Despite the overall positive relationship, the lack of a strong linear pattern between energy availability and canopy productivity can be explained at least in part by the conflicting effects of elevational and mesotopographic gradients. For example, we expect NDVI to generally decrease with decreased growing season length along an elevation gradient. However, we expect NDVI to increase in the case of snowbed or nival vegetation with a short growing season length along a mesotopographic gradient. I expect that numerous other, and perhaps more subtle, examples of

this kind of multi-directional relationship exist, and could well be linked to other factors such as nutrient and water availability, and frost stress. In this sense, the effect of growing season length on NDVI is context dependent, particularly at fine (2-15 m) scales. I would expect the relationship between growing season length and NDVI to improve as spatial grain increased, given that mesotopographic heterogeneity would be reduced and the pattern would follow an elevation gradient more closely. The weak relationship I found between energy availability and NDVI is echoed by a study conducted in the mountains of north-western Finland, in which the authors found that soil properties, topography and geomorphology combined explained only 33% of variation in biomass at 1 m resolution, and the relationships were non-linear (Suvanto *et al.* 2014). Clearly, predicting micro-scale heterogeneity in productivity using abiotic variables in alpine environments is a challenging task, and estimating snow cover duration does not enable straightforward predictions of both plant diversity and productivity.

Although these findings were critical stepping-stones in the advancement of my project, there are a number of aspects of the work that I was not satisfied with and which deserve further attention. First off, Chapter 1A was clearly lacking a spatial component. Of the 654,848 2 m grid cells I so proudly describe in the Methods section, I only utilized 100 in order to align with vegetation plots, and the rest of the analysis was non-spatial. In the fall of 2014, I participated in a field campaign with P. Choler and M. Corona (a fellow PhD student at the LECA), in which we sampled the presence or absence of thirty dominant species along a 100 m grid throughout the vegetated part of the Vallon de Roche Noire. While these data have not been exploited, a clear application would be to calibrate distribution models, either of species or recurring assemblages, using this database of over 500 points. Another possibility would be attempt to model the spatial distribution of the sub-alpine/alpine ecotone, which would necessitate accounting for a number of processes in addition to snow cover, including i) physical and animal disturbance, ii) plant interactions, iii) dispersal capacity, iv) soil properties and temperature regimes and v) inter-annual variability in snow cover and climate. Essentially, this project could constitute a thesis in its own right based on a process-based modeling approach.

Chapter 1B was disappointing in the sense that in addition to wanting to go further with analyses, the presented results can also be criticized and questioned. In response to the Chapter 1B manuscript, one reviewer wrote, “What would be actually new is to improve the estimation of GPP by explicitly accounting for the effects of topography, snow cover, canopy properties and

plant community information”. This was a frustrating response given that this is exactly what we endeavored to accomplish. Topography was built in to the snow cover model, canopy properties were derived from the hyperspectral image, and plant community information was provided by the community vegetation plots. The reviewer went on to cite a number of shortcomings, including i) fixing the light-use efficiency (LUE) term and not accounting for soil moisture or air temperature, ii) assuming a linear increase in NDVI from snowmelt to peak productivity, iii) circularity among correlated vegetation indices (NDVI, chlorophyll content and LAI) and iv) a lack of ground measures carried out during the campaign. Furthermore, we were criticized for using average decadal values for snow cover, air temperature and solar radiation rather than data specific to the campaign year (2008). While some of these difficulties were inherited and reflect the fact that I was trying to valorize previously acquired data without having been able to design the project from beginning to end, certain aspects of the analysis I carried out could nonetheless have been improved. Notably, soil humidity from the SAFRAN-Crocus model, which provided air temperature and solar radiation values, could have been used in the estimation of the light-use efficiency term. This would have posed a number of technical difficulties, however, given that values are based on simulated snowpack for 300 m elevation classes and would have had limited relevance at fine spatial scale. Still, it may have been better than simply fixing the LUE term. Also, I think that I could have better exploited community-level functional diversity metrics, which would have avoided the circularity issue by providing information on plant canopies that would have been independent of the hyperspectral image.

In general, in Chapter 1B I could have gone further exploring links between taxonomic and functional diversity and hyperspectral image data. Potential approaches included i) examining relationships between functional diversity and hyperspectral-derived vegetation indices (i.e. NDVI, LAI and chlorophyll content) or ii) using reflectance values of the over 300 spectral bands as input variables to predict functional diversity in a multivariate framework. Previous work conducted in central European grasslands employed branch and bound search algorithms to identify the spectral bands explaining the highest amount of variation in measured biomass and species richness (Psomas *et al.* 2011). To the best of my knowledge, however, links between hyperspectral data and plant functional diversity remain largely unexplored. Exploratory analysis of relationships between hyperspectral-derived leaf area index and functional diversity metrics showed significant relationships between LAI and plant height, leaf dry matter content

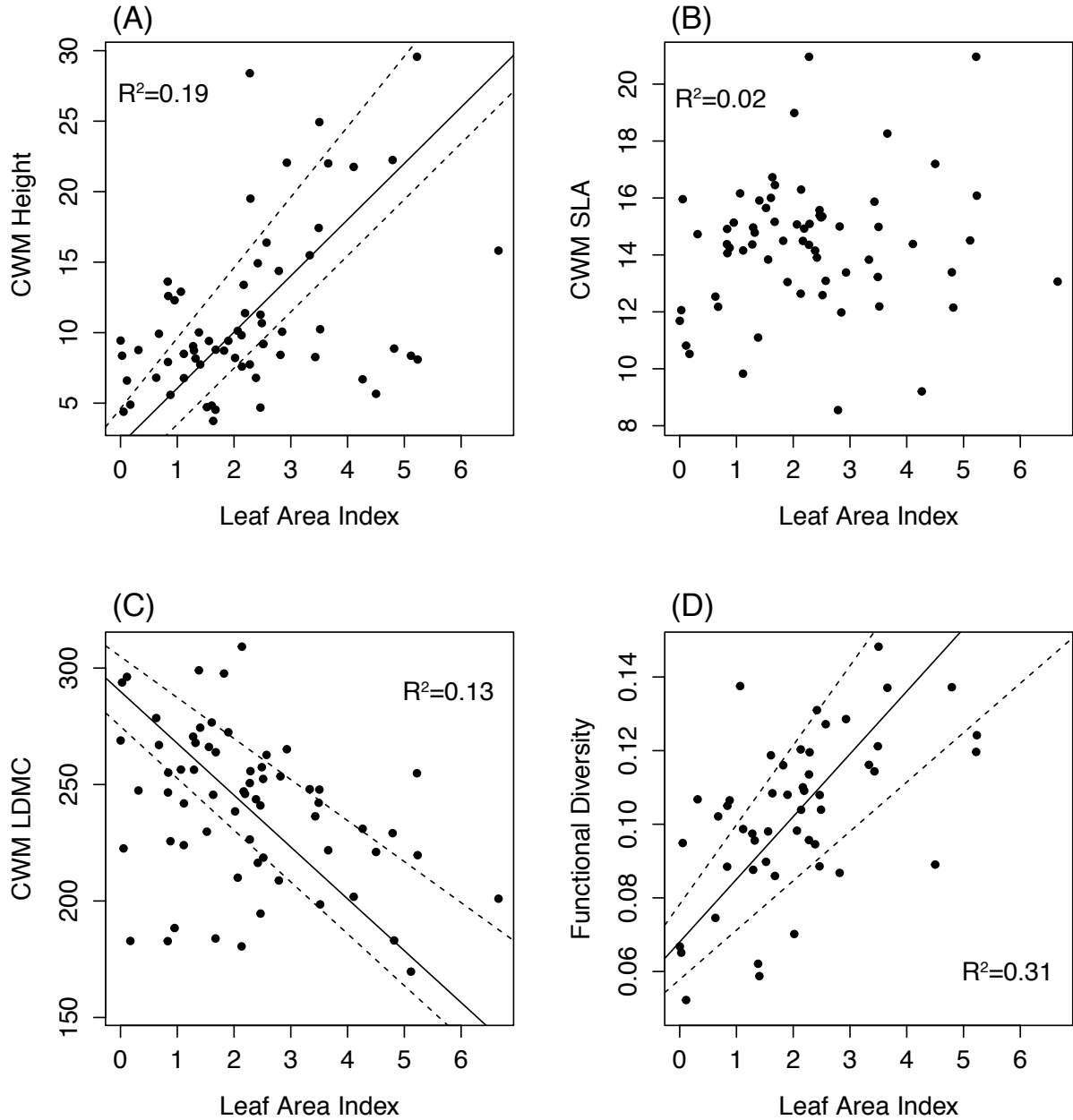


Figure 1. Standardized major axis regression between hyperspectral-derived leaf area index (LAI) and metrics of plant community functional diversity. Dashed lines show 95% confidence intervals of slope parameter estimates.

(LDMC), and multi-trait functional diversity (Figure 1). Given the usual co-variance between LDMC and specific leaf area (SLA), it was surprising that LAI and LDMC were significantly related, whereas no relationship existed between LAI and SLA. One possible explanation for this lack of trend could be high elevation plant communities located in scree fields with high SLA

(e.g. *Geum reptans*), which nonetheless have low LAI due to small amount of leaf area per unit of ground area. The relatively high R-squared values between LAI and functional diversity nonetheless highlights potential complementarity between optical information on plant canopy properties and field-measured functional diversity.

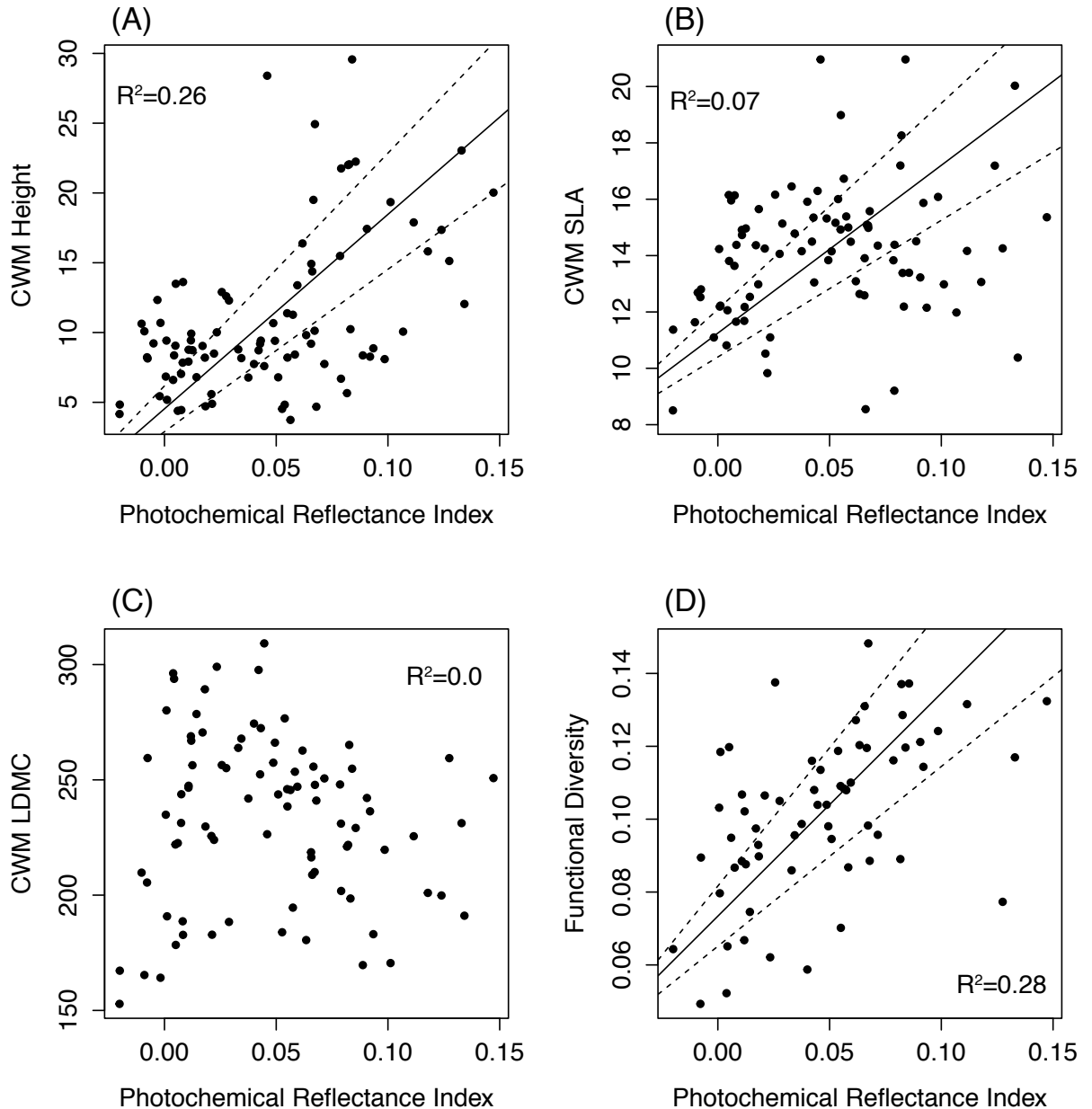


Figure 2. Standardized major axis regression between hyperspectral-derived photochemical reflectance index (PRI) and metrics of plant community functional diversity. Dashed lines show 95% confidence intervals of slope parameter estimates.

The photochemical reflectance index (PRI), which is a narrow-band index sensitive to xanthophyll pigment concentration, has been proposed as an optical measure of light-use efficiency (LUE; Grace *et al.* 2007). Quantifying spatial variation at the landscape scale is a key challenge in modeling gross primary productivity, and identifying a link between plant functional diversity and LUE would be a major insight in the realm of biodiversity ecosystem function studies. Significant-if-not-spectacular R-squared values found between PRI and functional diversity metrics were promising, although further work is needed to better understand these relationships. One important shortcoming of the trait data I used is that measures were not carried out during the hyperspectral flight. *In situ* trait measures would have enabled study of how functional traits contributed to optical measures of ecosystem functioning accounting for intraspecific trait variability, phenology and spatial context. I think that my preliminary analysis shows promising potential links, however a coordinated and premeditated study with both imagery and field measures is necessary in order to elucidate relationships between functional diversity to ecosystem functioning.

References

- Féret, J. B., & Asner, G. P. (2014). Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. *Ecological Applications*, 24(6), 1289-1296.
- Ford, K. R., Ettinger, A. K., Lundquist, J. D., Raleigh, M. S., & Lambers, J. H. R. (2013). Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-snow mountain landscape. *PloS one*, 8(6), e65008.
- Grace, J., Nichol, C., Disney, M., Lewis, P., Quaife, T., & Bowyer, P. (2007). Can we measure terrestrial photosynthesis from space directly, using spectral reflectance and fluorescence? *Global Change Biology*, 13(7), 1484-1497.
- Guerschman, J. P., Hill, M. J., Renzullo, L. J., Barrett, D. J., Marks, A. S., & Botha, E. J. (2009). Estimating fractional cover of photosynthetic vegetation, non-photosynthetic vegetation and bare soil in the Australian tropical savanna region upscaling the EO-1 Hyperion and MODIS sensors. *Remote Sensing of Environment*, 113(5), 928-945.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965-1978.

Kivinen, S., Kaarlejärvi, E., Jylhä, K., & Räisänen, J. (2012). Spatiotemporal distribution of threatened high-latitude snowbed and snow patch habitats in warming climate. *Environmental Research Letters*, 7(3), 034024.

Psomas, A., Kneubühler, M., Huber, S., Itten, K., & Zimmermann, N. E. (2011). Hyperspectral remote sensing for estimating aboveground biomass and for exploring species richness patterns of grassland habitats. *International Journal of Remote Sensing*, 32(24), 9007-9031.

Randin, C. F., Dedieu, J. P., Zappa, M., Long, L., & Dullinger, S. (2015). Validation of and comparison between a semidistributed rainfall–runoff hydrological model (PREVAH) and a spatially distributed snow-evolution model (SnowModel) for snow cover prediction in mountain ecosystems. *Ecohydrology*, 8(7), 1181-1193.

Suvanto, S., Le Roux, P. C., & Luoto, M. (2014). Arctic-alpine vegetation biomass is driven by fine-scale abiotic heterogeneity. *Geografiska Annaler: Series A, Physical Geography*, 96(4), 549-560.

Vionnet, V., Martin, E., Masson, V., Guyomarc'h, G., Bouvet, F. N., Prokop, A., ... & Lac, C. (2014). Simulation of wind-induced snow transport and sublimation in alpine terrain using a fully coupled snowpack/atmosphere model. *Cryosphere*, 8, p-395.

Chapter II

*Quantifying alpine plant community
habitat and growth responses:
application of satellite imagery*

Chapter II Introduction

Dense time series of multispectral satellite images with high ground resolution ($< 30\text{m}$) are only just now becoming available to ecologists. In order to make use of this information, ecologists must consider how to acquire, store and process large spatial datasets and apply remote sensing methods, which can be time consuming for non-specialists simply interested in the end-product. Google has anticipated this need by developing the Google Earth Engine (<https://earthengine.google.com/>), whose mission is to combine “a multi-petabyte catalog of satellite imagery and geospatial datasets with planetary-scale analysis capabilities” and make this information available to “scientists, researchers, and developers to detect changes, map trends, and quantify differences on the Earth’s surface”. While on the one hand this initiative facilitates data access for non-remote sensing specialists, on the other hand there is the potential problem of black box data processing methods and loss of control for scientists. Stating in a methods section that “Imagery was acquired from Google” is not the same as selecting an optical image processing technique from the literature based on a research question or application and detailing steps taken in terms of radiometric, atmospheric and topographic correction. On the other hand, the time saved may well be worth the loss in flexibility. Technical considerations aside, the other challenge that ecologists face in this context is determining what to do with these data, and specifically what novel questions might be addressed. In the field of alpine ecology in particular, regardless of how the data are acquired it is clear that high-resolution data on land surface dynamics opens up a number of interesting avenues of investigation at the interface between remote sensing and community ecology.

The goal of this chapter is to explore relationships between multi-temporal satellite imagery and plot-level measures of high-elevation plant diversity originating from field observations. With some notable exceptions (e.g. Fontana *et al.* 2008; Pottier *et al.* 2015; Randin *et al.* 2015), remote sensing and alpine plant ecology communities have advanced mostly in parallel with relatively few exchanges and collaborations. As the spatial and temporal resolution of available satellite imagery continues to improve, remote sensing presents an increasingly useful data source for plant ecologists interested in quantifying spatio-temporal variability in snow cover dynamics and plant phenology. In this chapter, the first question to be addressed is

whether or not satellite-based estimates of snow melt-out timing correspond with ground-based measures in topographically complex terrain. Using a framework initially proposed by Walker *et al.* 1993, the second challenge addressed consists of attempting to differentiate habitat for dominant alpine plant communities based on snow cover duration and peak productivity at the regional scale. I also test whether or not exposure to frost stress can be used as effectively as a third axis of environmental variation differentiating alpine plant communities. Finally, the third section is perhaps the most ambitious and least complete, but nonetheless presents an interesting approach and set of objectives. We take advantage of three consecutive highly contrasting snow cover years (2013-2015) in order to test whether or not NDVI responses of high elevation plant communities, for a given growing season length, are mediated by functional traits. The hypothesis is that communities with certain traits, i.e. taller canopies or higher SLA, will be able to track longer growing seasons while other communities might show a less flexible NDVI response to inter-annual variability in snow cover duration. Overall, all of these sub-questions attempt to explore potential complementarity between field surveys of plant diversity and dense time series of multi-spectral satellite imagery.

Chapter IIA

On the importance of high-resolution time series of optical imagery for quantifying the effects of snow cover duration on alpine plant habitat^{}*

^{*} Dedieu, J. P.⁺, **Carlson, B. Z.**⁺, Bigot, S., Sirguey, P., Vionnet, V., & Choler, P. (2016). On the Importance of High-Resolution Time Series of Optical Imagery for Quantifying the Effects of Snow Cover Duration on Alpine Plant Habitat. ⁺Denotes equal contributions as lead authors. *Remote Sensing*, 8(6), 481.



Article

On the Importance of High-Resolution Time Series of Optical Imagery for Quantifying the Effects of Snow Cover Duration on Alpine Plant Habitat

Jean-Pierre Dedieu^{1,2,3,*,†}, Bradley Z. Carlson^{4,5,6,†}, Sylvain Bigot^{1,2,3,6}, Pascal Sirguey⁷, Vincent Vionnet^{8,9} and Philippe Choler^{4,5,6,10}

¹ Laboratoire d'étude des Transferts en Hydrologie et Environnement, Université Grenoble Alpes, 460 rue de la Piscine, Saint Martin d'Hères 38400, France; sylvain.bigot@ujf-grenoble.fr

² Institut de Recherche pour le Développement, Laboratoire d'étude des Transferts en Hydrologie et Environnement, 460 rue de la Piscine, Saint Martin d'Hères 38400, France

³ Centre National de la Recherche Scientifique, Laboratoire d'étude des Transferts en Hydrologie et Environnement, 460 rue de la Piscine, Saint Martin d'Hères 38400, France

⁴ Université Grenoble Alpes, Laboratoire d'Ecologie Alpine, 2233 rue de la Piscine, Saint Martin d'Hères 38400, France; brad.z.carlson@gmail.com (B.Z.C.); philippe.choler@univ-grenoble-alpes.fr (P.C.)

⁵ Centre National de la Recherche Scientifique, Laboratoire d'Ecologie Alpine, 2233 rue de la Piscine, Saint Martin d'Hères 38400, France

⁶ Long Term Ecological Research Network "Zone Atelier Alpes", Saint Martin d'Hères 38400, France

⁷ University of Otago, National School of Surveying, P.O. Box 56, Dunedin 9054, New Zealand; pascal.sirguey@otago.ac.nz

⁸ Météo-France, Centre d'Etudes de la Neige, 1441 rue de la Piscine, Saint Martin d'Hères 38400, France; vincent.vionnet@meteo.fr

⁹ Centre National de la Recherche Scientifique, Centre d'Etudes de la Neige, 1441 rue de la Piscine, Saint Martin d'Hères 38400, France

¹⁰ Centre National de la Recherche Scientifique, Station Alpine Joseph Fourier, 2233 rue de la Piscine, Saint Martin d'Hères 38400, France

* Correspondence: jean-pierre.dedieu@univ-grenoble-alpes.fr; Tel.: +33-456-520-977

† These authors contributed equally to this work.

Academic Editors: Olivier Hagolle, Benjamin Koetz, Olivier Arino, Sylvia Sylvander, Clement Atzberger and Prasad S. Thenkabail

Received: 11 March 2016; Accepted: 2 June 2016; Published: 7 June 2016

Abstract: We investigated snow cover dynamics using time series of moderate (MODIS) to high (SPOT-4/5, Landsat-8) spatial resolution satellite imagery in a 3700 km² region of the southwestern French Alps. Our study was carried out in the context of the SPOT (Take 5) Experiment initiated by the Centre National d'Etudes Spatiales (CNES), with the aim of exploring the utility of high spatial and temporal resolution multispectral satellite imagery for snow cover mapping and applications in alpine ecology. Our three objectives were: (i) to validate remote sensing observations of first snow free day derived from the Normalized Difference Snow Index (NDSI) relative to ground-based measurements; (ii) to generate regional-scale maps of first snow free day and peak standing biomass derived from the Normalized Difference Vegetation Index (NDVI); and (iii) to examine the usefulness of these maps for habitat mapping of herbaceous vegetation communities above the tree line. Imagery showed strong agreement with ground-based measurements of snow melt-out date, although R^2 was higher for SPOT and Landsat time series (0.92) than for MODIS (0.79). Uncertainty surrounding estimates of first snow free day was lower in the case of MODIS, however (± 3 days as compared to ± 9 days for SPOT and Landsat), emphasizing the importance of high temporal as well as high spatial resolution for capturing local differences in snow cover duration. The main floristic differences between plant communities were clearly visible in a two-dimensional habitat template defined by the first snow free day and NDVI at peak standing biomass, and these differences were accentuated

when axes were derived from high spatial resolution imagery. Our work demonstrates the enhanced potential of high spatial and temporal resolution multispectral imagery for quantifying snow cover duration and plant phenology in temperate mountain regions, and opens new avenues to examine to what extent plant community diversity and functioning are controlled by snow cover duration.

Keywords: optical remote sensing; snow cover; mountains; NDSI; NDVI; alpine ecology

1. Introduction

1.1. Background and Rationale

Mountain regions are privileged areas for water and energy exchanges. Mountain rivers provide water supply to 40% of the world's population and are subject to high demographic and climate pressure [1]. In many mountain watersheds, the seasonal evolution of the snow pack is a key parameter influencing regional climate [2], water resource budgets [3], and ecosystem functioning and structure [4]. Within the context of global climate change [1,5], temperature rise in the European Alps has been pronounced and accompanied by rising snow lines and earlier melt-out dates [6,7]. Recent studies show that a continuous winter snow pack is becoming increasingly rare in Alpine catchments below 1200 m above sea level (a.s.l.) [8], although snow cover duration above 2000 m a.s.l. has been shown to be less sensitive to changes in air temperature [9]. Over the last few decades, observational studies of mountain vegetation have demonstrated rising tree lines in the Alps and Pyrenees in response to climate warming and land abandonment [10,11] as well as increasing species richness on Europe's temperate alpine summits [12].

Optical remote sensing provides the opportunity to address the question of snow cover regime changes at the regional scale, particularly in the context of mid-latitude study areas [13]. A decrease in snow-covered areas has been globally observed in the Northern Hemisphere since the end of the 1970s, when the first space borne optical sensors began to monitor the Earth's surface [14,15]. Different methods have been developed to compute changes in terms of snow cover area (SCA) and snow cover duration (SCD) [16,17], and have been applied (i) at the global scale with NOAA-AVHRR, SPOT-Vegetation and MODIS sensors; and (ii) at the regional scale with Landsat, SPOT and ASTER missions. The main parameters analyzed are the timing and duration of the melting season under current and future climate conditions [18,19]. Maps and statistics retrieved [13,20] are useful for a large panel of climate and environmental applications, including alpine ecology. Alpine ecologists are especially interested in snow cover maps in order to better understand and predict responses of high-elevation vegetation to climate change [21].

Temperate mountain grasslands are fundamentally limited by a short growing season, and spatial variability in energy availability is a key factor affecting the distribution of high-elevation plant species [22]. Growing season length, as determined by snow cover duration, has been associated with (i) patterns of taxonomic and functional diversity in alpine plant communities [23,24] as well as diversity patterns across plant and microbe trophic levels [25]; and (ii) ecosystem functioning, including primary productivity and phenology [26,27], and nutrient cycling [28]. Turnover in alpine plant diversity typically occurs over short distances (<50 m) in the form of complex mosaics that vary according to topographic heterogeneity [29], which necessitates quantifying changes in environmental conditions at this scale [30]. For plant ecologists interested in understanding and predicting responses of alpine plant communities to climate change, there is therefore a crucial need to map snow cover dynamics at high resolution and over broad spatial scales, both for the present and coming decades [31].

Prior to application of remote sensing-derived snow cover information, it is necessary to carry out ground validation and also to assess cross-scalar agreement between field measurements and imagery of varying spatial and temporal resolutions. Using MODIS imagery at the regional scale, strong

agreement was demonstrated between snow maps derived from the Normalized Difference Snow Index (NDSI) and ground-based measurements of snow height [32]. Also using MODIS, phenology metrics for above-tree line vegetation, including snow melt-out date, start of plant growth, and end of the growing season derived from the Normalized Difference Vegetation Index (NDVI) were validated with respect to ground measures of snow and plant height [33]. While at least one previous study has carried out quantitative comparison of snow cover area maps generated by Landsat ETM+ and MODIS satellites [34], studies testing the ability of dense time series of optical imagery at high spatial resolution (<30 m) to quantify snow cover duration in mountainous areas are lacking, and are necessary as the availability of high-resolution satellite imagery continues to increase.

A new technical step is in reach with the Sentinel-2 Copernicus program, including two optical platforms (2A launched successfully in June 2015 and 2B planned for 2016) with high temporal (5 days) and spatial (10 to 20 m) resolutions for coverage of $300 \times 300 \text{ km}^2$. These combined advantages offer to reduce data gaps caused by cloud cover, and, concerning snow, to improve accuracy for monitoring the timing of snow accumulation and snow melt-out relative to the larger repeat cycles of Landsat or SPOT missions. In order to simulate the Sentinel-2 revisit frequency and output products, the French Space Agency CNES (Centre National d'Etudes Spatiales), joined by the European Space Agency (ESA), implemented the SPOT (Take 5) Experiment, which consisted of moving the SPOT-4 and SPOT-5 satellites to a lower orbit before the end of their respective missions, in order to achieve five-day revisit capacity [35]. The two experiments took place respectively from February to June, 2013, for SPOT-4 (20 m resolution), and from April to September 2015, for SPOT-5 (10 m resolution) over worldwide selected sites, including our study area in the southwestern French Alps.

1.2. Goals and Objectives

Using images obtained from the SPOT (Take 5) Experiment, the objectives of this paper are: (i) to validate remote sensing observations of first snow free day derived from the Normalized Difference Snow Index relative to ground-based measurements for two snowmelt cycles (2013 and 2015); (ii) to generate regional-scale maps of first snow free day and peak productivity defined by the Normalized Difference Vegetation Index; and (iii) to examine the usefulness of these maps for habitat mapping of herbaceous vegetation communities above the tree line. The description of our study area, data sets and climate context are presented in Section 2. Section 3 provides methods for image processing, snow cover (NDSI) and NDVI mapping, validation of snow cover maps and intersection of remote sensing data with vegetation plots. Results are shown in Section 4 for validation of remote sensing estimates of snow melt-out date, regional-scale mapping of first snow free day and peak NDVI, and differentiation of alpine plant community habitat. These findings are discussed in Section 5, followed by our conclusions.

2. Study Area and Data Sets

2.1. Study Area

The SPOT (Take 5) study site (French Alps, Europe) is located at $45^{\circ}09'N$, $06^{\circ}10'E$, near the city of Grenoble. It is a high mountain area, centered on the Oisans massif, where 50% of the territory is located at an elevation of over 2000 m a.s.l., including both ski resorts and glaciers (Figure 1). Land cover above inhabited valleys is a combination of forest (mainly spruce, beech, larch and fir) interspersed with grasslands and subalpine heathlands, transitioning to alpine meadows (Figure 2), and finally rock, snowfield and glacier at the highest elevations. Our study area encompasses the Oisans mountain range in the Ecrins National Park, which is a long-term study site for both Météo France and the Long Term Ecological Research Network (LTER) "Zone Atelier Alpes" [36].

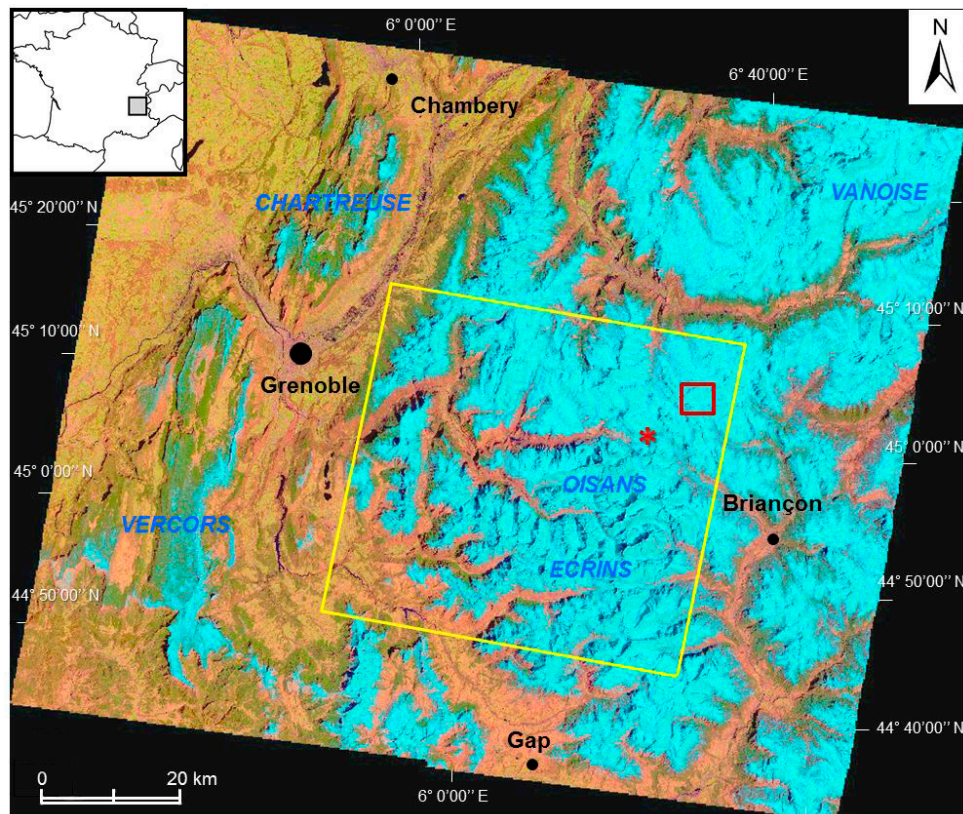


Figure 1. Location of study area, showing the overall SPOT-4 (Take 5) extent and the reduced SPOT-5 extent in **yellow**, which covers the Oisans massif and the Ecrins National Park. The **red** star shows the Figure 2 location and the **red** inset shows the “Massif des Cercès” area of Figure 5. The background image is a visible and infrared color composition (**green**, near infra-red and short-wavelength infrared channels) from a SPOT-4 scene acquired on 14 April 2013, with snow cover shown in **blue**. ©CNES-Cesbio.



Figure 2. Photo of spring snowmelt near the Col du Lautaret (Figure 1), showing characteristic spatial heterogeneity in snow cover duration and the differential timing of plant green-up. ©Philippe Choler/Station Alpine Joseph-Fourier.

2.2. Remote Sensing Data

The SPOT (Take 5) Experiment was carried out using SPOT-4 and 5 satellites. By combining both SPOT-4 sensors, it was possible to obtain an image tile of $110 \times 110 \text{ km}^2$, whereas the SPOT-5 images were registered under the regular size of $65 \times 65 \text{ km}^2$, using only a single sensor (Figure 1). The dataset was completed with Landsat-8 acquisitions available beginning in April 2013, and with near-daily MODIS images (L1B swath data product). The complete image collection was cropped to the SPOT-5 extent, in order to be consistent for image pre-processing, mapping and analysis. We used a digital elevation model (DEM) at 25 m resolution and a forest layer provided by the French National Institute Geographic Information (IGN) to remove pixels from the analysis that were forested and/or below 1800 m a.s.l. We selected the threshold of 1800 m a.s.l. in order to focus our study on snow cover dynamics and high-elevation plant communities above the tree line.

With spectral bands in the visible and infrared, the optical sensors of SPOT, Landsat and MODIS are appropriate to differentiate snow cover from other targets, particularly above the tree line, including vegetation, bare ground, water and clouds. The physical properties of snow retrieved by optical remote sensing are well documented, especially for energy balance or runoff modeling [37–39]. However, additional pre-processing steps are necessary in order to generate usable time series from multiple optical sensors, especially in the case of mountainous study areas [40].

2.3. Climate Context and Snow Cover Variability (1959–2015)

We provide re-analysis of climate and snow cover trends during the past six decades in order to put our study years (2013 and 2015) in context. Recent climate trends in the European Alps have had a strong impact on snow cover duration and environmental conditions for alpine plants [41]. Durand *et al.* [42] demonstrated a decline in snow cover duration in the French Alps between 1959 and 2005, particularly at low and medium elevations, caused by increases in air temperature coupled with changes in precipitation regimes [43–45]. With an increase in annual mean temperatures of $0.9 \text{ }^\circ\text{C}$, as compared to a global averaged increase of $0.6 \pm 0.2 \text{ }^\circ\text{C}$ [1], the European Alps have been strongly affected by recent climate change (Figure 3). Within the context of our study area, Figure 4 demonstrates inter-annual variability of the first snow free day for five elevation classes in the Oisans mountain range from August 1958 to August 2015. These results were obtained from a re-analysis of meteorological and snowpack conditions using the SAFRAN-SURFEX/Crocus-MEPRA model chain (S2M) [42,44,46]. At all elevations, snow melt-out date tends to occur earlier in the season during recent years as compared to past decades, although there is substantial year-to-year variability. At 1500 m a.s.l., the first snow free day occurred on average by Julian Day 119 for the period 1961–1990 and by Julian Day 106 over the period 1981–2010 (Figure 4). This trend was less pronounced at 2700 m a.s.l., where first snow free day advanced from Julian Day 182 to 172 between the 1961–1990 and 1981–2010 periods.

The years 2013 and 2015 were highly distinct compared to recent years in our study area in terms of precipitation, temperature and snow cover duration (Figures 3 and 4). Across all elevations, and as compared to average first snow free day values for 1981–2010, 2013 was characterized by exceptionally long-lasting snow cover, whereas snow melt-out occurred relatively early during the spring and early summer of 2015. Substantial climatic differences between study years 2013 and 2015 allowed us to validate our method of estimating the first snow free day for two highly contrasting snowmelt cycles.

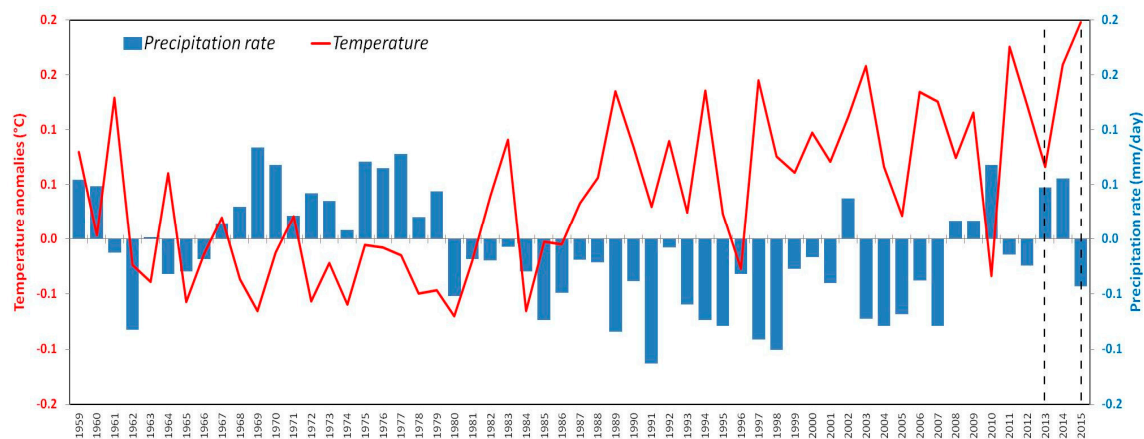


Figure 3. Inter-annual variability between 1959 and 2015 of annual average air temperature ($^{\circ}\text{C}$) and precipitation rate (mm/day) at 850 hPa in the French Alps, which is roughly equivalent to 1500 m a.s.l.. Data were obtained from the NCEP-NCAR (National Centers for Environmental Prediction/National Center for Atmospheric Research). Anomalies were calculated based on the 1961–1990 average; the alpine regional index is approximately 5.5° – $6.8^{\circ}\text{E}/44.5^{\circ}$ – 46°N . Vertical dashed black lines indicate the years considered in our study (2013 and 2015).

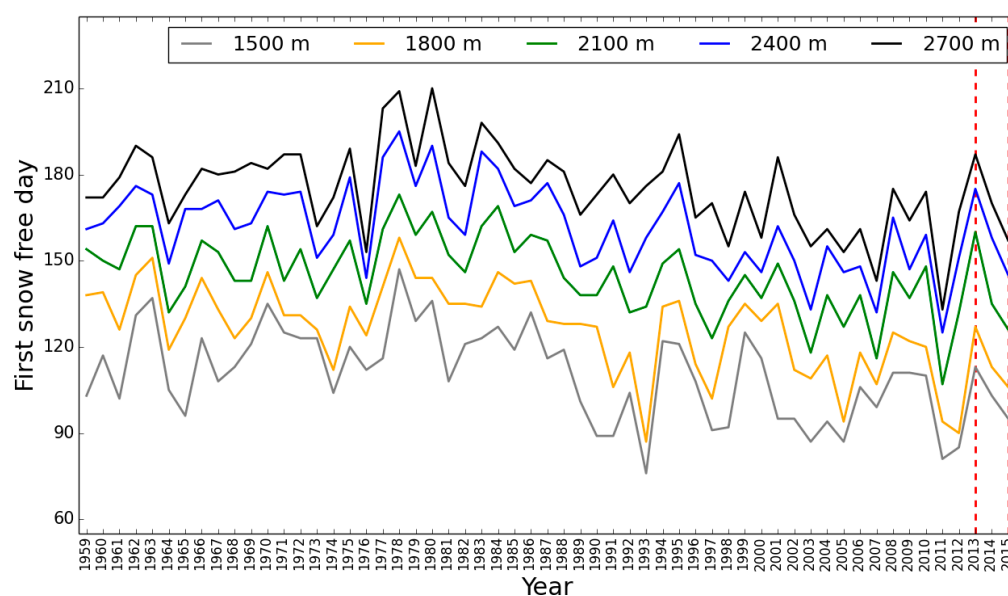


Figure 4. The first snow free day (in Julian Day) for different elevations in the Oisans mountain range from SAFRAN-SURFEX/Crocus-MEPRA model chain (S2M). Vertical dashed red lines indicate the years considered in our study (2013 and 2015).

3. Materials and Methods

3.1. Image Processing and Snow Cover Mapping

3.1.1. SPOT-4 and SPOT-5 and Landsat-8 Image Pre-Processing

In the framework of the SPOT (Take 5) Experiment, CNES-Cesbio provided SPOT-4 and SPOT-5 images at the top of the atmosphere (L1C) and top of the canopy (L2A) reflectance using the multi-sensor atmospheric correction and cloud screening (MACCS) algorithm [47]. The standard L2A product with “surface reflectance” (hereafter referred to as L2A-SRE) was further enhanced by applying correction methods originally proposed by Dymond and Sheperd [48,49] to account for

changes in illumination caused by slope angle and aspect, with the aim of providing a retrieved “flat reflectance” (hereafter referred to as L2A-FRE). Given that designated sites for the SPOT (Take 5) Experiment occurred across the globe, the Shuttle Radar Topography Mission (SRTM) 90 m product was used as the DEM for image processing. All processed SPOT (Take 5) images may be freely downloaded from the CNES-ESA web portal (<https://spot-take5.org>). To complete the time series for 2013 and 2015, we added available Landsat-8 images at 30 m resolution for both years, which were processed by the THEIA Land Data Center using the same atmosphere and slope-correction algorithms as for SPOT (Take 5) outputs. These data are also distributed with a free and open policy (<https://theia-land.fr>). Considering the L2A-FRE output as the optimal available product, particularly for early spring months characterized by low solar elevation, we acquired all SPOT and Landsat images for this study at this enhanced correction level. In total, we used thirty-eight high-resolution images (see Table S1 in Supplementary Material), including six SPOT-4 dates (2013), eleven SPOT-5 dates (2015), and twenty-one Landsat-8 dates (nine for 2013, twelve for 2015). SPOT and Landsat images with contrasting spatial resolutions (10–30 m, Table S1) were resampled to a baseline 25 m resolution using bilinear interpolation.

3.1.2. MODIS Image Processing

From February 2000 onward, the MODIS sensor onboard the Terra platform has acquired images worldwide with daily temporal resolution. The National Snow and Ice data Center (NSIDC) provides snow map products at daily and eight-day intervals [50,51]. However, the steep topography of our study area necessitated the use of an enhanced algorithm for detecting snow cover in mountainous terrain using MODIS data. MODImLab is a MATLAB toolbox allowing MODIS L1B swath data products (radiance at the top of atmosphere TOA) to be downloaded and processed automatically towards the production of binary snow maps and maps of sub-pixel snow fraction [52] snow albedo [53], and snow specific surface area [54]. In this study, MODImLab was used to process MODIS/TERRA L1B data using the image fusion approach, which allows for estimation of the short wave infrared band at 250 m spatial resolution [55].

3.1.3. Snow Cover (NDSI) and NDVI Mapping

Dozier [56] proposed a multispectral scheme with Landsat Thematic Mapper data for binary mapping of snow cover, by which each pixel is classified as snow, snow-free or cloud. This method relies on the Normalized Difference Snow Index (NDSI), which captures contrast between the high reflectance of snow in the green part of the solar spectrum (0.5 μm) and the low reflectance registered in the short wave infrared (SWIR) at 1.6 μm . The SWIR also provides the capability to discriminate snow from clouds, due to the increased absorption coefficient of ice compared to liquid water in the short-wave infrared:

$$NDSI = \frac{\rho_{\text{Green}} - \rho_{\text{SWIR}}}{\rho_{\text{Green}} + \rho_{\text{SWIR}}} \quad (1)$$

where ρ is the reflectance of the respective channel. Subsequently, a pixel in an un-forested area is mapped as snow covered when $NDSI > 0.4$ [56], which is referenced as a standard value by many publications in the literature since the initial paper of Dozier in 1989. This simple threshold-based approach was applied here to all sensors of our images dataset: SPOT, Landsat and MODIS in order to create binary snow maps. Table 1 summarizes the channels and respective wavelengths of the four sensors used in this study for NDSI and NDVI calculation. Concerning MODIS images, the mapping of snow from fused spectral bands was completed using the binary algorithm of the MOD10 Snow Product [50] based on the same 0.4 NDSI threshold. Additional tests on the visible and near-infrared bands, as well as a thermal test on the surface temperature, enable commission errors in water and dark areas to be reduced [51].

Table 1. Wavelength characteristics of the spectral bands used to identify snow cover for images acquired by the four sensors employed in this study.

Sensor	Resolution (m)	Wavelength (μm)			
		Green	Red	Near-Infrared	Shortwave Infrared
SPOT-4	20	0.50–0.59	0.61–0.68	0.78–0.89	1.58–1.75
SPOT-5	10	0.50–0.59	0.61–0.68	0.78–0.89	1.58–1.75
Landsat-8	30	0.53–0.59	0.64–0.67	0.85–0.88	1.57–1.65
MODIS	500	0.54–0.56	0.62–0.67	0.84–0.88	1.63–1.65

The separation of snow from clouds is a basic requirement of snow cover classifications using optical data and requires routines to discriminate snow on the ground from different types of cloud cover. Cloud masks were provided by CNES-Cesbio and were applied to Landsat and SPOT images, as demonstrated in Figure 5 (CNES product). Concerning MODIS images, MODImLab implements a cloud detection algorithm based on a selection of tests largely inspired from the MOD35 product [57], which was applied to MODIS reflective and emissive bands from the MOD021KM swath L1B products. Combining binary maps retrieved from the NDSI threshold with cloud masks generated snow cover maps at moderate (MODIS 250 m) and high (SPOT and Landsat at 25 m) spatial resolutions.

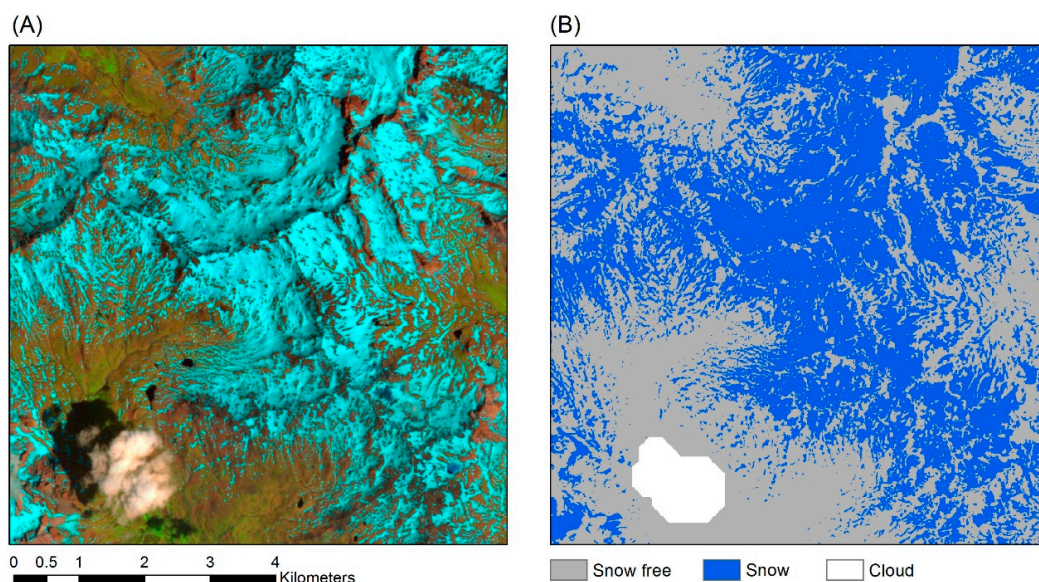


Figure 5. Example snow cover map based on the Normalized Difference Snow Index (NDSI) for a 56 km² in the Massif des Cerces (location provided in Figure 1), for 5 June 2015. (A) Visible and infrared color composite retrieved from a SPOT-5 image at 10 m resolution, showing snow cover in light blue; and (B) map of snow cover showing snow (blue), snow free areas (grey) and cloud/shadow cover (white) derived from a SPOT-5 image ©CNES-Cesbio.

The Normalized Difference Vegetation Index (NDVI), which measures plant photosynthetic activity, was calculated using pre-processed MODIS and SPOT/Landsat time series, using the following formula:

$$NDVI = \frac{\rho \text{ NIR} - \rho \text{ Red}}{\rho \text{ NIR} + \rho \text{ Red}} \quad (2)$$

where ρ is the reflectance of the respective red and near infrared channels, as described in Table 1 for each sensor. The same cloud masks used for snow cover mapping were applied to generate NDVI maps at 250 m (MODIS) and at 25 m (SPOT and Landsat). In addition to representing a proxy of plant biomass, NDVI has also been linked to species richness in the context of mountain grasslands [58].

It should be noted that with normalized indices such as NDSI and NDVI, the retrieved signal is not very sensitive to atmospheric effects in the context of high-elevation study areas [56]. Accordingly, we decided that it was not necessary to carry out atmospheric correction for MODIS images processed with MODImLab.

3.2. Vegetation Data and Ground Measurements of Snowmelt

We assembled a database of 1272 vegetation plots from subalpine grasslands, shrub and heathlands, and alpine meadows. Data were provided by the Conservatoire Botanique National Alpin (<http://www.cbn-alpin.fr/>) and the Ecrins National Park. Floristic surveys were conducted from 2000 to 2014 and consisted of recording all vascular plants occurring in a sampled area ranging from 10 m² to 25 m². The geo-location error of vegetation plots was less than 10 m. Vegetation plots below 1800 m a.s.l. were disregarded in order to exclude grassland patches interspersed with mountain forests.

Similarity-based cluster analysis was conducted using an agglomerative clustering technique [59]. First, floristic distances between vegetation plots were estimated using the Jaccard index, which is based on presence–absence data. Second, k clusters of vegetation plots were defined using the Partitioning Around Medoids (PAM) algorithm implemented in the *pam* function of the R package version 1.15.3 [60,61]. The resulting k clusters minimize the sum of dissimilarities between groups. Exploratory analyses were conducted using a prescribed number of clusters ranging from five to thirty. We identified that twelve clusters represented a fair compromise between having enough vegetation plots per cluster and adequately capturing plant community diversity in the targeted area. The floristic compositions of the resulting clusters are consistent with previous vegetation studies conducted in these mountain ranges [62].

Hourly soil temperatures in high elevation grasslands were recorded using miniaturized data loggers (Hobo pendant[®], Onset, Cape Cod, MA, USA) buried at 5 cm depth. During snow covered periods, subsurface soil temperatures did not exhibit circadian variations and temperature remained between −0.5 °C and 0.5 °C throughout the day. When snow melt-out occurs, daily amplitude increases significantly and the mean daily temperature rapidly rises above 0 °C. Our visual inspection of snow cover on a few instrumented sites clearly indicated that disappearance of snow coincides with the rise of subsurface soil temperature.

Snow depth measurements for 2013 and 2015 were obtained from (i) the Nivose network of Météo France consisting of high-altitude automatic weather stations; and (ii) from two automatic stations belonging to the experimental site of Col du Lac Blanc (2720 m a.s.l., Grandes Rousses range). At all stations, snow depth measurements were collected hourly using an ultra-sonic snow depth gauge.

3.3. Validation of Snow Cover Maps

Time series of snow cover maps derived from MODIS and from SPOT-4/5 and Landsat-8 (hereafter shortened to SL) were used to estimate the first snow free day for available ground measurements in 2013 and 2015. Eight (eleven) time series of soil temperature and four (seven) time series of snow height were available for 2013 and 2015, respectively. Time series of snow cover maps from MODIS and SL imagery were extracted for ground validation points for both years, and the median date between the last observation of snow cover (NDSI > 0.4) and the first snow free observation (NDSI < 0.4) was used to estimate the first snow free day in Julian Days. Considering that both ground-based and remote sensing based estimates were subject to error, standardized major axis regression [63] was used to fit a linear relationship between ground measurements and MODIS and SL estimates of first snow free day. R-squared was used to assess the strength of the relationship between remote sensing observations and ground-based measurements. Mean uncertainty was calculated for both MODIS and SL images and was defined as the average number of days between the last observation of snow cover and the first snow free observation. Mean error was estimated for both medium and high resolution imagery

and was defined as the average difference in Julian Days between remote sensing and ground-based observations of snow melt-out.

3.4. Mapping First Snow Free Day and Peak NDVI

We selected 2015 as an example year to carry out regional-scale mapping of the first snow free day and peak NDVI, and to explore the relevance of these maps for differentiating alpine plant community habitat. Images for 2015 consisted of eleven SPOT-5 scenes and twelve Landsat-8 scenes from 23 March to 8 September 2015 (Table S1). Given that no-data values were possible due to cloud cover or shadows, only pixels that were above 1800 m a.s.l., non-forested and that contained more than eleven non-NA observations were retained for analysis ($n = 4,580,421$). The same algorithm described above was used to estimate the first snow free day (Julian Day) for each pixel, based on the median date between the last observation of snow cover and the first snow free observation. Pixels which were snow free before the first available image (23 March) were set to no-data. The resulting map of the first snow free day was exported at 25 m resolution. NDVI at peak standing biomass (NDVI_{max}) was also estimated for each pixel by extracting the yearly maximum observed value of NDVI. The same protocol was used to estimate the first snow free day and NDVI_{max} using MODIS imagery for 2015, which was available from 1 February to 30 September ($n = 44,642$). Given the large number of MODIS observations, it was not necessary to remove pixels based on the number of cloud-free observations. Pearson's r was used to test for linear correlations between elevation (m a.s.l.) and the first snow free day (Julian Day), and between elevation and NDVI_{max} for a random sample of 5000 pixels iterated 100 times for both MODIS and SPOT and Landsat estimates of first snow free day. Lastly, first snow free day and NDVI_{max} were extracted for all vegetation plots for the year 2015, using both MODIS and SL time series maps. We anticipated an overall negative relationship between first snow free day and NDVI_{max} , with the expectation that a shorter growing season will lead to reduced peak standing biomass.

4. Results

4.1. Validation of Remote Sensing Estimates of the First Snow Free Day

Overall, ground-based physical measures of snow melt-out showed strong agreement with remote sensing observations. The date at which soil temperatures passed above 0°C and at which snow height reached 0 cm corresponded with NDSI values passing below 0.4, especially in the case of SPOT-4/5 and Landsat-8 and (SL) imagery (Figures 6 and 7). For the soil temperature plot shown in Figure 6A, MODIS (grey dashed line) overestimated the first snow free day relative to the soil temperature logger, whereas in Figure 6B, MODIS underestimated the first snow free day as determined by snow height. In both cases, topographic heterogeneity within 250 m pixels led to discrepancy between ground-based measurements of snow melt-out and NDSI observed by MODIS. The examples provided in Figure 6 demonstrate that if high spatial resolution images are available at the critical timing of snowmelt, it is possible to precisely determine the first snow free day even in topographically heterogeneous sites. The increased temporal resolution of MODIS relative to SL was evident due to the higher frequency of snow cover observations (Figure 6).

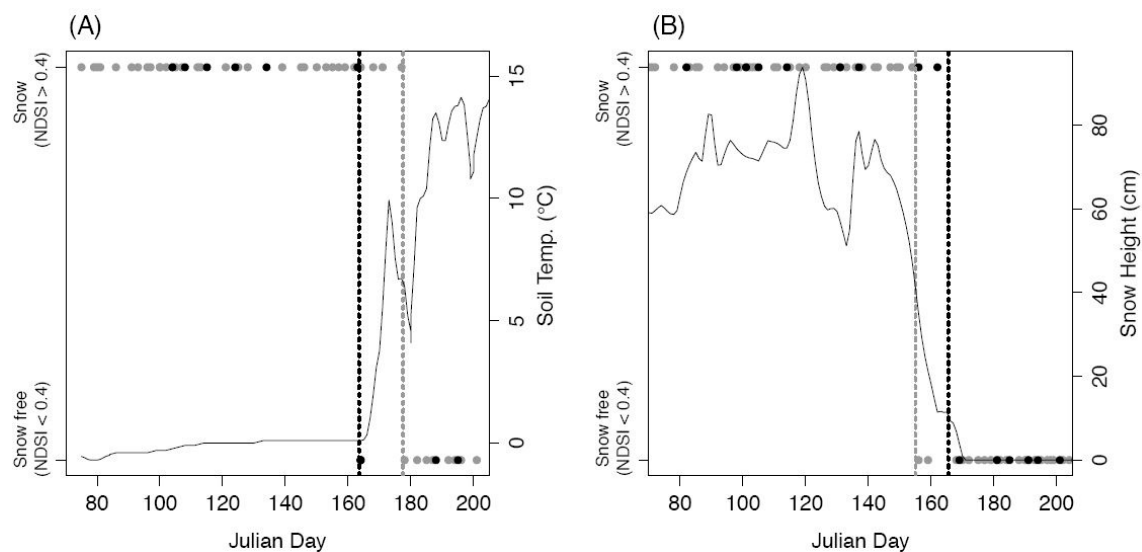


Figure 6. Time series observations for (A) a wind-blown dry alpine meadow dominated by *Kobresia mesuroides* located at 2648 m a.s.l. for 2013; and (B) a snow height monitoring station located in a topographic depression at 3100 m a.s.l. in the commune of La Grave for 2015. In (A), the line indicates running mean daily measures of soil temperature ($^{\circ}\text{C}$, $k = 3$). In (B), the line indicates running mean daily measures of snow pack height (cm, $k = 3$). Solid grey points show MODIS observations of snow cover, while solid black points show SPOT-5 and Landsat-8 observations of snow cover. The black dashed vertical line represents first snow free day estimated by SPOT and Landsat imagery, and the grey dashed vertical line represents the first snow free day estimated by MODIS.

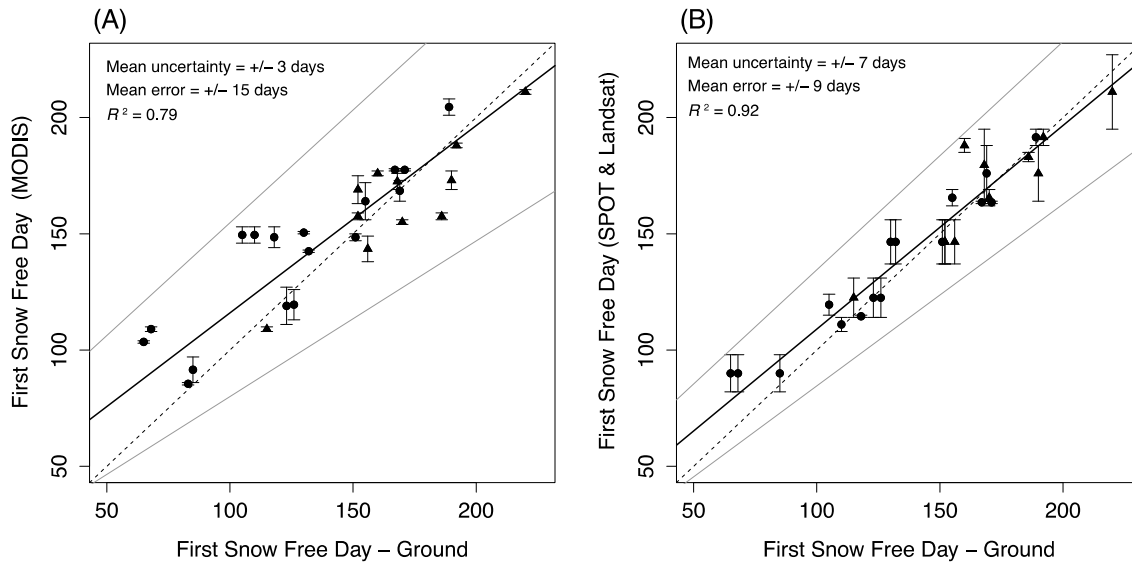


Figure 7. Ground-based measurements plotted relative to remote sensing-based estimates of the first snow free day for 28 observations in 2013 and 2015. Circles correspond to the first snow free day measured by soil temperature, and triangles correspond to first snow free day measured by snow height. Position on the y-axis represents the median Julian Day between the last snow and the first snow free observations (shown with error bars), as estimated by (A) MODIS; and (B) SPOT-5 and Landsat-8. The dashed line is the 1:1 trend line, whereas the solid line is the result of a standardized major axis regression between ground-based measurements and remote sensing observations. Grey lines indicate upper and lower confidence intervals for slope and intercept estimates.

4.2. Mapping the First Snow Free Day and Peak NDVI at the Regional Scale

Estimates of the first snow free day for 2015 varied from 31 March (Julian Day 90) to 4 September (Julian Day 247; Figure 8) for SL imagery and between 10 February (Julian Day 41) and 29 September (Julian Day 272) for MODIS imagery. The first snow free day was significantly correlated with elevation in the case of both MODIS and SL imagery; however, the correlation was stronger in the case of MODIS (0.76 as compared to 0.57 for SL imagery). Despite the overall positive trend between elevation and the first snow free day, we found substantial variation (up to 90 days) in melt-out timing along elevation isolines due to changes in slope orientation (Figure 8 inset). We considered changes in the first snow free day for similar elevations to represent the local effects of wind and topographic heterogeneity.

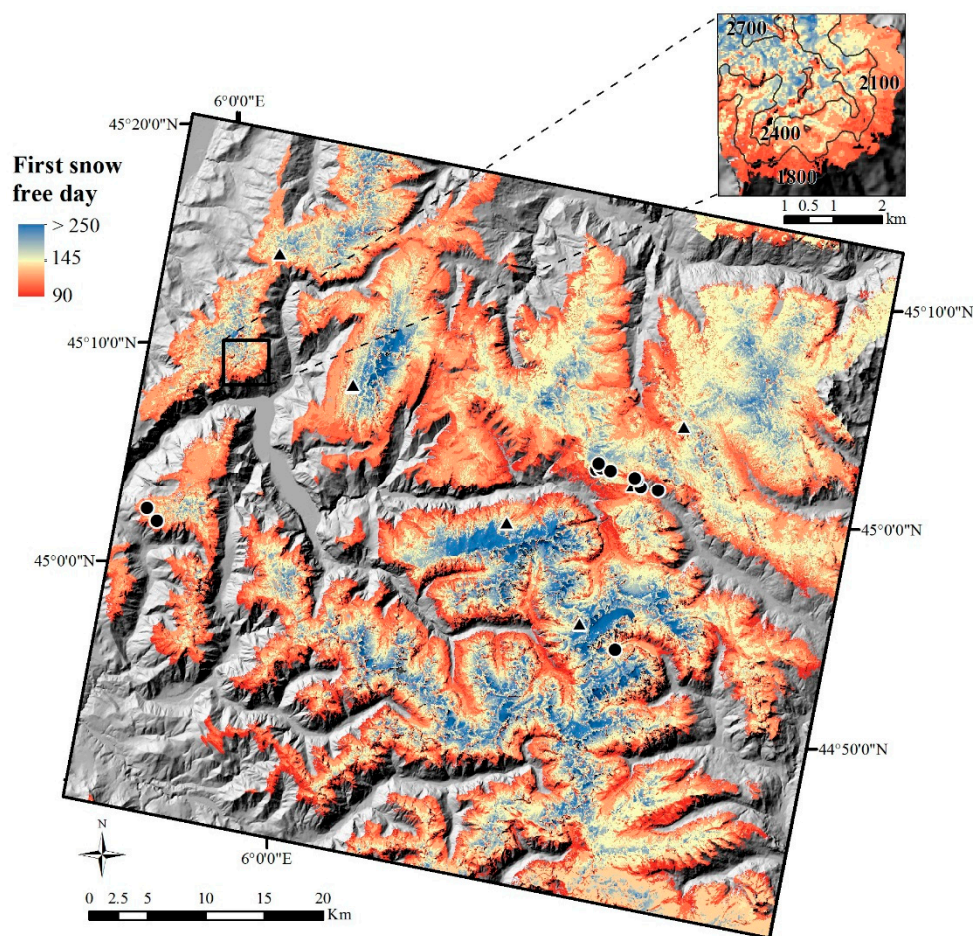


Figure 8. The first snow free day estimated using SPOT-5 and Landsat-8 imagery for 2015, expressed in Julian Days. Pixels have a 25 m spatial resolution and correspond to alpine areas above 1800 m a.s.l.. Points show the location of soil temperature loggers (circles) and snow height monitoring stations (triangles). The inset shows variation in snow cover duration relative to elevation isolines.

For MODIS imagery, peak NDVI (NDVI_{max}) varied from 0 to 0.85 with a mean of 0.48. When estimated with SL imagery, NDVI_{max} varied from 0 to 0.95 with a mean of 0.51 (Figure 9). Maximum values of NDVI above 0.90 (which represented the 0.95 quantile for SL imagery) likely reflected the localized presence of tree cover, despite our effort to remove these pixels from the analysis, or in isolated cases could have been the result of errors in cloud masks. The negative correlation between NDVI_{max} and elevation was somewhat stronger for MODIS than for SL imagery (-0.81 vs. -0.73). The inset in Figure 9 illustrates the high heterogeneity in NDVI_{max} at 25 m resolution, which reflects the patchy distribution of plant communities in high-elevation landscapes.

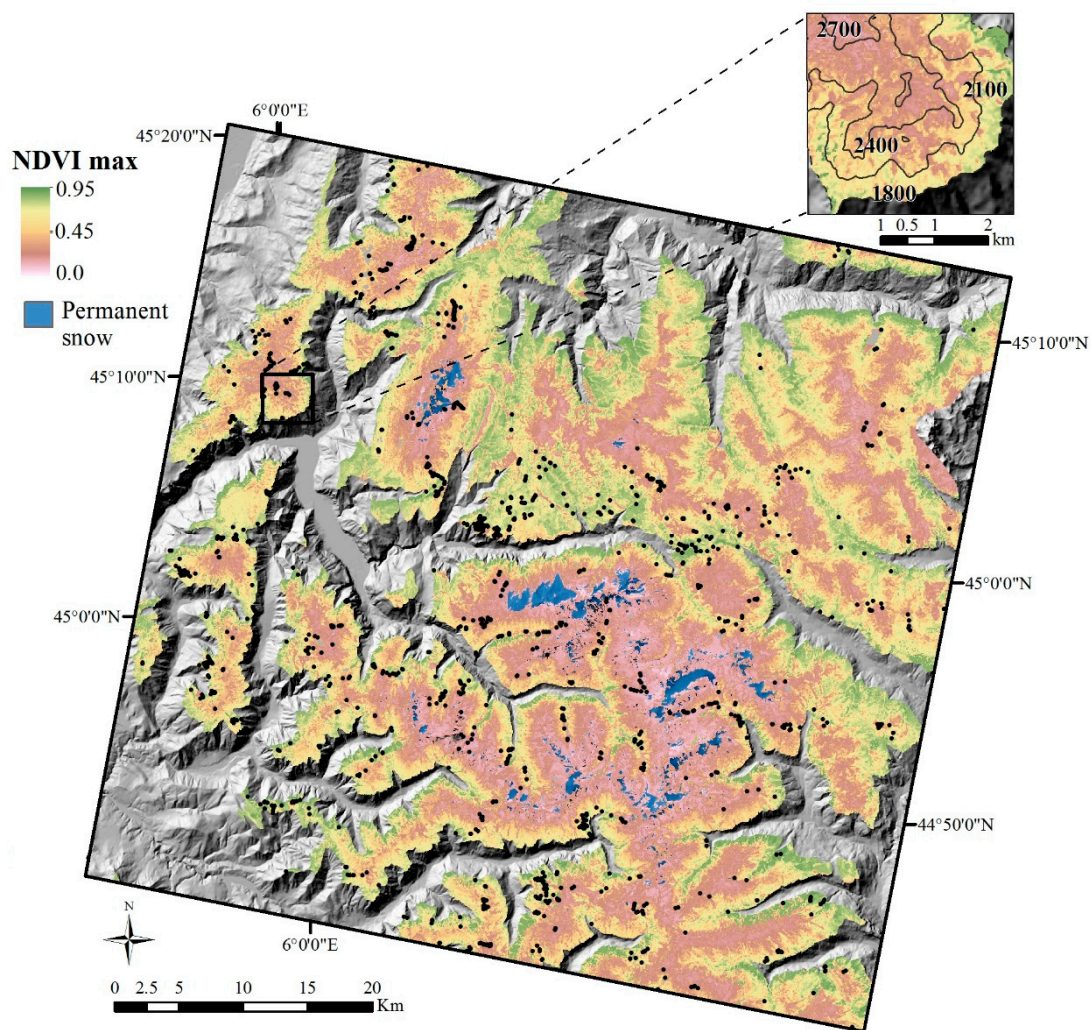


Figure 9. Peak NDVI (NDVI_{max}) estimated using SPOT-5 and Landsat-8 imagery for 2015. Pixels have a 25 m spatial resolution and correspond to alpine areas above 1800 m a.s.l. Points show the location of vegetation plots indicated at Section 3.2 ($n = 1272$). The inset shows variation in NDVI_{max} relative to elevation isolines. Permanent snow cover includes mostly glaciated surfaces.

4.3. Differentiating Alpine Plant Community Habitat by Peak NDVI and the First Snow Free Day

Dominant high-elevation plant communities were differentiated relative to the first snow free day and peak NDVI (NDVI_{max} ; Figure 10). The distribution of plant communities with respect to the first snow free day and NDVI_{max} was similar for axes derived from both MODIS and SL imagery, reflecting the turnover of plant communities along an elevation gradient. The higher temporal resolution of MODIS imagery was apparent due to a more continuous snow melt-out gradient, whereas SL imagery resulted in clustered points as a function of scene acquisition dates (Table S1). Estimation of NDVI_{max} at 25 m with SL imagery resulted in a general upward shift in NDVI values as compared to MODIS at 250 m (Figures 9 and 10), likely due to the higher fraction of vegetation cover contained within smaller pixels.

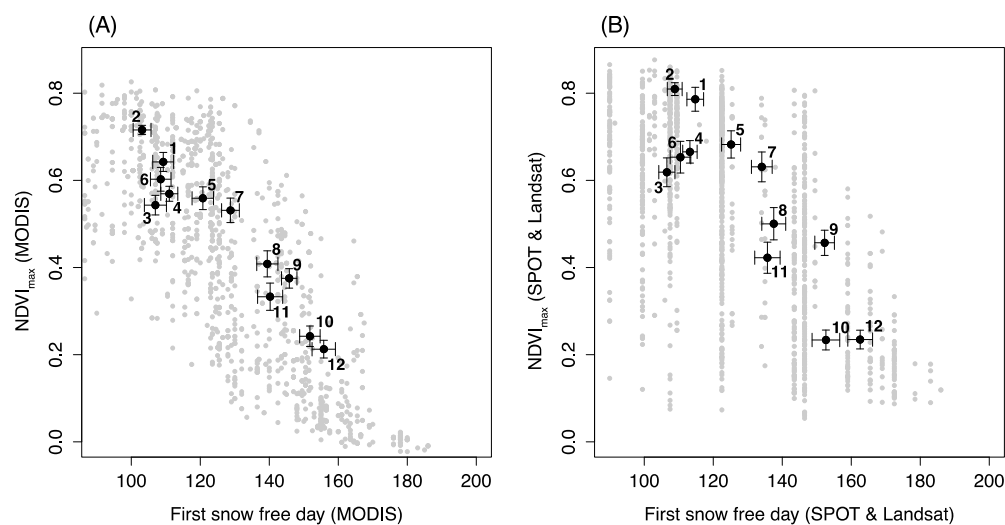


Figure 10. The first snow free day (Julian Day) and peak NDVI ($NDVI_{max}$) for 2015 represented by grey dots, measured by (A) MODIS; and (B) SPOT-5 and Landsat-8 images for 1272 vegetation plots. Black points and error bars represent the mean position with confidence intervals of the twelve plant communities detailed in Table 1. Values of NDVI close to 0 represent plant communities occurring in sparsely vegetated screes and talus. The overall upward shift in NDVI values for SPOT-5 and Landsat-8 imagery as compared to MODIS NDVI can be attributed to more homogenous plant cover occurring within smaller pixels. The error bars represent 95% confidence intervals around estimates of mean NDVI max and the first snow free day per plant community.

Subalpine grassland and shrub communities characterized by early snowmelt (Julian Day 100 to 110) and high NDVI (0.5 to 0.80) included communities 1, 2, 3, 4 and 6 (Figure 10; Table 2). Community 5, representing alpine dwarf shrub habitat, became snow free around Julian Day 120 with an $NDVI_{max}$ between 0.55 (MODIS) and 0.70 (SL). Moist subalpine to low-alpine grasslands (community 7), representative of a transition between subalpine and alpine vegetation, became snow free by Julian day 130 and displayed an $NDVI_{max}$ slightly lower than community 5. Communities 8, 9 and 11 corresponded to alpine grasslands occurring at similar elevations, including mesic alpine meadows, alpine snowbed and wind-blown, dry alpine meadows. As estimated by MODIS, these groups shared similar values of the first snow free day around Julian Day 140 and $NDVI_{max}$ around 0.4. SL imagery increased differentiation of alpine grassland communities, especially in the case of snowbed vegetation (community 9), along the first snow free day axis. Lastly, communities 10 and 12 were representative of talus and scree vegetation with low NDVI around 0.2 and a first snow free day after Julian day 150 (Figure 10; Table 2).

Table 2. Dominant co-occurring species and mean elevation (m a.s.l.) and habitat descriptions for twelve plant communities identified by clustering analysis.

Community	Mean Elevation	Description	Dominant Co-Occurring Species
1	1996	Mosaic of subalpine heath, shrub and tall herb communities	<i>Rhododendron ferrugineum</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis agrostiflora</i> , <i>Vaccinium uliginosum</i> , <i>Alnus alnobetula</i> , <i>Juniperus sibirica</i> , <i>Deschampsia flexuosa</i> , <i>Cacalia alliariae</i> , <i>Imperatoria ostruthium</i> , <i>Geranium sylvaticum</i>
2	2045	Tall subalpine grasslands and pastures	<i>Festuca paniculata</i> , <i>Nardus stricta</i> , <i>Meum athamanticum</i> , <i>Festuca nigrescens</i> , <i>Festuca violacea</i> , <i>Trifolium alpinum</i> , <i>Anthoxanthum odoratum</i> , <i>Vaccinium uliginosum</i> , <i>Carex sempervirens</i> , <i>Brachypodium rupestre</i>
3	2083	Dry subalpine to low-alpine meadows (on siliceous bedrocks)	<i>Festuca acuminata</i> , <i>Festuca laevigata</i> , <i>Juniperus sibirica</i> , <i>Sempervivum arachnoideum</i> , <i>Carex sempervirens</i> , <i>Helictotrichon parlatorei</i> , <i>Arctostaphylos uva-ursi</i> , <i>Festuca paniculata</i> , <i>Thymus praecox</i> , <i>Hieracium peleterianum</i>

Table 2. Cont.

Community	Mean Elevation	Description	Dominant Co-Occurring Species
4	2096	Subalpine heathlands	<i>Vaccinium myrtillus</i> , <i>Deschampsia flexuosa</i> , <i>Nardus stricta</i> , <i>Festuca paniculata</i> , <i>Carex sempervirens</i> , <i>Juniperus sibirica</i> , <i>Festuca nigrescens</i> , <i>Festuca violacea</i> , <i>Deschampsia flexuosa</i> , <i>Vaccinium uliginosum</i> , <i>Anthoxanthum odoratum</i>
5	2159	Prostrate alpine dwarf-shrub heaths	<i>Vaccinium uliginosum</i> , <i>Loiseleuria procumbens</i> , <i>Vaccinium myrtillus</i> , <i>Carex sempervirens</i> , <i>Nardus stricta</i> , <i>Rhododendron ferrugineum</i> , <i>Empetrum nigrum</i> , <i>Juniperus sibirica</i> , <i>Trifolium alpinum</i> , <i>Deschampsia flexuosa</i>
6	2178	Dry subalpine meadows (on non-siliceous bedrocks)	<i>Festuca laevigata</i> , <i>Sesleria caerulea</i> , <i>Helictotrichon sedenense</i> , <i>Helianthemum nummularium</i> , <i>Helictotrichon parlatoei</i> , <i>Festuca paniculata</i> , <i>Festuca violacea</i> , <i>Dryas octopetala</i> , <i>Alchemilla alpigena</i> , <i>Thymus praecox</i>
7	2338	Mesic to wet, subalpine to low-alpine pastures	<i>Plantago alpina</i> , <i>Nardus stricta</i> , <i>Festuca violacea</i> , <i>Festuca nigrescens</i> , <i>Salix herbacea</i> , <i>Trifolium thalii</i> , <i>Poa alpina</i> , <i>Leontodon pyrenaicus</i> , <i>Carex sempervirens</i> , <i>Polygonum viviparum</i>
8	2413	Mesic alpine meadows	<i>Carex curvula</i> , <i>Nardus stricta</i> , <i>Carex sempervirens</i> , <i>Gentiana alpina</i> , <i>Plantago alpina</i> , <i>Festuca halleri</i> , <i>Vaccinium uliginosum</i> , <i>Trifolium alpinum</i> , <i>Salix herbacea</i> , <i>Avenula versicolor</i>
9	2448	Alpine snowbed communities	<i>Salix herbacea</i> , <i>Alchemilla pentaphyllea</i> , <i>Plantago alpina</i> , <i>Omalotheca supina</i> , <i>Carex foetida</i> , <i>Nardus stricta</i> , <i>Luzula alpinopilosa</i> , <i>Alopecurus alpinus</i> , <i>Poa alpina</i> , <i>Sibbaldia procumbens</i>
10	2507	Alpine scree and open meadows	<i>Leucanthemopsis alpina</i> , <i>Cerastium pedunculatum</i> , <i>Saxifraga bryoides</i> , <i>Cacalia leucophylla</i> , <i>Luzula alpinopilosa</i> , <i>Doronicum grandiflorum</i> , <i>Cryptogramma crispa</i> , <i>Veronica alpina</i> , <i>Omalotheca supina</i> , <i>Oxyria digyna</i>
11	2528	Wind-blown, dry alpine meadows	<i>Kobresia myosuroides</i> , <i>Festuca halleri</i> , <i>Vaccinium uliginosum</i> , <i>Silene acaulis</i> , <i>Saxifraga bryoides</i> , <i>Juncus trifidus</i> , <i>Dryas octopetala</i> , <i>Carex curvula</i> , <i>Carex rupestris</i> , <i>Salix herbacea</i>
12	2701	Subnival scree vegetation	<i>Saxifraga bryoides</i> , <i>Leucanthemopsis alpina</i> , <i>Saxifraga oppositifolia</i> , <i>Silene acaulis</i> , <i>Oxyria digyna</i> , <i>Festuca halleri</i> , <i>Festuca violacea</i> , <i>Geum reptans</i>

5. Discussion

Our study proposes a simple method for estimating first snow free day from time series of multispectral imagery, which we validate for both high and moderate spatial resolution sensors with respect to ground measurements of snow melt-out date. We further demonstrate the ability of first snow free day and peak NDVI derived from high-resolution imagery to capture the floristic diversity of mountain plant communities located above the tree line. Although improving process-based models of snow accumulation and snowmelt in complex mountain terrain is an ongoing priority for snow scientists [64–66], and is necessary to forecast the effects of climate change on snow cover duration [21], simulating spatial heterogeneity of snowmelt in topographically complex study areas remains a difficult task [67,68]. Remote sensing thus represents a promising avenue for observing snow distribution patterns at regular intervals and over large spatial extents.

5.1. On the Importance of High-Resolution Time Series Imagery for Snow Cover Mapping

Optimized pre-processing routines are important to generate accurate output products in mountainous environments [69]. Taking these considerations into account, the SPOT-4/5 and Landsat-8 data pre-processed by CNES-Cesbio were made available with the choice of level 2A with surface reflectance correction (L2A-SRE), or with added slope correction to retrieve flat reflectance (L2A-FRE). The benefit of L2A-FRE processing is to ensure temporal consistency of surface reflectance values between SPOT-4/5 and Landsat-8 snow products. Furthermore, the SPOT (Take 5) Experiment generated Sentinel-2 proxy data by simulating high temporal (five-day) and spatial (10 m) resolution scene acquisition. These features are important given the spatial heterogeneity of snow cover duration widely observed in rugged terrain (Figures 2 and 5). For MODIS snow cover maps, the benefits of high temporal resolution for snow cover mapping were apparent in the form of low temporal uncertainty (Figures 6 and 7). Accuracy was somewhat lower as compared to SL imagery, however, due to the

relatively coarse spatial resolution of MODIS data, even after enhancement to 250 m resolution using the MODImLab process. Our results point to the importance of both high temporal and spatial resolution multispectral imagery for accurate monitoring of local-scale snow cover distribution and melting processes.

5.2. Perspectives on the Use of High-Resolution Imagery in Alpine Plant Ecology

Plant ecologists interested in modeling responses of alpine vegetation to environmental gradients require information on snow cover duration at the scale of observed turnover in plant communities, which typically occurs over distances <50 m in heterogeneous alpine environments (Figures 2 and 5) [29]. Figure 6A demonstrates the potential for high-resolution imagery to detect snow melt-out timing as determined by soil temperature for an alpine meadow community characteristic of topographically complex ridge crests, which is less accurately measured using moderate resolution imagery (MODIS). Although MODIS did not perform as well as high-resolution imagery, the enhanced snow cover product at 250 m resolution nonetheless showed strong agreement ground observations of snow melt-out (Figures 6 and 7). Our results thus support the use of MODIS, particularly for broad-scale phenological studies that take full advantage of the daily re-visit capacity, e.g., [70]. Finer studies of plant diversity patterns, however, would be better supported using snow cover information derived from high-resolution imagery.

For alpine ecologists, the new opportunities provided by high-resolution imagery are twofold. First, high-resolution data will increase our ability to carry out fine-scale mapping of high-elevation habitats over biogeographical scales. Previous attempts to map mountain habitats above the tree line have been fundamentally limited by the coarse resolution of source data [71]. Most importantly, there have been very few modeling studies accounting for snow cover dynamics in predicting spatial distribution of alpine plants and alpine communities, although see [72], which is rather surprising given that alpine plant ecologists have long recognized the pivotal role of snow cover for plant distribution [73]. In this study, we show that the first snow free day and the vegetation greenness during peak standing biomass provide a two-dimensional habitat template in which one can distinguish the dominant vegetation communities above the tree line. In particular, the effects of mesotopography, *i.e.*, elevation-independent topographic variability, on plant community composition are better captured when high spatial resolution data are used, as evidenced by the increased differentiation of snowbed communities (community 9) in Figure 10B. Ideally, a third axis consisting of exposure to mid-winter and spring frost events caused by frigid air temperatures and a shallow or absent snow pack would be used to further differentiate alpine plant community habitat. Field studies suggest that frost stress has a strong effect on alpine plant growth and community composition [23,74]. Acquiring this information from satellite imagery is challenging, however, due to shadows present in mid-winter imagery and also lack of information on snowpack height.

Second, high spatial and temporal resolution imagery will allow for testing of hypotheses relating plant diversity to ecosystem functioning at an unprecedented scale [75]. For example, time-integrated values of NDVI have been used as a surrogate for aboveground primary productivity in mountainous environments [27,76]. High-resolution data will enable relating these optically-derived proxies of ecosystem functioning to community-scale diversity metrics, whether taxonomic or functional. In addition, there will be new possibilities to investigate how inter-annual variability in snow cover duration cascades into ecosystem functioning and to what extent these dynamics are modulated by the plant composition of grasslands. Up to now, these relationships have been addressed with some disconnect between remote sensing and community ecology disciplines. We believe that the availability of high-resolution data may foster new lines of research in which plant community organization will be fully accounted for in diversity–climate relationships at regional or continental scales.

6. Conclusions

Through ground validation and comparison with moderate resolution products, our study demonstrates the utility of high-resolution time series imagery for mapping snow cover duration in alpine environments. In line with the objectives of the SPOT (Take 5) Experiment, our findings indicate the potential for data made available by the recently launched Sentinel-2 satellite to improve monitoring of snow cover dynamics and plant phenology in temperate alpine regions, which is an important task in the context of ongoing climate change. Specifically, we found that (i) high spatial resolution imagery improves estimates of local differences in snow melt-out induced by topographic heterogeneity; and (ii) that high temporal resolution remains essential in order to precisely detect snow melt-out timing and to capture peak productivity of alpine vegetation during the growing season. Regional-scale maps of the first snow free day and peak NDVI account for turnover in alpine plant communities in our study area and enable snow-vegetation studies at scales beyond what would be feasible using field measurements. The upcoming launch of new satellites (Sentinel-2B, Sentinel-3B *Venüs*) will continue to increase the availability of high spatial and temporal resolution multispectral imagery, which will improve the accuracy of time series studies dedicated to climate and ecological applications and allow for enhanced monitoring of snow and vegetation dynamics in mountain regions.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2072-4292/8/6/481/s1>, Table S1: List of satellite images available for 2013 and 2015.

Acknowledgments: The SPOT (Take 5) Experiments were proposed by CESBIO and implemented by CNES with the support of the European Space Agency. We are grateful to CNES for the selection of our *SPAMN* (SPOT-4) and *ECRINS* (SPOT-5) projects as test sites for the SPOT (Take 5) Experiments. Data were processed and delivered by CNES for the THEIA Land Data center and the authors wish to highly thank Olivier Hagolle from Cesium-CNES for the pre-processing of SPOT-4, SPOT-5 and Landsat-8 images and his reviewing of the image processing section of the paper. The MODIS Level-1B data were processed by the MODIS Adaptive Processing System (MODAPS) and the Goddard Distributed Active Archive Center (DAAC), which are archived and distributed by the Goddard DAAC. We thank the Météo France technical staff for maintaining instruments at the Col du Lac Blanc and in the Nivose network, and for handling data acquisition and storage. We thank Deborah Verfaillie (CNRM-GAME, CEN) for providing outputs of the S2M reanalysis. We thank Alexis Mikolajczak who assisted us in preparing vegetation plot data, and Cédric Dentant who provided data from the Ecrins National Park. We thank Jean-Paul Laurent for the monitoring of snow cover dynamics at the Lautaret pass in the framework of the FLUXALP project funded by the Labex OSUG@2020 (Investissements d'avenir—ANR10 LABX56). Thanks are also due to Vincent Thiérion from the National Institute for Environmental Science and Research (IRSTEA) for his technical help on the SPOT-4 part of the project, to Amélie Arnould for her contribution to the climate figures, and to Thomas Cavallo for his work on snow mapping with SPOT-4 images. Pascal Sirguey thanks the University of Otago, the Grenoble Institute of Technology (INP-Grenoble) and the University Grenoble-Alpes (UGA) for supporting his contribution to this work while on research and study leave in Grenoble. Finally, the authors thank the reviewers of this paper for their constructive comments on an earlier version of the manuscript. This research was conducted on the long-term research site Zone Atelier Alpes, a member of the ILTER-Europe network, and was supported by the Zone Atelier Alpes and by the Station Alpine J. Fourier (SAJF). The publication was funded by the Gestion et Impacts du Changements Climatique, Drôme: Eau, Climat Impacts liés aux Changements (GICC-DECLIC) program.

Author Contributions: Jean-Pierre Dedieu coordinated the *SPAMN* and *ECRINS* SPOT-Take 5 projects, supervised the paper, and was in charge of image processing and the snow mapping task. Bradley Z. Carlson carried out snow mapping, performed validation of snow cover maps, and analyzed plant communities with respect to available imagery. Sylvain Bigot was in charge of the climate data and analysis, and coordinated the GICC-DECLIC program. Pascal Sirguey developed the MODImLab toolbox and provided the expertise for processing of MODIS imagery. Philippe Choler provided data from soil temperature loggers, performed statistical analysis of vegetation data, and supervised the alpine ecology section of the paper. Vincent Vionnet provided data from snow height monitoring stations, analyzed data from the S2M reanalysis and assisted with the analysis of remote sensing and ground observations. The writing was led by Jean-Pierre Dedieu and Bradley Z. Carlson. All authors contributed to the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. PCC Report. *Working Group 1 Contribution to the IPCC Fifth Assessment Report, Climate Change 2013: The Physical Science Basis*; Cambridge University Press: Cambridge, UK, 2013; p. 1535.
2. Armstrong, R.L.; Brun, E. Snow and Climate. In *Physical Processes, Surface Energy Exchanges and Modeling*; Cambridge University Press: Cambridge, UK, 2010; p. 256.
3. Braun, L.; Weber, M.; Schütz, M. Consequences of climate change for runoff from Alpine regions. *Ann. Glaciol.* **2000**, *31*, 19–25. [[CrossRef](#)]
4. Seastedt, T.R.; Bowman, W.D.; Caine, T.N.; Mc Knight, D.; Townsend, A.; Williams, M.W. The landscape continuum: A model for high-elevation ecosystems. *Bioscience* **2004**, *54*, 111–121. [[CrossRef](#)]
5. EEA Report No 12/2012: *Climate Change, Impacts and Vulnerability in Europe*; European Environment Agency (EEA): Copenhagen, Denmark, 2012. [[CrossRef](#)]
6. Barnett, T.P.; Adam, J.C.; Lettenmaier, D.P. Potential impacts of warming climate on water availability in snow-dominated regions. *Nature* **2005**, *438*, 303–309. [[CrossRef](#)] [[PubMed](#)]
7. Beniston, M.; Uhlmann, B.; Goyette, S.; Lopez-Moreno, J. Will snow abundant winters still exist in the Swiss Alps in an enhanced greenhouse climate? *Int. J. Climatol.* **2010**, *31*, 1257–1263. [[CrossRef](#)]
8. Bavay, M.; Lehning, M.; Jonas, T.; Löwe, H. Simulations of future snow cover and discharge in Alpine headwater catchment. *Hydrol. Processes* **2009**, *23*, 95–108. [[CrossRef](#)]
9. Hantel, M.; Hirt-Wielke, L. Sensitivity of Alpine snow cover to European temperature. *Int. J. Climatol.* **2007**, *27*, 1265–1275. [[CrossRef](#)]
10. Gehrig-Fasel, J.; Guisan, A.; Zimmermann, N.E. Tree line shifts in the Swiss Alps: Climate change or land abandonment? *J. Veg. Sci.* **2007**, *18*, 571–582. [[CrossRef](#)]
11. Améztegui, A.; Brotons, L.; Coll, L. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Glob. Ecol. Biogeogr.* **2010**, *19*, 632–641.
12. Pauli, H.; Gottfried, M.; Dullinger, S.; Abdaladze, O.; Akhalkatsi, M.; Alonso, J.L.B.; Ghosn, D. Recent plant diversity changes on Europe's mountain summits. *Science* **2012**, *336*, 353–355. [[CrossRef](#)] [[PubMed](#)]
13. Hüsler, F.; Jonas, T.; Riffler, M.; Musial, J.P.; Wunderle, S. A satellite-based snow cover climatology (1985–2011) for the European Alps derived from AVHRR data. *Cryosphere* **2014**, *8*, 73–90. [[CrossRef](#)]
14. Brown, R.D. Northern Hemisphere snow cover variability and change. *J. Clim.* **2000**, *13*, 2339–2355. [[CrossRef](#)]
15. Lemke, P.; Ren, J.; Alley, R.B.; Allison, I.; Carrasco, J.; Flato, G.; Fujii, Y.; Kaser, G.; Mote, P.; Thomas, R.H.; et al. Observations changes in snow, ice and frozen ground. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge and New York University Press: New York, NY, USA, 2007; pp. 337–384.
16. Parajka, J.; Blösch, G. Validation of MODIS snow cover images over Austria. *Hydrol. Earth Syst. Sci.* **2006**, *10*, 679–689. [[CrossRef](#)]
17. Notarnicola, C.; Duguay, M.; Moelg, N.; Schellenberger, T.; Tetzlaff, A.; Monsoro, R.; Costa, A.; Steurer, C.; Zebisch, M. Snow Cover Maps from MODIS Images at 250 m Resolution, Part 1: Algorithm Description. *Remote Sens.* **2013**, *5*, 110–126. [[CrossRef](#)]
18. Beniston, M. Is snow in the Alps receding or disappearing? *WIREs Clim. Chang.* **2012**. [[CrossRef](#)]
19. Szczypta, C.; Gascoin, S.; Houet, T.; Hagolle, O.; Dejoux, J.F.; Vigneaux, C.; Fanise, P. Impact of climate and land cover changes on snow cover in a small Pyrenean catchment. *J. Hydrol.* **2015**, *521*, 84–99. [[CrossRef](#)]
20. Dedieu, J.P.; Lessard-Fontaine, A.; Ravazzani, G.; Cremonese, E.; Shalpykova, G.; Beniston, M. Shifting mountain snow patterns in a changing climate from remote sensing retrieval. *Sci. Total Environ. J.* **2014**, *493*, 1267–1279. [[CrossRef](#)] [[PubMed](#)]
21. Randin, C.F.; Dedieu, J.P.; Zappa, M.; Long, L.; Dullinger, S. Validation of and comparison between a semi distributed rainfall-runoff hydrological model (PREVAH) and a spatially distributed snow evolution model (SnowModel) for snow cover prediction in mountain ecosystems. *Ecohydrology* **2015**, *8*, 1181–1193. [[CrossRef](#)]
22. Körner, C. CO₂ exchange in the alpine sedge *Carex curvula* as influenced by canopy structure, light and temperature. *Oecologia* **1982**, *53*, 98–104. [[CrossRef](#)]
23. Choler, P. Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic. Antarct. Alp. Res.* **2005**, *37*, 444–453. [[CrossRef](#)]

24. Carlson, B.Z.; Choler, P.; Renaud, J.; Dedieu, J.P.; Thuiller, W. Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities. *Ann. Bot.* **2015**, *116*, 1023–1034. [[CrossRef](#)] [[PubMed](#)]
25. Fisk, M.C.; Schmidt, S.K.; Seastedt, T.R. Topographic patterns of above-and below ground production and nitrogen cycling in alpine tundra. *Ecology* **1998**, *79*, 2253–2266. [[CrossRef](#)]
26. Jonas, T.; Rixen, C.; Sturm, M.; Stoeckli, V. How alpine plant growth is linked to snow cover and climate variability. *J. Geophys. Res. Biogeosci.* **2008**, *113*, G03013. [[CrossRef](#)]
27. Choler, P. Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. *Biogeosciences* **2015**, *12*, 3885–3897. [[CrossRef](#)]
28. Freppaz, M.; Williams, B.L.; Edwards, A.C.; Scalenghe, R.; Zanini, E. Simulating soil freeze/thaw cycles typical of winter alpine conditions: Implications for N and P availability. *Appl. Soil Ecol.* **2007**, *35*, 247–255. [[CrossRef](#)]
29. Billings, W.D. Arctic and alpine vegetations: Similarities, differences, and susceptibility to disturbance. *BioScience* **1973**, *23*, 697–704. [[CrossRef](#)]
30. Scherrer, D.; Körner, C. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J. Biogeogr.* **2011**, *38*, 406–416. [[CrossRef](#)]
31. Carlson, B.Z.; Randin, C.F.; Boulangeat, I.; Lavergne, S.; Thuiller, W.; Choler, P. Working toward integrated models of alpine plant distribution. *Alp. Bot.* **2013**, *123*, 41–53. [[CrossRef](#)] [[PubMed](#)]
32. Klein, A.G.; Barnett, A.C. Validation of daily MODIS snow cover maps of the Upper Rio Grande River Basin for the 2000–2001 snow year. *Remote Sens. Environ.* **2003**, *86*, 162–176. [[CrossRef](#)]
33. Fontana, F.; Rixen, C.; Jonas, T.; Aberegg, G.; Wunderle, S. Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series—a comparison with *in situ* measurements. *Sensors* **2008**, *8*, 2833–2853. [[CrossRef](#)]
34. Molotch, N.P.; Margulis, S.A. Estimating the distribution of snow water equivalent remotely sensed snow cover data and a spatially distributed snowmelt model: A multi-resolution, multi-sensors comparison. *Adv. Water Resour.* **2008**, *31*, 1503–1514. [[CrossRef](#)]
35. Hagolle, O.; Sylvander, S.; Huc, M.; Claverie, M.; Clesse, D.; Dechoz, C.; Lonjou, V.; Poulain, V. SPOT-4 (Take 5): Simulation of Sentinel-2 Time Series on 45 Large Sites. *Remote Sens.* **2015**, *7*, 12242–12264. [[CrossRef](#)]
36. Bonet, R.; Arnaud, F.; Bodin, X.; Bouche, M.; Boulangeat, I.; Bourdeau, P.; Bouvier, M.; Cavalli, L.; Choler, P.; Delestrade, A.; *et al.* Indicators of climate: Ecrins National Park participates in long-term monitoring to help determine the effects of climate change. *Ecol. Mont-J. Prot. Mount. Areas Res.* **2016**, *8*, 44–52. [[CrossRef](#)]
37. Wiscombe, W.J.; Warren, S.G. A model for the spectral albedo of snow. I—Pure snow. *J. Atmos. Sci.* **1980**, *37*, 2712–2733. [[CrossRef](#)]
38. Dozier, J.; Painter, T. Multispectral and hyperspectral remote sensing of alpine snow properties. *Annu. Rev. Earth Planet Sci.* **2004**, *32*, 465–494. [[CrossRef](#)]
39. Rees, W.G. *Remote Sensing of Snow and Ice*; Taylor & Francis, CRC Press Book: Cambridge, UK, 2006; p. 285.
40. Riano, D.; Chuvieco, E.; Salas, J.; Aguado, I. Assessment of different topographic corrections in Landsat-TM data for mapping vegetation types. *IEEE Trans. Geosci. Rem. Sens.* **2003**, *41*, 1056–1061. [[CrossRef](#)]
41. Menzel, A.; Sparks, T.H.; Estrella, N.; Aasa, A.; Ahas, R.; Alm-Kübler, K.; Bissolli, P.; Braslavská, O.; Briede, A.; Chmielewski, F.; *et al.* European phenological response to climate change matches the warming pattern. *Glob. Chang. Biol.* **2006**, *12*, 1969–1976. [[CrossRef](#)]
42. Durand, Y.; Giraud, G.; Laternser, M.; Etchevers, P.; Mérindol, L.; Lesaffre, B. Reanalysis of 47 years of climate in the French Alps (1958–2005): Climatology and trends for snow cover. *J. Appl. Meteorol. Climatol.* **2009**, *48*, 2487–2512. [[CrossRef](#)]
43. Auer, I.; Böhm, R. HISTALP—Historical instrumental climatological surface time series of the Greater Alpine Region. *Int. J. Climatol.* **2007**, *27*, 17–46. [[CrossRef](#)]
44. Durand, Y.; Laternser, M.; Giraud, G.; Etchevers, P.; Lesaffre, B.; Mérindol, L. Reanalysis of 44 years of climate in the French Alps (1958–2002): Methodology, model validation, climatology, and trends for air temperature and precipitation. *J. Appl. Meteorol. Climatol.* **2009**, *48*, 429–449. [[CrossRef](#)]
45. Gobiet, A.; Kotlarsky, S.; Beniston, M.; Heinrich, G.; Rajczak, J.; Stoffel, M. 21st century climate change in the European Alps—A review. *Sci. Total Environ.* **2014**, *493*, 1138–1151. [[CrossRef](#)] [[PubMed](#)]

46. Vionnet, V.; Brun, E.; Morin, S.; Boone, A.; Faroux, S.; Le Moigne, P.; Martin, E.; Willemet, J.M. The detailed snowpack scheme Crocus and its implementation in SURFEX v7.2. *Geosci. Model Dev.* **2012**, *5*, 773–791. [[CrossRef](#)]
47. Hagolle, O.; Huc, M.; Villa Pascual, D.; Dedieu, G. A multi-temporal and multispectral method to estimate aerosol optical thickness over land, for the atmospheric correction of FormoSat-2, Venus and Sentinel-2 images. *Remote Sens.* **2015**, *7*, 2668–2691. [[CrossRef](#)]
48. Dymond, J.R.; Shepherd, J.D. Correction of the topographic effect in remote sensing. *IEEE Trans. Geosci. Remote Sens.* **1999**, *37*, 2618–2620. [[CrossRef](#)]
49. Shepherd, J.D.; Dymond, J.R. Correcting satellite imagery for the variance of reflectance and illumination with topography. *Int. J. Remote Sens.* **2003**, *24*, 3503–3514. [[CrossRef](#)]
50. Hall, D.K.; Riggs, G.; Salomonson, V.; Di Girolamo, N.; Bayr, K. Modis snow-cover products. *Remote Sens. Environ.* **2002**, *83*, 181–194. [[CrossRef](#)]
51. Hall, D.K.; Riggs, G. Accuracy assessment of the MODIS snow-cover products. *Hydrol. Process.* **2007**, *21*, 1534–1547. [[CrossRef](#)]
52. Sirguey, P.; Mathieu, R.; Arnaud, Y. Subpixel monitoring of the seasonal snow cover with MODIS at 250 m spatial resolution in the Southern Alps of New Zealand: Methodology and accuracy assessment. *Remote Sens. Environ.* **2009**, *113*, 160–181. [[CrossRef](#)]
53. Dumont, M.; Gardelle, J.; Sirguey, P.; Guillot, A.; Six, D.; Rabatel, A.; Arnaud, Y. Linking glacier annual mass balance and glacier albedo retrieved from MODIS data. *Cryosphere* **2012**, *6*, 1527–1539. [[CrossRef](#)]
54. Mary, A.; Dumont, M.; Dedieu, J.P.; Durand, Y.; Sirguey, P.; Milhem, H.; Mestre, O.; Negi, H.S.; Kokhanovsky, A.A.; Lafaysse, M.; *et al.* Intercomparison of retrieval algorithms for the specific surface area of snow from near-infrared satellite data in mountainous terrain, and comparison with the output of a semi-distributed snowpack model. *Cryosphere* **2013**, *7*, 741–761. [[CrossRef](#)]
55. Sirguey, P.; Mathieu, R.; Arnaud, Y.; Khan, M.; Chanussot, J. Improving MODIS spatial resolution for snow mapping using wavelet fusion and ARSIS concept. *IEEE Geosci. Remote Sens. Lett.* **2008**, *5*, 78–82. [[CrossRef](#)]
56. Dozier, J. Spectral signature of alpine snow cover from the Landsat Thematic Mapper. *Remote Sens. Environ.* **1989**, *28*, 9–22. [[CrossRef](#)]
57. Ackerman, S.; Strabala, K.; Menzel, W.; Frey, R.; Moeller, C.; Gumley, L. Discriminating clear sky from clouds with MODIS. *J. Geophys. Res.* **1998**, *103*, 32141–32157. [[CrossRef](#)]
58. Levin, N.; Shmida, A.; Levanoni, O.; Tamari, H.; Kark, S. Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. *Divers. Distrib.* **2007**, *13*, 692–703. [[CrossRef](#)]
59. Kaufman, L.; Rousseeuw, P.J. *Finding Groups in Data: An Introduction to Cluster Analysis*; John Wiley & Sons: Hoboken, NJ, USA, 2009; p. 368.
60. Maechler, M.; Rousseeuw, P.; Struyf, A.; Hubert, M.; Hornik, K. Cluster: Cluster Analysis Basics and Extensions. *R Package Vers.* **2014**, *2*, 56.
61. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2015.
62. Choler, P.; Michalet, R. Niche differentiation and distribution of *Carex curvula* along a bioclimatic gradient in the southwestern Alps. *J. Veg. Sci.* **2002**, *13*, 851–858. [[CrossRef](#)]
63. Warton, D.I.; Duursma, R.A.; Falster, D.S.; Taskinen, S. Smatr 3—An R package for estimation and inference about allometric lines. *Methods Ecol. Evol.* **2012**, *3*, 257–259. [[CrossRef](#)]
64. Mott, R.; Schirmer, M.; Bavay, M.; Grünwald, T.; Lehning, M. Understanding snow-transport processes shaping the mountain snow-cover. *Cryosphere* **2010**, *4*, 545–559. [[CrossRef](#)]
65. Winstral, A.; Marks, D.; Gurney, R. Simulating wind-affected snow accumulations at catchment to basin scales. *Adv. Water Resour.* **2013**, *55*, 64–79. [[CrossRef](#)]
66. Vionnet, V.; Martin, E.; Masson, V.; Guyomarc'h, G.; Bouvet, F.N.; Prokop, A.; Lac, C. Simulation of wind-induced snow transport and sublimation in alpine terrain using a fully coupled snowpack/atmosphere model. *Cryosphere* **2014**, *8*, 395–415. [[CrossRef](#)]
67. Egli, L.; Jonas, T.; Grünwald, T.; Schirmer, M.; Burlando, P. Dynamics of snow ablation in a small Alpine catchment observed by repeated terrestrial laser scans. *Hydrol. Process.* **2012**, *26*, 1574–1585. [[CrossRef](#)]
68. Revuelto, J.; Vionnet, V.; López-Moreno, J.I.; Lafaysse, M.; Morin, S. Combining snowpack modeling and terrestrial laser scanner observations improves the simulation of small scale snow dynamics. *J. Hydrol.* **2016**, *533*, 291–307. [[CrossRef](#)]

69. Teillet, P.M.; Guindon, B.; Goodeonugh, D.G. On the slope aspect correction of multispectral scanner data. *Can. J. Remote Sens.* **1982**, *8*, 84–106. [[CrossRef](#)]
70. Li, Z.; Yu, G.; Xiao, X.; Li, Y.; Zhao, X.; Ren, C.; Fu, Y. Modeling gross primary production of alpine ecosystems in the Tibetan Plateau using MODIS images and climate data. *Remote Sens. Environ.* **2007**, *107*, 510–519. [[CrossRef](#)]
71. Mùcher, C.A.; Klijn, J.A.; Wascher, D.M.; Schaminée, J.H. A new European Landscape Classification (LANMAP): A transparent, flexible and user-oriented methodology to distinguish landscapes. *Ecol. Ind.* **2010**, *10*, 87–103. [[CrossRef](#)]
72. Randin, C.F.; Vuissoz, G.; Liston, G.E.; Vittoz, P.; Guisan, A. Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the Western Swiss Alps. *Arctic. Antarct. Alp. Res.* **2009**, *41*, 347–361. [[CrossRef](#)]
73. Walker, D.A.; Halfpenny, J.C.; Walker, M.D.; Wessman, C.A. Long-term studies of snow-vegetation interactions. *BioScience* **1993**, *43*, 287–301. [[CrossRef](#)]
74. Wipf, S.; Stoeckli, V.; Bebi, P. Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Clim. Chang.* **2009**, *94*, 105–121. [[CrossRef](#)]
75. Violle, C.; Reich, P.B.; Pacala, S.W.; Enquist, B.J.; Kattge, J. The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 13690–13696. [[CrossRef](#)] [[PubMed](#)]
76. Rossini, M.; Cogliati, S.; Meroni, M.; Migliavacca, M.; Galvagno, M.; Busetto, L.; Cremonese, E.; Julitta, T.; Siniscalco, C.; di Cella, U.M.; *et al.* Remote sensing-based estimation of gross primary production in a subalpine grassland. *Biogeosciences* **2012**, *9*, 2565–2584. [[CrossRef](#)]



© 2016 by the authors; licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC-BY) license (<http://creativecommons.org/licenses/by/4.0/>).

Chapter IIB

*Habitat mapping of alpine snowbed and wind-blown
alpine meadows using multi-temporal satellite
imagery**

* **Carlson, B. Z.**, & Choler, P. Habitat mapping of alpine plant communities using multi-temporal satellite imagery. (**Unpublished manuscript**).

Introduction

Generating detailed and reliable habitat maps is an important task for conservation and land management. Available habitat schemes at the European-scale typically integrate static maps of geologic substrate, soil, topography, climate, vegetation and land cover to create classifications of broad habitat categories (e.g. Múcher *et al.* 2009; Múcher *et al.* 2010). In continental-scale mapping initiatives, alpine environments are often represented as a handful of classes, e.g. grassland, bare ground and glacier. Phenology metrics derived from multi-temporal remote sensing have been identified as important indicators of habitat distribution and applied for land cover mapping in the context of smaller study areas (e.g. Lucas *et al.* 2007), however the integration of multi-temporal imagery significantly increases the amount of time and effort for data processing. A recent study focused on mapping alpine plant community habitat made use of topographic proxies of snow cover duration, energy availability and temperature using a digital elevation model, while acknowledging the importance of integrating vegetation indices and snow cover dynamics in order to improve habitat models and differentiate the spatial distribution of alpine plant communities (Mikolajczak *et al.* 2015). Additionally, frost events have been identified as an important form of stress influencing alpine plant growth and distribution (Inouye 2008; Wheeler *et al.* 2014; Wipf *et al.* 2009), however this parameter has to the best of our knowledge not been incorporated as a predictive variable in habitat mapping studies.

In order to build on the two-dimensional habitat template based on first snow free day and peak NDVI proposed in Chapter IIA (Dedieu *et al.* 2016), two additional steps were taken here: i) time series were completed with images from the late fall and early winter in order to estimate the total duration of the snow free period (as opposed to only snow-melt out date); and ii) combining daily air temperature and snow cover data in order to estimate the occurrence of frost events between the beginning of March and the end of June.

Methods

The return of snow cover in the fall/early winter was estimated using the same approach as for the first snow free, i.e. the median date between the last snow-free observation and the first

snow-covered observation, based on the NDSI threshold of 0.4. The occurrence of frost events was estimated by summing the number of days with daily mean air temperature below 0°C and no snow cover. Air temperature values for 300 m elevation classes were derived from the SAFRAN meteorological model for the Oisans massif and provided by Météo France (Durand *et al.* 2009). The end of June was used as a cut-off date given that SAFRAN numerical simulations were unavailable at the time of this work after July 31, 2015, and also based on empirical work demonstrating that fully developed leaf tissues are more resistant to freezing events than developing tissues, and accordingly mid to late-summer episodes of freezing are less likely to affect plant growth and performance.

For the year 2015, we differentiated the twelve plant communities presented in Chapter IIA based on the total duration of snow free period (SFP), peak NDVI (NDVI_{max}) and the occurrence of frost events. We also calibrated simple habitat models, in this case generalized additive models in order to account for non-linear relationships (GAM; Wood 2006), in an attempt to differentiate the habitat of thermal alpine meadows from alpine snowbed communities. Utilized explanatory variables included: (1) the length of SFP, (2) NDVI_{max} , (3) the number of frost events and (4) the reflectance value of the green band from a SPOT-5 image acquired in early July, 2015. Other remote sensing studies have confirmed that the green band is more sensitive to chlorophyll content and the proportion of fresh biomass than the red, which is used for the estimation of photosynthetically active light absorption in the calculation of NDVI (Gitelson *et al.* 1996). Based on knowledge of the system and previous work on ridge-crest and snowbed communities (Björk and Molau 2007; Baptist and Choler 2008; Choler 2005), we expected the presence of snowbed communities to respond to long-lasting snow cover duration, rare occurrence of frost events and increasing probability of presence with increased reflectance in the green band. For thermal alpine meadows, we anticipated a longer snow free period, increasing probability of presence as the number of frost events increased and low probability of presence at high levels of reflectance in the green band. Spatial predictions are shown here only for snowbed communities. Continuous probability values were converted to a binary map of snowbed community presence/absence using an optimized threshold of the True Skill Statistic (Allouche *et al.* 2006).

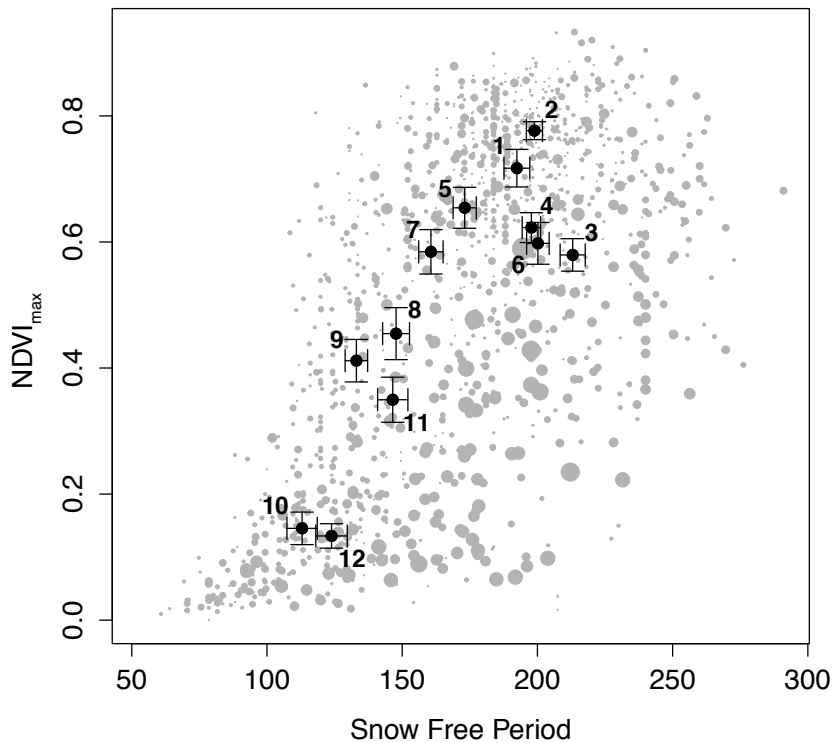


Figure 1. Vegetation plots (N=1272) plotted relative to length of the snow free period (days) and peak NDVI ($NDVI_{max}$) for 2015. Size of grey points is proportional to the occurrence of frost events. Black points and error bars represent the mean position with 95% confidence intervals of the twelve plant communities presented in Chapter 2A.

Preliminary results

In Figure 1, it is apparent that for a given length of snow free period, the highest values of $NDVI_{max}$ generally occur among vegetation plots exposed to the least number of frost events. This finding is congruent with our expectations as well as with observational studies demonstrating that frost events reduce plant performance in alpine environments by damaging leaf tissue (Gerdol *et al.* 2013; Inouye 2008). Quantifying frost occurrence provided a third axis with which to differentiate the high-elevation plant communities introduced in Chapter IIA. We can now state that community 3 (dry subalpine to low-alpine meadows on siliceous bed rock), which experienced the longest average snow free period of all studied plant communities in 2015, likely exhibited a lower $NDVI_{max}$ than communities 1 (subalpine heath and tall herb) and 2 (subalpine grassland and pasture) due to increased exposure to frost stress. Additionally, the higher $NDVI_{max}$ of community 9 (snowbed) relative to community 11 (alpine dry meadow) despite the shorter experienced growing season, can be attributed to increased frost exposure of ridge-crest alpine meadows. The additional information on frost exposure allows us to explain

some of the deviation from the overall positive relationship observed between snow free period and NDVI_{max} , i.e. residual variation in NDVI_{max} for a given level of snow free period can be attributed in part to varying degrees of frost stress. While these patterns have already been observed and documented in the literature, the key contribution here is to quantify spatial variation in fine-scale drivers such as frost events using a remote sensing approach, allowing for analysis of numerous vegetation plots at the regional scale.

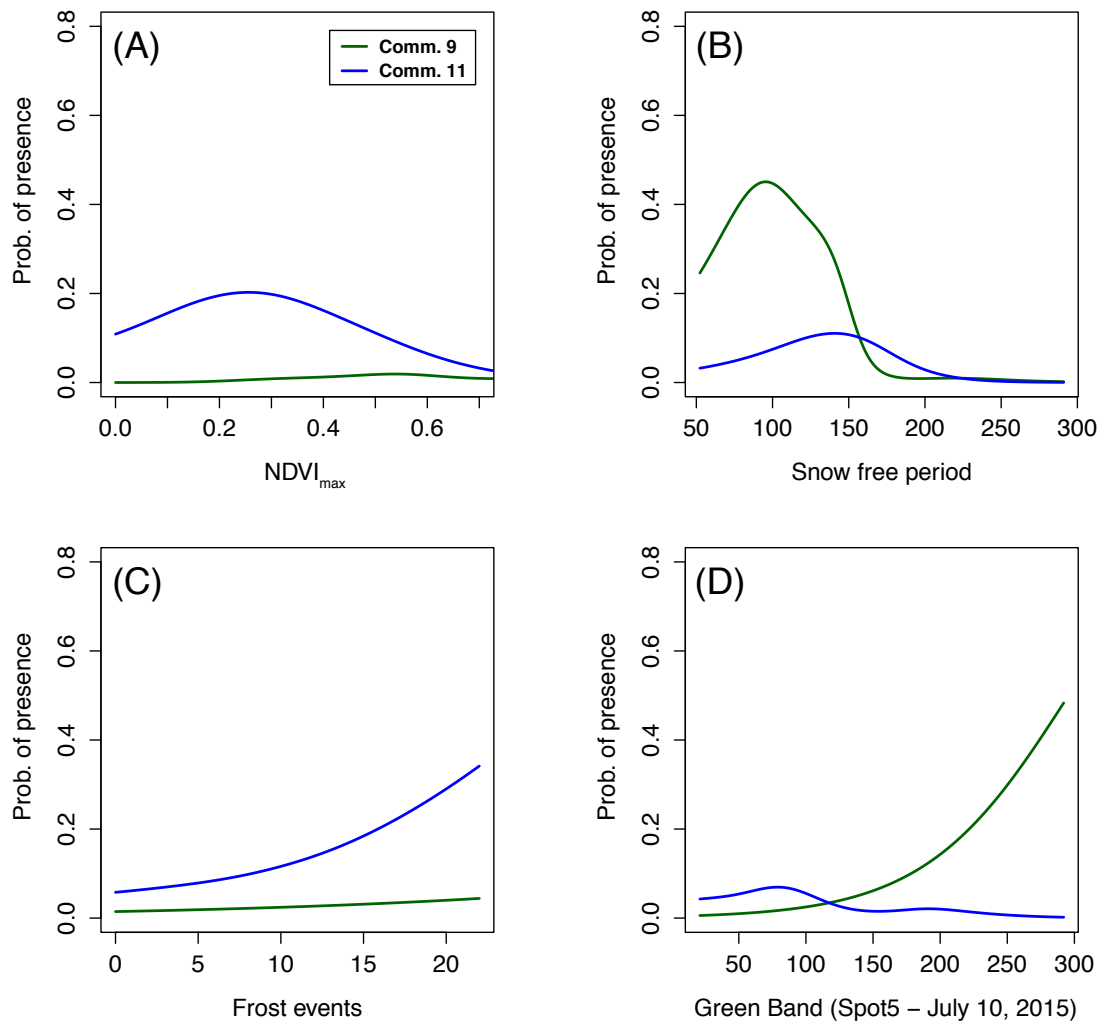
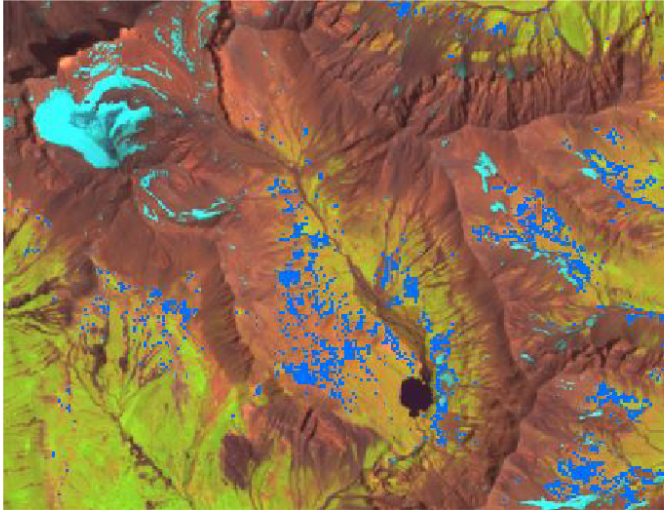


Figure 2. Generalized additive model (GAM) response curves for snowbed (Community 9) and wind-blown dry alpine meadow (Community 11) communities presented in Chapter 2A. Explanatory variables quantified for the year 2015 include (A) peak NDVI (NDVI_{max}), (B) the length of snow free period (days), (C) the occurrence of frost events and (D) the green band of a mid-summer SPOT-5 image representing the proportion of green biomass. Response curves were calculated by running the fitted model using fixed median values of non-focal explanatory values and a regular sequence from min. to max. of the focal explanatory variable.

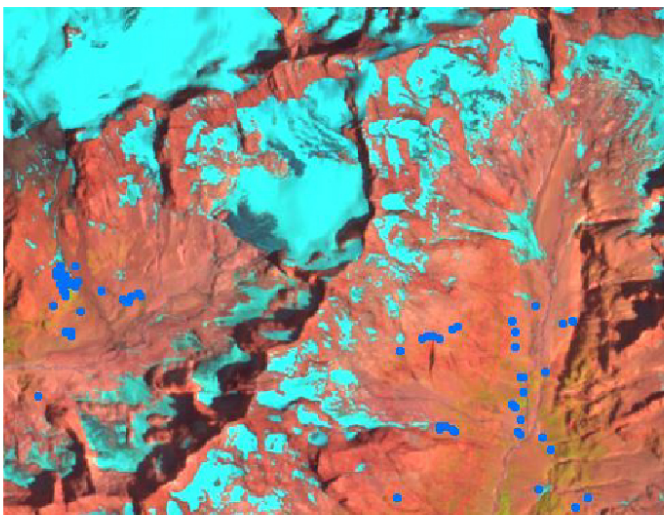
The next step was to establish statistical links between remote sensing-derived predictors and the observed spatial distributions of alpine plant communities. We attempted this exercise for communities 9 and 11 in particular, given that i) complex habitat mosaics formed by alpine snowbed and wind-blown alpine meadows cannot be differentiated along a simple elevation gradient and ii) these emblematic communities represent an important challenge for habitat modeling and conservation efforts in alpine environments. There is particular incentive to use direct variables in this context, i.e. snow free period rather than topographic proxies derived from a digital elevation model, given that topography-derived environmental indicators are static and have limited utility for monitoring programs seeking to understand vegetation responses to climatic trends and variability.

Our application of GAMs to predict the probability of presence of snowbed and wind-blown alpine meadow communities yielded promising initial results (Figure 2), showing response curves that were largely consistent with expectations. The probability of presence of snowbed communities responded strongly to snow free periods close to 100 days, whereas the peak for wind-blown meadows was situated around 140 days (Figure 2B). This difference of over a month in snow cover duration for adjacent habitats is consistent with field observations (Choler 2005). Snowbed communities showed no response to the occurrence of frost events (Figure 2C), which was somewhat surprising given the expectation of increased probability of presence at values close to 0. The probability of presence of wind-blown meadows, however, steadily increased with the number of frost events. Snowbed communities in particular also demonstrated a strong positive response to increased reflectance in the green band (Figure 2D). $NDVI_{max}$ turned out to be a poor predictor of snowbed and wind-blown meadow presence (Figure 2A), which could be attributed to the fact that $NDVI_{max}$ tended to differentiate communities along an overall elevation gradient but not necessarily along contrasting mesotopographic contexts (Figure 1). Given that NDVI is known to be relatively insensitive to the ratio of fresh vs. senescent biomass (Gittelsohn *et al.* 1996), it is possible that $NDVI_{green}$ (calculated using the green rather than red band) would better differentiate snowbed and wind-blown meadow communities, and would also reduce the number of explanatory variables considered.

(A)



(B)



0 1 km

Figure 3. Example GAM outputs of predicted snowbed community presence in the Ecrins National Park, indicated in dark blue, in (A) the Goléon valley above La Grave and (B) the Selle and Etançons valleys above la Bérarde. The scale bar is approximate.

Spatial projections of predicted snowbed presence were highly fragmented and occurred in small patches reminiscent of snowbed habitat distribution patterns observed in the field (personal observation; Figure 3). Validation is necessary, however, in order to verify whether or not model predictions in areas without vegetation plots correspond to actual zones of snowbed vegetation. It is also important to point out that botanists describe several different types of snowbed communities, including nival vegetation occurring on slopes without a pronounced topographic depression, and that inclusion of more vegetation plots over broader spatial scale would allow for more precise modeling of different snowbed communities. More generally, there

appears to be strong potential to combine field-based monitoring of snowbed vegetation with remote sensing observations in the context of a project recently launched by the Conservatoire Botanique National Alpin (CBNA) with the aim of monitoring responses of snowbed communities to climate change. The preliminary findings presented here should be viewed as a “proof-of-concept” prior to a more thorough analysis to be undertaken at the scale of the French Alps, ideally using newly available Sentinel-2 imagery.

References

- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology*, 43(6), 1223-1232.
- Baptist, F., & Choler, P. (2008). A simulation of the importance of length of growing season and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Annals of Botany*, 101(4), 549-559.
- Björk, R. G., & Molau, U. (2007). Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research*, 39(1), 34-43.
- Choler, P. (2005). Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research*, 37(4), 444-453.
- Dedieu, J. P., Carlson, B. Z., Bigot, S., Sirguey, P., Vionnet, V., & Choler, P. (2016). On the Importance of High-Resolution Time Series of Optical Imagery for Quantifying the Effects of Snow Cover Duration on Alpine Plant Habitat. *Remote Sensing*, 8(6), 481.
- Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B., & Mérindol, L. (2009). Reanalysis of 44 Yr of climate in the French Alps (1958-2002): methodology, model validation, climatology, and trends for air temperature and precipitation. *Journal of Applied Meteorology and Climatology*, 48(3), 429-449.
- Gerdol, R., Siffi, C., Iacumin, P., Gualmini, M., & Tomaselli, M. (2013). Advanced snowmelt affects vegetative growth and sexual reproduction of *Vaccinium myrtillus* in a sub-alpine heath. *Journal of Vegetation Science*, 24(3), 569-579.
- Gitelson, A. A., Kaufman, Y. J., & Merzlyak, M. N. (1996). Use of a green channel in remote sensing of global vegetation from EOS-MODIS. *Remote Sensing of Environment*, 58(3), 289-298.
- Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89(2), 353-362.

- Lucas, R., Rowlands, A., Brown, A., Keyworth, S., & Bunting, P. (2007). Rule-based classification of multi-temporal satellite imagery for habitat and agricultural land cover mapping. *ISPRS Journal of Photogrammetry and Remote Sensing*, 62(3), 165-185.
- Mikolajczak, A., Maréchal, D., Sanz, T., Isenmann, M., Thierion, V., & Luque, S. (2015). Modelling spatial distributions of alpine vegetation: A graph theory approach to delineate ecologically-consistent species assemblages. *Ecological Informatics*, 30, 196-202.
- Mucher, C. A., S. M. Hennekens, R. G. H. Bunce, J. H. J. Schaminee, and M. E. Schaepman. 2009. Modelling the spatial distribution of Natura 2000 habitats across Europe. *Landscape and Urban Planning* 92:148-159.
- Mücher, C. A., J. A. Klijn, D. M. Wascher, and J. H. J. Schaminée. 2010. A new European Landscape Classification (LANMAP): A transparent, flexible and user-oriented methodology to distinguish landscapes. *Ecological Indicators* 10:87-103.
- Nagendra, H., R. Lucas, J. P. Honrado, R. H. G. Jongman, C. Tarantino, M. Adamo, and P. Mairota. 2013. Remote sensing for conservation monitoring: Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecological Indicators* 33:45-59.
- Sakai, A., & Larcher, W. (2012). *Frost survival of plants: responses and adaptation to freezing stress* (Vol. 62). Springer Science & Business Media.
- Wheeler, J. A., Hoch, G., Cortés, A. J., Sedlacek, J., Wipf, S., & Rixen, C. (2014). Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia*, 175(1), 219-229.
- Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic change*, 94(1-2), 105-121.
- Wood, S. (2006). *Generalized additive models: an introduction with R*. CRC press.

Chapter IIC

*Linking functional diversity to productivity responses of alpine plant communities for three contrasting growing seasons (2013-2015)**

* **Carlson, B. Z.**, Thuiller, W. & Choler, P. Linking functional diversity to productivity responses of alpine plant communities for three contrasting growing seasons (2013-2015). (**Unpublished manuscript**).

Introduction

Understanding relationships between biodiversity and ecosystem functioning constitutes one of the most important ongoing fields of investigation in ecological research (Hooper *et al.* 2005). Experimental work has demonstrated significant effects of plant species richness on biomass (Tilman *et al.*, 2001), and more recent work has shown that in addition to species richness, multiple facets of biodiversity (including functional and phylogenetic diversity) correlate positively with plant productivity (Cadotte *et al.*, 2008). Particular emphasis has been placed recently on the promise of quantitative plant functional traits, defined as morphological, phenological or physiological features affecting plant performance, for predicting the impacts of global change on ecosystem functioning (Violle *et al.*, 2014). Quantifying plant diversity using the “common currency” of functional traits allows for both i) quantifying functional responses of plant communities along environmental gradients and ii) quantifying the effects of plant community traits, i.e. height and leaf area, on facets of ecosystem functioning such as aboveground biomass. In this simplified framework, a change in environmental conditions would enable predicting changes in plant community composition and trait values, and a change in plant trait values would enable predicting primary productivity (Díaz *et al.* 2007).

In parallel to recent advances in functional ecology, the remote sensing community has developed routines for generating spatially and temporally continuous estimates of gross primary productivity at the global scale (Running *et al.*, 2004). While more complex models accounting for incident solar radiation, temperature and moisture exist (Veroustraete, Sabbe & Eerens, 2002), the most straightforward approach to estimating annual aboveground productivity is to sum NDVI values observed at regular time intervals over the course of the growing season (e.g. Choler 2015). Field-measures of plant biomass are time consuming and by necessity limit spatial extent to local-scale studies areas, which can be frustrating in areas such as the French Alps where vegetation plots are widespread and numerous. Multi-temporal satellite imagery allows for spatially continuous estimates of primary productivity and provides the opportunity to assess biodiversity ecosystem function relationships at unprecedented scales. Although such an approach has been proposed in the literature (Violle *et al.* 2014), so far surprisingly little attention has been dedicated to exploring links between plant functional diversity and remote sensing-derived proxies of primary productivity.

The aim of this section is to explore productivity responses of high-elevation plant communities to inter-annual variability in snow cover duration. Given that we are studying three successive years (2013, 2014 and 2015), it can be assumed that changes in plant community composition between years were minimal. Accordingly, we can ask to what extent can the same plant canopies make use of highly contrasting growing season lengths, and also are productivity responses mediated by plant functional traits, namely height and specific leaf area? And lastly, does the occurrence of frost events reduce the capacity of plant communities to produce more biomass given a longer growing season? The same study area, vegetation plots and plant communities presented earlier in this chapter will be used for analysis, as well as estimates of plot-level functional traits and additional imagery for the years 2013 and 2014. Extending NDVI analysis through the fall and until the return of snow seemed particularly pertinent here given that autumn phenology has been identified as having a strong effect on inter-annual productivity (Choler 2015; Garonna *et al.* 2014). The three objectives of this section are to: (1) to place the 2013-2015 growing seasons in the context of the last 15 years; (2) to quantify NDVI responses of high-elevation plant communities for the three years; and (3) to explore relationships between variance in snow cover duration, frost stress, functional diversity and response capacity (in terms of productivity) of alpine plant communities.

Methods

Trait values for height, specific leaf area and leaf nitrogen content were assigned to species present in the study area using the TEEMBIO trait database. Species-trait and species-abundance tables for vegetation plots (N=1272) were combined to calculate community-weighted mean (CWM) and community-weighted variance (CWV) trait values for each community using an abundance threshold of 0.6 (i.e. if trait values were missing for species accounting for more than 40% of relative cover in a given community than the community trait value was set to no-data). Formulae for CWM and CWV calculation based on Garnier *et al.* (2004) are provided in the general introduction.

MODIS surface reflectance products covering the study area were downloaded for years between 2000 and 2015 from the Land Processes Distributed Active Archive Center (LP DAAC;

<http://e4ftl01.cr.usgs.gov/MOLT/>). Data consisted of composite reflectance, i.e. representing the highest cloud-free observed value over an 8-day period. Surface reflectance in the Red and Near-Infrared (NIR) were used to calculate NDVI at 250 m ground resolution. NDVI time series were used to estimate the start of the growing season ($\text{NDVI} > 0.1$), the peak (maximum NDVI) and the end of the growing season ($\text{NDVI} < 0.1$) for each vegetation plot. MODIS data and derived products were provided by P. Choler.

High-resolution images of varying spatial resolution (SPOT and Landsat) for the years 2013, 2014 and 2015 were resampled to the same 25 m grid (as in Dedieu *et al.* 2016) and were utilized to assess productivity responses of plant communities. Scene acquisition dates for the 73 analyzed images are provided in Figure 4. Due to the irregular time intervals between SPOT and Landsat images, in order to allow for comparison across years and among plant communities it was necessary to apply a smoothing algorithm. Observed NDVI values and associated image acquisition dates were extracted for 25 m grid cells corresponding to each plant community, and subsequently a loess regression was fitted between NDVI and date. Estimated model parameters were then used to predict NDVI values at a daily time interval, and snow-free values (when $\text{NDSI} < 0.4$) were retained for estimating the sum of growing season NDVI ($\text{NDVI}_{\text{int.}}$). The length of snow free period (nb. of days with $\text{NDSI} < 0.4$) and the occurrence of frost events (nb. of days between March and end of June with $\text{NDSI} < 0.4$ and air temperature $< 0^{\circ}\text{C}$) were estimated for all three years using the same approach described in the previous section. Finally, mean and variance of snow free period, $\text{NDVI}_{\text{int.}}$ and frost were calculated for each vegetation plot based on the three years of observations. In order to visualize NDVI responses for the twelve plant communities presented in Chapter IIA and for the three years, we also calculated the mean daily NDVI for each plant community and for each year.

Path analysis was carried out using the *lavaan* R package, with the goal of assessing causal relationships among observed variables (Grace *et al.* 2010). Hypothesized direct or indirect relationships between variables were assumed to be linear and acyclic, i.e. without feedbacks. We tested the direct effect of variance in SFP on variance in $\text{NDVI}_{\text{int.}}$, as previous work has shown that variation in snow free period accounts for most of variation in cumulated NDVI (Choler 2015). We also hypothesized that functional traits would respond to variance in snow free period and the occurrence of frost events, and that functional traits would in turn influence variance in $\text{NDVI}_{\text{int.}}$.

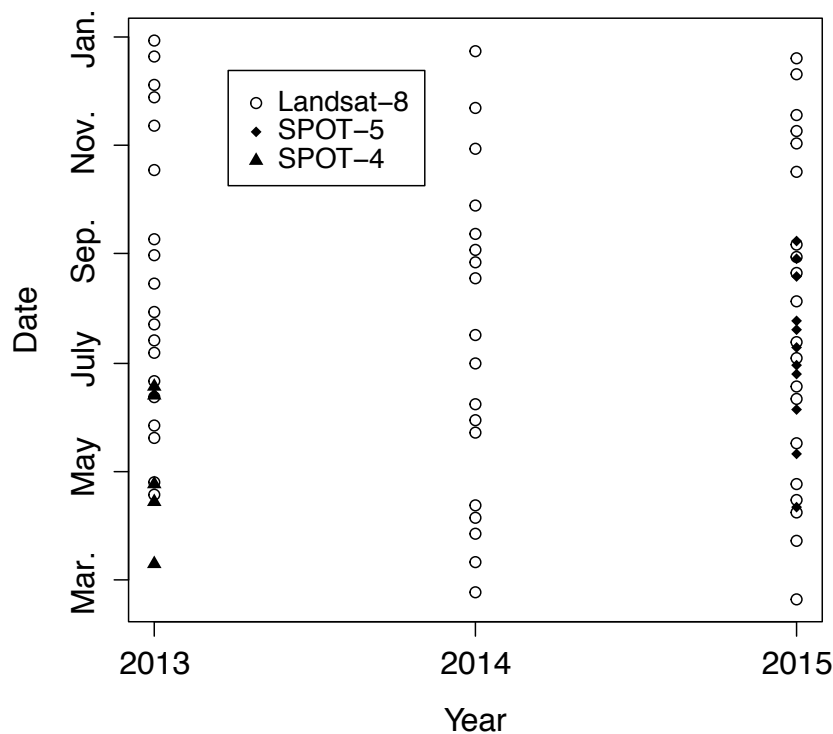


Figure 4. Acquisition dates for utilized Landsat-8, SPOT-4 and 5 images in 2013 (N=24), 2014 (N=18) and 2015 (N=31).

Preliminary results

The years 2013, 2014 and 2015 captured most of the variation in growing season length and timing of peak greenness observed in the study area during the last fifteen years (Figure 5). The 2013 growing season began late and ended early, and as shown in Figure 5 of Chapter IIA, was comparable to snow melt-out dates observed during the 1980s. By contrast, 2015 was characterized by early snow melt-out and an exceptionally long snow-free autumn, while 2014 was approximately intermediate between the two years (Figure 5). While attempting to study the effects of inter-annual variability on vegetation dynamics initially seems like a dubious exercise with only three years of observations, our analysis using MODIS imagery shows that these three particular years represented extremes in snow cover duration experienced by plant communities over the last fifteen years. The MODIS record placed our study years in context and supported the decision to carry out further analysis of community-level productivity using high-resolution Landsat and SPOT imagery for the years 2013-2015.

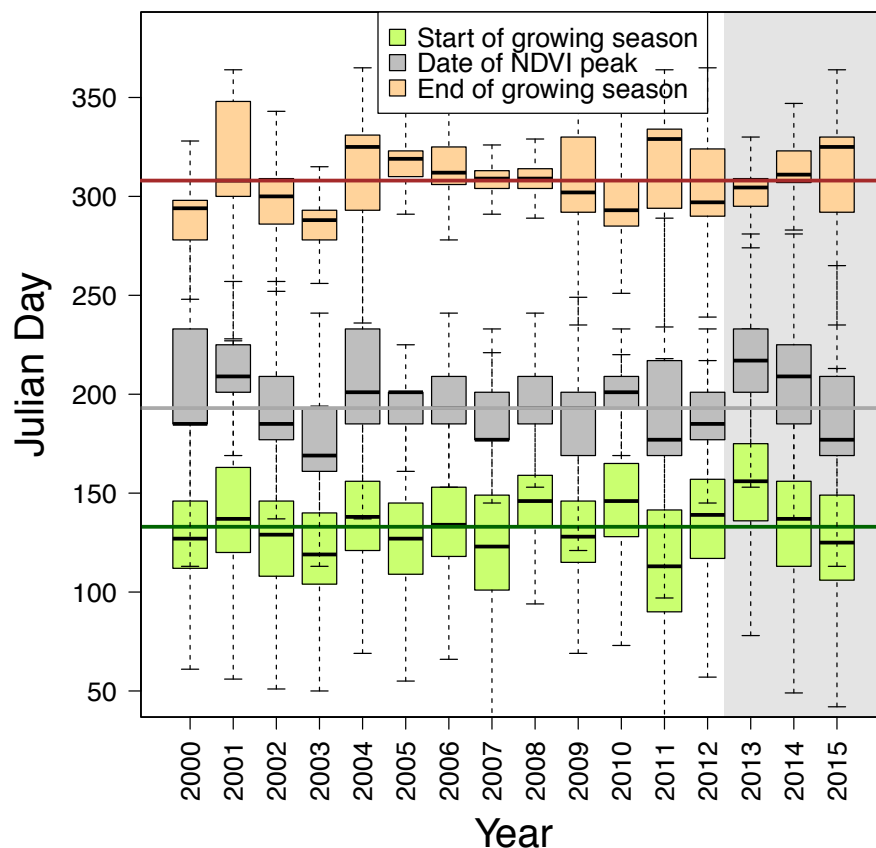


Figure 5. Start of the growing season (green), date of peak NDVI (grey) and the end of the growing season (orange) based on 8-day composite MODIS NDVI for the years 2000:2015. Start and end of the growing season were defined using an NDVI threshold of 0.1. Highlighted years indicate years of available high-resolution (SPOT and Landsat) imagery.

Average NDVI responses for the twelve studied plant communities and for the years 2013, 2014 and 2015 are shown in Figure 6. The decrease in NDVI with elevation is clearly visible based on the color scale, although particularly among sub-alpine communities there appears to be some mixing of NDVI trajectories independent of elevation. The contrasts in timing and length of growing seasons for the three study years suggested in Figure 5 are readily apparent in the NDVI trajectories of plant communities shown in Figure 6, with overall a “early and brief” season in 2013 and a “long and late” season in 2015. Despite substantial variation in growing season duration between years, it is interesting to note that the maximum NDVI values were fairly well preserved from one year to the next (Figure 6).

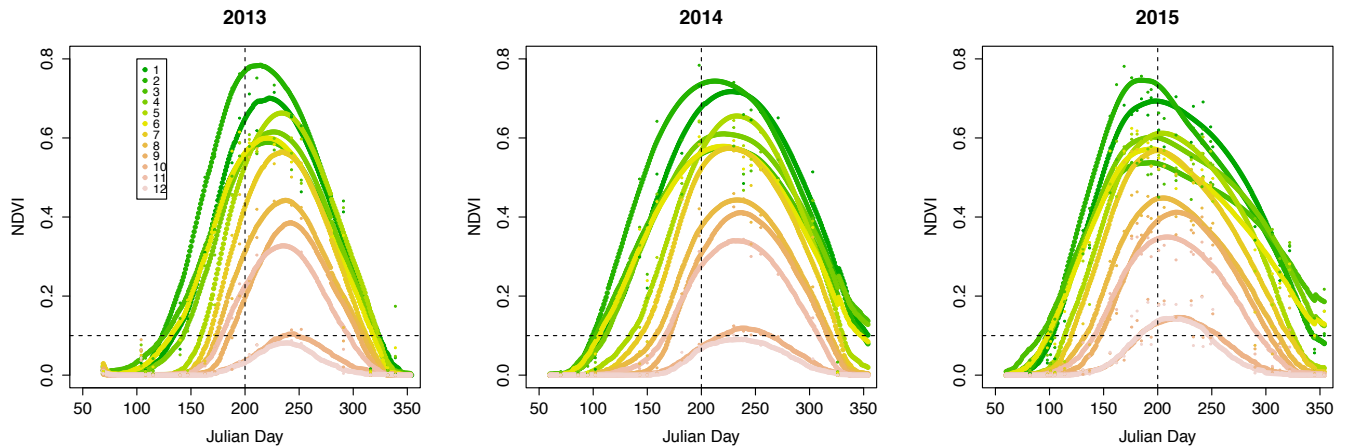


Figure 6. NDVI trajectories for twelve plant communities presented in Chapter 2A for the years 2013, 2014 and 2015. Colors correspond to the mean elevation of plant communities (dark green = low elevation, light orange = high elevation). Points show mean observed NDVI for each community based on imagery, while smoothed points are the mean daily NDVI values for each community resulting from a pixel-level loess interpolation of observed NDVI values.

At the community level, the NDVI trajectory of snowbed communities (community 9) consistently surpassed the NDVI of wind-blown alpine meadows (community 11), despite the later timing of green-up. This trend confirms that NDVI trajectories derived from imagery at 25 m resolution aligned with hypothesized snow cover and green-up dynamics at the scale of alpine plant communities, e.g. between ridge crest and snowbed contexts. While NDVI curves for 2013 and 2014 remained fairly “orderly”, in 2015 and after Julian Day 250 one can observe sudden disarray in the alignment of elevation-dependent NDVI responses. This may be attributed to two phenomena: i) an exceptionally dry mid- to late July (field observation; Julian Days 200-215), which may have limited productivity for certain communities and pushed the NDVI curve downward; and ii) in the context of the snow-free autumn (non-north facing aspects in the Oisans remained snow-free up to approximately 2600 m a.s.l. through Christmas, personal observation), certain plant communities may have been better able to “take advantage” of this abnormal prolongation of the potential growing season. It can be expected that evergreen shrubs such *Rhododendron ferrugineum* and *Juniperus* sp. (e.g. communities 1 and 5) expressed a higher NDVI signal relative to deciduous shrubs and grasslands by default. It is also possible that we over-estimated productivity late in the season, and as proposed in Chapter IIB, it would be worthwhile to re-run analyses using $NDVI_{green}$ in order to minimize this potential source of bias.

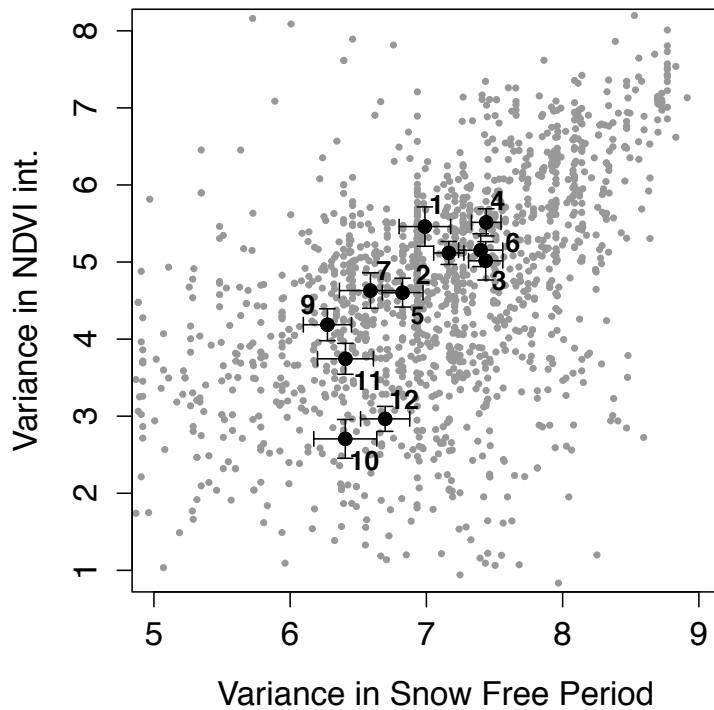


Figure 7. Vegetation plots (N=1272) plotted relative to variance in the length of the snow free period and variance in time-integrated NDVI (NDVI_{int.}) for the years 2013, 2014 and 2015. Black points and error bars represent the mean position with 95% confidence intervals of the twelve plant communities presented in Chapter 2A.

We found a strong positive relationship between variance in snow free period and variance in NDVI_{int.} (linear $R^2 = 0.41$, $P < 0.001$). Figure 7 shows the mean position of plant communities within this two-dimensional space with a clear gradient ranging from subalpine contexts with high variance in snow free period and in NDVI_{int.} to alpine contexts with low variance in snow free period and in NDVI_{int.}. Communities 3, 4 and 6, corresponding to dry sub-alpine meadows and sub-alpine heathlands, displayed the highest variance in both snow free period and in NDVI_{int.} (Figure 7), suggesting that early-melting subalpine communities were exposed to the highest inter-variability in snow free period. Interestingly, community 9 (snowbed) showed the lowest variance in snow free period as compared to all other communities but not in NDVI_{int.}. Low variation in the length of snow free period is consistent with the expectation that topography-related microhabitats buffer inter-annual variability in snow melt-out timing driven to a large degree by meteorological conditions. Given that experimental work in the same study system demonstrated that prolongation of the potential growing season did not lead to increases in snowbed productivity (Baptist *et al.* 2010), it is somewhat surprising to see the relatively high variance in NDVI_{int.} response for snowbed communities. It is possible, however, that non-snowbed vegetation with a more flexible response to growing season length also

contributed to observed NDVI signal within 25 m grid cells containing a mixture of different plant communities.

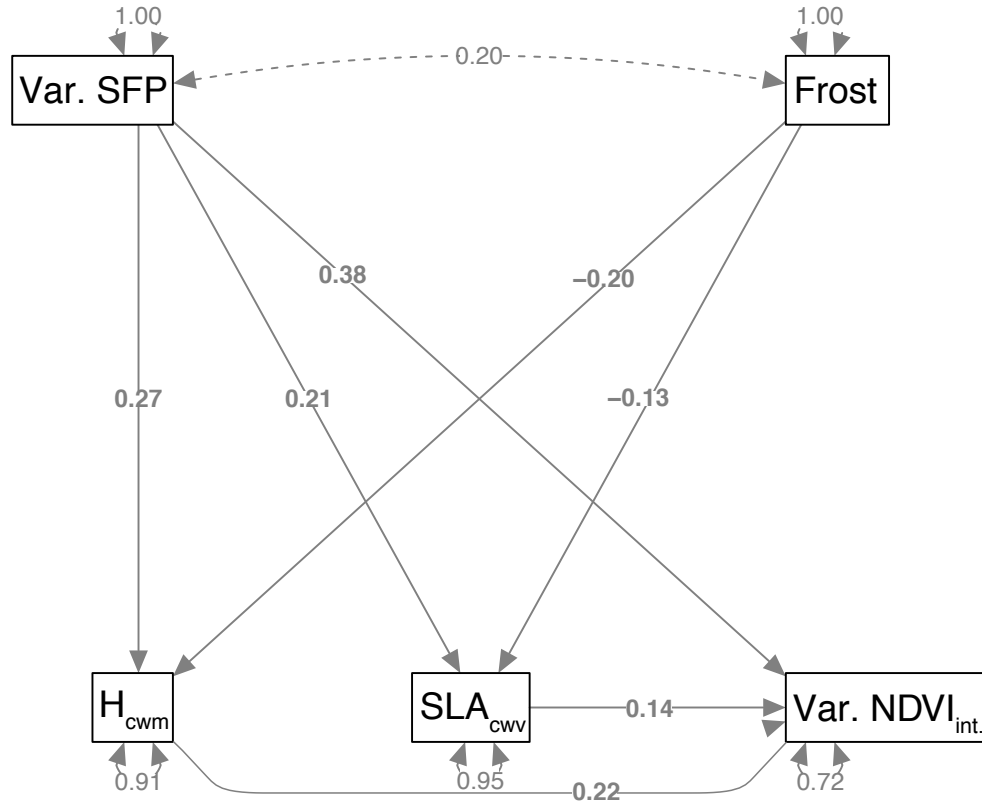


Figure 8. Path analysis showing relationships between variance in the length of snow free period (Var. SFP, 2013-2015), the occurrence of frost events (mean 2013-2015), community weighted mean plant height (H_{cwm}), community weighted variance specific leaf area (SLA_{cwv}) and variance in integrated NDVI (Var. NDVI_{int.}) for the years 2013-2015. Path coefficients are marked in bold, whereas co-variance and un-explained variance among variables are marked in non-bold.

Path analysis indicated statistically significant relationships between hypothesized causal relationships among variables (Figure 8). Following data exploration, only CWM plant height (H_{cwm}) and CWV specific leaf area (SLA_{cwv}) were retained for analysis, due to the fact that leaf nitrogen content had an excessive number of missing trait values for species, SLA_{cwm} did not respond significantly to any explanatory variable considered and H_{cwm} and H_{cwv} were highly co-linear. Path coefficients shown in Figure 8 confirmed the strong direct effect of variance in snow free period and variance in NDVI_{int.} initially found in Figure 7. Variance in snow free period also

had positive effects on both H_{cwm} and SLA_{cww} , which reflected findings shown in Chapter IA linking functional diversity to snow cover duration (Carlson *et al.* 2015). As hypothesized, the mean occurrence of frost events exhibited a negative effect on both functional trait metrics (Figure 8). H_{cwm} and SLA_{cww} had positive indirect effects on variance in $NDVI_{\text{int}}$, suggesting that plant functional traits partially mediated the NDVI response of plant communities, with higher values of H_{cwm} and SLA_{cww} enabling a more flexible NDVI response to changes in growing season length. While the signs of path coefficients were congruent with hypotheses, the addition of indirect effects of snow cover on NDVI response through community functional diversity did not increase in the amount of explained variation in the response variable (variance in $NDVI_{\text{int}}$). Accordingly, the most parsimonious model did not include functional traits, which contradicts the initial purpose and working hypotheses of this exercise. Further testing of path analyses with a full host of model performance metrics appears necessary before completely renouncing the approach adopted in this study.

A number of strategies could be adopted to improve this analysis. First, it may be more appropriate to use the log-response ratio (Hedges *et al.* 1999) of $NDVI_{\text{int}}$ for the years 2013 and 2015 rather than variance, given that only three years of observation were available for analysis. Second, recent work highlights the importance of weighting dominant versus rare species in the calculation of diversity metrics (Chalmandrier *et al.* 2015), and it would be worthwhile to test the sensitivity of community-weighted trait values to species dominance in the context of this analysis. We would expect that providing more weight to dominant species (as in standard CWM and CWV calculation) would provide better agreement with canopy-level estimates of NDVI from satellite imagery, however this assumption needs to be confirmed. Third, other facets of functional diversity (multi-trait estimates of divergence and convergence), taxonomic diversity (alpha and beta), as well as phylogenetic diversity metrics could be used to test for indirect effects of biodiversity on ecosystem function as quantified by NDVI response. Fourth, while path analysis is a useful framework for testing hypothesis causal links among multiple observed variables, the assumption of linear relationships is simplistic and likely does not correspond with the reality of the system. Accordingly, exploring other modeling strategies (random forest or GAM) constitutes a promising perspective for further testing effects of snow cover and plant diversity on response capacity to snow cover duration. Overall, there remains strong potential to

combine remote sensing with plot-level measures of community diversity to better understand links between biodiversity and ecosystem functioning.

References

- Baptist, F., Flahaut, C., Streb, P., & Choler, P. (2010). No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biology*, 12(5), 755-764.
- Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PloS one*, 4(5), e5695.
- Carlson, B. Z., Choler, P., Renaud, J., Dedieu, J. P., & Thuiller, W. (2015). Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities. *Annals of botany*, mcv041.
- Chalmandrier, L., Münkemüller, T., Lavergne, S., & Thuiller, W. (2015). Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. *Ecology*, 96(1), 143-153.
- Choler, P. (2015). Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. *Biogeosciences*, 12(12), 3885-3897.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, 104(52), 20684-20689.
- Dedieu, J. P., Carlson, B. Z., Bigot, S., Sirguey, P., Vionnet, V., & Choler, P. (2016). On the Importance of High-Resolution Time Series of Optical Imagery for Quantifying the Effects of Snow Cover Duration on Alpine Plant Habitat. *Remote Sensing*, 8(6), 481.
- Garonna, I., Jong, R., Wit, A. J., Múcher, C. A., Schmid, B., & Schaepman, M. E. (2014). Strong contribution of autumn phenology to changes in satellite-derived growing season length estimates across Europe (1982–2011). *Global change biology*, 20(11), 3457-3470.
- Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, 80(1), 67-87.
- Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80(4), 1150-1156.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... & Schmid, B. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, 75(1), 3-35.
- Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294(5543), 843-845.

Veroustraete, F., Sabbe, H., & Eerens, H. (2002). Estimation of carbon mass fluxes over Europe using the C-Fix model and Euroflux data. *Remote Sensing of Environment*, 83(3), 376-399.

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, 111(38), 13690-13696.

Chapter II Discussion

The findings of this chapter provide promising evidence of links between multi-temporal satellite imagery and patterns of high-elevation plant community diversity at the regional scale. Relative to the first objective identified in the introduction at the beginning of the chapter, disappearance of snow detected by SPOT and Landsat satellites was shown to strongly agree with ground-measures of snow melt-out. This simple validation exercise is highly useful to alpine ecologists, as it demonstrates that imagery can be used to move beyond isolated point measures to quantify snow cover duration at broad spatial scales.

The second habitat mapping objective was addressed by showing that floristic diversity responds consistently to gradients of peak NDVI and snow cover duration measured by satellite. This two-dimensional habitat template provides a biologically meaningful space within which to differentiate alpine plant community habitat, in the sense that energy availability and peak standing biomass are directly related to physiological constraints and responses of plant canopies. By contrast, a habitat template based on an elevation gradient and micro-topography index, for example, which could very well be statistically meaningful, would not have the same direct relevance for explaining plant community functioning. Admittedly, some modelers might take issue with the practice of using a vegetation-related variable (NDVI) to then in turn predict plant habitat, arguing that this approach is circular. In this case I view NDVI as an ecological indicator at the canopy level that corresponds to spatial turnover in plant communities, rather than as an environmental predictor in the classic sense.

The effort to include frost stress in Chapter IIB was less successful, and as mentioned in the discussion of IIA likely requires information on snowpack height in order to be more discerning. For example, I looked at several mid-winter satellite images of adjacent (same elevation) vegetation plots, one dominated by *Carex curvula* and the other characterized by *Nardus stricta*. Soil temperature loggers indicated freezing events occurring in the *Carex* plot but not for *Nardus*, and I wanted to see if the imagery captured these differences. In all images the both plots appeared to be snow covered, both visually and according the NDSI values. It seems likely that the *Carex* plot was covered by only a thin layer of wind-blown snow, whereas the *Nardus* plot likely had a substantial snowpack maintaining soil temperatures at 0°. This imperceptible difference from the perspective of the satellite nonetheless has important

implications for the environmental conditions experienced by those plant communities, and can account for the turnover in species composition among communities co-occurring at the same elevation. Detecting such fine differences in thermal and nival alpine regimes may be beyond the scope of satellite imagery, and would require measurements of snowpack height and wind effects.

Despite the limitations of satellite imagery, it is nonetheless exciting to imagine ten years from now when Sentinel-2 archives at 10 m ground resolution and 5-day time intervals will have built up and have become comparable to the MODIS archive that is currently available. Such a wealth of high-resolution information will allow for unprecedented study of growth responses to interannual variability in snow cover duration at the scale of turnover in plant communities, not to mention all manner of applications to be imagined. It is important to point out, however, that even the most precise satellite imagery will remain a tool for observation and monitoring. Having better maps of snow cover for the present does not necessarily translate to better maps of future snow cover duration, which remains a limitation for modelers interested in predicting future ecosystem responses to climate change. The same is true of NDVI, in the sense that generating the equivalent of a SPOT-5 NDVI map at 10 m for a future prediction period represents a monumental modeling challenge in its own right. All of this is to say that remote sensing-derived predictors are not flexible and readily transferable to future prediction periods, as is the case for example with Worldclim climate data. Despite these limitations, steady improvements in available satellite imagery will continue to enhance monitoring efforts and observation-based investigations of ecosystem functioning.

References

- Fontana, F., Rixen, C., Jonas, T., Aberegg, G., & Wunderle, S. (2008). Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series—a comparison with in situ measurements. *Sensors*, 8(4), 2833–2853.
- Pottier, J., Malenovský, Z., Psomas, A., Homolová, L., Schaepman, M. E., Choler, P., ... & Zimmermann, N. E. (2014). Modelling plant species distribution in alpine grasslands using airborne imaging spectroscopy. *Biology letters*, 10(7), 20140347.
- Randin, C. F., Dedieu, J. P., Zappa, M., Long, L., & Dullinger, S. (2015). Validation of and comparison between a semidistributed rainfall–runoff hydrological model

(PREVAH) and a spatially distributed snow-evolution model (SnowModel) for snow cover prediction in mountain ecosystems. *Ecohydrology*, 8(7), 1181-1193.

Walker, D. A., Halpenny, J. C., Walker, M. D., & Wessman, C. A. (1993). Long-term studies of snow-vegetation interactions. *BioScience*, 43(5), 287-301.

Chapter III

*Long-term monitoring of vegetation
changes in the French Alps*

Chapter III Introduction

As social and academic pressure to predict ecosystem responses to climate change continues to grow, long-term observation of historical landscape trajectories has become an increasingly important means of improving our understanding of natural systems and informing modelers. Monitoring programs are also an invaluable tool for land managers and conservation staff in need of quantitative tools to inform decision-making and policy. Long-term monitoring programs are traditionally carried out in the form of field campaigns with repeated measures over time. In the Alps, repeated floristic surveys of summit vegetation between 2001 and 2008 showed increases in the abundance of thermophilic species on European mountain summits (Gottfried *et al.* 2012). Recent studies have pointed out that summits are highly particular habitats representing a small surface area, and may not be representative of broader shifts in alpine vegetation downslope. For example, resurveying of vegetation plots in the Swiss Alps established during the 1970s showed that community composition had changed in the most snowbed plant communities due to the arrival of non-specialist grassland species, whereas other grassland communities remained quite stable (Matteodo *et al.* 2016). Another recent monitoring study found that changes in height and in alpha, beta and gamma diversity were highly community dependent and not systematic between the early 1990s and 2013 (Gritsch *et al.* 2016). In the Niwot Ridge LTER site in Colorado, Spasojevic *et al.* (2013) found site-wide increases in species richness and functional diversity, however the majority of observed variation was non-directional, reflecting the importance of transient shifts in community composition in response to stochastic population dynamics or inter-annual variability in climate. While the narrative related by Gottfried *et al.* (2012) of the upward march of thermophilic species is convenient in its simplicity, the use of species' temperature indicator values rather than direct measures of alpha and beta diversity has been questioned (Gritsch *et al.* 2016). Furthermore, a wide range of monitoring studies carried out in other alpine contexts show that observed changes are complex, often non-directional and plant community dependent. While long-term field monitoring campaigns remain an invaluable approach, future campaigns should seek to maximize spatial coverage, protocol standardization, international collaboration as well as measurement of environmental and biotic parameters in addition to floristic diversity (as exemplified by the recent launch of the ORCHAMP program in the French Alps).

In addition to field-based approaches, remote sensing can serve as a useful means of mapping shifts in vegetation structure over time. Historical aerial photographs have been frequently used to quantify changes in forest or shrub cover in both alpine and arctic contexts, allowing for quantification of ecotone dynamics at decadal time scales (e.g. Tape *et al.* 2006; Améztegui *et al.* 2010). Although the spatial resolution of commonly available historical satellite imagery does not allow for precise mapping of vegetation types or ecotone boundaries, satellite imagery has been employed to quantify long-term changes in the normalized difference vegetation index (NDVI) reflecting shifts in plant productivity. Analysis of greening (+NDVI) and browning (-NDVI) trends has been carried out in numerous study area contexts, including at the global scale (de Jong *et al.* 2011). One shortcoming of relying solely on satellite imagery, however, is the lack of ground-level information on processes and mechanisms of change. One approach to long-term monitoring using remote sensing is thus to combine optical trends with other lines of evidence (land-use data, climate data and field observations) in order to confirm patterns and assess potential drivers of vegetation change.

This section will present two articles utilizing multi-temporal remote sensing to quantify change in vegetation structure in the French Alps over the past decades. Chapter IIIA makes use of historical aerial photos to quantify changes in the forest-grassland ecotone in a natural reserve in a limestone massif to the southwest of Grenoble, the Vercors. Chapter IIIB applies the greening/browning framework to the Ecrins National Park located to the southeast of Grenoble, utilizing multi-spectral satellite imagery. The contributions and limitations of this work will be discussed at the end of the chapter.

Chapter IIIA

Long-term modeling of the forest-grassland ecotone in the French Alps: implications for land management and conservation^{}*

^{*} **Carlson, B. Z.**, Renaud, J., Biron, P. E., & Choler, P. (2014). Long-term modeling of the forest–grassland ecotone in the French Alps: implications for land management and conservation. *Ecological Applications*, 24(5), 1213-1225.

Long-term modeling of the forest–grassland ecotone in the French Alps: implications for land management and conservation

BRADLEY Z. CARLSON,^{1,4} JULIEN RENAUD,¹ PIERRE EYMARD BIRON,² AND PHILIPPE CHOLER^{1,3}

¹Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, Université Grenoble Alpes, F-38041 Grenoble, France

²Réserve Naturelle des Hauts Plateaux du Vercors, Parc Naturel Régional du Vercors, F-38250 Lans-en-Vercors, France

³Station Alpine Joseph Fourier, UMS CNRS-UJF 3370, Université Grenoble Alpes, F-38041 Grenoble, France

Abstract. Understanding decadal-scale land-cover changes has the potential to inform current conservation policies. European mountain landscapes that include numerous protected areas provide a unique opportunity to weigh the long-term influences of land-use practices and climate on forest–grassland ecotone dynamics. Aerial photographs from four dates (1948, 1978, 1993, and 2009) were used to quantify the extent of forest and grassland cover at 5-m resolution across a 150-km² area in a protected area of the southwestern French Alps. The study area included a grazed zone and a nongrazed zone that was abandoned during the 1970s. We estimated time series of a forestation index (FI) and analyzed the effects of elevation and grazing on FI using a hierarchical linear mixed effect model. Forest extent (composed primarily of mountain pine, *Pinus uncinata*) expanded from 50.6 km² in 1948 to 85.5 km² in 2009, i.e., a 23% increase in relative cover at the expense of grassland communities. Over the sixty-year period, the treeline rose by 118 m, from 1564 to 1682 m. Rapid forest expansion within the nongrazed zone followed the cessation of logging activities and was likely accelerated by climate warming during the 1980s. Within the grazed zone, the maintained presence of sheep did not fully counteract mountain pine expansion and led to highly contrasting rates of land-cover change based on the location of shepherds' cabins and water sources. Projections of FI for 2030 showed remnant patches of intensively used grasslands interspersed in a densely forested matrix. Our analysis of mountain land-cover dynamics provided strong evidence for forest encroachment into grassland habitat despite consistent grazing pressure. This pattern may be attributed to the disappearance of traditional land-use practices such as shrub burning and removal. Our findings prompt land managers to reconsider their initial conservation priority (i.e., the protection of a renowned mountain pine forest) and to implement proactive management strategies in order to preserve landscape heterogeneity and biological diversity. Projecting historical trends in the forest–grassland ecotone to 2030 provides stakeholders with a policy relevant tool for near-term land management.

Key words: ecotone dynamics; forest expansion; grassland conservation; grazing; mountain land-cover; remote-sensing.

INTRODUCTION

An understanding of historical shifts in the forest–grassland ecotone at the scale of a mountain reserve can provide the basis for future predictions of land cover and inform current land management and conservation decisions. Expansion of forest into subalpine and alpine grasslands during recent decades constitutes a global phenomenon that has been documented in mountain areas of North America (Briggs et al. 2005, Zald 2009), Europe (Kullman 2002, Gellrich and Zimmermann 2007, Améztegui et al. 2010), and Australia (Wearne and Morgan 2001). Shifts in the forest–grassland ecotone are relevant to broader issues of conservation

and land management. Forest expansion is known to reduce plant species richness at the landscape scale (Barbaro et al. 2001, Watkinson and Ormerod 2001, Dullinger et al. 2003b) and can also have a negative impact on umbrella wildlife species that depend on semiopen areas and ecotonal conditions (Suter et al. 2002, Schweiger et al. 2011). Forest expansion is of particular concern to land managers in grazed, mountainous areas due to associated increased fire risk and lowered pasture productivity (Lasanta et al. 2009). Mountain landscapes provide a unique opportunity to weigh the long-term influences of land-use practices and climate on observed shifts in extensively managed, seminatural ecosystems (Bartolomé et al. 2000). Additionally, protected mountain areas foster collaboration between land managers and ecosystem scientists in the shared aim of developing well-informed conservation plans.

Manuscript received 15 May 2013; revised 1 October 2013; accepted 23 October 2013; final version received 12 November 2013. Corresponding Editor (ad hoc): C. Tague.

⁴ E-mail: brad.z.carlson@gmail.com

Most studies on land-cover dynamics in mountain areas face the challenge of teasing apart the relative contributions of climate and land-use changes on spatial and temporal shifts in the forest–grassland ecotone (Gehrig-Fasel et al. 2007). The position of alpine treeline is defined by a temperature-dependent isotherm (Körner and Paulsen 2004). At the global scale, 52% of alpine treelines have manifested an upward shift in response to rising measured air temperatures (Harsch et al. 2009). Recorded temperatures in European mountain areas have risen significantly during the last century, with an approximate 2°C rise that is substantially higher than measured temperature rise in European lowlands (Beniston et al. 1997). Although climate change is expected to facilitate ongoing forest expansion in European mountain areas (Theurillat and Guisan 2001, Dullinger et al. 2003a), predicting future trajectories of forest expansion is complicated by observations of nonlinear, threshold-based responses of tree growth to rising temperatures and variable precipitation (Camarero and Gutiérrez 2007, Batllori et al. 2009).

In addition to climate, land-use practices are known to have a direct effect on the location of the forest–grassland ecotone, particularly in Europe where mountain landscapes have been shaped by human activities for centuries (Kaplan et al. 2009). Agricultural land abandonment, which has led to a decline in traditional mountain agricultural practices around the world over the course of the 20th century (Macdonald et al. 2000), has been identified as a driver of mountain forest expansion in the Pyrenees and Swiss Alps (Gellrich and Zimmermann 2007, Améztegui et al. 2010). Grazing of sheep and cattle represents a common form of land use in mountainous landscapes, and grazing practices are understood to have a direct effect on interactions between woody plant and grassland species (Cairns and Moen 2004). Decline in sheep stocking rates has furthermore been linked to landscape-scale forest expansion and habitat homogenization (Vicente Serrano et al. 2004). While debate exists in the literature concerning the direction and magnitude of grazing effects on mountain vegetation (Dalen and Hofgaard 2005, Sankey et al. 2006, Tømmervik et al. 2009), recent experimental evidence studies indicate that sheep grazing suppresses a treeline below its potential climatic limit (Speed et al. 2010). In addition to grazing impacts, related land-use practices such as shrub removal, burning, and logging can locally influence the location of the treeline (Körner 2007). Management decisions concerning brush removal are particularly important given that shrubs are known to facilitate *Pinus* installation in stressful habitats (Castro et al. 2004). Consequently, decline in grazing pressure and cessation of traditional land-use practices can lead to the rapid expansion of mountain forests (Tasser et al. 2007).

While the basic drivers of forest expansion in mountain environments are fairly well established, there is potential to improve methods of quantifying and

modeling historical vegetation dynamics in the context of conservation and land management. Long-term comparison between areas subjected to summer grazing and adjacent nongrazed zones allows for the investigation of contrasting disturbance regimes on ecotone dynamics and also, for distinction between climate and land-use drivers. The aims of this study are threefold: (1) to quantify, with high spatial and temporal resolution, forest and grassland cover at the scale of a French protected mountain area, the Réserve Naturelle des Hauts Plateaux du Vercors, hereafter RNHPV, (2) to develop a spatially explicit statistical model of forest–grassland ecotone dynamics in grazed and nongrazed zones, and (3) to provide insights for near-term land management policies. This study is the first to combine remote-sensing methods and linear mixed modeling in order to assess land-cover dynamics in an understudied region of the southwestern Alps characterized by high biodiversity and sensitivity to climate and land-use changes.

METHODS

Study area context

The RNHPV was established in 1985 and is located within the Vercors Regional Natural Park. The study area considered covers a 150-km² subset of the 170-km² RNHPV, as certain areas characterized by abrupt topography were excluded due to technical difficulties encountered when processing 1948 aerial imagery (Fig. 1B). The RNHPV covers a generally west-facing, karstic plateau composed of urgonian limestone spanning an elevation range from 1050 to 2431 m (Fig. 1). Situated at the transition zone between temperate and Mediterranean climate zones, the southern end of RNHPV is characterized by warmer temperatures (annual mean of 10.9°C vs. 7.2°C in the north) and reduced precipitation (annual sum of 1040 mm vs. 1649 mm in the north). Vegetation cover consists of a mosaic of deciduous and mixed forest (*Fagus sylvatica* and *Abies alba*) at lower elevations, coniferous forest (composed primarily of mountain pine, i.e., *Pinus uncinata*) and subalpine grassland at mid to upper elevations, and alpine grassland and sparsely vegetated ridge crests at the highest elevations (Fig. 1C; see Plate 1).

Climate change over the last 60 years (1958–2009) was documented using time series of temperature and rainfall from the SAFRAN meteorological model developed by Météo-France. Details on data description, methodology, and validation of SAFRAN for the French Alps are provided in Durand et al. (2009). Fluctuations in network density and data collection protocol may have contributed to bias and uncertainty in the SAFRAN climate series (see Vidal et al. [2010] for further discussion). Error associated with historical climate data had no bearing on our results, however, considering that we viewed these data as a contextual element for discussion rather than as an integral part of our analysis. We extracted the sum of June–July rainfall

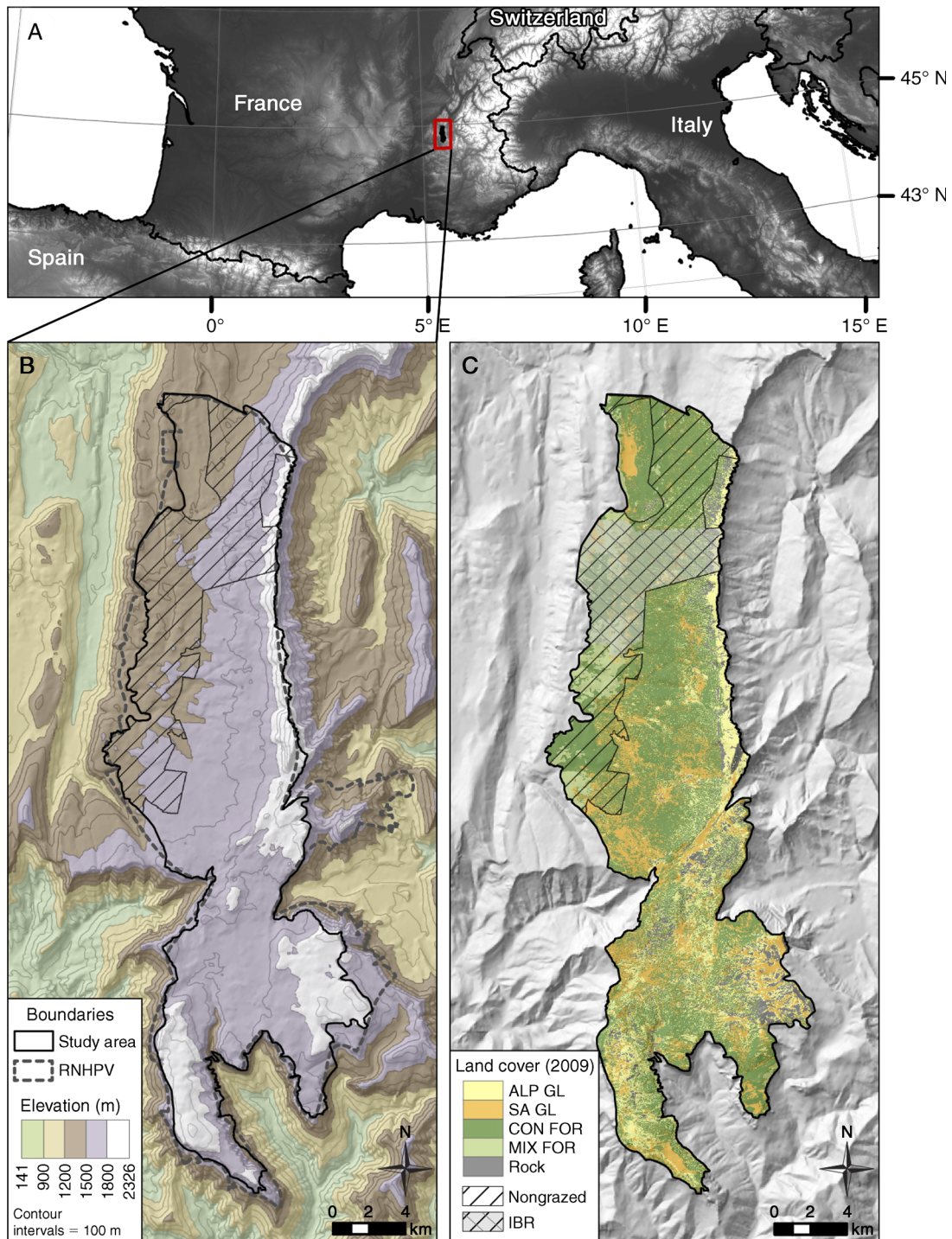


FIG. 1. (A) Location of the study area within the context of adjacent European mountain areas. (B) Relief map showing the topography of the study area and the boundaries of the RNHPV (Réserve Naturelle des Hauts Plateaux du Vercors). (C) Land cover in 2009 (ALP GL, alpine grassland; SA GL, subalpine grassland; CON FOR, coniferous forest; MIX FOR, mixed forest). The nongrazed zone is also indicated, as well as the location of the Integrated Biological Reserve (IBR).

(mm) and the mean July–August temperature ($^{\circ}\text{C}$), as previous studies indicated that mountain forest growth in the RNHPV was highly responsive to these two variables (Rolland et al. 1995, Rolland 2001).

Although human land use in the form of seasonal logging and sheep grazing on the Vercors plateau dates back to the 14th century, there is no historical evidence of permanent human settlement or habitation in the area currently comprising the RNHPV (Rolland 2001). The establishment of the RNHPV has promoted the conservation of mountain pine forest while encouraging the continuation of traditional summer transhumance of sheep from the French Mediterranean region. Sheep grazing within the nongrazed zone was progressively abandoned during the 1970s due to topographic constraints and difficulty of access (Fig. 1B). Moreover, a large part of this nongrazed zone was purchased by the state in the 1980s and became classified as an Integrated Biological Reserve (IBR) in 2011 (Fig. 1C). There has been no major anthropogenic disturbance in the area since the 1950s, although prior to this date coal mining and logging for the paper industry were widespread practices. The remainder of study area is referred to as the grazed zone (Fig. 1B), although management practices in this area range from intensive grazing to complete abandonment. Lastly, the term grazing practices is not limited to the direct effects of sheep presence and encompasses actions on the part of the shepherd, including the removal and burning of trees and shrubs.

Data preparation and image processing

Aerial imagery covering the study area was obtained for four dates (1948, 1978, 1993, and 2009). The 2009 mission consisted of 50-cm resolution digital color infrared (CIR) orthophotos. The 1948, 1973, and 1993 missions were airborne paper photographs. Images for these were scanned at 1000 dpi resolution and then orthorectified using direct linear transformation in Erdas Imagine (version 9.2, 2011; ERDAS, Huntsville, Alabama, USA). Approximately 25 ground control points (GCPs) were established per image, and it was ensured that root mean square error was inferior to 5 m. For each date, a mosaic was generated using histogram matching among images. Each mosaic was then imported into ArcGIS (version 10.1, 2010; ESRI, Redlands, California, USA) and orthorectified a second time using 200 GCPs and the spline transformation method in order to insure optimal superposition across dates.

A first supervised classification was applied to the CIR 2009 image to obtain a three-class land-cover map (forest, grassland, rock). Errors in the automated classification were then manually corrected using the initial mosaic as a reference. Based on the 2009 land-cover map, we fixed the rock class for the other three dates. We then carried out supervised classifications for the 1948, 1973, and 1993 mosaics using a threshold on the gray-scale band to distinguish between forest and

grassland. As for 2009, classification errors were corrected manually by means of visual comparison with the corresponding mosaic for the same year. All image classification was carried out using eCognition Developer (version 8.0, 2012; Trimble Navigation, Munich, Germany), while manual editing was performed in ArcGIS. Land cover maps for each date were resampled and exported at 5-m resolution, and 50 points were visually controlled and compared to the classified images in order to evaluate the accuracy of the classification. Confusion matrices showed in each case an overall accuracy varying between 0.88 and 0.96.

Estimates of forest and grassland surface area were calculated using a 50-m triangular irregular network (TIN) created from a 25-m digital elevation model (DEM). Use of the TIN allowed us to estimate surface area taking topography into account, which is of particular importance in mountainous study areas (Jenness 2004). In order to differentiate between densification within initially forested areas and encroachment into previously nonforested grasslands, we considered new forest in pixels that were less than 40% forested in 1948 to be the result of expansion and new forest in pixels that were more than 40% forested in 1948 to be the result of densification (see Améztegui et al. 2010).

A normalized forestation index (FI) was calculated for pixel (i) and for each date (j) using the following formula:

$$FI_{ij} = (F_{ij} - NF_{ij}) / (F_{ij} + NF_{ij}) \quad (1)$$

where F represents forest area and NF represents grassland area. FI values ranged from -1.0 (nonforested) to 1.0 (fully forested), and forested pixels were defined as those with an FI value >0 .

Modeling

We developed a hierarchical linear mixed model to analyze changes in FI over the last 60 years and to examine the effects of elevation and grazing on the direction and magnitude of these changes. Our longitudinal data set was comprised of N grid cells for which we estimated FI for the four dates. Because we have the same number of observations ($n = 4$) for all cells and because the observations are made at fixed years, the design is balanced. We implemented two separate models: one for grid cells located in the grazed zone and another for grid cells located in the nongrazed zone. Our modeling approach had two levels. The level-1 model corresponded to an exploratory analysis where trends in FI were examined for each cell. The regression of FI on year j for cell i was written

$$FI_{ij} = a_{0i} + a_{1i} \text{YEAR}_{ij} + \varepsilon_{ij} \quad (2)$$

where a_{0i} is intercept for cell i , a_{1i} is slope for cell i , and ε_{ij} represents cell-level error.

Based on this first data exploration, we hypothesized that a_{0i} and a_{1i} were dependent upon grid cell elevation,



PLATE 1. View of the Grand Veymont (2341 m) displaying the position of alpine treeline as well as the mosaic of subalpine grassland and mountain pine forest characteristic of the Vercors plateau (Vercors Regional National Park, France). Photo credit: Gilles Rayé.

and we implemented a level-2 model that used elevation as a linear predictor of the cell-specific parameters a_{0i} and a_{1i}

$$\begin{aligned} a_{0i} &= b_{00} + b_{01}\text{ELEV}_i + v_{0i}; \\ a_{1i} &= b_{10} + b_{11}\text{ELEV}_i + v_{1i}. \end{aligned} \quad (3)$$

Rearranging Eq. 2 and Eq. 3 yields

$$\begin{aligned} \text{FI}_{ij} &= b_{00} + b_{01}\text{ELEV}_i + b_{10}\text{YEAR}_{ij} \\ &+ b_{11}\text{ELEV}_i\text{YEAR}_{ij} + v_{1i}\text{YEAR}_{ij} + v_{0i} + \varepsilon_{it} \end{aligned} \quad (4)$$

where b represents coefficients for the two fixed effects YEAR and ELEV and their interaction, v are random effects and ε is cell-level error. Combined Eq. 4 has the form of a mixed linear model (Pinheiro and Bates 2000).

We centered the level-1 predictor (YEAR) by subtracting the value 1948 so that the intercept of the level-1 aligned with start of the study period. We assessed data normality by examining the distribution of the level-1 model residuals. We tested whether random intercepts and random slopes should be included in the model structure by comparing the log likelihood and the Akaike's information criteria of competing models. Because errors of repeated measures that are close in time may be correlated, we also tested the level-1 model for covariance structure (Wang and Goonewardene 2004). We found that including an autoregressive process of order 1 did not significantly

change model outputs. We did not include spatial autocorrelation in the model but examined a posteriori the spatial structure of model residuals using the Moran's I spatial autocorrelation test (Anselin 1995) in ArcGIS.

As a baseline, we modeled FI changes using a 1-ha grid cell resolution. To test for the effect of spatial aggregation of FI on model performance, we repeated all statistical analyses for finer (25 m, 50 m) and coarser (200 m, 400 m) grid cell resolutions. Model performance was evaluated using several goodness-of-fit statistics: R^2 , mean absolute error (MAE), and root mean square error (RMSE). Additionally, we partitioned the mean squared error (MSE) into its systematic and unsystematic components as described by Willmott (1982). Statistical analyses were done within the R software environment (R Development Core Team 2013). For linear mixed models, we used the nlme library (Pinheiro et al. 2012).

RESULTS

Remote-sensing analysis

Forest–grassland maps generated for the RNHPV in 1948, 1978, 1993, and 2009 indicated a strong and consistent expansion of forest extent at the expense of subalpine and alpine grassland communities (Figs. 1 and 2). Forest surface area expanded from 50.6 km² in 1948 to 85.5 km² in 2009, representing an increase in relative

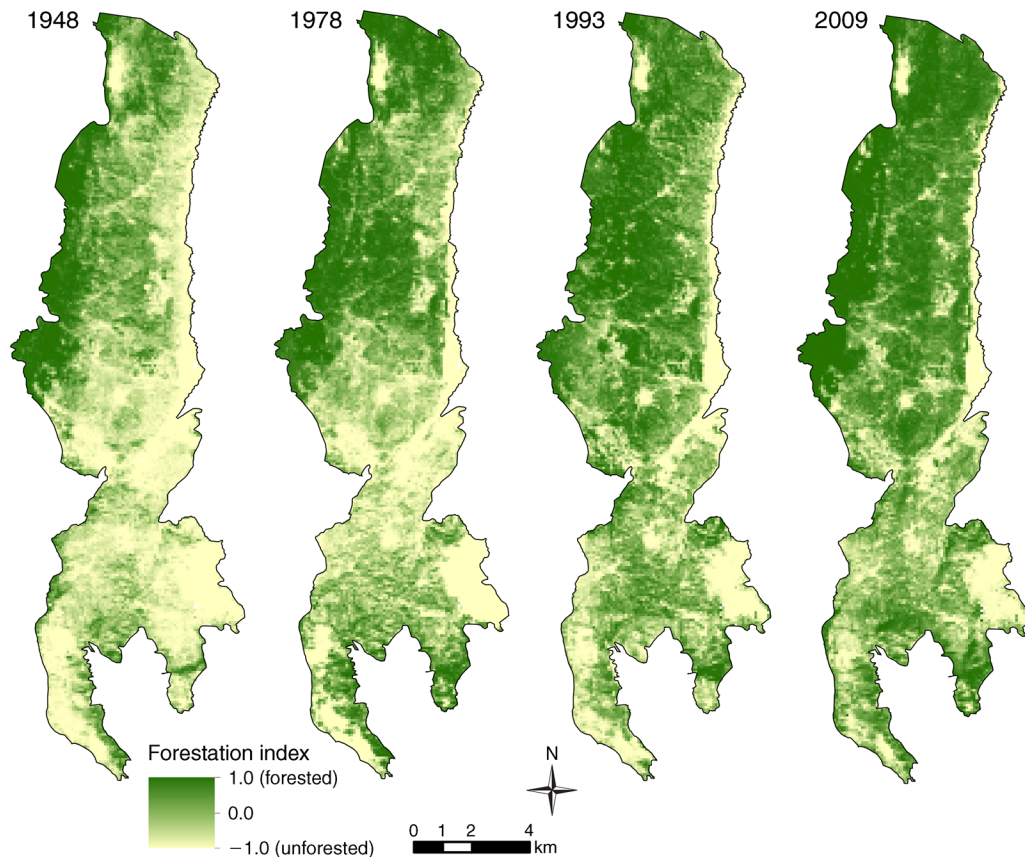


FIG. 2. Forestation index (FI) for the four dates considered (1948, 1978, 1993, and 2009).

composition from 34% to 57% of the study area. Over the same period, the surface area of grassland communities diminished from 87.0 to 52.8 km². Of the estimated 34.2 km² of new forest established between 1948 and 2009, 16% of this growth took the form of densification within preexisting forest in 1948, while 84% occurred as expansion into previously nonforest grasslands. The majority (75%) of forest expansion occurred below 1700 m. Between 1948 and 2009, the median elevation of forested pixels rose from 1481 to 1570 m (+89 m). The upper limit of forested pixels increased from 1564 to 1682 m (+118 m) over the course of the study period. Based on available vegetation maps (Villaret and Genis 2004) and field validation, we concluded that the bulk of new forest over the past 60 years primarily composed of *Pinus uncinata*.

FI analysis relative to elevation and year

Based on the level-1 model, we found a relationship between slope (change in FI) and intercept (FI in 1948) within the nongrazed zone (Fig. 3A). Grid cells that were initially forested in 1948 tended to exhibit little change over the course of the study period. With the exception of very low initial FI values (close to -1.0), there was a negative relationship between intercept and

slope. In other words, the greater the extent of forest in 1948, the lower the ensuing rate of forestation.

Elevation classes were distributed nonrandomly across the scatter plot. Highly forested grid cells in 1948, showing little change in FI, tended to be located in the low-elevation class (1200–1500 m). Partially forested grid cells with high slopes were represented by the mid-elevation class (1500–1800 m). Finally, initially nonforested grid cells that remained as such were located above 1800 m. An empirical function was used to capture these changes in FI in the absence of land-use practices (Fig. 3A). By contrast, high variability in the relationship between initial FI and change in FI was observed within the grazed zone (Fig. 3B). This was especially true for mid-elevation grid cells where a larger range of FI changes is apparent, and which may have been related to varying intensity of grazing practices. This elevation class was the best represented throughout the study area (Fig. 1B), and therefore this region contributed the most to the observed variability in FI change in the RNHPV (Fig. 3C). The most prominent areas showing deforestation between 1948 and 2009 corresponded with localized fires that occurred during the 1970s and sporadic logging activity (P. E. Biron, *personal observations*; Fig. 3C).

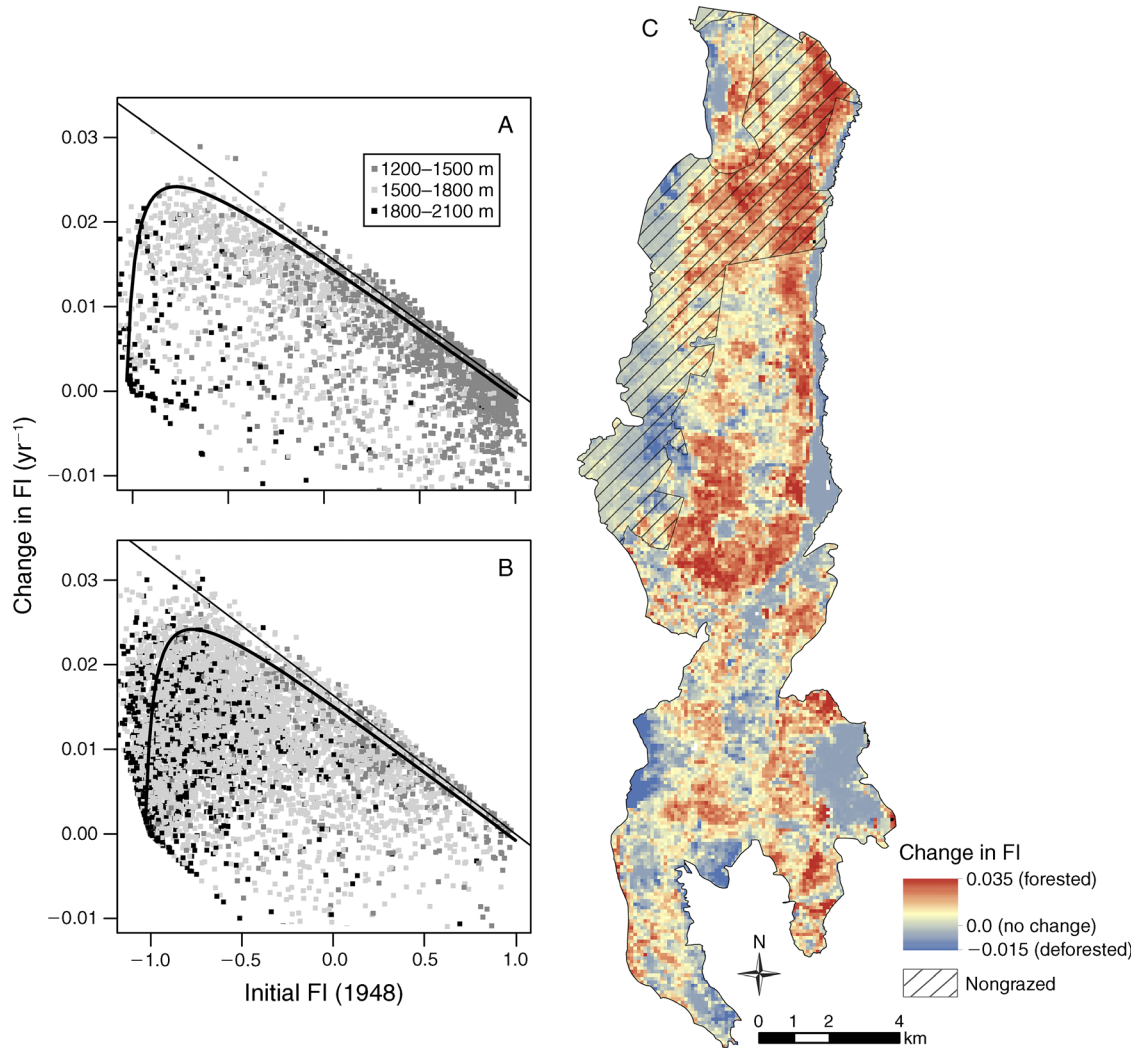


FIG. 3. Plot of initial FI (1948 intercept) and change in FI (slope) for (A) nongrazed and (B) grazed pixels as estimated by the level-1 model applied to each 1-ha grid cell (details in *Methods: Modeling*). The upper envelope was fit using a rational function. Elevation classes are shown in grey scale. (C) Change in FI (slope) values mapped for each 1-ha grid cell, as estimated by the level-1 model. High slope values represent areas that became forested between 1948 and 2009, while negative values indicate areas that became deforested during this time.

TABLE 1. Rank fit among model candidates.

Fixed effects	Random intercept	Random slope	Correlation structure	Grazed area ($N = 3102$)			Nongrazed area ($N = 1499$)		
				LogLik	AIC	dAIC	LogLik	AIC	dAIC
Time		x		−9390	16789	6059	−4182	8373	4594
Time	x			−6301	12610	1880	−2817	5643	1864
Time	x	x		−5899	11811	1081	−2444	4901	1122
Time × elevation		x		−7049	14110	3380	−2644	5301	1522
Time × elevation	x			−5724	11459	729	−2042	4097	318
Time × elevation	x	x		−5357	10730	0	−1881	3779	0
Time × elevation	x	x	x	−5357	10732	2	−1881	3781	2

Notes: Slope and intercept columns indicate whether the model included random slope and intercept parameters for each grid cell. N is the number of 1-ha grid cells. LogLik is the log-restricted-likelihood, AIC is the Akaike information criterion, dAIC is the difference in AIC compared with the best model.

TABLE 2. Interval estimates for all effects, and *F* ratios for the fixed effects, included in the final model.

Effects	Grazed area (<i>N</i> = 3102)					Nongrazed area (<i>N</i> = 1499)	
	Value	Lower	Upper	df	<i>F</i>	Value	
Fixed							
Intercept	2.42	2.23	2.6	1, 9304	3449	5.92	
Time	2.3×10^{-2}	1.96×10^{-2}	2.63×10^{-2}	1, 9304	4941	-4.37×10^{-2}	
Elevation	-1.76×10^{-3}	-1.87×10^{-3}	-1.66×10^{-3}	1, 3100	3100	-3.73×10^{-3}	
Time \times elevation	-7.8×10^{-6}	-9.74×10^{-6}	-5.77×10^{-6}	1, 9304	9304	3.28×10^{-5}	
Random							
SD(intercept)	0.35	0.334	0.361			0.37	
SD(slope)	5.16×10^{-3}	4.96×10^{-3}	5.57×10^{-3}			5.6×10^{-3}	

Notes: *N* is the number of 1-ha grid cells. $P < 0.001$ for all fixed effects. In accordance with Pinheiro and Bates (2000), *F* values are not included for random effects.

Model selection

Of the ten different model configurations tested, the best performing level-2 model (in terms of both log likelihood and AIC) included an interaction effect between time and elevation, a random slope and random intercept per grid cell, and no additional parameter for correlation structure (Table 1). Table 2 shows the fixed and random effect coefficients, as well as their confidence intervals for the selected model. Testing for the effect of grid cell size showed that the percentage of systematic error increased at finer resolutions, whereas the percentage of nonsystematic error increased at coarser resolutions (Table 3). Goodness-of-fit statistics (R^2 and RMSE) were marginally better at the coarser 200 m and 400 m resolutions. Finally, varying the number of pixels included in the model did not significantly affect model performance (Table 2).

Residuals of the linear mixed effects models for grazed and nongrazed zones showed significant spatial structure ($P < 0.001$) for all four dates considered, however the spatial patterns were not consistent across years (see Appendix). For example, the slight change in forest extent in the central part of the reserve from 1948 to

1978 (Fig. 2), followed by the rapid expansion of forest in this sector between 1978 and 1993, caused the model to overestimate FI in 1978 and subsequently to underestimate it in 1993. Both the models for grazed and nongrazed zones tended to underestimate forest expansion at the alpine treeline ecotone in 2009. Based on this detailed analysis of model performance, we concluded that a linear mixed model was sufficiently robust to represent observed trends in forest–grassland ecotone dynamics.

Aligning vegetation change with climate trends

No generalized trend was apparent in the sum of June/July rainfall between 1958 and 2009, although intermittent dry summers were evident (e.g., 1962, 1988, 1995, and 2003; Fig. 4A). Over the same time period, it was possible to detect an approximate 2°C rise in mean July/August temperatures within the RNHPV (Fig. 4B), which was consistent with 20th-century temperature trends observed throughout the Alps (Beniston et al. 1997). The bulk of this warming in the RNHPV appeared to have occurred over a fifteen-year period between 1980 and 1995, which coincided with a period

TABLE 3. Effect of spatial aggregation on fixed effects at varying resolutions.

Cell resolution (m)	Number of grid cells	r^2	SMA intercept	SMA slope	Systematic error (%)	Unsystematic error (%)	RMSE	MAE
Grazed								
25	3013	0.91	−0.036	0.83	34	66	−0.21	0.23
50	3077	0.93	−0.028	0.86	28	72	−0.14	0.19
100	3102	0.94	−0.024	0.88	26	74	−0.12	0.16
100	1551	0.94	−0.025	0.88	25	75	−0.10	0.16
100	387	0.94	−0.030	0.88	26	74	−0.10	0.16
200	1580	0.95	−0.023	0.89	23	77	−0.08	0.14
400	404	0.95	−0.021	0.90	20	80	−0.06	0.13
Nongrazed								
25	1432	0.91	0.088	0.81	38	62	0.26	0.19
50	1455	0.93	0.072	0.84	32	68	0.22	0.16
100	1499	0.93	0.069	0.85	31	69	0.19	0.14
100	749	0.92	0.075	0.84	33	67	0.20	0.16
100	187	0.94	−0.030	0.88	34	66	0.19	0.15
200	792	0.95	−0.023	0.89	29	71	0.18	0.14
400	213	0.95	−0.021	0.90	27	73	0.16	0.13

Note: MAE is mean absolute error, RMSE is root mean square error, SMA is standardized major axis.

TABLE 2. Extended.

Nongrazed area ($N = 1499$)			
Lower	Upper	df	F
5.64	6.2	1, 4495	1765
-4.88×10^{-2}	-3.87×10^{-2}	1, 4495	506
-3.92×10^{-3}	-3.55×10^{-3}	1, 1497	1562
2.94×10^{-5}	3.61×10^{-5}	1, 4495	84
0.352	0.388		
5.21×10^{-3}	6.01×10^{-3}		

of accelerated forest expansion within the grazed zone (Fig. 4).

Forecasting FI in 2030

Using the level-2 model, we extrapolated FI values for the year 2030. Projected forestation occurred in the form

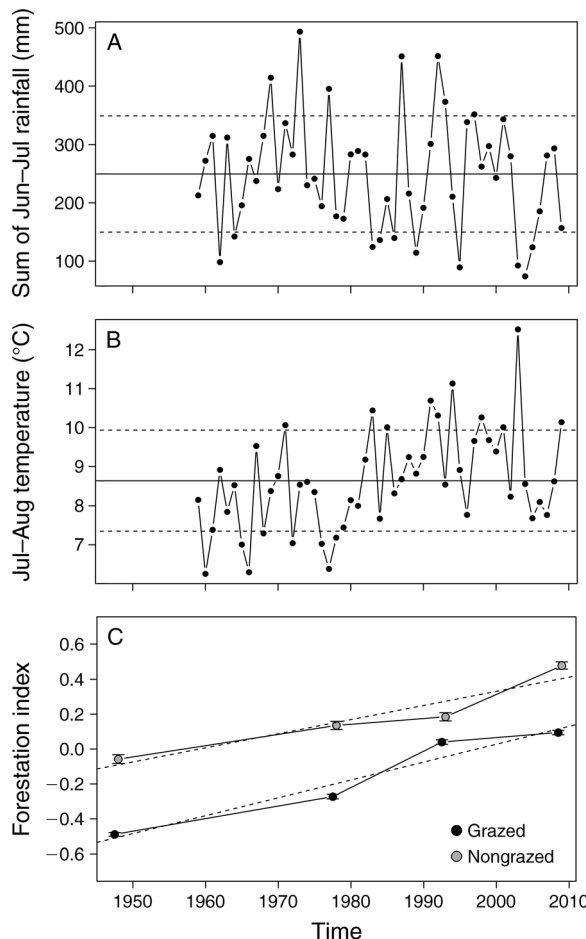


FIG. 4. (A) Sum of June–July rainfall (mm) between 1958 and 2009. (B) Mean July–August temperatures between 1958 and 2009. (C) Mean FI for 1948, 1978, 1993, and 2009 plotted for grazed and nongrazed zones. Bars indicate the upper and lower 95% confidence limits of the standard error of the sample mean.

of expansion and densification below the upper limit of forested pixels. Mean FI across the study area increased from 0.61 in 2009 to 0.65 in 2030, although this increase was inconsistent across grazed and nongrazed zones. Mean FI did not increase within the nongrazed zone between 2009 and 2030, suggesting that forest saturation had occurred by 2009 and that maximum FI had already

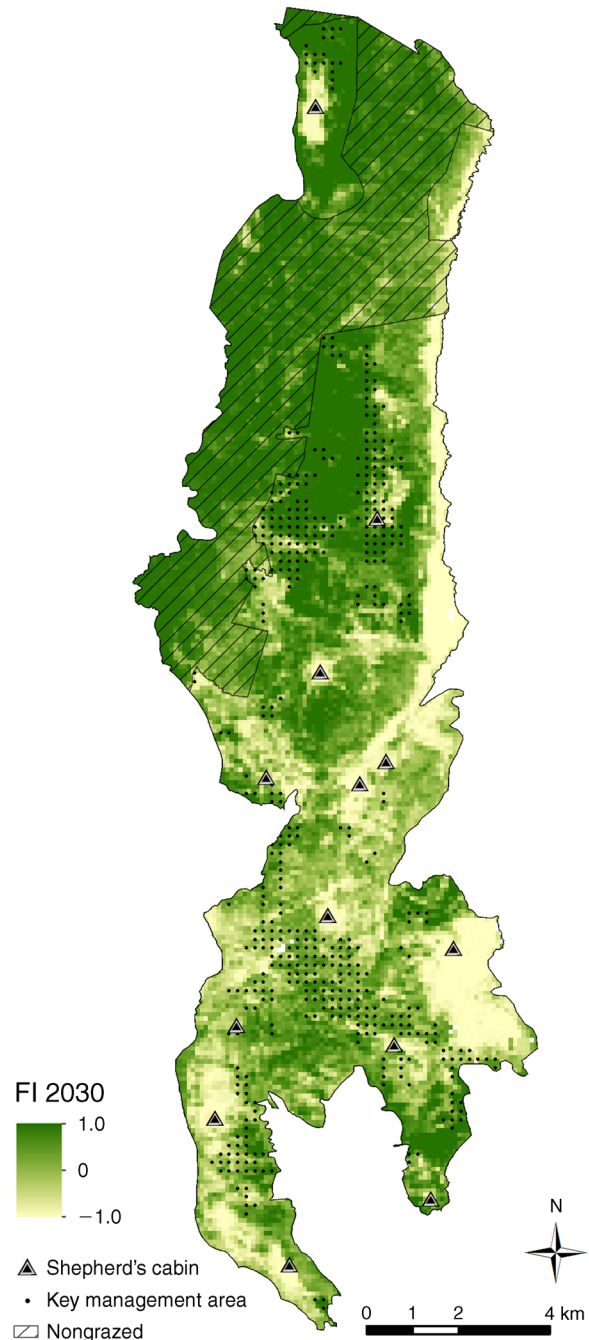


FIG. 5. Projected FI for 2030 based on the linear mixed effects model with the present location of shepherds' cabins indicated. Dots indicate key management areas predicted to become forested between 2009 and 2030.

been reached. In the grazed zone, the mean increase in FI from 0.50 to 0.59 indicated that a forest expansion dynamic was still underway in 2009. Noticeably, projected land cover manifests an increased contrast between open pastures in the vicinity of shepherds' cabins and surrounding densely forested areas (Fig. 5). Grid cells projected to become 15% more forested between 2009 and 2030 were considered to be key management areas, where near-term action on the part of land managers would be the most effective (Fig. 5).

DISCUSSION

The strong dynamic of mountain pine expansion at the expense of grassland habitat observed in the RNHPV is consistent with other reports from European mountain areas (Kullman 2002, Gellrich and Zimmermann 2007, Améztegui et al. 2010). This study improves on these previous works by (1) applying automated image classification techniques to estimate high-resolution (5 m) forest and grassland extent, (2) considering multiple dates in order to obtain finer temporal resolution and generate more robust land cover projections, and (3) using a long-term comparison of adjacent grazed and nongrazed zones.

Climate and mountain pine expansion in the RNHPV

The coincidence of rising mean summer temperatures and accelerated forest expansion during the 1980s suggests that warming in the RNHPV may have contributed to mountain pine installation and growth. Dendrochronological data collected in the French Alps have shown that the growth of *Pinus uncinata* responds positively to rising air temperatures and that *Pinus uncinata* germination and growth is more tightly coupled to interannual climatic variation than *Picea abies*, *Larix decidua*, or *Pinus cembra* (Rolland et al. 1998). The future trajectory of *Pinus uncinata* growth in response to climate change remains uncertain, however, as moisture may become an increasingly important limiting factor (Vittoz et al. 2008). Evidence from the Pyrenees and the Swiss Alps suggests that temperatures above a certain threshold lead to increased rates of evapotranspiration and drought stress that limit mountain pine growth (Rigling et al. 2002, Camarero and Gutiérrez 2007). In the RNHPV, previous studies provide evidence that decreased precipitation during the growing season can severely restrict the seedling establishment and sapling growth of mountain pine (Rolland 2001). Increasing frequency of extreme drought could exacerbate this phenomenon in the near future. For example, field observations indicated that the 2003 summer heat wave resulted in widespread mortality among juvenile pines (Biron, *personal observation*).

Our phenomenological model based on elevation and time does not include climatic variables that have been used in previous studies to model forest dynamics (e.g., Dullinger et al. 2004, Lischke et al. 2006, Wiegand et al. 2006). In particular, our use of topography as a static

explanatory variable represents environmental conditions indirectly and does not allow for explicit consideration of climate change in the model. The influence of climate on vegetation cover can nonetheless be inferred, however, given that our model was fit to historical changes in forest cover over a 60-year period. A further strength of our modeling approach was the ability to isolate the effect of land use vs. climate change on vegetation dynamics by means of long-term comparison of grazed and nongrazed areas, something largely overlooked by previous studies. Despite its simplicity, we demonstrate that our method is a straightforward and effective framework that meets the needs of land managers and that can be implemented with minimal data requirements. Although climate forcing remains a key contextual factor, our findings suggest that incorporating agricultural practices and socioeconomic trajectories into models of vegetation dynamics should be the first priority for future studies in managed ecosystems.

Identifying the role of land use in forest–grassland ecotone dynamics

Our comparison of grazed and nongrazed zones allowed us to infer the effects of grazing practices on observed land-cover dynamics. As found in other studies of forest expansion in mountainous areas (Gehrig-Fasel et al. 2007, Améztegui et al. 2010), the highest rates of mountain pine growth in the RNHPV occurred between 1500 and 1800 m, where both suitable climatic conditions and the presence of nurse shrubs enabled pine installation (Castro et al. 2004). Within the nongrazed zone, we suggest that the observed expansion of *Pinus uncinata* was largely the result of postdisturbance succession dynamics. Coal extraction in the nongrazed zone persisted through the 1950s, and the burst of forest growth observed between 1948 and 1978 followed the cessation of this industry (Fig. 2; Rolland 2001). Similarly, the demise of logging for the paper industry during the 1960s was connected to the subsequent boom in forest extent observed between 1978 and 1993 (Figs. 1 and 2). We conclude that the synergistic effect of changes in disturbance regimes and climate warming during the 1980s promoted the high rates of change in FI observed throughout the nongrazed zone (Fig. 4C).

Within the grazed zone, highly variable rates of vegetation change between 1948 and 2009 can be explained in part by the local influence of sheep grazing activity (Cairns and Moen 2004). The fact that a substantial portion of grazed pixels between 1500 and 1800 m remained nonforested for the duration of the study period indicates that grazing and related practices counteracted natural succession dynamics and allowed for the persistence of grasslands (Speed et al. 2010). On the one hand, the spatial concentration of flocks of sheep around infrastructure (shepherds' cabins and water sources) created locally overgrazed areas. On the

other hand, the decline of shrub removal practices at the landscape scale contributed to overall mountain pine densification and expansion. The combination of these two factors contributed to an increasingly polarized landscape, at the expense of grassland habitat and semiopen areas. It is interesting to note that important shifts in land cover took place even though the total number of sheep in the RNHPV remained fairly constant during the study period (~ 1.1 sheep/ha; Billet 2004). Consistent with these trends, our projected land-cover map in 2030 (Fig. 5) shows isolated patches of grassland within an increasingly forested landscape matrix.

Implications for conservation

Ongoing mountain pine expansion threatens to reduce habitat diversity and biological diversity in the RNHPV through the homogenization of land cover, a phenomenon that has already been documented in other mountain areas (Dullinger et al. 2003a, Vicente Serrano et al. 2004, Briggs et al. 2005, Haugo et al. 2011), as well as locally within the Vercors Regional Natural Park (Barbaro et al. 2001). Extensively managed, species rich, and calcareous grasslands in European mountain areas have been shown to decline over the last three decades and have thus been identified as a high conservation priority by the European Union Habitats Directive (Toland et al. 2008). The cessation of grazing activities and subsequent reduction in the abundance of subalpine and alpine grassland species has the potential to diminish plant diversity at the scale of vegetation communities within the RNHPV. Evidence from a comparable mountain system in South Tyrol, Italy indicates that the combination of land abandonment and land-use intensification in extensive grasslands leads to decreased species richness at the landscape scale (Tasser and Tappeiner 2002). In addition to reducing the habitat of diverse grasslands, forest expansion can have consequences for protected, emblematic animal species. For example, the black grouse (*Tetrao tetrix*) and the capercaillie (*Tetrao urogallus*) require a mosaic of open and semiforested habitats and are therefore vulnerable to landscape homogenization (Imbert and Rousset 1997, Suter et al. 2002, Schweiger et al. 2011).

Formulating a land management response to mountain pine expansion is particularly delicate in the RNHPV given that one of the primary aims of the reserve's creation was to protect what is known to be the largest *Pinus uncinata* forest in France (Rolland 2001). Although mountain pine expansion dynamics were underway well before the creation of the RNHPV, recent awareness of this phenomenon has compelled land managers to reconsider the initial conservation objectives of the RNHPV. For example, reserve officials have recently authorized shepherds to locally remove shrubs or trees, while ensuring that these practices are accompanied by scientific monitoring programs to assess their impact on vegetation dynamics.

In a broader context, mountain pine expansion is related to a number of other issues currently confronting land managers. First, several external drivers outside of the control of reserve officials have the potential to cause increasingly concentrated grazing: (1) more frequent droughts in southern France may reduce the productivity of Mediterranean pastures and incite more shepherds to bring their flocks to mountain areas such as the Vercors for extended summer periods, (2) the recent reemergence of the wolf in the Vercors has prompted shepherds to concentrate their flocks in open areas where it is easier to survey sheep and also to confine flocks at night (Espuno et al. 2004), (3) shepherds' growing demand for comfort tends to increase the proportion of time spent in the vicinity of cabins, and finally, (4) sheep races have been selected for increased weight at the expense of water stress tolerance, which renders flocks more dependent on water sources. Second, the RNHPV does have the ability to counteract grazing concentration by authorizing shrub burning and tree removal and also by implementing a broader network of equipped water points in order to avoid localized high stocking rates. Authorized shrub clearing in the Spanish Mediterranean mountains between 1986 and 2005 led to increased available pasture for sheep and also served to reduce the severity of naturally occurring fires (Lasanta et al. 2009). Based on previous work relating controlled fire-regimes to increased landscape heterogeneity and successful grassland conservation (Fuhlendorf and Engel 2004), we recommend that reserve officials implement a rotation system whereby shepherds would be allowed to burn a small area of shrubland in a different location once a season. Also, given that the location of water sources has been linked to the demography of surrounding shrub populations known to facilitate mountain pine expansion (Hunt 2001, Batllori et al. 2009), requiring shepherds to move water sources or vary the source used could help disperse flocks across a broader spatial area. Considering that sheep grazing alone is insufficient to restore and maintain areas of grassland habitat (Bartolomé et al. 2000), the implementation of a spatially heterogeneous disturbance regime seems necessary to preserve and restore grassland habitat beyond the immediate vicinity of shepherds' cabins. Specifically, we recommend that land managers concentrate their actions on zones of current grassland that are susceptible to become forested in 2030 according to our model (Fig. 5).

CONCLUSION

Our results establish a conclusive link between the presence of sheep grazing and related practices and the maintenance of grasslands. As such, our study is consistent with others that have recommended conservation strategies based on the continuation of traditional mountain land-use practices (Zervas 1998, Bartolomé et al. 2000, Dullinger et al. 2003a). We advocate that land managers in the RNHPV continue to encourage the

presence of transhumant grazing and associated land-use practices as a means of maintaining biologically diverse patchworks of forest and grassland habitat. The simple modeling approach used here represents a policy-relevant tool that provides land managers with a readily applicable protocol for assessing long-term land-cover changes in protected mountain areas. By identifying key locations where the intervention of land managers would be the most effective, our study also provides tools and guidelines for planning conservation strategies.

ACKNOWLEDGMENTS

This work was done within the framework of CAMELEON, a research project funded by the European ERA-NET Circle-2 (Climate Impact Research and Response Coordination for a Larger Europe) Mountain subnetwork. We thank Yves Durand (Météo France), Yann Buthion (Parc Naturel Régional du Vercors), Guy Lempérière, Manar Hatem, Abderrahim Bouasria, and Benoit Perrimond for their valuable input and discussions on this work. This research was conducted within the long-term research site Zone Atelier Alpes, a member of the ILTER-Europe network.

LITERATURE CITED

- Améztegui, A., L. Brotons, and L. Coll. 2010. Land use changes as major drivers of mountain pine (*Pinus uncinata*) expansion in the Pyrenees. *Global Ecology and Biogeography* 19:632–641.
- Anselin, L. 1995. Local Indicators of Spatial Association—LISA. *Geographical Analysis* 27:93–115.
- Barbaro, L., T. Dutoit, and P. Cozic. 2001. A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. *Biodiversity and Conservation* 10:119–135.
- Bartolomé, J., J. Franch, J. Plaixats, and N. G. Seligman. 2000. Grazing alone is not enough to maintain landscape diversity in the Montseny Biosphere Reserve. *Agriculture, Ecosystems and Environment* 77:267–273.
- Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to global warming. *Global Ecology and Biogeography* 18:460–472.
- Beniston, M., H. F. Diaz, and R. S. Bradley. 1997. Climatic change at high elevation sites: an overview. *Climate Change* 36:233–251.
- Billet, S. 2004. Histoire, Pastoralisme Evolution du milieu naturel sur les Hauts Plateaux du Vercors. Report. U.R. Agricultures et Milieux Montagnards, Groupement de Grenoble (CEMAGREF), Grenoble, France.
- Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243–254.
- Cairns, D. M., and J. Moen. 2004. Herbivory influences tree lines. *Journal of Ecology* 92:1019–1024.
- Camarero, J. J., and E. Gutiérrez. 2007. Response of *Pinus uncinata* recruitment to climate warming and changes in grazing pressure in an isolated population of the Iberian System (NE Spain). *Arctic, Antarctic and Alpine Research* 39:210–217.
- Castro, J., R. Zamora, J. A. Hódar, and J. M. Gómez, and L. Gómez-Aparicio. 2004. Benefits of using shrubs as nurse plants for reforestation in mediterranean mountains: a 4-year study. *Restoration Ecology* 12:352–358.
- Dalen, L., and A. Hofgaard. 2005. Differential regional tree line dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research* 37:284–296.
- Dirnböck, T., S. Dullinger, and G. Grabherr. 2003. A regional impact assessment of climate and land use change on alpine vegetation. *Journal of Biogeography* 30:1–17.
- Dullinger, S., T. Dirnböck, and G. Grabherr. 2003a. Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps (Austria). *Arctic, Antarctic, and Alpine Research* 35:434–441.
- Dullinger, S., T. Dirnböck, J. Greimier, and G. Grabherr. 2003b. A resampling approach for evaluating the effects of pasture abandonment on subalpine plant diversity. *Journal of Vegetation Science* 14:243–252.
- Dullinger, S., T. Dirnböck, and G. Grabherr. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invisibility. *Journal of Ecology* 92:241–252.
- Durand, Y., M. Latenser, G. Giraud, P. Etchevers, B. Lesaffre, and L. Merindol. 2009. Reanalysis of 44 years of climate in the French Alps (1958–2002): methodology, model validation, climatology, and trends for air temperature and precipitation. *Journal of Applied Meteorology and Climatology* 48:429–449.
- Espuno, N., B. Lequette, M. L. Pouille, P. Migot, and J. D. Lebreton. 2004. Heterogenous response to preventive husbandry during wolf recolonization of the French Alps. *Wildlife Society Bulletin* 32:1195–1208.
- Fuhlendorf, S. D., and D. M. Engel. 2004. Application of the fire-grazing interaction to restore a shifting mosaic of tallgrass prairie. *Journal of Applied Ecology* 41:604–614.
- Gehrig-Fasel, J., A. Guisan, and N. E. Zimmermann. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science* 18:572–582.
- Gellrich, M., and N. E. Zimmermann. 2007. Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: a spatial statistical modelling approach. *Landscape and Urban Planning* 79:65–76.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to global warming. *Ecology Letters* 12:1040–1049.
- Haugo, R. D., C. B. Halpern, and J. D. Bakker. 2011. Landscape context and long-term tree influences shape the dynamics of forest–meadow ecotones in mountain systems. *Ecosphere* 2:art91.
- Hunt, L. P. 2001. Heterogenous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology* 38:238–252.
- Imbert, M., and E. Rousset. 1997. Gestion des habitats naturels en faveur du tetras lyre dans le département de la Drôme: démarche expérimentale. *Biodiversité* 51–53.
- Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. *Wildlife Society Bulletin* 32:829–839.
- Kaplan, J. O., K. M. Krumhardt, and N. Zimmermann. 2009. The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28:3016–3034.
- Körner, C. 2007. Climatic treelines: conventions, global patterns, causes. *Erdkunde* 61:316–324.
- Körner, C., and J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31:713–732.
- Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* 90:68–76.
- Lasanta, T., J. Arnáez, M. P. Errea, L. Ortigosa, and P. Ruiz-Flano. 2009. Mountain pastures, environmental degradation, and landscape remediation: the example of a Mediterranean policy initiative. *Applied Geography* 29:308–319.
- Lischke, H., N. E. Zimmermann, J. Bolliger, S. Rickebusch, and T. J. Löffler. 2006. Treemig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling* 199:409–420.

- Macdonald, D., J. R. Crabtree, G. Wiesinger, T. Dax, N. Stamou, P. Fleury, J. Gutierrez Lazpita, and A. Gibon. 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management* 59:47–69.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-PLUS*. Springer-Verlag, New York, New York, USA.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2012. nlme: linear and nonlinear mixed effects models. R package version 3.1-103. <http://cran.r-project.org/web/packages/nlme/index.html>
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Rigling, A., O. Bräker, G. Schnitzer, and F. Schweingruber. 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-pinion in the Valais (Switzerland). *Plant Ecology* 163:105–121.
- Rolland, C. 2001. Influence du pâturage sur la germination et la survie des semis à pin à crochets dans la Réserve Naturelle des Hauts Plateaux du Vercors. Centre d'Ecologie Alpine, Grenoble, France.
- Rolland, C., J. Florence-Schueler, and J. Cooper. 1995. A comparison of the growth of mountain pine and spruce (*Pinus uncinata* Ram. and *Picea abies* Karst.) on a karstified calcareous flag in a temperate, mid-altitude mountain area (Vercors, France). *Revue de Géographie Alpine* 83:17–32.
- Rolland, C., V. Petitcolas, and R. Michalet. 1998. Changes in radial tree growth for *Picea abies*, *Larix deciduas*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees* 13:40–53.
- Sankey, T. T., C. Montagne, L. Graumlich, R. Lawrence, and J. Nielsen. 2006. Twentieth century forest–grassland ecotone shift in Montana under differing livestock pressure. *Forest Ecology and Management* 234:282–292.
- Schweiger, A. K., U. Nopp-Mayr, and M. Zohmann. 2011. Small-scale habitat use of black grouse (*Tetrao tetrix* L.) and rock ptarmigan (*Lagopus muta helvetica* Thienemann) in the Austrian Alps. *European Journal of Wildlife Research* 58:35–45.
- Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2010. Experimental evidence for herbivore limitation of the treeline. *Ecology* 91:3414–3420.
- Suter, W., R. F. Graf, and R. Hess. 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology* 16:778–788.
- Tasser, E., and U. Tappeneir. 2002. Impact of land use change on mountain vegetation. *Applied Vegetation Science* 5:173–184.
- Tasser, E., J. Walde, U. Tappeiner, A. Teutsch, and W. Noggler. 2007. Land use changes and natural reforestation in the Eastern Central Alps. *Agriculture, Ecosystems and Environment* 118:115–129.
- Theurillat, J. P., and A. Guisan. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* 50:77–109.
- Toland, J., W. Jones, J. Eldridge, E. Thorpe, and E. O'Hara. 2008. LIFE and Europe's grasslands: restoring a forgotten habitat. Office for Official Publications of the European Communities, Luxembourg.
- Tømmervik, H., B. Johansen, J. A. Riseth, S. R. Karlsen, B. Solberg, and K. A. Hogda. 2009. Above ground biomass changes in the mountain birch forests and mountain heaths of Finnmarksvidda, northern Norway. *Forest Ecology and Management* 257:244–257.
- Vicente Serrano, S. M., T. Lasanta, and A. Romo. 2004. Analysis of the spatial and temporal evolution of vegetation cover in the Spanish central Pyrenees: the role of human management. *Environmental Management* 34:802–818.
- Vidal, J. P., E. Martin, L. Franchistéguy, M. Baillon, and J. M. Soubeyrou. 2010. A 50-year high-resolution atmospheric reanalysis over France with the Safran system. *International Journal of Climatology* 30:1627–1644.
- Villaret, J. C., and J. M. Genis. 2004. Site Natura 2000–I27. Landes, pelouses, forêts et habitats rocheux des Hauts Plateaux du Vercors. Cartographie de la végétation et des habitats et Atlas cartographique. Conservatoire botanique national alpin 2:1–34.
- Vittoz, P., B. Rulence, T. Largey, and F. Freléhoux. 2008. Effects of climate and land use change on the establishment and growth of cembra pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the central Swiss Alps. *Arctic, Antarctic and Alpine Research* 40:225–232.
- Wang, Z., and L. A. Goonewardene. 2004. The use of mixed models in the analysis of animal experiments with repeated measures data. *Canadian Journal of Animal Science* 84:1–11.
- Watkinson, A. R., and S. J. Ormerod. 2001. Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology* 28:233–237.
- Wearne, L. J., and J. W. Morgan. 2001. Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. *Arctic, Antarctic, and Alpine Research* 33:369–377.
- Wiegand, T., J. J. Camarero, N. Ger, and E. Gutiérrez. 2006. Abrupt population changes in treeline ecotones along smooth gradients. *Journal of Ecology* 94:880–892.
- Willmott, C.J. 1982. Some comments on the evaluation of model performance. *Bulletin of the American Meteorological Society* 63:1309–1313.
- Zald, H. S. 2009. Extent and spatial patterns of grass bald land cover change (1948–2000), Oregon Coast Range, USA. *Plant Ecology* 201:517–529.
- Zervas, G. 1998. Quantifying and optimizing grazing regimes in Greek mountain systems. *Journal of Applied Ecology* 35:983–986.

SUPPLEMENTAL MATERIAL

Appendix

Level-2 model residuals for the four dates considered (1948, 1978, 1993, and 2009) ([Ecological Archives A024-071-A1](#)).

Supplement

Forest/nonforest rasters for the four dates considered, a 25-m resolution digital elevation model, and a shapefile representing the nongrazed area ([Ecological Archives A024-071-S1](#)).

Chapter IIIB

*Observed long-term greening of alpine vegetation in a protected area of the French Alps**

* **Carlson, B. Z.**, Dentant, C., Bonet, R., Thuiller, W. & Choler, P. Observed long-term greening of alpine vegetation in a protected area of the French Alps. (**In prep.**).

Introduction

Changes in the productivity of vegetation cover observed by satellite can provide insight into ground-level shifts in the structure and functioning of terrestrial ecosystems (Kerr and Ostrovsky 2003; Pettorelli *et al.* 2005). Potential drivers of spatial and temporal trends in vegetation greening (increased productivity) and browning (decreased productivity), often quantified using the Normalized Difference Vegetation Index (NDVI), include climate or land-use change (Jia *et al.* 2003; Metternicht *et al.* 2010), disturbance (Goetz *et al.* 2005) or plant succession dynamics (Walker *et al.* 1995). NDVI provides an optical proxy of standing biomass and photosynthetic activity (Myneni and Williams 1994), and when integrated over time can generate a number of metrics for the study of vegetation dynamics, including the duration of the growing season, peak greenness, and rates of green-up and senescence (Busetto *et al.* 2010). In temperate mountain ecosystems such as the European Alps, quantifying potential shifts in NDVI is of high interest in order to monitor responses of alpine vegetation to global change and to complement observational field data. Furthermore, shifts in the productivity of mountain forests and grasslands have strong implications for a number of ecosystem services in alpine landscapes, including carbon storage (Rossini *et al.* 2012) and erosion control through root systems (Meusbürger *et al.* 2010).

Greening and browning dynamics in alpine study areas have received substantially less attention than in Arctic and sub-Arctic regions, where multiple field and remote sensing-based studies indicate widespread patterns of greening driven by shrub expansion into tundra during recent years (Tape *et al.* 2006; Myers-Smith *et al.* 2011). However, there are a number of reasons to expect temporal trends in NDVI in the context of the European Alps, including recent increases in air temperature above the global average increase (Beniston 2005), decreases in snow cover duration below 2000 m above sea level (a.s.l.; Hantel and Hirt-Wielke 2007), glacier retreat and ensuing plant colonization (Cannone *et al.* 2008), tree line rise and forest expansion (Carlson *et al.* 2014; Gehrig-Fasel *et al.* 2007), and observed changes in plant diversity observed on European summits (Pauli *et al.* 2012). In the French Alps in particular, reanalysis of historical climate data shows an average increase of 1° C since the late 1950s (Durand *et al.* 2009a), and a significant decrease in the length of snow cover duration since the late 1980s (Durand *et al.* 2009b). One possible explanation for the lack of NDVI trend studies in alpine environments is

that the 1 km spatial resolution of the widely used Advanced Very High Resolution Radiometer satellite (AVHRR) is poorly suited to quantify change heterogeneous mountain landscapes (Fontana *et al.* 2008). One study using AVHRR images over Europe between 1982 and 1999 showed an overall increase in NDVI (up to 0.1), however the authors did not report significant greening trends for mountainous areas in particular (Julien *et al.* 2006).

The Moderate Resolution Imaging Spectroradiometer satellite (MODIS), which was launched in 1999 and provides 8-day composite NDVI products at 250 m resolution, currently enables unprecedented opportunity to carry out NDVI trend analysis over more than 15 years in temperate mountain study areas. A recent study utilizing MODIS NDVI between 2000 and 2012 demonstrated that inter-annual variability in the productivity of alpine grasslands in the French Alps is largely determined by snow free period, although temporal trends in peak NDVI were not investigated specifically (Choler 2015). Considering that MODIS spectral data have been used for vegetation trend analysis at the global scale (Zhao and Running 2010), and have been validated with respect to ground measurements and other sensors (Fisher and Mustard 2007), trends in NDVI detected with MODIS can be considered to represent actual changes in vegetation cover as opposed to sensor artifacts. In an alpine context, however, the 250 m ground resolution limits the interpretation of NDVI trends with respect to alpine plant communities distributed at fine spatial resolution (Virtanen and Ek 2014).

With the launch of the Landsat-8 satellite in 2013, the Landsat data program continues to provide the longest available record of earth surface observations at the relatively high ground resolution of 30 m (Roy *et al.* 2014). Given that spectral bands and sensor characteristics are not identical across platforms, however, careful image processing is necessary in order to render time series analysis possible using scenes acquired by different Landsat satellites (Chander *et al.* 2009; Roy *et al.* 2016). The higher spatial resolution of Landsat imagery as compared to MODIS allows for the quantification of changes in NDVI closer to the spatial resolution of both (i) drivers of vegetation change, for example grazing or other land-use practices and (ii) heterogeneity of alpine habitats and plant communities (Dedieu *et al.* 2016). A study conducted using Landsat-5 imagery in the Pyrenees, for example, demonstrated decreases in NDVI in areas characterized by intensive grazing and increases in NDVI in un-managed alpine grasslands between the late-1980s and the late 2000s (Gartzia *et al.* 2016). To complement existing research on NDVI dynamics in temperate mountain ecosystems, we believe that there is a need to consider results from multiple

satellite platforms to confirm greening and browning trends in alpine areas, and also to intersect satellite data with independent, ground-level field observations in order to attribute observed changes to specific habitats and vegetation communities.

In this observational study, we investigated changes in peak NDVI in a 918 km² protected area of the southwestern French Alps. We chose to focus our study on the Ecrins National Park in order to take advantage of exceptionally high-quality field data on the spatial distribution of land cover types, plant communities and the presence of domestic grazing. To investigate the question of recent greening or browning in the Ecrins National Park, we sought to (i) quantify trends in peak NDVI (NDVI_{max}) between 2000 and 2015 using both MODIS and Landsat satellites; (ii) identify which land cover types and plant communities show the most change; (iii) determine if NDVI max trends were initiated in the last 15 years or were already underway during the late 1980s and 1990s; and (iv) to test for differences in NDVI max trends between grazed and non-grazed areas, assuming that land abandonment would be a more important factor within grazed areas. We also made use of a biological reserve within the Ecrins National Park, which has not been subject to human passage or land-use during the study period, in order to test for climate-related changes in vegetation productivity. Finally, we used aerial photographs to provide examples of vegetation change in the Ecrins National Park and to propose possible ground-level mechanisms contributing to observed shifts in NDVI_{max}.

Methods

Field mapping and vegetation sampling

The Ecrins National Park covers an expansive alpine area including the Oisans, Thabor, Pelvoux, Champsaur and Grand Rousses massifs with over 150 summits over 3000 m a.s.l.. Elevation gradients range from 700 to 4100 m a.s.l.. Bedrock in the interior of the park consists of granite and ancient gneiss on the highest summits, with zones of sedimentary rock frequently occurring in peripheral areas of the park. Floristic diversity in the Ecrins National Park is rich, reflecting influences from the Mediterranean and northern alpine floras. Between 1995 and 2000, park staff carried out exhaustive field mapping of habitats within the Ecrins National Park at the polygon level, primarily collecting data on land cover and the presence or absence of domestic

grazing during the summer months. Land-cover classes utilized in this study are listed in the legend of Figure 1A. In 1995, the 689 ha Lauvitel Natural Reserve was designated within the park for the study and monitoring of ecosystem dynamics. Land-use was non-existent in the area prior to 1995, and currently the reserve is inaccessible to the public.

We assembled a database of 3390 vegetation plots from mountain forest, subalpine grasslands, shrub and heathlands, alpine meadows and rock and scree habitats. Data were provided by the Conservatoire Botanique National Alpin (<http://www.cbn-alpin.fr/>) and the Ecrins National Park. Floristic surveys were conducted from 2000 to 2015 and consisted of recording all vascular plants occurring in a sampled area of 100 m². The geo-location error of vegetation plots was less than 10 m. Using a clustering algorithm detailed in (Dedieu *et al.* 2016), we grouped vegetation plots into fifteen plant communities representative of turnover in plant community diversity in our study area.

N	Community	Mean elevation	Dominant co-occurring species
114	1	1039	<i>Papaver rhoeas</i> , <i>Cirsium arvense</i> , <i>Polygonum aviculare</i>
232	2	1125	<i>Lonicera xylosteum</i> , <i>Fraxinus excelsior</i> , <i>Fragaria vesca</i>
64	3	1329	<i>Sorbus aria</i> , <i>Abies alba</i> , <i>Acer opalus</i>
341	4	1411	<i>Achillea millefolium</i> , <i>Dactylis glomerata</i> , <i>Lotus corniculatus</i>
178	5	1546	<i>Urtica dioica</i> , <i>Rubus idaeus</i> , <i>Dryopteris filix-mas</i> , <i>Rubus idaeus</i>
420	6	1617	<i>Festuca laevigata</i> , <i>Teucrium chamaedrys</i> , <i>Lotus corniculatus</i>
301	7	1774	<i>Vaccinium myrtillus</i> , <i>Rhododendron ferrugineum</i> , <i>Geranium sylvaticum</i>
143	8	1786	<i>Potentilla erecta</i> , <i>Bartsia alpina</i> , <i>Carex davalliana</i>
361	9	1959	<i>Geranium sylvaticum</i> , <i>Lotus corniculatus</i> , <i>Trifolium pratense</i>
517	10	2013	<i>Poa alpina</i> , <i>Plantago alpina</i> , <i>Nardus stricta</i>
323	11	2160	<i>Juniperus communis</i> , <i>Carex sempervirens</i> , <i>Anthoxanthum odoratum</i>
220	12	2341	<i>Helictotrichon sedenense</i> , <i>Poa alpina</i> , <i>Festuca violacea</i>
134	13	2799	<i>Leucanthemopsis alpina</i> , <i>Saxifraga oppositifolia</i> , <i>Silene acaulis</i> subsp. <i>Bryoides</i>
19	14	2830	<i>Eritrichium nanum</i> , <i>Artemisia eriantha</i> , <i>Ranunculus glacialis</i>
10	15	2837	<i>Cerastium pedunculatum</i> , <i>Poa laxa</i> , <i>Agrostis rupestris</i>

Table 1. Dominant co-occurring species, number of vegetation plots (N), mean elevation (m a.s.l.) for fifteen plant communities identified by clustering analysis.

Image processing and NDVI calculation

MODIS surface reflectance products covering the study area were downloaded for the months of June, July and August between 2000 and 2015 from the Land Processes Distributed Active Archive Center (LP DAAC; <http://e4ftl01.cr.usgs.gov/MOLT/>). Data consisted of

composite reflectance, i.e. representing the highest cloud-free observed value over an 8-day period. Surface reflectance in the Red and Near-Infrared (NIR) were used to calculate the Normalized Difference Vegetation Index ($\text{NIR} - \text{Red} / \text{NIR} + \text{Red}$).

Level 1T Landsat-5 (Thematic Mapper), Landsat-7 (ETM+, SLC-on) and Landsat-8 (OLI) images were obtained from the Landsat Earth Explorer data portal managed by the United States Geologic Survey (USGS; <http://earthexplorer.usgs.gov>). In order to align with available MODIS imagery, we downloaded Landsat images covering the Ecrins National Park for the months of June, July and August for the years 1984, 1985 and 1987 (Landsat-5), 2000, 2001 and 2002 (Landsat-7) and 2013, 2014 and 2015 (Landsat-8). We did not to use Landsat-7 images from 2003 onward due to damage occurring to the Scan Line Corrector in May, 2003. Figure S1 shows the distribution of dates for utilized Landsat-5, 7 and 8 images. Following standard methodology (Chander *et al.* 2009; Roy *et al.* 2016), we converted Landsat-5, 7 and 8 spectral bands from calibrated digital numbers to top-of-atmosphere (TOA) reflectance. Prior to processing, all bands were re-projected from Universal Transverse Mercator to the Lambert Conformal Conic coordinate system. Recent studies (Holden and Woodcock 2016; Roy *et al.* 2016) demonstrate that NDVI measured by Landsat-8 is systematically higher than NDVI measured by Landsat-7, largely due to higher measured reflectance in the near-infrared band. To account for this, we applied a linear transformation function calibrated at the scale of the conterminous United States by Roy *et al.* (2016) to convert Landsat-8 NDVI values to Landsat-7 NDVI equivalence.

NDVI_{max} trend estimation

In order to estimate peak photosynthetic activity within the Ecrins National Park, peak NDVI (NDVI_{max}) values were extracted for each grid cell and for each study year (for MODIS, 2000:2015, and for Landsat, 1984, 1985, 1987, 2000:2002 and 2013:2015). We considered that extracting NDVI_{max} for the months of June, July and August would account for most of the variation in plant phenology due to inter-annual climate variability and also differences in elevation and plant strategy. For our analysis, we retained grid cells (i) with a mean MODIS NDVI_{max} value above 0.1 for the 2000:2015 period; (ii) that were less than 3000 m a.s.l., given that vegetation above this elevation in the Ecrins National Park is largely cliff-dwelling and not well-suited to analysis using space-borne moderate resolution remote sensing data; and (iii) that corresponded to forest, dense scrub, 10-40% and 40-60% tree and shrub and cover, dwarf shrub,

grassland, mineral and vegetated mineral land cover classes (Figure 1A; glacier, wetland, ravines and water bodies were excluded). In total, this filtering process left us with 32,796 grid cells at 250 m resolution for analysis. In order to assess trends in MODIS NDVI between 2000 and 2015, Theil-Sen single median linear regression (Sen 1968) was applied to each grid cell using year as the explanatory variable and NDVI_{max} as the response variable, and slope parameters were extracted for each grid cell.

We then sought to assess agreement between MODIS and Landsat sensors in regard to changes in NDVI_{max} between 2000 and 2015. To ensure temporal consistency, we retained only the years in common to both sensors (2000:2002 and 2013:2015). To ensure spatial consistency, we calculated the mean of 30 m Landsat NDVI_{max} values within 250 m MODIS grid cells. For both sensors and at 250 m resolution, we calculated the log-response ratio of NDVI_{max} for each grid cell (Δ NDVI_{max}; Hedges *et al.* 1999), as follows:

$$\Delta \text{NDVI}_{\text{max}} = \ln (\text{NDVI}_{\text{max 2013:2015}} / \text{NDVI}_{\text{max 2000:2002}})$$

where \ln is the natural logarithm, NDVI_{max 2013:2015} is the mean NDVI_{max} for the years 2013:2015, and NDVI_{max 2000:2002} is the mean NDVI_{max} for the years 2000:2002. For spatial comparison, we mapped Δ NDVI_{max} for both sensors and calculated overlap between positive and negative change in NDVI_{max}.

In order to take advantage of the higher ground resolution and longer historical record of Landsat imagery, we also calculated the log-response ratio of NDVI_{max} at initial 30 m resolution. We applied the same selection criteria as for analysis with MODIS at 250 m (less than 3000 m a.s.l., mean NDVI_{max} for the period 2000:2015 above 0.1, and only the land cover classes of interest, see above), which resulted in 1,997,476 grid cells for analysis. Δ NDVI_{max} was calculated (1) between periods 1984, 1985 and 1987 and 2000:2002, and (2) between periods 2000:2002 and 2013:2015. To align layers, i) the land cover map was resampled from 100 m to 30 m using the nearest neighbor algorithm and ii) a digital elevation model at 25 m resolution provided by the French National Institute of Geographic Information (IGN) was resampled to the same 30 m grid using bilinear interpolation. For each 30 m grid cell, we also assigned 0 or 1 based on the presence or absence or potential grazing activity. Finally, for each of the 3390

vegetation plots, we extracted values for $\Delta \text{NDVI}_{\text{max}}$ for both time periods, elevation and land cover.

To assess changes in NDVI in the absence of land-use pressure, $\Delta \text{NDVI}_{\text{max}}$ for the period 1984:2015 were extracted specifically for the Lauvitel Natural Reserve. Using a stratified random sampling routine, $\Delta \text{NDVI}_{\text{max}}$ values for grid cells occurring in comparable topographic contexts from locations throughout the park (equivalent range of elevation and slope aspects) were extracted in order to compare NDVI change in the Lauvitel Natural Reserve to vegetation dynamics at the scale of the park.

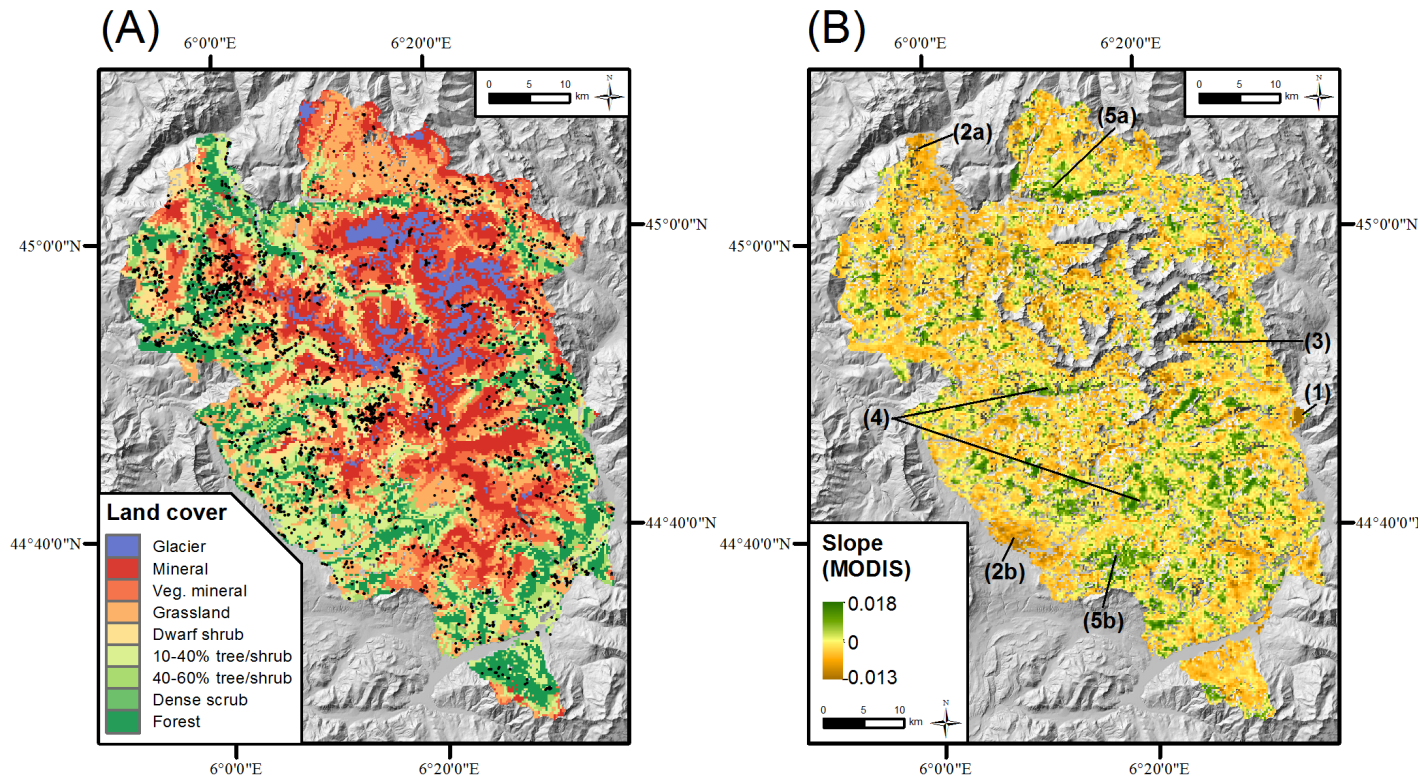


Figure 1. (A) Land cover classes corresponding to the year 2000 for the Ecrins National Park. Black points represent the location of vegetation plots ($N = 3324$). (B) Linear slope coefficients between year and MODIS NDVI max for each 250m grid cell between 2000 and 2015. Numbers and leader lines show the location of examples cited in the text (Results paragraph 1).

Results

Spatial trends in MODIS and Landsat NDVI_{max}

The distribution of NDVI_{max} slope values estimated using MODIS NDVI time series had a slight positive skew (mean = 0.0014, max. = 0.018, min. = -0.013) and values were highly spatially structured (Figure 1B). Areas of concentrated negative slope values shown in dark brown in Figure 1B could generally be attributed to local factors, i.e. (1) a fire occurring in a sawmill in the town of Argentière-la-Bessée in April, 2010; (2a-b) areas of agricultural activity; and (3) a forest that was demolished by either avalanche or landslide activity in a steep valley, according to aerial photos. Areas of concentrated positive slope values shown in dark green were more widespread, and typically occurred in the interior region of the park at mid- to high elevations. South-facing slopes above east-west oriented valleys showed fairly consistent greening trends (4), as well as grassland plateaus (5a-b; Figure 1B). Overall, 56% of grid cells had a slope value above 0.001, 16% had a slope value below -0.001 and the remaining 28% had slope values between -0.001 and 0.001.

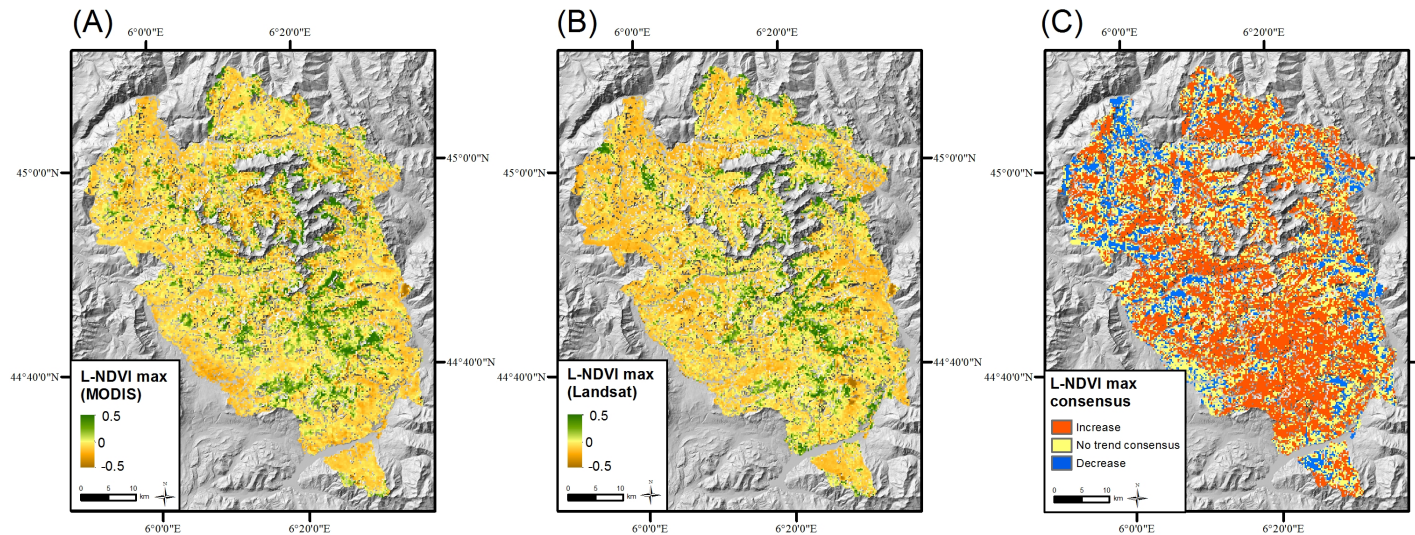


Figure 2. (A) Log-response ratio between mean values of NDVI max for the periods 2000:2002 and 2013:2015 (Δ NDVI max) derived from MODIS (A) and Landsat (B). (C) Overlap of positive (orange) and negative (blue) changes in Δ NDVI max between MODIS and Landsat sensors. Yellow corresponds to areas where (1) sensors lacked consensus on directional change or (2) both MODIS and Landsat detected no change. The spatial resolution of grid cells is 250 m.

Values of NDVI_{max} at 250 m resolution estimated from Landsat and MODIS imagery were highly correlated across study years (Pearson's $R = 0.95$, $P < 2.2\text{e-}16$), although MODIS NDVI was on average higher than Landsat NDVI. The higher values of MODIS NDVI could be due to both sensor differences as well as the higher temporal resolution of MODIS imagery, capable of capturing subtle variation in the timing of peak vegetation greenness. Given our interest in proportional change, however, we did not consider this absolute difference between MODIS and Landsat NDVI to be problematic. The spatial distributions of log-response ratios of NDVI_{max} ($\Delta \text{NDVI}_{\text{max}}$) derived from Landsat and MODIS sensors showed strong agreement (Figure 2), and were spatially coherent with respect to the distribution of slope values shown in Figure 1B. In Figure 2C and according to both Landsat and MODIS, 52% of grid cells were characterized by an increase in $\Delta \text{NDVI}_{\text{max}}$, 34% showed no consensus trend and 15% were characterized by a consensus decrease in $\Delta \text{NDVI}_{\text{max}}$. These results indicated concordance between trends detected by MODIS and Landsat as well as an overall greening tendency accompanied by localized areas of browning in the Ecrins National Park since 2000 (Figure 2).

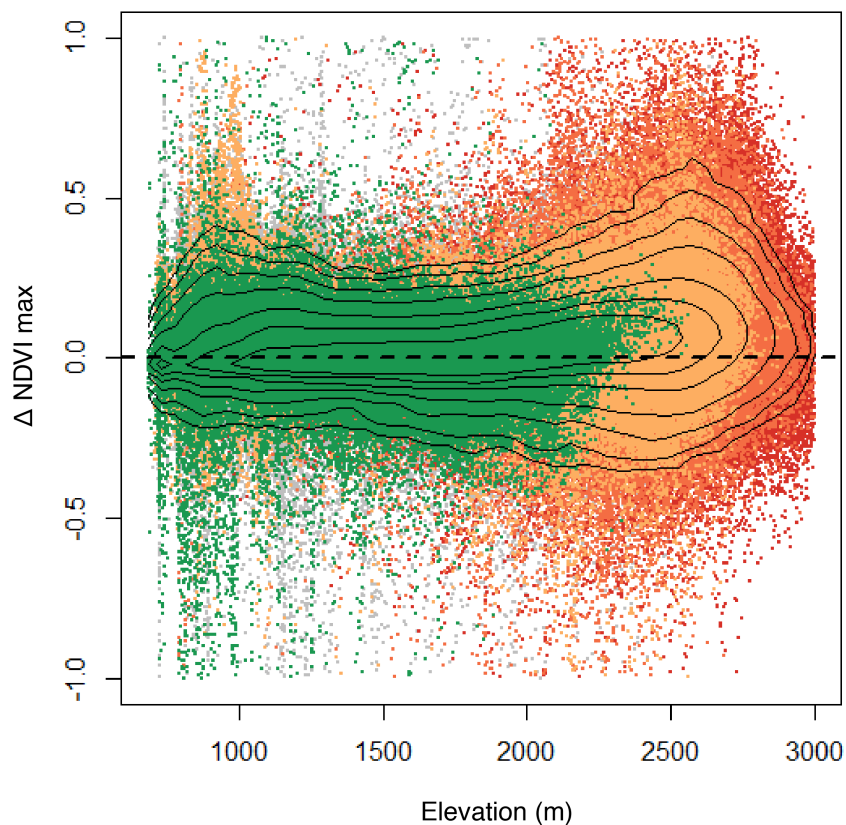


Figure 3. (A) Log-response ratio between mean values of NDVI max for the periods 2000:2002 and 2013:2015 (Δ NDVI max) relative to elevation (m a.s.l.) for 30 m Landsat grid cells ($N = 1,996,307$). Green points represent forest, light orange points represent grasslands, dark orange points represent vegetated scree and talus, red points represent sparsely vegetated scree and talus and grey points represent all other Delphine land cover classes. Grid cells with Δ NDVI max above 1 or less than -1 were considered outliers and removed from the analysis.

Change in $NDVI_{max}$ in relation to topography, land cover, plant communities

Given the general consensus between spatial and temporal trends in $NDVI_{max}$ estimated by MODIS and Landsat between 2000 and 2015, we proceeded with analysis at the initial 30 m ground resolution of Landsat 5-8 imagery. Contour lines shown in Figure 3 indicate that across elevations (between 800 and 3000 m a.s.l.), consistently more than half of Δ $NDVI_{max}$ values were positive. At low elevations (<1000 m a.s.l.), certain grasslands were characterized by pronounced increases in $NDVI_{max}$ while a number of forested pixels showed radical decreases in

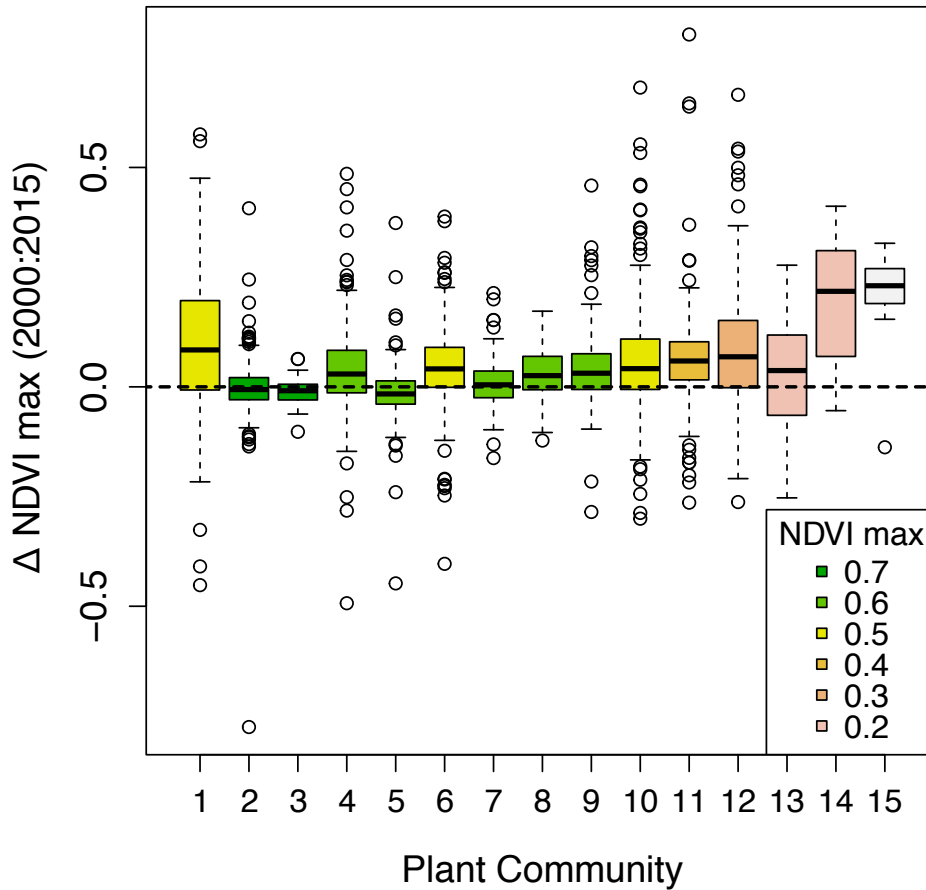


Figure 4. Boxplots of log-response ratio between mean values of NDVI max for the periods 2000:2002 and 2013:2015 (Δ NDVI max) for dominant plant communities in the Ecrins National Park. Color corresponds to mean NDVI max across study years for each plant community (described in Table 1). NDVI max and Δ NDVI-max values were derived from Landsat imagery at 30 m.

NDVI_{max}, although these observations fell outside of contour lines (Figure 3). Mid-elevations (between 1000 and 2000 m a.s.l.) exhibited a consistent majority greening trend across land cover classes with only a small proportion of Δ NDVI_{max} values above 0.5 or below -0.5. Above 2000 m a.s.l. and in non-forested habitats, contour lines indicated a peak in positive Δ NDVI_{max} values in grassland, vegetated mineral and mineral land cover classes. Specifically, the highest values of Δ NDVI_{max} were concentrated at 2500 m a.s.l. (Figure 3).

Plant communities ordered according to mean elevation exhibited a similar pattern as compared to land cover types (Figure 4). Only four communities showed a distribution of Δ NDVI_{max} centered at 0, including communities 2 (montane shrub), 3 (montane forest), 5 (nettle and raspberry) and 7 (sub-alpine shrub; Table 1). All other communities had positive median values of Δ NDVI_{max} (Figure 4). Low-elevation grasslands found in clearings and fields (community 1), showed exceptionally high values of Δ NDVI_{max} with first and third quartiles entirely above 0. Additionally, plant communities above 2000 m a.s.l. exhibited high values of Δ NDVI_{max}, including alpine grasslands (communities 10 and 13), dwarf shrub (community 11) and scree and talus vegetation located at the highest elevations (communities 13-15; Table 1; Figure 4).

	% Greening (1984:2015)	% Browning (1984:2015)	% Greening (beginning in 2000)	% Browning (beginning in 2000)
Forest	35.68	0.47	1.99	61.85
Grassland	66.90	1.06	7.55	24.48
Veg. mineral	68.38	1.54	7.99	22.09
Mineral	55.44	2.99	16.43	25.13
All	56.63	1.27	7.15	34.95

Table 2. Percentage of grid cells showing greening (Δ NDVI max > 0) or browning (Δ NDVI max < 0) trends during the study period for each land cover class.

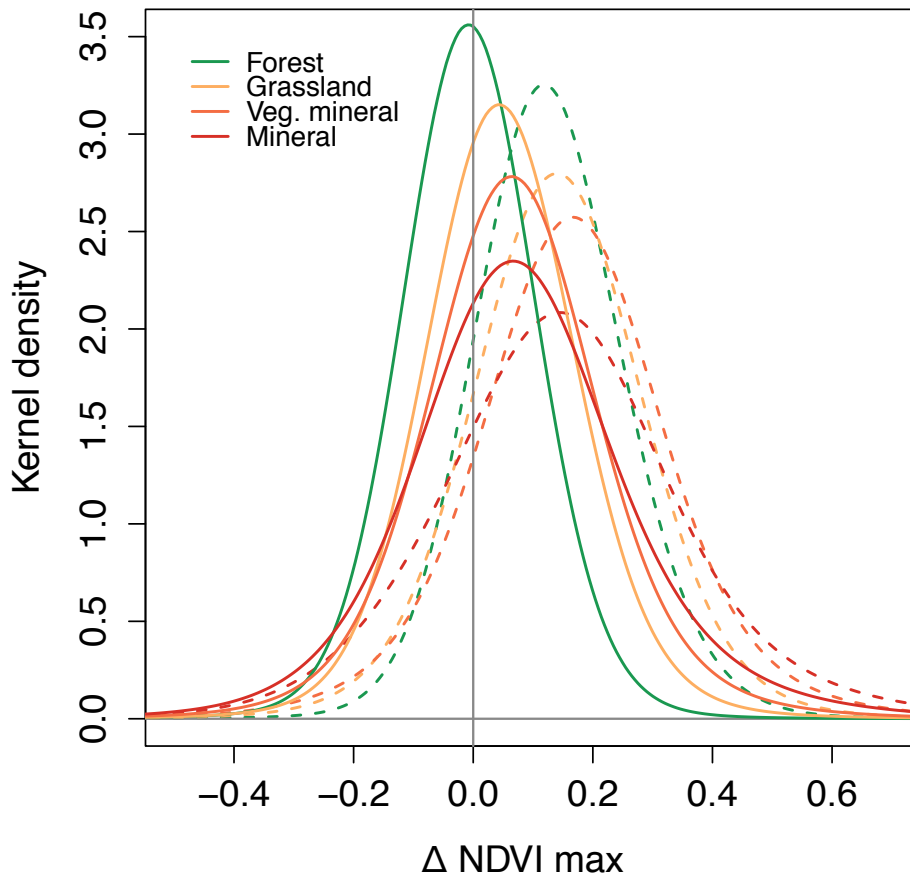


Figure 5. Kernel density of Δ NDVI max values between 1984 and 2002 (dashed lines) and between 2000 and 2015 (solid lines). Colors correspond to land cover classes. Bandwidth was fixed using the standard deviation of the original data.

Temporal origins of greening and browning dynamics and land-use context

Across land cover classes, greening trends in the Ecrins National Park were stronger between 1984 and 2002 as compared to between 2000 and 2015 (Figure 5). Thirty-six percent of forests exhibited greening between 1984 and 2015, whereas over 50% of grasslands, vegetated mineral and mineral land cover classes showed consistent greening over the same period (Table 2). Less than two-percent of 30 m grid cells in the study area were characterized by browning between 1984 and 2015, however 35% of grid cells (and 62% of forest) began browning from 2000 onward. While overall only 7% of the park showed greening dynamics beginning in 2000, 16% of mineral grid cells showed increases in NDVI_{max} initiated after 2000 (Table 2). Greening

dynamics were both predominant in the Lauvitel Natural Reserve and representative of $\Delta \text{NDVI}_{\text{max}}$ values sampled from comparable topographic contexts elsewhere in the park (Figure 6). Furthermore, increase in NDVI_{max} was significantly higher in areas subject to domestic grazing for both time periods (1984:2002 and 2000:2015; Figure 7). In both Figures 6 and 7, the slow-down of greening dynamics indicated in Figure 5 is clearly visible.

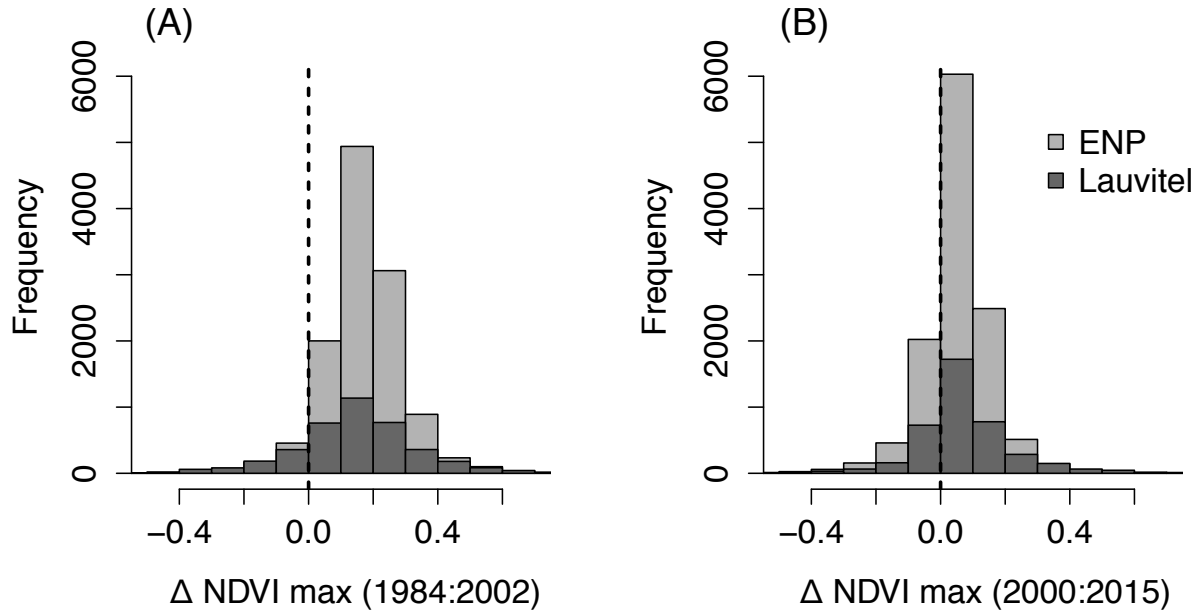


Figure 6. Histograms of $\Delta \text{NDVI}_{\text{max}}$ values between 1984 and 2002 (A) and between 2000 and 2015 (B) for a natural reserve (dark grey; Lauvitel) and for 12000 grid cells randomly sampled from equivalent topographic contexts throughout the Ecrins National Park (ENP).

Discussion

Our study combined time series from multiple satellites (MODIS, Landsat-5, 7, 8) with independent field data to investigate changes in peak plant productivity in a French high mountain national park over the last thirty years. We found overall concordance between trends detected by Landsat and MODIS satellites, which supported full exploitation of the Landsat record at 30 m ground resolution. Increases in NDVI_{max} over the last sixteen years (2000:2015)

were concentrated in above-tree line habitats at high elevation (~ 2500 m a.s.l.), suggesting that the main greening dynamic in our study area was not forest expansion or tree line rise but rather increased productivity of alpine grassland and scree communities. The long-term (1984:2015) Landsat record indicated ongoing greening trends in over half of the Ecrins National Park, once again mostly in non-forested land cover classes, as well as recent greening dynamics initiated since 2000 in high-elevation scree habitats. We also found that increase in NDVI_{max} was more pronounced between 1984 and 2002 than between 2000 and 2015, suggesting a slowing of greening dynamics during recent years. Although we did not detect widespread long-term browning trends ($<2\%$ of the study area), approximately a third of the Ecrins National Park showed decreases in NDVI_{max} over the last fifteen years. Observed greening in a natural reserve without human activity suggests that climate change in our study area, and in particular warming air temperatures and decreased snow cover duration (Durand *et al.* 2009a-b; Dedieu *et al.* 2016), has contributed to increases in high-elevation plant productivity independent of the effects of land-use. Higher overall values of greening in areas subject to grazing nonetheless indicate that shifts in land-use practices (e.g. land abandonment) can locally accelerate greening dynamics in addition to climate.

Potential causes of alpine vegetation greening

We attribute shifts in NDVI_{max} at low elevation (<1500 m a.s.l.; Figure 3) largely to the effects of local land-use practices, including agriculture, grazing and forestry. Specifically, we consider the increase in NDVI_{max} in montane fields and grasslands (communities 1 and 4; Figure 4; Table 1) to be linked to forest expansion since 2000 following pasture abandonment. This interpretation is supported by a previous modeling study testing the effects of land-use on vegetation structure in the Ecrins National Park, which found that land abandonment lead to forest densification and expansion at the expense of grassland communities (Boulangeat *et al.* 2014). Observational studies elsewhere in the Alps (Carlson *et al.* 2014) and Pyrenees (Améztegui *et al.* 2010) also point to the widespread nature of land-use related forest expansion throughout

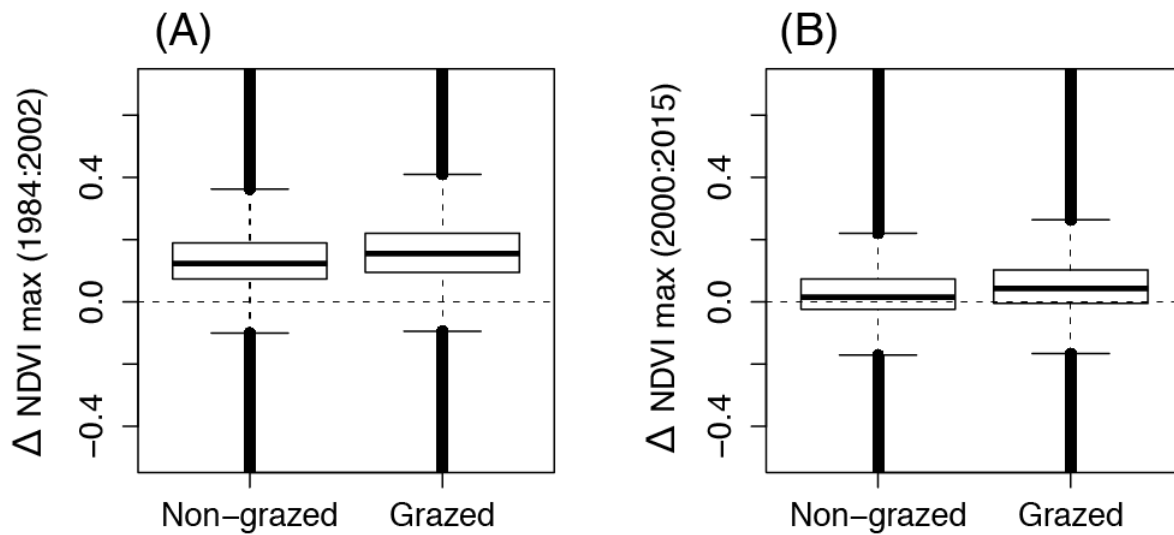


Figure 7. Boxplots of Δ NDVI max values between 1984 and 2002 (A) and between 2000 and 2015 (B) for non-grazed and grazed areas.

European mountain ranges. Other disturbances in addition to grazing affecting the position of the forest-grassland ecotone include fire and logging, however we consider that these drivers are relevant only for small, isolated areas of the Ecrins National Park. Although the NDVI_{max} of forest plant communities remained largely stable between 2000 and 2015 (community 3; Table 1; Figure 4), the increase in NDVI_{max} for one-third of forest land cover between 1984 and 2015 (Table 2) suggests that climate warming and decreases in snow cover duration at low elevations (Durand *et al.* 2009a-b) may have contributed to gradual greening in certain montane forests throughout the park.

The strongest observed greening trends occurred in the context of high-elevation (>2000 m a.s.l.) plant communities and habitats. More than half of grassland, vegetated mineral and mineral habitats within the Ecrins National Park showed consistent increases in NDVI_{max} between 1984 and 2015 (Table 2). In the case of dense alpine grasslands (i.e. Figure 8 A-C), we hypothesize that increases in NDVI_{max} may have been the result of gradual densification and increases in the height of herbaceous plant cover, although this hypothesis would require verification using repeat measures of standing biomass. It is also possible that the encroachment of short-stature shrubs such as *Vaccinium uliginosum* and *Juniperus communis nana* has

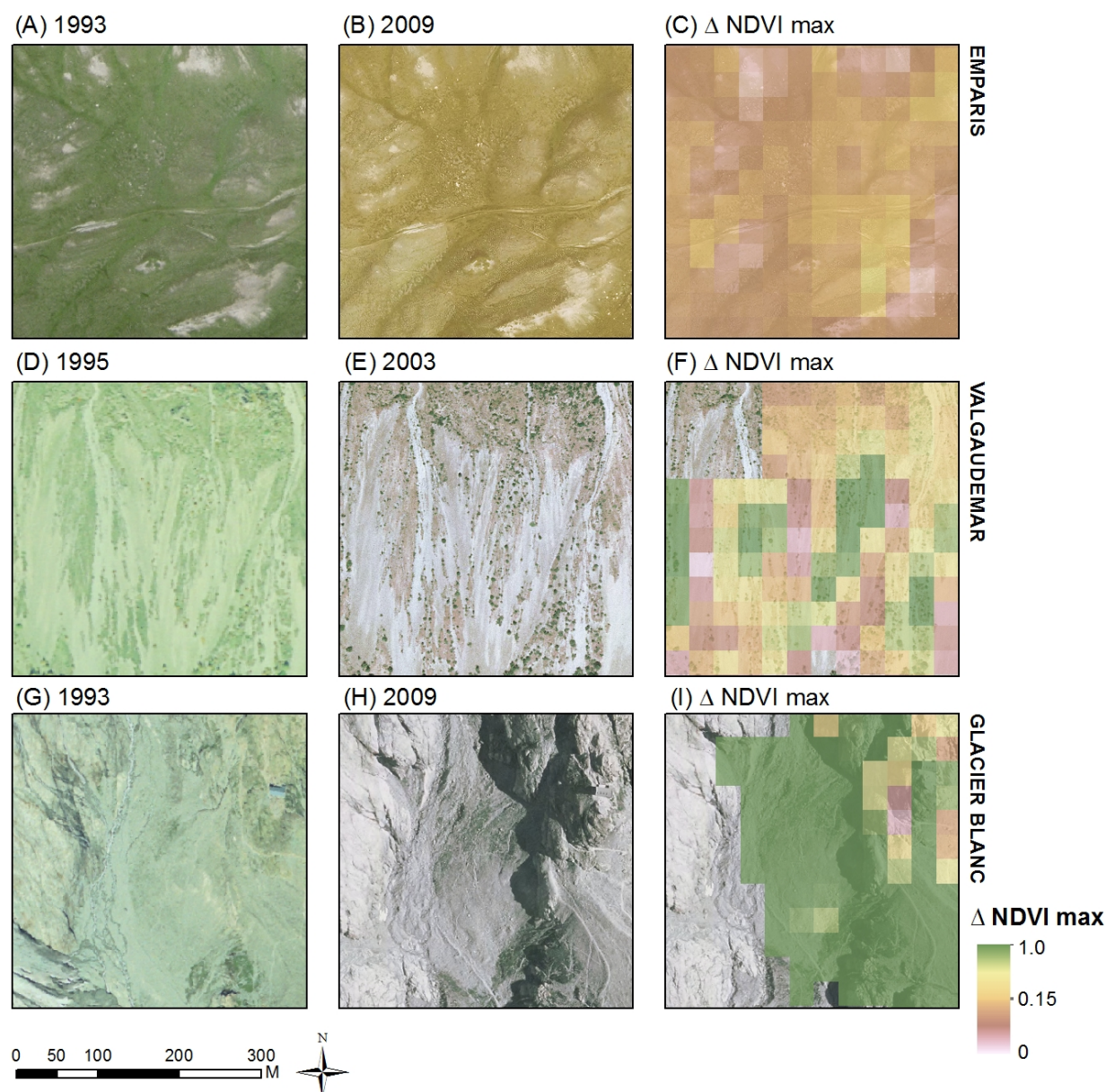


Figure 8. Historical aerial photos (A-B, D-E, G-H) and maps of the log-response ratio between mean values of NDVI max for the periods 2013:2015 and 2000:2002 (Δ NDVI max; C, F, I) for selected sites displaying increases in NDVI max. Ground resolution of Δ NDVI max values is 30 m. As mapped in 2000, panels (A-C) correspond to scree and talus, (D-F) correspond to vegetated scree and talus and (G-I) to grassland.

contributed to the NDVI_{max} signal. Expansion of dwarf shrubs has been observed in the nearby central Italian Alps at elevations up to 2500 m a.s.l. (Cannone *et al.* 2007). Higher observed rates of greening in grazed areas of the Ecrins National Park (Figure 7) suggest that changing land-use practices likely have contributed to both shrub encroachment and increased grassland

productivity. Further work including data on the spatial intensity of grazing, however, would be necessary in order to quantify potential effects of grazing on grassland productivity.

In terms of climate, considering that the length of the snow free period has been identified as the main driver of productivity in this system (Choler 2015), we find it plausible that the reduction in snow cover duration since the 1980s contributed to observed increases in peak grassland productivity. This hypothesis could also help to explain the higher rates of greening observed between 1984 and 2002 as compared to more recent years, given the occurrence of a “step effect” of sudden increase in air temperature and decrease in snow cover duration occurring in the late 1980s followed by more gradual climate change during recent years (Durand *et al.* 2009a-b). Pronounced greening in the Lauvitel Natural Reserve (Figure 6), where it is forbidden even for hikers to pass through, provides strong support for the occurrence of climate-driven increases in alpine grassland productivity in the Ecrins National Park. It is also possible that increased atmospheric deposition of nitrogen has contributed observed increases in high-elevation plant productivity, which has been observed and cited as an important process in other temperate alpine study systems (Seastedt *et al.* 2004).

Habitats classified as vegetated scree in 2000 exhibited the most widespread greening dynamics between 1984 and 2000 as compared to other land cover classes (68%, Table 2). As illustrated in Figure 8 D-F, steep screes with shrubs and small trees already present appear to have become more densely colonized since the early 1990s, leading to an increase in measured NDVI_{max} signal. In addition to the more general climate change context, it is possible that plant colonization dynamics in steep terrain are partially responsible for this trend, as plant establishment contributes to slope stability (Meusburger *et al.* 2010), which could further facilitate plant colonization. Field observations suggest that the pioneer tree *Pinus cembra* in particular has colonized steep rock faces in many areas of the park during recent years and could be contributing to the widespread increase in NDVI_{max} in the vegetated mineral land cover class.

The highest proportional changes in NDVI_{max} between 2000 and 2015 occurred in the scree land cover class (i.e. less than 10% vegetated scree and talus; Figure 3). Figure 4 demonstrates that the average NDVI_{max} of scree and talus plant communities is less than 0.2, which indicates that we quantified small absolute differences in NDVI_{max} that were nonetheless proportionally significant. We propose two mechanisms that could be responsible for greening trends in this context. First, glacier retreat during recent decades has been especially pronounced

in the southern French Alps (Gardent *et al.* 2010), and as described elsewhere in the Alps (i.e. Raffl *et al.* 2006), has been followed in Ecrins National Park by plant colonization of ice-free moraines. This process is illustrated in Figure 8 G-I and in Figure 9, where vegetation colonized a recently de-glaciated zone and caused a dramatic proportional increase in $NDVI_{max}$. Second, in addition to vegetation dynamics in peri-glacial areas, we believe it is possible that the decrease in snow cover duration since the 1980s may have led to the emergence of a brief growing season in high-elevation contexts previously characterized by perennial snowfields. Although we expect that colonization in these contexts likely consists of sparse scree vegetation, with time this



Figure 9. View of the Glacier Blanc area shown in panels G-I of Figure 8, showing areas of greening detected by satellite in the wake of glacier retreat. Photo courtesy of H. Gerardi.

process could lead to the emergence of novel snowbed communities with a high proportion of plant cover. If combined with NDVI trend analysis, field surveys, historical aerial photos and high-resolution topographic data could be used to establish monitoring programs to test this hypothesis.

Implications of long-term greening dynamics and main conclusions

Increased plant productivity in alpine environments has a number of implications for ecological functioning and land management in protected mountain areas such as the Ecrins National Park. For example, increased biomass in alpine grasslands and in rocky areas could affect the spatial distribution of herbivore habitat, both (i) from the perspective of shepherds optimizing herd location in the context of domestic grazing; and (ii) for wild herbivores optimizing foraging strategy based on vegetation quality and availability (e.g. Grignolio *et al.* 2003). A study from the Austrian Alps measured significant herbivory of nival vegetation up to 3000 m a.s.l. (Diemer 1996), which suggests that shifts even in high-elevation plant composition may have implications for higher trophic levels. Also, higher plant cover in alpine and nival habitats may contribute to slope stability and soil water retention capacity, particularly in the context of unstable glacial moraines and steep scree slopes. Decreased erosion would have strong implications for mountain runoff forecasting (Lehning *et al.* 2006) and slope-related risk assessment in alpine watersheds (Descroix and Mathys 2003). Finally, the combination of ongoing glacier retreat and more prevalent plant cover at high elevation has the potential to affect landscape aesthetics and perception, particularly for tourists associating snow and rock with a pristine high-mountain environment and who travel to the mountain areas such as the Ecrins National Park with this landscape image in mind. Given that observed changes in plant cover so far have been incremental, however, we consider this point to be something to bear in mind for the future rather than an immediate land management issue.

This work provides evidence for long-term greening of alpine vegetation in a protected area of the French Alps, especially in above-tree line grasslands and screes. We hypothesize that increasing air temperatures, decreased snow cover duration and local shifts in pastoral activity are the main drivers of observed greening dynamics. Although we restricted our study to the Ecrins National Park in order to take advantage of available field data, future studies should expand the spatial scale considered and test for greening and browning trends at the scale of the European

Alps. In addition to quantifying extrinsic factors affecting changes in peak productivity, i.e. grazing pressure or climate forcing, further fieldwork is necessary to elucidate vegetation dynamics contributing to the measured greening signal, i.e. shrub encroachment, expansion of herbaceous plant cover, increases in plant height and biomass or colonization by pioneer tree species. Perhaps most promising is the opportunity to combine multi-temporal satellite imagery with repeat field surveys of plant diversity and community composition, in order to explore links between biodiversity and ecosystem functioning in mountain environments.

References

- Améztegui, A., Brotons, L., & Coll, L. (2010). Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecology and Biogeography*, 19(5), 632-641.
- Beniston, M. (2005). Mountain climates and climatic change: an overview of processes focusing on the European Alps. *Pure and Applied Geophysics*, 162(8-9), 1587-1606.
- Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulkhak, S., Zimmermann, N.E. & Thuiller, W. (2014). Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. *Ecography*, 37(12), 1230-1239.
- Busetto, L., Colombo, R., Migliavacca, M., Cremonese, E., Meroni, M., Galvagno, M., Rossini, M., Siniscalco, U., Morra di Cella, U. & Pari, E. (2010). Remote sensing of larch phenological cycle and analysis of relationships with climate in the Alpine region. *Global Change Biology*, 16(9), 2504-2517.
- Carlson, B. Z., Renaud, J., Biron, P. E., & Choler, P. (2014). Long-term modeling of the forest–grassland ecotone in the French Alps: implications for land management and conservation. *Ecological Applications*, 24(5), 1213-1225.
- Cannone, N., Diolaiuti, G., Guglielmin, M., & Smiraglia, C. (2008). Accelerating climate change impacts on alpine glacier forefield ecosystems in the European Alps. *Ecological Applications*, 18(3), 637-648.
- Cannone, N., Sgorbati, S., & Guglielmin, M. (2007). Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment*, 5(7), 360-364.
- Chander, G., Markham, B. L., & Helder, D. L. (2009). Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment*, 113(5), 893-903.
- Choler, P. (2015). Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. *Biogeosciences*, 12(12), 3885-3897.

- Descroix, L., & Mathys, N. (2003). Processes, spatio-temporal factors and measurements of current erosion in the French southern Alps: a review. *Earth Surface Processes and Landforms*, 28(9), 993-1011.
- Dedieu, J. P., Carlson, B. Z., Bigot, S., Sirguey, P., Vionnet, V., & Choler, P. (2016). On the Importance of High-Resolution Time Series of Optical Imagery for Quantifying the Effects of Snow Cover Duration on Alpine Plant Habitat. *Remote Sensing*, 8(6), 481.
- Diemer, M. (1996). The incidence of herbivory in high-elevation populations of *Ranunculus glacialis*: a re-evaluation of stress-tolerance in alpine environments. *Oikos*, 486-492.
- Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B., & Mérindol, L. (2009a). Reanalysis of 44 Yr of climate in the French Alps (1958-2002): methodology, model validation, climatology, and trends for air temperature and precipitation. *Journal of Applied Meteorology and Climatology*, 48(3), 429-449.
- Durand, Y., Giraud, G., Laternser, M., Etchevers, P., Mérindol, L., & Lesaffre, B. (2009b). Reanalysis of 47 years of climate in the French Alps (1958-2005): Climatology and trends for snow cover. *Journal of Applied Meteorology and Climatology*, 48(12), 2487-2512.
- Fisher, J. I., & Mustard, J. F. (2007). Cross-scalar satellite phenology from ground, Landsat, and MODIS data. *Remote Sensing of Environment*, 109(3), 261-273.
- Fontana, F., Rixen, C., Jonas, T., Aberegg, G., & Wunderle, S. (2008). Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series-a comparison with in situ measurements. *Sensors*, 8(4), 2833-2853.
- Gardent, M., Rabatel, A., Dedieu, J. P., & Deline, P. (2014). Multitemporal glacier inventory of the French Alps from the late 1960s to the late 2000s. *Global and Planetary Change*, 120, 24-37.
- Gartzia, M., Pérez-Cabello, F., Bueno, C. G., & Alados, C. L. (2016). Physiognomic and physiologic changes in mountain grasslands in response to environmental and anthropogenic factors. *Applied Geography*, 66, 1-11.
- Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, 18(4), 571-582.
- Goetz, S. J., Bunn, A. G., Fiske, G. J., & Houghton, R. A. (2005). Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 102(38), 13521-13525.
- Grignolio, S., Parrini, F., Bassano, B., Luccarini, S., & Apollonio, M. (2003). Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. *Folia Zoologica*, 52(2), 113-120.
- Hantel, M. and Hirt-Wielke, L. Sensitivity of Alpine snow cover to European temperature. *International Journal of Climatology*. 2007, 27(10), 1265-1275.
- Holden, C. E., & Woodcock, C. E. (2016). An analysis of Landsat 7 and Landsat 8 underflight data and the implications for time series investigations. *Remote Sensing of Environment*.
- Jia, G. J., Epstein, H. E., & Walker, D. A. (2003). Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters*, 30(20).

- Julien, Y., Sobrino, J. A., & Verhoef, W. (2006). Changes in land surface temperatures and NDVI values over Europe between 1982 and 1999. *Remote Sensing of Environment*, 103(1), 43-55.
- Kerr, J. T., & Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends in Ecology & Evolution*, 18(6), 299-305.
- Lehning, M., Völksch, I., Gustafsson, D., Nguyen, T. A., Stähli, M., & Zappa, M. (2006). ALPINE3D: a detailed model of mountain surface processes and its application to snow hydrology. *Hydrological Processes*, 20(10), 2111-2128.
- Metternicht, G., Zinck, J. A., Blanco, P. D., & Del Valle, H. F. (2010). Remote sensing of land degradation: Experiences from Latin America and the Caribbean. *Journal of Environmental Quality*, 39(1), 42-61.
- Meusburger, K., Konz, N., Schaub, M., & Alewell, C. (2010). Soil erosion modelled with USLE and PESERA using QuickBird derived vegetation parameters in an alpine catchment. *International Journal of Applied Earth Observation and Geoinformation*, 12(3), 208-215.
- Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K., Macias-Fauria, M., Sass-Klassen, U., Esther, L. & Ropars, P. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509.
- Myneni, R. B., & Williams, D. L. (1994). On the relationship between FAPAR and NDVI. *Remote Sensing of Environment*, 49(3), 200-211.
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F. & Ghosn, D. (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. *Science*, 336(6079), 353-355.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20(9), 503-510.
- Raffl, C., Mallaun, M., Mayer, R., & Erschbamer, B. (2006). Vegetation succession pattern and diversity changes in a glacier valley, Central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 38(3), 421-428.
- Rossini, M., Cogliati, S., Meroni, M., Migliavacca, M., Galvagno, M., Busetto, L., Cremonese, E., Julitta, T., Siniscalco, C., Morra di Cella, U. & Colombo, R. (2012). Remote sensing-based estimation of gross primary production in a subalpine grassland. *Biogeosciences*, 9(7), 2565-2584.
- Roy, D. P., Kovalskyy, V., Zhang, H. K., Vermote, E. F., Yan, L., Kumar, S. S., & Egorov, A. (2016). Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. *Remote Sensing of Environment*.
- Roy, D. P., Wulder, M. A., Loveland, T. R., Woodcock, C. E., Allen, R. G., Anderson, M. C., Helder, D., Irons, J.R., Johnson, D.M., Kennedy, R. & Scambos, T. A. (2014). Landsat-8: Science and product vision for terrestrial global change research. *Remote Sensing of Environment*, 145, 154-172.
- Seastedt, T. R., Bowman, W. D., Caine, T. N., McKNIGHT, D. I. A. N. E., Townsend, A., & Williams, M. W. (2004). The landscape continuum: a model for high-elevation ecosystems. *Bioscience*, 54(2), 111-121.

Sen, P. K. (1968). Estimates of the regression coefficient based on Kendall's tau. *Journal of the American Statistical Association*, 63(324), 1379-1389.

Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686-702.

Virtanen, T., & Ek, M. (2014). The fragmented nature of tundra landscape. *International Journal of Applied Earth Observation and Geoinformation*, 27, 4-12.

Walker, D. A., Auerbach, N. A., & Shippert, M. M. (1995). NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska. *Polar Record*, 31(177), 169-178.

Walther, G. R., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16(5), 541-548.

Zhao, M., & Running, S. W. (2010). Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science (New York, NY)*, 329(5994), 940.

Supplementary material

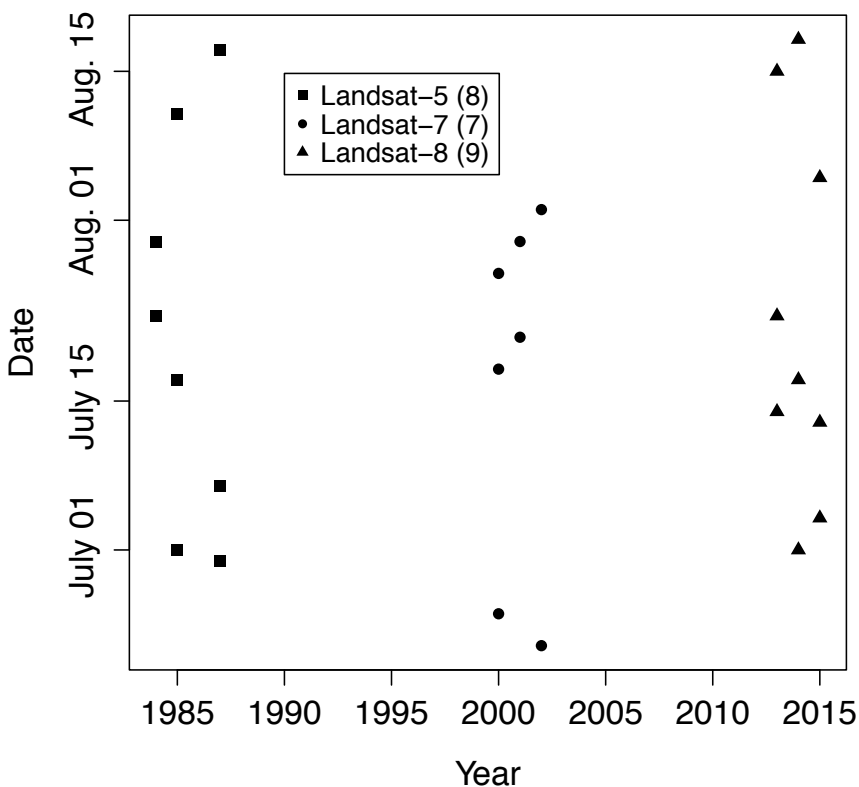


Figure S1. Acquisition dates for utilized Landsat-5, 7 and 8 images.

Chapter III Discussion

Evidence presented from the Vercors and Ecrins protected areas around Grenoble attest to important decadal-scale shifts in vegetation structure and functioning in the context of recent climate and land-use changes. In the Vercors, the dramatic expansion of mountain pine appears to be largely driven by modified sheep grazing practices, although pine growth has likely been encouraged by warmer temperatures some shifts in the upper treeline (reflecting climatic limits) were detected. In the Ecrins, increase in NDVI was higher on average in grazed areas, which also points to a potential interaction between land-use and climate drivers. The observed greening in the Lauvitel Natural Reserve, however, is an important indicator of systemic change in alpine vegetation independent of altered regimes of domestic grazing or other forms of mountain land-use.

While I found it a worthwhile exercise to report changes in vegetation structure in local protected areas and collaborate with park scientific staff, I am somewhat disappointed by the descriptive approach adopted in this chapter. Ideally, I would have liked to align spatial changes in vegetation (tree cover or NDVI) with co-varying drivers, including snow cover duration, air temperature and land-use intensity data. This approach would have enabled a stronger link to previous chapters, and also would have perhaps provided conclusive evidence concerning the causes of observed changes. In my defense, I was unable to find GIS layers of historical drivers that would have been appropriate for a modeling approach. Data from Météo France and the SAFRAN-CROCUS model were highly useful for providing context in terms of massif-scale evolution of air temperature and snow cover duration, however coarse outputs would have been poorly suited to modeling spatial heterogeneity in vegetation dynamics. Although a current map of grazing intensity and timing exists for the Ecrins National Park, information is associated with large polygons rather than spatially specific zones, and historical data are lacking. Also I think that both studies would have benefitted from *in situ* field observations, either of mountain pine population and colonization dynamics or of changes in height, biomass and community composition in the case of the Ecrins study. It is worth mentioning that a monitoring program was carried out in the Ecrins National Park measuring changes in the relative cover of vegetation strata (grasses, as well as shrubs and trees <1 m to >4m) for 124 sites. Intersection with NDVI

trends did not show strong agreement (Figure 1), which could be linked to the following explanations: i) changes in vegetation cover were estimated visually, often from across the valley, and are subject to bias; ii) field-measured sites did not overlap with areas of the most pronounced change detected by satellite. It is also possible that changes in NDVI did not adequately reflect changes in vegetation structure, however this seems counterintuitive and would require further field validation.

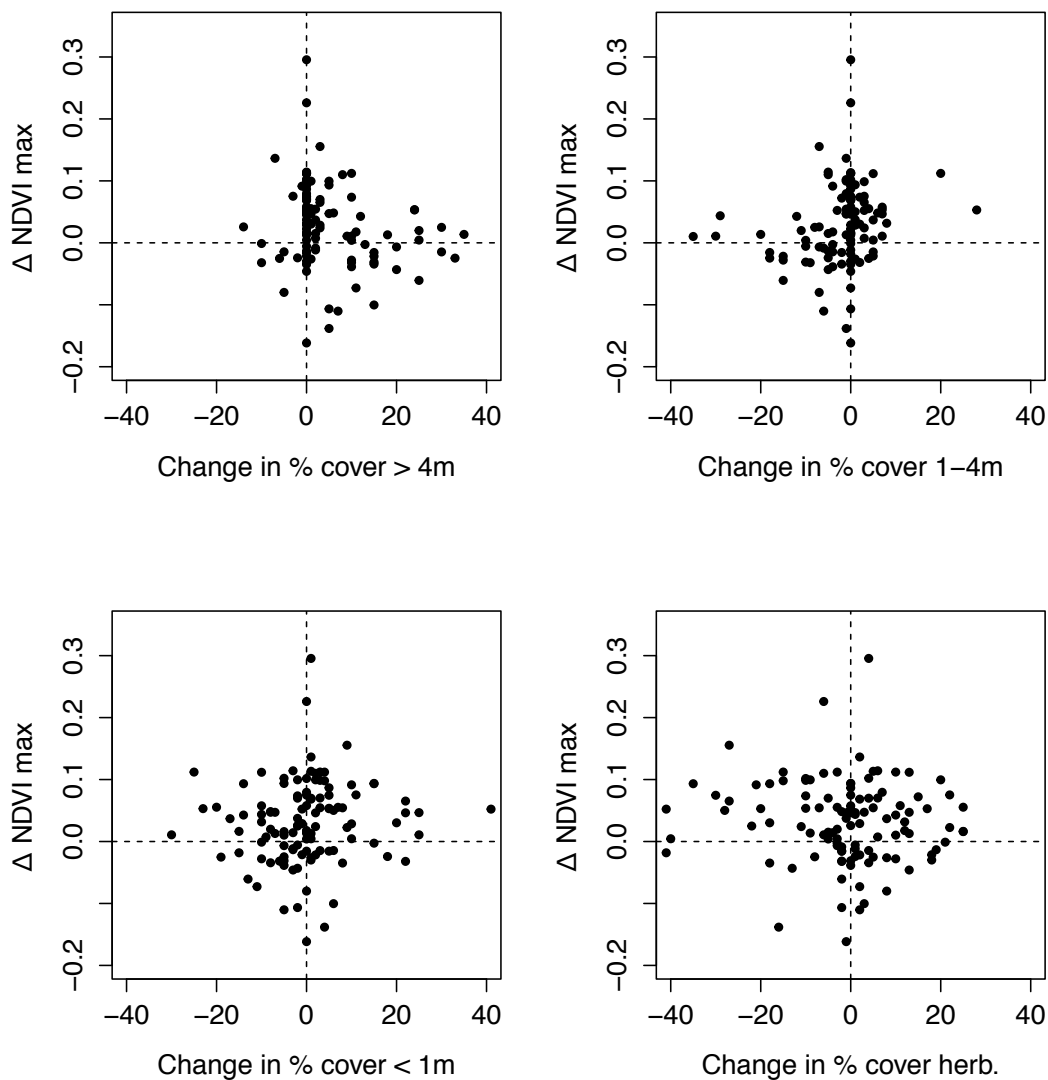


Figure 1. Log-response ratio values of NDVI_{max} for the period 2000:2015 extracted for 124 polygons in the Ecrins National Park. For each polygon, visual estimates of change in the percent cover of vegetation strata were carried out between the late 1990s and the 2010-2015 period. None of the shown relationships expressed a significant correlation.

Overall, it seems that there is great potential synergy between remote sensing and field-based long-term monitoring campaigns, given that the two approaches have complementary characteristics. A purely remote sensing based approach enables quantifying spatial variation in landscape dynamics over time, however fails to quantify ground-level changes and local mechanisms affecting the observed optical signal. By contrast, field-monitoring approaches provide detailed information on subtle changes and mechanisms, but are quickly restricted to a handful of points and produce data that can be difficult to extrapolate over time and space. Future monitoring campaigns conducted in alpine areas should seek to maximize complementarity between the two approaches, which calls for close collaboration between the scientific staff of protected areas and academic researchers.

References

- Améztegui, A., Brotons, L., & Coll, L. (2010). Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecology and Biogeography*, 19(5), 632-641.
- de Jong, R., de Bruin, S., de Wit, A., Schaepman, M. E., & Dent, D. L. (2011). Analysis of monotonic greening and browning trends from global NDVI time-series. *Remote Sensing of Environment*, 115(2), 692-702.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J. L. B., ... & Krajči, J. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), 111-115.
- Gritsch, A., Dirnböck, T., & Dullinger, S. (2016). Recent changes in alpine vegetation differ among plant communities. *Journal of Vegetation Science*.
- Matteodo, M., Ammann, K., Verrecchia, E. P., & Vittoz, P. (2016). Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps. *Ecology and Evolution*.
- Tape, K. E. N., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686-702.

Conclusion and perspectives

“Science needed its rare geniuses, but it also needed its foot soldiers.”

-Lily King, Euphoria

This work contributes to existing knowledge of the drivers affecting alpine plant community distribution and functioning in the context of the French Alps. Although study areas, data and approaches vary considerably from one chapter to the next, the overarching goal consists of improving understanding of how alpine plant communities respond to environmental gradients in a global change context. The links between Chapters I and II are readily apparent, considering that Chapter I explores the statistical and ecological relevance of quantifying snow cover duration in relation to diversity patterns, and Chapter II proceeds to utilize estimated gradients of snow cover duration information to predict alpine plant habitat and growth responses at the regional scale. While stating that snow cover has strong effects on alpine plant communities is not a novel conclusion in alpine ecology, Chapter I nonetheless attempts to make this message explicitly clear to the modeling community, for whom quantifying spatial variation in snow cover is far from standard practice. Chapter II establishes a clear link between multi-temporal satellite imagery and vegetation plots recorded by field botanists, which opens up a number of interesting possibilities including improved habitat mapping and monitoring of plant community responses to inter-annual variability in snow cover duration and climate. In its current form, the last section of Chapter II fails to establish a strong connection between functional traits (leaf area and height) and NDVI responses to variation in growing season length. However, quantifying the effects of diversity on ecosystem functioning along environmental gradients, as proposed in Violle *et al.* (2014), remains an exciting perspective that I only began to address in this work. Relative to Chapters I and II, Chapter III marks a fundamental change in approach – essentially, time replaces snow cover duration and temperature on the X-axis, and vegetation responses are analyzed from an observational standpoint. Nonetheless, reported changes in vegetation structure, especially in Chapter IIIB, provide novel insight into historical trends and ongoing vegetation dynamics occurring in the French Alps. Both the study in the Vercors and the Ecrins are an

invitation to go further, to carry out field experiments and to align remote sensing trends with spatio-temporal drivers of vegetation change.

The remainder of this concluding section will be dedicated to the discussion of perspectives emerging out of my work thus far. My approach to this section is simple: if I had another three years to continue pursuing alpine ecology work at the LECA or elsewhere, what would I like to do? In many ways I think these emerging ideas are the most representative of the journey of the past three years, reflecting interactions and discussions I had over the course of my work, development in my own interests and understanding of the system, and also ongoing goals that were part of my early work and which are still unresolved. For me this balance of continuity and fresh momentum constitutes the most motivating aspect of research, both looking back and moving forward.

I) Improving alpine snowpack models at high spatial resolution

Although much work effort has been put into process-based snowpack modeling on the part of snow scientists around world, quantifying physical processes determining fine-scale snow distribution in areas of complex mountain topography remains an ongoing challenge (Vionnet *et al.* 2014). This is a major obstacle, considering that without the ability to forecast snowpack dynamics at fine spatial scales, alpine ecologists will be hard pressed to make meaningful predictions about the response of high-elevation plant communities to climate change during the coming decades. As someone neither trained in physics, numerical modeling or snow science, I will not pretend to have the solution “key in hand”, as the French say. Instead, throughout this section I will relate some of the ideas discussed with V. Vionnet at the Centre d’Etudes de la Neige (CEN) throughout my project, with the intention of i) clearly expressing the processes that are key to take into account from a plant ecology perspective and ii) proposing potential field-based and modeling strategies for improving snowpack models.

Lehning *et al.* (2008) introduced the concepts of inhomogenous precipitation and preferential snow deposition in mountainous environments (Figure 1), which result from interactions between precipitation, wind and topography. They argued that while erosion and snow redistribution processes are important, irregular snow deposition in the absence of erosion

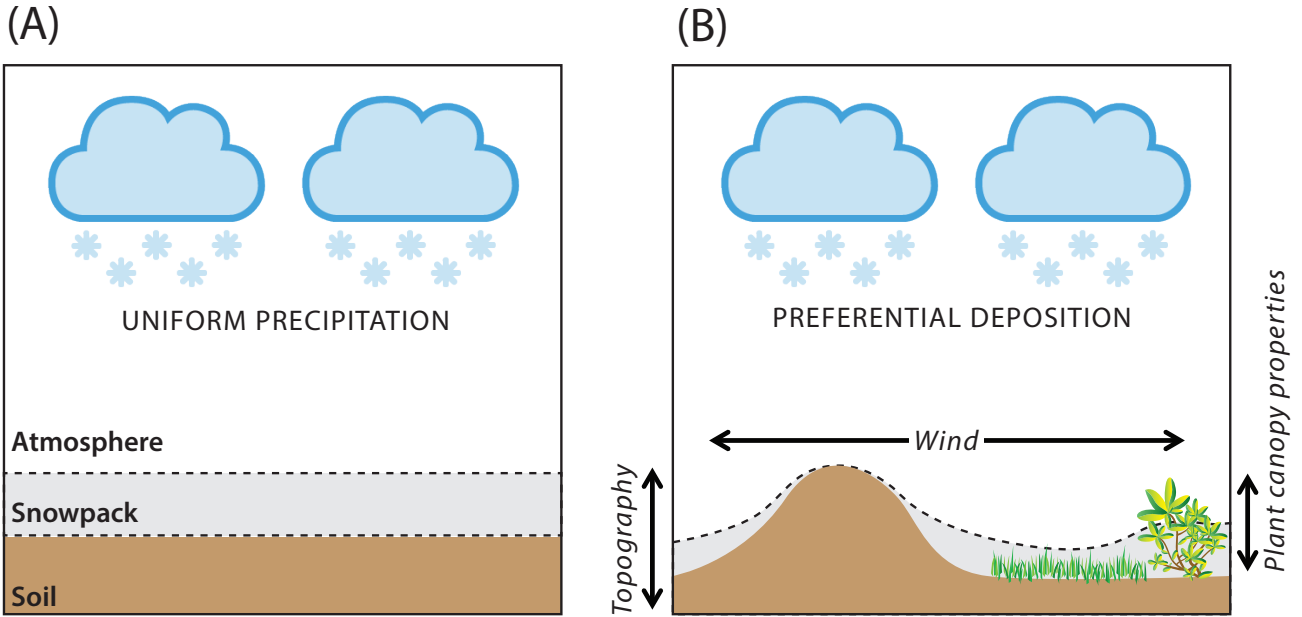


Figure 1. (A) Illustration of a uniform precipitation snowpack model, in which snowpack dynamics are uniform for a given spatial or topographic entity. (B) Illustration of a preferential deposition snow deposition model, in which snow accumulation is influenced by wind and local topography and vegetation.

introduces a great deal of initial spatial variability in snowpack depth, and that this single process might be easier to quantify and incorporate into a modeling framework. Although they concluded their work stating they were unable to capture heterogeneity beyond the “ridge-scale”, i.e. broad differences between windward and leeward slopes, their work nonetheless introduced a key idea that has since been applied by other snow scientists. Winstral *et al.* (2012) hypothesized that information on wind speed, topography and vegetation could be used to re-scale “sheltered” snow accumulations to estimate snow depth in wind-affected sites. Accounting for wind, vegetation and topography effects on snow accumulation greatly improved agreement between a satellite image of spring snow distribution and model outputs (Figure 2). More recently, Vionnet *et al.* (2014) combined an atmospheric and a snowpack model to quantify snow erosion and redistribution processes during wind events. Three-dimensional simulations of blowing snow in the absence of additional snowfall demonstrated overall agreement with the observed effects of wind in the study area, however the model failed to capture heterogeneity below a 50 m leeward/windward scale.

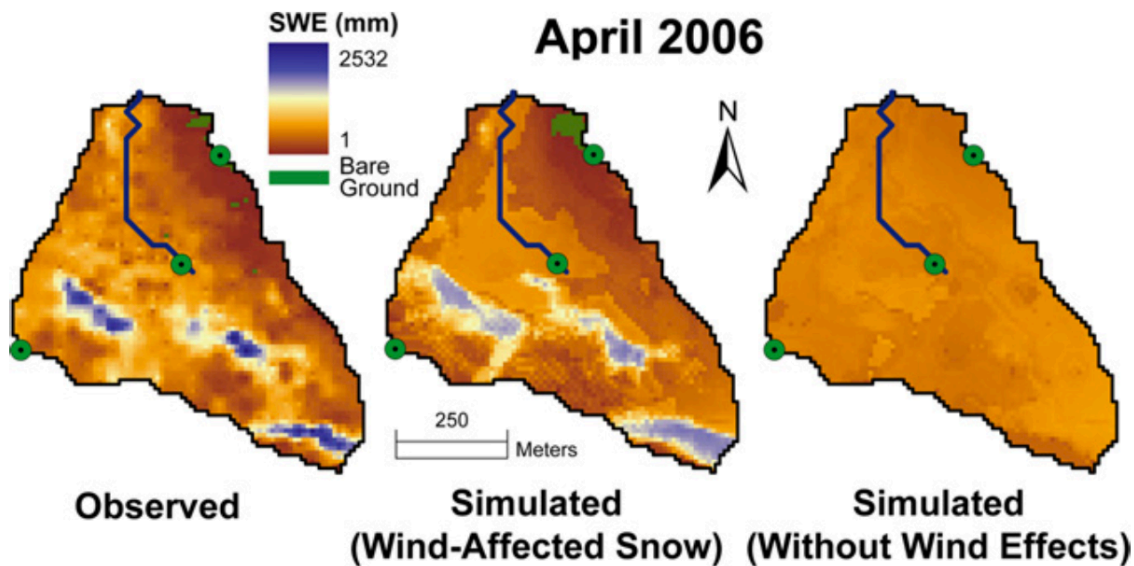


Figure 2. Figure 6 from Winstral *et al.* (2012) showing measured and modeled snow water equivalent (SWE) in a high-elevation watershed in southwestern Idaho. Modeling was carried out on a 10 m grid.

From a plant ecologist's perspective, this fine-scale, intra-slope heterogeneity is of the highest interest for prediction patterns of plant distribution and functioning. Following discussions with V. Vionnet, I think that the Winstral approach of quantifying preferential deposition in the absence of snow erosion perhaps holds the most promise for short-term advances in the accuracy of snowpack model outputs at fine spatial scales. That said there are a number of aspects of Winstral's work that could be improved upon, at least from a conceptual perspective, in order to better suit applications to study areas in the Alps. Overall, however, it seems that the concept of using local information on topography and vegetation to redistribute a given input of precipitation in the form of snow across the landscape has strong potential.

In terms of vegetation, the clear imperative consists of integrating continuous and quantitative plant traits into snow accumulation functions. The effects of plant canopy traits on snowpack dynamics have been demonstrated by Sturm *et al.* (2001) in an Arctic context, who showed that increased LAI, stem diameter and plant height resulted in deeper snowpack along a wind vector (Figure 3). Hyperspectral imagery, acquired by plane or by drone, emerges as an optimal data source for this task, given its ability to generate spatially continuous maps of plant canopy properties. Vegetation indices derived from hyperspectral imagery that could be utilized

in this context include leaf area index and cellulose (stem) area index. Although this point requires further research, the cellulose area index is of particular interest as it quantifies the amount of non-photosynthetic vegetation per unit of ground area (Nagler *et al.*, 2013), which

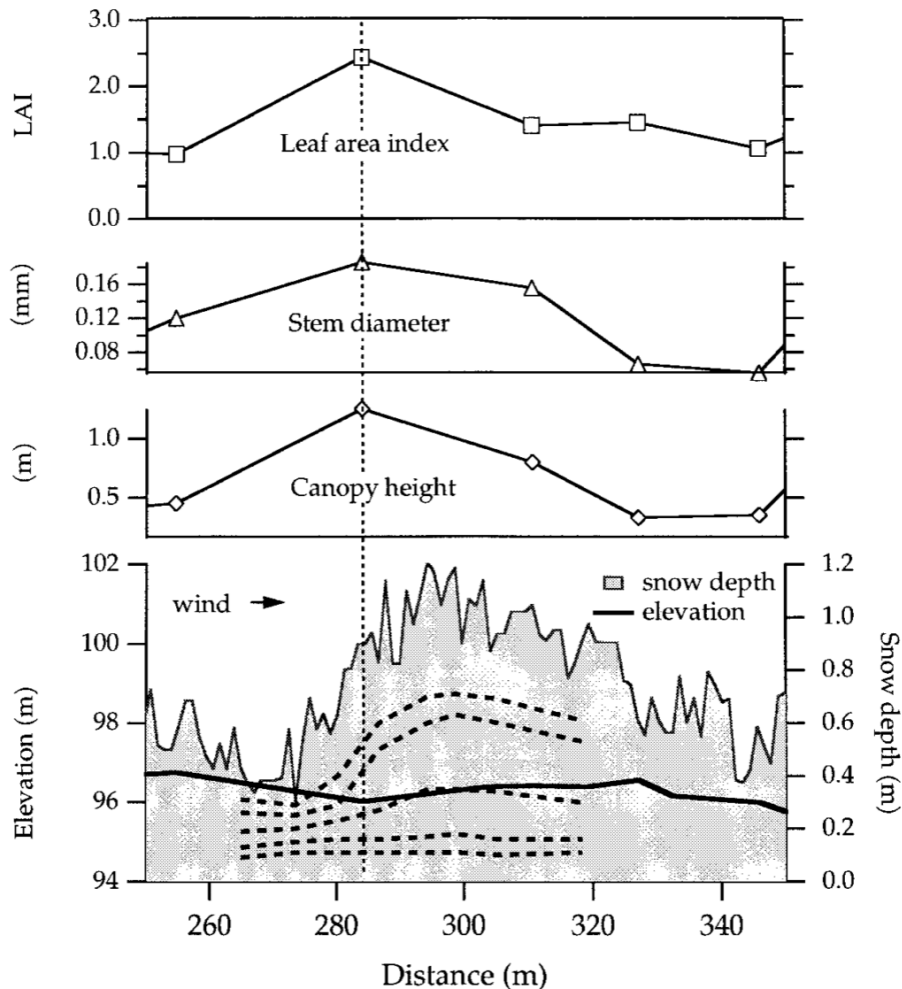


Figure 3. Figure 2 from Sturm *et al.* (2001) showing covariation in shrub canopy properties and snow depth along a wind vector in Prudhoe Bay, Alaska.

could potentially be used as a proxy for the amount of stem tissue affecting snow pack properties. Furthermore, terrestrial laser scanning (TLS) represents a promising means of quantifying spatio-temporal variation in the height of both snowpack (Revuelto *et al.* 2014) and plant canopies (Lefsky *et al.* 2002). Combining time series of snowpack height captured by TLS and spatial variation in plant canopy properties would allow for modeling the effects of vegetation structure on seasonal snow cover dynamics, including “snow-up”, mid-winter accumulation and melting.

In terms of topography, the approach utilized by Winstral *et al.* (2013) could be reproduced using a high-resolution digital elevation model derived from TLS or airborne LIDAR.

One point of discussion, however, concerns a fundamental difference between the Rockies and the Alps, which is that prevailing winds tend to be much more consistent in North America than in European mountain systems. In this respect, defining a prevailing wind vector and quantifying relative exposure would be overly simplistic in Alpine study areas, where weather systems arrive from multiple directions and topography locally redirects and influences wind dynamics. To address this challenge, at least two approaches appear to be feasible: i) carry out numerical simulation of wind fields over complex topography, as in Vionnet *et al.* (2014); or ii) adopt an empirical approach based on the assumption that wind is omnipresent in high-alpine environments and interacts with topography in a consistent manner. In the first case, computational limits and spatial accuracy readily emerge as potential shortcomings. In the second, computation and implementation would be straightforward using a metric such as the topographic position index (TPI), but spatial accuracy might suffer if wind vectors are not explicitly quantified. In both cases, field validation using TLS imagery would be necessary in order to compare the performance of the two methods.

The SAFRAN-CROCUS chain, hereafter referred to as CROCUS, constitutes the best available operational snowpack model for the French Alps, and the starting point for any improved snow distribution outputs of interest to plant ecologists. In its current form, CROCUS generates estimates of snowpack height and snow water equivalent for the broad topographic classes previously described (300 m elevation classes, slope aspect and two categories of slope angle). When mapped, these values result in blocks based on underlying topographic categories and are of limited use for fine-scale studies of plant diversity and functioning. An ambitious approach to improving the spatial resolution and accuracy of CROCUS would consist of building preferential deposition into the model structure, accounting for topography and vegetation as previously suggested. My sense is that this would be a major undertaking and in any case would be entirely dependent on the research goals and priorities of the CEN. A less ambitious approach would consist of using TLS data to fit empirical snow redistribution functions. In other words, for a given snowpack height at a given time step and topographic class, one could downscale height values using a function based on fine-scale information on topography and canopy properties. This approach could prove to be effective at the scale of a watershed, such as the Vallon de Roche Noire, however the data-intensive nature of the inputs and study-area specificity of empirical relationships fitted between inputs and snow accumulation could quickly limit the

application of this approach at broad spatial scales. Building topography and vegetation into the underlying physical model undoubtedly constitutes the most promising avenue for generating future maps of snow cover distribution at scales of biogeographic interest.

II) Positive feedback mechanisms driving shrub cover in an alpine context

The northward expansion and densification of birch, willow and alder shrubs has been extensively documented throughout Arctic and subarctic regions during recent decades (Tape *et al.* 2006; Forbes *et al.* 2010; Ropars and Boudreau 2012). Conversion of herbaceous tundra to mixed shrub and forest tundra decreases surface albedo and increases NDVI (Blok *et al.* 2011), leads to a deeper winter snow pack and increases winter soil temperatures as well as the depth of the permafrost active layer in summer (Sturm *et al.* 2001). A further hypothesis states that warmer soil temperatures caused by shrub densification foster soil microbial activity and enhance nitrogen availability for plants, leading to positive feedback loops between climate warming and shrub growth (Sturm *et al.* 2005). An experimental study conducted in the Canadian Yukon comparing soil temperature, snow depth, litter decomposition rates and nitrogen availability between tundra and shrub canopies found that shrub canopies substantially increased mid-winter snow depth and soil temperature, however nutrient dynamics were not significantly altered by shrub cover (Myers-Smith and Hik 2013). A recent study conducted at Blyon Island in the Canadian Arctic found that in addition to increasing snow height, the formation of low-density depth hoar was more pronounced under shrubs than in neighboring herb tundra, which improved insulation of underlying soil (Dominé *et al.* 2016). Furthermore, woody stems absorbed more short-wave radiation and provided hotspots that accelerated melting. Taken together, processes linked to shifts in the shrub-tundra ecotone are expected to have complex and multidirectional effects on carbon fluxes in high-latitude ecosystems, which are of critical importance for global-scale circulation models (Pearson *et al.* 2013).

In this context, surprisingly little research attention has been dedicated to shrub dynamics in the Alps, although many of the hypothesized feedbacks between climate, soil properties and

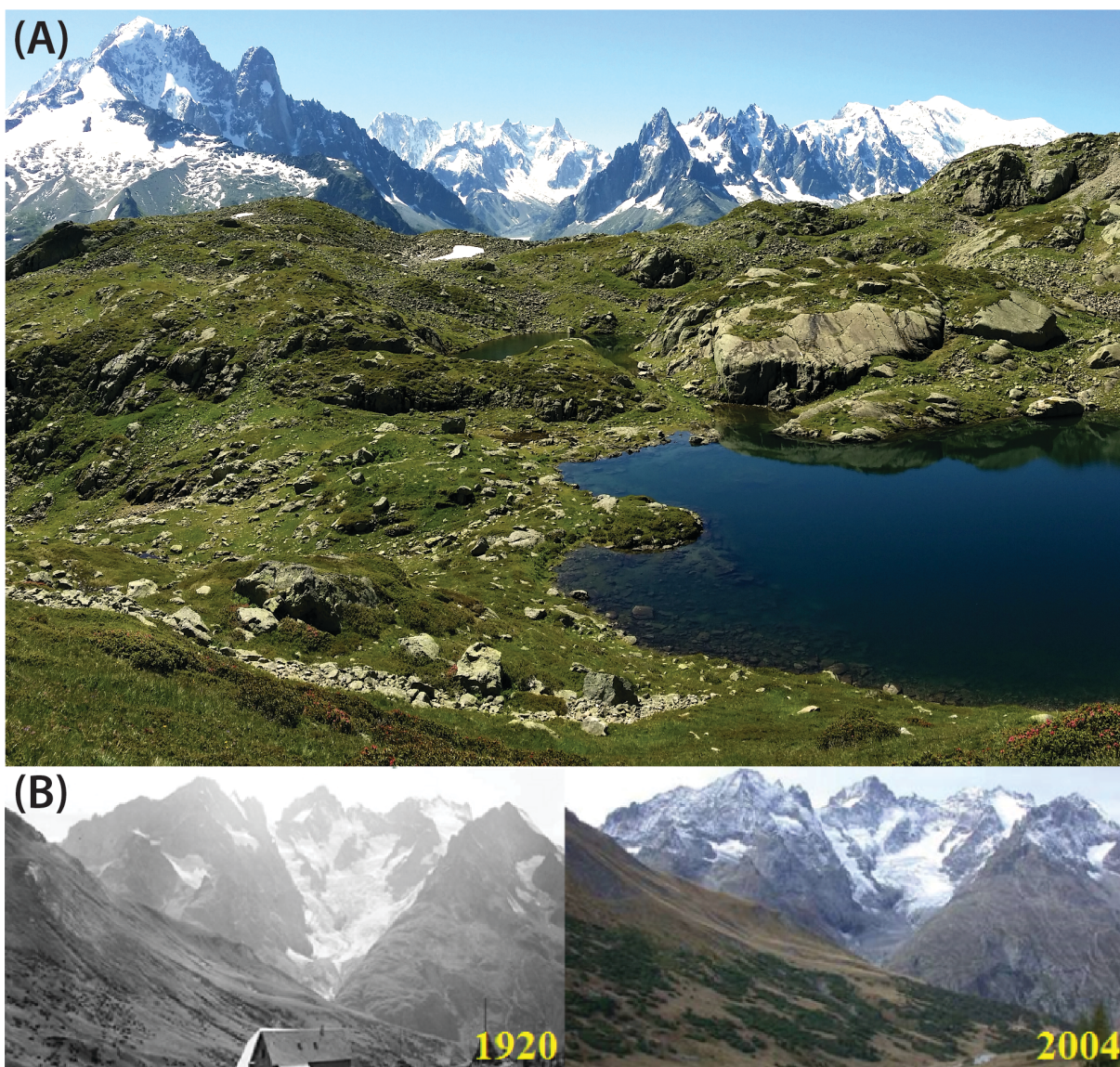


Figure 4. (A) Example of a typical “jumble” of bare rock, grassland and shrub cover in the Mont Blanc massif. Shrubs appear in dark green and are comprised of *Rhododendron ferrugineum*. Although they are not visible in the photo, shrub cover on the wind-exposed ridge in the mid-ground of the photo consists of dwarf prostrate *Loiseleuria procumbens*. (B) Repeat photography showing the expansion of shrubs (mostly *Alnus viridis*) at the Col du Lautaret in the Ecrins National Park. Source: P. Choler (LECA/SAJF)

shrub density developed in high-latitude regions could be applied or at least tested in temperate alpine study areas (see Myers-Smith *et al.* 2011 for a complete list of drivers). While permafrost is not a widespread feature of vegetated alpine landscapes, and implications for the global carbon budget are less critical than in the case for high-latitude regions, increases in shrub cover

nonetheless have strong potential repercussions on plant diversity, plant-plant interactions, plant-soil feedbacks and biomass production in an alpine context. Shrubs are abundant throughout the subalpine belt of the Alps (Figure 4A), ranging from tall multi-stemmed *Alnus* sp., *Salix* sp. and *Rhododendron ferrugineum*, to erect dwarf *Vaccinium* sp. and *Juniperus* sp., to prostrate dwarf shrubs such as *Loiseleuria procumbens*. Height can be quite variable for certain shrub species in the Alps and is highly dependent on elevation and topographic context. Recent increase in the cover of *Alnus viridis* has been identified as a widespread dynamic in the northern French Alps (Anthelme *et al.* 2007; Figure 4B), and a diachronic mapping study conducted in the central Italian Alps reported increases in shrub cover between 1953 and 2003 (Cannone *et al.* 2007). The latter study was carried out at the scale a single slope and is based on repeated categorical phytosociological mapping, however, and in my view strong and widespread observational evidence of changes shrub cover in the Alps is currently lacking in the literature. Lacking further still are studies investigating local drivers of shrub dynamics in the Alps and potential consequences of increasing shrub cover on ecosystem functioning.

There is strong reason to expect recent changes in shrub cover in response to climate and land-use changes during recent decades. One possible explanation for the relative scarcity of observational studies on shrub dynamics in the Alps, however, is related to the difficulty of quantifying shrub cover in heterogeneous alpine landscapes. Field mapping of shrub cover would be laborious and in the short-term limited to current distribution patterns. Shrub mapping using remote sensing is a challenging task in alpine environments, given that shrubs are typically interspersed within a jumbled matrix of grasses, bare ground and tree cover and do not present a clear spectral target (Figure 4A). Spectral unmixing methods have been applied to map fractional shrub cover in a semi-arid ecosystem (Sohn and McCoy 1997), but to the best of my knowledge have not been attempted in the case of shrub cover in the Alps. In my view, it would be worthwhile to attempt to quantify change in the percent cover of dominant shrub species using spectral unmixing and a combination of field data on the size and location of homogenous shrub patches (end members), hyperspectral data and multispectral satellite imagery. Repeat aerial photography, likely limited to color photographs in order to be able to visually identify shrubs, would constitute a complementary approach for identifying historical changes in the shrub ecotone. Long-term field monitoring programs would also constitute an important cross-validation of changes in NDVI or shrub cover identified using satellite imagery. Methodological

details aside, the necessary first step seems to be establishing whether or not there is a dynamic underway, assessing the magnitude of change, and beginning to identify potential drivers of shrub dynamics within alpine landscapes.

In order to better understand the drivers and consequences of landscape-scale shrub cover dynamics, it seems promising to test aspects of the snow-shrub hypotheses developed in arctic ecosystems in the context of alpine field sites. Figure 5 proposes a modified feedback loop (from Sturm *et al.* 2005) adapted to shrub dynamics in the alpine zone. The overall approach would be to measure physical and biological parameters in adjacent grass and shrub communities, while selecting a range of representative dominant species. For example, *Nardus stricta* and *Carex sempervirens* communities could be sampled alongside common shrubs such as *Rhododendron ferrugineum*, *Juniperus communis nana* and *Vaccinium uliginosum*, with an appropriate number of replicates per target species. The remainder of the fieldwork would consist of measuring the hypothesized links proposed in Figure 5. Temperature loggers at 2 m above the ground and at 5 cm in the soil could be used to quantify snow cover duration, soil temperature regimes and growing degree days. Mid-winter visits to field sites would be necessary in order to measure snowpack height, as well as other physical parameters such as stratigraphy and grain properties. More advanced physical measures of snow such as thermal conductivity would require collaboration with experts at the CEN. In addition it would be worth checking for the presence of burrowing small mammals within the snowpack in order to assess possible effects of animal populations on snowpack structure. The protocol described in Myers-Smith *et al.* (2013) could be used to measure nitrogen availability and soil litter decomposition rates during the growing season, as well as canopy properties such as height, stem diameter and leaf area index. It would be particularly interesting to compare melt rates in adjacent shrub and grass sites, and to test whether or not higher absorption of radiation by shrub canopies leads to consistent differences in snow melt-out date. Collectively, this work would contribute to snow-shrub research conducted in Arctic and subarctic regions, and would provide potentially new insight into shrub dynamics and consequences for ecosystem functioning in the Alps.

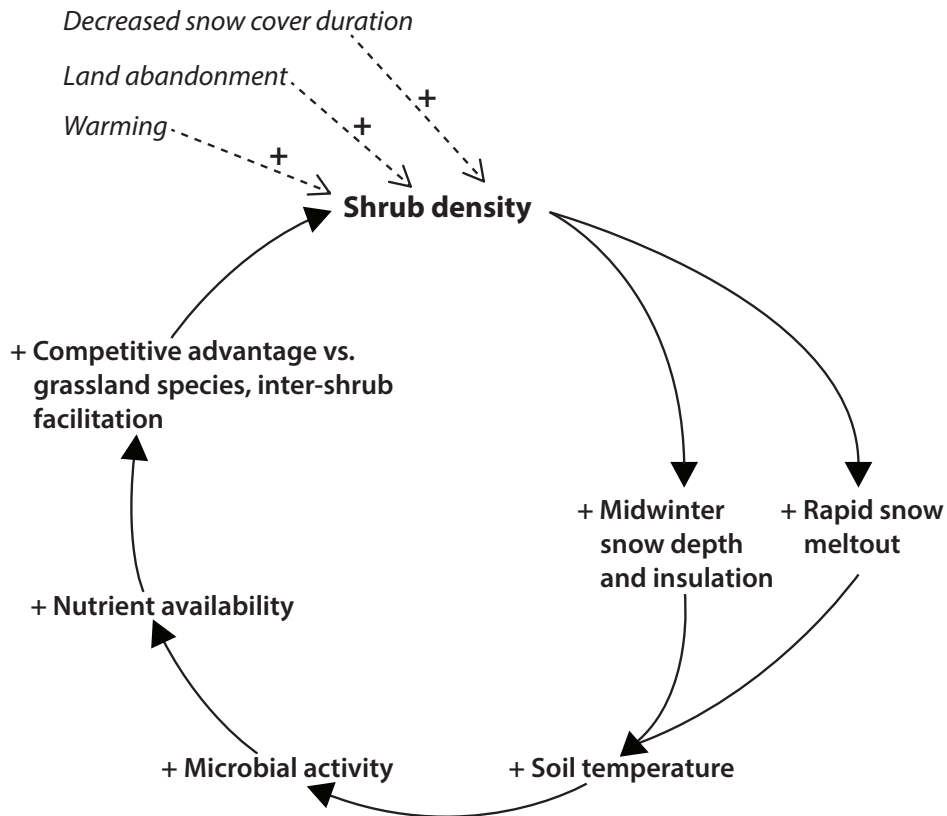


Figure 5. Hypothesized positive feedback loop influencing shrub expansion at the alpine-subalpine ecotone, modified from Sturm *et al.* (2005).

III) A proposed integrated framework for modeling alpine plant distribution

Solid knowledge of the key processes driving alpine plant distributions and community structure is especially important in the context of global change, as steep environmental gradients render alpine landscapes susceptible to abrupt shifts in plant distribution and abundance over short time scales. Modeling the spatial distribution of alpine plants over time requires the integration of a wide range of processes unique to this complex system. While the limitations of correlative species distribution models (SDMs) have been reviewed in detail (Thuiller *et al.* 2008), alpine landscapes pose additional challenges that have only begun to be addressed in the SDM literature (Guisan *et al.* 2009; Engler *et al.* 2011). These challenges include accounting for

micro-scale variation in plant-level abiotic conditions, snow cover duration and its effect on plant communities (Wipf *et al.* 2009), shift in the strength and direction of biotic interactions along stress gradients (Choler *et al.* 2001), geomorphic disturbance in periglacial environments (le Roux and Luoto 2013), spatial-temporal shifts in alpine and sub-alpine land-use practices (Dirnböck *et al.* 2003), and near- to mid-term changes in land cover (i.e. treeline elevation and glacier extent, see Engler *et al.* 2011 for a discussion of this problem). Scale-dependent and hierarchical mechanisms acting upon the distribution of alpine plants require a renewed approach, where mechanisms driving species distribution and community structure are explicitly integrated into a single framework (Thuiller *et al.* 2013). Recent studies aimed at disentangling the primary drivers affecting alpine plant distribution have rendered an integrated modeling approach feasible, where both correlative and process-based elements can be combined in a single modeling framework (e.g. Boulangeat *et al.* 2012).

Based on the work in Carlson *et al.* (2013), I now present a potential methodological framework aimed at developing an integrated alpine biodiversity model. Although I did not focus my project on the ideas presented in this work, the content of this paper remains pertinent to ongoing challenges in alpine ecology from a modeling standpoint and constitutes an important perspective moving forward. Given the contributions of co-authors to this text, I will use “we” for the remainder of the section. The proposed approach is based on three steps: (1) dynamic modeling of sub-alpine and nival ecotone position as a means of delineating alpine zone boundaries over time (Figure 6); (2) modeling of species habitat within the alpine zone, taking into account micro- and meso-topography, snow cover duration, geomorphic disturbance, climate and the biotic environment and (3) integrating habitat models with spatially explicit meta-population models of demography (Figure 7).

As a first step, we propose combining dynamic models of the sub-alpine (upper limit of treeline and shrubs) and the nival (lower-limit of glaciers) ecotones in order to account for shifts in alpine zone boundaries over time (Figure 6). The model *TreeMig* (Lischke *et al.* 2006) provides an example of an already existing spatial and temporal gap model that takes into account climate and land-use change, biotic interactions and dispersal, and that can be used to reconstruct tree species successions when colonizing below and migrating at the treeline ecotone. The use of a dynamic dominant vegetation model (e.g. FATE-HD, Boulangeat *et al.* 2014) represents an alternative solution that could be applied to model both treeline and shrub extension over time. We propose

the use of grazing intensity and frequency (land-use), climate mean and variability, substrate, biotic interactions and dispersal as input variables in this initial ecotone model. Remote sensing could also be used to validate predictions of treeline and shrub position for the present. In order to model the nival ecotone using state of the art techniques, collaboration with glaciologists would be necessary. Existing climate-based algorithms of glacier volume (e.g. Jouvet *et al.* 2008) based on historical glacier dynamics could be applied to novel study areas, where historical glacier inventories and data availability are becoming sufficient to model future trajectories of glacier extent (e.g. Gardent *et al.* 2013). Generating a dynamic clip of an alpine study area over time would increase the accuracy of predictions and improve the efficiency of model calculations, given that only areas of potential alpine plant habitat would be taken into account.

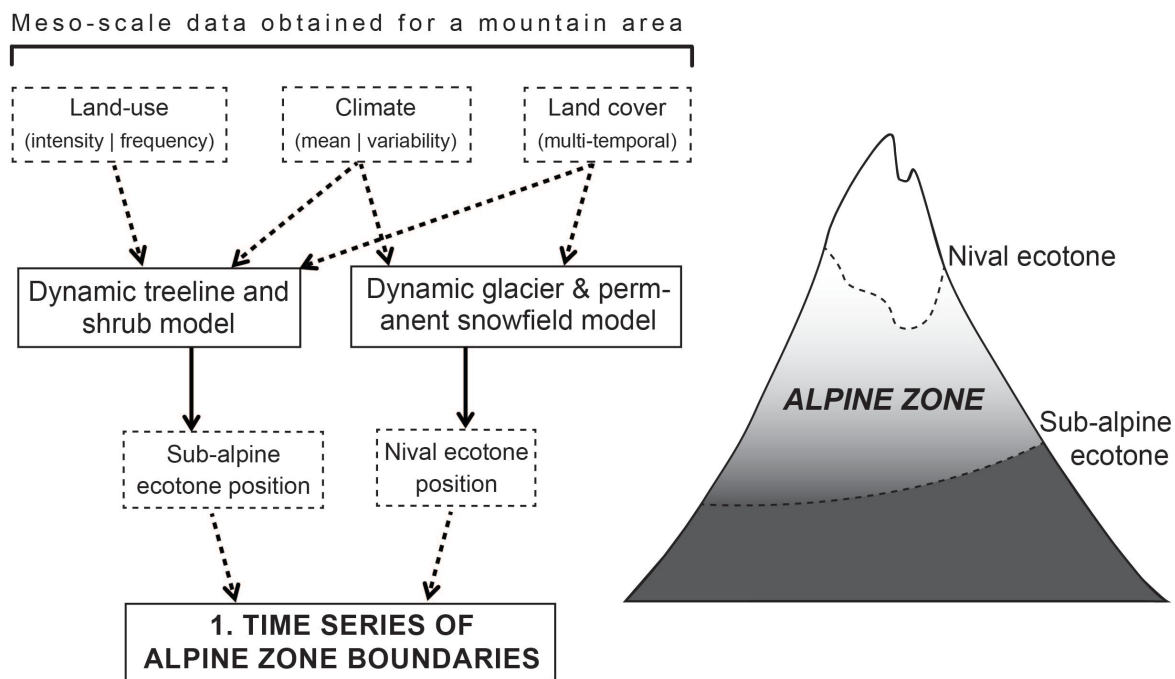


Figure 6. Meso-scale (~50m) dynamic modeling of alpine zone boundaries. The lower limit is defined by a time series of treeline and shrub position, while the upper limit is defined by a time series of glacier/nival extent. Dashed lines indicate input variables and solid lines indicate sub-models.

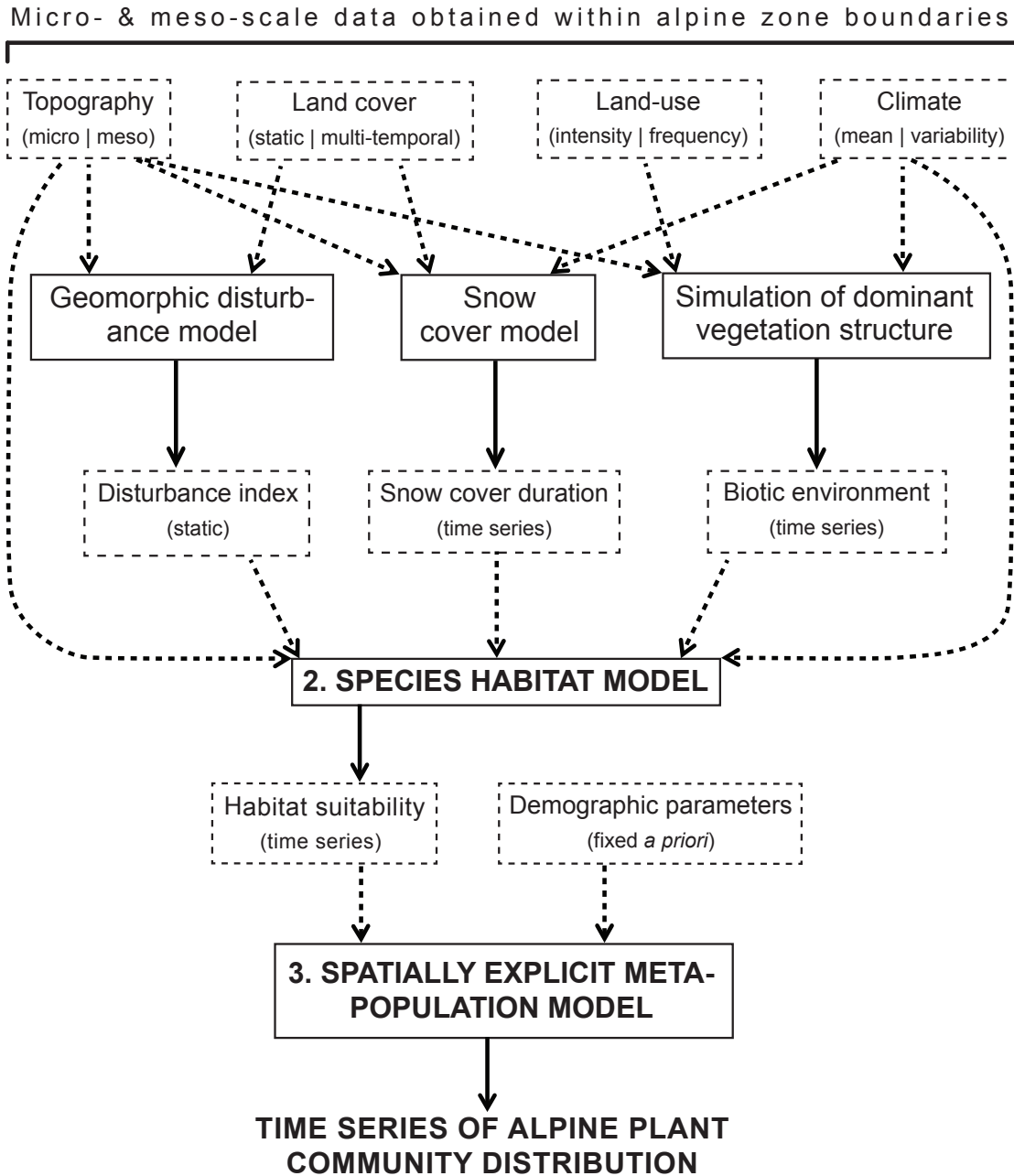


Figure 7. Fine-scale (<10m) modeling of suitable habitat (1) and spatial-temporal population dynamics (2) within alpine zone boundaries (Figure 6). Dashed lines indicate input variables and solid lines indicate sub-models.

Within established alpine zone boundaries (Figure 7), we propose developing a dynamic habitat model that takes into account the most important drivers of alpine plant distribution. Throughout this phase, remote sensing would play a key role in both data acquisition and model validation. Input variables would consist of micro- (VHR DEM) and meso-topography (medium-

resolution DEM), land cover, spatially explicit grazing intensity and frequency data and climate variables representing both mean and extreme tendencies. A process-based snowpack model, as discussed in earlier in section I and accounting for climate, topography and potentially vegetation, constitutes an essential cornerstone of an integrated alpine biodiversity model. Predicted snow cover duration could be combined with air temperature data in order to estimate snow-free growing degree days as well as the occurrence of frost events. Geomorphic disturbance and periglacial landforms could be modeled using remote sensing and topographic data, and incorporated as an explanatory variable in the form of a continuous and spatially explicit index (e.g. Randin *et al.* 2009). Incorporation of alpine-specific abiotic drivers would thus serve to refine areas of predicted favorable habitat. With predicted seed presence as a starting point, biotic interactions (including competition for light and soil nutrients, and biotic interactions induced by of plant canopy) could be then simulated at the level of dominant functional groups using a dynamic plant succession model (e.g. FATE-HD).

The goal of the third step (Figure 7) would be to model population dynamics within and adjacent to zones of favorable habitat using established meta-population modeling methods (Hanski 1999). Dominant functional groups could be split open in order to simulate population dynamics at the species level. A spatially explicit version of the incidence function based on metapopulation theory (Hanski 1999) would form the basis for simulating species abundance and turnover (Thuiller *et al.* 2013). Initially this approach would need to be tested for a small number of species before application at the community level. For a species within a patch, the input parameters for one or multiple species would consist, in principle, of the following geo-localized demographic data: probability of presence, colonization rate, fecundity, dispersal capacity and distance to other patches, extinction rate and carrying capacity (as determined by environmental conditions) (Thuiller *et al.* 2013). If these parameters are unavailable for certain species, a Bayesian framework or Approximate Bayesian Computing could be used to make robust inferences from available data (e.g. repeated surveys, Pagel and Schurr 2012), but this strategy remains to be evaluated in our context. This approach would enable simulation of source/sink dynamics where unviable populations are maintained in non-favorable areas due to the proximity of source populations (Pagel and Schurr 2012). The output of a spatially explicit metapopulation model would consist of estimates of alpine plant abundance, ideally at 10 m resolution or less in order to capture plant distribution in the form of micro-refugia.

While the broad methodology outlined here could take a multitude of forms in an applied context, we advocate that an integrated model of alpine plant distribution (Figures 6 and 7) should ideally include (1) dynamic ecotone modeling in order to account for shifts in alpine zone extent over time; (2) climate variables reflecting variability and extremes in addition to mean meteorological conditions; (3) a predictive model of snow cover duration driven by climate variables and accounting for topography and vegetation; (4) proxies of the biotic environment that account for shifts in species interactions induced by climate change; (5) realistic and spatially explicit proxies of geomorphic disturbance mechanisms in periglacial environments and; (6) process-based modeling of population dynamics and community structure within shifting zones of favorable habitat. Our review of the literature indicates that the tools and methods necessary to account for these drivers already exist independently, and that the main challenge now consists of efficiently combining different drivers affecting alpine plant distribution. Initially, we recommend approaching sections of Fig. 3 (i.e. snow cover duration, geomorphic disturbance, post-glacial retreat succession dynamics) and developing heuristic modeling frameworks for these separate processes before assembling multiple processes into a broader integrated model. Additionally, model calibration and validation should be accompanied by field experiments and monitoring programs, designed to generate observational data and improve understanding of the system. Examples include community transplant experiments along elevation gradients (e.g. Poll *et al.* 2009), as well as field and remote sensing-based mapping of plant functional groups for validation purposes.

Improved alpine biodiversity models will allow for more precise forecasting of plant distributions and vulnerability in response to global changes, which is essential to regional-scale conservation efforts in mountain areas. Developing a comprehensive integrated model of alpine plant distribution will require inter-disciplinary collaboration among biogeographers, biostatisticians, community ecologists, glaciologists and geologists, as well as the continuation and enhancement of long-term alpine monitoring programs.

Conclusion

Throughout this work, I have endeavored to present a number of novel applications of remote sensing, all aimed at improving our understanding of patterns of diversity and functioning

of high-elevation vegetation in the French Alps. Although I did not go so far as to model future scenarios of biodiversity or ecosystem functioning, my analysis of current patterns and observed historical trends provides new evidence of how temperate alpine plant communities may respond to ongoing climate and land-use change, and opens up a number of interesting research perspectives. Chapter I demonstrates the importance of quantifying snow cover duration for predicting patterns of plant taxonomic and functional diversity, and also highlights the ongoing challenge of modeling spatial gross primary productivity dynamics in alpine landscapes. In Chapter II, I explore the utility of satellite imagery for quantifying environmental conditions experienced by alpine plant communities, and further show how metrics of snow cover duration and peak productivity can be used to model alpine plant community habitat and growth responses to contrasting snow cover regimes. Chapter III provides new evidence of recent changes occurring in high-elevation plant communities in the French Alps in a climate and land-use change context. Analysis of the forest-grassland ecotone in the Vercors Regional Park shows a strong dynamic of forest expansion in response to overall climate warming and local shifts in grazing-related land-use practices, which supports findings from other studies conducted elsewhere in the Alps and Pyrenees. In the second part of Chapter III, for the first time I present evidence of greening dynamics in a protected area of the French Alps, the Ecrins National Park. I propose that a decrease in snow cover duration and pronounced warming occurring in the 1980s likely contributed to increased canopy productivity in high alpine contexts, and are driving functional changes in alpine environments in the absence of land-use change. Taken collectively, rather than pushing a specific aspect alpine ecology forward, my work helps to fill out our working knowledge of alpine plant communities and serves to solidify a number of field-based observations by carrying out robust spatial analyses.

References

- Anthelme, F., Villaret, J. C., & Brun, J. J. (2007). Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale. *Journal of Vegetation Science*, 18(3), 355-362.
- Blok, D., Schaepman-Strub, G., Bartholomeus, H., Heijmans, M. M., Maximov, T. C., & Berendse, F. (2011). The response of Arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature. *Environmental Research Letters*, 6(3), 035502.
- Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulhak, S., Zimmermann, Z. & Thuiller, W. (2014). Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. *Ecography*, 37(12), 1230-1239.
- Boulangeat, I., Gravel, D., & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, 15(6), 584-593.
- Cannone, N., Sgorbati, S., & Guglielmin, M. (2007). Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment*, 5(7), 360-364.
- Carlson, B. Z., Randin, C. F., Boulangeat, I., Lavergne, S., Thuiller, W., & Choler, P. (2013). Working toward integrated models of alpine plant distribution. *Alpine Botany*, 123(2), 41-53.
- Choler P, Michalet R and Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82: 3295-3308.
- Dirnböck T, Dullinger S, and Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, 30, 1-17.
- Domine, F., Barrere, M., & Morin, S. (2016). The growth of shrubs on high Arctic tundra at Bylot Island: impact on snow physical properties and permafrost thermal regime. *Biogeosciences Discussions*, 2016, 1-28.
- Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M. B., ... & Choler, P. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17(7), 2330-2341.
- Forbes, B. C., Fauria, M., & Zetterberg, P. (2010). Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, 16(5), 1542-1554.
- Gardent, M., Rabatel, A., Dedieu, J. P., & Deline, P. (2014). Multitemporal glacier inventory of the French Alps from the late 1960s to the late 2000s. *Global and Planetary Change*, 120, 24-37.
- Guisan A, Theurillat JP and Klenast F (2009) Predicting the potential distribution of plant species in an alpine environment. *Journal of Vegetation Science*, 9, 65-74.
- Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.

- Jouvet J, Picasso M, Rappaz J, Blatter H, Huss M and Funk M (2008) Numerical simulation of Rhone's glacier from 1874 to 2100. *JST Presto Symposium on Mathematical Sciences towards Environmental Problems* (Hokkaido University technical report series in mathematics), 136: 1-9.
- Lefsky, M. A., Cohen, W. B., Parker, G. G., & Harding, D. J. (2002). Lidar Remote Sensing for Ecosystem Studies. *BioScience*, 52(1), 19-30.
- Lischke, H., Zimmermann, N. E., Bolliger, J., Rickebusch, S., & Löffler, T. J. (2006). TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, 199(4), 409-420.
- Roux, P. C., & Luoto, M. (2014). Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. *Journal of Vegetation Science*, 25(1), 45-54.
- Lehning, M., Löwe, H., Ryser, M., & Raderschall, N. (2008). Inhomogeneous precipitation distribution and snow transport in steep terrain. *Water Resources Research*, 44(7).
- Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., ... & Ropars, P. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509.
- Myers-Smith, I. H., & Hik, D. S. (2013). Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow-shrub interactions. *Ecology and Evolution*, 3(11), 3683-3700.
- Nagler, P. L., Inoue, Y., Glenn, E. P., Russ, A. L., & Daughtry, C. S. T. (2003). Cellulose absorption index (CAI) to quantify mixed soil-plant litter scenes. *Remote Sensing of Environment*, 87(2), 310-325.
- Pagel, J., & Schurr, F. M. (2012). Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography*, 21(2), 293-304.
- Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3(7), 673-677.
- Poll, M., Naylor, B. J., Alexander, J. M., Edwards, P. J., & Dietz, H. (2009). Seedling establishment of Asteraceae forbs along altitudinal gradients: a comparison of transplant experiments in the native and introduced ranges. *Diversity and Distributions*, 15(2), 254-265.
- Randin, C. F., Vuissoz, G., Liston, G. E., Vittoz, P., & Guisan, A. (2009). Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the Western Swiss Alps. *Arctic, Antarctic, and Alpine Research*, 41(3), 347-361.
- Revuelto, J., López-Moreno, J. I., Azorin-Molina, C., Zabalza, J., Arguedas, G., & Vicente-Serrano, S. M. (2014). Mapping the annual evolution of snow depth in a small catchment in the Pyrenees using the long-range terrestrial laser scanning. *Journal of Maps*, 10(3), 379-393.
- Ropars, P., & Boudreau, S. (2012). Shrub expansion at the forest-tundra ecotone: spatial heterogeneity linked to local topography. *Environmental Research Letters*, 7(1), 015501.

- Sohn, Y., & McCoy, R. M. (1997). Mapping desert shrub rangeland using spectral unmixing and modeling spectral mixtures with TM data. *Photogrammetric Engineering and Remote Sensing*, 63(6), 707-716.
- Sturm, M., Holmgren, J., McFadden, J. P., Liston, G. E., Chapin III, F. S., & Racine, C. H. (2001). Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate*, 14(3), 336-344.
- Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., ... & Romanovsky, V. E. (2005). Winter biological processes could help convert arctic tundra to shrubland. *Bioscience*, 55(1), 17-26.
- Tape, K. E. N., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686-702.
- Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT and Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 137-152.
- Thuiller, W., Münkemüller, T., Lavergne, S., Mouillot, D., Mouquet, N., Schiffrers, K., & Gravel, D. (2013). A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology Letters*, 16(s1), 94-105.
- Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, 111(38), 13690-13696.
- Winstral, A., Marks, D., & Gurney, R. (2013). Simulating wind-affected snow accumulations at catchment to basin scales. *Advances in Water Resources*, 55, 64-79.
- Wipf S, Stoeckli V and Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, 94, 105-121.

Supplementary Material

Article S1

*Working toward integrated models of alpine plant
distribution**

* **Carlson, B. Z.**, Randin, C. F., Boulangeat, I., Lavergne, S., Thuiller, W., & Choler, P. (2013). Working toward integrated models of alpine plant distribution. *Alpine Botany*, 123(2), 41-53.

Working toward integrated models of alpine plant distribution

Bradley Z. Carlson · Christophe F. Randin ·
Isabelle Boulangeat · Sébastien Lavergne ·
Wilfried Thuiller · Philippe Choler

Received: 15 April 2013 / Accepted: 23 July 2013
© Swiss Botanical Society 2013

Abstract Species distribution models (SDMs) have been frequently employed to forecast the response of alpine plants to global changes. Efforts to model alpine plant distribution have thus far been primarily based on a correlative approach, in which ecological processes are implicitly addressed through a statistical relationship between observed species occurrences and environmental predictors. Recent evidence, however, highlights the shortcomings of correlative SDMs, especially in alpine landscapes where plant species tend to be decoupled from atmospheric conditions in micro-topographic habitats and are particularly exposed to geomorphic disturbances. While alpine plants respond to the same limiting factors as plants found at lower elevations, alpine environments impose a particular set of scale-dependent and hierarchical drivers that shape the realized niche of species and that require explicit consideration in a modelling context. Several recent studies in the European Alps have successfully integrated both correlative and process-based elements into distribution models of alpine plants, but for the time being a single integrative modelling framework that includes all key drivers remains elusive. As a first step in working toward a comprehensive integrated model applicable to

alpine plant communities, we propose a conceptual framework that structures the primary mechanisms affecting alpine plant distributions. We group processes into four categories, including multi-scalar abiotic drivers, gradient dependent species interactions, dispersal and spatial-temporal plant responses to disturbance. Finally, we propose a methodological framework aimed at developing an integrated model to better predict alpine plant distribution.

Keywords Alpine plants · Alpine-specific drivers · Integrated approach · Species distribution modelling

Introduction

Solid knowledge of the key processes driving alpine plant distributions and community structure is especially important in the context of global change, as steep environmental gradients render alpine landscapes susceptible to abrupt shifts in plant distribution and abundance over short time scales (Frei et al. 2010; Gottfried et al. 2012). A further research challenge consists of forecasting shifts in alpine community structure resulting from the dual threat of colonization by upward-migrating thermophilic species and by conventional alien invasive species (Guisan and Theurillat 2000; Pauchard et al. 2009).

Modelling the spatial distribution of alpine plants over time requires the integration of a wide range of processes unique to this complex system (Gottfried et al. 1999). While the limitations of correlative species distribution models (SDMs, sensu Guisan and Thuiller 2005) have been reviewed in detail (Thuiller et al. 2008; Dormann 2007; Elith and Leathwick 2009), alpine landscapes pose additional challenges that have only begun to be addressed in the SDM literature (Guisan et al. 2009; Engler et al. 2011). These

B. Z. Carlson (✉) · I. Boulangeat · S. Lavergne · W. Thuiller ·
P. Choler
Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553,
Univ. Grenoble Alpes, 38041 Grenoble, France
e-mail: carlsonb@zbr.ujf-grenoble.fr

C. F. Randin
Botanisches Institut der Universität Basel, Schönbeinstrasse 6,
4056 Basel, Switzerland

P. Choler
Station Alpine J. Fourier, UMS CNRS-UJF 3370,
Univ. Grenoble Alpes, 38041 Grenoble, France

challenges include accounting for micro-scale variation in plant-level abiotic conditions (e.g. Scherrer and Körner 2011), snow cover duration and its effect on plant communities (Hejman et al. 2006; Wipf et al. 2009), shift in the strength and direction of biotic interactions along stress gradients (Choler et al. 2001; Michalet et al. 2006), geomorphic disturbance in periglacial environments (Randin et al. 2009a; le Roux and Luoto 2013), spatial–temporal shifts in alpine and sub-alpine land-use practices (Dirnböck et al. 2003; Vittoz et al. 2008; Gehrig-Fasel et al. 2007) and near- to mid-term changes in land cover (i.e. treeline elevation and glacier extent, see Engler et al. (2011) for a discussion of this problem). Scale-dependent and hierarchical mechanisms acting upon the distribution of alpine plants require a renewed approach, where mechanisms driving species distribution and community structure are explicitly integrated into a single framework (Thuiller et al. 2013). Recent studies aimed at disentangling the primary drivers affecting alpine plant distribution have rendered an integrated modelling approach feasible, where both correlative and process-based elements can be combined in a single modelling framework (Boulangeat et al. 2012a; see Dormann et al. (2011) for definitions of *hybrid* vs. *integrated* models).

The purpose of this review was to assemble the most pertinent drivers of alpine vegetation distribution into an integrative and conceptual framework that could later be applied to improve the predictive power and transferability of alpine flora distribution models (hereafter referred to as *alpine biodiversity models*). We group processes affecting alpine plant distribution into four categories: hierarchical abiotic drivers, gradient-dependent species interactions, dispersal and spatial–temporal plant responses to disturbance in alpine landscapes. Although methodological details will not be addressed here, we will discuss specific tools and approaches for both (1) enhancing the fit of projections of alpine plant distribution relative to observed distributions and (2) improving the accuracy of future predictions by incorporating the most pertinent explanatory variables affecting the biogeography of alpine plants. We conclude by proposing a methodological approach aimed at integrating key drivers into an applied modelling context.

Hierarchy and scale of influence of abiotic drivers

The alpine zone is defined at its lower boundary by the limit of the tree life (hereafter referred to as treeline, Körner and Paulsen 2004; Körner et al. 2011) as well as the upper limit of sub-alpine shrubs (Körner 2003), and at its upper boundary by the presence of permanent snowfields, glaciers and steep rock formations characteristic of the alpine–nival ecotone (Gottfried et al. 1998). Sub-alpine and nival boundaries are

best defined at the meso-scale [10–100 m, see Billings (1973) for a definition of scales], given that ecotones in high mountain landscapes are often defined by transitional zones rather than spatially precise shifts (Körner 2007). During recent decades, both the upper treeline (Harsch et al. 2009) and the shrub upper margin (Kullman 2002), as well as the lower limit of permanent snowfields and glaciers (Paul et al. 2007) have moved upward in elevation in response to climate change. Given that trends of treeline rise and glacier retreat are expected to continue in the near future, we propose applying dynamic models of sub-alpine and nival ecotone position to better delineate the upper and lower limits of potential habitat for alpine plants over time.

Within the alpine zone, the prevailing importance of climate and micro/meso topography in determining plant distribution is well established (Billings and Bliss 1959; Billings 1973; Bowman et al. 1993). Abiotic conditions are considered to be especially strong drivers of alpine plant distribution due to the tight coupling between plant physiology and the harsh climatic conditions found in alpine environments (Bliss 1971). In alpine landscapes where human disturbance is minimal, physiological responses to abiotic stress gradients primarily shape the fundamental limits of species' niches and determine the upper elevational limit of plant distributions (Normand et al. 2009). Complex mountain topography leads to micro-scale (1–10 m) heterogeneity in plant-level abiotic conditions as well as the presence of micro-refugia known to buffer plant species from long-term changes in regional climate (Dobrowski 2010).

Although their overall importance is unquestioned, debate and uncertainty arise in a modelling context concerning which abiotic drivers limit alpine plant distribution the most directly, how to measure them and how such factors might affect plant distribution when considered at multiple scales (Randin et al. 2009b; Scherrer and Körner 2011). Commonly used explanatory variables in correlative SDMs such as air temperature, soil texture, solar radiation and moisture indices represent proxies of direct physiological or resource gradients controlling patterns of plant distribution (sensu Austin and Smith 1989). A number of alpine plant modelling studies have used micro-topographic input variables (slope and aspect) to approximate variation in environmental conditions and resources such as heat sum, soil water availability and snow cover duration (e.g. Gottfried et al. 1999; Lassueur et al. 2006; Randin et al. 2009a). In this section, we discuss (1) the meso-scale distribution of sub-alpine and nival ecotones and give a brief overview of existing modelling approaches; (2) micro-scale abiotic drivers of plant distribution within the alpine zone and (3) the effects of seasonal snow cover on plant distribution in addition to potential methods for modelling snow cover dynamics in alpine environments.

Sub-alpine ecotone distribution

The position of the sub-alpine ecotone is known to be affected by both temperature and land-use drivers (Dullinger et al. 2003). On a global scale, treeline has been shown to correspond with mean annual growing season temperatures of 6.7 ± 0.8 °C (Körner and Paulsen 2004). This definition was later refined to include a minimum growing season length of 94 days (constrained by the first and last transition of a weekly average of daily mean air temperature of 0.9 °C) and a mean air temperature during that period of at least 6.4 °C (Körner et al. 2011). Although it has not been described systematically, the upper limit of shrub distribution is also known to be sensitive to temperature (Kullman 2002) in addition to the presence of herbivores (Olofsson et al. 2009). In the case of both treeline and the upper limit of shrubs, non-elevation specific drivers such as alpine land-use (especially grazing), geomorphic disturbance and substrate can locally modify ecotone location and physiognomy (Körner 2007; Marcias-Fauria and Johnson 2013).

Ideally, a dynamic sub-alpine ecotone model aimed at defining the lower limit of the alpine zone would incorporate meso-scale climate variables in addition to the aforementioned non-elevation specific drivers affecting treeline and shrub location. Biotic interactions between pioneer trees and shrubs should also be taken into account (e.g. Dullinger et al. 2003), considering that shrubs are known to facilitate tree installation by providing ‘safe-sites’ for seed germination (Batllori et al. 2009). While the *TreeMig* model (Lishcke et al. 2006) is applicable only to trees and does take into account geomorphology, it does provide an example of a process-based ecotone model that combines the abiotic environment, competition for light and soil water and dispersal. Very recently, high-resolution light detection and ranging (LIDAR) imagery was used to map treeline location in the Swiss Alps and to validate a process-based model of tree growth based on climate variables (Coops et al. 2013). The combination of advanced remote-sensing technology with physiology-based ecotone modelling represents a promising approach for continuing to improve models of the lower limit of the alpine zone.

Nival ecotone distribution

Perhaps due to its less striking appearance and the reduced amount of associated plant biomass, the upper limit of the alpine zone has received a fraction of the attention dedicated to the lower alpine treeline ecotone (but see Gottfried et al. 1998; Pauli et al. 2003). The lower limit of alpine glaciers is a complex entity affected by climate (temperature and snow fall), the extent and elevation of the upper accumulation zone, ice flow dynamics and topography (Haeberli and Beniston 1998). Climate-induced glacier retreat causes the

nival ecotone to shift upward and enables plant succession dynamics to occur in un-colonized glacier forelands. In Coastal Alaska, *Dryas* shrubs are documented within 30 years of glacial retreat, followed by alder shrubs within 50 years and spruce within 100 years (Chapin et al. 1994; Boggs et al. 2010). Although the timing and species composition of successional changes undoubtedly vary by region, rates of post-glacial succession measured in Alaska suggest that this process occurs within the prediction period considered by most modelling studies (50–100 years).

The accelerating retreat of alpine glaciers necessitates the incorporation of dynamic models of ice extent into alpine biodiversity models. Inclusion of a fixed binary mask of glacier cover for the duration of a prediction period will lead to underestimates of potential habitat for pioneer alpine species (Engler et al. 2011). Independently of SDM studies, multi-temporal satellite imagery, climate data and three-dimensional modelling techniques have been used to model the trajectory of glacier extent and mass-balance in the Swiss and French Alps (Paul et al. 2007; Jouvet et al. 2008; Dumont et al. 2012). We recommend that these studies should be viewed as the basis for incorporating glacier retreat dynamics into predictions of alpine plant distribution.

Micro-scale abiotic drivers

Within the alpine zone, micro-topography constitutes a particularly important filter affecting plant distribution and community structure (Billings 1973). Recent work suggests that climate-induced extinction of alpine flora could be buffered by the presence of micro-refugia, where locally favourable conditions are conserved by nuances in aspect and slope angle (Dobrowski 2010). Indeed, the use of medium resolution (25–50 m) digital elevation models (DEMs) leads to overly coarse estimates of abiotic conditions and fails to account for micro-climates generated by complex mountain topography (Scherrer and Körner 2011). Predictions of alpine plants based on meso-scale topographic variables and downscaled climate data thus run the risk of over-estimating habitat loss as a result of climate change (Randin et al. 2009b; Engler et al. 2011).

The use of remote-sensing derived very high-resolution digital elevation models (VHR DEMs, <10 m resolution) to estimate topographic variables has been shown to improve the predictive power of SDMs in an alpine setting (Lassueur et al. 2006). In this study, although slope retained the same predictive power when considered at 1 and 25 m resolution, aspect (indirectly reflecting energy inputs) became a more significant explanatory variable when calculated at the micro-scale. In a more recent study, data-loggers buried at 3 cm soil depth on a uniformly oriented slope in the Swiss alpine zone (>2,150 m a.s.l.) demonstrated substantial variation in ground surface temperatures (Scherrer and Körner

2011). Their results show that temperature variability and extremes are better predictors of alpine plant presence than mean temperature trends. The significance of soil temperature as a predictor of plant distribution also highlights the importance of distinguishing between meteorological temperature (air temperatures > 2 m above ground) and experienced temperature from a plant perspective (soil and air temperatures within 20 cm of the ground surface). Identifying surface temperature at micro-scales is especially critical in an alpine setting where plants are decoupled from atmospheric conditions and a distance of 2 m can cause greater temperature fluctuations than the most extreme IPCC climate scenario (Scherrer and Körner 2011).

In a predictive modelling context, downscaling climate variables using a VHR DEM may be more effective than using micro-scale topographic variables that infer abiotic conditions indirectly (e.g. Lassueur et al. 2006 using aspect as a proxy for solar radiation). The incorporation of micro-scale estimates of temperature, moisture index and solar radiation has the potential to capture micro-refugia in future, climate-based predictions of alpine plant distribution. While downscaling climate variables is standard practice for extrapolating isolated measures of meteorological temperature across complex mountain topography, algorithms become increasingly complicated at finer resolutions and correlations between measured temperatures in situ and modelled temperatures are known to decrease at higher elevations (Fridley 2009). Accordingly, the extent of modelling areas may be limited due to the computational demands of applying downscaling algorithms at micro-resolutions. Although methodological hurdles exist, in our view downscaled climate variables at a resolution finer than 10 m have important potential to improve predictions of alpine plant distribution.

Snow cover dynamics

Patterns of seasonal snowmelt in alpine landscapes are found to occur with surprising consistency from one year to the next (Walsh et al. 1994) and are known to have a direct effect on the abiotic constraints acting upon plant distribution (Billings and Bliss 1959; Choler 2005; Keller et al. 2005). Accounting for snow cover dynamics and their future evolution is of particular importance because snow cover impacts yearly regimes of temperature, soil water content and light (Baptist and Choler 2008). These induced changes can also indirectly affect the outcome of biotic interactions, considering that early snow melting sites represent stressful conditions where facilitation among species has been shown to predominate (Choler et al. 2001; Wipf et al. 2006).

As a first approach, several studies have incorporated static maps of snow cover into SDMs in alpine environments (e.g. Dirnböck et al. 2003; Hirzel et al. 2006), although this

method over-simplifies the dynamic nature of snowmelt processes. At least one study has incorporated a simulation of snow accumulation, transport and melting into an alpine plant modelling study (Randin et al. 2009a). Inclusion of snow cover improved the fit of spatial projections within the study area but did not enhance the transferability of the model when it was applied to other mountain systems. The authors attribute this lack of predictive power to the fact that the mechanistic snow model used (see Tappeiner et al. 2001) did not take snow distribution by avalanches into account, which is known to be a major factor in determining the location of persistent snowfields (Butler et al. 2007).

In the Swiss Alps, a snow cover simulation model (Zappa 2008) was developed to predict snow cover duration based on abiotic variables (temperature, precipitation, solar radiation and moisture). A recent pilot study validated the output of this model relative to observed snowmelt patterns obtained from multi-temporal SPOT imagery and found the model to be an excellent predictor of snow cover duration in high mountain areas over a 3-year period (Dedieu et al. 2012). In our view, future studies should consider estimated snow cover duration as a predictive variable of alpine plant distribution.

Dynamic species interactions along environmental gradients

Although correlative SDMs implicitly address competition and facilitation dynamics by projecting the realized niche of species (Guisan and Thuiller 2005), this desirable property is nonetheless unable to account for altered biotic interactions from range shifts resulting from environmental change (Meier et al. 2010). Examining sub-alpine and montane species (up to 2,600 m) in Western Europe, Lenoir et al. (2008) documented an average upward shift in species range optimum of 29 m per decade during the twentieth century. Upward shifts in European alpine plant distribution have been detected both over the past century (Frei et al. 2010) and also more recently between 2001 and 2008 (Gottfried et al. 2012; Pauli et al. 2012). Varying responses among species will lead to novel sets of biotic interactions that pose a critical challenge for building reliable biodiversity models (Meier et al. 2010; Kissling et al. 2011; Thuiller et al. 2013).

While emphasis has been placed on the need to explicitly incorporate competition into SDMs (Guisan and Zimmermann 2000), a rich literature in community ecology points out the equal importance or even predominance of facilitation in stressful environments (Callaway et al. 2002; Michalet et al. 2006). Through localized nutrient concentration, sheltering from wind and enhanced thermal regulation, intra and inter-specific facilitation enables alpine plants to expand their realized niche in the face of

increasingly severe environmental conditions. It has been demonstrated that within the same species or among consistent species pairs, the direction of biotic interactions shifts along abiotic stress gradients (Choler et al. 2001; Callaway et al. 2002).

Kissling et al. (2011) propose a strategy for quantitatively modelling multi-directional biotic interactions at the community level using *interaction currencies*. In this approach, biotic interactions are defined indirectly through species' relationships with a mediating currency, which can be designated as either a resource or an abiotic condition known to drive species distribution. Ground surface temperature, for example, could act as an interaction currency mediating biotic interactions in alpine landscapes. For a particular range of temperatures, *interaction coefficients* could be assigned to each species (or functional group) to quantify the effect of soil temperature on species' relative competitive ability. Certain species would thus be favoured by high competition and low abiotic stress, while others would benefit from low competition due to their ability to cope with high abiotic stress. The use of interaction currencies could, therefore, account for shifting species interactions (e.g. from competition to facilitation) in a climate change context.

A second approach to modelling multi-directional biotic interactions was developed by Boulangeat et al. (2012a). In their regional-scale biodiversity model, the authors indirectly accounted for species interactions by assigning a biotic environment index to focal species based on a dataset of 2170 co-occurring species documented within the study area. Index values of repulsion and attraction were determined relative to observed co-distribution patterns and environmental niche data (Boulangeat et al. 2012a). The method is limited in the sense that it uses phenomenological indices that do not allow for the isolation of biotic interactions from other local environmental factors affecting co-distribution patterns. Moreover, shifts in biotic interactions induced by climate change, as well as interactions between newly co-occurring species, cannot be explicitly taken into account using such fixed co-occurrence indices (Thuiller et al. 2013).

A third approach to modelling competition and facilitation dynamics among alpine plants involves incorporating the presence of one or several dominant species as predictive variables. Pellissier et al. (2010) used the probability of presence of *Empetrum nigrum*, a dominant species in Norwegian tundra, to improve predictions of 29 co-occurring species. Functional traits were measured for subordinate species and used to infer the direction of interactions with *E. nigrum*, i.e. facilitation, competition or neutrality. Thus, in addition to standard topo-climatic predictors, probability of presence of *E. nigrum* was used as a proxy for community assemblage processes.

For all three approaches mentioned above (interaction currencies, co-occurrence indices and dominant species

predictors), the size of the interaction matrices (and thus model complexity) could be reduced by consolidating species into functional groups (Kissling et al. 2011). In our view, an improved approach for predictive modelling of alpine plant interactions would involve using a dynamic dominant vegetation model (e.g. FATE, Midgley et al. 2010) to simulate plant succession processes based on abiotic drivers. In this approach, species are grouped into dominant functional groups representative of both functional and taxonomic diversity (Boulangeat et al. 2012b). After initial seed presence is determined based on a habitat suitability model, competition among co-occurring functional groups within the same pixel is then mechanistically modelled taking into account annual growth and competition for light (Midgley et al. 2010). In order to address biotic interactions among herbaceous alpine plants, four improvements would have to be made upon the existing framework : (1) plant phenology should be taken into account to simulate coexistence between early and late growing plants; (2) in addition to determining light availability, plant stature could be used as a proxy for localized shifts in environmental conditions such as protection from wind exposure and buffering of temperature, e.g. by canopy, which would address facilitation dynamics in harsh alpine environments; (3) competition for available soil nutrients (e.g. nitrogen) in addition to light should be included and (4) interactions between plant succession and soil nutrient composition should be incorporated. This last point is particularly relevant in periglacial zones, where positive feedback mechanisms between plant installation and soil nutrients are known to affect vegetation composition over time (Chapin et al. 1994). Modelling the biotic environment using dominant functional groups is justifiable given that biotic interactions are known to be of less importance in plant communities lacking dominant species (Meier et al. 2010). Climate change would affect the predicted habitat distribution of dominant functional groups, which would begin to address the problem of modelling shifts in biotic interactions relative to abiotic drivers (Kikvidze et al. 2011).

Dispersal and spatial configuration of habitats

A recent work emphasizes the importance of patch configuration, seed dispersal and site availability as drivers of alpine plant distribution (Dullinger et al. 2011). An experimental study manipulated alpine snow bed plants to investigate whether species were limited primarily by abiotic conditions or by dispersal (Dullinger and Hülber 2011). Successful establishment of transplanted individuals underpinned the importance of seed dispersal and patch connectivity as drivers of distribution in a meta-population system of specialized alpine species (Dullinger and Hülber

2011). Such findings suggest that post-Little Ice Age recolonization dynamics may be at the origin of the observed phenomenon of increasing species richness within the alpine zone and that dispersal rather than abiotic conditions could be the primary factor limiting species distribution (Kammer et al. 2007). Additionally, detection of a lag time between climate warming and observed demographic response suggests that dispersal limitation leads to the accumulation of extinction debt within alpine plant populations (Dullinger et al. 2012). Incorporating sub-models of seed dispersal into alpine biodiversity models is thus necessary to simulate alpine plant population dynamics within areas of suitable habitat (e.g. Engler et al. 2009).

Reconstructing colonization patterns and distinguishing between short-term (adjacent colonization over the span of a century) vs. long-term (evolutionary scale patterns linked to long-term climate change and species migration) dispersal constitutes an on-going challenge in the field of alpine biogeography (Schönswetter et al. 2005; Winkworth et al. 2005; Puscas et al. 2008). Considering that long-term dispersal begins to play a significant role at broad spatial and temporal scales, it is probably sufficient to only consider short-term dispersal mechanisms when forecasting alpine plant distribution at the regional scale within a 100-year prediction period. Although we have focused on dispersal here, other species traits are understood to affect the long-term distribution of alpine plants. For example, a recent study identified that clonal reproduction can allow the persistence of plant populations in alpine habitats for up to several hundred thousand years (De Witte et al. 2012). Thus, accounting for reproductive strategies may be an important predictor of long-term plant persistence in the face of dramatic climate fluctuations.

Spatial-temporal responses of alpine plants to geomorphic disturbance and land-use change

Alpine environments are subject to a number of disturbance processes that are particular to this system and which affect vegetation distribution at varying spatial and temporal scales (Nichols et al. 1998). First, human land-use and associated agro-pastoral practices constitute an important form of disturbance in many alpine environments, especially in densely populated mountain ranges such as the European Alps (Gelrich and Zimmermann 2006; Vittoz et al. 2008). Second, slope and freezing temperatures engender a host of mechanical disturbance processes in periglacial environments that affect vegetation distribution, including solifluction, cryoturbation, avalanches and rockslides (Johnson and Billings 1962; Butler et al. 2007). The goal of this section is to review the findings of studies that have considered alpine-specific forms of disturbance in a modelling context.

Alpine land-use

Disturbance processes linked to human land-use and mountain agriculture represent an important non-elevation specific driver of alpine vegetation distribution. In Europe, mountain areas have been inhabited and subject to anthropogenic deforestation and agro-pastoral practices for multiple centuries (Kaplan et al. 2009), and the long-term presence of traditional mountain agricultural in sub-alpine and alpine valleys has typically led to the persistence of diverse and stable plant communities (Tappeiner et al. 2008). Since the mid-twentieth century, land abandonment in mountain areas has become a widespread phenomenon throughout Europe and much of the world, as large-scale agriculture has oriented cultivation toward less steep and more productive slopes (Gelrich and Zimmermann 2006). Recent studies in the Pyrenees and Swiss Alps have made direct links between declining human agricultural activity and rapid forest densification and encroachment into grassland communities over the past 50 years (Gehrig-Fasel et al. 2007; Améztegui et al. 2010). In densely populated mountain ranges, shifts in land-use have been found to be a more direct driver of vegetation change than climate change (Gehrig-Fasel et al. 2007).

Despite its unquestioned effect on sub-alpine and alpine plant distribution, surprisingly few studies have considered land-use scenarios in an alpine vegetation modelling context (but see Dirnböck et al. 2003; Lischke et al. 2006 for tree-line). In the North Eastern Calcareous Alps of Austria, Dirnböck et al. (2003) obtained approximate dates of abandonment for land parcels throughout a 150-km² study area and developed two scenarios based on either the continuation of current practices or total land abandonment. SDMs applied to 85 plant species showed that land abandonment, when coupled with climate change, leads to accelerated habitat reduction for alpine species. Recently, Midgley et al. (2010) introduced a framework for integrating disturbance processes (e.g. mowing and grazing) with habitat suitability and dispersal at the level of plant functional groups. By explicitly taking into account the influence of agro-pastoral practices on vegetation dynamics, plant succession models that incorporate both grazing intensity and frequency seem to have strong potential to improve alpine biodiversity models.

Geomorphic disturbance

Patterns of sub-alpine and alpine vegetation distribution are structured by geomorphic processes. For example, the location of treeline can be limited by underlying lithology, locally suppressed by avalanche and rock fall couloirs and constrained by mass-wasting events (Körner 2003; Butler et al. 2007). Opportunist, non-dominant species are able to

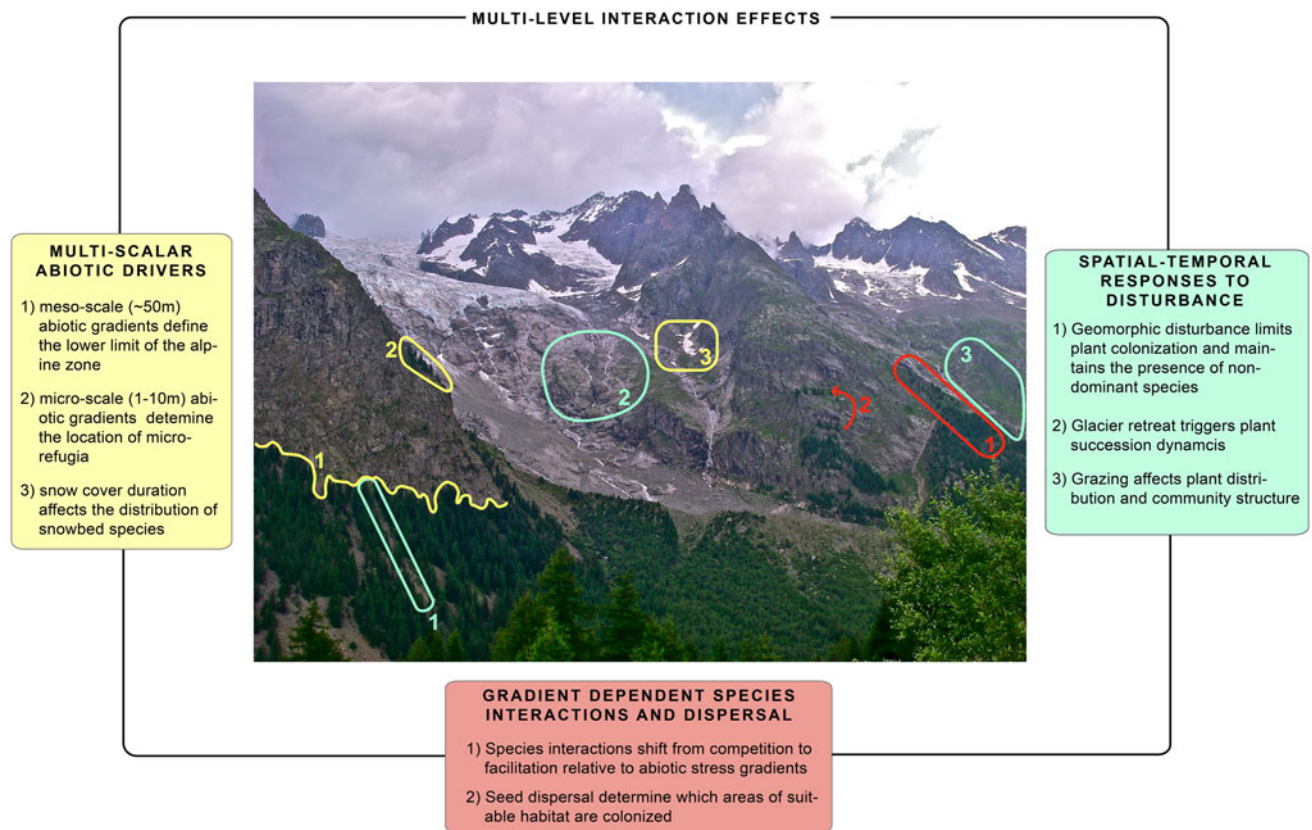


Fig. 1 Key drivers and processes affecting alpine plant distribution and their locations in a high mountain landscape

persist in sub-alpine and alpine communities by means of disturbance events that remove competitors and create temporarily favourable conditions (Chesson 2000). For example, shade-intolerant *Larix decidua* is able to endure in sub-alpine landscapes dominated by shade-tolerant *Abies alba* due to frequent disturbance events in the form of snow avalanches and landslides that create gaps (Bebi et al. 2009). Geomorphic disturbance thus affects species distribution by precluding plant growth in certain areas and by enabling resilient species to persist in disturbed sites that would otherwise be occupied by more competitive species.

We are aware of a handful of studies that have incorporated geomorphic disturbance variables directly into SDMs of alpine plant distribution (Brown 1994; Randin et al. 2009a; le Roux and Luoto 2013). Randin et al. (2009a) developed a disturbance index, ranging from areas of developed, stable soil with high vegetation cover to areas of bare rock covered by patchy vegetation and subject to continuous erosion and seasonal cycles of avalanche and rock fall. On average, the inclusion of a geomorphic disturbance variable only slightly improved the fit and predictive power of SDMs, although contributions were highly species-specific. The authors pointed out that use of a semi-quantitative index imposed artificial

boundaries on the landscape and that a continuous geomorphic index based on a VHR DEM might have had better explanatory power (Randin et al. 2009a). Le Roux and Luoto (2013) showed that the use of variables representing solifluction, fluvial activity and nivation in addition to standard climate predictors significantly improved the spatial predictions of alpine plant distribution and community composition.

VHR DEMs derived from advanced remote-sensing products (e.g. LIDAR) have been used to improve spatial estimates of geomorphic disturbance in high mountain environments (Kasai et al. 2009). Avalanche couloirs, proportion of bare ground, scree fields and evidence of cryoturbation can all be detected using high-resolution satellite imagery (e.g. Walsh et al. 1998), and the integration of this information could be used to develop spatially continuous indices of geomorphic disturbance. Considering that geomorphic disturbance in high mountain environments is a by-product of broader topographic factors (Körner et al. 2011) that are unlikely to fluctuate systematically in response to climate change, the priority should be on developing models of periglacial disturbance for current mountain landscapes (e.g. Marmion et al. 2008). In our view, static, spatially continuous estimates of geomorphic

disturbance ought to be sufficient to improve the predictive power of alpine biodiversity models when integrated with other dynamic drivers.

A proposed integrated framework for modelling alpine plant distribution

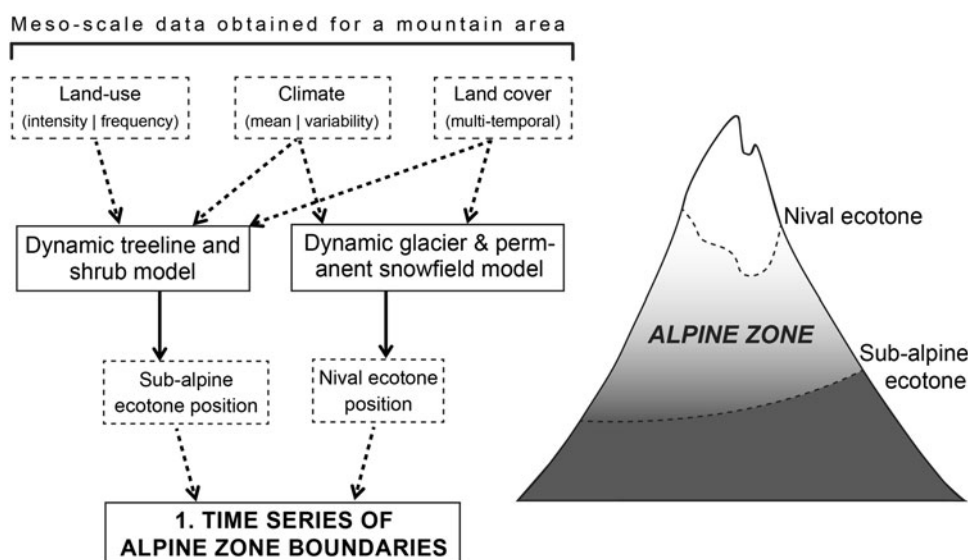
We now present a potential methodological framework aimed at developing an integrated alpine biodiversity model. Our approach is based on three steps: (1) dynamic modelling of sub-alpine and nival ecotone position as a means of delineating alpine zone boundaries over time (Fig. 2); (2) modelling of species habitat within the alpine zone, taking into account micro- and meso-topography, snow cover duration, geomorphic disturbance, climate and the biotic environment and (3) integrating habitat models with spatially explicit meta-population models of demography (Fig. 3).

As a first step, we propose combining dynamic models of the sub-alpine (upper limit of treeline and shrubs) and the nival (lower-limit of glaciers) ecotones to account for shifts in alpine zone boundaries over time (Fig. 2). The model *TreeMig* (Lischke et al. 2006) provides an example of an already existing spatial and temporal gap model that takes into account climate and land-use change, biotic interactions and dispersal (Rickebusch et al. 2007) and which can be used to reconstruct tree species successions when colonizing below and migrating at the treeline ecotone. The use of a dynamic dominant vegetation model (e.g. FATE, Midgley et al. 2010) represents an alternative solution that could be applied to model both treeline and shrub extension over time. We propose the use of grazing intensity and frequency (land-use), climate mean and variability (as outlined by

Körner et al. 2011), substrate, biotic interactions and dispersal as input variables in this initial ecotone model. Remote-sensing could also be used to validate predictions of treeline and shrub position for the present (e.g. Coops et al. 2013). In order to model the nival ecotone using state of the art techniques, collaboration with glaciologists would be necessary. Existing climate-based algorithms of glacier volume (e.g. Jouvet et al. 2008) based on historical glacier dynamics in the Swiss Alps (e.g. Kääb et al. 2002) could be applied to novel study areas, where historical glacier inventories and data availability are becoming sufficient to model future trajectories of glacier extent (e.g. Gardent et al. 2012). Generating a dynamic clip of an alpine study area over time would increase the accuracy of predictions and improve the efficiency of model calculations, given that only areas of potential alpine plant habitat would be taken into account.

Within established alpine zone boundaries (Fig. 3), we propose developing a dynamic habitat model that takes into account the most important drivers of alpine plant distribution. Throughout this phase, remote sensing would play a key role in both data acquisition and model validation. Input variables would consist of micro- (VHR DEM) and meso-topography (medium-resolution DEM), land cover, spatially explicit grazing intensity and frequency data and climate variables representing both mean and extreme tendencies. Multi-temporal remote-sensing could furthermore be used to calibrate a climate and topography-based model of snow cover duration (e.g. Dedieu et al. 2012). Geomorphic disturbance and periglacial landforms could be modelled using remote sensing and topographic data and incorporated as an explanatory variable in the form of a continuous and spatially explicit index (e.g. Randin et al. 2009a). Incorporation of alpine-specific abiotic drivers would thus serve to refine

Fig. 2 Meso-scale (~50 m) dynamic modelling of alpine zone boundaries. The lower limit is defined by a time series of treeline and shrub position (sub-alpine ecotone), while the upper limit is defined by a time series of glacier/nival extent (nival ecotone). *Dashed lines* indicate input variables and *solid lines* indicate sub-models



areas of predicted favourable habitat. With predicted seed presence as a starting point, biotic interactions (including competition for light and soil nutrients and biotic interactions induced by of plant canopy) could be then simulated at the level of dominant functional groups using a dynamic plant succession model (e.g. FATE, Midgley et al. 2010).

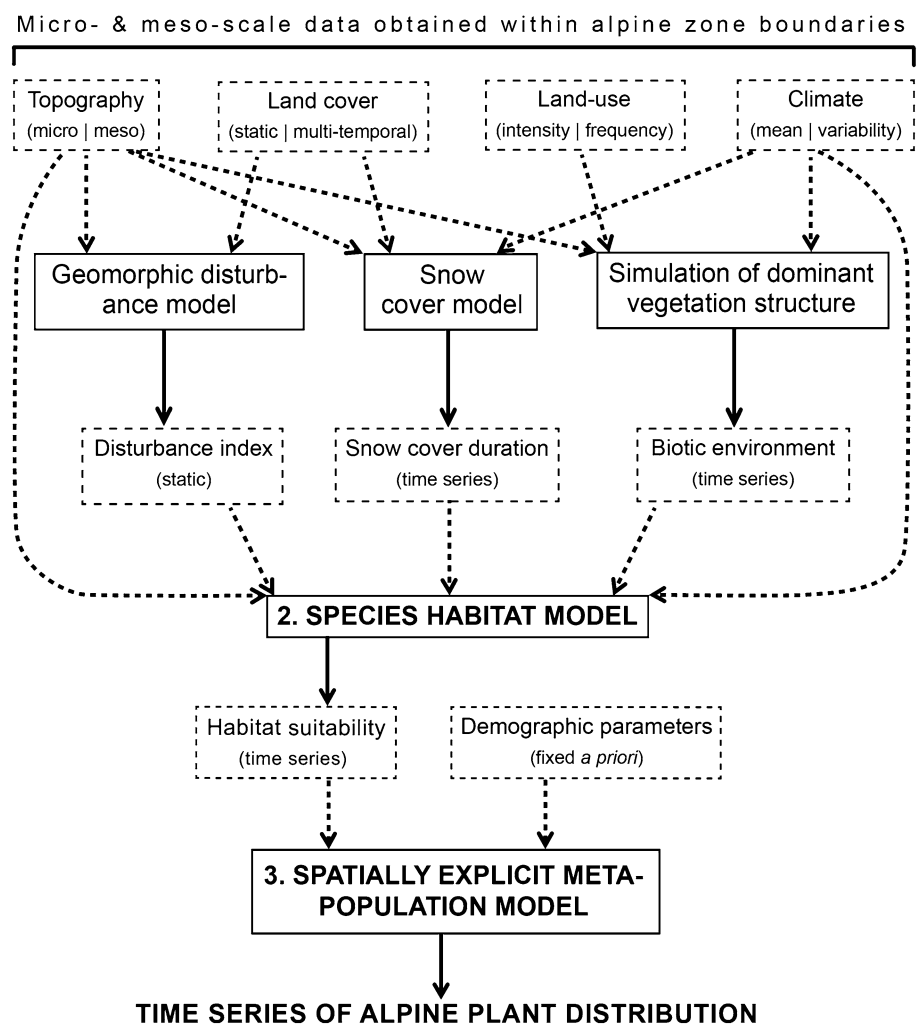
The goal of the third step (Fig. 3) would be to model population dynamics within and adjacent to zones of favourable habitat using established meta-population modelling methods (Hanski 1999). Dominant functional groups could be split open to simulate population dynamics at the species level. A spatially explicit version of the incidence function based on metapopulation theory (Hanski 1999) would form the basis for simulating species abundance and turnover (Thuiller et al. 2013). Initially this approach would need to be tested for a small number of species before application at the community level. For a species within a patch, the input parameters for one or multiple species would consist, in principle, of the following geo-localized demographic data: probability of presence, colonization rate, fecundity, dispersal capacity and distance to other patches,

extinction rate and carrying capacity (as determined by environmental conditions) (Thuiller et al. 2013). If these parameters are unavailable for certain species, a Bayesian framework or Approximate Bayesian Computing could be used to make robust inferences from available data (e.g. repeated surveys, May et al. 2013; Pagel and Schurr 2012), but this strategy remains to be evaluated in our context. This approach would enable simulation of source/sink dynamics where unviable populations are maintained in non-favourable areas due to the proximity of source populations (Pagel and Schurr 2012). The output of a spatially explicit meta-population model would consist of estimates of alpine plant abundance, ideally at 10 m resolution or less to capture plant distribution in the form of micro-refugia.

Conclusion

We have assembled the key drivers of alpine plant distribution into a conceptual framework aimed at developing an integrated model alpine plant distribution (Fig. 1). While the

Fig. 3 Micro-scale (<10 m) modelling of suitable habitat (1) and spatial-temporal population dynamics (2) within alpine zone boundaries (Fig. 2). *Dashed lines* indicate input variables and *solid lines* indicate sub-models



broad methodology outlined here could take a multitude of forms in an applied context, we advocate that an integrated model of alpine plant distribution (Figs. 2, 3) should ideally include (1) dynamic ecotone modelling to account for shifts in alpine zone extent over time; (2) climate variables reflecting variability and extremes in addition to mean meteorological conditions; (3) a predictive model of snow cover duration driven by climate variables; (4) proxies of the biotic environment that account for shifts in species interactions induced by climate change; (5) realistic and spatially explicit proxies of geomorphic disturbance mechanisms in periglacial environments and; and (6) process-based modelling of population dynamics and community structure within shifting zones of favourable habitat. Our review of the literature indicates that the tools and methods necessary to account for these drivers already exist independently and that the main challenge now consists of efficiently combining different drivers affecting alpine plant distribution. Initially, we recommend approaching sections of Fig. 3 (i.e. snow cover duration, geomorphic disturbance, post-glacial retreat succession dynamics) and developing heuristic modelling frameworks for these separate processes before assembling multiple processes into a broader integrated model.

Improved alpine biodiversity models will allow for more precise forecasting of plant distributions and vulnerability in response to global changes, which is essential to regional-scale conservation efforts in mountain areas. Developing a comprehensive integrated model of alpine plant distribution will require inter-disciplinary collaboration among biogeographers, biostatisticians, community ecologists, glaciologists and geologists, as well as the continuation and enhancement of long-term alpine monitoring programmes.

Acknowledgments The research leading to these results has received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement No. 281422 (TEEMBIO) and from the ERA-NET CIRCLE (Mountain Group) (CAMELEON).

References

- Améztegui A, Brotons L, Coll L (2010) Land-use changes as major drivers of mountain pine (*Pinus uncinata*) expansion in the Pyrenees. *Glob Ecol Biogeogr* 19:632–641
- Austin MP, Smith TM (1989) A new model of continuum concept. *Vegetation* 83:35–47
- Baptist F, Choler P (2008) A simulation of the importance of length of growing season and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Ann Bot* 101:549–559
- Battlori E, Camarero JJ, Ninot JM, Gutiérrez E (2009) Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to global warming. *Glob Ecol Biogeogr* 18:460–472
- Bebi P, Kulakowski D, Rixen C (2009) Snow avalanche disturbances in forest ecosystems: state of research and implications for management. *For Ecol Manage* 257:1883–1892
- Billings WD (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *Bioscience* 23:697–704
- Billings WD, Bliss LC (1959) An alpine snowbank environment and its effects on vegetation, plant development and productivity. *Ecology* 40:388–397
- Bliss LC (1971) Arctic and alpine plant life cycles. *Annu Rev Ecol Syst* 2:405–438
- Boggs K, Klein SC, Grunblatt J, Boucher T, Koltun B, Sturdy M, Streveler GP (2010) Alpine and sub-alpine vegetation chronosequences following deglaciation in coastal Alaska. *Arct Antarct Alp Res* 42:385–395
- Boulangeat I, Gravel D, Thuiller W (2012a) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecol Lett* 15:584–593
- Boulangeat I, Philippe P, Abdulhak S, Douzet R, Garraud L, Lavergne S, Lavorel S, Van Es J, Vittoz P, Thuiller W (2012b) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Glob Change Biol* 18:3464–3475
- Bowman W, Theodose T, Schardt J, Conant R (1993) Constraints of nutrient availability on primary production in two alpine Tundra communities. *Ecology* 74:2085–2097
- Brown DG (1994) Predicting vegetation types at treeline using topography and biophysical disturbance variables. *J Veg Sci* 5:641–656
- Butler DR, Malanson GP, Walsh SJ, Fagre D (2007) Influences of geomorphology and geology on alpine treeline in the American West—More important than climatic influences? *Phys Geogr* 28:434–450
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848
- Chapin SF, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol Monogr* 64:149–175
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Choler P (2005) Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arct Antarct Alp Res* 37:444–453
- Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308
- Coops NC, Morsdorf F, Schaepman ME, Zimmermann NE (2013) Characterisation on an alpine treeline using airborne LIDAR data and physiological modeling. *Glob Change Biol*. doi:10.1111/gcb.12319
- De Witte LC, Armbruster GFJ, Gielly L, Taberlet P, Stöcklin J (2012) AFLP markers reveal high clonal diversity and extreme longevity in four key Arctic-alpine species. *Mol Ecol* 21:1081–1097
- Dedieu JP, Randin CF and Zappa M (2012) Validation par télédétection spatiale de l'enneigement dans les Alpes autrichiennes pour l'approvisionnement en eau de la ville de Vienne. 25ème Colloque de l'Association Internationale de Climatologie, Grenoble, France
- Dirnböck T, Dullinger S, Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *J Biogeogr* 30:1–17
- Dobrowski S (2010) A climatic basis for micro-refugia: the influence of terrain on climate. *Glob Change Biol* 17:1022–1035
- Dormann CF (2007) Promising the future? Global change projections of species distributions. *Basic Appl Ecol* 8:387–397

- Dormann CF, Stanislaus J, Cabral J, Chuinne I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2011) Correlation and process in species distribution models: bridging a dichotomy. *J Biogeogr* 39:2119–2131
- Dullinger S, Hülber K (2011) Experimental evaluation of seed limitation in alpine snow bed plants. *PLoS ONE* 6(6):e21537
- Dullinger S, Dirnböck T, Grabherr G (2003) Patterns of shrub invasion into high mountain grasslands of the northern calcareous Alps, Austria. *Arct Antarct Alp Res* 35:434–441
- Dullinger S, Mang T, Dirnböck T, Ertl S, Gatttringer A, Grabherr G, Leitner M, Hülber K (2011) Patch configuration affects alpine plant distribution. *Ecography* 34:576–587
- Dullinger S, Gatttringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzer C, Leitner M, Mang T, Caccianiga M, Dirnböck T, Ertl S, Fischer A, Lenoir J, Svenning JC, Psomas A, Schmatz DR, Silc U, Vittoz P, Hülber K (2012) Extinction debt of high-mountain plants under 21st century climate change. *Nat Climate Change* 2:619–622
- Dumont M, Gardelle J, Sirguey P, Guillot A, Six D, Rabatel A, Arnaud Y (2012) Linking annual glacier mass balance and glacier albedo retrieved from MODIS data. *Cryosphere* 6:1527–1539
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Syst* 40:677–697
- Engler R, Randin CF, Vittoz P, Czaka T, Beniston M, Zimmermann NE, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal matter? *Ecography* 32:34–35
- Engler R, Thuiller W, Dullinger S, Zimmermann N, Araújo M, Pearman P, Le Lay G, Piedallu C, Albert C, Choler P, Coldea G, de Lamo X, Dirnböck T, Gégout JC, Gómez-García D, Heegaard E, Høistad F, Nogués-Bravo D, Normand S, Puşcaş M, Sebastian MT, Stanisci A, Theurillat JP, Trivedi M, Vittoz P, Guisan A (2011) 21st century climate change threatens mountain flora unequally across Europe. *Glob Change Biol* 17:2330–2341
- Frei E, Bodin J, Walther GR (2010) Plant species' range shifts in mountainous areas: all uphill from here? *Bot Helv* 120:117–128
- Fridley JD (2009) Downscaling climate over complex terrain: high fine scale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains)*. *J Appl Meteorol Climatol* 48:1033–1049
- Gardent M, Rabatel A, Dedieu JP, Deline P, Schoeneich P (2012) Analysis of the glacier retreat in the French Alps since the 1960s based on the new glacier inventory. *Geophys Res Abstr*, 14, EGU2012-8984-1, 9th EGU General Assembly, Wien
- Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? *J Veg Sci* 18:571–582
- Gellrich M, Zimmermann N (2006) Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: A spatial statistical modelling approach. *Landsc Urb Plan*, (LAND-1362), 12 pp
- Gottfried M, Pauli H, Grabherr G (1998) Prediction of vegetation patterns at the limits of plant life: a new view of alpine-Nival ecotone. *Antar Arct Alp Res* 30:207–231
- Gottfried M, Pauli H, Reiter K, Grabherr G (1999) A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Divers Distrib* 5:241–251
- Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barancok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, Kazakis G, Krajci J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P, Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A, Theurillat JP, Thomaselli M, Villar L, Vittoz P, Vogiatzakis I, Grabherr G (2012) Continent-wide response of mountain vegetation to climate change. *Nat Climate Change* 2:111–115
- Guisan A, Theurillat JP (2000) Assessing alpine plant vulnerability to climate change: a modelling perspective. *Integr Assess* 1:307–320
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Guisan A, Zimmermann N (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186
- Guisan A, Theurillat JP, Klenast F (2009) Predicting the potential distribution of plant species in an alpine environment. *J Veg Sci* 9:65–74
- Haeblerli W, Beniston M (1998) Climate change and its impacts on glaciers and permafrost in the alps. *AMBIO* 27:258–265
- Hanski I (1999) Metapopulation ecology. Oxford University Press, USA
- Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to global warming. *Ecol Lett* 12:1040–1049
- Hejman M, Dvorak JJ, Kocianova M, Pavlu V, Nezerkova M, Pavlu V, Nezerkova P, Vitek O, Rauch O, Jenik J (2006) Snow depth and vegetation pattern in a late-melting snowbed analyzed by GPS and GIS in the Giant Mountains, Czech Republic. *Arct Antarct Alp Res* 38:90–98
- Hirzel A, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presence. *Ecol Model* 199:142–152
- Johnson PL, Billings WD (1962) Alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol Monogr* 32:105–135
- Jouvet J, Picasso M, Rappaz J, Blatter H, Huss M, Funk M (2008) Numerical simulation of Rhone's glacier from 1874 to 2100. In: JST Presto Symposium on Mathematical Sciences towards Environmental Problems (Hokkaido University technical report series in mathematics) 136: 1–9
- Kääb A, Paul F, Maisch M, Hoelzle M, Haeblerli W (2002) The new remote sensing derived Swiss glacier inventory: II. First results. *Ann Glaciol* 34:363–366
- Kammer PM, Schöb C, Choler P (2007) Increasing species richness on mountain summits: upward migration due anthropogenic climate change or re-colonization. *J Veg Sci* 18:301–306
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quat Sci Rev* 28:3016–3034
- Kasai M, Ikeda M, Asahina T, Fujisawa K (2009) LiDAR-derived DEM evaluation of deep-seated landslides in a steep and rocky region of Japan. *Geomorphology* 113:57–69
- Keller F, Goyette S, Beniston M (2005) Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Clim Change* 72:299–319
- Kikvidze Z, Michalet R, Brooker RW, Lohengrin AC, Lortie CJ, Pugnaire FL, Callaway RM (2011) Climate drivers of plant-plant interactions and diversity in alpine communities. *Alp Bot* 121:63–70
- Kissling WD, Dormann CF, Groeneveld J, Hickler T, Kühn I, McInerny GJ, Montoya JM, Römermann C, Schiffrers K, Schurr FM, Singer A, Svenning JC, Zimmermann NE, O'Hara RB (2011) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *J Biogeogr* 39:2163–2178
- Körner C (2003) Alpine plant life, 2nd edn. Springer, Heidelberg
- Körner C (2007) Climate treelines: conventions, global patterns, causes. *Erdkunde* 61:316–324
- Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *J Biogeogr* 31:713–732

- Körner C, Paulsen J, Spehn EM (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alp Bot* 121:73–78
- Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J Ecol* 90:68–76
- Lassueur T, Joost S, Randin C (2006) Very high resolution digital elevation models: do they improve models of plant species distribution? *Ecol Model* 198:139–153
- Le Roux PC, Luoto M (2013) Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. *J Veg Sci*. doi:10.1111/jvs.12059
- Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771
- Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ (2006) TreeMig: a forest-landscape model for simulating spatial and temporal patterns from stand to landscape scale. *Ecol Model* 199:409–420
- Marcias-Fauria M, Johnson EA (2013) Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proc Nat Acad Sci USA*. doi:10.1073/pnas.1221278110
- Marmion M, Hjort J, Thuiller W, Luoto M (2008) A comparison of predictive models in modelling the distribution of periglacial landforms in Finnish Lapland. *Earth Surf Proc Land* 33:2241–2254
- May F, Giladi I, Ristow M, Ziv Y, Jeltsch F (2013) Metacommunity, mainland-island system or island communities? Assessing the regional dynamics of plant communities in a fragmented landscape. *Ecography* 36:842–853
- Meier ES, Kienast F, Pearman PB, Svenning JC, Thuiller W, Araújo MB, Guisan A, Zimmermann NE (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33:1038–1048
- Michalet R, Brooker RW, Cavieres LA, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM (2006) Do biotic interactions shape both sides of the hump-backed model of species richness in plant communities? *Ecology* 82:3295–3308
- Midgley GF, Davies ID, Albert CH, Altwegg R, Hannah L, Hughes GO, O'Halloran LR, Seo C, Thorne JH, Thuiller W (2010) BioMove: an integrated platform simulating the dynamic response of species to environmental change. *Ecography* 33:612–616
- Nichols WF, Killingbeck KT, August PV (1998) The influence of geomorphological heterogeneity on biodiversity: a landscape perspective. *Conserv Biol* 12:371–379
- Normand S, Treier UA, Randin C, Vittoz P, Guisan A, Svenning J-C (2009) Importance of abiotic stress as a range determinant for European plants: insight from species' responses to climatic gradients. *Glob Ecol Biogeogr* 18:437–449
- Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob Change Biol* 15:2681–2693
- Pagel J, Schurr FM (2012) Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Glob Ecol Biogeogr* 21:293–304
- Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arévalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougall K, Millar CI, Naylor BJ, Parks CG, Rew LJ, Seipel T (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Front Ecol Environ* 7:479–486
- Paul F, Kääb A, Haeblerli W (2007) Recent glacier changes in the Alps observed by satellite: consequences for future monitoring strategies. *Glob Planet Change* 31:111–122
- Pauli H, Gottfried M, Grabherr G (2003) Effects of climate change on the alpine and Nival vegetation of the alps. *J Mt Ecol* 7:3–12
- Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Calzado RF, Ghosn D, Holten JJ, Kanka R, Kazakis G, Kollar J, Larsson P, Moiseev P, Loiseev D, Molau U, Molero Mesa J, Nagy L, Pelino G, Puscas M, Rossi G, Stanisci A, Syverhuset AO, Theurillat JP, Tomaselli M, Unterluggauer P, Villar P, Grabherr G (2012) Recent plant diversity changes on Europe's mountain summits. *Science* 336:353–355
- Pellissier L, Bräthen KA, Pottier J, Randin C, Vittoz P, Dubuis A, Yoccoz NG, Torbjørn A, Zimmermann NE, Guisan A (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of Tundra plants. *Ecography* 33:1004–1014
- Puscas M, Taberlet P, Choler P (2008) Post-glacial history of the dominant alpine sedge *Carex curvula* in the European Alpine System inferred from nuclear and chloroplast markers. *Mol Ecol* 17:2417–2429
- Randin C, Liston G, Vittoz P, Guisan A (2009a) Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the Western Swiss Alps. *Arct Antarct Alp Res* 41:347–361
- Randin C, Engler R, Normand S, Zappa M, Zimmermann NE, Pearman PB, Vittoz P, Thuiller W, Guisan A (2009b) Climate change and plant distribution: local models predict high-elevation persistence. *Glob Change Biol* 15:1557–1569
- Rickebusch S, Lischke H, Bugmann H, Guisan A, Zimmermann NE (2007) Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. *Forest Ecol Manag* 246:251–263
- Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J Biogeogr* 38:406–416
- Schönschetter P, Stehlik I, Holderegger R, Tribsch A (2005) Molecular evidence for glacial refugia of mountain plants in the European Alps. *Mol Ecol* 14:3547–3555
- Tappeiner U, Tappeiner G, Aschenwald J, Tasser E, Ostendorf B (2001) GIS-based modelling of spatial pattern of snow cover duration in an alpine area. *Ecol Model* 138:265–275
- Tappeiner U, Borsdorf A, Tasser E (2008) Mapping the Alps: Society–Economy–Environment. Spektrum Akademischer, Heidelberg
- Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspect Plant Ecol Evol Syst* 9:137–152
- Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schiffrers K, Gravel D (2013) A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol Lett*. doi:10.1111/ele.12104
- Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O (2008) Low impact of climate change on sub-alpine grasslands in the Swiss Northern Alps. *Glob Change Biol* 15:209–220
- Walsh SJ, Butler DR, Allen TR, Malanson GP (1994) Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *J Veg Sci* 5:657–672
- Walsh SJ, Butler DR, Malanson GP (1998) An overview of scale, pattern, and process relationships in geomorphology: a remote sensing and GIS perspective. *Geomorphology* 21:183–205
- Winkworth R, Wagstaff S, Glenny D, Lockhart P (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Org Divers Evol* 5:237–247
- Wipf S, Rixen C, Mulder CPH (2006) Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Glob Change Biol* 12:1496–1506

Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change* 94:105–121

Zappa M (2008) Objective quantitative spatial verification of distributed snow cover simulations: an experiment for entire Switzerland. *Hydrol Sci J* 53:179–191

Article S2

*Accounting for treeline shift, glacier retreat and
primary succession in mountain plant distribution
models* *

* **Carlson, B. Z.**, Georges, D., Rabatel, A., Randin, C. F., Renaud, J., Delestrade, A., Zimmermann, N., Choler, P. & Thuiller, W. (2014). Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models. *Diversity and Distributions*, 20(12), 1379-1391.



Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models

Bradley Z. Carlson^{1*}, Damien Georges¹, Antoine Rabatel², Christophe F. Randin^{3,4}, Julien Renaud¹, Anne Delestrade^{5,6}, Niklaus E. Zimmermann⁴, Philippe Choler^{1,7†} and Wilfried Thuiller^{1†}

¹Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, University Grenoble Alpes, BP 53, 38041 Grenoble, France, ²Laboratoire de Glaciologie et Géophysique de l'Environnement, UMR CNRS-UJF 5183, University Grenoble Alpes, BP 96, 38402 Grenoble, France, ³Botanisches Institut der Universität Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland, ⁴Swiss Federal Research Institute WSL, Zürcherstr. 111, HL-E22, 8903 Birmensdorf, Switzerland, ⁵Centre de Recherche sur les Ecosystèmes d'Altitude, 67, lacets de Belvédère, 74400 Chamonix-Mont-Blanc, France, ⁶Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, University de Savoie, 73376 Le Bourget du Lac, France, ⁷Station Alpine J. Fourier, UMS CNRS-UJF 3370, University Grenoble Alpes, BP 53, 38041 Grenoble, France

†Co-senior authors.

*Correspondence: Bradley Z. Carlson, Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, University Grenoble Alpes, BP, 53, 38041 Grenoble, France.
E-mail: brad.z.carlson@gmail.com

ABSTRACT

Aim To incorporate changes in alpine land cover (tree line shift, glacier retreat and primary succession) into species distribution model (SDM) predictions for a selection of 31 high-elevation plants.

Location Chamonix Valley, French Alps.

Methods We fit linear mixed effects (LME) models to historical changes in forest and glacier cover and projected these trends forward to align with 21st century IPCC climate scenarios. We used a logistic function to model the probability of plant establishment in glacial forelands zones expected to become ice free between 2008 and 2051–2080. Habitat filtering consisted of intersecting land cover maps with climate-driven SDMs to refine habitat suitability predictions. SDM outputs for tree, heath and alpine species were compared based on whether habitat filtering during the prediction period was carried out using present-day (static) land cover, future (dynamic) land cover filters or no land cover filter (unfiltered). Species range change (SRC) was used to measure differences in habitat suitability predictions across methods.

Results LME predictions for 2021–2080 showed continued glacier retreat, tree line rise and primary succession in glacier forelands. SRC was highest in the unfiltered scenario (–10%), intermediate in the dynamic scenario (–15%) and lowest in the static scenario (–31%). Tree species were the only group predicted to gain overall range by 2051–2080. Although alpine plants lost range in all three land cover scenarios, new habitat made available by glacier retreat in the dynamic land cover scenario buffered alpine plant range loss due to climate change.

Main conclusions We provide a framework for combining trajectories of land cover change with SDM predictions. Our pilot study shows that incorporating shifts in land cover improves habitat suitability predictions and leads to contrasting outcomes of future mountain plant distribution. Alpine plants in particular may lose less suitable habitat than standard SDMs predict due to 21st century glacier retreat.

Keywords

Chamonix Valley – French Alps, habitat filtering, land cover dynamics, remote sensing, species range change.

INTRODUCTION

High mountain environments are characterized by steep environmental gradients that lead to abrupt changes in land cover over short distances (Billings, 1973). The alpine tree

line (Körner, 2007) and the alpine-nival ecotone (Gottfried *et al.*, 1998) represent obvious and prominent boundaries in mountain landscapes that define areas of potential habitat for many plant species. Recent studies employing species distribution models (SDMs; Guisan & Thuiller, 2005) to predict

mountain plant occurrence have focused largely on bioclimatic variables, such as temperature, precipitation, edaphic conditions (Dubuis *et al.*, 2013), or biotic predictors (Pellissier *et al.*, 2010). Climate-driven SDMs, however, run the risk of generating spurious predictions if land cover and its temporal changes are not considered. In mountain landscapes, urban areas, tree cover, bare rock or glaciers may preclude the presence of certain plant species regardless of climate conditions. Previous mountain plant modelling studies have dealt with the problem of heterogeneous land cover in two ways, either focusing on small-extent study areas with consistent habitat types (e.g. Dullinger *et al.*, 2011) or at broader scales, using present-day land cover maps to define areas of suitable habitat for mountain plants in the future (e.g. Randin *et al.*, 2009; Engler *et al.*, 2011).

The use of a present-day land cover map to filter predictions of species distribution in 2080 becomes problematic given that land cover in mountain environments is dynamic and known to change over comparably short time-scales. Abundant literature points to recent and ongoing phenomena of glacier retreat (e.g. Rabatel *et al.*, 2012, 2013), tree line rise (Kullman, 2002; Harsch *et al.*, 2009; Elliott, 2011) and upward shifts in alpine plant distribution in response to climate change (Gottfried *et al.*, 2012). Land abandonment and land use intensification have been connected to the expansion of mountain tree species and the loss of grassland habitat in the Pyrenees and in the Alps (Gehrig-Fasel *et al.*, 2007; Améztegui *et al.*, 2010; Carlson *et al.*, 2014). In alpine environments, climate-induced glacier retreat has caused the alpine-nival ecotone to shift upward and enabled rapid primary plant succession dynamics to occur during colonization of glacier forelands (Pauli *et al.*, 2003; Boggs *et al.*, 2010; Burga *et al.*, 2010). Collectively, such land cover shifts have taken place over recent decades and can be expected to continue to play a strong role in shaping mountain landscapes during the prediction period considered by most modelling studies (the next 50–100 years).

The primary aim of this study was to refine climate-based SDM predictions using dynamic land cover maps, and to test this approach on a selection of 31 plants in the Chamonix Valley, French Alps. We considered tree line rise, glacier retreat and primary succession as relevant land cover changes in determining the distribution of high mountain plants. We sought to understand the effect of using modelled land cover to define suitable habitat for plants during a 2021–2080 century prediction period, and to compare these results to predictions generated by previous approaches (either no habitat filtering or static filtering based on a present-day land cover map). To model land cover, we used historical aerial photographs to document past shifts in forest and glacier extent and then projected these trends forward in time using a linear mixed modelling approach. We classified present-day SPOT satellite imagery to include other land cover classes in our analysis in addition to forest and glacier. A logistic model was used to predict the probability of plant colonization in ice-free areas following glacier retreat. For both

present-day and future land cover maps, we defined favourable habitat for plant species during the prediction period using a typology of six land cover classes. Our pilot study tests this novel methodological approach on high-elevation plants of the French Alps and lays the groundwork to better account for shifts in land cover in future studies aimed at forecasting 21st century mountain plant distribution.

METHODS

Study area context

The study area included a 122 km² sector covering the south-eastern side of the Chamonix Valley and the French side of the Mont Blanc mountain range (Figs 1c and 2). The elevation gradient of the study area spans a range from approximately 1000 m above sea level (m a.s.l.) in the valley floor to 4122 m a.s.l. at the summit of the Aiguille Verte, over a horizontal distance of approximately 5 km (Fig. 2). Glaciers are currently estimated to cover 19% of the study area (23 km²). Vegetation is typical of a granitic landscape in the northern French Alps (e.g. Lauber & Wagner, 2008). As part of the interior Alps, the climate of the Mont Blanc range is classified as continental. The Mont Blanc side of the Chamonix Valley has no official protection status and thus has been subject to a high degree of human disturbance in the form of pastoral activities and mountain tourism since the late 19th century (Sauvy, 2001). Since the 1970s, many of the slopes surrounding the Chamonix Valley have also been developed for the ski industry by the Compagnie des Remontées Mécaniques de Chamonix-Mont-Blanc (Sauvy, 2001). Although the influence of land use on vegetation in the Chamonix Valley was not explicitly considered in this study, it is important to emphasize that observed vegetation dynamics took place in a context of a heavily human-altered landscape.

Land cover mapping

Forest

Aerial photographs covering the study area were obtained for three dates (1952, 1979 and 2008; Fig. 1a). The 2008 mission consisted of 50-cm-resolution digital colour infrared (CIR) orthophotographs. The 1952 and 1979 missions were airborne paper photographs obtained from the French *Institut National de l'Information Géographique et Forestière* (IGN). Photographs were scanned at 1000 dpi resolution and then ortho-rectified using direct linear transformation in Erdas Imagine [version 9.2 (2011) Huntsville, AL, USA]. Approximately 25 ground control points (GCPs) were used per image, and it was ensured that the root mean square error was less than 5 m. For each date, an image mosaic was generated using histogram matching among images. Each mosaic was then imported into ArcGIS [version 10.1 (2010) Redlands, CA, USA] and ortho-rectified a second time using 200

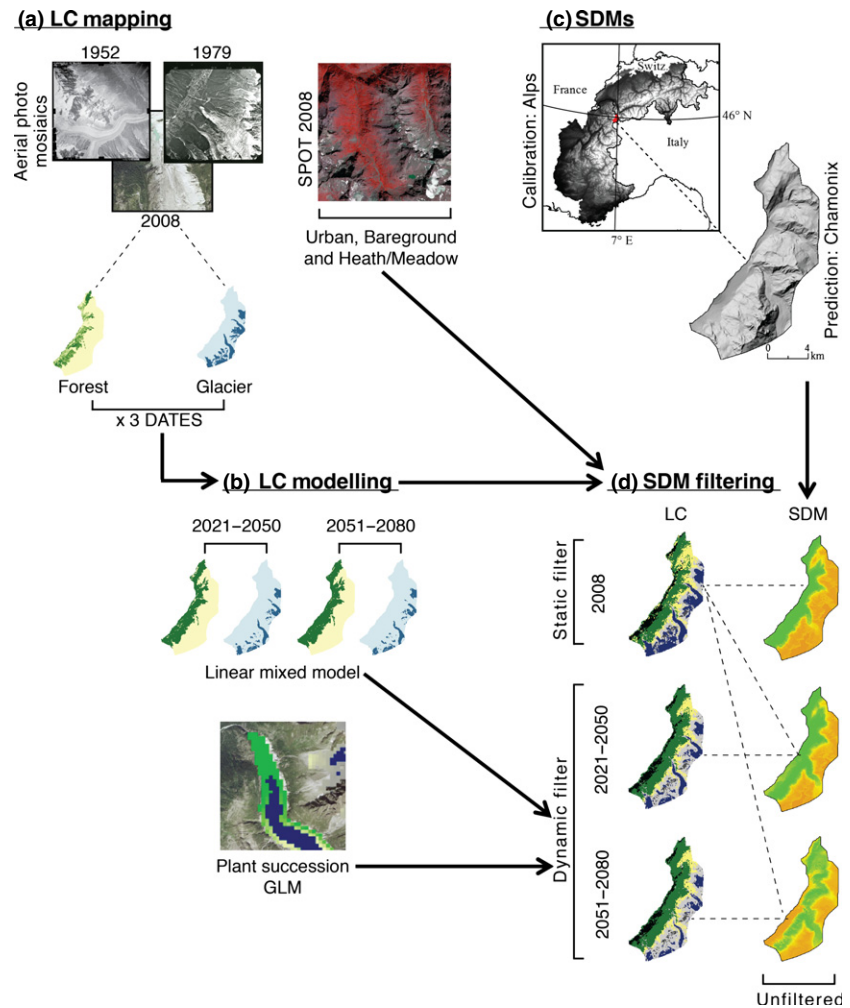


Figure 1 Overview of the methodological approach utilised. Dashed lines represent data manipulation within a step, while solid arrows represent transitions between steps. LC = land cover; SDMs = species distribution models.

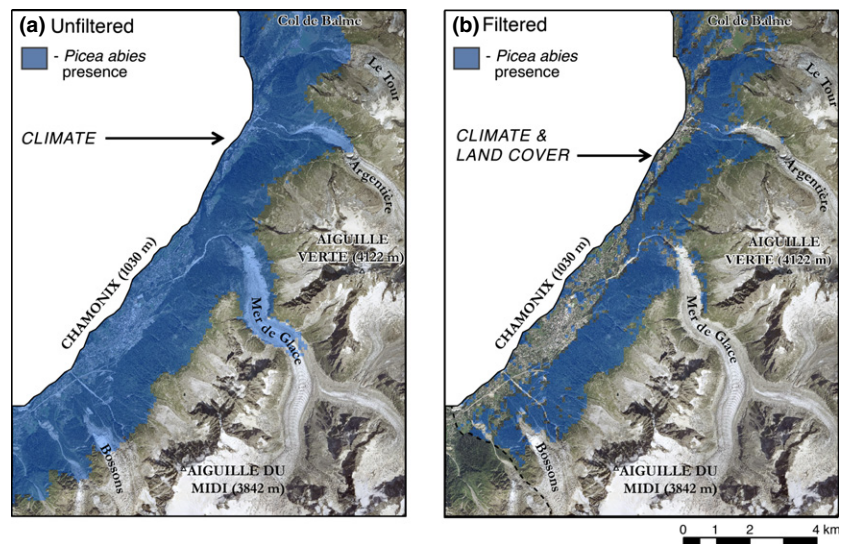


Figure 2 Example of using land cover to filter species distribution model predictions for the present-day period in the Chamonix Valley. (a) Predicted presence of *Picea abies* representing the unfiltered species distribution model output. (b) Predicted presence of *Picea abies* representing the species distribution model output filtered by present-day land cover. The dashed line on (b) indicates the extent of available land cover data.

GCPs and the spline transformation method to ensure optimal superposition across dates. A supervised classification in eCognition Developer [version 8.0 (2012) Munich, Germany] was applied to the 1952, 1979 and 2008 mosaics to obtain a

two-class forest/non-forest land cover map. Automated classification was then adjusted manually by comparison with the original mosaics, and forest cover maps were exported as 5-m raster layers.

Glacier

Glacier outlines were manually delineated for three historical dates: 1850, 1952 and 2008. Present-day moraine location was used as a signature to map maximum ice extent during the Little Ice Age, with 1850 being used as an approximate representative date (Gardent *et al.*, 2012). Orthophotographs with a 50 cm resolution were used to map glacier extent in 1952 and 2008 at a scale of approximately 1 : 1000 (Gardent *et al.*, 2012; Rabatel *et al.*, 2012). This method, although more time-consuming than automatic delineation, enabled higher mapping accuracy, especially in the case debris-covered glaciers.

Land cover modelling

A normalized Forestation Index (FI) and Glacier Index (GI) were calculated for pixel (*i*) and for each date (*j*) using the following formulas (eqn. 1 and 2):

$$FI_{ij} = (F_{ij} - NF_{ij}) / (F_{ij} + NF_{ij}) \quad (1)$$

$$GI_{ij} = (G_{ij} - NG_{ij}) / (G_{ij} + NG_{ij}) \quad (2)$$

where *F* represents forest area and *NF* non-forest area, and *G* represents glacier area and *NG* non-glacier area. Values ranged from −1.0 (non-forested or non-glaciated) to 1.0 (fully forested or fully glaciated). A hierarchical linear mixed effects (LME) model was used to analyse changes in FI over the last 60 years and changes in GI over the last 160 years (Fig. 1b). The longitudinal data set comprised *N* grid cells for which FI and GI were estimated for the three dates considered. Because there is the same number of repeated observations (*n* = 3) for all cells, and because the observations are made at fixed years, the design was balanced. The discrepancy in temporal extent between FI and GI analyses can be attributed to the lack of forest cover data for the mid-19th century. In the case of glaciers, we sought to consider to the longest available record in order to assess the hypothesis of linear recession over time.

Based on data exploration, it was hypothesized that FI and GI were dependent upon grid cell elevation, slope and date (eqn. 3 and 4):

$$FI_{ij} = a_i + b_{01}SLOPE_i + b_{02}ELEV_i + b_{03}YEAR_{ij} + b_{04}ELEV_i * YEAR_{ij} + v_{0i} + v_{1i}YEAR_{ij} + \varepsilon_{ij} \quad (3)$$

$$GI_{ij} = a_i + b_{01}SLOPE_i + b_{02}ELEV_i + b_{03}YEAR_{ij} + b_{04}ELEV_i * YEAR_{ij} + v_{0i} + v_{1i}YEAR_{ij} + \varepsilon_{ij} \quad (4)$$

where *i* corresponds to each pixel and *j* to each date considered, *a* represents model intercepts, *b* represents coefficients for the fixed effects SLOPE, ELEV and YEAR and their interaction, *v* are random effects and ε is a cell-level error. Combined equations (3) and (4) have the form of a mixed linear model (Pinheiro & Bates, 2000).

LME models were fit at 1, 2, 3, 4 and 5 ha resolutions using the *nlme* library (Pinheiro *et al.*, 2012) in the R software environment (R Core Team, 2013). Model performance was tested using AIC, log likelihood and Pearson's correlation coefficients calculated between observed and predicted values. Random effects residuals were also considered for each model as an estimate of the explanatory power of input variables. Fitted models were then projected to the years 2021–2080, and model predictions were averaged to align with IPCC time periods 2021–2050 and 2051–2080. Continuous maps of FI and GI for the five resolutions considered were converted to point features and resampled to a baseline 100 m resolution using the kriging function in ArcGIS with a circular semivariogram. Future FI and GI were converted into binary forest/non-forest and glacier/non-glacier maps at 100 m resolution using the optimal threshold value that minimized false positives and maximized true positives for observed dates (Thuiller *et al.*, 2009). Finally, projected maps of forest and glacier for 2021–2050 and for 2051–2080 were integrated with a current land cover map derived from SPOT satellite imagery so as to include urban areas, meadow and heath and bare ground (see Appendix S1).

A logistic regression model was used to predict the probability of plant colonization of glacier forelands following glacier retreat. Plant presence or absence based on the 2008 mosaic was detected at 100 m resolution within glacial forelands that became deglaciated between 1850 and 2008. Elevation, sum of annual solar radiation derived from a digital elevation model and distance to the front of the nearest glacier in 2008 were aggregated to grid cells, and a generalized linear model (GLM) was fit to observed data. After recalculating distance according to modelled ice extent, the GLM model was then applied to grid cells anticipated to become deglaciated between 2008 and 2051–2080. The aforementioned protocol was used to convert continuous probability values into a map of predicted plant presence–absence, and areas of presence were reclassified from bare ground to meadow/heath for the 2051–2080 land cover map. Accordingly, a seamless and dynamic land cover map from 2008 to 2051–2080 was generated 100 m resolution at the extent of the study area.

Species distribution model filtering

Species distribution models (SDMs) based on four bioclimatic variables and one regional climate scenario were calibrated at the scale of the French and Swiss Alps and were then projected at 100 m resolution for the prediction period (see Appendix S2, Fig. S1). In addition to climate suitability, land cover maps for 2008, 2021–2050 and 2051–2080 were used to define areas of favourable habitat for the 31 selected plant species. Favourable habitat for tree species was defined as forest land cover, while favourable habitat for alpine species was defined as meadow/heath and bare ground land cover. Favourable habitat for heath species was defined as bare ground, meadow/heath and forest land cover to enable

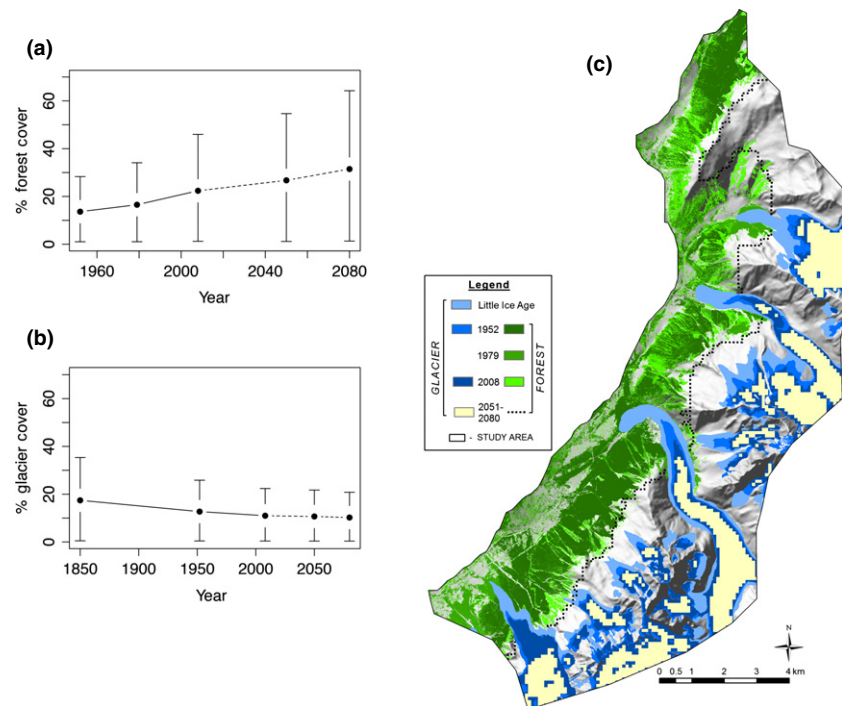


Figure 3 Percentage of forest (a) and glacier (b) cover averaged among 1 ha grid cells ($N = 12,242$) across the study area for the three historical dates considered (1952, 1979 and 2008 for forest and 1850, 1952 and 2008 for glacier), showing 95% confidence intervals. Solid lines represent historical land cover data, while dashed lines represent predicted land cover. (c) Juxtaposition of historical land cover data with predicted tree line and glacier position for 2051–2080.

both understorey coexistence of heath and forest (e.g. Nilsson & Wardle, 2005) and expansion of heath into non-vegetated areas, as has been observed in the study area during recent years (personal observation, A. Delestrade). For each species and for three dates (2008, 2021–2050 and 2051–2080), SDM outputs were multiplied by a binary habitat filter (0 for non-favourable, 1 for favourable) that excluded species from areas designated as unsuitable (Fig. 1d). Three scenarios were considered: (1) a *static* land cover filter, which consisted of multiplying the 2008 land cover map with SDM outputs for 2021–2050 and for 2051–2080, (2) a *dynamic* land cover filter, which consisted of multiplying SDM outputs for 2021–2050 and for 2051–2080 with projected land cover maps for the respective time periods and (3) *unfiltered* SDM outputs that were not intersected with land cover data. Predicted species range change (SRC; % predicted range gain – % predicted range loss) was used to assess the effect of land cover filtering on habitat suitability predictions. Finally, a pairwise Wilcoxon rank sum was used to test for differences in SRC results among unfiltered, dynamic and static land cover scenarios.

RESULTS

Past and future land cover change

Historical land cover consistently reflected increasing forest cover as well as the diminishing extent of glaciers (Table 2). Glaciers covered 30% of the study area in 1850 as compared to 19% in 2008, whereas relative forest cover increased from 17% in 1952 to 26% of the study area in 2008. Observed forest expansion can be fit by a positive linear trajectory

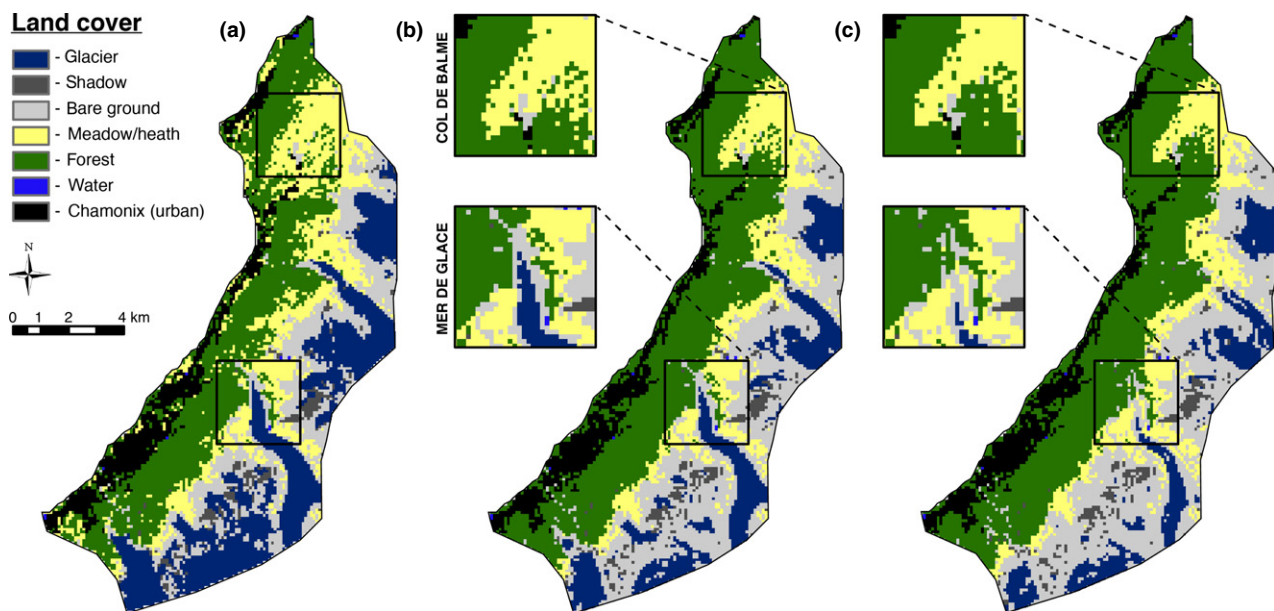
($P < 0.001$) between 1952 and 2008, while glacier expansion can be fit by a negative linear trend ($P < 0.001$) between 1850 and 2008. Historical shifts at the scale of the study area thus supported the use of a linear model to predict future trends in land cover dynamics (Fig. 3). Among the five resolutions that were tested, the 300-m-resolution FI model and 100-m-resolution GI model were retained to model forest and glacier extent over time (see Appendix S3; Tables S1 and S2). Predicted land cover scenarios for forest and glacier reflected ongoing forest expansion and glacier retreat (Table 1). Although glacier cover continued to decrease at a roughly constant rate during the prediction period, increase in forest cover between 2021–2050 and 2051–2080 slackened ($< 2 \text{ km}^2$ gain) in comparison with observed historical changes. Forest expansion was particularly noticeable in the vicinity of the Col de Balme (see inset in Fig. 4). The model for plant succession predicted the expansion of meadow/heath communities in 2051–2080 into areas that were glaciated in 2008 (see the Mer de Glace inset, Fig. 4).

Land cover filtering of species distribution models

For the duration of the prediction period and for all species considered, proportional loss in suitable habitat was equivalent across land cover scenarios (57–58%) (Table 2). Proportional gain in suitable habitat was highest for unfiltered SDMs (49%), intermediate when the dynamic filter was applied (43%) and lowest in the case of the static filter (27%). Absolute range gain and loss were substantially higher in the unfiltered scenario, however, given that current and future species distributions in this scenario were not restricted by land cover maps. Overall species range change

Table 1 Relative cover of forest and glacier for observed (1850 to 2008) and predicted (2021–2080) time periods (– indicates that no data were available for this date).

		Observed				Predicted	
Year		1850	1952	1979	2008	2021–2050	2051–2080
Forest	% Cover		17	20	26	36	37
	Area (km ²)	–	20.59	24.23	32.16	43.48	45.5
Glacier	% Cover	30	22	–	19	14	10
	Area (km ²)	36.87	26.71	–	22.96	16.61	11.73

**Figure 4** Land cover filters used to define areas of favourable habitat for the 36 plant species considered: (a) 2008 (b) 2021–2050 and (c) 2051–2080. Inset maps represent modelled plant succession dynamics on the foreland of the Mer de Glace Glacier and in the Col de Balme agro-pastoral area.

(SRC) was highest in the unfiltered scenario (–10%), intermediate in the dynamic scenario (–15%) and lowest in the static scenario (–31%). Pairwise differences in SRC among unfiltered, dynamic and static scenarios were significant ($P < 0.001$). Delta SRC between dynamic and static filtering methods was highest among tree species (+25%), followed by alpine plants (+20%), and was surprisingly low among heath species (+2%; Table 2).

Application of the three different land cover scenarios (dynamic, static and unfiltered) led to contrasting range gain predictions for the three plants groups considered (tree, heath and alpine). *Pinus cembra*, a pioneer tree species in the Chamonix Valley, gained 101 ha in the dynamic scenario as compared to only 10 ha in the static scenario (Table 1). Below the tree line, montane species such as *Fagus sylvatica* gained substantially more range in the dynamic land cover scenario. As a group, tree species gained the most range in 2021–2050 when the dynamic filter was applied (Fig. 5a). However, as rates of modelled forest expansion declined for the 2051–2080 period, median species range gain for trees shifted to being higher in the case of the unfiltered SDM.

When compared to the static scenario, heath species gained more range over the prediction period in the dynamic scenario due to modelled glacier retreat and primary succession. In the dynamic scenario, montane shrubs such as *Salix caprea* gained the most range (+2318 ha) while the expansion of more cryophilous subalpine species such as *Empetrum nigrum* was restricted by thermal limits and glacier cover (+34 ha; Table 1). Throughout the prediction period, alpine plants gained the most range in the case of the dynamic filter, even as compared to the unfiltered scenario (Fig. 5a). Expected gain in suitable habitat for alpine plants was therefore higher based on combined climate and land cover change relative to climate change alone. Across land cover scenarios, suitable habitat loss was greatest for alpine/nival species such as *Ranunculus glacialis* and *Saxifraga oppositifolia* and was lowest for transition subalpine/alpine species such as *Trifolium alpinum* and *Dryas octopetala* (Table 1).

Trees were the only species group to maintain average positive SRC throughout the prediction period in all three scenarios (Fig. 5b). Heath species exhibited neutral SRC across scenarios for 2021–2050, which shifted to negative

Table 2 Predicted range change in 2051–2080 relative to current distributions for dynamic, static and unfiltered land cover scenarios by species and vegetation group

		Dynamic LC					
	Species	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC
Tree	<i>Populus tremula</i>	27	1659	1196	1.60	70.94	69.34
	<i>Betula pendula</i>	854	1193	216	41.72	10.55	−31.17
	<i>Betula alba</i>	1696	332	506	83.63	24.95	−58.68
	<i>Alnus incana</i>	0	442	1528	0.00	345.70	345.70
	<i>Acer pseudoplatanus</i>	490	2073	1799	19.12	70.19	51.07
	<i>Larix decidua</i>	407	1608	728	20.20	36.13	15.93
	<i>Picea abies</i>	517	2836	1009	15.42	30.09	14.67
	<i>Pinus cembra</i>	1692	574	101	74.67	4.46	−70.21
	<i>Pinus uncinata</i>	1306	822	1029	61.37	48.36	−13.02
	<i>Fagus sylvatica</i>	237	1332	2756	15.11	175.65	160.55
Heath	<i>Salix caprea</i>	197	3530	2318	5.286	62.195	56.909
	<i>Arctostaphylos uvaursi</i>	2491	766	1560	76.481	47.897	−28.585
	<i>Calluna vulgaris</i>	363	10	22	97.319	5.898	−91.421
	<i>Rhododendrum ferrugineum</i>	2224	2268	328	49.51	7.302	−42.208
	<i>Vaccinium myrtillus</i>	2239	3260	683	40.716	12.42	−28.296
	<i>Vaccinium uliginosum</i>	3433	5	40	99.855	1.163	−98.691
	<i>Vaccinium vitisidaea</i>	2412	3294	179	42.271	3.137	−39.134
	<i>Empetrum nigrum</i>	3661	629	34	85.338	0.793	−84.545
	<i>Sorbus chamaemespilus</i>	3377	340	1375	90.853	36.992	−53.861
	<i>Juniperus sibirica</i>	2181	1744	555	55.567	14.14	−41.427
Alpine	<i>Ranunculus glacialis</i>	2353	393	956	85.69	34.81	−50.87
	<i>Dryas octopetala</i>	1115	1908	1873	36.88	61.96	25.07
	<i>Salix herbacea</i>	2539	674	1081	79.02	33.65	−45.38
	<i>Linaria alpina</i>	2177	862	1094	71.64	36.00	−35.64
	<i>Carex curvula</i>	3256	205	706	94.08	20.40	−73.68
	<i>Silene acaulis</i>	2172	1256	1311	63.36	38.24	−25.12
	<i>Festuca halleri</i>	3276	110	669	96.75	19.76	−76.99
	<i>Sedum alpestre</i>	3330	153	621	95.61	17.83	−77.78
	<i>Trifolium alpinum</i>	1399	2010	797	41.04	23.38	−17.66
	<i>Gentiana acaulis</i>	1784	1808	823	49.67	22.91	−26.75
	<i>Saxifraga oppositifolia</i>	3592	14	9	99.61	0.25	−99.36
	Mean	1832.16	1229.35	900.06	57.72	42.52	−15.20

Static LC						Unfiltered					
Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC
27	1659	627	1.60	37.19	35.59	183	2958	985	5.83	31.36	25.53
854	1193	128	41.72	6.25	−35.47	2250	1373	162	62.10	4.47	−57.63
1696	332	413	83.63	20.37	−63.26	2341	380	2036	86.04	74.83	−11.21
0	442	1234	0.00	279.19	279.19	96	1078	1959	8.18	166.87	158.69
490	2073	1062	19.12	41.44	22.32	1507	2859	4919	34.52	112.67	78.15
407	1608	363	20.20	18.02	−2.18	568	2253	4410	20.14	156.33	136.19
517	2836	272	15.42	8.11	−7.31	1545	4373	2799	26.11	47.30	21.19
1692	574	10	74.67	0.44	−74.23	2893	1626	3466	64.02	76.70	12.68
1306	822	693	61.37	32.57	−28.81	1827	1259	4636	59.20	150.23	91.02
237	1332	1967	15.11	125.37	110.26	966	2046	3572	32.07	118.59	86.52
197	3530	2115	5.286	56.748	51.462	673	4444	3485	13.15	68.11	54.95
2491	766	1490	76.481	45.748	−30.734	3018	978	3080	75.53	77.08	1.55
363	10	22	97.319	5.898	−91.421	506	10	24	98.06	4.65	−93.41
2221	2271	231	49.443	5.142	−44.301	2592	3826	2715	40.39	42.30	1.92
2238	3261	496	40.698	9.02	−31.678	3100	4328	2466	41.73	33.20	−8.54
3432	6	38	99.825	1.105	−98.72	5328	51	669	99.05	12.44	−86.62
2409	3297	19	42.219	0.333	−41.886	2974	6194	1209	32.44	13.19	−19.25

Table 2 Continued

Static LC						Unfiltered					
Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC
3658	632	10	85.268	0.233	−85.035	5399	2982	329	64.42	3.93	−60.49
3377	340	1331	90.853	35.808	−55.044	3964	418	4363	90.46	99.57	9.11
2180	1745	488	55.541	12.433	−43.108	2540	2509	2542	50.31	50.35	0.04
2353	393	216	85.69	7.87	−77.82	3686	1396	891	72.53	17.53	−55.00
1066	1957	945	35.26	31.26	−4.00	3161	2764	2526	53.35	42.63	−10.72
2539	674	214	79.02	6.66	−72.36	3827	1972	879	65.99	15.16	−50.84
2177	862	216	71.64	7.11	−64.53	4122	2107	891	66.17	14.30	−51.87
3256	205	190	94.08	5.49	−88.59	5541	720	814	88.50	13.00	−75.50
2171	1257	250	63.33	7.29	−56.04	3711	2808	1028	56.93	15.77	−41.16
3276	110	204	96.75	6.03	−90.73	5861	413	836	93.42	13.33	−80.09
3330	153	184	95.61	5.28	−90.32	6517	483	681	93.10	9.73	−83.37
1386	2023	302	40.66	8.86	−31.80	3594	2906	593	55.29	9.12	−46.17
1778	1814	247	49.50	6.88	−42.62	4227	2724	665	60.81	9.57	−51.24
3592	14	1	99.61	0.03	−99.58	6964	38	4	99.46	0.06	−99.40
1829.55	1231.97	515.42	57.64	26.91	−30.73	3080.03	2073.42	1923.68	58.36	48.53	−9.84

SRC for most species in 2051–2080. For alpine plants in 2021–2050, SRC was negative in the unfiltered and static land cover scenarios, yet switched to being neutral when the dynamic filter was applied. Although alpine plants lost overall range in all three land cover scenarios for the 2051–2080 period (Fig. 5b), the least loss occurred when the dynamic filter was used to define suitable habitat (+13% relative to the unfiltered and +19% relative to the static scenarios; Table 1).

DISCUSSION

The main finding of this study was to show that the consideration of historical trends in land cover projected forward to the 21st century significantly altered SDM predictions for mountain plants. To the best of our knowledge, this approach is unique in that it combines historical remote sensing with species distribution models in a high mountain context. It differs from previous attempts to refine SDM predictions in alpine environments that used very high-resolution explanatory variables (Randin *et al.*, 2009) or that took into account mechanistic processes such as the lag time associated with plant dispersal (Dullinger *et al.*, 2012), although ideally these different approaches should be combined (Carlson *et al.*, 2013). Our results support the conclusion that mountain plants could lose less range due to climate change than standard SDMs predict (Randin *et al.*, 2009; Engler *et al.*, 2011).

Predicted land cover change in the Chamonix Valley

Linear mixed effects modelling of shifts in glacier and forest extent combined with a logistic model of plant succession in the wake of glacier retreat allowed for anticipation of land cover changes during the 2021–2080 prediction period considered in this study. The resulting dynamic land cover filters

included two succession processes that were absent from the static (2008) land cover filter (for definitions of succession, refer to Connell & Slatyer, 1977). The first process consisted of a secondary succession dynamic in the form of forest expansion and upper tree line shift, which was particularly pronounced in agro-pastoral zones such as the mid-elevation (approximately 2100 m a.s.l.) Col de Balme sector (Fig. 4). Although the use of time and topography as explanatory variables did not allow for disentanglement of climate and land use drivers in this study, evidence from elsewhere in the Alps points to land abandonment as the primary driver of forest expansion in subalpine areas below the potential physiological tree line (Gehrig-Fasel *et al.*, 2007; Améztegui *et al.*, 2010; Carlson *et al.*, 2014). It appears likely that shifts in land use practices occurring in a climate warming context also contributed to the rapid increase in forest cover documented in the Chamonix Valley between 1952 and 2008, and to predicted forest expansion between 2021 and 2080. The second process imbedded in the dynamic land cover model consisted of simulating glacier retreat and ensuing primary succession dynamics. The predicted presence of forest and heath/meadow land cover classes in areas expected to become free of ice between 2008 and 2050 aligned both with observed historical changes in the study area (Fig. S2) and with observations of primary plant succession in glacier forelands from the Swiss Alps (Burga *et al.*, 2010).

In the case of forest land cover modelling, our empirical approach aimed to capture information contained in aerial photos and to generate future scenarios of forest extent based on historical rates of change. While tree line position at the regional scale can be reliably predicted by temperature, variation at local scales is largely due to non-elevation specific drivers such as land use and geomorphic disturbance (Körner, 2007; Case & Duncan, 2014). Here, we did not attempt to disentangle the factors determining tree line position, but rather sought to quantify local trajectories of tree

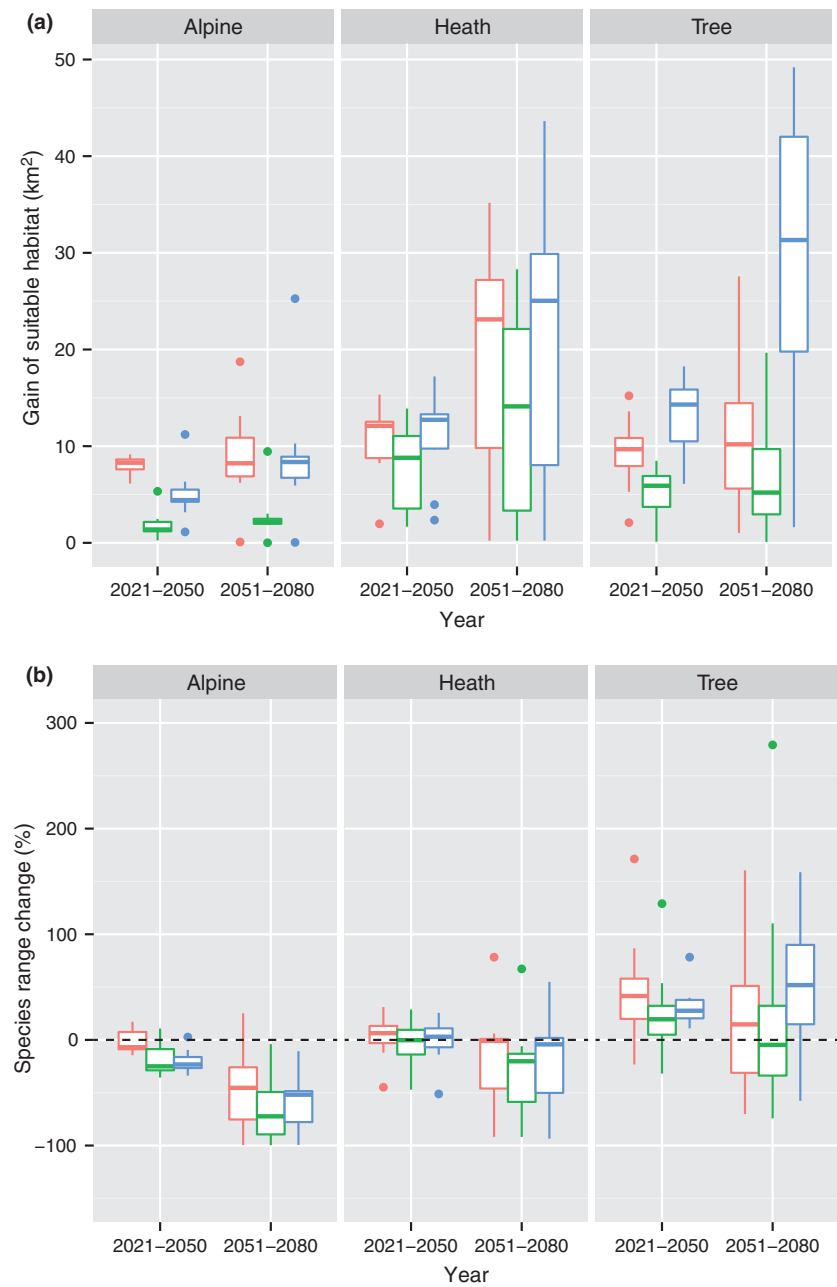


Figure 5 (a) Predicted gain in suitable habitat (km²) for 2021–2050 and for 2051–2080 for the three plants groups and the three land cover scenarios considered. (b) Predicted species range change (%) for 2021–2050 and for 2051–2080 for the three plants groups and the three land cover scenarios considered. Red boxplots correspond to the dynamic land cover scenario, green box plots to the static land cover scenario, and blue boxplots to the unfiltered SDM output.

line shift ultimately resulting from the combined effects of climate, disturbance linked to land management and geomorphology, and biological constraints (competition and dispersal). For example, although climate is not addressed as an explicit driver of forest expansion, the land cover model was fit to observed shifts in tree line occurring in the context of 20th century climate change. Our goal was thus to estimate the overall extent of forest over time using the land cover model, and then to predict the distribution of tree species within this broader matrix based on climate suitability. We consider that combining the land cover model with SDM outputs provides complimentary information and that retaining the intersection of the two models adds fine-grained spatial heterogeneity to habitat suitability predictions

that are otherwise largely based on temperature isotherms (Fig. 2).

For glacier modelling, predictive scenarios of glacier retreat generated during this study were simplified (two-dimensional) and did not explicitly address processes known to drive glacier retreat dynamics, such as climate (air temperature and snow fall), the extent and elevation of upper accumulation zones, ice flow dynamics and topography (Haeberli & Beniston, 1998). While our approach was useful for generating future scenarios of glacier extent based on historical trends, other studies predicting the accelerated loss of ice over the next decades indicate that we likely under-estimated 21st century glacier retreat in our study area (Jouvet *et al.*, 2009; Huss *et al.*, 2010). Finally, the correlative approach

used here to model plant succession dynamics in deglaciated areas did not account for factors such as seed dispersal, substrate, or soil moisture, nutrient and mineral content, all of which are known to influence the rate and location of primary succession in glacier forelands (Chapin *et al.*, 1994; Fastie, 1995; Rydgren *et al.*, 2014).

Future studies that integrate glacier retreat with biodiversity forecasting should combine mechanistic models of tree line (e.g. Lischke *et al.*, 2006) and glacier retreat (e.g. Jouvét *et al.*, 2009) with innovative, process-based tools for modelling primary plant succession in glacier forelands. In this study, incorporating nonlinear, transformative change in the land cover model was not statistically feasible due to the limited number of historical observations (three dates) of forest and glacier extent. However, the comparable linear trends observed for both forest and glacier cover change over the past multiple decades suggest that our projected land cover trends may not differ much from a more mechanistic approach, unless strong breaks in climate and land use trends occur in the near future.

Effects of land cover filtering on predicting species distributions

Combining 21st century land cover change with SDM outputs led to contrasting predictions of habitat suitability for the 31 mountain plants considered. Among tree species, the greatest proportional differences in species range gain between dynamic and static land cover scenarios were obtained by tree line species such as *Pinus cembra* and *Picea abies* (Table 1). Accounting for forest expansion in the dynamic land cover filter allowed tree line species to track climate changes by moving upward, as opposed to being limited by the fixed tree line barrier imposed by the static land cover filter. In both static and dynamic land cover scenarios, however, strict habitat filtering based on forest land cover excluded tree co-occurrence with meadow or heath communities, or in favourable microsites known to enable the installation of pioneer tree individuals above tree line (e.g. Batllori *et al.*, 2009). We used tree line to define the upper limit of tree suitable habitat, considering that the abundance and biomass of isolated trees located above tree line was minimal. Furthermore, the underlying land cover model accounted for tree succession into areas of meadow/heath and bare ground. When the dynamic filter was applied to trees such as *Fagus sylvatica* and *Acer pseudoplatanus*, higher amounts of gain in suitable habitat relative to other land cover scenarios could be attributed to below tree line forest densification and colonization dynamics (Table 1).

Consideration of overall species range change (SRC) allowed for comparison of the effects of the three different land cover scenarios (Fig. 5b). When the dynamic filter was applied, the greater predicted habitat gain and SRC for trees in 2021–2050 suggested that modelled forest expansion in the dynamic filter outpaced habitat gain due to predicted climate change alone. In 2051–2080, however,

greater SRC among trees for the unfiltered SDM showed that climate-induced range change surpassed forest expansion predicted by the land cover model. Such findings align with a recent study conducted in the French Alps, which showed that the expansion of tree species responded rapidly to land use change, but exhibited prolonged lag times in response to climate change (Boulangeat *et al.*, 2014). Also, given the reliance of our land cover model on extrapolating observed historical changes, our predictions are likely to be less pertinent for the more distant 2051–2080 time period.

Heath species posed a particular challenge in this land cover filtering exercise, as their thermal limits do not align with either tree line or alpine-nival ecotone boundaries, and their biogeography spans a broad range of intermediate mountain habitats. Additionally, the present-day distribution of heath communities is difficult to detect using remote sensing, due to the frequent occurrence of heath as forest understorey species and also their similar spectral signal relative to grasslands. Given that we were unable to quantify historical changes in the distribution of heath species, and the broad range of habitat types in which they occur, we decided to not to restrict favourable habitat for this group except by glacier cover. Even so, the neutral to negative trend in SRC predicted in the dynamic scenario likely underestimates the future prevalence of heath species in the study area. Contrary to our model predictions, recent observation of heath expansion and invasion of alpine zones in the Chamonix Valley would suggest that heath species are likely to be beneficiaries of warming mountain habitats during the 21st century (A. Delestrade, personal observation).

For the eleven alpine plant species considered, the shift from positive SRC in 2021–2050 to net negative SRC in 2051–2080 when the dynamic land cover filter was used (Fig. 5b) aligns with the hypothesis that alpine plant range loss will occur gradually (Dullinger *et al.*, 2012). Although we considered the ‘full dispersal’ scenario here, it has been shown that dispersal limitation causes alpine plants to lag behind climate shifts and to persist in marginal conditions before reaching a critical extinction threshold (Dullinger *et al.*, 2012). Such findings suggest that the consequences of climate change may require multiple decades to become fully apparent in alpine plant communities. In our results, the observed tipping point for alpine plants from SRC gain in 2021–2050 to loss in 2051–2080 could be due to upward shifts in suitable habitat in the context of conically shaped mountain summits (Körner *et al.*, 2011). When alpine plants move upward in elevation to track favourable climate conditions, inevitably they lose ground due to the decreasing amount of available surface area. Despite the predicted loss of suitable alpine habitat due to 21st century regional climate warming (Engler *et al.*, 2011), it has been suggested that alpine plants will be able to persist locally by means of topographically defined micro-refugia (Randin *et al.*, 2009; Scherrer & Körner, 2011). Our findings contribute to the hypothesis that climate-driven SDMs might over-predict

alpine plant habitat loss by pointing out that the loss of alpine plant habitat could be further mitigated by new habitat made available by glacier retreat.

CONCLUSION

The results of this study point to the rich potential of combining trajectories of land cover change with species distribution modelling methods as a means of better understanding the response of mountain ecosystems to 21st century climate change. We show that remotesensing-derived land cover information can refine both current and future predictions of habitat suitability for plant species. We further demonstrate that when rates of glacier loss, primary succession and forest expansion are taken into account in addition to traditional climate drivers, high-elevation plants are predicted to lose less overall range than when mountain land cover is held constant. Although in this study we combined land cover modelling with species distribution models, the approach used here could readily be applied to filter the predictions of more complex, process-based biodiversity models applied to mountainous regions.

ACKNOWLEDGEMENTS

The research leading to this paper received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007–2013 Grant Agreement no. 281422 (TEEMBIO). Collaboration and data sharing was facilitated by the Mont Blanc Atlas project (<http://atlas-montblanc.org>), initiated by the Centre de Recherche sur les Ecosystèmes d'Altitude (CREA). Most of the computations presented in this paper were performed using the CIMENT infrastructure (<https://ciment.ujf-grenoble.fr>), which is supported by the Rhône-Alpes region (GRANT CPER07_13 CIRA: <http://www.ci-ra.org>) and France-Grille (<http://www.france-grilles.fr>). We thank the SO/SOERE GLACIOCLIM (CNRS/Univ. Grenoble Alpes/IRD) and the LabEx OSUG@2020 (funded by the 'Programme d'Investissements d'Avenir' from the French government implemented by the ANR), for the funding of the orthorectification, georeferencing and mosaicing of 1952 aerial photographs.

REFERENCES

- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.
- Améztegui, A., Brotons, L. & Coll, L. (2010) Land-use changes as major drivers of mountain pine (*Pinus uncinata*) expansion in the Pyrenees. *Global Ecology and Biogeography*, **19**, 632–641.
- Anandhi, A., Frei, A., Pierson, D.C., Schneiderman, E.M., Zion, M.S., Lounsbury, D. & Matonse, A.H. (2011) Examination of change factor methodologies for climate change impact assessment. *Water Resources Research*, **47**, W03501.
- Battlori, E., Camarero, J.J., Ninot, J.M. & Gutiérrez, E. (2009) Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* treeline ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography*, **18**, 460–472.
- Billings, W.D. (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience*, **23**, 697–704.
- Boggs, K., Klein, S.C., Grunblatt, J., Boucher, T., Koltun, B., Sturdy, M. & Streveler, G.P. (2010) Alpine and subalpine vegetation chronosequences following deglaciation in coastal Alaska. *Arctic, Antarctic and Alpine Research*, **42**, 385–395.
- Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne, S., Lavorel, S., Van Es, J., Vittoz, P. & Thuiller, W. (2012) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Global Change Biology*, **18**, 3464–3475.
- Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulhak, S., Zimmermann, N.E. & Thuiller, W. (2014) Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. *Ecography*, **37**, 01–10.
- Burga, C.A., Krüsi, B., Egli, M., Wernli, M., Elsener, S., Zieffle, M., Fischer, T. & Mavris, C. (2010) Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): straight forward or chaotic? *Flora*, **205**, 561–576.
- Carlson, B.Z., Randin, C.F., Boulangeat, I., Lavergne, S., Thuiller, W. & Choler, P. (2013) Working toward integrated models of alpine plant distribution. *Alpine Botany*, **132**, 41–53.
- Carlson, B.Z., Renaud, J., Biron, P.E. & Choler, P. (2014) Long-term modelling of the forest grassland ecotone in the French Alps: implications for conservation and pasture management. *Ecological Applications*, **24**, 1213–1225. doi:10.1890/13-0910.1.
- Case, B.S. & Duncan, R.P. (2014) A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position. *Ecography*, **37**, 001–014.
- Chapin, F.S., Walker, L.R., Fastie, C.L. & Sharman, L.C. (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, **64**, 149–175.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.
- Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P. & Guisan, A. (2013) Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science*, **24**, 593–606.

- Dullinger, S., Mang, T., Dirnböck, T., Ertle, S., Gattringer, A., Grabherr, G., Leitner, M. & Hülber, K. (2011) Patch configuration affects alpine plant distribution. *Ecography*, **34**, 576–587.
- Dullinger, S., Gattringer, A., Thuiller, W. *et al.* (2012) Extinction debt of high-mountain plants under 21st century climate change. *Nature Climate Change*, **2**, 619–622.
- Elliott, G.P. (2011) Influences of 20th century warming at upper treeline contingent on local-scale interactions: evidence from a latitudinal gradient in the Rocky Mountains, USA. *Global Ecology and Biogeography*, **20**, 46–47.
- Engler, R., Thuiller, W., Dullinger, S. *et al.* (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330–2341.
- Fastie, C.L. (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, **76**, 1899–1916.
- Gardent, M., Rabatel, A., Dedieu, J.P., Deline, P. & Schoen-
eich, P. (2012) Analysis of the glacier retreat in the French Alps since the 1960s based on the new glacier inventory. *Geophysical Research Abstracts*, **14**, . EGU2012-8984-1, 9th EGU General Assembly, Wien, 22–27 April 2012.
- Gehrig-Fasel, J., Guisan, A. & Zimmermann, N.E. (2007) Treeline shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science*, **18**, 572–582.
- Gottfried, M., Pauli, H. & Grabherr, G. (1998) Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Antarctic, Arctic and Alpine Research*, **30**, 207–231.
- Gottfried, M., Pauli, H., Futschik, A. *et al.* (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Haeblerli, W. & Beniston, M. (1998) Climate change and its impacts on glaciers and permafrost in the Alps. *Ambio*, **27**, 258–265.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global meta-analysis of treeline response to global warming. *Ecology Letters*, **12**, 1040–1049.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Huss, M., Juvet, G., Farinotti, D. & Bauder, A. (2010) Future high-mountain hydrology: a new parameterization of glacier retreat. *Hydrology & Earth System Sciences Discussions*, **7**, 345–387.
- IPCC (2000) *Special report on emission scenarios*. Cambridge University Press, Cambridge, UK, 570 pp.
- Juvet, G., Huss, M., Blatter, H., Picasso, M. & Rappaz, J. (2009) Numerical simulation of Rhonegletscher from 1874 to 2100. *Journal of Computational Physics*, **228**, 6426–6439.
- Körner, C. (2007) Climate treelines: conventions, global patterns, causes. *Erdkunde*, **61**, 316–324.
- Körner, C., Paulsen, J. & Spehn, E.M. (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany*, **121**, 73–78.
- Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68–77.
- Lauber, K. & Wagner, G. (2008) *Flora Helvetica*. Feddes Repertorium, Bern.
- Lischke, H., Zimmermann, N.E., Bolliger, J., Rickebusch, S. & Löffler, T.J. (2006) Treemig: a forest-landscape model for simulating spatial and temporal patterns from stand to landscape scale. *Ecological Modelling*, **199**, 409–420.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.
- Nilsson, M.C. & Wardle, D.A. (2005) Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, **3**, 421–428.
- Pauli, H., Gottfried, M. & Grabherr, G. (2003) Effects of climate change on the alpine and nival vegetation of the alps. *Journal of Mountain Ecology*, **7**, 3–12.
- Pellissier, L., Bräthen, K.A., Pottier, J., Randin, C., Vittoz, P., Dubuis, A., Yoccoz, N.G., Torbjørn, A., Zimmermann, N.E. & Guisan, A. (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography*, **33**, 1004–1014.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed effects models in S and S-PLUS*. Springer-Verlag Inc., New York, NY.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. & the R Development Core Team (2012) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-103.
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Rabatel, A., Dedieu, J.-P., Letréguilly, A. & Six, D. (2012) Remote sensing monitoring of the evolution of glacier surface area and equilibrium-line altitude in the French Alps, *Proceedings of the 25th symposium of the International Association of Climatology*, 5–8 September 2012, Grenoble, France.
- Rabatel, A., Letréguilly, A., Dedieu, J.-P. & Eckert, N. (2013) Changes in glacier equilibrium-line altitude in the western Alps from 1984 to 2010: evaluation by remote sensing and modeling of the morpho-topographic and climate controls. *The Cryosphere*, **7**, 1455–1471.
- Randin, C., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W. & Guisan, A. (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.
- Rouse, J.W. Jr, Hass, R.H., Deering, D.W., Schell, J.A. & Harlan, J.C. (1974) Monitoring the vernal advancements

- and retrogradation (green wave effect) of natural vegetation. NASA/GSFC, Final Report. Greenbelt, MD, 1 137.
- Rydgren, K., Halvorsen, R., Töpper, J.P. & Njøs, J.M. (2014) Glacier foreland succession and the fading effect of terrain age. *Journal of Vegetation Science*. doi:10.1111/jvs.12184.
- Samuelsson, P., Jones, C.G., Willén, U., Ullerstig, A., Gollvik, S., Hansson, U., Jansson, C., Kjellström, E., Nikulin, G. & Wyser, K. (2011) The Rossby Centre Regional Climate model RCA3: model description and performance. *Tellus A*, **63**, 4–23.
- Sauvy, A. (2001) *Chamonix d'un siècle à l'autre*. Editions Art-haud, Paris.
- Scherrer, D. & Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406–416.
- Thuiller, W., Lafourcade, B., Engler, R. & Araujo, M.B. (2009) BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- Zimmermann, N.E. & Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science*, **10**, 469–482.
- Zimmermann, N.E., Edwards, T.C., Moisen, G.G., Frescino, T.S. & Blackard, J.A. (2007) Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *Journal of Applied Ecology*, **44**, 1057–1067.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 SPOT satellite imagery.

Appendix S2 Species distribution modelling.

Appendix S3 Land cover model selection.

Figure S1 Model performance, estimated by the true skill statistic (TSS), by vegetation group.

Figure S2 Glacier retreat and plant succession on the Mer de Glace Glacier between 1952 and 2008.

Table S1 Model evaluation parameters for forest and glacier linear mixed models relative to grid cell resolution. Akaike's information criteria (AIC), log likelihood and random effects residuals were used to assess the ability of fixed effects to explain between grid cell variation in FI and GI. Resolutions that appear in bold were retained for forest index (FI) and glacier index (GI) modelling.

Table S2 Range change metrics for predicted forest cover in 2021–2050 and in 2051–2080 for different grid cell resolutions. The 300 m resolution is in bold as this was the grid cell size that was retained and integrated into the dynamic land cover filter.

BIOSKETCH

Bradley Z. Carlson is currently a PhD student working on the EMABIO team at the Laboratory of Alpine Ecology (LECA) in Grenoble, France. His project is focused on integrating remote sensing data into models of plant distribution in high-elevation landscapes.

Author contributions: W.T., P.C., A.D. and B.Z.C. conceived the ideas; N.Z., C.F.R. and D.G. collected data and built species distribution models; J.R. carried out habitat mapping using satellite imagery; A.R. provided historical glacier extent data and expertise; B.Z.C. performed the majority of data analysis, including land cover modelling, and led the writing.

Editor: Mathieu Rouget