Dynamique et restauration d'une steppe méditerranéenne après changements d'usages (La Crau, Bouches-du-Rhône, France)

Renaud Jaunatre

Université d'Avignon et des Pays de Vaucluse

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Dynamics and restoration of a Mediterranean steppe after changes in land-use (La Crau, Southern-France)

Dynamique et restauration d'une steppe Méditerranéenne après changements d'usages (La Crau, Bouches-du-Rhône, France)

Renaud JAUNATRE

Soutenance prévue le 7 Décembre 2012 devant le jury composé de :

Richard HOBBS	Professeur University of Western Australia	Rapporteur
Martin ZOBEL	Professeur University of Tartu, Estonia	Rapporteur
Rob MARRS	Professeur University of Liverpool, UK	Examinateur
François MESLEARD	Directeur de recherche, Tour du Valat Professeur associé Université d'Avignon et des Pays de Vaucluse	Examinateur
Jonathan MITCHLEY	Docteur University of Reading, UK	Examinateur
Elise BUISSON	Maître de Conférences, H.D.R. Université d'Avignon et des Pays de Vaucluse	Directrice
Thierry DUTOIT	Directeur de Recherche CNRS Université d'Avignon et des Pays de Vaucluse	Co-directeur

Thèse préparée au sein de l'Institut Méditerranéen de Biodiversité et d'Écologie

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« Vous arrivez devant la nature avec des théories, la nature flanque tout par terre. »

Pierre-Auguste Renoir d'après G. Coquiot (1925)

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Introduction

I.1. General context: from biodiversity to ecosystem restoration

Ecosystem restoration has been identified as one approach to slow down the loss of biodiversity and to protect all the biodiversity-based goods and services from which humankind benefits. The term "biodiversity" appeared for the first time in a publication in Wilson's book *Biodiversity* (1988). The term was highlighted during the 1992 Earth Summit at Rio de Janeiro when the Convention on Biological Diversity focused on developing national strategies for the conservation and sustainable use of biodiversity was presented (Convention on Biological Diversity, 1992). Biodiversity can be broken down into three types: genetic (diversity of genes within a species), specific (diversity among species) and ecosystemic (diversity of higher level of organization). A wide and ever-increasing range of studies have shown the importance of biodiversity for ecosystem functioning (Hooper et al., 2005) and also for the maintenance of current civilizations (Millennium Ecosystem Assessment, 2005; Rands et al., 2010). The term 'Ecosystem services' describes the whole range of services and goods provided free by natural ecosystems which would represent significant costs if it became necessary to replace them (Westman, 1977; Costanza et al., 2007; Daily and Matson, 2008) (e.g. food production, pollination, erosion control, flood mitigation, etc.). 'Ecosystem services' is therefore a useful concept which can be brandished for the purpose of putting pressure on public policy-makers (Ring et al., 2010; Nahlik et al., 2012). Despite the growing interest in Biodiversity, the pressure put on it is constantly on the increase (Rands et al., 2010). Biodiversity is threatened both by the direct impact of anthropogenic activities and by indirect impact through climate change (Vitousek et al., 1997). Two recent notions may serve to illustrate the extent of this phenomenon: the earth's sixth mass extinction definition (Barnosky et al., 2011), and the Anthropocene era definition (Crutzen, 2002; Zalasiewicz et al., 2011), which both highlight the growing and long-lasting impact of humankind on Earth. The discipline of conservation biology was developed in this context with the aim of finding possible ways of putting a stop to the biodiversity crisis. Three main lines of action may help to reduce biodiversity loss: i) when no specific threat to an ecosystem is identified, it is simply a matter of maintaining the conditions which have driven the ecosystem to its current state (e.g. maintenance of a fire regime and extensive herbivore grazing in African savannahs); ii) when a species or ecosystem is endangered (i.e. many threats have been identified and/or the remaining total area or population is small), the species or area should benefit from conservation measures, from protection (e.g. ban on hunting, protected areas) to *ex-situ* conservation and reproduction; iii) when the ecosystem has been destroyed, the last resort is ecosystem restoration. Management, protection or restoration are applied actions which require in-depth understanding of the ecosystem's functioning and processes if it is to be implemented effectively. The aims of Conservation Biology, as well as Restoration Ecology in the specific case of ecosystem restoration, are to transfer the principles of ecology, biogeography, population genetics, economics, sociology, and anthropology, philosophy and other related theoretical disciplines into applied actions to control the decline of biodiversity (Meffe and Carroll, 1997). Insights provided by these scientific disciplines are currently of particular importance, especially as major international institutions have set quantified objectives for conservation and restoration (Millennium Ecosystem Assessment, 2005; Convention on Biological Diversity, 2011). This thesis focuses both on the theoretical understanding of ecosystem dynamics and on concrete applied ecosystem restoration, on the basis of a study of the La Crau area ecosystem.

I.2. Thesis aims and main organization

The aims of the thesis are to provide insights into both the dynamics of a Mediterranean steppe after changes in land-use and the implementation of techniques which could be applied to restore this ecosystem after severe anthropogenic disturbance (Figure I.1).

The basic questions addressed in this thesis are:

-What are the main drivers of plant community recovery? (**Chapter 1**)

-Is this ecosystem resilient in the face of severe anthropogenic disturbances? (**Chapter 2**)

-How can the recovery or restoration of a community be assessed ? (**Chapter 3**)

-How can we restore this community? (**Chapter 4**)

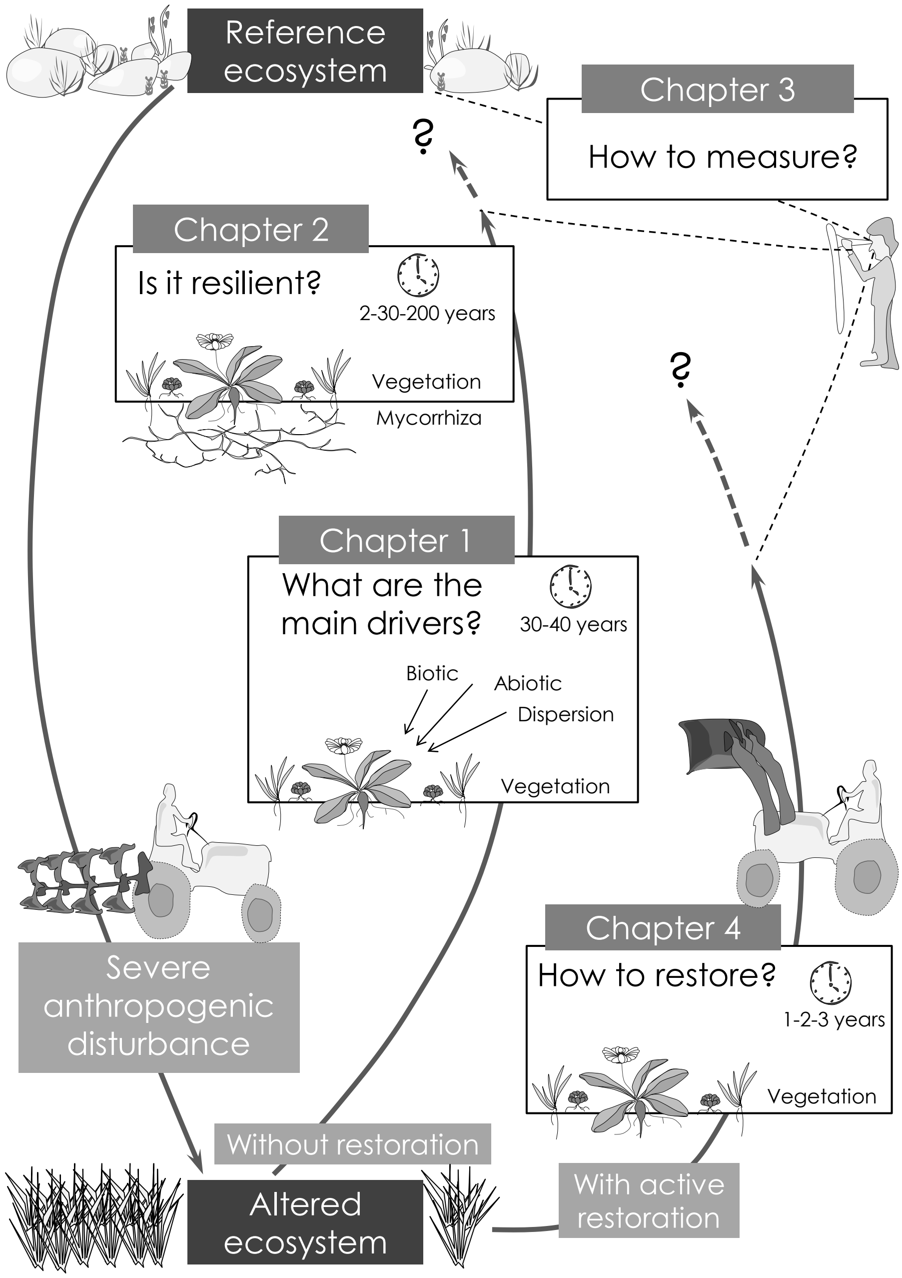


Figure I.1: General schema of the thesis organization

Land-use changes and especially the abandonment of intensive cultivation can provide an appropriate focus for the study of vegetation recovery and community assembly (Cramer et al., 2008; Prach and Walker, 2011). Theoretical models of plant community establishment usually describe a regional species pool that is constrained by three filters: dispersion, abiotic and biotic (Keddy, 1992; Zobel, 1997; Fattorinni and Halle, 2004; Lortie et al., 2004; Guisan and Rahbek, 2011). The aim of **Chapter 1** is to measure in plant community secondary successions the part of variability attributable to each filter (Figure I.1). This study examined plant communities after abandonment of cultivation in the La Crau area. Former arable fields were selected and characterized by their location on geological and climatic gradients, and by taking into account land use in their surroundings over time. We recorded plant species richness and composition, and carried out soil analyses. Former arable fields were compared with each other and with areas where no abrupt anthropogenic exogenous disturbance had occurred and where only traditional sheep grazing systems had been in use for several thousand years. The relative effect of filters was determined by partitioning the variance of community characteristics attributable to each filter.

The remaining difference found in the course of this study, even after 30 years of abandonment, raised the question of whether the ecosystem is resilient to exogenous disturbances and whether all of its components have the same resilience. A growing number of studies show the advantage of taking into account the interactions between vegetation, soil and mycorrhizae in order to understand the organization and dynamics of plant communities (van der Heijden et al., 1998). These three ecosystem components interact continuously, either positively or negatively, but little research has focused on the resilience of these interactions. The aim of the **second chapter** was therefore to measure the resilience of these three components after a cultivation episode in the La Crau area. We selected a gradient of crop abandonment: 2 years - 35 years - 150 years and the reference steppe. We surveyed plant community characteristics and soil chemical properties and we measured the mycorrhizal infestation of four species with contrasting abundances in disturbed and undisturbed areas.

When spontaneous succession does not lead to the reference community trajectories, active ecological restoration has to be implemented (Manchester et al., 1999; Prach and Pyšek, 2001; Török et al., 2011). The Strategic Plan for Biodiversity 2011-2020 sets as an objective the restoration of 15% of degraded ecosystems by 2020 (Convention on Biological Diversity, 2011). This challenge raises at least two major questions: i) how to restore and ii) how to measure the restoration success of given ecosystems? Measurement of restoration success is necessary as a basis for assessment of the achievement of the objectives and for tailoring management practices to the objectives. Numerous studies are being conducted with the aim of attempting to work out synthetic indices to assess ecosystem diversity or integrity in the context of global change (Balmford et al., 2003). Nevertheless, at the community level, there is no index that allows the assessment of community integrity with regard to its restoration or resilience, despite the fact that a wide range of indicators are used, such as species richness, Shannon diversity, multivariate analyses or similarity indices. We have therefore developed two new indices, as explained in the **third chapter**, disentangling missing and higher abundances and providing additional insights that may be useful for management purposes.

If 15% of degraded ecosystems have to be restored before 2020, research into how to restore a defined reference ecosystem is of primary concern, not only at small experimental scale but also at large applicable scale. The aims of the **fourth chapter** are to determine whether it is possible to restore a low productive species-rich ecosystem after the abandonment of intensive cultivation and to determine which restoration techniques provide the best restoration results. Experiments were carried out within a 357ha rehabilitation project, with the aim of recreating an herbaceous sheep-grazed habitat. We applied on the rehabilitated area i) nurse species seeding, ii) topsoil removal, iii) hay transfer and iv) soil transfer, to restore a steppe plant community with the last French Mediterranean steppe as a reference ecosystem. These four techniques, applied for the first time at large scale on a Mediterranean herbaceous ecosystem, were monitored during three years.

Before presenting the results of the four chapters, the following sections of the Introduction will present the conceptual and theoretical framework as well as the specificities of the study site.

I.3. Restoration ecology

I.3.1. Historical background

The first documented restoration projects are attributed to Aldo Leopold in the 1930's, with the Wisconsin Madison University and the Civilian Conservation Corps workers team (Jordan III et al., 1987). This work was carried out following the dust bowl disasters, resulting from a combination of intensive cultivation and severe drought, which devastated American Midwest landscapes and led to widespread famine. Aldo Leopold and his team's idea was "[…] to reconstruct, primarily for the use of the university, a sample of original Wisconsin — a sample of what Dane County looked like when our ancestors arrived here in the 1840s...[…]" (Meine, 2009). These are the first documented restoration actions aimed at recreating a defined ecosystem, but the restoration of some ecosystem functions had already been carried out in other places. For instance in France, the "*Restauration des Terrains en Montagnes*" society (Mountainous Area Restoration society) undertook actions to reduce soil erosion by reforestation (Combes, 1989). Since then, many restoration projects have been implemented (e.g. some non-exhaustive reviews: Walker et al. (2004); Palmer et al. (2005); Rey Benayas et al. (2009) and Kiehl et al. (2010)) with a wide diversity of aims and outcomes, which require more precise definition.

I.3.2. Restoration ecology: definition, aims and semantics

Restoration ecology is the science that develops and tests a body of theory focused on repairing damaged ecosystems (Palmer et al., 1997) and is therefore closely linked to ecological restoration which, according to the Society for Ecological Restoration, is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration International Science and Working Policy Group, 2004). The distinction between certain terms may require definition, mainly those concerning differences in restoration objectives. Restoration *sensu stricto* is the re-establishment of all attributes of the reference ecosystem, including species-richness, composition, structure and function; whereas rehabilitation objectives focus on the re-establishment of some functions or services or partial re-establishment of ecosystem attributes (Figure I.2). Many projects have *sensu stricto* restoration objectives but in view of their actual results they should perhaps be reclassified as rehabilitation projects (Hobbs, 2007). Both restoration *sensu stricto* and rehabilitation focus on a historical pre-existing reference ecosystem, while reclamation can be used in the context of industrial or mine degraded lands for the purposes of terrain stabilization, public health and safety, or landscape improvement (e.g. the re-establishment of plant cover in mining sites in order to prevent toxic dust dispersion) (Society for Ecological Restoration International Science and Working Policy Group, 2004). Reclamation can also be used as a synonym for reallocation (Aronson et al., 1993; Muller et al., 1998) with a target ecosystem as an objective, but in contrast to rehabilitation or restoration, the target is an ecosystem which has been chosen for various reasons, such as improving biodiversity or providing ecosystem services (e.g. creation of wetlands in the context of mitigation banks in the United States) (Figure I.2).

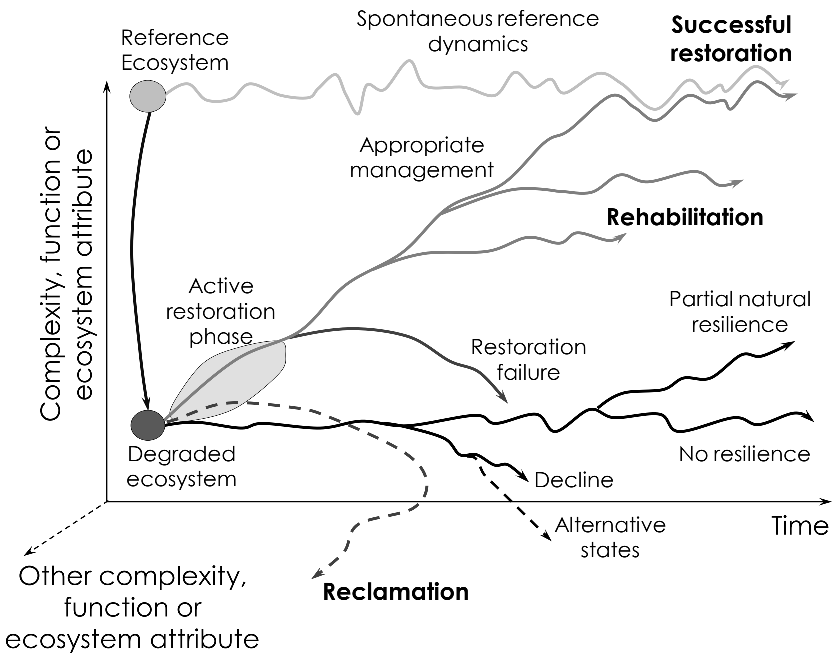


Figure I.2: General model illustrating the different restoration terms, in a three dimensional plot: time; complexity or ecosystem function characterizing reference ecosystem; and other complexity, function or ecosystem attributes which do not characterize the reference ecosystem. This third dimension is expressed by dashed lines. Modified from Aronson et al. (1993) and Buisson (2011).

I.3.3. Reference ecosystem

All the different terms used to describe restoration *sensu lato* are linked to the definition of restoration objectives. The vision of how an impaired ecosystem should be after restoration is called the reference (Clewell and Aronson, 2007). The choices of restoration objectives are unavoidably subjective (Choi, 2004), are always a trade-off between different objectives (Bullock et al., 2011) and are determined by historical considerations, ecological values, social acceptance and economic feasibility. Historical considerations can differ geographically: in the New World or in Australia, the historical reference is usually the ecosystem before European settlement (Swetnam et al., 1999) whereas in Europe the historical reference is usually the state before an anthropogenic severe disturbance (e.g. intensive cultivation). Ecological values include species or habitat with conservation values, biodiversity or potential habitat for rare and/or endemic and/or threatened species. A restoration project needs social acceptance to be successful, a counter-example is the restoration of the wetlands on which Chicago was built that would clearly not prove acceptable (Choi, 2007). Economic feasibility is an important limiting factor which will determine the scale and intensity of active restoration taking into account current technical knowledge (Cairns, 2000).

The reference can be defined as an actual area or as a written description (Society for Ecological Restoration International Science and Working Policy Group, 2004). Several authors have criticized a too narrow view of the reference, which could be either unsuited to the current environmental conditions (i.e. in view of global change) or an unattainable goal (Pickett and Parker, 1994; Hobbs and Norton, 1996). On the other hand, the reference ecosystem is viewed as a valuable tool as a basis for setting objectives, identifying restoration needs and assessing restoration success (Aronson et al. (1993); Clewell and Aronson (2007); Giardina et al. (2007) and **Chapter 3**). More than a simple static state, the reference should reflect the range of variability potentially illustrated by spatial or temporal variation of the natural ecosystem (Society for Ecological Restoration International Science and Working Policy Group, 2004; Hilderbrand et al., 2005). In order to express the natural dynamics, the goal could be a reference trajectory (Aronson et al., 1993), and the restored ecosystem should therefore show the same resilience to common variability under environmental conditions (Figure I.2). The notion of target species is directly linked to the concept of reference ecosystem. These species are the species present in the reference and are usually contrasted with non-target species which are species absent from the reference ecosystem. Reducing the number of non-target species can be an objective but just like the native/non-native distinction, it should be used with caution (Davis et al., 2011). It should be stressed that even target species can become competitive and their over-abundance can represent a threat to successful restoration. For this reason in **Chapter 3**, the indices developed will distinguish target and non-target abundances rather than species.

I.3.4. Restoration ecology and related disciplines

The choice and description of references and the choice of methodologies to achieve restoration goals are the core of restoration ecology, which cannot easily be distinguished from community ecology (Figure I.3; Palmer et al. (1997)). Theoretical ecology provides useful fundamental knowledge for restoration ecology which in turn provides frameworks and insights into how ecological restoration should be carried out (Figure I.3; Falk et al. (2006)). On the other hand, ecological restoration provides opportunities to implement restoration ecology experiments, which have been viewed as an acid test for fundamental ecology theories since the early stages of restoration ecology (Figure I.3; Bradshaw (1987)).

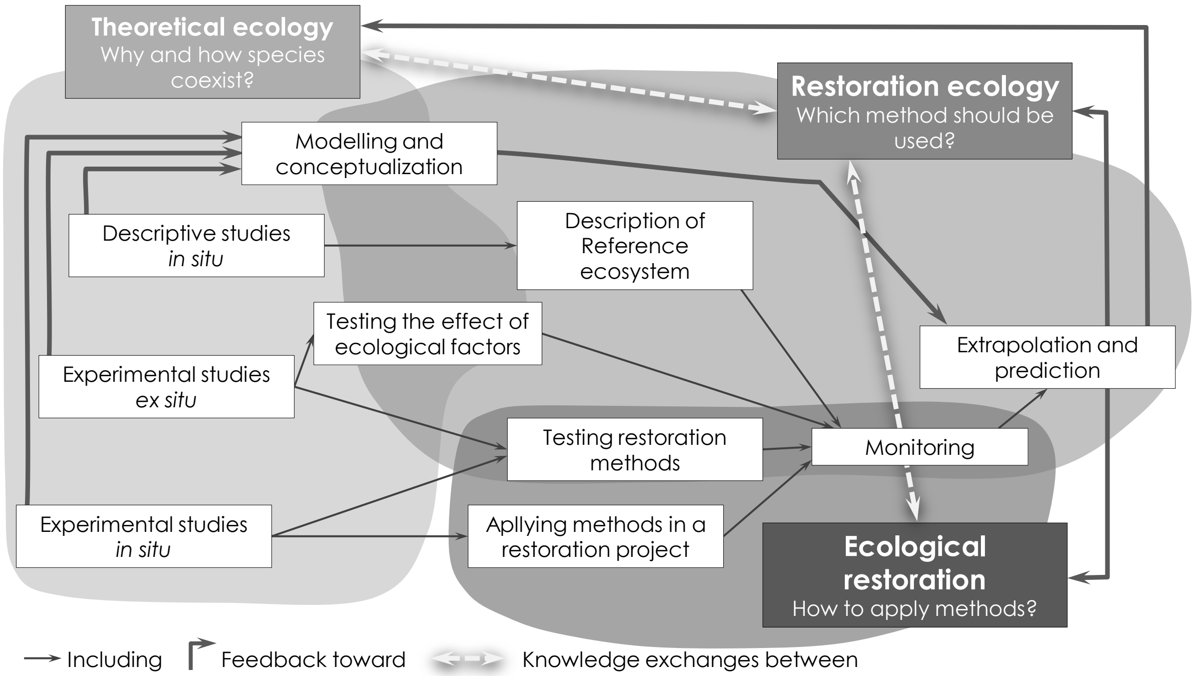


Figure I.3: Interrelations between theoretical ecology, restoration ecology and ecological restoration. This model is based on three model from Prach et al. (2001), Falk et al. (2006), and Buisson (2011), adapted.

I.4. Community Ecology

I.4.1. The science of community ecology

Community ecology includes a wide range of topics and among them succession and disturbance are two major issues which are relevant for restoration ecology and in particular in the context of this thesis. Community ecology is the science that focuses on the patterns and processes underlying the diversity, abundance and composition of species in a community (Vellend, 2010). Although this is the main focus of a whole scientific discipline, the definition of a community is not straightforward. Since the beginning of community ecology, there have been two divergent approaches to the concept of community: the *organismic concept* and the *individualistic continuum concept* of community. The organismic view is holistic and deterministic: the underlying idea is that the community is an entity which arises and matures toward a unique stable endpoint depending on climatic conditions: the climax (Clements, 1916, 1936). The individualistic continuum concept is individualistic and mechanistic: community boundaries cannot be defined because the community is only the result of the sum of individual dynamics of populations determined by each species' characteristics (Gleason, 1926, 1939). The broadly accepted view currently lies somewhere between these two extreme views (Verhoef and Morin, 2010), and one of the basic way of defining a community is to place it on a hierarchical scale on this sequence: […] > population > community > ecosystem > landscape > […]. The population is a group of individuals of the same species, the ecosystem is the whole system including living organisms and physical factors (Tansley, 1935), a set of different ecosystems, usually including an anthropic dimension is the landscape level (Troll (1939) cited by Burel and Baudry (1999)). A community can therefore be defined as "an assemblage of populations of living organisms in a prescribed area or habitat" (Krebs, 1972). Despite some criticism of community ecology as a discipline (Lawton, 1999; Ricklefs, 2008), useful advances have been made towards understanding and conceptualizing communities, especially with regard to succession, disturbances and community assembly, and this is directly relevant for restoration ecology.

I.4.2. Succession

The simplest way of defining succession is species change over time, or turnover (Walker and Moral, 2003). Although it is tempting to define it as evolution, as a synonym of development, this should be avoided in order to avoid confusion with the Darwinian sense of evolution. In the present definition of succession, there is also a matter of scale: historical reconstructions of very long-term changes (i.e. paleoecological studies), and temporal variability around a relatively stable state (i.e. the carousel model of Maarel et Sykes (1993)) are two kinds of vegetation changes which are generally not included in the definition of succession (Walker and Moral, 2003).

Among the numerous ways of describing succession, a widely used dichotomy is the primary/secondary distinction, in which should both be considered as endpoints of a continuum rather than a clear-cut distinction (White and Jentsch, 2001). This discriminates successions through their characteristics at the beginning. Primary succession occurs on sterile substrate with low nutrient content (e.g. lava or glacial moraine) (Walker and Moral, 2003) whereas secondary succession occurs on substrate were biotic content is not null: a seed bank or soil biota may remain, and soil nutrient content is not a limiting factor (e.g. vegetation recovery after cultivation abandonment or forest regeneration after a hurricane) (Cramer et al., 2007).

One of the first succession models is the *relay floristic model* of Clements (1916) in which early-successional species establish at the beginning, then perish as the late-successional species establish and persist to form the succession endpoint. Another model is the *initial floristic model* (Egler, 1954) where all, both early- and late-successional species, are present at the beginning of succession. In the early stages, early-successional species dominate, and late-successional species remain at very low abundance. As time goes by, early-successional species decline and late-successional species tend to dominate. A very influential explanation of succession was the three models of succession developed by Connell et Slatyer (1977): the *facilitation*, *tolerance* and *inhibition* models. The *facilitation* model is when early-successional species establish and alter the environment in such a way that it becomes more suitable for late-successional species. The *tolerance* model is when early-successional species establish and alter the environment in such a way that it excludes other species except those that can tolerate the competition of early-successional species, which then, with time, end up dominating. The last model is the *inhibition* model, when early-successional species establish and alter their environment in such a way that it prevents any other species from establishing; late-successional species will establish only when early-successional species die. As a disturbance is basically at the origin of almost all successions, it is essential to the succession concept.

I.4.3. Disturbance

Many authors have given definitions of disturbances, two of which are widely used: the definition by Pickett and White (1985): a relatively discrete event in time that alters the structure of a population, community or ecosystem; and the definition by Grime (1977): a constraint that limits the plant biomass by causing its destruction. The disturbance is usually opposed to stress which is a limitation of the production of biomass (Grime, 1977). The distinction between stress and disturbance is not always straightforward, as the same event can be considered as a stress or a disturbance, depending on the organism of interest. For a given organism, the event can be considered as stress until organism tolerance is exceeded, when the tolerance is exceeded, this leads to its death or a significant loss of biomass and is therefore considered as a disturbance (Sousa, 1984). A disturbance has to be characterized in order to assess its effect on a population, community or ecosystem. Sousa, (1984) defined several attributes of disturbance: the extent, i.e. the size of the disturbed area; the magnitude, including intensity: i.e. the strength of the disturbing force, and severity: i.e. the damage caused by the disturbance; the frequency, i.e. the number of disturbances per period of time and the predictability, i.e. the variance of the mean time between disturbances. Two distinctions are made to characterize disturbances: i) disturbance may be either exogenous: i.e. if the disturbance event originates outside of the system (e.g. avalanche, storm) or the disturbance can be considered as endogenous when the disturbance event originates inside the system (e.g. a senescent tree fall). Sometimes the cut-off line between the two is difficult to determine: for instance a fire can be considered exogenous when its origin is a thunderstorm, but fire intensity can be increased by organic compounds released by the vegetation and therefore the fire can be considered as endogenous for ecosystems such as matorral. ii) natural or anthropogenic disturbance is also a common dichotomy which distinguishes man-made disturbance from other disturbances, even if a natural disturbance can have the same effects as an anthropogenic disturbance (e.g. large herbivore herds and traditional itinerant mixed domestic grazing).

The notion of resilience is closely linked to the disturbance concept. A distinction should be made between ecological resilience, referred to hereafter as resistance, and engineering resilience, hereafter resilience. Resistance represents the amount of energy needed to change ecosystem properties, or the maximum level of disturbance that the ecosystem can withstand without any significant changes (Carpenter et al., 2001; Walker, Holling, et al., 2004; Van Nes and Scheffer, 2007). One way to represent resistance is a basin of attraction, of which the size is a measure of the maximum disturbance that an ecosystem can undergo without shifting to another state (Figure I.4; Van Nes and Scheffer (2007)). Resilience is the capacity of an ecosystem to return to the original state following a disturbance event (Holling, 1973) and it can be represented by the slope of the basin of attraction (Figure I.4; Van Nes and Scheffer (2007)). Hysteresis occurs when an event moves the community into a state that cannot be recovered from by the application of the reverse event alone (i.e. alternative stable state (Beisner et al., 2003)). In the same representation used before for resistance and resilience, hysteresis occurs when the difference in levels when moving from the new state is higher than the difference in levels when moving from the pre-disturbance state ((Beisner et al., 2003); Figure I.4).

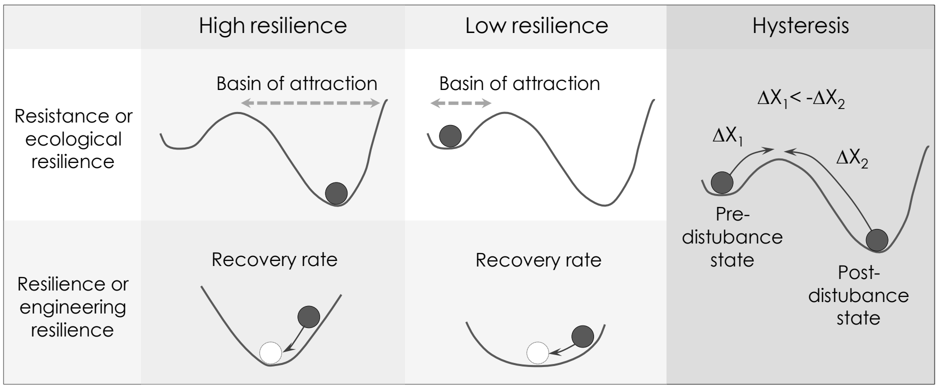


Figure I.4: Conceptual representation of resistance, resilience and hysteresis with the ball-in-cup analogy. Potential states of the ecosystem are represented by the line, with the position of the ball on this line representing the state of the community (e.g. diversity, complexity, etc.) (adapted from Beisner et al. (2003) and Van Nes and Scheffer (2007)).

Disturbance is commonly viewed as a driver of biodiversity and organism coexistence, allowing maximum diversity at an intermediate disturbance frequency or intensity: this is the so-called “Intermediate Disturbance Hypothesis” (Connell, 1978). Many aspects of what had been a general and widely accepted hypothesis have now been refuted. Empirical evidence does not always support the Intermediate Disturbance Hypothesis: in a review, less than 20% of studies out of 116, found that the predicted species-richness peak was at intermediate disturbance

(Mackey and Currie, 2001). Rather, different shapes of disturbance-diversity relationships occur, such as positive monotonic relationships which are the most common after the lack of relationship (Mackey and Currie, 2001). These empirical results are confirmed by modeling which found "coexistence regions" not only at intermediate but also at high disturbance intensity depending on disturbance frequency, while the model found "coexistence regions" at intermediate or extreme (very low or very high) disturbance frequency, depending on disturbance intensity (Miller et al., 2011). Moreover, it has been theoretically refuted that the major mechanisms thought to be behind this hypothesis could imply a diversity peak at intermediate disturbance (i.e. competition decreasing, interruption of progress toward a competitive exclusion equilibrium and interchanging of identity of competitive dominant species recapped in Fox, (in press)). Despite the lack of a general model, numerous case studies describe the effect of different kinds of disturbance on community characteristics, in particular two disturbances that will be discussed in this thesis: extensive grazing and intensive cultivation.

Grazing can have various impacts on grassland plant communities: by removing biomass (defoliation), it alters the growth of individuals and can alter interactions by limiting light competition of grazed individuals. Moreover, trampling can induce microsite disturbances and hence the creation of safe sites. Although urine and faeces deposition can alter nutrient cycles, when herds sleep in limited locations, these depositions are restricted to patches corresponding to sleeping areas (Gibson and Brown, 1992; Milchunas and Lauenroth, 1993; Isselin-Nondedeu et al., 2006; Gibson, 2009). Through its effects on individual growth and fitness, grazing can alter community diversity and structure. The trade-off between relative grazing tolerance and competitive ability (Fynn et al., 2005) can induce a reduced number of mainly competitive species at low grazing intensity, lower competition allowing a higher diversity at intermediate grazing intensity and a reduced number of mainly relatively grazing tolerant species at high grazing intensity. These effects depend on environmental conditions and are summarized in a model based on grazing intensity, moisture and the evolutionary history of grazing (Milchunas et al., 1988; Milchunas and Lauenroth, 1993). It predicts that in areas with long evolutionary history of grazing, the relationship found between grazing intensity and diversity is between a monotonic negative and a humped back relationship, whether environmental conditions are semi-arid or subhumid. More recent models include the potential existence of alternative stable states when vegetation changes induced by grazing have passed a threshold, which prevents the vegetation from recovering with the restoration of the previous grazing regime alone (Westoby et al., 1989; Beisner et al., 2003). Grazing is widely used to maintain open and species-rich plant communities (Gibson and Brown, 1992; Barbaro et al., 2001), especially in areas where domestic grazing is not only a diversity driver but also a cultural practice (Dutoit, Thinon, et al., 2009).

In contrast to grazing, the intensive cultivation of vegetation does not have a long history. Plant communities are therefore rarely adapted to its impact: removal of both above- and below-ground biomass through plowing, relatively long-term inhibition of growth or germination through tillage or herbicides and increase in nutrient content through fertilization. Mainly due to the lack of permanent seed banks of the pre-cultivation communities (Hutchings and Booth, 1996; Bossuyt and Honnay, 2008) and to the high densities of more competitive species allowed by increased fertility (Marrs, 2002; Standish et al., 2008), former cultivation usually has a long-term impact on plant communities. The causes and effects of intensive cultivation are in sharp contrast to the causes and effects of extensive grazing and the two phenomena should therefore not be considered as the same type of disturbance (cf Table I.1). In this study, the study site (i.e. the La Crau area, see Introduction section I.5) is influenced by two kinds of disturbances, extensive sheep grazing and intensive cultivation (Table I.1). For simplicity sake, disturbed areas will be taken to correspond to previously cultivated or at least plowed areas, and cultivation will be considered as a synonym of severe exogenous anthropogenic disturbance, whereas undisturbed areas will correspond to uncultivated or unplowed areas, even if these areas have undergone and are still undergoing grazing disturbance.

As a basis for organizing ideas on how processes influence succession and community assembly, community ecologists have developed numerous conceptual models, some of which will be described in more detail.

Table I.1: Characteristics of two different types of disturbance in the La Crau area: extensive sheep grazing and intensive cultivation

Disturbance	Extensive sheep grazing	Intensive cultivation
Origin	-Endogenous	-Exogenous
Time	-For 6000 years	-second half of 20th century only
	-Repeated event	-One time event
	-During 6 months every year	-During 5-20 years
Magnitude (Severity)	- Only a partial amount of biomass is removed at the individual level	- The whole biomass is removed at community level
Predictability	-Very high	-Very low
Frequency	-Once per year for 6000 years	-Once during the whole history of the La Crau ecosystem
Extent	-Over the whole remaining La Crau steppe area or abandoned cultivation	-Several extensive areas (5-500ha each)

I.4.4. Community assembly models

One of the main models used to describe plant community assembly is the filter model, in which a global species pool is constrained by three filters: dispersion, abiotic and biotic filters to select the final species and individuals of the final community (Keddy, 1992; Zobel, 1997; Fattorinni and Halle, 2004; Lortie et al., 2004; Guisan and Rahbek, 2011).

The first filter is dispersion: species have to be able to join the community either from external species pools (*via* seed rain) or from internal species pools (i.e. from the seed bank). As predicted by the island biogeographical model of MacArthur and Wilson (1967), the larger the community location and the less distant the species pool (considering time and/or space), the higher the probability is of a species reaching a community. This theoretical model has been confirmed by several studies on the proximity of species pools (Pärtel et al., 1998; Pärtel and Zobel, 1999; Cook et al., 2005).

The second filter is the abiotic filter: species have to be able to withstand the environmental conditions. The range of environmental conditions within which a species can live, i.e. its niche (Grinnell, 1917), determines its ability to germinate, grow and reproduce under given abiotic conditions. Without any influence of other species, a species occupies its fundamental niche and when biotic interactions alter the niche either by reducing it or by enlarging it, a species occupies its realized niche (Bruno et al., 2003).

The third filter is the biotic filter: individuals of a species have to be able to withstand biotic interactions, i.e. interactions with other members of the same species (intraspecific), with other plant species (interspecific) or with other organisms. Competition occurs when the resource (i.e. light, space, pollinators or nutrients) is limited and an individual by its own presence or consumption reduces the resource available for another individual, possibly leading to its exclusion (Grime, 1973). This negative interaction has been considered for a long time as the most determinant interaction in plant communities. Facilitation is the fact that the presence of one individual increases the germination, growth or reproduction of another individual. It is now widely recognized that it also plays a significant role in plant community assembly (Callaway, 2007; Brooker et al., 2008). Interactions with other organisms act as a filter but can also can alter filters, either with negative effects (e.g. predation) or with positive effects (e.g. zoochory, mutualisms). One example of other organisms which exert a significant effect on communities is soil microorganisms (van der Heijden et al., 1998). Mycorrhizae can improve growth, survival and reproduction success and thus can significantly influence the ability of a species to establish in a community and therefore influence the whole plant community (Grime et al., 1987; Koide and Lu, 1992; Stanley et al., 1993; Heppell et al., 2002; O'Connor et al., 2002).

One criticism of the filter model has been the hierarchy of the filters, and the possible interactions between each filter have therefore to be integrated in the model. Biotic interactions can change the ability of a species to withstand environmental conditions (Bruno et al., 2003) or even to disperse in the community (Römermann, Tackenberg, et al., 2005). It is especially important that these interactions be particularly integrated when this model is interpreted in a restoration context. Sometimes for example, environmental conditions are suitable for species A but competition with species B prevents species A from establishing. The alteration of abiotic conditions in a way that makes them still suitable for species A but no longer suitable for species B can therefore allow the establishment of species A (e.g. Charpentier et al. (1998)).

Components of the filter model are differently affected by historical ecological conditions or by a severe anthropogenic exogenous disturbance (Fattorinni and Halle, 2004). For instance in dry grassland, historical ecological conditions mainly determine the abiotic filter, and through feedback between filters, the internal species pool and the community itself, indirectly exert an influence on the actual community. A severe exogenous anthropogenic disturbance, such as cultivation, can induce a significant alteration of the internal species pool, and can change environmental conditions and hence biotic interactions, which will indirectly exert an effect on the actual plant community (Figure I.5).

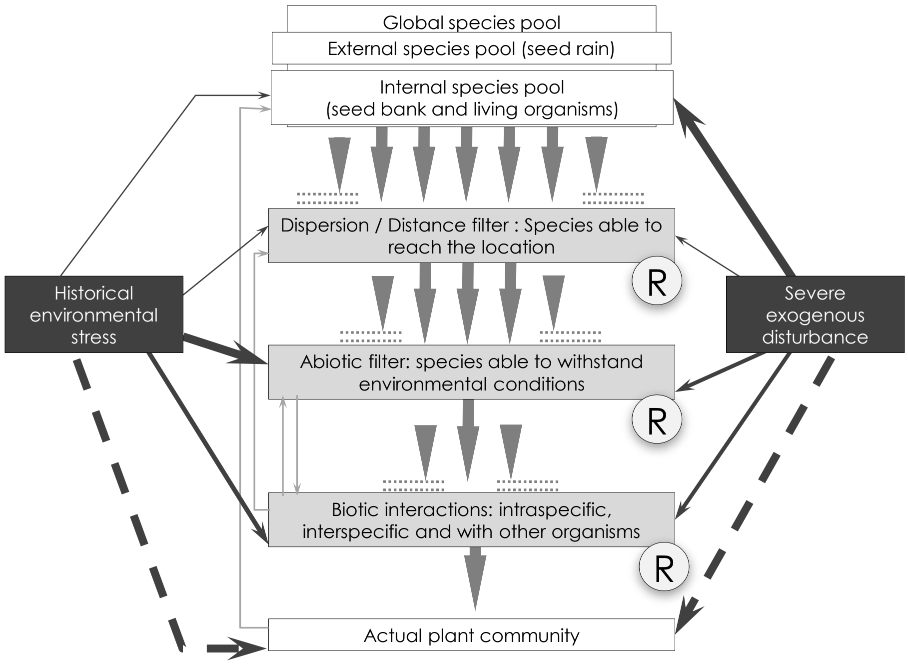


Figure I.5: Filter model of plant community. White boxes represent species pools, eitherinternal, external or actual plant community. Light grey boxes represent filters: dispersion, abiotic and biotic. Large grey arrows represent species able to pass and those which are stopped by filters. Thin arrows represent feedback occurring within filters or within species pools. This model is adapted from (Keddy, 1992; Zobel, 1997; Lortie et al., 2004; Guisan and Rahbek, 2011). Dark grey boxes represent two examples of particular conditions: historical environmental stress and severe exogenous anthropogenic disturbance and their potential effects on filters and species pools (the larger the arrow is, the greater the effect is expected to be) and their potential indirect effect (dashed line) on the actual plant community (adapted from (Fattorinni and Halle, 2004)). Discs marked with an "R" represent the restoration lever which can potentially be used in active restoration.

Such filter models could give the impression that with sufficient knowledge of the species pool, and of environmental conditions, the end result is highly predictable and thus that the succession course could be manipulated toward a designed reference for the purposes of ecological restoration (Luken, 1990; Hilderbrand et al., 2005). New advances in theoretical ecology, mainly using neutrality concepts and historical contingency, advocated a more complex and stochastic view of community assembly (Hubbell, 2001; Chase, 2003; Chave, 2004; Fukami, 2010). The development of corpus around alternative stable or transient states, which is in between the two extreme views totally deterministic and totally stochastic, has provided significant insights for restoration ecology (Suding, 2004; Hobbs et al., 2008; Fukami and Nakajima, 2011).

I.4.5. From community ecology to ecological restoration

The transfer of the filter model into the ecological restoration context could be made on the basis of the threshold concepts (Whisenant, 1999; Hobbs and Harris, 2001; Briske et al., 2006), in which filters are viewed as restoration levers that have to be manipulated to reach a reference community (Figure I.5). Those restoration levers have been used in several restoration experiments, whether dispersion filters (Kiehl et al., 2010), abiotic filters (Verhagen et al., 2001) or biotic filters (Mitchley et al., 1996; Padilla and Pugnaire, 2006; Pywell et al., 2007). In this thesis, **Chapter 1** focuses on determining the importance of each of these filters for the spontaneous recovery of plant communities after intensive cultivation and **Chapter 4** assesses restoration techniques which act on these restoration levers.

I.5. Characteristics of the La Crau study area

I.5.1. From world grassland biomes to Mediterranean steppe

Grasslands are ecosystems where the vegetation is dominated by grasses (Allen et al., 2011). They are the most extensive ecosystem in the world, covering more than 50,000,000km² over all the continents (Gibson, 2009). Most of the grasslands are related to severe climatic conditions (e.g. low temperature, drought, etc.) or frequent disturbances (e.g. fires, grazing, etc.) (Gibson, 2009). Grassland provides several ecosystem goods and services, such as recreational areas (e.g. African savannahs which are very attractive for tourism), carbon storage (comparable to that of forests considering its extent) or food production. Production of domestic livestock is the most widespread use of grasslands (Gibson, 2009) and results in the ecosystem historically associated with human land-uses, i.e. cultural landscape (Birks et al., 1989). Grasslands are an important repository of biodiversity, they account for forty of the world's 234 Centers of Plant Diversity (each with >1000 vascular plants with >10% endemism) and are usually habitats for large herbivores, arthropods or birds (Gibson, 2009). Despite all of these characteristics, grasslands are subject to three major threats: alteration by agriculture, fragmentation and non-native species invasion (Saunders et al., 1991; Poschlod and WallisDeVries, 2002; Fargione et al., 2009). The Mediterranean basin is one of the 25 hotspots of biodiversity and is host to many Mediterranean grasslands, several of which may qualify as steppe (Medail and Quezel, 1997; Myers et al., 2000). According to the Forage and Grazing Terminology committee, steppe is "Semi-arid, sparse to rolling grassland characterized by short to medium-height grasses occurring with other herbaceous vegetation and occasional shrubs" (Allen et al., 2011). The designation 'steppe' is usually attributed when the origin of these ecosystems is driven by climatic conditions and especially a mean annual rainfall between 100 and 400mm for arid and semi-arid steppe (Le Houérou, 2001). When other factors, such as agricultural practices (e.g. grazing), are as important as climatic factors with regard to their origin, the word pseudo-steppe is usually preferred. The total surface area of Mediterranean steppe has considerably declined in the last decades and now covers only 3,700,00ha in the European part of the Mediterranean basin and 63,000,000ha in North Africa (Le Houérou, 1995). The study site for this study, the La Crau area, qualifies as Mediterranean pseudo-steppe and like all endangered ecosystems, it merits investigation in order to understand its dynamics for the purposes of conservation or restoration (Valladares and Gianoli, 2007; Méndez et al., 2008).

I.5.2. Geographical and Geological context

The La Crau area is a wide flat area of more than 45,000ha located between the towns of Arles, Salon-de-Provence, Istres and Fos-sur-mer and between the Alpilles range, the Berre Lagoon and the Camargue wetland natural areas (43°33'N, 4°52'E; Figure I.6.A). This georgraphical area corresponds to the former Durance river bed which, in different successive flows, has deposited stones from its catchment basin: Ecrins, Queyras and Devoluy, corresponding to the French southern part of the Alps mountain range. The Durance river bed ran through the La Crau area from the period of sea shrinkage (Pliocene, -2,000,000BP) until the Orgon threshold reduction stage (-12000BP) (Roux and Colomb, 1986) (Figure I.6.A). Several geological areas can be distinguished corresponding to different times and origins of stone deposits. The "old La Crau", mainly represented by *Arles Crau*, is issued from deposits from the early Pleistocene (-2,000,000BP – -600,000BP). The "young Crau" is issued from deposits from the second part of the Pleistocene: -600,000BP – -100,000BP for the

Luquier Crau, mainly of Riss origin, and -100,000BP – -10,000BP for the *Miramas Crau*, mainly of Würm origin (Roux and Colomb, 1986) (Figure I.6.B).

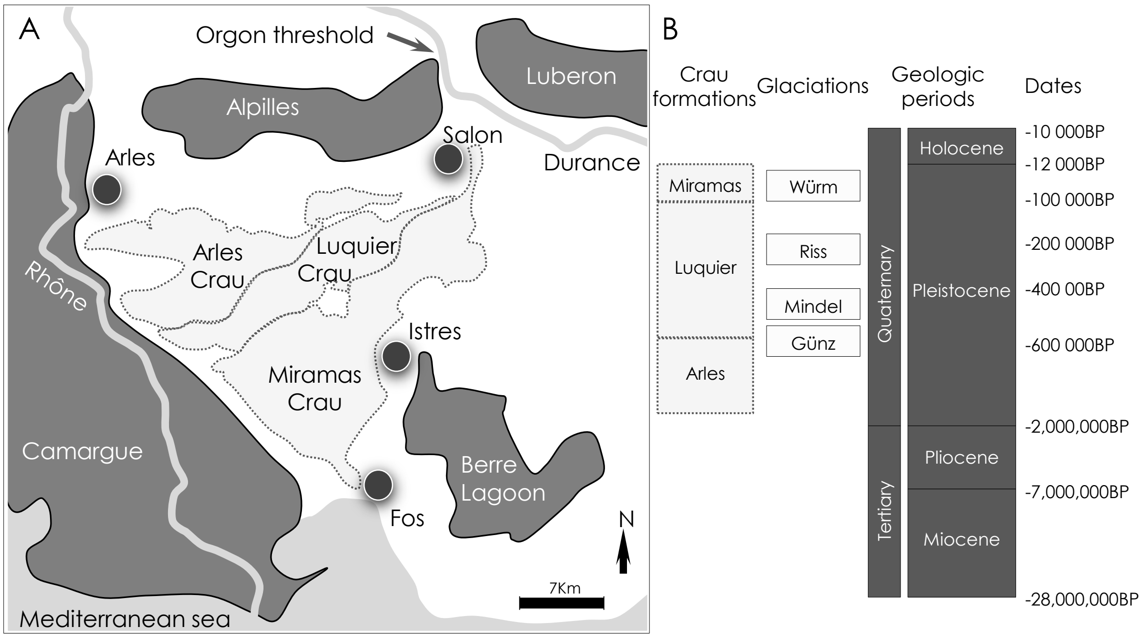


Figure I.6: Geological and geographical background of the La Crau area: map (A) and timeline (B).

I.5.3. Climate

The La Crau area has a meso-Mediterranean climate characterized by three months of summer drought, a mild winter (average temperature of 7°C and rare frosts), 400 to 600mm of rain precipitation per year, mainly in autumn (50%) (Figure I.7.A), a high number of hours of sunshine per year (>2800) and a very frequent and strong wind. The wind is an essential component of the La Crau climate, with 300 days of wind per year, including 70 days with wind speeds higher than 20km.h-1, mainly caused by the Mistral which is a north/north-westerly wind (Figure I.7.B). This wind increases soil desiccation and sunlight and lowers winter temperatures. Another major component of the Mediterranean climate is the high inter-annual variability: for example, between 1997 and 2006, a southern La Crau area meteorological station recorded an average yearly precipitation of 561mm but with a minimum of 394mm and a maximum of 823mm. In order to illustrate the inter-annual variability, we have provided ombrothermic diagrams for the study period which show that 2010 and 2011 were rather humid compared to 2012 (Figure I.7.C). Despite the relatively small area covered by the La Crau area, a small but significant environmental condition gradient occurs between north and south and is reflected by a phenological time lag of approximately 5 to 10 days (phenological events occur earlier in southern areas) (Bourrely et al., 1983).

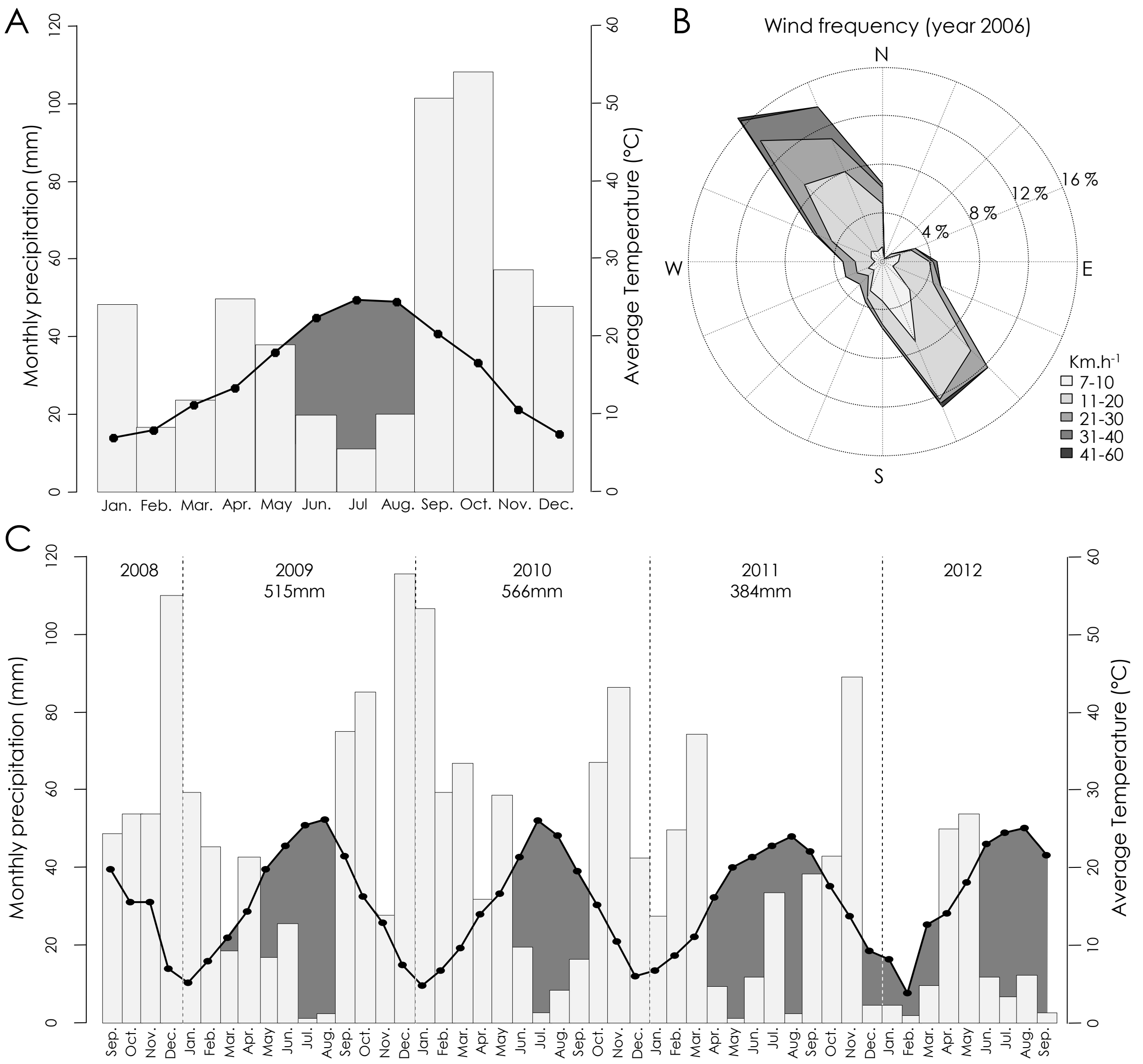


Figure I.7: Ombrothermic diagrams and wind rose for the La Crau area. A and B are an ombrothermic diagram and a wind rose representing average precipitations, and wind frequency calculated for the "Grand Carton" meteorological station (43°33'49N; 4°52'01E) during the 1997-2006 period (INRA CSE data (Wolff et al., 2009)). C represents successive ombrothermic diagrams calculated for the study time span (Sept 2008 – Sept 2012) in Istres (43°30'45N; 4°59'18E; data from Meteociel, an amateur meteorologist database, www.meteociel.fr/climatologie/villes.php). On both A and C ombrothermic diagrams, dark grey areas represent the drought period when precipitation is below 2*average temperature (Gaussen and Bagnouls, 1957).

I.5.4. Ecological characteristics of the La Crau area

The geological history of the La Crau area has resulted in a particular soil, composed of a stony layer (with low phosphorus and potassium content (Duclos,

1994) and with 40-70% of stones) overlying an almost impermeable calcareous conglomerate layer which makes the water table unavailable for plant roots. This characteristic soil, combined with the climatic conditions and several millennia of itinerant sheep grazing (Badan et al., 1995; Henry et al., 2010) has resulted in the only French Mediterranean pseudo-steppe (Devaux et al., 1983; Buisson and Dutoit, 2006). This ecosystem is characterized by its unique species-rich plant community dominated by *Brachypodium retusum* (Pers.) P. Beauv., *Asphodelus ayardii* Jahand. & Maire, *Thymus vulgaris* L. and *Stipa capillata* L. (Devaux et al., 1983). The plant community is characterized by a high number of annual species, such as *Vulpia* spp., *Linum trigynum* L., *Aegilops ovata* L., *Euphorbia exigua* L., *Asterolinon linum-stellatum* (L.) Duby, *Evax pygmaea* (L.) Brot., *Logfia gallica* (L.) Coss. & Germ., *Plantago bellardii* All., *Salvia verbenaca* L., and *Taeniaterum caput-medusa* (L.) Nevski. As noted earlier, the word steppe is usually used to describe vegetation with cover discontinuity due to climatic conditions. In the La Crau ecosystem, when sheep grazing is removed, the discontinuity in the vegetation cover disappears (Henry, 2005), thus the proper term for describing the La Crau area would indeed be 'pseudo-steppe'. However for the sake of clarity, because it has already been widely used in La Craurelated literature and because sheep grazing is the traditional and historical land-use, the word 'steppe' will be used hereafter (Devaux et al., 1983). The La Crau steppe is also a haven for birds, reptiles and insects (Buisson and Dutoit, 2006). The La Crau area hosts the only French breeding population and / or the largest French population of steppe birds, such as *Pterocles alcata* (pin-tailed sandgrouse), *Tetrax tetrax* (little bustard) or *Falco naumanni* (lesser kestrel) (Cheylan et al., 1983). The La Crau pseudo-steppe also provides a habitat for the largest population of *Lacerta lepida* (jeweled lizard) and for endemic arthropods: *Prionotropis hystrix rhodanica* (hedgehog grasshopper) and *Acmaeoderella perroti* (Crau jeweled beetle) (Foucart and Lecoq, 1998; Cheylan and Grillet, 2005). Traditional land-use is itinerant sheep grazing, which has been carried out there for thousands of years throughout the 45,000 ha area (Henry et al., 2010).

I.5.5. Conservation issues for the La Crau area

From the 45,000ha ecosystem created by the Durance river former delta, only 11,500ha remained in the early 2000's. Irrigation initiated by the Craponne canal in 1559, allowed has since made possible the development of the La Crau hay meadows. Market gardening was practiced between the 1970's and 1980's (most of which is now abandoned). The recovery of the vegetation in these old fields is the study focus of **Chapters 1 and 2**), quarries, military activities and industrialization from the early 20th century until the present day, and intensive fruit cultivation which began in 1980's, have all contributed to the decline of the original steppe area (Deverre, 1996; Gaignard, 2003; Buisson & Dutoit 2006) (Figure I.8). These many disturbances affecting the La Crau ecosystems have occurred despite the calls for protection which began in 1975, leading to the designation of a 11,816ha European Union Special Protection Area in 1990, the designation of a NATURA 2000 management plan in 1999, and finally the creation of the National Reserve in 2001 to protect a 7,411ha area (Buisson and Dutoit, 2006) (Figure I.8).

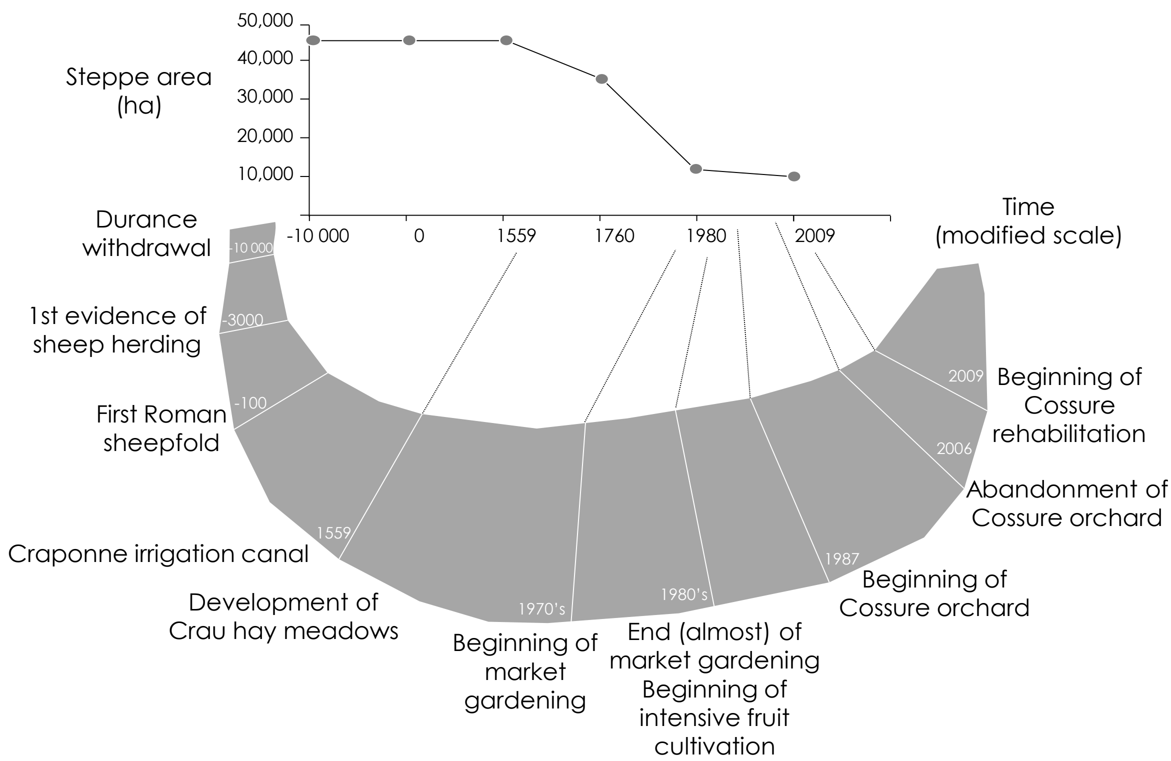


Figure I.8: History of decline of steppe area. The above plot shows the steppe area relative to time (data from Wolff et al. (2009)). The plot below is a timeline of the main events which have led to losses and gains in steppe areas. Scales have been modified; the scale of the timeline is for graphic purposes only.

The conservation objectives were taken to a new level in 2008 with the implementation of the first French habitat bank in Cossure, the focus of **Chapter 4**. Cossure is a former orchard, where cultivation started in 1987 and was abandoned in 2006 and which was bought in 2008 by a state-owned sovereign fund, *CDC Biodiversité,* with the aim of rehabilitating a herbaceous area in order i) to recreate a breeding and wintering habitat for endangered steppe birds, ii) to reconnect fragmented patches of the national reserve, and iii) to reintroduce traditional sheep grazing. Concomitantly to these conservation actions in the La Crau area, several research questions have been addressed.

I.5.6. The La Crau area as a research model

Four major periods can be distinguished in the history of the acquisition of knowledge of La Crau (Buisson et al., 2004). From 1805 to the mid 1970's, the study of La Crau was mainly focused on the description of the ecosystem, especially the plant community (*Asphodeletum fistulosi* (Molinier and Tallon, 1950)) and the behavior patterns of steppe bird species, such as *Pterocles alcata* or *Tetrax tetrax* (Frisch, 1965). Cheylan (1975) was the first author to warn the scientific community of the threats facing this unique ecosystem. Several studies were then carried out to identify the value of and threats to the La Crau area which led to publication of a special issue in the journal *Biologie Ecologie Méditerranéenne* (vol. 10, 1983). From the 1990's to the years 2000, studies focused on the impact of management practices either on the pastoral system (Cheylan and Demandolx-Dedons, 1998), on the vegetation (Masip, 1991) or on the avifauna (Wolff et al., 2002). From the years 2000 on, the La Crau area has been the focus of research on a range of scientific questions mainly dealing with dynamics and restoration (Buisson et al., 2004; Dutoit, Buisson, et al., 2011). The origin of its vegetation has been assessed on the basis of paleoecological studies (Henry, 2009). Abandoned cultivated fields were used to determine the spontaneous recovery of steppe vegetation (Buisson, 2005; Römermann, Dutoit, et al., 2005) and of steppe beetles (Fadda, 2006). These abandoned areas have also been used for this thesis, with the inclusion of landscape characteristics of the surroundings of abandoned areas (**Chapter 1**), and mycorrhizal infestation measures and a longer time gradient since abandonment (**Chapter 2**). The lack of resilience even to simple soil disturbance (Coiffait-Gombault et al., 2012a) has highlighted the need for restoration research, which has been conducted on the restoration of abiotic conditions (Buisson, 2005), seeding structuring species for restoring biotic filter (Coiffait-Gombault, 2011) or hay transfer for restoring dispersion filters (Coiffait-Gombault et al., 2011). These questions of restoration are further explored in **Chapters 3 and 4** of this thesis and in three other current theses concerning the impact of the different vegetation restoration treatments on Orthoptera and Coleoptera, in complement to the research undertaken for this thesis (Alignan, In prep), the use of ants as ecological engineers for the restoration of the spatial structure and dynamics of vegetation (*Messor barbata*, (Bulot, In prep)) or the biological management of a colonizing species (*Rubus* spp.) induced by land use changes and landscape fragmentation of the original steppe vegetation (Masson, In prep).

The La Crau area as a research model can be rather challenging, involving both drawbacks and advantages. Although the uniqueness of the La Crau ecosystem could detract from the generalization of the conclusions of the study, obvious parallels could be drawn between the La Crau area and other species-rich, grazed ecosystems, such as the Dehesas in Spain, Montado in Portugal, semi-arid steppe of North Africa or even lesser Mediterranean ecosystems, such as calcareous grasslands. A major drawback of La Crau area is the complexity of its vegetation: i) the high number of species both at small-scale (approximately 40 species for $4m^2$) and at large-scale (approximately 500 species occur in steppe or abandoned cultivation areas), ii) the high climatic variability and unpredictability, iii) the high intra-specific phenotypic variability (e.g. *Senecio vulgaris* L., which is a common French species described in the Bonnier Flora as a 10-30cm species (Bonnier, 1985), does not exceed 2cm in the steppe and <1cm adult individuals are regularly found). This complexity prevents us from using simple and precise models and calls for the use of multivariate analyses or the development of integrative indices (**Chapter 3**). The fact that the La Crau steppe is protected prevents any destructive research on this ecosystem. The counterpart of its high conservation value is that all the research undertaken is requested by stakeholders with the aim of transferring the acquired knowledge for management application purposes.

For all these reasons, the La Crau area represents a sometimes difficult but exciting challenge for advancing the understanding of vegetation dynamics or the application of restoration techniques, which are the subjects of later chapters. The question of the main drivers of plant community recovery will be addressed in **Chapter 1**, while the question of long-term resilience to severe anthropogenic disturbances will be addressed **Chapter 2**. **Chapter 3** will discuss how the recovery or restoration of a community can be assessed and **Chapter 4** how this community may be restored.

Transition to chapter 1

The **Chapter 1** examines plant communities after abandonment of cultivation in order to determine what the main driver of plant community recovery is: dispersion, abiotic or biotic filter (Figure T1.1)? To address this question, the vegetation of forty former arable fields is compared and interpreted in the light of their soil characteristics, their location on a geological and climatic gradient and their land uses in their surroundings.

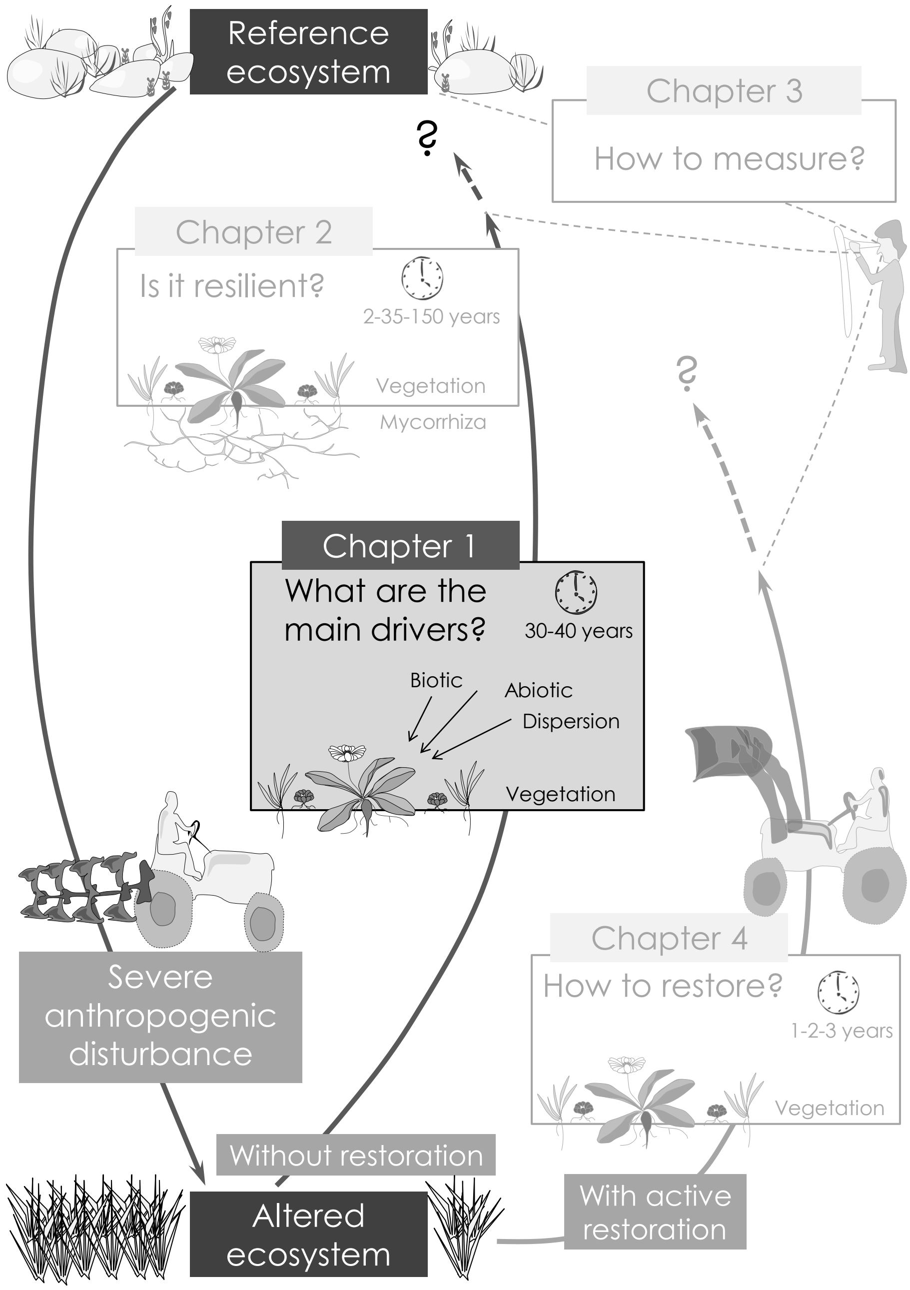


Figure T1.1: Location of Chapter 1 in the general thesis organization.

The La Crau Mediterranean steppe ecosystem. Photo credit: R. Jaunatre

Vegetation relevés carried out in a former arable field. Photo credit: R. Jaunatre

CHAPTER 1 - Mediterranean steppe vegetation after intensive agriculture abandonment is driven first by abiotic factors and second by dispersion

Renaud Jaunatre, Elise Buisson, Thierry Dutoit

(submitted to Agriculture Ecosystems & Environment the 15th of August 2012)

1.1. Introduction

Impact of land-use changes is a major topic in conservation biology, especially concerning abandonment of intensive agriculture (Stoate et al., 2009). Such conversion from intensive cultivation to extensive pastures always raises the issue of the ecosystem's ability to recover its pre-cultivation state of semi-natural grassland (Cramer et al., 2007). Many authors have attempted to link known processes to theoretical models that summarize how communities establish (Keddy, 1992; Zobel, 1997; Fattorinni and Halle, 2004; Lortie et al., 2004; Guisan and Rahbek, 2011). Most of these models are structured by filters that constrain community composition from a regional species pool. The first filter is dispersion: species have to be able to disperse toward the community. This ability depends both on the landscape matrix and on the dispersability of species found in adjacent areas (Gibson and Brown, 1991; Pärtel and Zobel, 1999; Lindborg and Eriksson, 2004; Herault and Thoen, 2009). The second is the abiotic filter: species have to be able to germinate, grow and reproduce under given environmental conditions, and this ability depends on each species' physiological capability. The last one is the biotic filter: the occurrence and nature of biotic interactions alter the first two filters either by enhancing their mesh, e.g. by increasing dispersion or by facilitating growth or establishment in limiting environmental conditions; or by reducing their mesh, e.g. by competitive exclusion (Bruno et al., 2003; Lortie et al., 2004). The aim of this paper is to measure the importance of each of these theoretical filters in driving secondary succession plant community after agricultural abandonment.

Secondary succession is an essential concern in plant ecology (Cramer et al., 2007, 2008), not only for theoretically-driven studies (Connell and Slatyer, 1977; Prach and Walker, 2011), but also for conservation and restoration perspectives (Luken, 1990; Walker et al., 2007). Estimating how dispersion, abiotic factors and biotic interactions influence the recolonization of old fields has rarely been addressed (except, for example, by de Blois et al. (2001) ; and Vellend et al. (2007)), especially in Mediterranean systems (Bonet, 2004). One reason could be that addressing this issue requires a variegated landscape (McIntyre and Barrett, 1992) with various patches under secondary succession that are still more or less surrounded by the reference ecosystem, i.e. the ecosystem in which no abrupt anthropogenic exogenous disturbance has occurred (McIntyre and Hobbs, 1999). The La Crau area in southeastern France is a steppe ecosystem that used to be partly used for open-field melon cultivation starting in the 1970's; cultivation was abandoned progressively between 1975 and 1988 (Römermann, Dutoit, et al., 2005). It therefore provides the ideal setting, which when coupled with variation partitioning (Borcard et al., 1992) allows us to tackle the following question: which part of the variability amongst secondary succession plant communities could be attributed to each filter? This question is important from a both theoretical and a management standpoint (de Blois et al., 2001), and can provide significant insight into plant community dynamics from a restoration perspective (Naveh, 1994).

1.2. Materials and Methods

1.2.1 Site description

The La Crau area is the last remaining xeric steppe in southeastern France (ca. 10,000ha; c. 43°33' N, 4°52' E; Figure 1.1) and has been shaped by i) a Mediterranean climate with mean annual temperature of 15°C, a variable annual sum of precipitation between 400 and 600mm concentrated in autumn, four months of summer drought, and more than 110 days with a >50km.h^{-1} wind; ii) 40cm deep soil composed with about 50% of silicaceous stones overlaying a conglomerate layer, making the alluvial water table unavailable to the roots of plants and iii) a population of itinerant sheep that have grazed there over the past several thousand years (Devaux et al., 1983; Buisson and Dutoit, 2006). This has led to a unique and species-rich plant community composed mainly of annuals and dominated by *Brachypodium retusum* Pers. and *Thymus vulgaris* L.. Most of the species are oligotrophic species, i.e. they are able to grow well in a stressful environment. This community characterizes the reference ecosystem in this study and will henceforth be referred to as *steppe*. The 45,000ha of original steppe was characterized by relatively homogeneous vegetation before being fragmented by various anthropogenic disturbances, in particular, cultivation (Devaux et al., 1983; Buisson and Dutoit, 2006). Melon cultivation occurred in the La Crau area between 1971 and 1988, most of the fields have been subsequently abandoned; they now contain different plant communities dominated by *Bromus* species (Römermann, Dutoit, et al., 2005).

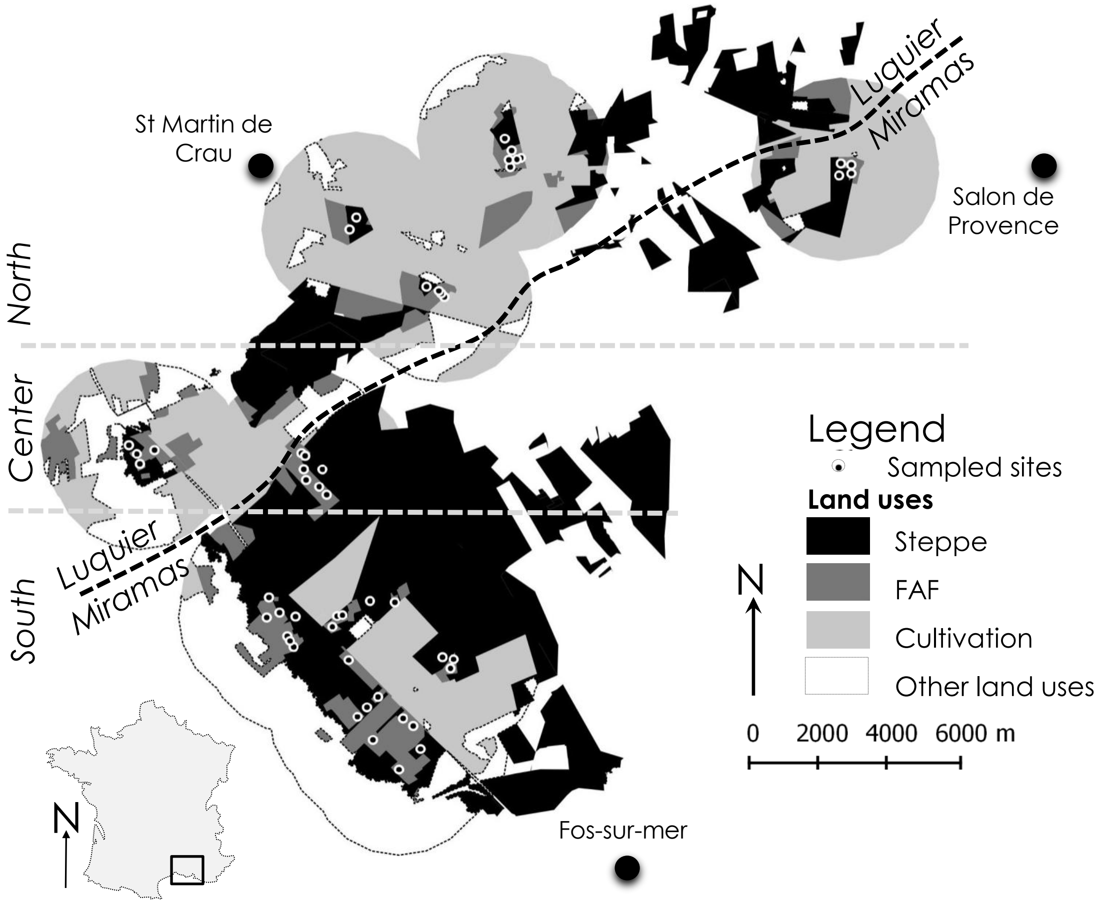


Figure 1.1. Map of the La Crau area. The three main towns are shown. The thick dashed lines delineate geological zones: Luquier and Miramas (black) and climatic gradient zones: North, Center and South (grey). Steppe habitats are shown for the whole area whereas other GIS land covers are shown only within a 2400m radius surrounding sampled areas. The category "Other land uses" represents a few potentially very different land uses (i.e. roads, wetlands, buildings, etc.) and were not used in analyses.

1.2.2. Field selection

Mapping based on aerial photographs enabled us to identify more than 220 areas that i) appear as steppe on the earliest photographs available (1947); ii) show evidence of cultivation in later photographs (1955 – 1971 – 1975 – 1978 – 1979 – 1984 – 1988) and, iii) were abandoned prior to the most recent set of photographs(i.e. abandoned between 1978 and 1988). To avoid the introduction of an additional source of variability, we focused only on open-field melon cultivation and not on large plastic tunnel fields that left less-disturbed trackways between the tunnels (Römermann, Dutoit, et al., 2005). Forty of these former arable fields, hereafter called FAF, were chosen in order not to have two fields sharing the same characteristics (age, landscape, etc.). The distance between any two sampled sites varies between 120m and 20km (Figure 1.1).

1.2.3. Model description

The model used to explain plant community assembly is composed with the following three filters: dispersion, abiotic and biotic (Keddy, 1992; Lortie et al., 2004). Each filter is approximated by an association of explanatory variables that are known in the literature to affect plant community composition, and for which data are available (Figure 1.2).

Dispersion is a stochastic process that depends on propagule availability in the seed bank or in the seed rain. It is widely recognized that most of the species from dry grasslands do not produce a permanent seed bank (Graham and Hutchings, 1988a). This has also been demonstrated in La Crau (Römermann, Dutoit, et al., 2005). On the other hand the seed rain depends both on the landscape matrix and on the dispersability of species found in adjacent areas (Gibson and Brown, 1991; Pärtel and Zobel, 1999; Lindborg and Eriksson, 2004; Herault and Thoen, 2009). We thus included land uses in the areas surrounding FAF as explanatory variables of the dispersion filter. As the probability of a propagule of one species joining a community is increased with time, we also included the age of cultivation abandonment (determined on the basis of available aerial photographs) as a dispersion explanatory variable.

The abiotic filter in FAF depends on environmental conditions that prevailed before the disturbance, and on how the disturbance changed these characteristics. In the La Crau area there is a relative geological and climatic gradient determined by moisture and geological formation. Southern areas receive less precipitation and dry faster in late spring than northern ones, leading to a 5-10 day phenological lag with few differences in vegetation composition (Devaux et al., 1983). We distinguished three classes by their climatic gradient: North, Center and South (Figure 1.1). Two geological formations can be distinguished in La Crau: Miramas and Luquier soils, which were formed at different periods, respectively 300,000–120,000 BP and 120,000–30,000 BP (Colomb and Roux, 1978) (Figure 1.1). Luquier soils contain slightly more phosphorus and potassium and less clay (Duclos, 1994). Soil characteristics were also added to the model as they integrate both differences due to the geological and climatic gradient and also the differences that are due to cultivation legacies (Foster et al., 2003).

The biotic filter depends on how present organisms can modify other species' abundance. During FAF recolonization, target species (i.e. species from the reference ecosystem that was not cultivated = steppe species) have to face dense cover of ruderals or more opportunistic species (Öster et al., 2009; Baeten et al., 2009). Hence we approximated the biotic filter by indicators of potential competition in FAF (Buisson, 2005): percentage of total vegetation cover, average vegetation height and sum of abundances (estimated by Braun-Blanquet coefficient) of the three most abundant species in each quadrat (hereafter named abundance of dominant species).

Filters, their explanatory variables and other unmeasured variables may not be randomly distributed in space, and hence may be spatially correlated. Borcard et al. (1992) suggest taking space into account when trying to explain community structure by explanatory variables in order to discriminate what can be explained only by the explanatory variable, only by space, and by both. We thus used space (XY geographic coordinates) as an indirect explanatory variable in our model (Figure 1.2).

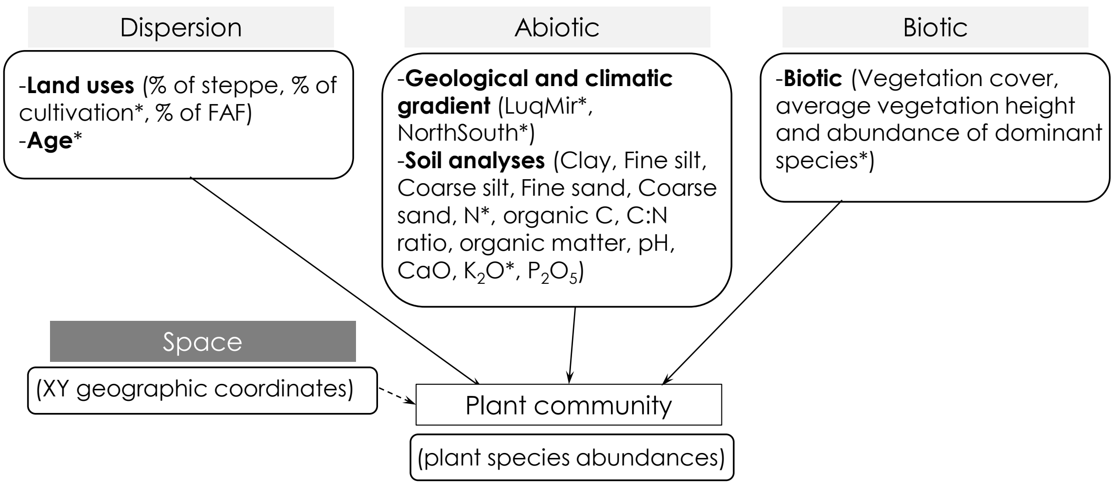


Figure 1.2: Conceptual model of FAF (Former Arable Fields) plant community drivers: Dispersion, Abiotic and Biotic are the three filters expected to have a direct effect on plant community (full-lined arrows) and the space factor is expected to have an indirect effect (dashed-line arrow). Groups of explanatory variables are in bold and measured variables in brackets. Asterisks indicated selected explanatory variables in the parsimonious RDA model.

1.2.4. Land use characterization

We identified all land uses within a 900m radius circle around the centre of each field in order to reflect the species pool available to each field since cultivation stopped. Land use classes were: steppe, cultivation and FAF. The 900m radius was chosen as a trade off between i) a smaller radius that would have caused the landscape factors to be especially influenced by the area of each field, and ii) a larger radius that would have made the landscape factors of two fields close together almost identical. For each class, spatio-temporal percentages were calculated using Geographical Information System (GIS) software: Quantum GIS 1.5.0 'Thetys' (Quantum GIS Development Team, 2010).

1.2.5. Vegetation and soil sampling

Vegetation sampling was carried out at the center of each of the forty FAF and of eleven steppe areas from all geographical zones of the La Crau area (Figure 1.1) in three 4m² quadrats. A Braun-Blanquet coefficient (Braun-Blanquet et al., 1952) was given to all plant species recorded. For each plot, there are three values for each vegetation parameter and one value for all other parameters (soil, landscape, etc.): we therefore used the mean values of vegetation parameters on three quadrats for further analyses. For soil analyses, a subsample of 70g of soil was gathered in each of the three quadrats in the topsoil layer (0-10cm) before being pooled to obtain one 210g soil sample for each FAF. They were then sieved with a 2mm mesh sieve. Analyses were carried out by the INRA (Institut National de la Recherche Agronomique). Granulometry: percentage content of clay (<0.002mm), fine silt (0.002-0.02 mm), coarse silt (0.02-0.05mm), fine sand (0.05-0.2mm) and coarse sand (0.2-2mm), nutrient analysis (organic C, total N, P_2O_5 (Olsen et al., 1954), $CaCO_3$, CaO, K_2O) and water pH were measured according to the methods described in Baize (2000).

1.2.6. Statistical analyses

Diversity was assessed using both richness and Shannon evenness (Pielou, 1969) and was compared with univariate tests: statistical differences between steppe and FAF were measured with Wilcoxon tests, as data were not normally distributed. Vegetation composition was analyzed using multivariate methods.

In order to study the vegetation of steppe and FAF together, a Non-metric Multidimensional Scaling (NMDS) ordination was performed on the vegetation matrix to ordinate quadrats according to their plant community characteristics (Borcard et al., 2011). A permutation test was performed to test the difference in ordination of FAF and steppe vegetation.

In order to study FAF vegetation in more details, we carried out three more multivariate analyses on Hellinger transformed FAF vegetation data to be able to use Redundancy Analyses (RDA) (Legendre and Gallagher, 2001). 1) A parsimonious RDA was performed with a reduced number of explanatory variables in the model as it is advised by Borcard et al., (2011) (Figure 1.2). The forward selection method retains 7 out of the 22 explanatory variables, making it possible to obtain an RDA model with all variance inflation factors below 10. This RDA was followed by permutation tests making it possible to test the effect of explanatory variables on RDA ordination. According to permutation tests, pH has no significant effect on ordination ($p=0.067$) and was thus removed from the parsimonious RDA model. The 6 selected explanatory variables used in the parsimonious RDA model are: North/South (VIF=7.11), N (VIF=1.51), Luquier/Miramas (VIF=2.76), % of cultivation in the landscape (VIF=3.20), K_2O (VIF=1.91), and abundance of dominant species (VIF=1.89) (Figure 1.2). 2) In order to discriminate the influence of the three filters, we used Borcard et al. (1992)'s variation partitioning method to measure the variation in FAF plant community explained by dispersion, abiotic and biotic filters, alone or combined together with space. 3) We then assessed the importance of each group of explanatory variables (GEV; Figure 1.2): landscape, age, geological and climatic gradient, soil and biotic, relative to space importance. Four successive RDAs allowed us to calculate fractions of the total variation explained: i) by GEV, ii) by space, and iii) by the spatially-structured GEV (Borcard et al., 1992).

Two lists of species (steppe and FAF) were established in order to test for correlation between their abundance and explanatory variables. Species of the two lists are species present both in FAF and in steppe but showing significant differences in abundances between steppe and FAF according to a Wilcoxon test. The fifteen steppe species are: *Aira cupaniana* Guss, *Asphodelus ayardii* Jahand. & Maire, *Carduus nigrescens* Vill., *Carlina corymbosa* L., *Erodium cicutarium* (L.) L'Hérit., *Euphorbia exigua* L., *Logfia gallica* (L.) Coss. & Germ., *Galium murale* (L.) All., *Galium parisiense* L., *Hypochaeris glabra* L., *Linum trigynum* L., *Poa bulbosa* L., *Sanguisorba minor* Scop., *Sherardia arvensis* L. and *Thymus vulgaris* L. and the seven FAF species are: *Calamintha nepeta* (L.) Savi, *Diplotaxis tenuifolia* (L.) DC., *Lepidium* *graminifolium* L., *Lobularia maritima* (L.) Desv., *Rostraria cristata* (L.) Tzvelev, *Rumex pulcher* L. and *Verbascum sinuatum* L.. Correlations were assessed using one-tailed Spearman rank-based correlation test. One-tailed tests were chosen because we had a priori hypotheses on the correlation between explanatory variables and species abundances (Ruxton and Neuhäuser, 2010). Concerning land uses in the surroundings, we expected steppe to provide steppe species propagules and cultivation or FAF to provide more ruderals (*sensu* Grime et al. (1988)), hence FAF species propagules. We thus tested for a negative correlation between % of cultivation and % of FAF and steppe species abundances, and a positive correlation with FAF species abundances. As cultivation has changed soil characteristics towards less oligotrophic conditions (Römermann, Dutoit, et al., 2005; Buisson et al., 2006), we expected steppe species to be positively correlated with fine sand and coarse sand that lower water retention, and C:N ratio and organic matter but negatively correlated with clay, fine silt, coarse silt, pH, $CaCO_3$, P_2O_5, CaO and K_2O. We tested for opposite relationships between these soil parameters and FAF species abundances. Concerning biotic explanatory variables, as we only measured variables related to competition interactions, we tested for negative relationships i) between these variables and steppe species abundances, and ii) between these variables and FAF species abundances. Concerning biotic explanatory variables, as cumulative abundances of dominant species are related to competition interactions, we tested for negative relationships i) between these variables and steppe species abundances, and ii) between these variables and FAF species abundances.

All the analyses were conducted using R 2.13.0 (R Development Core Team, 2011). Univariate analyses were done with the R package "stats" and multivariate analyses with the packages "ade4" (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007), "packfor" (Dray et al., 2011) and "vegan" (Oksanen et al., 2008).

1.3. Results

1.3.1. Steppe and FAF vegetation

In total, 158 plant species are recorded: 148 in 120 FAF quadrats (40x3 quadrats) and 122 in 33 steppe quadrats (11x3 quadrats). Despite the high number of overlapping species, mean species richness is significantly higher in steppe areas (39.3±1.7 vs 32.2±1.3; W=332, p=0.011). Similarly, Shannon evenness, although slightly different, is significantly higher in steppe areas than in FAF (0.47±0.001 vs 0.46±0.002; W=356, p=0.001). The major vegetation trend, shown by the NMDS (Figure 1.3), is a difference between steppe and FAF plant communities (permutation test n=999, r^2=0.164, p<0.001). Steppe vegetation is characterized by species such as *Asphodelus ayardii* Jahand. & Maire, *Brachypodium retusum* (Pers.) P. Beauv. or annuals like *Brachypodium distachyon* (L.) P. Beauv. or *Plantago bellardii* All.. FAF vegetation is characterized by species, such as *Bromus spp.*, *Hordeum murinum* L., and *Carduus pycnocephalus* L., even if some FAF seem to include some oligotrophic species present in both steppe and some FAF e.g. *Sherardia arvensis* L., *Carthamus lanatus* L. or *Aegilops ovata* L..

1.3.2. Relationship between explanatory variables and FAF plant communities

The whole reduced RDA model constrains 39% of variance (Figure 1.4). The first axis of the RDA ordination computed on the FAF plant communities distinguishes FAF with higher abundances of dominant species, characterized by higher abundances of *Bromus* spp. or *Calamintha nepeta* (L.) Savi. This negative end of axis 1 is also correlated with a higher percentage of cultivation around the FAF. On the other side along this first axis, FAF are mainly characterized by forbs, such as *Carthamus lanatus* L., *Hypochaeris glabra* L., *Trifolium* spp., or *Sideritis romana* L.. The second axis is correlated with total nitrogen and potassium, as well as the geological position (Luquier-Miramas). These explanatory variables seem to discriminate oligotrophic communities with species like *Brachypodium distachyon* (L.) P. Beauv. or *Linum trigynum* L. and less oligotrophic communities with species like *Hordeum murinum* L. and *Polycarpon tetraphyllum* (L.) L.. The North/South gradient is correlated with both axes, northern FAF appearing more correlated with higher potassium values and a higher % of cultivation in the surroundings.

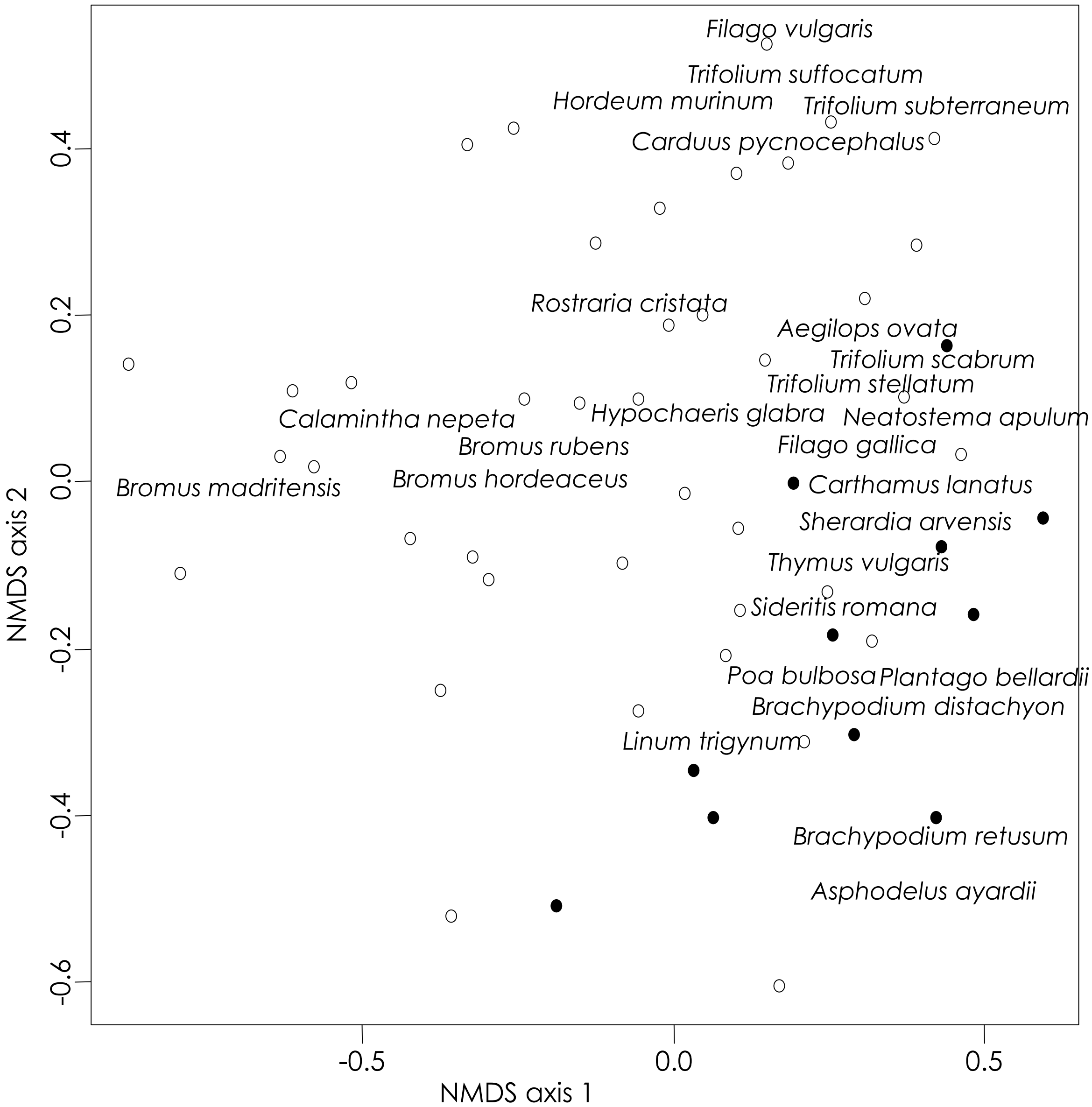


Figure 1.3. Steppe (filled circles, n=11) and FAF (open circles, n=40) ordination based on NMDS of plant community composition, final stress=0.19. For clarity purpose, only the 27 most correlated species are shown (out of 130).

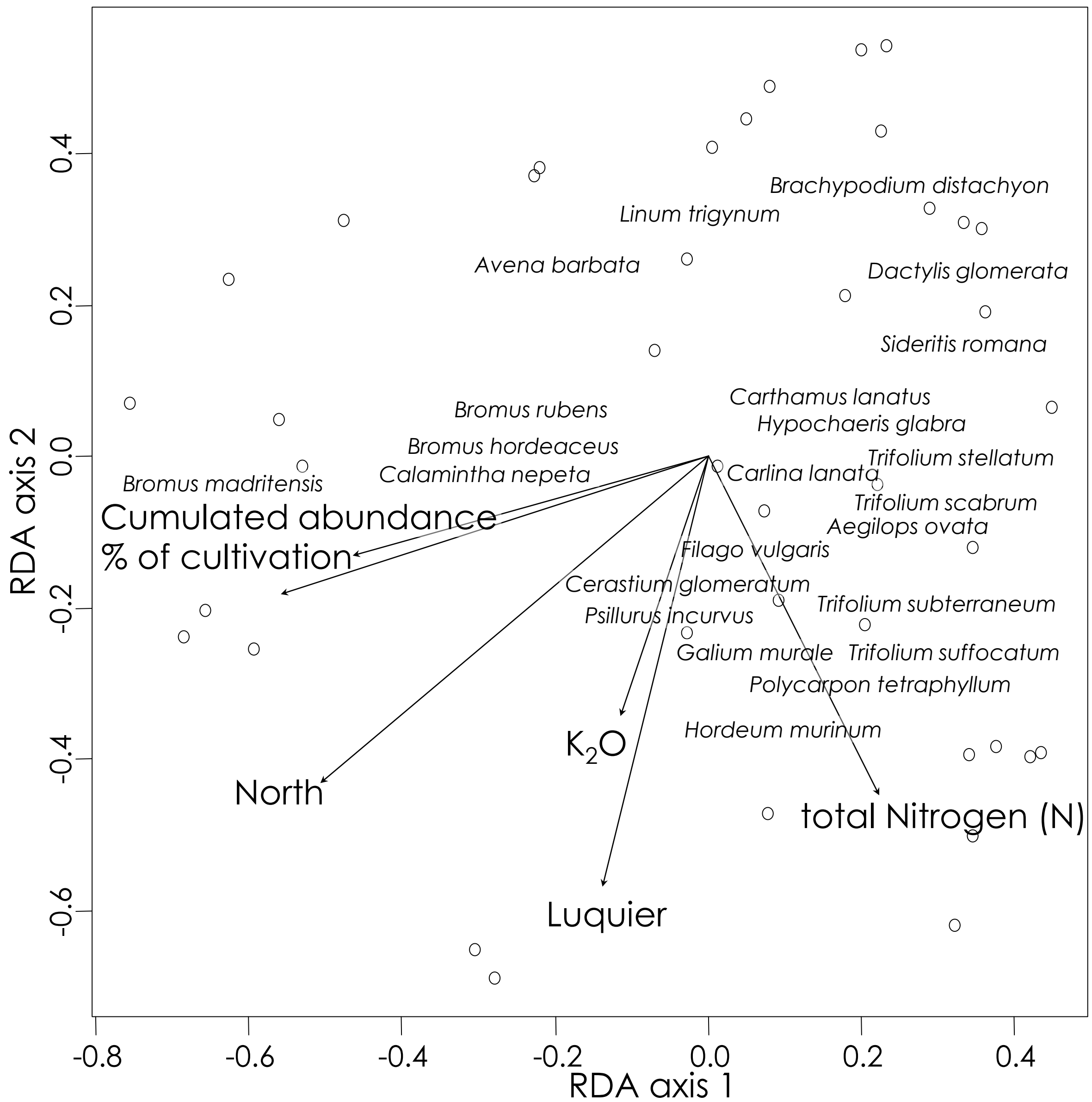


Figure 1.4. FAF (n=40) ordination based on the most parsimonious RDA model of plant community composition. In the interest of clarity, only the 23 most correlated species are shown (out of 111) and all explanatory variables of the most parsimonious model are shown. The proportion of constrained inertia is 36.8%.

1.3.3. Variation partitioning

The variation in FAF plant communities explained by the three filters is unbalanced: the abiotic filter alone explains 13% of the model while the dispersion and biotic ones explain respectively 4% and 1% (Figure 1.5). Explanatory variables are inter-correlated, either between themselves (3%) or via their spatial structure (12%). A great part of the variance in FAF plant communities remains unexplained by our filters (63%).

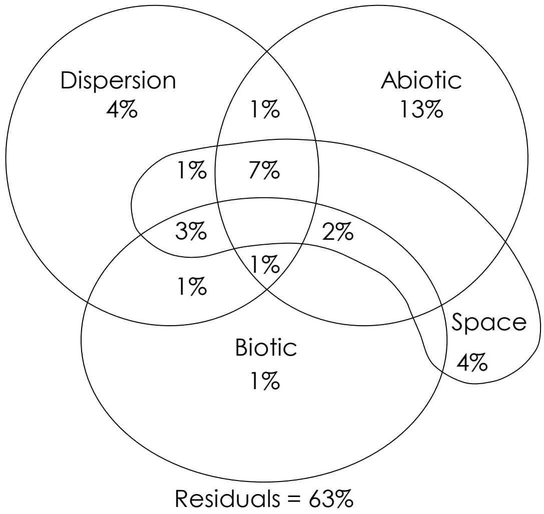


Figure 1.5. Venn diagrams representing the four fractions of variation partitioning: Dispersion, Abiotic, Biotic and Space on vegetation of FAF. Empty cells occur when explained variation is below 0.1%.

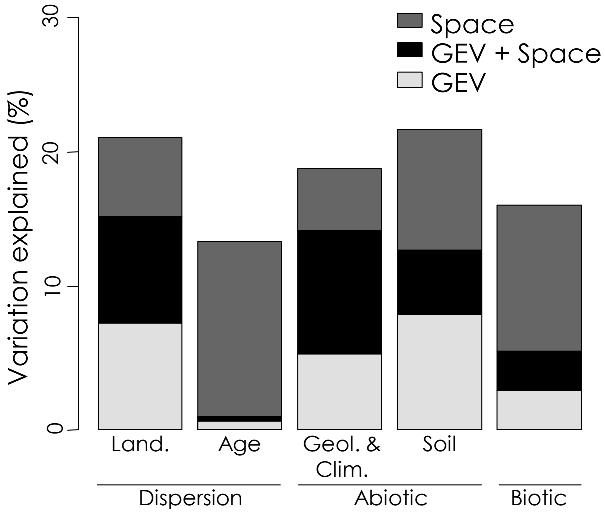


Figure 1.6. Variation in FAF plant communities explained by filters and groups of explanatory variables (GEV). Variation is partitioned into three fractions: spatial component only (Space), spatially structured explanatory variables (Space + GEV) and explanatory variables only (GEV). Explanatory variables are: Land.: land uses in the surroundings, Age: time since cultivation abandonment, Geol. and Clim.: information on geological formation and on North/South gradient, Soil: physical and chemical soil variables, Biotic: vegetation cover, average vegetation height and abundances of dominant species.

A closer look at the filters, via GEV (Group of Explanatory Variables), shows that landscape, i.e. land uses in the surroundings since cultivation abandonment, accounts for 15% of the explained variation, of which half is also explained by spatial structure (Figure 1.6). Age since last cultivation explains a very small part of FAF plant communities: less than 1%. The geology and climate gradient explains a great amount of the FAF plant community variation (14%), but a large part of the explained variation is also explained by space (9%). Meanwhile, soil explains less of the variation (13%) but a smaller part of the explained variation is also explained by space (5%). The biotic filter explains a smaller part of the variation in the FAF plant community variation: 6% of which 3% is also explained by space.

1.3.4. Relationships between explanatory variables and steppe or FAF species abundances

Correlations between the abundances of characteristic species and explanatory factors are diametrically opposed whether we consider steppe or FAF species (Table 1.1). There is a statistically significant correlation between landscape and FAF species: their abundances decrease with increasing steppe percentage and increase with increasing cultivation percentage. In contrast, steppe species abundances are not significantly correlated with landscape in the surrounding environment. Age since cultivation abandonment is not correlated, either with FAF or with steppe species abundances. Concerning abiotic conditions, granulometry is only correlated with FAF species: their abundances significantly increase with higher clay and fine silt proportions while they significantly decrease with fine sand. Some chemical characteristics (organic carbon, nitrogen, organic matter, pH and calcium carbonate) are not significantly correlated with species abundances. The C:N ratio is positively correlated with steppe species abundances, while phosphorus and potassium contents are negatively correlated. As for FAF species abundances, these are positively correlated with phosphorus, calcium oxide and potassium content. If we consider the biotic filter, we find that only the abundances of dominant species in FAF are negatively correlated with steppe species abundances in FAF. There is no significant relationship between FAF species abundances and the other measured variables.

Table 1.1: Influence of explanatory variables on FAF (Former Arable Fields) and steppe species abundances. The given p value comes from the one-tailed rank-based Spearman's correlation test. The sign indicates whether we tested for a negative (–) or positive (+) relationship between explanatory variables and abundances.

Explanatory variable	Steppe species			FAF species		
Dispersion		p value			p value	
% of Steppe	+	0.191	NS	-	<0.001	***
% of Cultivation	-	0.083	.	+	0.002	**
% of FAF	-	0.717	NS	+	0.715	NS
Age	+	0.873	NS	-	0.635	NS
Abiotic		p value			p value	
Clay	-	0.244	NS	+	0.002	**
Fine silt	-	0.6	NS	+	0.015	*
Coarse silt	-	0.736	NS	+	0.177	NS
Fine sand	+	0.122	NS	-	0.023	*
Coarse sand	+	0.869	NS	-	0.175	NS
Organic carbon	+	0.354	NS	-	0.736	NS
Total N	-	0.395	NS	+	0.207	NS
C:N ratio	+	0.015	*	-	0.266	NS
Organic matter	+	0.366	NS	-	0.744	NS
PH	-	0.269	NS	+	0.22	NS
$CaCO_3$	-	0.752	NS	+	0.261	NS
P_2O_5	-	0.004	**	+	0.002	**
CaO	-	0.167	NS	+	<0.001	***
K_2O	-	0.003	**	+	0.002	**
Biotic		p value			p value	
Average vegetation height	-	0.346	NS	-	0.195	NS
Vegetation cover	-	0.106	NS	-	0.578	NS
Abundance of dominant species	-	0.031	*	-	0.731	NS

1.4. Discussion

As reported in many studies that have focused on community resilience (Tomanek et al., 1955; Coffin et al., 1996; Meiners et al., 2002; Bonet and Pausas, 2004), even more than 30 years after disturbance, the species richness and evenness of the plant communities that colonized the disturbed sites are still lower than, and the composition is still considerably different from, those from steppe areas. Actual differences are usually explained by the low dispersion of target species (Hutchings and Booth, 1996) or the durable establishment of non-target species and associated negative feedback (McCain et al., 2010). In this study we explain this within the framework of theoretical filters (Keddy, 1992; Lortie et al., 2004).

Community composition depends both on the regional species pool and on the local species pool (Pärtel et al., 1996; Alard and Poudevigne, 2002). At a finer observational scale, the landscape species pool, here approximated by the landscape surrounding each former arable field (FAF), explains a great amount of the variation in the FAF plant communities. Fields surrounded by cultivation exhibit a higher abundance of more competitive species like *Bromus* spp. while those surrounded by steppe exhibit a higher abundance of steppe species and lower cover of FAF species. Differential dispersal limitation can cause wide species-specific deviations in the probability of finding a species from the landscape species pool in the community (Grace, 2001). Non-target species are favored by frequently disturbed areas (Deutschewitz et al., 2003) and the presence of reference areas in the vicinity promotes the dispersal of target species to the community (Tansley and Adamson, 1925; Cook et al., 2005). This is especially true when most of the target species have poor dispersal abilities (Primack and Miao, 1992) or low colonization rate (Buisson and Dutoit, 2004; Buisson et al., 2006). Time since abandonment surprisingly does not have any effect on FAF plant communities' characteristics. One hypothesis could be that FAF communities have reached alternative stable states (Beisner et al., 2003) or at least alternative transient states (Fukami and Nakajima, 2011). The fact that rapid community shifts occur rather at the beginning of the succession (Foster and Tilman, 2000; Bonet and Pausas, 2004) and (Coiffait-Gombault et al., 2012a) in La Crau seems to be a more valuable explanation of the absence of age effect, especially considering the relatively short gradient of age between the oldest and the youngest former arable field (21-31 years).

Our results show that abiotic conditions are the major determinant of FAF plant communities, whether we consider all species, FAF species or steppe species. Theoretical models predict that once a species reaches a site, environmental conditions and biotic interactions will determine its establishment in the community (Keddy, 1992; Lortie et al., 2004). Soil characteristics (phosphorus, potassium and calcium oxide) exert a differential effect on FAF and steppe species, as the latter are favored by low concentration values. Nutrient enrichment does not prevent target species development but enhances competition of non-target species due to their dense cover (Huenneke et al., 1990). Steppe species abundances are significantly negatively correlated with abundance of dominant species of FAF. Dominance by more competitive and ruderal species on soil with higher nutrient contents can lead to a decline of target species (Yurkonis and Meiners, 2004), which is why it is sometimes difficult to disentangle biotic and abiotic filters. Sowing steppe species in FAF abiotic conditions or in steppe abiotic conditions does not influence their establishment (Coiffait-Gombault et al., 2012b); we can therefore hypothesize that it is due to increased effect of competition more than a direct effect of abiotic conditions. This hypothesis is moreover confirmed by the fact that steppe species abundances are negatively correlated with abundance of dominant species.

We deliberately did not consider positive interactions, which can exert a significant role in determining a plant community (Brooker et al., 2008). Two other potential biotic interactions have not been studied: sheep herds and microorganisms. Sheep grazing has been reintroduced on all FAF almost immediately after cultivation abandonment. Microorganisms, such as soil bacteria or mycorhizal fungi can exert a strong influence on plant community (Van Der Heijden et al., 1998; O'Connor et al., 2002) but identification of these interactions requires time consuming protocols which could not have been applied within the framework of this study on a scale sufficient to cover the La Crau area with its 51 sites.

The fact that we have fewer steppe quadrats than FAF quadrats does not allow testing for a stronger differentiation of steppe communities according to geological and climatic gradient. Nevertheless, it has already been shown that very old communities show more differentiation issued from long-term interaction with microclimatic or the geologic variation: e.g. in the La Crau area (Römermann, Dutoit, et al., 2005) and in abandoned quarries in the Czech republic (Novák and Prach, 2003). However, it is important to stress that such differentiation is even noticeable via the RDA, and variation partitioning, which have enabled us to demonstrate the effect of geologic and climatic gradient on species composition.

Variation partitioning is a very useful tool to assess the relative importance of drivers within any model, especially when several factors are implied and are possibly correlated with each other (Borcard et al., 1992). The way we modeled the main drivers enabled us to obtain a relatively high amount of explained variation (37%) compared to other published variation partition assessments (e.g. 25% on Hungarian arable weeds (Pinke et al., 2012), 32% on tropical pteridophytes (Jones et al., 2010) or 40% on South-West Canadian old-fields (Benjamin et al., 2005)). The low dispersal abilities of steppe species (Buisson and Dutoit, 2004; Buisson et al., 2006) and the large regional species pool of up to 500 species (La Crau area, Saatkamp, pers. com.) may explain the high amount of stochasticity found in analyses (Chase, 2003).

FAF plant communities are still different from the pre-cultivation vegetation, even 30 years after the transition to an extensive pasture. Considering the current difference, a full recovery of the reference community will take a very long time or lead to an alternative degraded stable state (Beisner et al., 2003; Cramer et al., 2008), and measuring relative importance of drivers of formerly disturbed plant communities is of great concern for conservation and restoration (Luken, 1990; Walker et al., 2007). Our results show that the three theoretical filters are important in determining plant community composition. Nevertheless the abiotic filter seems to exert the greatest effect, followed by the dispersion filter and last of all, the biotic filter. Based on our results, it is clear that restoration efforts for such former arable field vegetation, should focus on i) choosing fields surrounded by the high steppe percentage areas; ii) forcing the dispersal of target species; and iii) lowering arable weed species competition abilities.

Transition to chapter 2

The remaining differences between former arable field and steppe that we found in **Chapter 1** even after 30 years of abandonment raised two questions: i) Is this ecosystem really resilient to exogenous disturbances in the long term? And ii) Do all its components have the same rate of resilience? A growing number of studies show the advantage of taking into account the interactions between vegetation, soil and mycorrhizae in order to understand the organization and dynamics of plant communities (van der Heijden et al., 1998). These three ecosystem components interact continuously, either positively or negatively, but little research has focused on the resilience of these interactions. The **Chapter 2** therefore aims at assessing the resilience of soil characteristics, mycorrhizal infestation and plant communities after a cultivation episode. The study focuses on four cultivation periods, from 150 years to 2 years since cultivation abandonment (Figure T2.1).

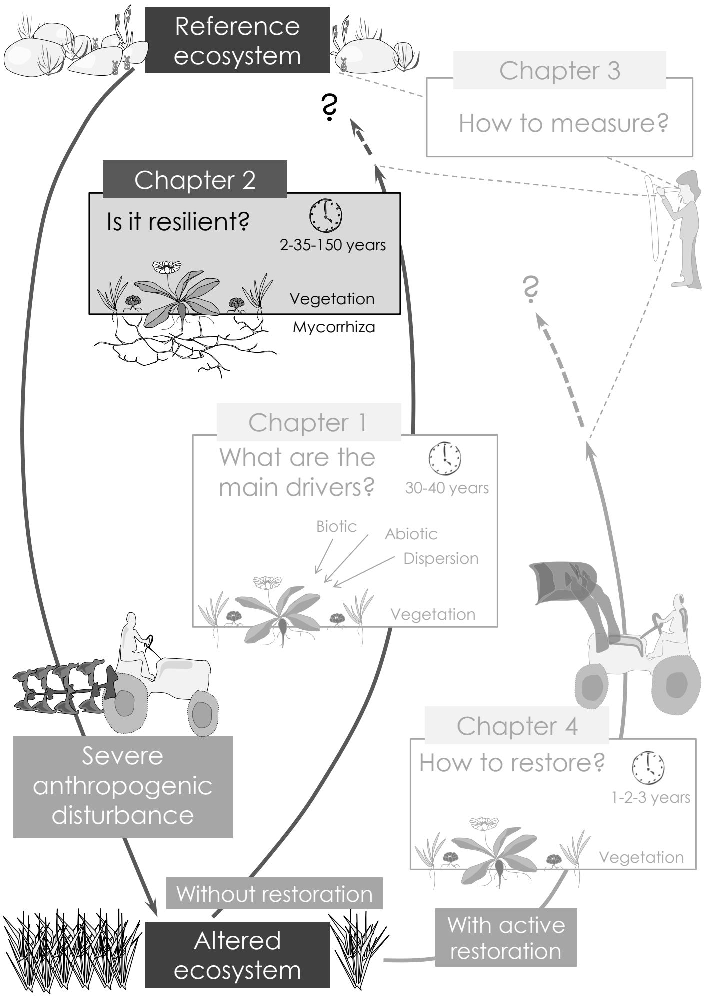


Figure T2.1: Location of Chapter 2 in the general thesis organization.

A 35 year-old abandoned field. Photo credit: R. Jaunatre

Gathering roots for mycorrhizal infestation assessment. Photo credit: R. Jaunatre

CHAPTER 2 - A multi-level approach to assess the resilience of a mature ecosystem to disturbance

Renaud Jaunatre, Elise Buisson, Thierry Dutoit

2.1. Introduction

Land-use changes have lead to major alterations of ecosystems all around the world in the recent decades (Vitousek et al., 1997; Rands et al., 2010). Due to progress in agronomy in the last century, agriculture intensification has spread even to low productive ecosystems, which are therefore currently highly threatened (Huston, 2005; Millennium Ecosystem Assessment, 2005). Understanding how changes in land-uses can alter these ecosystems has important implications, especially in a context where environmental authorities encourage limitation of biodiversity loss and restoration of ecosystem (Millennium Ecosystem Assessment, 2005; Convention on Biological Diversity, 2011). In this context, land abandonment is viewed as a great opportunity both to recover former ecosystems and to study ecosystem natural or spontaneous dynamics and resilience (Prach and Walker, 2011).

Understanding succession after disturbance is of special interest in order to use its patterns and processes to restore disturbed ecosystems, especially using natural or near-natural restoration techniques (i.e. with the least active intervention possible) (Řehounková and Prach, 2008; Prach and Hobbs, 2008). Disturbance characteristics have to be defined to understand their effects on ecosystems. According to Grime (1977), a disturbance is a constraint that limits plant biomass by causing its destruction. Sousa (1984) defined several attributes of disturbance: i) the extent: the size of the disturbed area; the magnitude, including ii) intensity: the strength of the disturbing force, and iii) severity: the damage caused by the disturbance; iv) the frequency: the number of disturbances per amount of time and v) the predictability: the variance of the mean time between disturbances. If values had to be given to each of these attributes for cultivation disturbance, they would be high, except the predictability and frequency: i) they occur over a wide extent: wider than the scale at which community processes occur (Peterson et al., 1998; Huston, 1999), ii) compared to the components of most cultivated ecosystems, the strength of the disturbing force is high (e.g. chisel plow *vs.* roots), iii) the severity is high: almost all mature organisms die during a cultivation event. Due to all these characteristics, cultivation will be further defined as a severe anthropogenic disturbance. Although a high recovery of ecosystems seems to occur after endogenous or historical disturbances, such as fire or grazing (Harrison and Shackleton, 1999; Lavorel, 1999), a severe anthropogenic disturbance, such as cultivation, shows low resilience in many ecosystem types (Bellemare et al., 2002; Dupouey et al., 2002; Römermann, Dutoit, et al., 2005; Elmore et al., 2007; Gustavsson et al., 2007).

Despite the growing number of studies showing interest in taking into account mycorrhizal interactions to understand plant community dynamics (Grime et al., 1987; O'Connor et al., 2002; van der Heijden and Horton, 2009; Bever et al., 2010), there is a marked asymmetry between the study of plants and that of mycorrhizae due to the fact that the study of mycorrhizae is more difficult (Bever et al., 2001). Mycorrhizae can be found in most plant communities (van der Heijden and Sanders, 2002) and a meta-analysis has shown that they build interactions with more than 80% of plant species and 92% of families (Wang and Qiu, 2006). Mainly through the increased volume available for prospection, mycorrhizae increase plant water (Allen, 1982; Augé, 2001) and phosphorus uptake (Bolan, 1991; Koide, 1991). They also increase the growth of plant individuals and of their descendants (Koide and Lu, 1992; Heppell et al., 2002). All these impacts therefore suggest a potentially marked impact on plant communities, and it has been shown that they can modify competition between plants and their coexistence within a community (Grime et al., 1987; Zobel and Moora, 1995; Hartnett and Wilson, 1999; Smith et al., 1999; Bever, 2002) as well as structure (Wilson and Hartnett, 1997; O'Connor et al., 2002), richness and composition of plant communities (Gange et al., 1993; Francis and Read, 1994; Zobel and Moora, 1995; Hart et al., 2003).

In the context of multiple studies which are carried out on plant community dynamics or restoration in the La Crau Mediterranean steppe (cf. Introduction section I.5.6. and Dutoit et al. (2011)), it seems important to have a first insight into the behavior of mycorrhizae. The objective of this study is therefore i) to measure the short-, mid- and long-term effects of a severe anthropogenic disturbance on three components of a Mediterranean steppe ecosystem: the plant community, soil chemical parameters and mycorrhizal infestation and ii) to identify the difference in recovery rates of these three ecosystem components (Alard et al., 1998).

2.2. Materials and methods

2.2.1. Study area

The La Crau area is the last xeric steppe of south-eastern France (ca. 10,000ha) and has been shaped by i) a dry Mediterranean climate, ii) a particular 40cm-deep soil composition with about 50% of silicaceous stones overlying an almost impermeable conglomerate layer, making the alluvial water table unavailable to the roots of plants and iii) itinerant sheep grazing over a period of several thousand years (Devaux et al., 1983; Buisson and Dutoit, 2006). This has led to a unique and species-rich association of plants composed mainly of annuals and dominated by *Brachypodium retusum* Pers. and *Thymus vulgaris* L.. The steppe, in which the only endogenous disturbance was sheep grazing, has lost more than 80% of its original 45,000 ha area due to exogenous anthropogenic disturbances (Buisson and Dutoit, 2006). Our study focuses on three of them, all were cultivation settled on the original steppe and are now abandoned: a vineyard abandoned approximately 150 years ago (AF-150), melon cultivation fields abandoned 35 years ago (AF-35) and an orchard abandoned in 2006 which had undergone its last disturbance comparable to plowing in 2009, two years before sampling (**Chapter four** and Jaunatre et al. (2012)) (AF-2) (Figure 2.1). The steppe was used as a control where no severe anthropogenic disturbance occurred according to available historical information (Cassini et al., 1778). Our study has a chronosequence approach. Despite the many advantages of diachronic studies, space for time substitution or synchronic studies allows the surveying of a longer time span and have already been proved to be relevant (Debussche et al., 1996; Foster and Tilman, 2000).

2.2.2. Sampling

As the former vineyard and the former orchard are unique, we focused on the two areas located around these two abandoned fields, which are relatively close together compared to the whole La Crau area (Figure 2.1). Therefore, two steppe sites (ST-6000) and two AF-35 sites were selected, one of each close to the AF-150 or close to the AF-2. In each of the six sites selected, three sampling areas were set (Figure 2.1C), where mycorrhizal infestation, vegetation, microbial community and soil were sampled (Figure 2.1D).

2.2.3. Soil analyses

In each sampling area, three 70g sub-samples of soil were gathered (Figure 2.1D) and pooled together to constitute one soil sample. They were sieved with a 2mm mesh sieve for analyses carried out by the INRA (Institut National de la Recherche Agronomique). Granulometry (percentage content of clay (<0.002 mm), fine silt (0.002-0.02 mm), coarse silt (0.02-0.05 mm), fine sand (0.05-0.2 mm) and coarse sand

(0.2-2 mm)), nutrient analysis (organic C, total N, P_2O_5 (Olsen et al., 1954), CaO, and K_2O) and water pH were measured according to the methods described in Baize (2000).

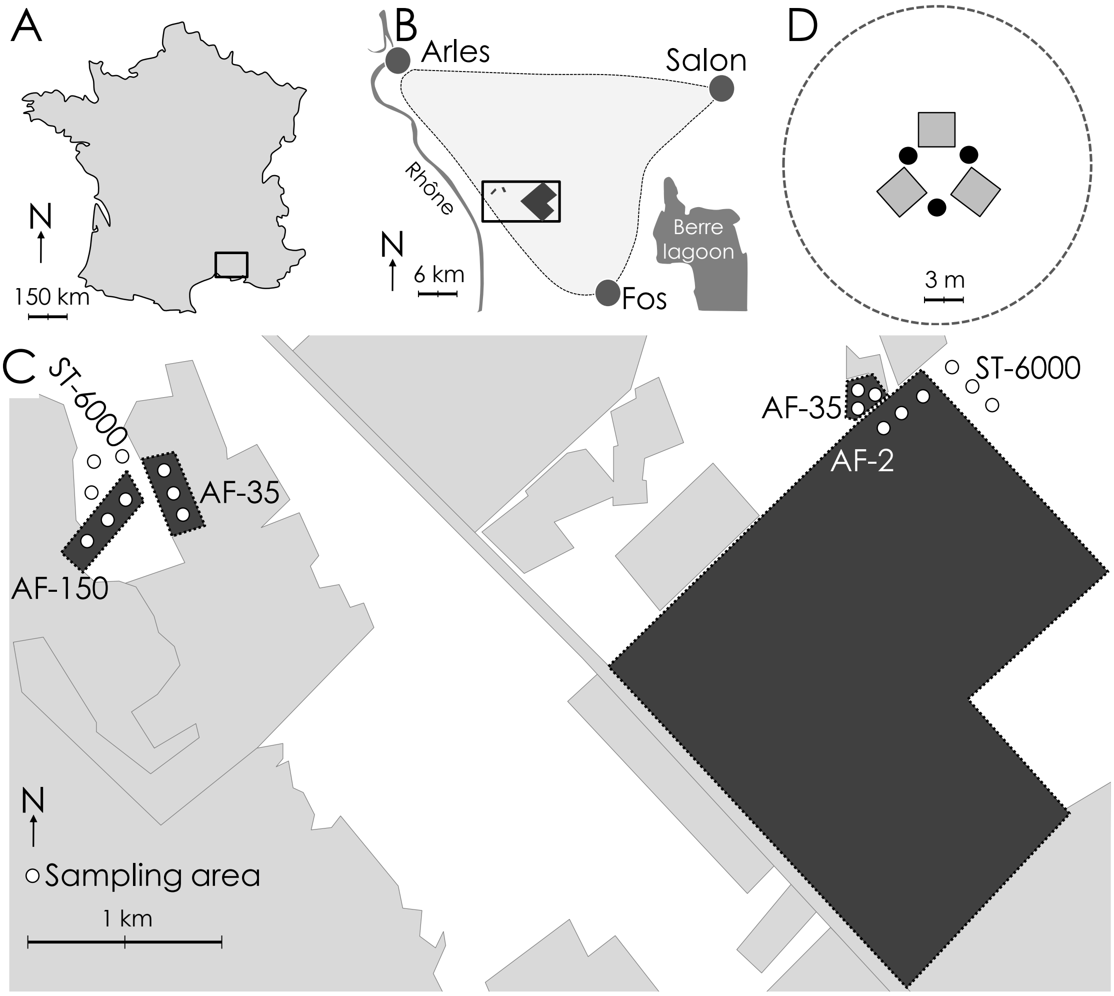


Figure 2.1: **Study site and sampling design**. A: location of the La Crau area in France. B: location of study area in the La Crau area. C: location of the sites: the two steppe sites (ST-6000), and in the fields abandoned 150 (AF-150), 35 (AF-35 ×2) and 2 (AF-2) years ago. White areas represent the steppe, dark grey areas represent sampled abandoned fields and light grey areas represent other land uses (forest, roads, former or present cultivations). D: Detail of sampling area, the large circle represents the 25 m diameter prospected area to find individuals of the four species for mycorrhizal infestation assessment, the grey squares represent the three 2x2m quadrats where plant species abundances were recorded and the black dots represent the three soil samples before they were pooled for soil physical and chemical analyses and microbial community analysis.

2.2.4. Vegetation survey

Vegetation relevés were made on three 2x2m quadrats for each sampling area and a Braun-Blanquet coefficient was assigned to each plant species recorded (Braun-Blanquet et al., 1952). Moreover, average height and vegetation cover were estimated in each quadrat.

2.2.5. Mycorrhizal infestation

Colonization was assessed on four species occurring almost all along the gradient decribed above: i) *Carthamus lanatus* L. which is an Asteraceae more abundant in the steppe, ii) *Carduus pycnocephalus* L. which is an Asteraceae more abundant in the abandoned fields, iii) *Brachypodium distachyon* (L.) P. Beauv. which is a Poaceae more abundant in the steppe and iv) *Bromus madritensis* L. which is a Poaceae more abundant in the abandoned fields. Roots were colored with the black Schaeffer ink and vinegar coloration method (Vierheilig et al., 1998). Total percentage of mycorrhizal infestation: internal hyphae, vesicles or arbuscules, were counted with the magnified intersections method (McGonigle et al., 1990).

2.2.6. Data analysis

In order to have a global overview on the soil parameters and on plant communities, multivariate analyses were performed: a Principal Component Analysis (PCA) for soil parameters and a Non-metric Multi Dimensional Scaling (NMDS) for plant community (Borcard et al., 2011). As data were conformed to parametric assumptions, analyses of variance (ANOVA) followed by Tukey Honest Significant Difference post-hoc tests were performed to compare values between the four field ages for soil nutrient contents, vegetation species-richness, Shannon index, Shannon evenness and mycorrhizal infestation. However parametric assumption were not reached for vegetation average height and percentage of cover, we therefore performed Kruskal-Wallis tests and pairwise Wilcoxon tests with a p-value adjustment according to Benjamini-Hochberg's method. All the analyses were conducted with R 2.13.0 (R Development Core Team, 2011), univariate analyses with its package "stats" and multivariate analyses with its packages "ade4" (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007) and "vegan" (Oksanen et al., 2008).

2.3. Results

2.3.1. Soil analyses

The ordination of samples by their soil characteristics (Figure 2.2) discriminates the four ages of the gradient. The first axis (35.2%) discriminates a gradient of age from the 2 year-old abandoned field (AF-2), to the 35 year-old abandoned field (AF-35) and to the 150 year-old abandoned field (AF-150) and the steppe (ST-6000), with significant decreasing concentration of P_2O_5, pH and K_2O (Figure 2.3). The second axis (24.5%) discriminates the steppe (ST-6000) and the oldest abandoned field (AF-150), with apparently more carbon and nitrogen, despite the fact that there is no significant difference when each soil variable is tested separately with post hoc tests for these two sites (Figure 2.3).

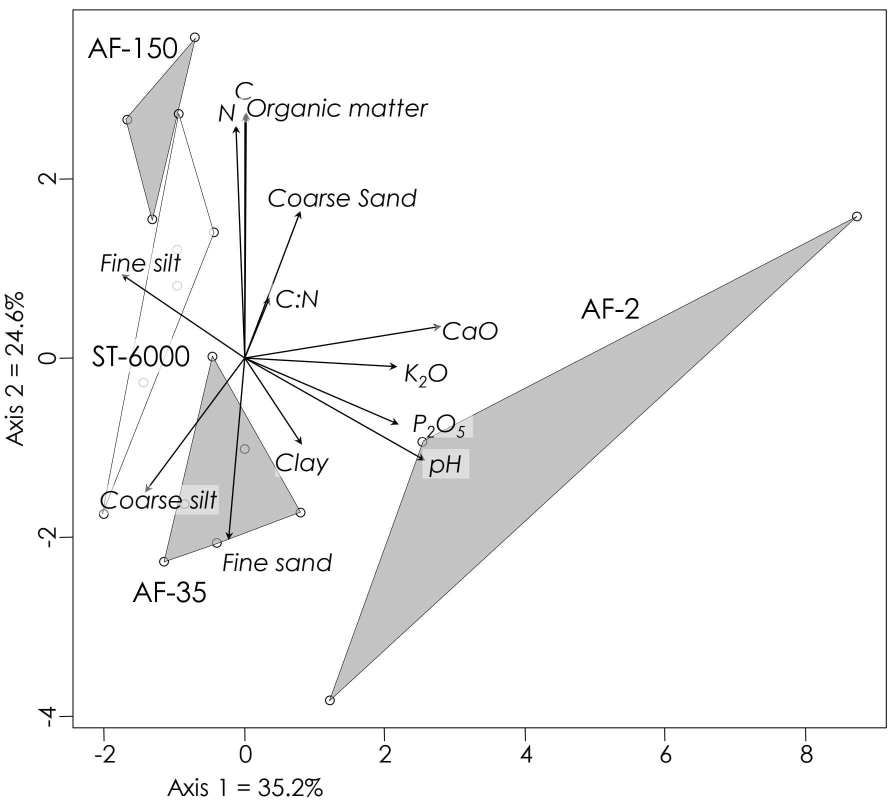


Figure 2.2: Ordination plot of the Principal Component Analysis based on soil granulometry and nutrient contents in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Arrows represent soil variables (Coarse sand, Fine sand, Coarse silt, Fine silt, Clay, Organic matter, C/N: Carbon:Nitrogen ratio; C: total carbon; N: total nitrogen; K_2O: potassium, P_2O_5: Olsen phosphorus (Olsen et al., 1954); CaO: Calcium oxide and pH). Polygons surround the points corresponding to one age class.

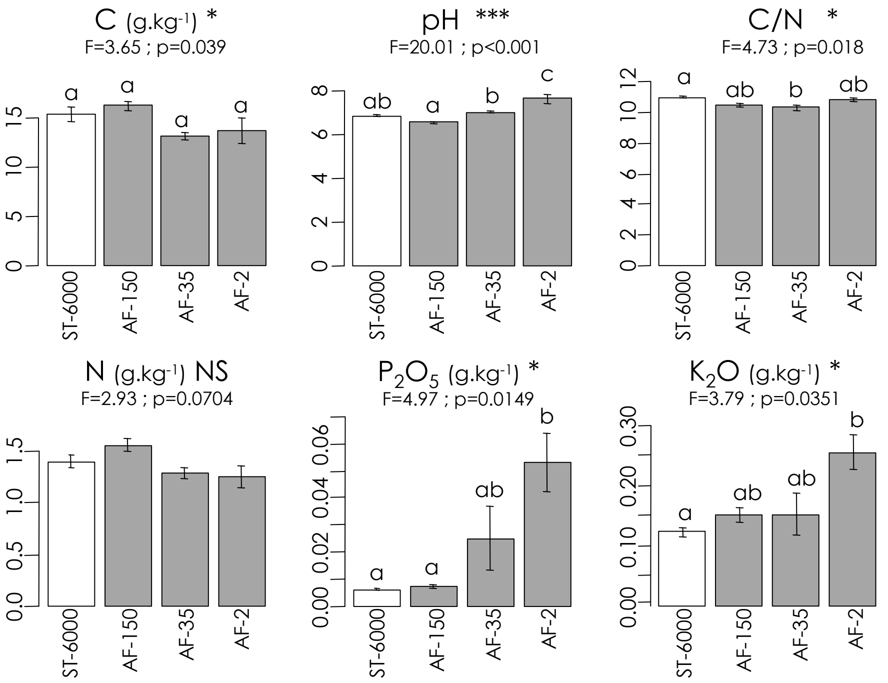


Figure 2.3: Soil nutrient contents in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Mean values±standard error of Carbon (C), Nitrogen (N), C/N ratio (C/N), Phosphorus (P_2O_5), and Potassium (K_2O) in steppe (ST-6000) and abandoned fields (AF-2/35/150). Bars having a common letter are not significantly different according to Tukey Honest Significant Difference post-hoc test (p>0.05).

2.3.2. Vegetation survey

For all the plant community measured variables, the youngest abandoned field (AF-2) is significantly different (Figure 2.4), with lower species-richness, Shannon index and Evenness and higher average height and vegetation cover. Average height and vegetation cover are not different within the three other communities. However, species-richness and Shannon index are significantly lower in the AF-35 compared to the ST-6000 or AF-150. Moreover, Evenness is significantly lower in AF-35 than in the ST-6000. The oldest abandoned field (AF-150) does not show significant differences with the ST-6000 for all the five plant community variables (Figure 2.4). The differences in plant community variables are also discernible in plant community compositions (Figure 2.5). AF-2 is dominated by *Bromus madritensis* L., *Bromus lanceolatus* Roth and *Carduus pycnocephalus* L.. AF-35 is also characterized by Poaceae and Asteraceae (*Bromus hordeaceus* L., *Bromus rubens* L., *Carthamus lanatus* L. etc.). AF-150 and ST-6000 are very close, sharing many species (e.g. *Aegilops ovata* L., *Brachypodium distachyon* (L.) P. Beauv., *Carlina corymbosa* L., *Erodium cicutarium* (L.) L'Hérit. or

Plantago bellardii All.), even if some ST-6000 species are absent from AF-150 (e.g. *Brachypodium retusum* (Pers.) P. Beauv.).

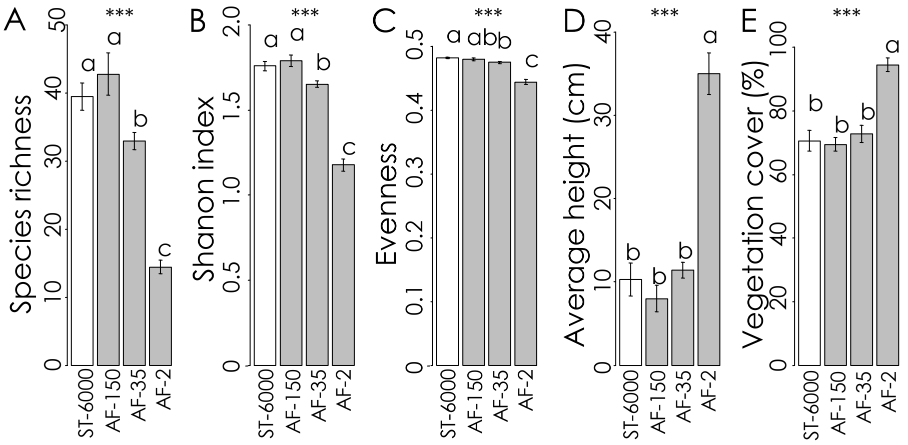


Figure 2.4: Mean values of species-richness (A), Shannon index (B), Shannon evenness (C), average height (D) and percentage of vegetation cover (E) in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Error bars represent standard error, bars sharing a common letter are not significantly different (Tukey HSD multiple comparison tests, except for the average height and percentage of vegetation cover of which data do not fulfill parametric assumption: pairwise Wilcoxon tests with a p-value adjustment according to Benjamini-Hochberg's method; p>0.05).

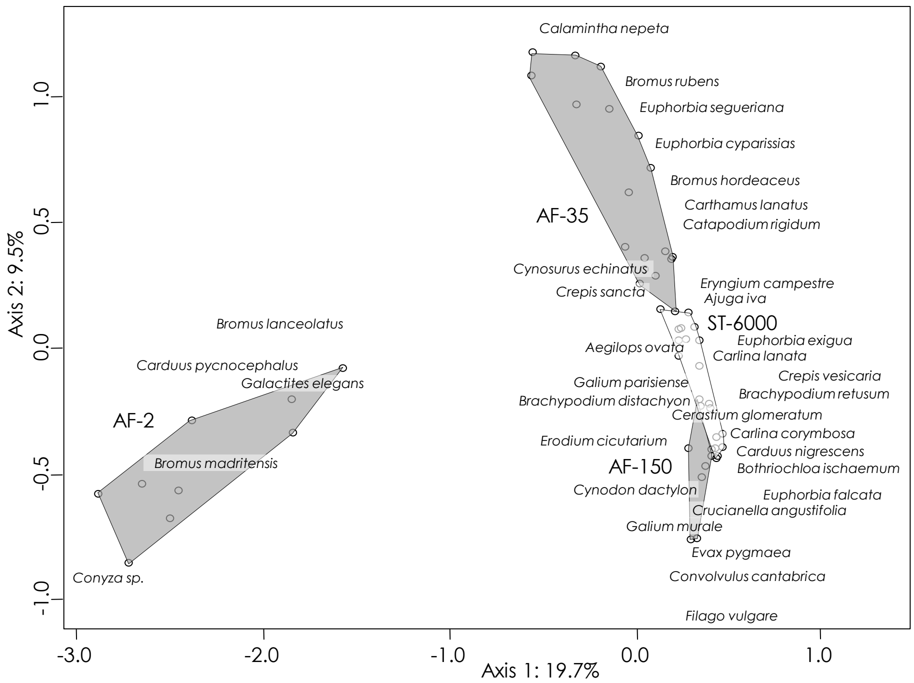


Figure 2.5: Ordination plot of the Correspondence analysis based on vegetation abundances on steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Based on 54 relevés and 110 species of which the 35 most correlated with the axes are shown. Polygons surround the points corresponding to one age class.

2.2.3. Mycorrhizal infestation

Mycorrhizal infestation is significantly lower when abandonment is recent for three species (*Brachypodium distachyon*: df=2, F=4.16, p=0.025; *Bromus madritensis*: df=3, F=5.81, p=0.002 and *Carduus pycnocephalus*: df=2, X2=7.38, p=0.025; Figure 2.6) but not for *Carthamus lanatus* (df=2, F=2.39, p=0.11). For *C. pycnocephalus* and *B. madritensis,* there is only a significant difference between AF-2 and ST-6000. *B. distachyon* shows a significant difference in mycorrhizal infestation between AF-35 and ST-6000. However, mycorrhizal infestation is not significantly different between ST-6000 and AF-150 for any of the measured species (Figure 2.6).

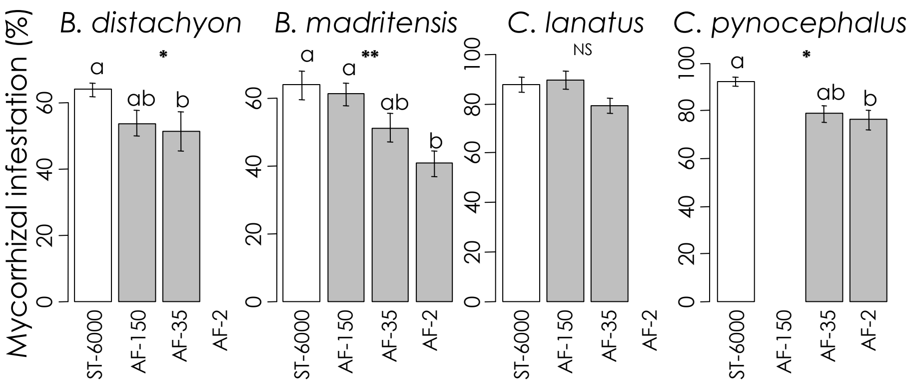


Figure 2.6: Mean values of species-richness (A), Shanon index (B), evenness (C), average height (D) and percentage of vegetation cover (E) in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Error bars represent standard error, bars sharing a common letter are not significantly different (Tukey HSD multiple comparison test, p>0.05). Missing bars occur when the species could not be found in any plot of the abandoned field.

2.4. Discussion

Our results show that soil characteristics are discriminated over time on the cultivation abandonment gradient, with lower pH and content of potassium and phosphorus in the older fields. These results are consistent with results found in other studies where potassium and phosphorus contents were negatively correlated with time since last cultivation (Wong et al., 2010) or where high soil phosphorus content was able to maintain even 25 years after cessation of fertilization (Smits et al., 2008; Henkin et al., 2010). Soil characteristics are known to be very important in determining the plant community (Janssens et al., 1998; Kulmatiski et al., 2006). Despite the fact that in our abandoned fields soil phosphorus content remains below the level of 0.05g.kg^{-1}, suggested to be the threshold value for limiting establishment of species-rich plant community (Janssens et al., 1998), it can have effect on the long-term, even after the recovery of lower values (Semelová et al., 2008).

Like those for soil, plant community characteristics follow the gradient of time since cultivation abandonment. The more recently abandoned fields have lower species-richness, Shannon indices and Shannon evenness and they have higher average height and vegetation cover. Moreover, the vegetation composition, which is mainly dominated by grasses such as *Bromus* spp. in the most recently abandoned fields, gains in diversity and in forbs as time since last cultivation increases. Such slow recolonization was observed in other ecosystems after severe disturbances (Tomanek et al., 1955; Coffin et al., 1996; Meiners et al., 2002; Bonet and Pausas, 2004). However, after 150 years, the vegetation composition of the abandoned field is close to the steppe but still slightly different, especially because of the steppe dominant species which is missing (i.e. *B. retusum*).

These results are in accordance with previous studies, such as that of Öster et al. (2009) which found that half of the species were able to colonize abandoned fields after 50 years, or that of Dupouey et al. (2002) which found differences in plant communities still significant more than 2000 years after a cultivation event in a present forested plant community.

Mycorrhizal infestations follow similar patterns to those of soil and plant community characteristics: the mycorrhizal infestation rate increases with time since cultivation abandonment for three species and has no significant relationship for the fourth. These results are in accordance with studies that have shown that soil disturbance can decrease mycorrhizal infestation (Jasper et al., 1989). Agricultural practices are indeed known to have impacts on mycorrhizal communities (Douds et al., 1995; Jansa et al., 2003) or mycorrhizal reproduction dynamics (Oehl et al., 2009), and that areas cultivated with more input show less mycorrhizal infestation (Douds et al., 1995; Mäder et al., 2000). Time since the last disturbance is determinant on mycorrhizal communities (Fitzsimons et al., 2008) or infestation (Eriksson, 2001), which is concomitant to our results which show that mycorrhizal infestation recovers and is not significantly different from the steppe after 35 years, except for *B. distachyon*. It seems interesting to stress that the species which shows the lowest resilience of mycorrhizal infestation rate (*B. distachyon*), is also the phylogenetically closest species from *B. retusum*. *B. retusum* is not present at any location of this old abandoned field despite the fact that it is the dominant species of the steppe and that it is present at the abandoned field boundaries, and despite the fact that all measured environmental parameters are not significantly different. Low seed production and fertility, and hence poor dispersion abilities have already been hypothesized (Buisson et al., 2006; Coiffait-Gombault et al., 2012a). According to the slow recovery of mycorrhizal infestation rates of a phylogenetically close species, it can be hypothesized that concomitant to a low seed production, *B. retusum* suffers from a lack of mycorrhizal interaction to establish in abandoned fields.

From the results given by this study, it seems that mycorrhizal infestation resilience is faster than vegetation resilience. The vegetation dynamics can be explained by a filter model (Keddy, 1992; Zobel, 1997; Fattorinni and Halle, 2004; Lortie et al., 2004; Guisan and Rahbek, 2011): i) plant species have to be able to disperse, which depends on species dispersion abilities and proximity of source site (Gibson and Brown, 1991; Pärtel and Zobel, 1999; Lindborg and Eriksson, 2004; Herault and Thoen, 2009); ii) plant species have to be able to withstand environmental conditions, which depends both on historical environmental conditions and on disturbance legacies (Foster et al., 2003) and iii) the first two filters will be modified by biotic interactions and will depends on the presence of facilitators or competitors in the community (Bruno et al., 2003). This model allows explaining the low resilience of plant after cultivation in the La Crau area: species have low dispersal abilities and no permanent seed bank (Graham and Hutchings, 1988b; Römermann, Dutoit, et al., 2005), we have shown in this study that soil nutrient content are still different, even on the long term for phosphorus, and finally some species are more able to compete with these higher nutrient contents (Öster et al., 2009; Baeten et al., 2009), especially if they had benefited from priority effect due to chance or better abilities to disperse (Fukami et al., 2005).

Concerning the mycorrhizae, it seems conceivable to apply a similar model to explain their recovery after a severe anthropogenic disturbance, as it has been suggested by Lekberg et al. (2007). If mycorrhizae have been suppressed during the cultivation event (but we do not have any data on mycorrhizal infestation of plants during cultivation in the La Crau), they have to disperse to the disturbed area, which can be relatively fast (Allen, 1989) due mainly to wind dispersion of very light propagules (spores) compared to plant (seeds) (Warner et al., 1987). Non-killed hyphae can also be an important source of mycorrhizae but is highly affected by soil disturbance (Jasper et al., 1989; Brundrett and Abbott, 1994). Mycorrhizal infestation then depends on environmental conditions: the more the nutrients are available, the less mycorrhizal infestation there is (Koide, 1991). Finally, mycorrhizal infestation depends on biotic interaction. Despite the fact mechanical soil disturbance plays a greater role than plant communities in the determination of myccorhizal communities (Schnoor et al., 2011), it has been shown that plant species-richness can increase the diversity and fitness of mycorrhizae (Burrows and Pfleger, 2002). Moreover, diversity of mycorrhizae that infect an individual depends on the diversity of the whole plant community (van de Voorde et al., 2010), and the composition of the plant community has a significant effect on the composition of the mycorrhizal community (Johnson, 1993; Eom et al., 2000).

The results given by this study are a first step to exploring the relationship between environmental conditions, plant communities and mycorrhizae. They have shown that with time, these three indicators are getting closer to the undisturbed state, and that at a human lifespan scale, a complete unassisted resilience is not possible. After 35 years, some of the proxy we used, such as species-richness, plant community composition and species-richness, soil phosphorus content and mycorrhizal infestation did not reach their previous disturbance characteristics. After 150 years, all the proxies were similar to the reference, except plant community composition which still appears to be different. Moreover, trying to link the different components and to find how dynamics of resilience of one component could affect the restoration of others would allow finding the 'limiting components' which could affect, slow down or stop the restoration dynamics of the whole ecosystem. The way mycorrhizal communities affect plant communities are complex: as for plants, not all mycorrhizal species have the same role in ecosystems (Hart et al., 2003). The effects of mycorrhizae on plants are species-specific (Hoeksema et al., 2010), but also depend on environmental conditions (Grime et al., 1987; Hartnett and Wilson, 1999; Kytöviita et al., 2003). This is a call to carry further research on how other ecosystem elements can affect plant community recovery, and to study how they could be used to accelerate this recovery in a restoration context (Allen, 1989; Herrera et al., 1993; Callaway et al., 2001; Kardol et al., 2009).

Transition to Chapter 3

In **Chapter 1** and **Chapter 2**, we have shown that even after a period exceeding human life-span, spontaneous succession is unlikely to lead to the steppe ecosystem. Active restoration is therefore needed to try to recover areas of such non-resilient ecosystems (Cramer et al., 2008; Prach and Hobbs, 2008; Hölzel et al., 2012). The Strategic Plan for Biodiversity 2011-2020 sets as an objective the restoration of 15% of degraded ecosystems by 2020 (Convention on Biological Diversity, 2011). This challenge raises at least two major questions: i) how to restore and ii) how to measure restoration success? These questions are tackled in **Chapter 3** and **Chapter 4** within the framework of the Cossure project: the first habitat bank in France.

T3.1. French nature protection legislation framework and habitat bank

Since 1976, the French nature protection law (*loi relative à la protection de la nature n°76-629*) has defined the "Avoid – Reduce – Compensate" triptych. The Avoid step means that all impact on natural habitat due to anthropogenic actions must be avoided. However, if a project is of major general interest, it may be allowed. The project therefore has to be designed in such a way that environmental impact is minimized as far as is practicable: this is the Reducing step (Figure T3.1). For unavoidable impact, compensatory mitigation is required to replace the loss in order to lead to no net loss of biodiversity, i.e. the compensation actions are intended to create an amount of biodiversity equivalent to the loss induced by unavoidable residual impact (ten Kate et al., 2004). Compensation can consist in: undertaking positive management interventions either to restore an area or to improve environmental management of a protected area: protecting new areas of biodiversity, funding ecological research, or since 2008, buying habitat mitigation bank units.

Habitat banking (or mitigation banking) is *ex-ante* (i.e. before impact) and *ex-situ* (i.e. not just next to the impacted ecosystem) compensation. An accredited establishment creates or recreates habitat by restoration or management and sells the biodiversity gain (biodiversity units) to planners who have to compensate for their future habitat destruction. The first habitat banking is currently being experimented in France by CDC Biodiversité with the Cossure project (Chabran, 2011; Chabran and Napoléone, 2012).

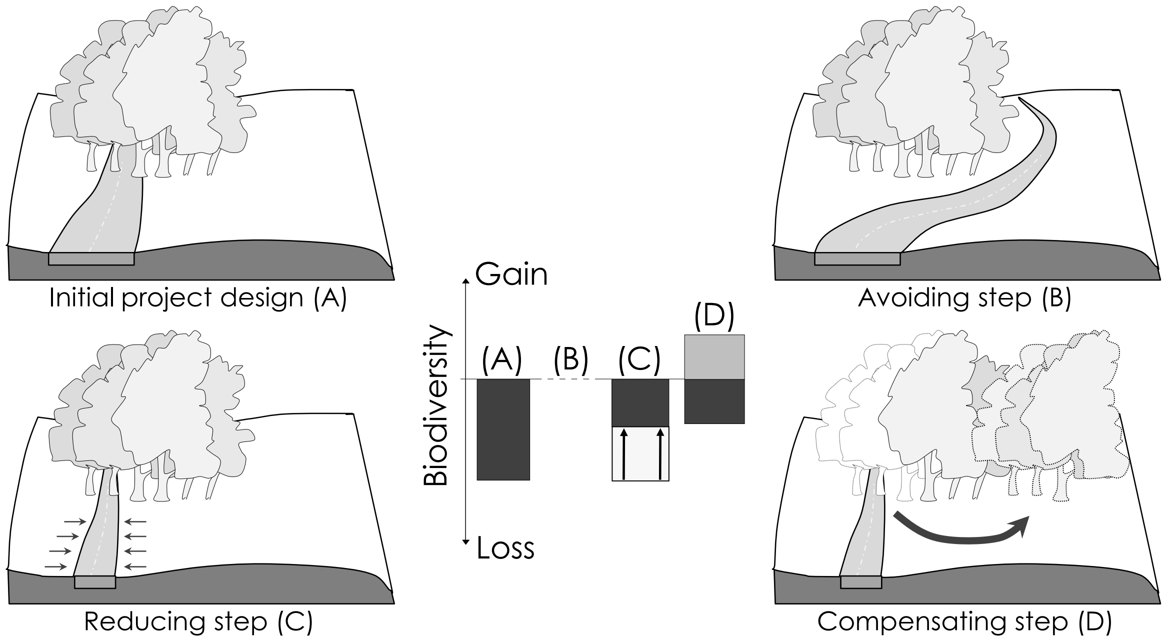


Figure T3.1: Diagram representing the Avoid-Reduce-Compensate triptych and its impact on the biodiversity of a small forest grove (adapted from a drawing of Champres, DIREN de La Réunion, (2008) and Rio Tinto, (1992)). Biodiversity is impacted by the initial project design (A), impacts are null if the new design avoids the defined biodiversity (Avoid step: B), the Reduce step (C) allows to minimize the impact and the Compensate step (D) allows to recreate the amount of biodiversity lost by the residual impact.

T3.2. The Cossure project

The French government launched its first experiment with habitat banking in the La Crau area in 2008. The choice of the La Crau area for experimenting habitat banking in France was not arbitrary. The only French Mediterranean steppe constitutes a unique plant community, a habitat for the only French breeding population and / or the largest French populations of some steppe birds, the largest population of a protected reptile species and a habitat for endemic arthropods one of which is considered as 'critically endangered' (*Prionotropis hystrix rhodanica* (hedgehog grasshopper) (IUCN, 2010)). From the 45,000ha of ecosystem created by the Durance river former delta, only 11,500ha remained in the early 2000's, mainly due to urban planning and cultivation (Deverre, 1996; Gaignard, 2003) (Figure T3.2). The constant reduction of the steppe area was slowed down with the creation of the National Reserve (Buisson and Dutoit, 2006) and conservation was taken to a new level in 2008 with the implementation of the French first habitat bank in Cossure.

Cossure is a former orchard, cultivated from 1987 and abandoned in 2006, and was bought in 2008 by a state-owned sovereign fund, CDC Biodiversité. The main aim is thus to rehabilitate a herbaceous area in order i) to recreate a breeding and wintering habitat for endangered steppe birds, ii) to reconnect fragmented patches of the national reserve and iii) to reinstall traditional sheep grazing. This rehabilitated area would then be used as a 'biodiversity unit'.

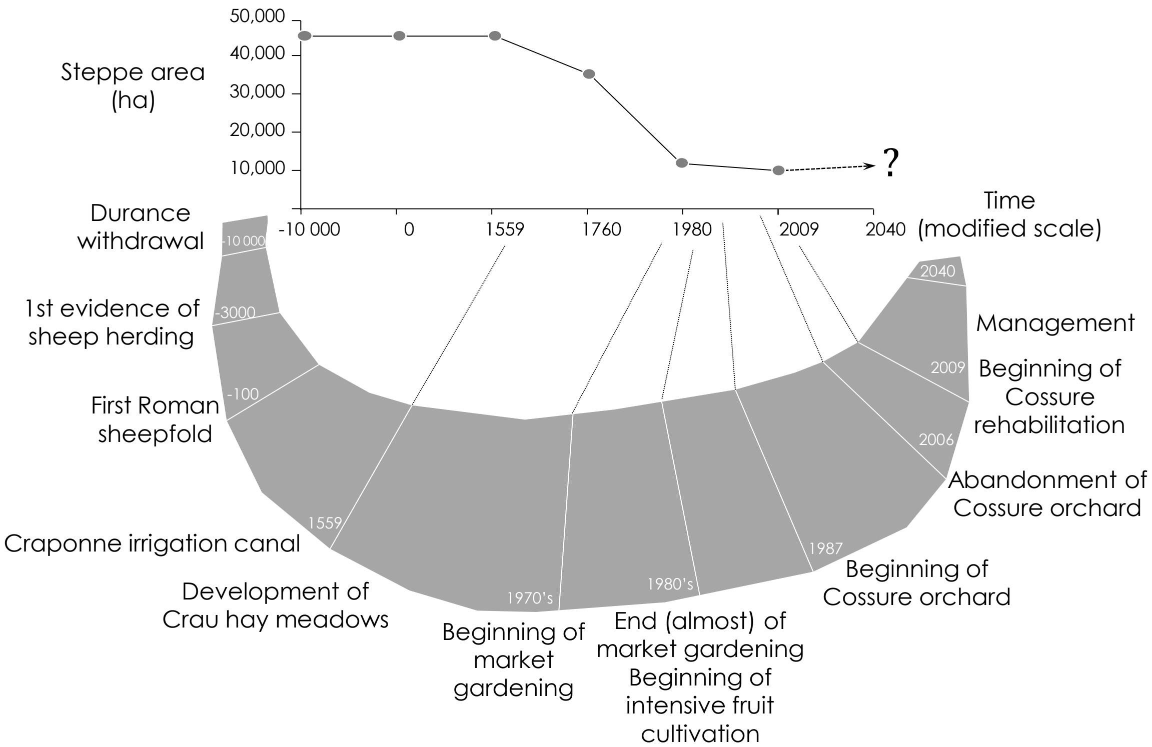


Figure T3.2: History of steppe area gains and losses. The above plot shows the steppe areas relative to time (data from Wolff et al. (2009)), the dashed line represents an estimation of the ultimate aim of the research carried out within the Cossure project. The plot below is a timeline of the main events which have led to losses and gains in steppe areas. Scales have been altered; the scale of the timeline is for graphic purposes only.

T3.3. Design a project involving numerous stakeholders

Although the whole project was financially supported by CDC Biodiversité funds, decisions, from the project framework to its implementation, were taken collectively. Many different stakeholders are involved in the project. The stakeholders come into three categories:

i) environmental managers, NGO: National Reserve managers (CEN-PACA(*Conservatoire d'Espaces Naturels de Provence Alpes Côtes d'Azur*) and

Chambre d'Agriculture des Bouches-du-Rhône), the *Direction Régionale de l'Environnement, de l'Aménagement et du Logement* (regional agency for the environment, development and housing), a reporter from the *Conseil Scientifique Régional du Patrimoine Naturel* (regional scientific council for natural patrimony), the *Direction Départementale de l'Agriculture et de la Forêt* (regional agency for agriculture and forests) and the *Société d'Aménagement Foncier et d'Etablissement Rural* (country planning agency).

ii) project manager (CDC Biodiversité),

iii) scientists with various roles (researchers who will undertake experiments, advisory experts and members of scientific committees who monitor the project outline: National Reserve and CDC Biodiversité).

All the stakeholders were as far as possible included in the discussions to ensure an ongoing dialogue. This time consuming process of involvement made it possible to tailor the project to stakeholders' expectations on a day-to-day basis (Jaunatre et al., 2011).

The different stakeholders did not share the same expectations. Scientists prefer the application of a range of techniques, repeated many times and spatially randomized equally over the whole area, in order to produce data valid for publication. For environmental managers, such as those from the neighbouring Nature Reserve, techniques have to fit to the aims of their management plan and have to be compatible with traditional land-uses. Project manager looks for the lowest price with the best potential results covering the largest area. The whole project in its final form is a trade-off, determined during the numerous meetings the main purpose of which was to prioritize everyone's objectives, but also to bring certain opportunities to the foreground (Figure T3.3). Two examples of dialogues which have led to trade-offs or opportunities are the control areas and the topsoil removal techniques.

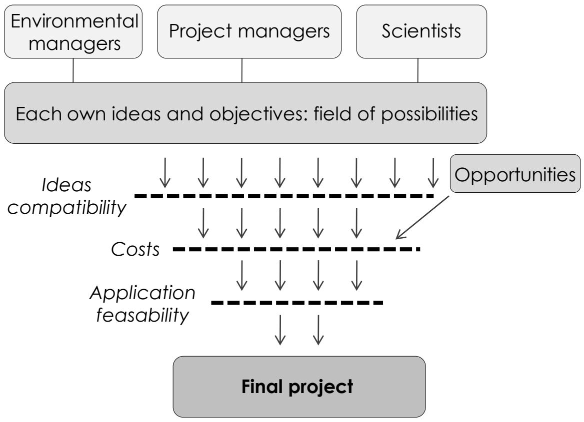


Figure T3.3: Conceptual diagram of the project design. Arrows represent ideas and concepts which are filtered by the constraints represented by dashed-lines (reproduced from Jaunatre et al. (2011)).

T3.4. A trade-off found in the definition of control areas

Scientists emphasized the importance of real control areas with dead fruit trees to identify potential perch effects on plant succession (Pausas et al., 2006). An area such as this was incompatible, firstly with the objective of steppe birds come back and secondly with health and safety rules on fruit tree disease (Plum pox *virus*). The trade-off found was to keep a small area without soil leveling but where trees were removed in order to create a pseudo-control plot.

T3.5. Opportunity to implement an additional experiment: topsoil removal

One of the weekly meetings pointed out the need for soil material to build a mound to prevent sheep from falling into a gravel pit. Without this constant dialogue, the material would have probably been brought from a quarry. Instead, the meeting allowed the scientists to take the opportunity presented by this requirement to apply a new treatment: topsoil removal. This treatment had not been proposed before because of its cost and the problem of storage of the removed soil (Klimkowska, Dzierża, et al., 2010). In the end, topsoil removal was applied on 0.1ha and made it possible to build the required mound at virtually no cost. With an appropriate dialogue organization and decision chain, all the stakeholders were able to express their point of view, thus allowing decisions to be taken very rapidly bearing in mind all the priorities in a way that proved enriching for the final project (Figure T3.3).

T3.6. Decisions relative to the rehabilitation work

Immediately after the former orchard was bought, analyses of fauna, flora and soil were carried out in order to check that trying to restore the area would be better than letting it recover spontaneously. Soil presented higher nutrient content, plant and faunal communities had low species-richness and were composed mainly of common species (Dutoit, Jaunatre, et al., 2009). This initial state inventory provided several items of information relevant to further decisions about rehabilitation works.

The first, and certainly the most important point, was that almost no protected species or habitat was found within the abandoned orchard but only common species and low conservation value habitats (Dutoit, Jaunatre, et al., 2009), which in a sense validated the choice of trying to restore this area.

The only protected species found in Cossure was *Phyllitis scolopendrium* (L.) Newman, protected at regional level, in 11 of the 26 wells formerly used for irrigation. These wells were used for tree irrigation and exhibit relatively species-rich fern communities (3.61±0.31 fern species by well with a maximum of 6 fern species). The wells, which it had been intended to close for safety reasons, were therefore preserved.

Mounds of approximately 50cm were built to provide more soil for fruit tree roots during orchard establishment. Vegetation and soil characteristics were found not to differ at the top of the mounds or in between two mounds (Dutoit, Jaunatre, et al., 2009). Therefore for the restoration of vegetation, leveling the mounds was not needed. However, it was pointed out during the meetings that the holes created by pulling up trees could be dangerous for sheep, and that steppe birds need a totally flat area to recolonize: it was therefore decided to level the mounds.

The initial state inventory revealed that orchard's edges had a higher species-richness than the abandoned orchard, and community composition and soil characteristics were closer to those of the steppe. It was thus decided, in order to minimize the impact of rehabilitation works, to leave these edges allowing spontaneous succession to occur where the conditions appeared to be the best (fewer plowing events, less fertilizers and herbicides).

T3.7. Rehabilitation work and restoration experiments

The rehabilitation works consisted in cutting down, crushing and exporting fruit trees (200,000) and windbreak poplars (100,000) in 2009. Soils were then leveled and sheep grazing was finally reintroduced in spring 2010 (Dutoit, 2010). Thus, a potentially large area was rehabilitated and remnant patches of suitable habitat for steppe birds could be reconnected. Additional ecological restoration experiments were carried out in order to restore the original pseudo-steppe vegetation and its associated entomofauna (Orthoptera, Coleoptera). The short-term objectives of these experiments are to limit the colonization of unwanted plant species and to improve the establishment of target species just after the end of the rehabilitation phase. Long-term objectives are to restore pseudo-steppe plant community richness, composition and structure. Four restoration techniques were implemented on the rehabilitated area and are discussed in **Chapter 4**. In all the treatments, soil, faunal and plant communities were monitored in order to provide information for management purposes (mainly sheep grazing pressure) and insights on restoration success. Thoughts on how to define restoration success and how to measure it have led to the definition of new indices to measure restoration success, presented in **Chapter 3**.

The **Chapter 3** objective is to develop and discuss new indices allowing measuring the resilience or restoration of community structure: either focusing on the proportion of the species abundance in the reference community represented in the restored community or focusing on the proportion of the species abundance in the restored community which is higher than in the reference community (Figure T3.4).

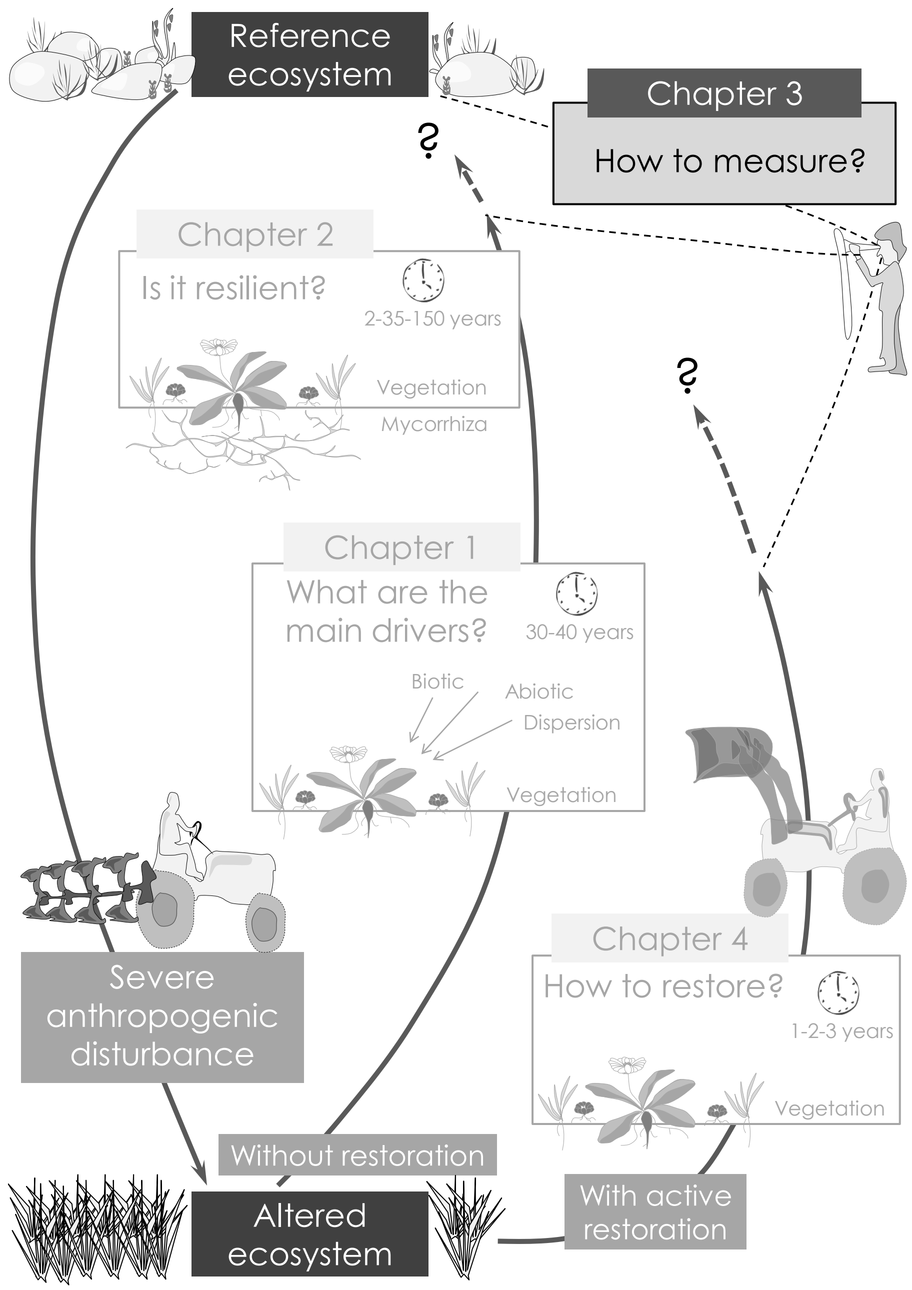


Figure T3.4: Location of Chapter 3 in the general thesis organization.

The La Crau steppe plant community (*Bellis sylvestris* autumnal flowering).
Photo credit: R. Jaunatre

The La Crau steppe plant community (*Salvia verbenaca, Evax pygmaea, Bromus hordeaceus, Trifolium subterraneum, Logfia gallica, Bellis sylvestris, Eryngium campestre, Asphodelus ayardii, Brachypodium retusum*, etc.). Photo credit: R. Jaunatre

CHAPTER 3 - New synthetic indicators to assess community resilience and restoration success

Renaud Jaunatre, Elise Buisson, Isabelle Muller, Hélène Morlon,

François Mesléard, Thierry Dutoit

(accepted with major revision in Ecological Indicators the 27th August 2012)

3.1. Introduction

The Strategic Plan for Biodiversity 2011-2020 sets as an objective the restoration of 15% of degraded ecosystems by 2020 (Convention on Biological Diversity, 2011), and this challenge raises at least two major questions: i) How to restore and ii) how to measure restoration success of said ecosystems? The first question has been addressed and is still being addressed in a multitude of ecological systems and geographical areas (see for example Perrow and Davy (2002)) and for various restoration aims. Restoration targets are diverse: from rehabilitation, which is the restoration of one or some target ecosystem functions, to the restoration *sensu stricto,* which is the restoration of the whole ecosystem, i.e. its richness, composition, structure and functions (Society for Ecological Restoration International Science and Working Policy Group, 2004). Restoration is advocated for stopping the global erosion of biodiversity (Millennium Ecosystem Assessment, 2005; Nellemann et al., 2010), and is imposed by law in many countries for ecosystem destruction or degradation offsets (ten Kate et al., 2004). However, a recent meta-analysis conducted over 89 ecological restoration projects concluded that although restored ecosystems provide more biodiversity and ecosystem services than degraded ecosystems, these parameters still do not reach those of reference ecosystems (Benayas et al., 2009).

A community is defined as "an assemblage of populations of living organisms in a prescribed area or habitat" (Krebs, 1972). A multitude of indicators can be used to characterize a community (e.g. patchiness, nutrient cycling rate, interaction intensities, etc. (Noss, 1990)). To assess restoration success, most measures of biodiversity are related to abundance, species richness, diversity, growth, or biomass of organisms (Ruiz-Jaen and Mitchell Aide, 2005). As strengthened by the analysis of 80 recent (2007-2011) papers comparing restored and reference communities, species richness and abundances are the most commonly used indicators of restoration (Appendix 3). Species-richness is one of the simplest ways to describe a community (Magurran, 2004), however, many authors admit that species-richness, as well as diversity index (Shannon, Pielou, etc.), cannot be used alone (Noss, 1990). Indeed, completely different communities can be characterized by the same species-richness and diversity values. Our review analysis also pointed out an absence of consensus on indicators of community structure integrity: various multivariate analyses and various similarity-dissimilarity indices are widely used (52.5%

and 20% of the studies respectively) (Appendix 3). Nevertheless, all these indicators can have some drawbacks. Multivariate analyses are designed to maximize the variance while reducing the number of dimensions and provide a good overview of plant community composition and help to distinguish different plant communities (McGarigal et al., 2000; Borcard et al., 2011). While some methods allow us to significantly distinguish groups (McArdle and Anderson, 2001; Borcard et al., 2011), it is difficult to assess the magnitude of these differences between groups and impossible to compare, for example, the same restoration technique in two different ecosystems. Moreover, these types of analyses are not commonly used by practitioners because it is difficult to communicate their results to the general public. One-dimension measure, even if it summarizes more (and consequently reduces the amount of) information, is easier to interpret and can solve the problem of assessing magnitude differences. Examples of one-dimension community comparison measure are the widely used similarity-dissimilarity indices (such as Sorensen or Bray-Curtis) but these indices can be difficult to interpret: the dissimilarities can be attributed either to lower abundances of target species (i.e. species present in the reference community), or to higher abundances of target or non-target species compared with the reference community. These two explanations, which can occur concurrently, do not have the same implications in terms of community dynamics and hence of further management (Luken, 1990).

The objective of this work is therefore to develop an assessment method of community structure integrity after restoration (i.e. to measure restoration success) or after disturbance (i.e. to measure resilience) that measures the two types of community dissimilarities: lower and higher abundances in the restored or degraded community compared to reference communities. We have developed two indices giving additional insights on community states: the first index measures the proportion of the species abundance in the reference community represented in the restored or degraded community, and the second index measures the proportion of the species abundance in the restored or degraded community which is higher than in the reference community. We illustrate the use of these indices with fictitious communities, with an application to resilience and with an application to restoration in order to discuss the contribution of the new indices compared with existing ones, their perspective of utilization and limits.

3.2. Materials and methods

3.2.1. Indices description

The goal of our indices is to measure resilience or restoration success in a given community (the assessed community, AC), by comparison with a series of communities used as a reference (RC). Using a series of reference communities is crucial, as we expect undisturbed areas to present possible large variations in composition. Each community is characterized by a list of species each associated with a number (n) which reflects their abundance on a given area at a given date: size, biomass, abundance coefficient, percentage of cover, etc. The assessed community may be composed of target species (Clewell and Aronson, 2007), i.e. species present in the reference community, but also of non-target species. The idea behind our indices is to distinguish the species lower in abundance in the assessed community than in the reference communities, from the species higher in abundance in the assessed community than in the reference communities.

For a given species i, we note $\Delta_{i,j} = |n_{i,AC} - n_{i,j}|$ the absolute difference between the abundance in the assessed community and the abundance in reference community j. We indicate with a subscript whether the abundance in the assessed community is lower ($\Delta^{-}_{i,j}$) or higher ($\Delta^{+}_{i,j}$) than in the reference community.

We define 3 indices:

1) The Community Structure Integrity Index (CSII) measures the average proportion of species' abundance in the reference communities represented in the assessed community, and is defined as:

$$\mathrm{CSII} = \overline{\left(\frac{\sum_{i=1...S} \left(n_i - \Delta^{-}_{i,j} \right)}{\sum_{i=1...S} n_{i,j}} \right)}^{j=1..K}$$

with S the total number of species over all communities and K the total number of reference communities. The overbar stands for the arithmetic mean over all reference communities. The CSII index thus focuses on the "deficit" of abundance in the assessed community. It takes values between 0 and 1, and equals 1 when all species in the assessed communities are at least as abundant as in the reference communities.

2) The normalized Community Structure Integrity Index ($CSII_{norm}$) is a normalized version of CSII. Indicators which represent measurable portions of a reference are the easiest to interpret and therefore the most convincing (Duelli and Obrist, 2003; Balmford et al., 2005). We calculate a normalized value of CSII as: $CSII_{norm} = \frac{CSII}{CSII_{RC}}$

with $CSII_{RC}$ the arithmetic mean of CSII calculated over all reference communities. Hence, reference communities have an average $CSII_{norm}$ value of 1; this allows a meaningful comparison of $CSII_{norm}$ values across ecosystems with different heterogeneity of reference communities.

3) The Higher Abundance Index (HAI) measures the average proportion of species' abundance in the assessed community higher than the reference communities, and is defined as:

$$\mathrm{HAI} = \overline{\left(\frac{\sum_{i=1...S} \Delta^{+}_{i,j}}{\sum_{i=1...S} n_{i,AC}} \right)}^{j=1...K}$$

where the overbar stands for the arithmetic mean over all reference communities. HAI considers both target species having a higher abundance in the assessed community than in the reference community and non-target species. No normalized version of HAI was developed as it is already a relative value to the whole assessed community structure.

We calculated the 3 indices and compared them to standard indicators in three case studies: one with fictitious communities, one in which resilience is assessed after disturbance, and one in which restoration is assessed.

3.2.2. Fictitious case study

New methods need to be tested rigorously before being applied to real data. We created fictitious communities which allowed us to confirm that the new indices show differences when they occur and do not show differences when they do not occur. We defined 10 types of fictitious communities: one reference, and nine assessed community types where the increase in target species abundances (T0, T0.5 and T1 having respectively 0×, 0.5× and 1× the abundance of target species in the reference) and the increase in non-target abundances (N0, N0.5 and N1 having respectively 0×, 0.5× and 1× the abundance of non-target species) were crossed, resulting in the following community types: T0N0, T0N0.5, T0N1, T0.5N0,T0.5N0.5, T0.5N1, T1N0, T1N0.5 and T1N1 (Figure 3.1). As it is important that fictitious communities are the closest to what they are supposed to simulate (Zurell et al., 2010), we simulated 10 samples for each community type (representing the samples which could be surveyed in a community assessment), within which species abundances were characterized by means and variances similar to those found in an example of real plant communities assessed in a restoration context (**Chapter 4** and Jaunatre et al. (2012)).

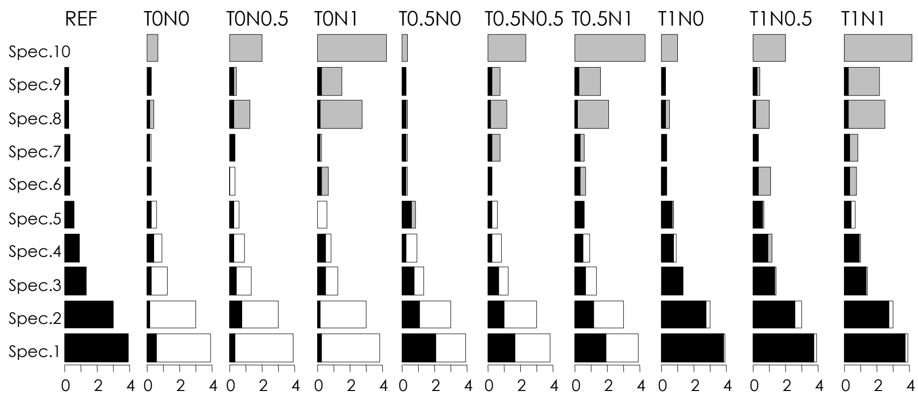


Figure 3.1: Structure of the eight fictitious communities. White areas are missing abundances, black areas are abundances up to reference community abundances and grey areas are abundances higher than the reference community abundances. REF is the reference community, and the nine others are assessed community types where the increase in target species abundances (T0, T0.5 and T1 having respectively 0×, 0.5× and 1× the abundance of target species in the reference) and the increase in non-target abundances (N0, N0.5 and N1 having respectively 0×, 0.5× and 1× the abundance of non-target species). Data are mean±SE, two bars with no letter in common are significantly different according to Tukey Honestly Significant Differences comparisons ($p<0.05$).

3.2.3. Application to the resilience of a Mediterranean steppe after ploughing.

La Crau area is the last xeric steppe in south-eastern France (ca. 10,000ha; c. 43°33’ N, 4°52’ E) and has been shaped by i) a Mediterranean climate: a mean annual temperature of 15°C, a variable annual sum of precipitation between 400 and 600mm concentrated in autumn and spring, with four months of summer drought, and more than 110 days with a >50km*h^{-1} wind; ii) 40cm deep soil composed with about 50% of silicaceous stones overlying a conglomerate layer, making the alluvial water table unavailable to the roots of plants and iii) itinerant sheep grazing over a period of several thousand years (Devaux et al., 1983; Buisson et al., 2006). Although this area is protected by a French National Reserve status, a 5.7ha area was accidentally ploughed in August 2010. Once the Reserve authorities were aware of the incident, the area was steamrollered in order to reduce the effects of ploughing. Vegetation relevés were carried out in order to assess the impact of such a disturbance: nine 4m² quadrats were surveyed in the ploughed area and the unploughed area (reference community) in May 2011. Standard indicators and the three indicators presented above were calculated for both areas.

3.2.4. Application to the restoration by hay transfer of a Mediterranean meso-xeric grassland

The Camargue natural areas (Rhône Delta, south of France, 140,000ha) have drastically declined with the combined effects of industrialization and agricultural development (Lemaire et al., 1987). Currently, opportunities arise to rehabilitate them on abandoned cultivated plots. The 70ha Cassaïre site (c. 43°31' N, 4°44' E), is mostly composed of former rice fields. The upper elevation of the site (3m above sea level) is currently being restored by transferring hay from reference xero-halophytes communities of the Tour du Valat domain (Mesléard et al., 2011) located 10km away from the restoration site. The hay was previously gathered by air-vacuuming in summer 2010 and transferred on five mesocosms (15m × 5m × 40cm deep) randomly disposed on the site. Hay material was applied on a 2m × 10m plot (hay density=11.5g*m^{-2}). Five control mesocosms where no hay transfer was applied were also randomly disposed. A vegetation survey was carried out in the hay transfer and the control using 50cm × 50cm grids in each mesocosm subdivided into 25 10cm × 10cm cells for each species recorded, giving a frequency. Five grids were also randomly surveyed in the reference community.

3.2.5. Analyses

We calculated standard indicators for the three case studies (Table 3.1): species richness, Shannon index, Shannon evenness (Pielou, 1969) which are indicators of diversity, and Sorensen similarity and Bray-Curtis similarity (i.e. 1-Bray-Curtis dissimilarity index) which are both indicators of composition. The Sorensen index does not take abundances into account, while the Bray-Curtis index does (Borcard et al., 2011). In order to have one value of similarity for each assessed community sample, we calculated the mean of similarities between that sample and each reference community sample. Then, in order to have one value of similarity for each reference community sample, we calculated the mean of similarities between that sample and each reference community sample. We also calculated the three new indices (HAI, CSII and $CSII_{norm}$,) for the three case studies.

Table 3.1: Description of standard indicators and of the new indices developed.

Indicators	Description of the indicators
Species-richness	Number of different species recorded in a delimited area.
Shannon index	Shannon index is a diversity index which expresses a ratio of proportion of species abundance relative to the whole community. The more one species dominates the community compared to other species, the higher Shannon index is. It is limited between 0 and a maximum potential which increases with species-richness.
Shannon evenness	Shannon evenness maximum potential value depends on the species-richness of the assessed community. Shannon evenness is relative to this potential maximum and is therefore limited to 1.
Sorensen similarity index	Sorensen similarity index is a similarity index between two samples which take into account only composition, not species abundance. It increases when two communities are close and is limited between 0 and 1.
Bray-Curtis similarity index	Bray-Curtis similarity index is a similarity index between two samples which take into account composition and species abundance. It increases when two communities are close and is limited between 0 and 1. Usually, Bray-Curtis dissimilarity is used but for clarity's sake, we used the similarity (1-Bray-Curtis similarity).
Community Structure Integrity Index (CSII)	CSII is an index calculated between a sample and one or several samples of a reference community. It measures the proportion of the species abundance in the reference community represented in the assessed community. It increases when target species abundance increases until their abundance reach those of reference community. It is limited between 0 and 1.
Normalized Community Structure Integrity Index ($CSII_{norm}$)	$CSII_{norm}$ is similar to the CSII but is normalized in a way that when it is calculated in the reference community it takes a 1 value. It is also limited between 0 and 1.
Higher Abundance Index (HAI)	HAI is an index calculated between a sample and one or several samples of a reference community. It measures the proportion of the species abundance in the assessed community which is higher than in the reference community. It increases when non-target species abundance increases or when target species abundance increases above their abundance in reference community. It is limited between 0 and 1.

After checking conformity to parametric conditions we performed T-tests for the Mediterranean steppe case study and an ANOVA followed by Tukey HSD post hoc tests for the fictitious and the Mediterranean xero-halophyte grassland case study to compare indicators between communities.

All calculations and analyses were performed with the package "stats" and "vegan" in R 2.13.0 (R Development Core Team, 2011) and we used the R code given in Appendix 4 for our three new indices (CSII, $CSII_{norm}$ and HAI) calculations and abundances plotting.

3.3. Results

3.3.1. Fictitious case study

Species-richness and Shannon index increased or decreased independently of which species occur in the assessed community. Obviously, the smaller species-richness was found in the T0N0 community and the highest species-richness in the T1N1 community (Figure 3.1 & 2). The Shannon evenness, which is independent of species-richness, was the highest in the community with low abundances, and was not significantly different between the reference and the other community types. Sorensen similarity and Bray-Curtis similarity increased when target species abundances increased, but only Bray-Curtis similarity decreased when non-target species abundances increased. There was no significant difference in Bray-Curtis similarity indices between the T0.5N0 community, where target species abundances was lower than in the reference and non-target species abundances null, and the T1N1 community, where target species abundances were equal to the reference and non-target species abundances higher. CSII and CSIInorm increased only when target-species abundances increased and were not significantly different from the reference when all the target species had the same abundance as in the reference. CSII and CSIInorm were not influenced by the increase in non-target species abundances. On the contrary, HAI was significantly influenced by the increase in non-target species but not by target species abundances. However, when the overall abundance of community decreased, the HAI increased.

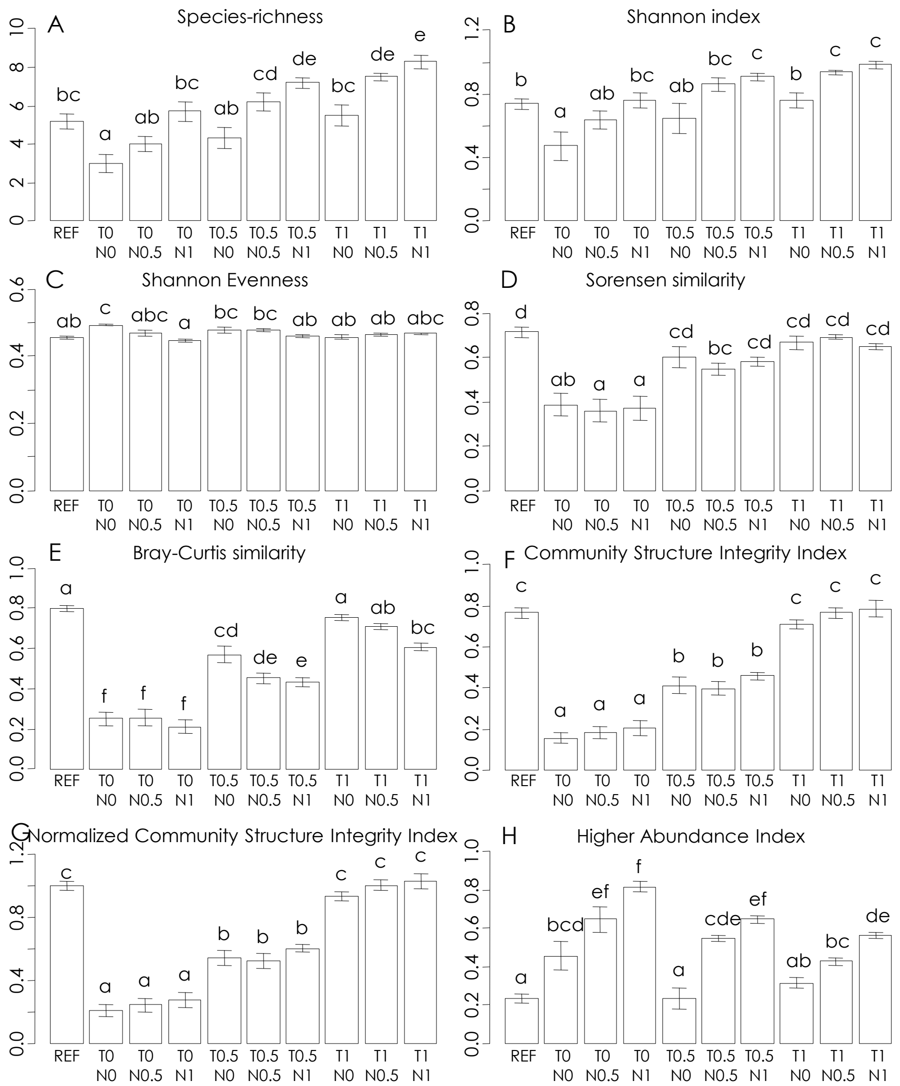


Figure 3.2: Comparison of standard indicators (Species-richness, Shannon index, Shannon evenness, Sorensen similarity index, Bray-Curtis similarity index (1-Bray-Curtis dissimilarity index) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance Index) in the ten fictitious communities. REF is the reference community, and the nine others are assessed community types where the increase in target species abundances (T0, T0.5 and T1 having respectively 0×, 0.5× and 1× the abundance of target species in the reference) and the increase in non-target abundances (N0, N0.5 and N1 having respectively 0×, 0.5× and 1× the abundance of non-target species). Data are mean±SE, two bars with no letter in common are significantly different according to Tukey Honestly Significant Differences comparisons ($p<0.05$).

3.3.2. Resilience of a Mediterranean steppe

The reference and ploughed communities shared numerous species (Figure 3.3), as expressed by their similar species-richness (Table 3.2). However many species have different abundances: some have higher abundance in the reference community (e.g. *Brachypodium distachyon*) or are absent in the ploughed community (e.g. *Brachypodium retusum*), whereas some have higher abundances in the ploughed community (e.g. *Bromus madritensis*), or were not recorded at all in the reference community (e.g. *Polycarpon tetraphyllum*). These differences in abundance were poorly shown by diversity indices: Shannon index was significantly different (1.68±0.04 in the reference vs. 1.61±0.07 in the ploughed community; p=0.04) but Shannon evenness was not significantly different (p=0.38). As for indices dealing with community composition (Sorensen similarity index, Bray-Curtis similarity index) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance Index) we found significant differences between the reference and ploughed communities (Table 3.2). Sorensen and Bray-Curtis similarities were higher in the reference community than in the assessed community (ploughed community). The mean $CSII_{norm}$ reached 0.41 in the ploughed community meaning that 59% of the reference community was destroyed by the ploughing event. The reference community had a mean $CSII_{norm}$ of 1, while it had a mean CSII of 0.71. The reference community had a mean HAI of 0.29 significantly different from the ploughed community mean HAI of 0.64 meaning that 64% of the abundance in the ploughed community came from species in higher abundance than in the reference communities.

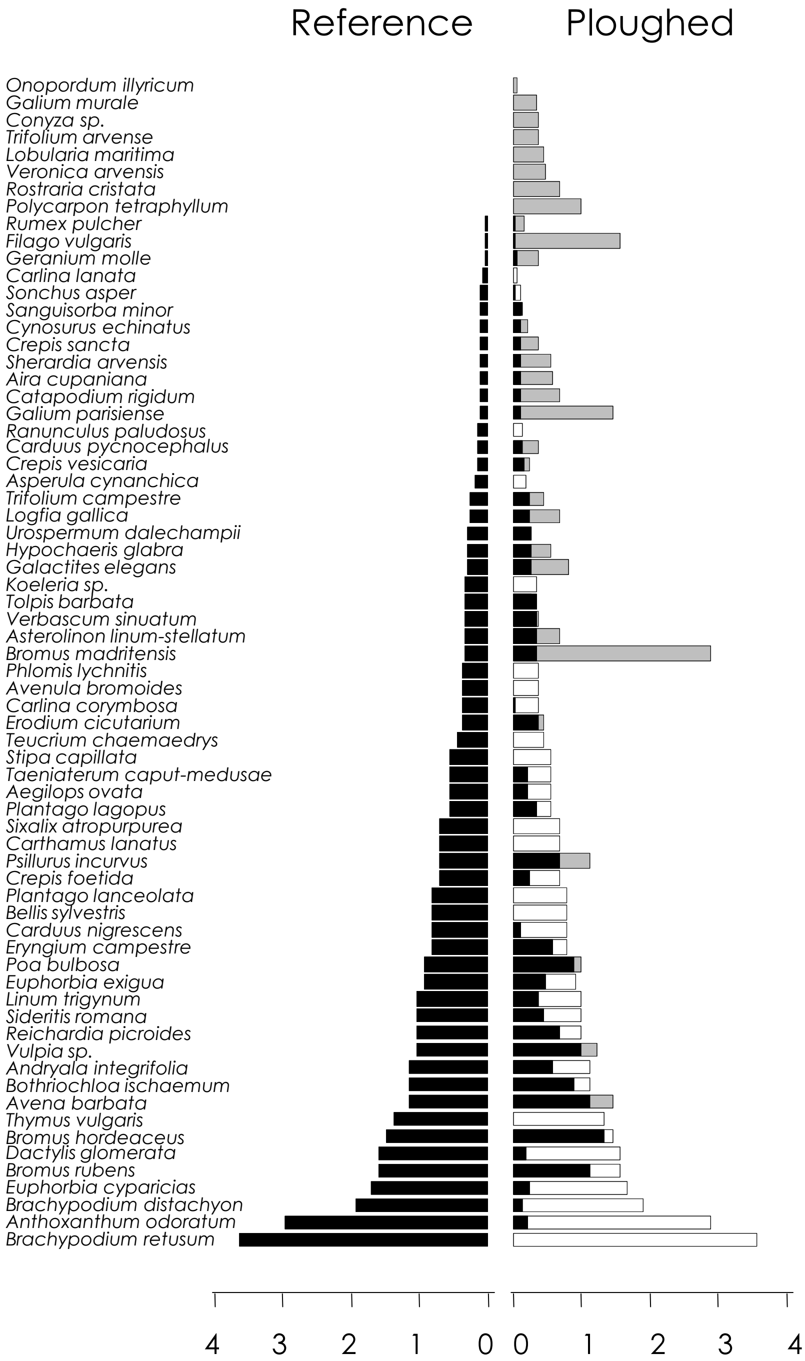


Figure 3.3: Mean abundances of reference community and ploughed communities (assessed community) (n=9). Black areas represent mean abundances in the reference communities. White areas represent mean missing abundances in the ploughed community, grey areas represent mean abundances in the ploughed community up to the mean abundances in the reference community and yellow areas represent abundances which are higher than in the reference community. For clarity purposes, only species which occur in more than 3 samples are shown (67 of the 119 species).

Table 3.2: Comparison of standard indicators (species-richness, Shannon index, Shannon evenness, Sorensen similarity index and Bray-Curtis similarity (i.e. 1-Bray-Curtis dissimilarity)) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance Index) between the reference community and the ploughed area. Reported values are means ± confidence interval (95%), t is the statistic of the t test, df the degree of freedom and the p value (no sign: p>0.05; *: p<0.05; **: p<0.01 and ***: p<0.001).

	Reference	Ploughed area	t	df	p	
Species-richness	33.78±2.88	29.67±4.43	1.90	14	0.078	
Shannon index	1.68±0.04	1.61±0.07	2.27	13	0.041	*
Shannon evenness	0.48±0	0.48±0	0.92	14	0.375	
Sorensen similarity index	0.71±0.02	0.4±0.08	9.71	9	<0.001	***
Bray-Curtis similarity index	0.71±0.02	0.31±0.06	14.50	10	<0.001	***
Community Structure Integrity Index	0.71±0.03	0.29±0.08	12.00	10	<0.001	***
normalized Community Structure Integrity Index	1.00±0.04	0.41±0.11	12.00	10	<0.001	***
Higher Abundance Index	0.29±0.03	0.64±0.04	-17.47	14	<0.001	***

3.3.3. Restoration of a Mediterranean meso-xeric grassland

The restored hay transfer community shared more species with the reference community than with the control community (Figure 3.4). However, as in the resilience case study, some species showed different abundances: some had higher abundance in the reference community (e.g. *Galium murale*) or were completely absent in the restored community (e.g. *Brachypodium phoenicoides*) whereas some had higher abundances in the restored community (e.g. *Bromus hordeaceus*), or were not recorded in the reference community (e.g. *Polygonum aviculare*). We did not find any differences in the Shannon index and species richness between reference and hay transfer community (Table 3.3). Nevertheless, Sorensen similarity index, Bray-Curtis similarity index and the three new indices ($CSII_{norm}$, CSII and HAI) were significantly different between the 3 communities (p<0.001 for the five indices). Sorensen and Bray-Curtis similarities were the highest in the reference community and the lowest in the control. The mean $CSII_{norm}$ of the control was 0.01, meaning that only 1% of the reference community abundance was expressed in this community. It reached a mean of 0.20 for the restored community, meaning that according to our index, 20% of the reference community has been restored. In the reference community the mean of the $CSII_{norm}$ and the CSII were respectively of 1 and 0.67. In this reference community the value of the mean HAI (0.32) was significantly different from the restored or the control (respectively 0.77 and 0.99) meaning the control community corresponded to 99% of the abundance of target species higher than the reference community or of non-target species.

Table 3.3: Comparison of standard indicators (species-richness, Shannon index, Shannon evenness, Sorensen similarity index and Bray-Curtis similarity (i.e. 1-Bray-Curtis dissimilarity)) and the three new indices (Community Structure Integrity Index, normalized Community Structure Integrity Index and Higher Abundance index) between the reference community, the hay transfer community and the control community. Reported values are means ± confidence interval (95%), F is the statistic of the ANOVA test, df the degree of freedom and p the p value (NS: p>0.05; *: p<0.05; **: p<0.01 and ***: p<0.001). Values on a line with a common letter are not significantly different (Tukey HSD test with a p-value adjustment according to Bonferroni's method).

	Reference	Hay transfer	Control	F	df	p	
Species-richness	34.80±4.95 a	25.00±12.49 a	9.60±8.31 b	18.69	2	<0.001	***
Shannon index	1.60±0.09 a	1.41±0.22 a	0.85±0.68 b	8.71	2	0.005	**
Shannon evenness	0.45±0.02	0.45±0.03	0.44±0.05	0.26	2	0.77	NS
Sorensen similarity index	0.71±0.05 a	0.25±0.16 b	0.03±0.07 c	102.90	2	<0.001	***
Bray-Curtis similarity index	0.59±0.06 a	0.16±0.13 b	0.01±0.01 c	128.86	2	<0.001	***
Community Structure Integrity Index	0.67±0.07 a	0.13±0.13 b	0.00±0.01 c	170.56	2	<0.001	***
Normalized Community Structure Integrity Index	1±0.11 a	0.20±0.19 b	0.01±0.02 c	176.56	2	<0.001	***
Higher Abundance index	0.32±0.04 a	0.77±0.18 b	0.99±0.02 c	94.10	2	<0.001	***

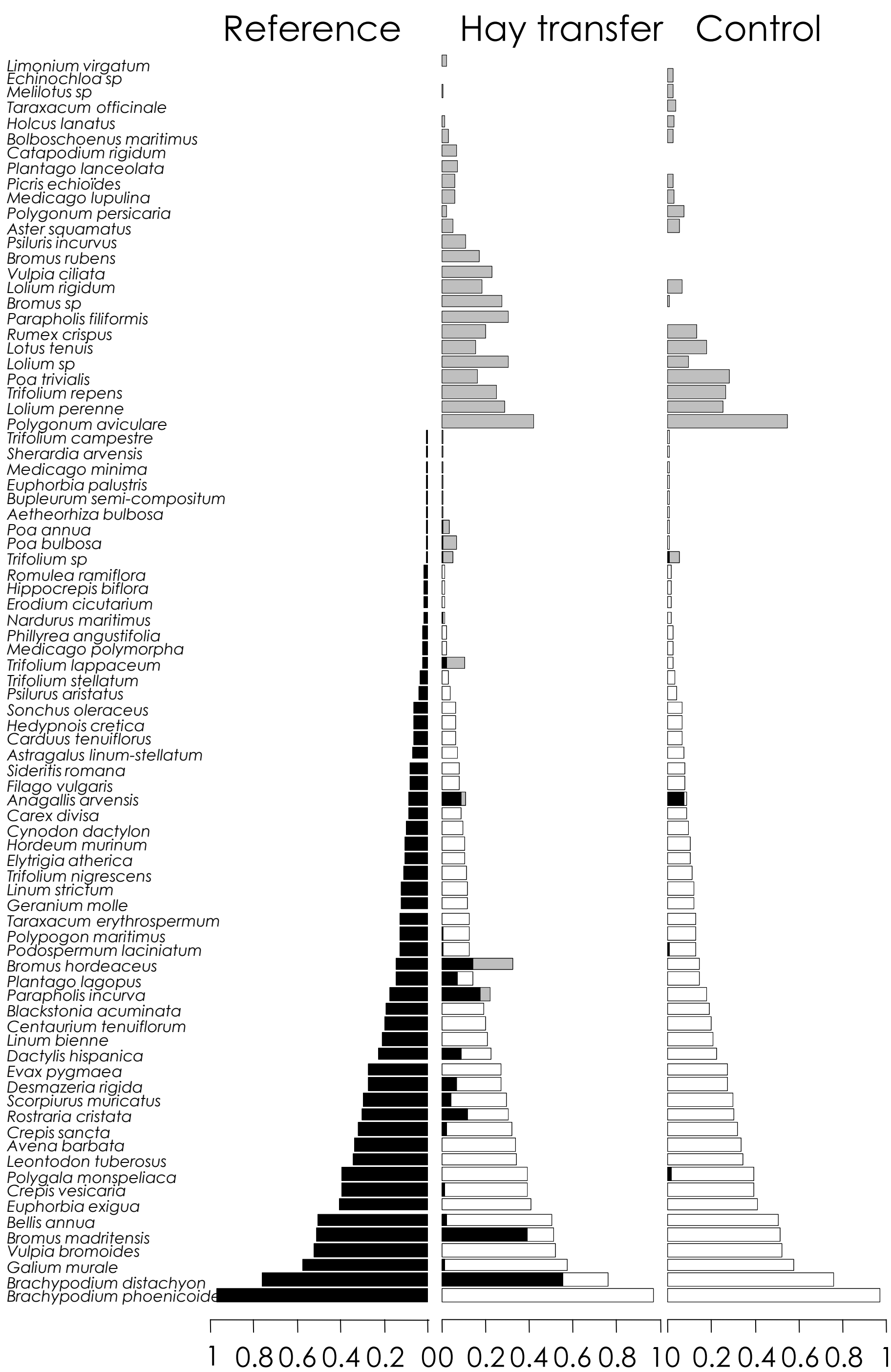


Figure 3.4. Mean abundances of reference, hay transfer and control communities (n=5). Black areas represent the mean abundances in the reference communities, white areas represent mean missing abundances in hay transfer and control communities, grey areas represent mean abundances in ploughed community up to the mean abundances in the reference communities and yellow areas represent mean abundances which are higher than in the reference communities. For clarity purposes, only species which occur in more than 2 samples are shown (83 on 97 species).

3.4. Discussion

3.4.1. Comparison of standard indicators with CSII and HAI

Among the numerous indicators used to assess diversity (functional diversity, β diversity, etc.), some standard indicators are widely used in conservation biology (species-richness, Shannon or Shannon evenness) and provide useful information on community states. Nevertheless, when measuring resilience or restoration, they have to be cautiously interpreted. In our case studies we found no significant differences in the species-richness and evenness between the restored or ploughed community and their respective references, although the communities showed great differences in composition. More seriously, sometimes diversity indicators are higher in the assessed community than in the reference, despite the fact that the community is dominated by non-native or ruderal species (Balcombe et al., 2005). Even if species-richness and evenness were similar in the assessed communities and in their respective reference, we cannot consider that the meso-xeric grassland has been fully restored by hay transfer and that the ploughed steppe has fully recovered after one year. Similarity indices, which permit the comparison of the composition of two communities, are used to assess restoration or resilience (Appendix 3). Some similarity indices, however, do not take abundance into account (e.g. Sorenson, Ochiai, etc. (Borcard et al., 2011)). Those indices cannot detect dissimilarities between two communities of identical composition but of different structure, as our fictitious communities example shows. Structure may be a determinant for ecosystem functioning (Chapin et al., 1997). Indices which depend on community structure should thus be preferred when assessing resilience or restoration (e.g. Bray-Curtis, etc. (Borcard et al., 2011)). In our case studies the Bray-Curtis similarity index is the standard indicator which expresses the largest difference between reference and assessed communities. Nonetheless, such indices, when deviating from the maximum similarity (i.e. 1 for similarity indices, 0 for dissimilarity indices), may reflect two different kinds of patterns: the species in the assessed community may have lower abundances than those in the reference community, or they may have higher abundances. Our three new indices permit disentangling these two different patterns, which can occur simultaneously. This is particularly illustrated by the fictitious case study. Indeed, when the abundances were higher in the assessed than in the reference community, Bray-Curtis similarity decreased. On the contrary, the CSSI does not depend on abundances that were higher than in the reference community and thus does not decrease. The similarity decreasing is expressed in the Higher Abundance Index, which then deviates from 0. The ploughed steppe community and the restored xero-halophytic grassland community had $CSII_{norm}$ of 0.41 and 0.20 respectively meaning that according to our indices, assessed communities contain 41% and 20% of abundances of their respective reference communities. Their mean HAI were 0.64 for the ploughed steppe community and 0.77 for the restored meso-xeric grassland community, meaning that, according to our indices, the assessed communities contained 64% and 77% of their respective total abundance which are higher abundances (i.e. non-target species or abundances of target species are higher than mean reference abundances).

3.4.2. Contribution of CSII and HAI to community assessment interpretation

The choice of an indicator depends on what one wants to measure, and on the objectives with which the measures are taken (Duelli and Obrist, 2003). Moreover, (Balmford et al., 2005) advocates using indicators that are rigorous, repeatable, and widely and easily understandable. $CSII_{norm}$ and HAI indices both represent easily understandable measurements for conservation biologists of a community state: $CSII_{norm}$ is the proportion of the reference community structure which can be found in the assessed community whereas HAI is the proportion of the assessed community structure that is represented by higher abundances than in the reference community. Knowing whether a community has a “deficit” of target species abundance or is characterized by higher abundances is of primary interest for practitioners who want to manage ecological succession (Luken, 1990; Kiehl and Pfadenhauer, 2006).

3.4.3. Applications of indices to restoration ecology and biological conservation

Low values of CSII express a lack of target species in the assessed community. Therefore identifying the reasons why these species do not reach the reference community abundances is of primary interest. If target species do not disperse, the propagule source may be too far away or the target species do not produce sufficiently dispersible propagules: management can be focused on strengthening dispersion processes (see Kiehl et al., (2010) for review). For example, the restored meso-xeric grassland case study shows that dispersion strengthening by hay transfer increases CSII value. Environmental conditions may be too far from the growth optimum of target species, in which case management should involve trying to restore suitable conditions (Bakker and Berendse, 1999; Dorland et al., 2005). Target species may also be in competition with non-target species (D'Antonio et al., 2003), which will be expressed with high values of HAI. Management should then involve trying to decrease abundances of these species with higher abundances, whether it concerns target species or not (Donath et al., 2003; Murray and Marmorek, 2003). More than a static measurement, these indices may be used to monitor the succession of assessed communities. Increasing CSII values could show that dispersion strengthening is not necessary. On the contrary, an increase of HAI, even if the values are low, can indicate the need for managing higher abundance (Donath et al., 2003; Haywood, 2009). In both real case studies, HAI are significantly higher than in the reference community. If HAI increases during forthcoming years, the actual site management, extensive sheep grazing, will have to be adapted to reduce higher abundance. Otherwise these species with higher abundance may have a negative feedback on the CSII values and thus threaten the maintenance of community integrity success.

3.4.4. Limits and constraints of CSII and HAI use

Particular attention should be paid to data gathering before performing indices calculations. Whether it is for assessing resilience or restoration efficiency, the definition and characterization of reference ecosystems are crucial (White and Walker, 2008). A broad part of ecological restoration literature deals with this issue (Ehrenfeld and Toth, 1997; Egan, 2001). In order to avoid bias in HAI or CSII calculations, similar community characterization protocol should be used in reference and assessed ecosystems (same sample size, working effort, plant identification skills and date of sampling). Communities are not static entities and, at least in the framework of restoration, the reference should be all the manifested or potential states that occur within a given historical and spatial variation (Landres et al., 1999; Society for Ecological Restoration International Science and Working Policy Group, 2004). Therefore, reference community characterization should take into account the natural variability of the reference, both spatially and temporally (White and Walker, 2008). Calculation of CSII and HAI should be performed in both the reference and assessed communities. Indeed the indices give information on the reference community variability and heterogeneity and allow statistical analyses comparing the reference and assessed communities. These comparisons provide an overview of the assessed community but do not account for the whole complexity of an ecosystem: functional, spatial or dynamic attributes are eluded. Therefore these indices should be used in addition to standard indicators or more specific ones adapted to each case study (see for example Raab and Bayley (2012)). Moreover, in a context of the evaluation of a restoration project, assessment of one community of the whole ecosystem is not sufficient to draw conclusions on the project. Several communities should be assessed (i.e. plants, insects, birds, mammals, microbes, etc.), as well as environmental characteristics (i.e. soil chemistry, disturbance regime, etc.) or landscape-scale indicators (i.e. fragmentation, etc.) (Palmer et al., 2005; Tasser et al., 2008).

3.4.5. Perspective of use and development of CSII and HAI

All species do not necessarily have the same status in a community, whether they could exert a more significant role in ecosystem functioning or services (Funk et al., 2008; Bullock et al., 2011) or they could be of high conservation value. It could have been relevant to give more weight to high conservation value species in the calculation of CSI indices or to give more weight to species with a high invasion potential for the HAI. However, these resulting indices would deviate from the original goal of these indices: measuring in an easily interpretable way the difference from a reference community.

To our knowledge, no meta-analyses have tried to measure the abilities of ecological restoration projects to restore reference community integrity. It has been proved that restoration exerts a significant positive effect on diversity or ecosystem services (Benayas et al., 2009). Regarding the high differences sometimes existing between standard indicators and CSII in our case studies, it would be interesting to perform these indices calculations in such meta-analyses.

Metaphorically speaking, if we compare restoration with assembling a jigsaw puzzle, species-richness would be equivalent to the colour palette of the puzzle and Shannon index, or evenness, would be the correct equilibrium of colours, whereas CSII could be compared to the number of correct pieces of the puzzle. This metaphor leads to two comments: 1) It seems obvious that even the correctly balanced color palette is not enough to complete the puzzle if 50% of the pieces are missing; 2) Even with all the pieces, they have to be assembled adequately to obtain the desired picture. To our knowledge, there is no indicator which measures this community configuration (apart from random/aggregated distribution) although it has been proved to exert a significant effect on ecosystem functioning (Maestre, Castillo-Monroy, et al., 2012). Consideration of how to measure the state of a community in a framework of restoration or resilience assessment should be continued to set realistic and measurable goals for ecosystem management as noticed by Ehrenfeld and Toth (1997).

Transition to chapter 4

Restoration ecologists have identified a series of steps to maximize the likelihood of achieving diverse restoration goals in a restoration project (Hobbs and Norton, 1996; Giardina et al., 2007). The Cossure project presented in **Transition to Chapter 3** has followed most of these steps (Figure T4.1).

(1) Identification of the reference system
Description of the La Crau area floral and faunal communities, paleoecology and archeology .

(2) Identify processes leading to degradation and restoration needs
Identification of first threats in 1975, creation of National Reserve in 2001, and assessment of natural resilience in several studies.

(3) Develop methods to reverse or ameliorate the degradation
First works on environmental conditions recreation, then small-scale dispersion reinforcement or structuring species seeding.

(4) Determination of realistic goals
Numerous meeting with local stakeholders, National Reserve and the CDC Biodiversité led to the objective of the rehabilitation of a steppe like habitat for the return of steppe birds.

(5) Identification of monitoring Indices
The whole project is assessed through several of its components: economic and social implications and ecological implications, birds, reptiles, ants, orthoptera, coleoptera and vegetation, involving mainly composition, diversity, presence of conservation interest species but also new indicators of community structure integrity.

(6) Implementation of restoration
After the former orchard bought in 2007, the 357ha rehabilitation works began in 2008 and end in 2009.

(7) Monitoring, documentation and communication
According ot the 5th step, the whole project is monitored and results are annually discussed with stakeholders and CDC Biodiversité and presented in an annual report. Results are also communicated in national and international conferences (REVER, the french network of ecological restoration; the Society for Ecological Restoration; the International Association of Vegetation Science) but also at local scale towards non-scientific people (round table, open doors days).

Figure T4.1 : Detailed key processes of the Cossure project based on Giardana et al. (2007) and Hobbs & Norton (1996) conceptual schemes. References for each steps are given hereafter: (1) (Molinier and Tallon, 1950; Cheylan, 1975; Devaux et al., 1983; Badan et al., 1995; Henry et al., 2010); (2) **Chapter 1**, 2 and (Cheylan, 1975; Buisson and Dutoit, 2004, 2006; Römermann, Dutoit, et al., 2005; Coiffait-Gombault et al., 2012a); (3) (Buisson, 2005; Coiffait-Gombault et al., 2011, 2012b); (4) **Transition to Chapter 3** and (Jaunatre et al., 2011); (5) **Chapter 3**, 4 and (Bulot, In prep; Alignan, 2010; Wolff, 2011; Chabran and Napoléone, 2012); (6) **Chapter 4** and (Jaunatre et al., 2012); (7) (Dutoit, Jaunatre, et al., 2009, 2011).

The reference ecosystem has been identified by several studies (cf **Introduction section I.5**), as well as the processes of degradation and restoration needs (cf **Chapter 1 and 2**). The development of restoration methods applicable for the La Crau steppe plant community has begun less than ten years ago with Buisson's thesis (2005) and went on with Coiffait-Gombaut's thesis (2011). These previous studies, combined with discussions with stakeholders allowed determining the aims of Cossure project and what components of the project were going to be assessed (**Transition to Chapter 3** and Jaunatre et al. (2011)). Moreover **Chapter 3** gave a thought focused on the way to measure the restoration of communities within this project. After the implementation of rehabilitation and restoration, the project was monitored and results are given in the **fourth chapter**.

Objectives of **Chapter 4** are to know if it is possible to restore a low productive species-rich ecosystem after intensive cultivation, and to determine which restoration techniques provide the best restoration result (Figure T4.2). Experiments were carried out within a 357ha rehabilitation project, aiming to recreate an herbaceous sheep-grazed habitat. Four techniques were assessed: i) nurse species seeding, ii) topsoil removal, iii) hay transfer, and iv) soil transfer, with the steppe plant community as restoration target.

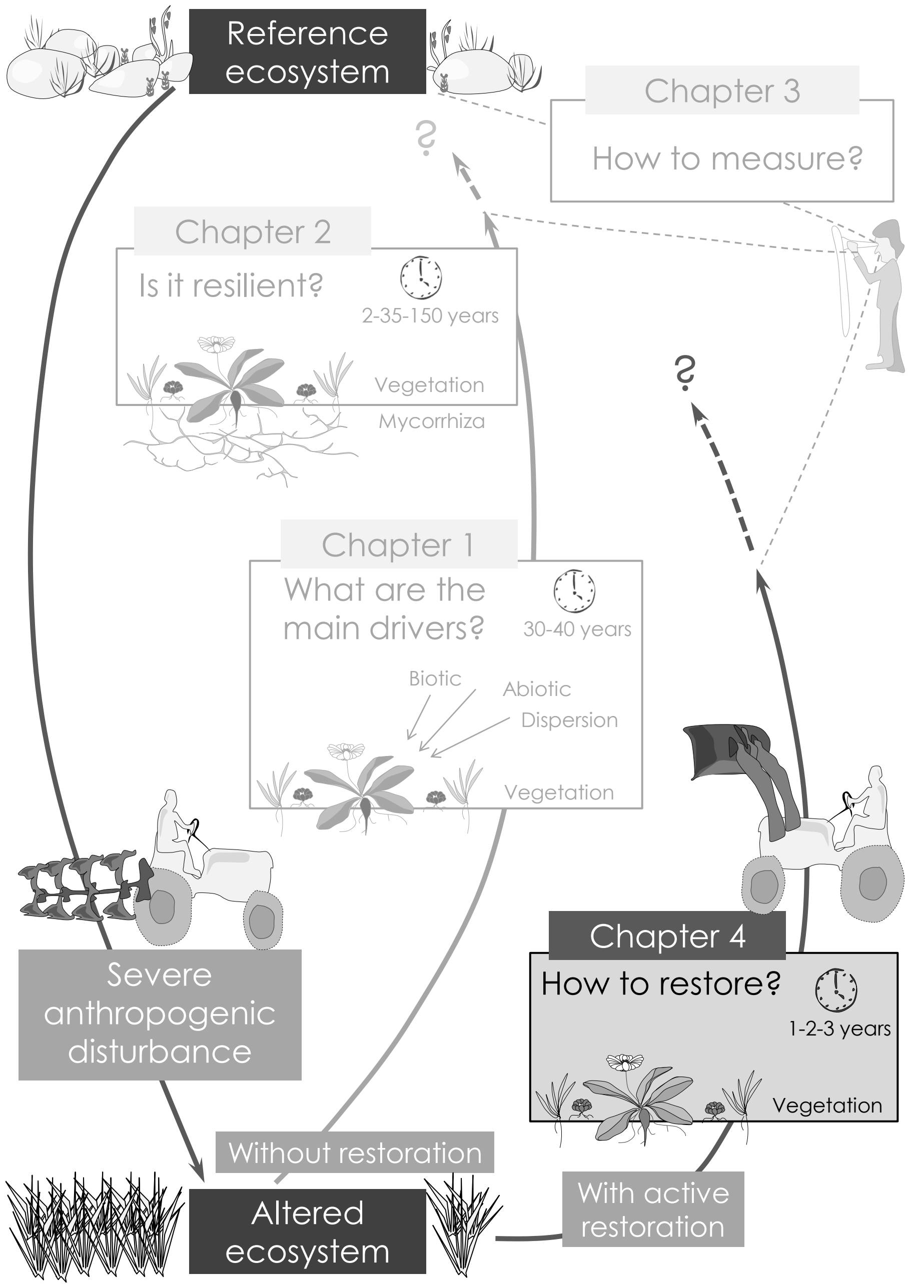


Figure T4.2: Location of Chapter 4 in the general thesis organization.

Former Cossure orchard rehabilitation: removing of peach trees. Photo credit: R. Jaunatre

Former Cossure orchard restoration experiment: soil transfer. Photo credit: R. Jaunatre

CHAPTER 4 - Using ecological restoration to restore an abandoned intensive cultivation in a Mediterranean rangeland

Renaud Jaunatre, Elise Buisson, Thierry Dutoit

4.1. Introduction

Restoring ecosystems has been identified as one of the possible tools to slow down biodiversity loss (Millennium Ecosystem Assessment, 2005). Ecosystem restoration is becoming an increasingly common mitigation measure or management tool in environmental conservation, especially since the Convention on Biological Diversity (2011) stated that 15% of degraded ecosystems should be restored by 2020. Research on restoration techniques is therefore of primary concern, not only at small experimental scales but also at large scale. Large scale experiments have already been conducted in some ecosystems (e.g. Donath et al. (2007) in flood meadows; Shaish et al. (2008) in coral reef), but there is still a need to undertake such experiments in Mediterranean rangelands which still cover more than 3,700,000ha (Dehesas and Montado ecosystems) in the Iberian peninsula and more than 63,000,000ha in North Africa (Le Houérou, 1995; Valladares and Gianoli, 2007; Méndez et al., 2008).

The abandonment of intensively cultivated areas provide obvious locations on which large scale experiments can be carried out to restore semi-natural ecosystems with extensive land-use, integrated into the current agricultural landscapes (Cramer et al., 2007; Buisson et al., 2009). Ecosystems which have evolved with long-term severe environmental constraints, whether biotic (e.g. grazing) or abiotic (e.g. dryness), and which have then been cultivated, often pass biotic and abiotic thresholds (Whisenant, 1999), because this type of disturbance is long-lasting and/or at large scale. Although spontaneous succession may present many advantages in ecological restoration (Rehounková and Prach, 2006; Walker et al., 2007; Prach and Hobbs, 2008; Jirova et al., 2012), it can result in ecosystems that are totally different from the chosen reference ecosystem (Manchester et al., 1999; Prach and Pyšek, 2001; Török et al., 2011) when this has been created and maintained by earlier human land uses and is thus better defined as a cultural ecosystem (Clewell and Aronson, 2007). This is especially true when soil has been nutrient-enriched, leading to increased competition (Marrs, 2002), and when target species propagules are no longer available, either because the seed bank has been depleted (Hutchings and Booth, 1996; Bossuyt and Honnay, 2008) or because of their dispersal limitation (Bakker et al., 1996; Münzbergová and Herben, 2005). Such disturbed ecosystems may need active restoration (Cramer et al., 2008; Prach and Hobbs, 2008; Hölzel et al., 2012), which should focus on lowering non-target species abundance and on improving target species dispersion (Walker, Stevens, et al., 2004; Baer et al., 2008; Dickson and Busby, 2009; Kiehl et al., 2010). Among the numerous restoration techniques that have been developed (see Fagan et al. (2008); Kiehl et al. (2010) and Török et al. (2011) for reviews), we tested four on areas of between 3 to 60 ha: nurse species seeding, topsoil removal, hay transfer and soil transfer.

The possibility of changing the facilitation-competition balance by introducing new species (Gómez-Aparicio, 2009) has led to the use of nurse species. For example, the species-richness of former arable land has been increased by seeding hemiparasitic species of the *Rhinanthus* genus in order to reduce dominant species density (Davies et al., 1997; Pywell et al., 2007). Seeding species can act as a filter on community composition because they can use up nutrients without being competitive several years after restoration, given the environmental conditions of the site. The established sown mixture can indeed drive succession from an inhibition to a tolerance model of succession (Connell and Slatyer, 1977). Rapid cover and nutrient consumption can inhibit arable weed species density in the first years via priority effects (Ross and Harper, 1972; Kardol et al., 2012). We therefore tested the effects of seeding nurse species to inhibit rapidly the dense cover of non-target species.

By decreasing nutrients, as well as by removing the permanent seed bank of weeds (Davy, 2002), topsoil removal in former agricultural areas has proven to favor low productive plant communities (Aerts et al., 1995; Patzelt et al., 2001; Verhagen et al., 2001; Allison and Ausden, 2004). We therefore tested this treatment for the first time on a large scale in a Mediterranean environment.

Dispersion has been identified as a major limiting factor for spontaneous succession of target communities (Hutchings and Booth, 1996; Bischoff, 2002). Strengthening this dispersion is becoming a major topic in ecological restoration (Kiehl, 2010; Kiehl et al., 2010; Hölzel et al., 2012). As commercial regional seed mixtures (Jongepierová et al., 2007) are rarely available for species-rich communities, the reintroduction of propagules gathered on the reference ecosystem can be a very efficient solution (Kiehl et al., 2010). The transfer of hay material and soil material were both tested in this study. Hay transfer is a well known technique and is widely used in northern Europe for restoration experiments (Hölzel and Otte, 2003; Rasran et al., 2006; Kiehl et al., 2010). This technique has however never been tested on a large scale in drier ecosystems. Vacuum harvesting of seeds that have already fallen on the ground was used because it has been proven to successfully gather species in north-western Europe (Stevenson et al., 1997; Riley et al., 2004) and previously in a small scale experiment in Mediterranean plant communities (Coiffait-Gombault et al., 2011).

Soil transfer can be used to transfer propagules, either by transferring intact turves, fragmented turves or bulk soil, and has already produced successful results in recreating species rich plant communities (Pywell et al., 1995; Bullock, 1998; Vécrin and Muller, 2003). Gathering bulk soil is cheaper and easier and the restoration success is similar to whole turf transfer for species richness and composition (Good et al., 1999). Although this technique requires having an area which will be destroyed, it is expected to be very efficient for transferring seeds, but also propagules and associated microorganisms. It is also expected to lower nutrient content by mixing soil from the reference ecosystem with that from the degraded site.

Apart from fire and overgrazing disturbances (D'Antonio et al., 2003), Mediterranean ecosystem restoration issues have been poorly addressed despite the fact that these ecosystems are particularly threatened by anthropogenic disturbances (Underwood et al., 2009). In the present study, we assessed the efficiency of four restoration treatments applied at a large scale with the aim of restoring a Mediterranean species-rich steppe community. The two main barriers to the spontaneous recolonization of plants that have been identified are dispersal limitation of target species and the high dispersal and establishment potential of non-target species, in particular due to increased fertility in the former cultivation area (Buisson, 2005). Experiments were carried out within a 357ha rehabilitation project, the aim of which is to recreate herbaceous sheep-grazed habitat for steppe birds. We applied on the rehabilitated area i) nurse species seeding, ii) topsoil removal, iii) hay transfer and iv) soil transfer, in order to restore a Mediterranean rangeland plant community with the last French Mediterranean steppe as a reference ecosystem. These four restoration techniques, applied for the first time at large scale on a Mediterranean herbaceous ecosystem, were monitored over a three year period. The aims of the present study are to assess the feasibility of restoring large areas of low productive species-rich ecosystem following intensive cultivation and to determine which restoration techniques provide the best restoration results in the short term.

4.2. Material and methods

4.2.1. Study site

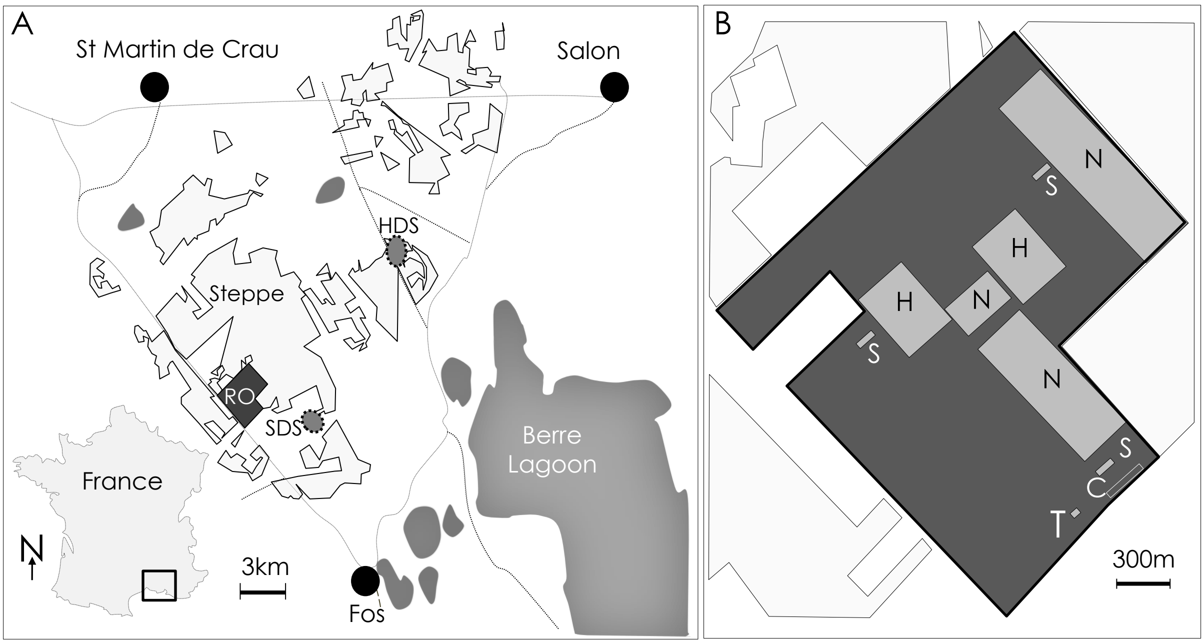


Figure 4.1: A, location of the La Crau area in France and location of the remnant patches of steppe (light grey), rehabilitated orchard (RO, black), the hay donor site (HDS; dark grey) and the soil donor site (SDS; dark grey); B, experimental design of restoration treatment on former Cossure orchard (C: control; N: nurse species seeding; T: topsoil removal; REH: rehabilitated area; H: Hay transfer; and S: soil transfer) (Jaunatre et al., 2012).

The La Crau area, the only French Mediterranean steppe, has been shaped by millennia of interactions between soil, climatic conditions and sheep grazing (Devaux et al., 1983; Badan et al., 1995; Henry et al., 2010) (Figure 4.1A). The 40 cm deep soil is made up of 50% of silicaceous stones and lies on a calcareous conglomerate which cannot be penetrated by plant roots (Devaux et al., 1983). The climate is Mediterranean, with high interannual variability, with an average of 540 mm yearly precipitation, mainly in spring and autumn, and 110 days per year with a more than $50 km.h^{-1}$ wind (Devaux et al., 1983). Traditional extensive sheep grazing has taken place in the La Crau area for more than 2000 years (Badan et al., 1995; Henry et al., 2010) as in many typical Mediterranean rangelands (Le Houérou, 1995). This xeric steppe, located in the South of France, is a unique species-rich plant community composed mainly of annuals and dominated by *Brachypodium retusum* Pers. and *Thymus vulgaris* L.. Despite the fact that the steppe of La Crau is a unique ecosystem, these experiments provide insights on restoration technique efficiency that are relevant to other relatively semi-dry Mediterranean rangeland ecosystems, such as the Dehesas in Spain, Montado in Portugal and the steppe of north Africa (Le Houérou, 1995).

4.2.2. Restoration aims in a rehabilitation project

All the restoration treatments tested were applied within a larger rehabilitation project: in 2006, a 357 ha orchard located approximately in the centre of the steppe area (Figure 4.1A) and adjacent to the largest remnant patch of steppe (6,500 ha), was abandoned in 2008. Among the dead, or almost dead, fruit trees, the vegetation was mainly dominated by grasses such as *Avena barbata* Link and *Bromus madritensis* L., with some forbs such as *Galium aparine* L., *Crepis foetida* L. or *Lactuca seriola* L.. The rehabilitation project within which the restoration treatments were applied began in 2009 with the aim of re-creating a herbaceous steppe-like habitat for steppe birds. Vegetation and soil characteristics were studied before rehabilitation and the whole area was homogenous (multivariate ordination results not shown). The rehabilitation treatment consisted in i) cutting down and exporting trees from the abandoned orchard (200,000 peach trees and 100,000 poplars used for hedgerows; ii) leveling soils; and iii) reintroducing traditional sheep grazing in spring 2010. This rehabilitation was applied over the whole area, it is thus considered spatially homogenous regarding soil characteristics and potential vegetation. The study focuses on four additional ecological restoration treatments applied on the rehabilitated area (Jaunatre et al., 2012): nurse species seeding, topsoil removal, hay transfer and soil transfer. The short-term objective of this restoration experiment is to limit the colonization of unwanted plant species and to improve the establishment of characteristic species just after the end of the rehabilitation phase. The mid-term objective is to re-direct the plant community along the desired successional pathway toward the steppe in order to reach a plant community with steppe characteristics: species-richness, composition and structure on a very longer-term (>30 years).

4.2.3. Restoration treatments

More details on the Restoration treatments can be found in Jaunatre et al. (2012). The three nurse species (*Lolium perenne* L., *Festuca arundinacea* Schreb. and *Onobrychis sativa* Lam) were chosen for their palatability, their purchase availability, their ability to rapidly cover bare ground, but also for their low competitive ability under Mediterranean environmental conditions and their actual presence in the artificial meadows of the La Crau area (Devaux et al., 1983). They were sown on 60ha (Figure 4.1B). The topsoil removal treatment consisted in removing the nutrient-rich upper soil layer, down to a depth of 20cm over a 3250m² area (Figure 4.1B). The hay material used for hay transfer was gathered by a leaf vacuum truck in summer at a donor site located less than 5km away from the restoration site (Figure 4.1A). The material was then spread with a 1:3 ratio (gathering seeds on 1ha, then spreading them on 3ha) over two 10ha areas in the rehabilitated orchard (Figure 4.1B). The material for soil transfer is the 20cm upper soil layer of a 1ha steppe patch of which the destruction was previously planned for construction work, located less than 2km away from the restoration site (Figure 4.1A). The gathering of bulk soil, the transport and the spreading at 1:3 ratio on three 1ha areas (Figure 4.1B) were carried out within one day in early September a few hours before the first significant autumn rains. Hay and soil donor sites used to be connected by sheep grazing from Neolithic times to the establishment of cultivation in the La Crau area in the 1970's (Fabre, 1997). The control is a 2ha area (Figure 4.1B) where trees were removed for safety purposes but soils were not levelled (Jaunatre et al., 2011).

As in Hölzel & Otte (2003), the aim was to assess the efficiency of these treatments applied on a large scale for restoration. Non-scientific constraints imposed by the multiple stakeholders of the project lead to the application of each treatment on few large areas rather than classic scientific experimental design with many small ones. However, the only difference between multiple sampling within one or few large treatment areas and one sample on numerous small treatment areas is that the treatment has not been applied in the areas between samples. Such areas without restoration treatment do not make sense and cannot be approved within a large scale restoration project (Jaunatre et al., 2011).

4.2.4. Soil seed bank and seed sources

Germination potential was assessed from five types of samples: four types of soil seed bank and one hay seed bank. The four types of soil seed bank were collected from the control, the rehabilitated area, the topsoil removal, and from the soil donor site. Each seed bank was estimated according to the concentrated seedling emergence method (Ter Heerdt et al., 1996) with ten 2L soil samples. Ten hay seed bank samples were spread on the same substrate as the soil seed bank samples: a 1:4 compost:vermiculite mix. All the samples were randomly arranged in a greenhouse and germinations were counted, identified and removed each week during 3 months. These data were used to estimate germinated seed species-richness and the numbers of germinated seeds from target and non-target species. Target species were species found in the reference steppe communities (Molinier and Tallon, 1950).

4.2.5. Vegetation survey

On the steppe, the control, the rehabilitated area, the nurse species seeding, the hay transfer and the soil transfer, 18 2×2 m quadrats were surveyed. For topsoil removal, which covered too small an area for such an extensive survey, 9 2×2 m quadrats were surveyed. Quadrats were all placed at least 20 meters from the edge of the area were the treatment was applied. Each year in May from the first (2010) to the third (2012) year after treatment application, on each quadrat, plant species were identified and a Braun-Blanquet abundance-dominance coefficient was given to each recorded plant species (Braun-Blanquet et al., 1952), and average vegetation height and vegetation cover were measured.

4.2.6. Soil analyses

Analyses were carried out on 30 samples of soil from the abandoned orchard before rehabilitation (in 2008), five samples from the soil donor site (in 2009) and six samples in each of the following: control, rehabilitated area, nurse species seeding, topsoil removal and soil transfer (in 2012). For each sample, three 70g subsamples of soil were randomly gathered in a 35m² area before being pooled and sieved with 2mm mesh sieve for analyses carried out by the INRA (Institut National de la Recherche Agronomique). Nutrient analysis (organic C, total N, C:N, P_2O_5 (Olsen et al., 1954), CaO and K_2O) and water pH were measured following standard methods (Baize, 2000).

4.2.7. Data analysis

As data of species-richness of germinated seeds and number of germinated seeds from target or non-target species were not in conformity with parametric conditions, comparison between treatments were performed with non-parametric tests: a Kruskal-Wallis test, followed by a pairwise Wilcoxon comparisons with a p-value adjustment according to the Benjamini-Hochberg's method if a significant difference was found (Benjamini and Hochberg, 1995).

Soil characteristics were ordinated by a Principal Component Analysis (PCA) and vegetation composition characteristics were ordinated by a Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarity (Borcard et al., 2011). In order to assess plant community restoration success, we used the normalized Community Structure Integrity Index ($CSII_{norm}$) and Higher Abundance Index (HAI). The $CSII_{norm}$ measures the proportion of the species abundance in the steppe community represented in the restored community, and HAI measures the proportion of the species abundance in the restored community which is higher than in the steppe community (**Chapter 3**).

Parametric conditions were not reached for the testing of interactions between years and treatment, so we did not test this interaction. However, as data from above-ground vegetation (species-richness, Shannon index, Shannon evenness (Pielou, 1969), average height, vegetation cover, $CSII_{norm}$ and HAI) were in conformity with parametric conditions considering the effect of year or treatment, ANOVA and Tukey Honest Significant Differences post hoc tests were performed to compare means between treatments in the third year or within a treatment between years.

All the analyses were conducted with R 2.13.0 (R Development Core Team, 2011), univariate analyses with its package "stats" and multivariate analyses with its packages "ade4" (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007) and "vegan" (Oksanen et al., 2008).

4.3. Results

4.3.1. Seed germination potential

The species richness of the seed bank significantly decreased from the control to the rehabilitated area to the topsoil removal (Figure 4.2A); species-richness average was below 8 for all types, and the maximum species-richness was 15 in one control sample. Seed bank species-richness from the soil donor site was similar to that of the rehabilitated area and seed bank species-richness of the hay material was similar to that of the control. The number of germinated seeds showed contrasting results whether we considered target or non-target species (Figure 4.2B-C). The control showed the highest number of non-target germinated seeds with a mean of 177.7±77.3 germinated seeds per sample mainly represented by *Chenopodium album* L. and *Cardamine hirsuta* L.. However, it showed a very low mean number of target germinated seeds: 1.2±0.5 seeds (*Linaria arvensis* (L.) Desf. or *Trifolium campestre* Schreber). The rehabilitated area showed a slightly higher but not significantly different number of non-target germinated seeds compared to the topsoil area both represented by the same species as in the control. None of the target species germinated in either of these treatments. The soil donor site and hay material had a relatively low number of non-target germinated seeds mainly represented by *Anagallis* sp. for the soil donor site and *Senecio vulgaris* L. for the hay material. Nevertheless, a significant number of target species seeds germinated in the soil donor site (19.5±5.9 germinated seeds) and hay material (34.4±7.1 germinated seeds), mainly represented by *P. bulbosa* and *Brachypodium distachyon* (L.) P. Beauv. for soil donor site and by *B. distachyon* and *Plantago lagopus* L. for the hay material.

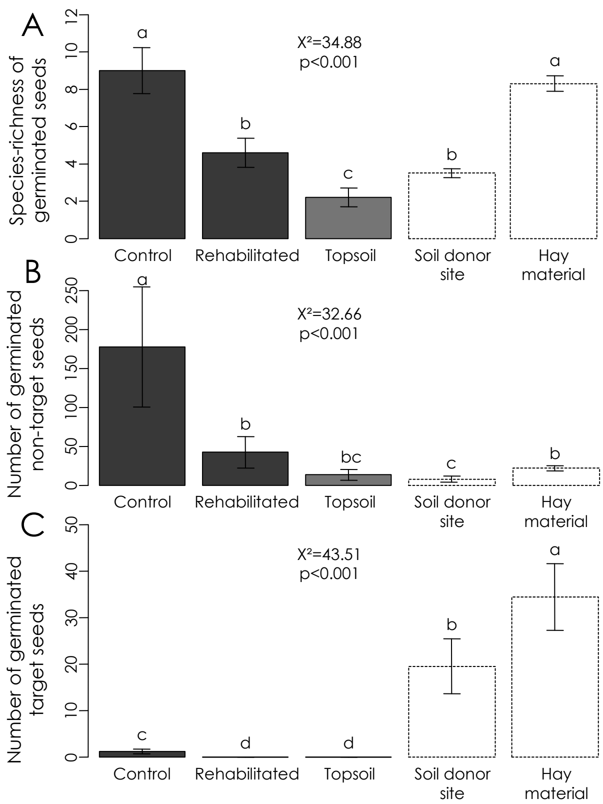


Figure 4.2: Species-richness of germinated seeds (A) and number of germinated seeds of non-target (B) and target (C) species from the seed bank of the control (dark grey), rehabilitated area (dark grey) and topsoil removal (light grey) as well as from the seed bank the soil donor site (white) and from the hay material (white). Kruskal-Wallis Chi-squared and its corresponding p-value are shown above each graphic. Bars showing common letters do not have any significant differences according to pairwise multiple comparisons with Benjamini-Hochberg p adjustment (Benjamini and Hochberg, 1995).

4.3.2. Effects of rehabilitation and restoration on soil properties

The ordination based on soil properties showed a nutrient content gradient on the first axis (62.4%) (Figure 4.3). Samples from the control in 2012 and from the abandoned orchard before rehabilitation in 2008 were in the same range of relatively high nutrient content (carbon, nitrogen, potassium and phosphorus). At the opposite end of the scale were the steppe, soil donor site and topsoil removal samples. The rehabilitated area, nurse species seeding and soil transfer areas were in between and are ordered along this gradient from the higher nutrient content (rehabilitated area) to the lower nutrient content (soil transfer). The ordination showed a pH and C:N gradient on the second axis (18.1%), with lower pH and higher C:N in the steppe samples and higher pH and lower C:N in the topsoil removal samples.

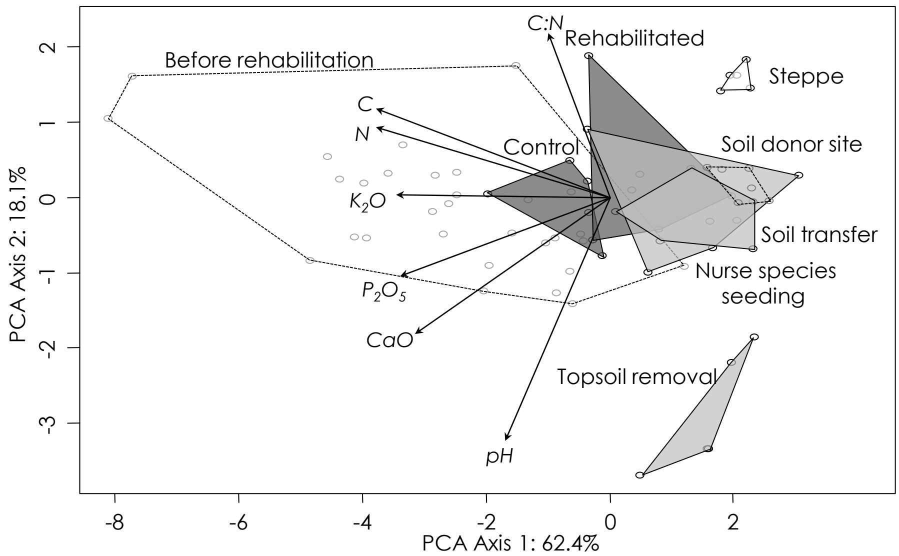


Figure 4.3: PCA ordination based on 71 soil samples analysis. Samples from each treatment (2012) are grouped by full lines: Steppe in white, soil transfer, topsoil removal and nurse species seeding in light grey and Rehabilitated area and Control in dark grey. Samples from the abandoned orchard before rehabilitation (2008) are grouped with dashed lines, as well as samples from the soil donor site (2009). Arrows represent soil variables (C:N: Carbon:Nitrogen ratio; C: total carbon; N: total nitrogen; K2O: potassium, P2O5: Olsen phosphorus (Olsen et al., 1954); CaO: Calcium oxide and pH).

4.3.3. Effects of rehabilitation and restoration on plant community characteristics

In the control, rehabilitated area and hay transfer, species-richness diminished from the first to the second year and recovered their value in the third year (Figure 4.4A). In nurse species seeding and soil transfer, species-richness did not show any significant differences between years. Topsoil removal showed a significant increase in species-richness from the first to the third year whereas the steppe showed a significant decrease during these years. In the third year, the highest species-richness was found in the steppe (32.94±1.33) but was not significantly different from the species-richness in topsoil removal (27.11±1.33) or soil transfer (28.72±1.8) treatments (Table 4.1). The rehabilitated area and hay transfer treatments showed intermediate species-richness (around 15) whereas nurse species seeding and the control showed the lowest species-richness (around 10). In the third year, Shannon index and Shannon evenness showed patterns similar to those of species-richness except that the topsoil removal area showed significantly lower values than the steppe (Table 4.1).

Average height showed the same dynamics in all treatments over the three years, except the steppe which was stable (Figure 4.4B): it increased between the first and the second year to reach mean values above 20cm (with a maximum of 48cm in the control), and it significantly decreased in the third year. That last year, the highest average height was in the control (15±1.28cm) and the lowest in the steppe (6.22±0.68cm), other treatments showed average heights around 10cm (Table 4.1). Vegetation cover tended to decrease from the first to the third year, except in the topsoil removal area (Figure 4.4C). In the third year, vegetation cover was highest in the control (93.11±1.78%) and lowest in topsoil removal (47.56±8.63%) and the steppe (58.61±2.77%) and showed intermediate values around 70% in other treatments (Table 4.1).

Table 4.1: Plant community characteristics for each treatment after 3 years (2012): control, rehabilitated area (Rehab.), nurse species seeding (Nurse), topsoil removal (Topsoil), hay transfer (Hay T.), soil transfer (Soil T.) and steppe. The given values are means±standard errors, df, F and p correspond to the degree of freedom, the F value and p value resulting from ANOVAs testing for the effect of treatment on each variable. Within a row, two cases with a common letter have significantly different values according to Tukey Honest Signicant Differences post hoc tests.

	ANOVA	Control	Rehab.	Nurse	Topsoil	Hay T.	Soil T.	Steppe
Species-richness ($4m^2$)	df=6 F=51.43 p<0.001	11.78±1.09 ab	15.61±1.41 b	9.61±0.81 a	27.11±1.33 c	13.91±0.87 ab	28.72±1.8 c	32.94±1.33 c
Shannon Index	df=6 F=44.68 p<0.001	1.03±0.04 ab	1.19±0.06 ab	0.98±0.03 a	1.56±0.02 c	1.17±0.04 b	1.54±0.04 cd	1.68±0.02 d
Shannon Evenness	df=6 F=16.02 p<0.001	0.425±0.005 ab	0.444±0.007 ab	0.441±0.004 a	0.474±0.003 c	0.451±0.004 b	0.464±0.004 cd	0.483±0.002 d
Average Height (cm)	df=6 F=10.17 p<0.001	15±1.28 a	9.33±0.53 b	9.56±0.65 b	10.67±0.82 b	9.91±0.57 b	10.94±0.81 b	6.22±0.68 c
Vegetation cover	df=6 F=10.31 p<0.001	93.11±1.78 a	68.33±4.39 bc	66.94±2.83 bc	47.56±8.63 d	73.64±2.61 b	74.17±2.22 b	58.61±2.77 cd
normalized Community Structure Integrity Index	df=6 F=197.24 p<0.001	0.034±0.005 a	0.111±0.014 b	0.039±0.006 a	0.257±0.019 b	0.099±0.012 c	0.442±0.042 d	1.00±0.036 e
Higher Abundance Index	df=6 F=314.78 p<0.001	0.946±0.007 a	0.872±0.012 b	0.935±0.008 a	0.783±0.008 c	0.872±0.012 b	0.674±0.019 d	0.334±0.009 e

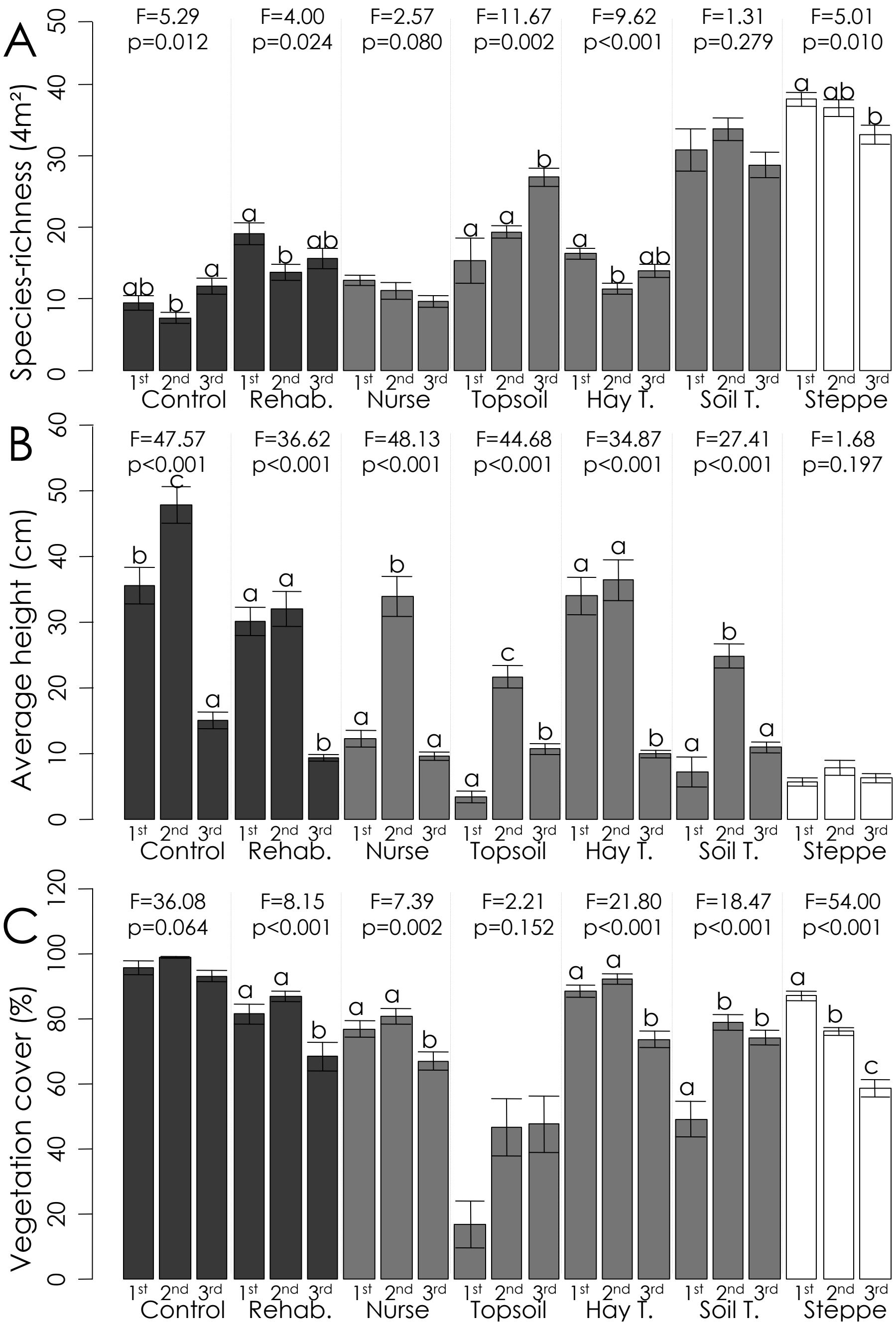


Figure 4.4: Means and standard errors of species-richness (4m²) (A), average height (cm) (B) and vegetation cover (%) (C) for the first three years (1st: 2010; 2nd: 2011; 3rd:2012) for each treatment: steppe (white), for restoration techniques (soil transfer (Soil T.), hay transfer (Hay T.), topsoil removal (Topsoil) and nurse species seeding (Nurse); light grey), for rehabilitated area (Rehab.; dark grey) and control (dark grey). The F and p value of ANOVA performed within each treatment to compare years are shown above the bars. Within a treatment, bars showing common letters do not have any significant differences according to Tukey Honest Signicant Differences post hoc tests.

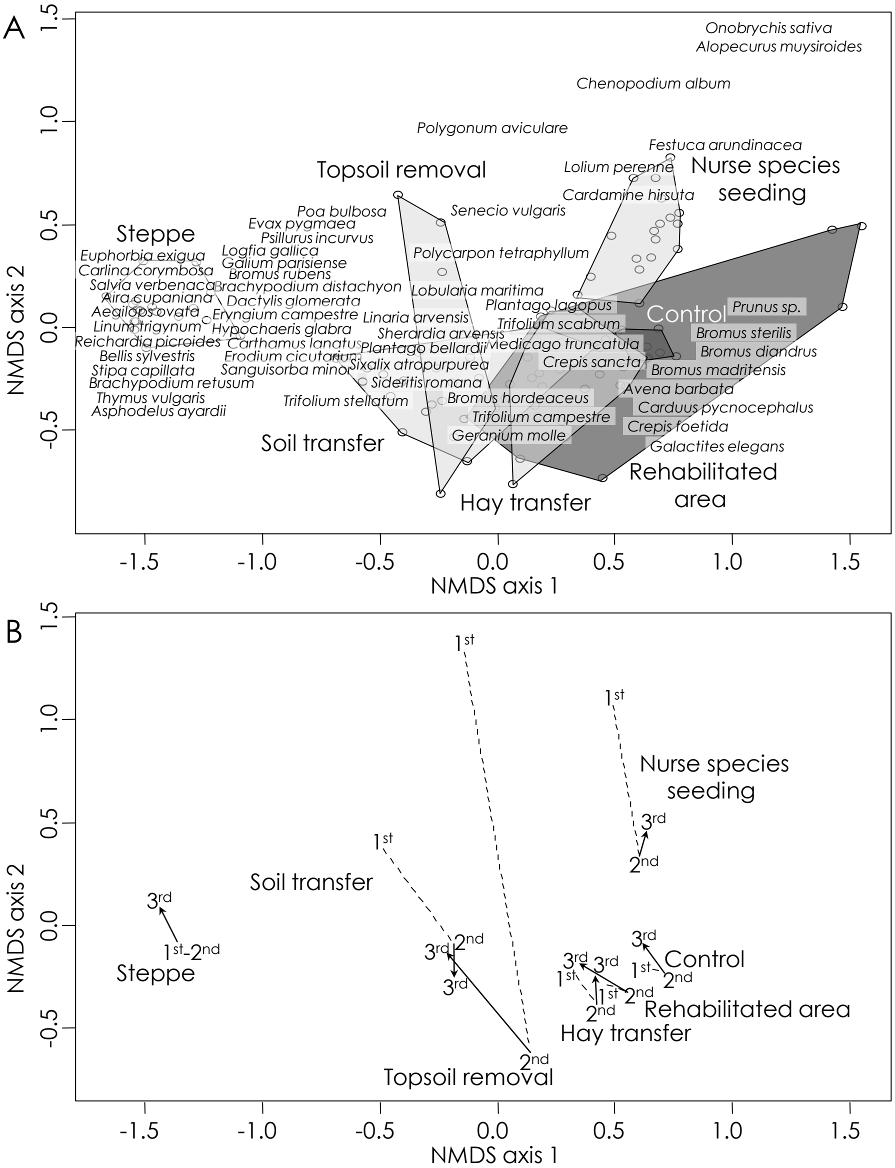


Figure 4.5: NMDS ordination based on 324 2x2m vegetation samples and the 149 species present in at least 3 samples. The A plot shows only the 2012 samples (open circles) grouped by treatments: steppe in white, soil transfer, hay transfer, topsoil removal and nurse species seeding in light grey and Rehabilitated area and control in dark grey. In the interests of clarity, only the 53 best correlated species are shown. The B plot shows the succession of vegetation for each treatment, according to the position of their barycenter, dashed lines represent the succession from the first year (1; 2010) to the second year (2; 2011), full arrows represent the succession from the second year to the third year (3; 2012).

4.3.4. Effects of rehabilitation and restoration on plant community composition

The NMDS ordination showed a gradient of plant community compositions from the steppe to the rehabilitated area, control and nurse species communities (Figure 4.5A). The control was very similar to the rehabilitated area community: dominated by grasses and thistles such as *Bromus diandrus* Roth, *B. madritensis*, *A. barbata*, *Carduus pycnocephalus* L. or *Galactites elegans* (All.) Soldano. The trajectories of their barycenter showed very slow dynamics from the first year to the third year (Figure 4.5B). Nurse species seeding was well discriminated on the ordination plot, characterized by the sown species: *L. perenne*, *F. arundinacea* and *O. sativa*. The trajectory showed a marked shift from the first year to the second year, characterized by a decrease of *O. sativa*, *Alopecurus muysiroides* Hudson and *C. album*. The hay transfer community was confounded with the rehabilitated area community, but on the steppe side of the gradient, characterized by more target forbs, such as *P. lagopus*, *Sixalix atropurpurea* (L.) Greuter et Burdet, *Sherardia arvensis* L.. The trajectory of its barycenter was like that of the rehabilitated area: very small changes occurred in composition and abundance of species from the first to the third year. The topsoil removal community was the one with the strongest dynamics (Figure 4.5B), from community dominated by ruderals, such as *Senecio vulgaris* L. or *Polycarpon tetraphyllum* (L.) L. or *Polygonum aviculare* L. to community very close to the soil transfer community. In the third year, these two communities were the closest to the steppe and were characterized by many target species, such as *Plantago bellardii* All., *Poa bulbosa* L., *B. distachyon*, *Eryngium campestre* L. or *Logfia gallica* (L.) Coss. & Germ.. The steppe was still well discriminated on the ordination by its characteristic species, such as *B. retusum*, *Stipa capillata* L., *T. vulgaris* or *Asphodelus ayardii* Jahand. & Maire.. The steppe showed almost no changes in plant composition and abundances from the first to the third year (Figure 4.5B).

The $CSII_{norm}$ did not show significant differences between years in the control and the rehabilitated area where it stayed relatively low (below 0.15) (Figure 4.6A). The nurse species seeding showed a slight significant increase from the first to the second year and the hay transfer from the second to the third year, but both stayed below 0.15 as well. The topsoil removal showed an increase of its $CSII_{norm}$ over the three years to reach 0.25±0.02 in the third year (Table 4.1). The soil transfer was the restoration treatment with the highest $CSII_{norm}$ from the first to the third year (0.44±0.04), but remained significantly different from the steppe (1.0±0.03). The HAI was relatively high in the control and rehabilitated area (above 0.8) and did not change over the years (Figure 4.6B). In nurse species seeding, topsoil removal and hay transfer, the HAI decreased and reached its lowest value in the third year. In the soil transfer, the HAI increased after the first year and decreased from the second to the third year. The highest HAI in the third year was found in the control and nurse species seeding (above 0.93; Table 4.1), rehabilitated area and hay transfer had intermediate values (around 0.87) whereas topsoil removal (0.783±0.008) and soil transfer (0.674±0.019) had the lowest values but still higher than the steppe (0.334±0.009).

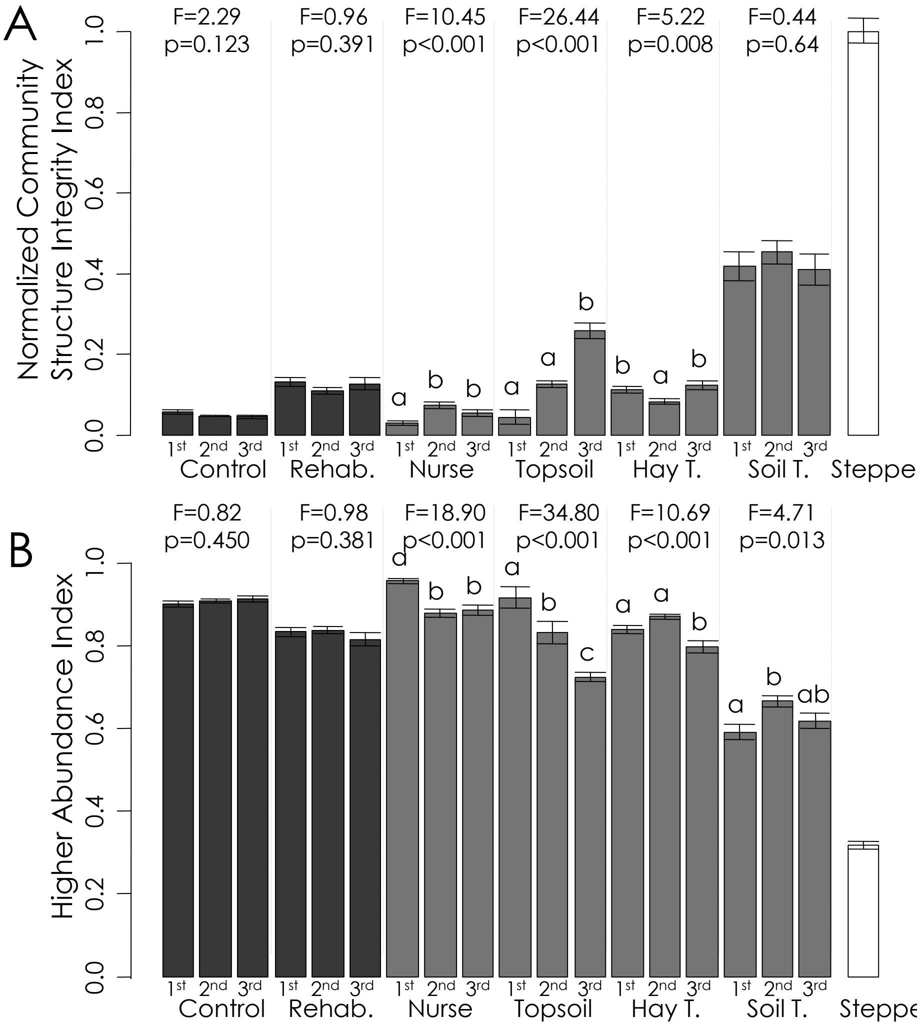


Figure 4.6: Means and standard errors of normalized Community Structure Integrity Index (A) and Higher Abundance Index (B) for the first three years (1st: 2010; 2nd: 2011; 3rd:2012) for each treatment: steppe (white), for restoration techniques (soil transfer (Soil T.), hay transfer (Hay T.), topsoil removal (Topsoil) and nurse species seeding (Nurse); light grey), for rehabilitated area (Rehab.; dark grey) and control (dark grey). The F and p value of ANOVA performed within each treatment to compare years are shown above the bars. Within a treatment, bars showing common letters do not show any significant differences according to Tukey Honest Signicant Differences post hoc tests.

4.4. Discussion

Spontaneous succession potential can be estimated by seed bank studies (Willems and Bik, 1998). Our results confirmed previous studies that have shown that the seed banks of previously cultivated areas rarely contain seeds from the target community but rather ruderal ones (Thompson and Grime, 1979; Graham and Hutchings, 1988a; Hutchings and Booth, 1996; Stroh et al., 2002; Buisson et al., 2006). Via priority effect (Ross and Harper, 1972; Kardol et al., 2012), this non-target seed bank can form dense cover that may affect the establishment of recolonizing target species (Baer et al., 2008; Standish et al., 2008). This pattern was observed on the rehabilitated area, where grasses, such as *A. barbata* or *Bromus* spp. dominated right from the first year (Jaunatre et al., 2012). Moreover, soil nutrient content is still affected by the cultivation legacy. Nitrogen is very labile and decreased to values similar to those of the steppe in three years, while potassium and phosphorus are still significantly higher. After the cessation of fertilization, long-term effect on plant communities persists (Dupouey et al., 2002; Jacquemyn et al., 2003; Smits et al., 2008; Královec et al., 2009), even if soil parameters have recovered their pre-fertilization values (Semelová et al., 2008). These environmental conditions resulted in high average height and vegetation cover which may have had a negative effect on germination and growth of less competitive light demanding target species (Hautier et al., 2009). The low recruitment of target species in the rehabilitated area, revealed by their stable low species-richness and composition, may be rooted in this heightened competition due to higher nutrient content (Henry et al., 2004). Succession toward a low productive community may be increased by biomass removal, for instance through mowing or grazing. Nevertheless, previous studies on the La Crau steppe ecosystem have shown that the plant community is still different in terms of composition and species-richness 30 years after the abandonment of cultivation (**Chapter 1**; (Römermann, Dutoit, et al., 2005; Buisson et al., 2006)) and more than 200 years after the abandonment of cultivation (**Chapter 2**). As spontaneous succession did not provide successful results with regard to the aim of restoration of the reference plant community, a more active restoration has to be considered in order to accelerate or to make possible its recovery (Cramer et al., 2008; Prach and Hobbs, 2008; Hölzel et al., 2012).

Topsoil removal allowed the reduction of the number of non-target species in the seed bank to levels as low as that of the seed bank of the steppe. Moreover, the nutrient content was significantly lowered by topsoil removal, as was expected in view of results from other ecosystems (Aerts et al., 1995; Patzelt et al., 2001; Verhagen et al., 2001; Allison and Ausden, 2004; Klimkowska, Kotowski, et al., 2010). As in Allison and Ausden's experiment (2004), pH and calcium content were increased by topsoil removal. This can be explained by the crumbling of the calcareous conglomerate top and/or the breaking of some calcareous stones during topsoil removal. As in Patzelt et al. (2001), in the early stage of restoration, we found low species-richness and ruderal species in the areas where the topsoil was removed (Jaunatre et al., 2012). In the following years, species-richness and target vegetation composition recovered as nutrient availability decreased (Temperton et al., 2012). This resilience was probably enhanced by the almost complete absence of competition, with dense cover of grasses (Allison and Ausden, 2004; Kiehl et al., 2006). Nevertheless, if a suitable habitat for the characteristic species of the reference steppe seems to have been restored by this method, the slow increase of species-richness between 2010 and 2013 shows that dispersal limitation is equally an active filter to limit the natural colonization of top soil removal sites.

Hay transfer showed very few changes compared to first year results (Jaunatre et al., 2012): species-richness was no higher than in the rehabilitated area and although it exhibited some target forbs, such as *P. lagopus*, *S. arvensis* or *S. atropurpurea*, the composition was still very close to that of the rehabilitated area. These results differ from those obtained in other hay transfer experiments where richness of target species increased significantly during the first years (Hölzel and Otte, 2003; Donath et al., 2007; Edwards et al., 2007; Coiffait-Gombault et al., 2011). A first hypotheses which could explain the low success of this hay transfer is the date of hay gathering, which was carried out in August. According to a local plant phenological study, this date corresponds to the seed dispersion period of several species but numerous other studied species disperse their seeds a few weeks earlier (Bourrely et al., 1983). The repetition over time of seed gathering can maximize the number of target species (Stevenson et al., 1997) and may be a solution to improve restoration success. A second hypothesis to explain the low success of hay transfer is the high density of more competitive species (mainly *A. barbata* and *Bromus* spp.). Seed mixture containing many low competitive species should be applied on appropriate substrate, for example, topsoil removal prior to hay transfer has shown successful results (Patzelt et al., 2001; Hölzel and Otte, 2003; Klimkowska, Kotowski, et al., 2010).

A lower cost solution may be to wait for the decrease in the high nutrient content due to cultivation legacies, as well as the decrease in vegetation cover and height (Bartha et al., 2003) using grazing, before transferring hay. Nevertheless, managers of large-scale projects may be reluctant to accept the staggering application of restoration processes over several years. A third hypothesis could be the low density of spread hay material: 1ha gathered, transferred on 3ha. This ratio is nevertheless close to the range applied on other dry grasslands (7:1-1:3, Kiehl et al., (2010)) and which has proved to be successful. Moreover, increasing the density would mean increasing the cost per hectare, and would require finding enough suitable donor areas.

As soil transfer is based on the destruction of a portion of the reference area, it cannot be a substitute for *in situ* conservation (McLean, 2003). Nevertheless this technique has provided very positive results. Soil nutrient content was not affected by soil transfer, in contrast to what sometimes occurs in habitat or turf translocation (Trueman et al., 2007). Only pH and calcium were higher than at the soil donor site. Such increases have already been noticed when soils are moved in the La Crau area (Coiffait-Gombault et al., 2012a) and can be attributed to the calcareous stones breaking during soil gathering. Right from the first year, species-richness recovered values similar to those of the steppe (Jaunatre et al., 2012), and have not significantly changed since then. Moreover the composition was close to that of the steppe, including many target species, as was observed in previous soil transfers in other ecosystems (Bullock, 1998; Good et al., 1999; Box, 2003; Trueman et al., 2007). However, vegetation structure is slightly different from the steppe, especially during the second year which was characterized by marked higher rainfall. This structure change is reflected in the restoration indices: the normalized Community Structure Integrity Index did not change over the three years, revealing stability in target species abundances, whereas the HAI increased, revealing an increase in non-target abundances compared to the steppe. These higher abundances are again explained by the density of grasses, such as *A. barbata* and *Bromus* spp.. The decrease of the HAI in 2012 is a more positive result, especially if this tendency can be maintained with grazing in the future (Gibson and Brown, 1992; Stroh et al., 2002). Several restoration projects using soil transfer have failed to maintain a high conservation value due to unsuitable management practices (Bullock, 1998; Box, 2003). The wide difference between the low potential which could be expected from the seed bank study and the mainly positive results obtained from the field vegetation in soil transfer has already been noticed and attributed either to the difference in volume (Willems and Bik, 1998; Jaunatre et al., 2012) or the difference in environmental conditions (Stevenson et al., 1997).

Nurse species seeding was the treatment with the lowest species-richness and the composition that differed most widely from that of the steppe. The $CSII_{norm}$ was lower than 0.04, and not significantly different from that of the control, which means that less than 4% of the steppe community has been restored. The short-term objective was to increase the abundance of target species and to lower the abundance of non-target species. The first objective was not achieved after three years. The second objective was partially achieved: non-target species which dominated in rehabilitated area, such as *A. barbata* and *Bromus* spp., had very low abundance in nurse species seeding. Nevertheless two of the sown (but non-target) species dominated: *F. arundinacea* and *L. perenne*. However the relatively low average height and vegetation cover generated by this technique could provide safe sites for further colonization of target species, especially if the sown grasses decrease with environmental conditions (Mitchley et al., 1996). The future dynamics of the community is unknown, but this raises questions, which are of interest in community ecology: i) will the sown species maintain their abundance? Some evidence seems to indicate that their abundance will decrease: the actual decrease in vegetation cover (mainly composed of the sown species), and the harsh environmental conditions for two non-Mediterranean species; ii) will safe sites be colonized by non-target species instead of target species? Some non-target species are already present in low abundance and their dispersion will be easier than for target species which will have to disperse from the surrounding steppe. There is a risk that *A. barbata* and *Bromus* spp. will colonize and saturate the released safe sites. However in the rehabilitated area where they currently dominate, they had benefited from the absence of competition from other established species. In the nurse species seeding safe sites, microsites will not have the same environmental conditions: sown species can exert at least low competition for light, soil water and nutrients. Without totally excluding the non-target grasses by competition, the sown nurse species can exert enough competition to prevent them from dominating and to allow safe sites to be established by target-species (Davies et al., 1997; Pywell et al., 2007). Such hypothetic interactions have to be monitored and confirmed both by models and in field studies, but this could be an interesting and innovative way to modify the spontaneous succession in ecosystems where the dynamics is arrested by some early succession competitive species (Connell and Slatyer, 1977).

Controlling grazing pressure on a large scale is not an easy task and the actual pressure is usually the result of a trade-off between the expected biomass production and the sheep breeders' ability to increase or decrease the number of sheep. This trade-off does not always meet the needs associated with restoration objectives, considering the climate variability. In the first two years of this restoration experiment, considering the relatively high spring precipitation in 2010 (191% of average precipitation in the January-April period) and 2011 (116%), the grazing pressure was relatively low for the first years (399 days*sheep^{-1}*ha^{-1}) and increased in 2011 and 2012 (618 days*sheep^{-1}*ha^{-1}). The differences in vegetation height and cover were significant between the grazed and ungrazed control only in 2012 (results not shown), which combines both higher grazing pressure and lower spring precipitation (48% of average precipitation in the January-April period). Grazing has been proved to be an efficient method to remove preferentially nutrient rich biomass (Stroh et al., 2002; Jacquemyn et al., 2003). However, the deposition of faeces may redistribute phosphorus (Henkin et al., 2010) and sheep should be only allowed to graze during the day and be kept in the sheepfold at night (Marrs, 1985). As this has been the traditional way of sheep herding in the La Crau area for more than 2000 years (Badan et al., 1995; Fabre, 1997; Henry et al., 2010), this beneficial management system will be applied in the long-term over the whole of the restored area (Meffre et al., 2011). The results obtained on vegetation argue in favor of carrying on with relatively high grazing pressure in order to encourage the establishment of target species (Gibson and Brown, 1992).

These experiments conducted at La Crau have shown that the current knowledge in ecological restoration can provide a basis for restoring some ecosystem components at least partially, and improving biodiversity and habitat quality compared to former intensive cultivation or to the natural resilience. The rehabilitation project resulted in the creation of a large area dominated by grasses and which constitutes a favorable habitat for numerous steppe birds (Wolff, 2011), but with vegetation that is different from that of the steppe. Even if some target species were successfully transferred by hay transfer, increasing the number of target species was not achieved by the end of the third year. Nurse species seeding seems to provide a suitable area for target species colonization, but probable competition with grasses has to be monitored. The best results are obtained by topsoil removal and soil transfer which allowed recovery of the species-richness and, partially of the composition. Nevertheless these relatively positive results were obtained at high economic and ecological costs and resulted in lower biodiversity compared to the reference, as in a review of 89 restoration projects (Benayas et al., 2009). This partial success, highlights the importance of *in situ* conservation of natural habitats in preference to possible restoration after their destruction.

Transition to Discussion

Chapter 4 assessed four restoration techniques applied on a large scale in the Cossure rehabilitation project. Several complementary experiments have been carried out within this project in order to assess the efficiency of combination or modification of the way each technique was applied. These complementary experiments have been monitored but due to lack of significant results in the short term, they have not been presented in this thesis. Nevertheless, we can provide a summary of preliminary results concerning i) various combinations of nurse species, ii) different hay transfer ratios, iii) combinations of topsoil removal with other techniques and iv) different methods of soil transfer.

TD.1. Combinations of sown nurse species

The objective was to measure the effect of each sown species on the restoration outcome. Three blocks were implemented, containing six 20x50m plots where species were sown alone or in combination: *Lolium perenne* L.; *Festuca arundinacea* Schreb.; *Onobrychis sativa* Lam; *L. perenne*-*O. sativa*; *L. perenne*-*F. arundinacea*; *F. arundinacea*-*O. sativa*. In each plot, a vegetation relevé was carried out on a 2x2m quadrat. For the three years, the results did not show any significant differences concerning plant community characteristics (e.g. species-richness, vegetation cover, etc.). Composition was obviously linked to the sown species identity but the difference was not as marked as could have been expected: some species were indeed present in plots were they were not planned to be sown. This could be explained by the fact that the size of plots was rather small considering the tool used to sow these treatments: a broadcast seeder. Thus, if sown species identity exert a significant differential effect on plant community characteristics, this effect could have been masked by the unplanned mixing of species.

TD.2. Different hay transfer ratios

The objective was to determine what transfer ratio between the gathering area and the transferring area allows the best transfer success. Six blocks were set, containing three 20x50m plots where hay was transferred with a 3:1; 1:1 or 1:3 ratio. As with the previous experiment, no significant difference was found between the different ratios. In the **Chapter 4**, one hypothesis to explain the low establishment of target species was the competition with dense cover of grasses such as *Bromus* spp.

or *A. barbata*. Even if it has been shown that increasing target species density may allow increasing their establishment (Dickson and Busby, 2009), the grass density has to be lowered in our case to overcome the competition (Henry et al., 2004; Dickson and Busby, 2009).

TD.3. Topsoil removal in combination with other restoration techniques

The objective was to test the efficiency of topsoil removal combined with other restoration techniques (nurse species seeding; hay transfer and soil transfer) and to measure how topsoil removal can improve their efficiency. We have already shown in **Chapter 4** that topsoil removal can decrease non-target seed bank and nutrient availability. The hypotheses were therefore that topsoil removal can decrease competition, increase species-richness and similarity to reference and especially the latter two when species dispersion is strengthened (i.e. when combined with hay or soil transfer). Within the topsoil removal area (0.5ha), no technique (further named as rehabilitated without topsoil), nurse species seeding, hay transfer and soil transfer were applied on three repeated 10x10m plots. Three vegetation relevés on 2x2m quadrats were carried out on each plot. In order to assess the effect of topsoil removal, we compared these relevés with those carried out in **Chapter 4** without topsoil removal. Results after three years show that competition, approximated with average height and vegetation cover, was not significantly decreased by topsoil removal for rehabilitated or nurse species seeding (Figure TD.1A & B). However average height was significantly decreased by topsoil removal with soil transfer, and vegetation cover was also significantly decreased by topsoil removal with hay transfer and soil transfer. Specie-richness and Bray-Curtis similarity were significantly increased by topsoil removal for all the techniques (Figure TD.1C & D). Hay transfer has a species-richness not significantly different from the steppe only with topsoil removal, and its Bray-Curtis similarity is higher than rehabilitated only when topsoil is removed. Our hypotheses are therefore confirmed by this experiment. Topsoil removal allows improvement of the effect of other restoration techniques and confirmed that a combination of hay transfer with topsoil removal is an effective way to restore species-rich plant communities (Patzelt et al., 2001; Hölzel and Otte, 2003; Klimkowska, Kotowski, et al., 2010). However the substantial costs involved in this operation need to be reduced (Klimkowska, Dzierża, et al., 2010). An alternative currently being assessed in another thesis (Bulot, In prep), is soil compaction. At a lower cost, it could decrease soil nutrient availability and space available for roots, and thus decrease the density of potentially competitive species.

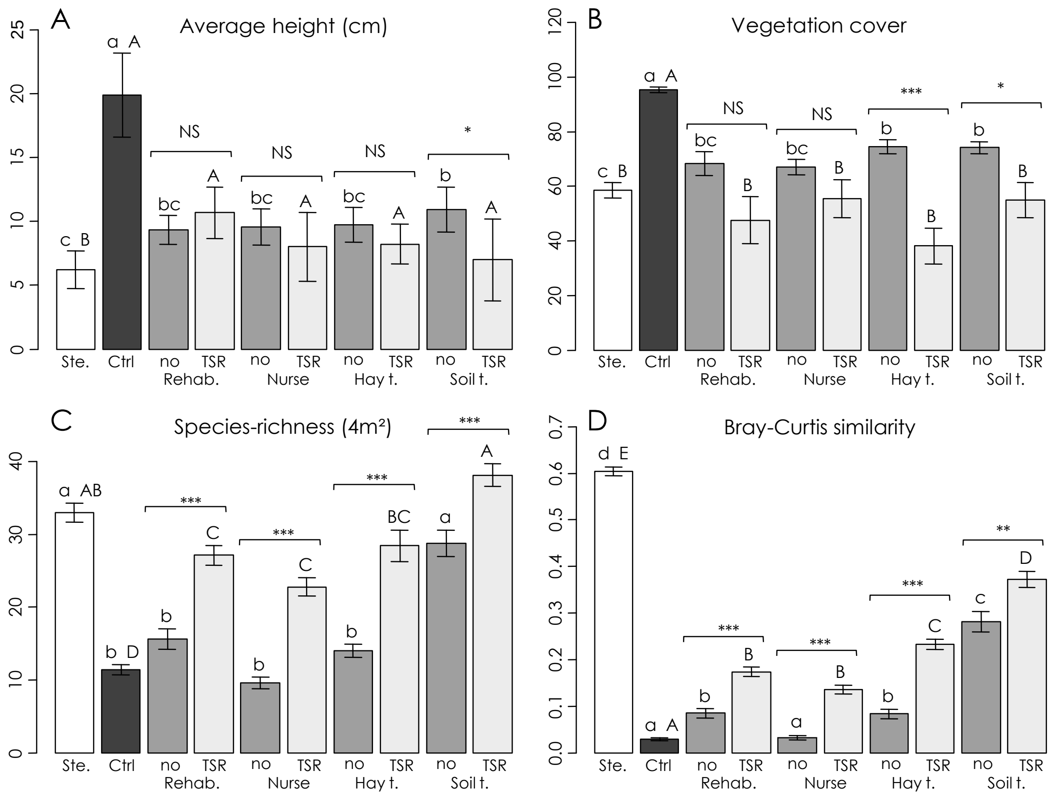


Figure TD.1: Effect of topsoil removal on average height (cm) (A), vegetation cover (%) (B), species-richness (4m²) (C) and Bray-Curtis similarity (D). Average±standard error of the Steppe (Ste.) and control (Ctrl) compared to rehabilitated area (Rehab.), nurse species seeding (Nurse), hay transfer (Hay t.) and soil transfer (Soil t.), either without topsoil removal (no) or with topsoil removal (TSR). Bars showing common letters do not show any significant differences according to Tukey Honest Significant Differences post hoc tests ($p>0.05$), without topsoil removal (lower case letters) and with topsoil removal (upper case letters). Within a technique, asterisks indicate significant differences according to t tests between with or without topsoil removal (***: $p<0.001$; **: $p<0.01$; *: $p<0.05$ and NS: $p>0.05$).

TD.4. Soil transfer: spreading excavated soil or transferring macroturf?

Soil transfer applied on a large-scale on the Cossure project was carried out by spreading excavated soil, which allowed a decrease in the ratio between gathered and transferred area (**Chapter 4**). On another restoration site (next to the donor site, Figure 4.1, **Chapter 4**) on a small experimental scale, macroturf transfer was compared to spreading excavated soil in order to measure the potential loss of diversity induced by the latter technique. Five 5x5m macroturf transfers and three 5x5m excavated soil spreading areas were implemented, and one vegetation relevé on a 2x2m quadrat was carried out on each transfer. After two years, the results show that species richness and Shannon evenness are not different from the steppe and between the two soil transfer methods (Figure TD.2.A & B). The plant community composition is very similar to what has been previously found with the bulk soil transfer described in **Chapter 4**. This is reflected by similar values of $CSII_{norm}$ or HAI. However, the macroturf transfer has a significantly higher $CSII_{norm}$ than excavated soil spreading, which could be explained by a better success of target perennial transfer, such as the steppe dominant *B. retusum* (Figure TD.2.C, D & E). These results are in accordance with previous studies which have shown similar results between excavated soil spreading or macroturf transfer (Good et al., 1999; Kiehl et al., 2010), but show that these methods can have varying success depending on transferred species characteristics (Aradottir, 2012). Roots of *B. retusum* seem very sensitive to soil disturbance, as almost no individuals are able to survive excavated soil spreading (**Chapter 4**; Jaunatre et al. (2012)) or soil disturbance alone (**Chapter 3 section 3.3.2.**; Coiffait-Gombault et al. (2012a)). Macroturf transfer is indeed up to now the only method which allows transferring *B. retusum*. A possible optimization of soil transfer could be a combination of i) macroturf transfer, which allows transferring the steppe dominant species: *B. retusum* with ii) excavated soil spreading, which allows the transfer of most of the species and reduces the area of donor site necessary to restore a given area.

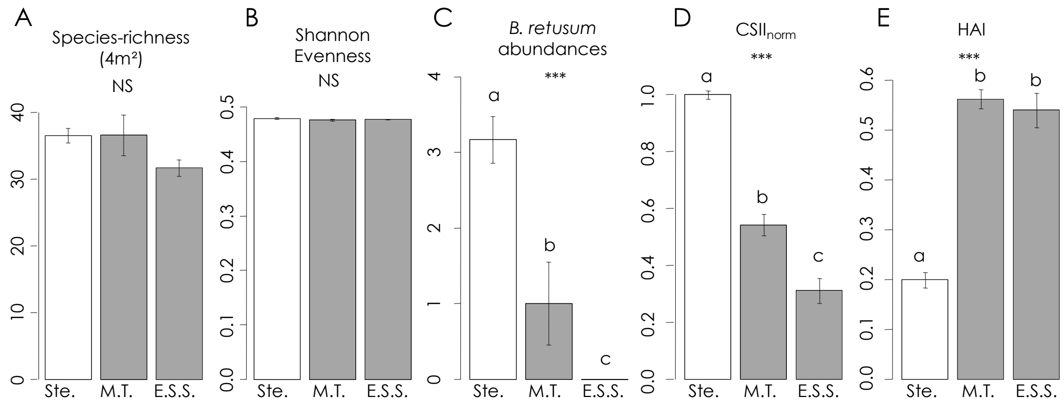


Figure TD.2: Effects of soil transfer type on several plant community parameters: Average±standard error of Species-richness (4m²) (A); Shannon evenness (B); *Brachypodium retusum* abundance (C), normalized community structure integrity index ($CSII_{norm}$) (D) and higher abundance index (HAI) (E) for steppe (Ste.), macroturf transfer (M.T.) and excavated soil spreading (E.S.S.). Stars represent the p value of the Analyses of Variance (***: $p<0.001$; **: $p<0.01$; *: $p<0.05$ and NS: $p>0.05$); bars showing common letters do not show any significant differences according to Tukey Honest Significant Differences post-hoc tests ($p>0.05$).

Brachypodium retusum, the dominant plant of the La Crau steppe of chich the biology remains to be studied. Photo credit: R. Jaunatre

One of the two sheep flocks on the rehabilitated area of the Cossure former orchard. Photo credit: R. Jaunatre

General Discussion

The thesis was focused on dynamics and restoration of a Mediterranean steppe after changes in land-uses (Figure D.1). **Chapter 1** showed a slow resilience after 30-40 years, and that the main driver of abandoned field plant communities is the abiotic filter, followed by the dispersion and biotic filters. **Chapter 2** confirmed the slow resilience, even in the long-term (150 years) for vegetation but showed that soil and mycorrhizal infestation was resilient in the mid-term (35 years). **Chapter 3** developed 3 indices allowing a new assessment of community resilience or restoration, while **Chapter 4** assessed several restoration techniques, and showed that the restoration of some plant community characteristics are possible and that soil transfer showed the best results, followed by topsoil removal, and then nurse species seeding and hay transfer.

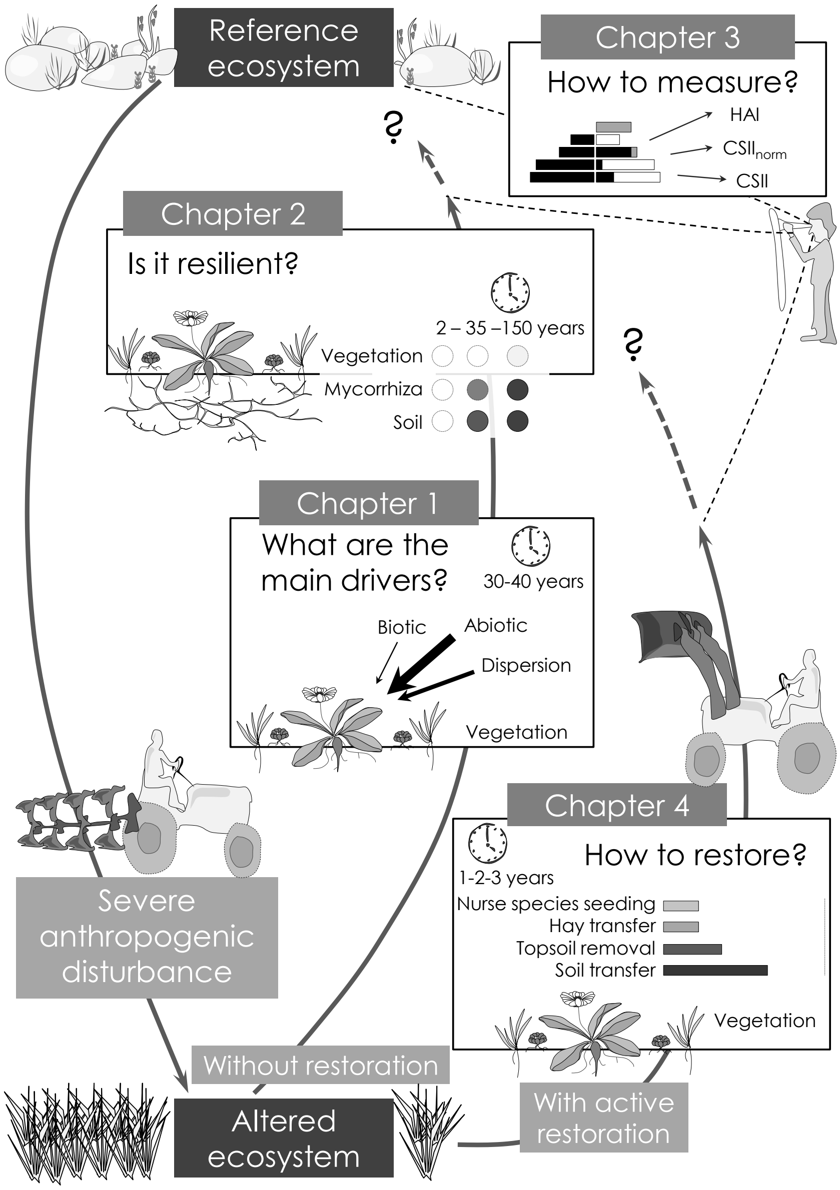


Figure D.1: Main insights of the thesis replaced in the general outlook of thesis organization.

D.1. Insights on plant community dynamics after severe disturbance

D.1.1. The slow resilience of the La Crau steppe

Previous studies have shown that after severe anthropogenic disturbance, plant community characteristics come closer to those of the pre-disturbance state (e.g. increasing species-richness and target abundances) over time (Meiners et al., 2002; Bonet and Pausas, 2004). These results are confirmed by **Chapter 2**, which shows an increased species-richness, and a composition which is closer to that of the steppe with time since last cultivation. This positive effect of time seems observable on a long time scale while it is not on a shorter time scale: in **Chapter 1**, the time-scale was 30 to 40 years since last cultivation and the time did not have any significant effect on the plant community. Despite this positive effect of time on a long time scale, the studies carried out in **Chapter 1** and **2** confirm that the La Crau steppe plant community is not resilient in the mid-term (30-40 years) or in the long-term (150 years). Such mid-term effects of severe anthropogenic disturbance have already been highlighted by previous studies in the La Crau area (Buisson and Dutoit, 2004; Römermann, Dutoit, et al., 2005; Coiffait-Gombault et al., 2012a) and very long-term effects have already been reported in other ecosystems (Forey and Dutoit, in press; Wells et al., 1976; Dupouey et al., 2002; Öster et al., 2009). Actual differences with the pre-disturbance state are usually explained by the fact that communities which were cultivated often passed biotic and abiotic thresholds (Whisenant, 1999). For the long or mid-term effect, we show that soil characteristics on the abandoned fields were slightly different from the steppe, but with no significant differences. This means that after three decades, the abiotic characteristics recovered. Moreover, we found in **Chapter 2** that after 35 years, three out of four species had recovered their pre-disturbance mycorrhizal infestation rate and after 150 years the three species found had recovered their pre-disturbance mycorrhizal infestation rate. As abiotic conditions recover and as at least some biotic interactions seem to recover, two hypotheses can explain the low resilience of the plant community: i) the low target-species propagule availability (production, dispersion, recruitment), either because the seed bank was depleted (Hutchings and Booth, 1996; Bossuyt and Honnay, 2008) or because of dispersal limitation (Bakker et al., 1996; Münzbergová and Herben, 2005) and ii) a durable establishment of non-target species and increased competition (Marrs, 2002; McCain et al., 2010), which can have long lasting effects due to priority effects even if abiotic conditions recovered (Semelová et al., 2008).

D.1.2. Drivers of plant community recovery

Concomitant to the 'why no resilience?' question, there is the 'what determines the recovery?' question. As it is presented earlier in the thesis (Introduction section I.4.4), the filter model is a useful model which provides a framework to understanding plant community assembly (Keddy, 1992; Pärtel and Zobel, 1999; Fattorinni and Halle, 2004; Lortie et al., 2004; Guisan and Rahbek, 2011) and hence to understanding plant community recovery. In **Chapter 1** we measured which part of the variability amongst secondary succession plant communities could be attributed to each filter. Our results show that, given the proxies used to characterize each filter, the most important was the abiotic filter, followed by the dispersion filter and finally the biotic filter (Figure D.2). Moreover we found that soil characteristics (phosphorus, potassium and calcium) exert a differential effect on both steppe and non-target species, the latter being favored by higher nutrient contents. Nutrient enrichment does not necessarily prevent target species from establishing but can enhance competition of non-target species due to their dense cover (Huenneke et al., 1990; Yurkonis and Meiners, 2004; Buisson et al., 2006). This is corroborated by the fact that steppe species abundances are significantly negatively correlated with the abundance of the dominant species of abandoned fields. We also found a significant effect of landscape in the surrounding on abandoned field plant communities: fields surrounded by cultivation exhibit a higher abundance of abandoned field characteristic species while those surrounded by steppe exhibit a higher abundance of steppe species. This confirms the importance of the species pool in the local surroundings of the community for the development of the target community (Tansley and Adamson, 1925; Pärtel et al., 1996; Alard and Poudevigne, 2002; Cook et al., 2005).

D.1.3. Convergence of results obtained with community dynamics and restoration

This graduation of filter importance is also confirmed by the results obtained in **Chapter 4** with restoration technique application. Indeed, the most convincing results were obtained with techniques which modify the abiotic conditions (soil transfer and topsoil removal), and then by techniques which strengthen dispersion if abiotic conditions have been restored (soil transfer or hay transfer combined with topsoil removal) (Figure D.2). In **Chapter 1** we measured the respective importance of each filter, without being able to rank them. **Chapter 4** and the complementary studies reported in the **transition to discussion** confirmed **Chapter 1** conclusions and previous studies that show that dispersion is a limiting factor for the La Crau steppe vegetation (Buisson and Dutoit, 2004; Römermann, Dutoit, et al., 2005; Buisson et al., 2006; Coiffait-Gombault et al., 2011), and also show that without controlling soil conditions, strengthening dispersion appears to be ineffective. This is in accordance with the threshold model with an ascendency of abiotic threshold (Whisenant, 1999).

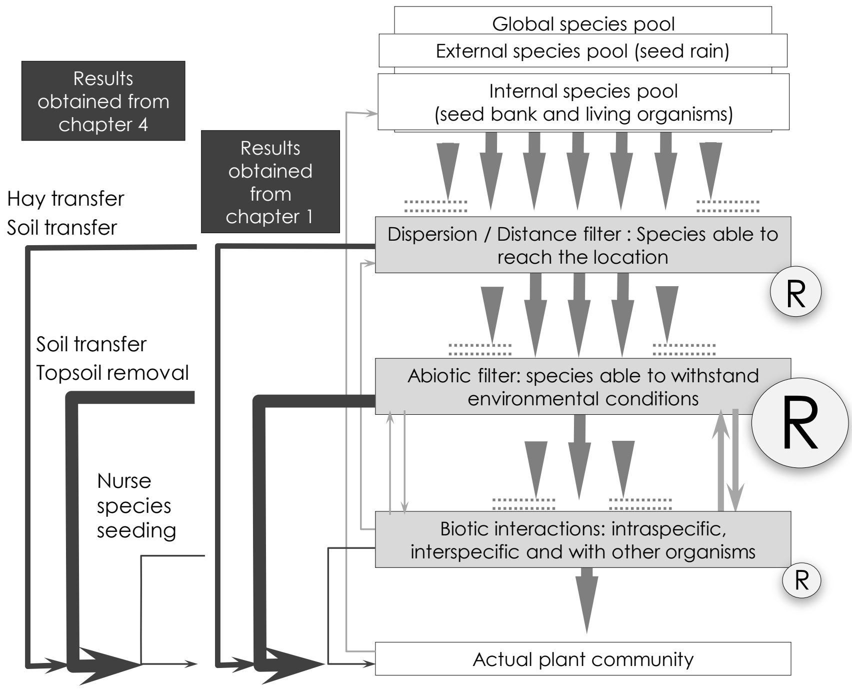


Figure D.2: Insights of Chapter 1 and 4 replaced in the filter model framework. White boxes represent species pools, either internal or external, and actual plant community. Light grey boxes represent filters: dispersion, abiotic and biotic. Large grey arrows represent species able to pass and those which are stopped by filters. Thinner grey arrows represent feedback occurring within filters or with species pools. This model is adapted from (Keddy, 1992; Zobel, 1997; Fattorinni and Halle, 2004; Lortie et al., 2004; Guisan and Rahbek, 2011). Dark grey arrows represent the effect of filters on actual plant community expected with the results obtained in **Chapter 1** or 4, the larger the arrow is, the greater the effect is expected to be. Discs marked with an "R" represent the restoration levers which can potentially be used in active restoration, the wider the disc, the more important the corresponding restoration lever, according to our findings in the La Crau area.

Concerning the La Crau area steppe plant community restoration we can therefore rank the 3 filters (Figure D.2): first the abiotic filter has to be restored, followed by the dispersion filter. The biotic filters comes third for several reasons: i) no positive interactions between plants have been identified so far (Coiffait-Gombault, 2011), ii) interactions with other organisms are poorly known in the La Crau area, although **Chapter 2** shows that in at least for three species out of the four, the mycorrhizal infestation rate is resilient in the mid-term, iii) negative interactions (mainly competition), are directly linked to environmental conditions, and thus an indirect effect on competition is expected if the abiotic filter is used as a restoration lever: either by decreasing nutrient contents or by increasing sheep grazing (while it can also be considered as a biotic interaction, grazing decreases nutrient availability and creates gaps).

D.2. Insights on plant community restoration

D.2.1. What are the benefits of restoration?

A very important question in restoration is « Do we know enough to intervene? » (Hobbs et al., 2011). From the work conducted in this thesis, in the La Crau area context, we know that: i) inaction will lead, in the short term, to a low species-richness and grassland dominated with species considered as relatively competitive by target species because of, among other things, their density (**Chapter 4**) and perhaps a species-rich but still different community on the very long-term especially without the dominant perennial grass species (**Chapter 2**); ii) active rehabilitation allows a fast recovery of a suitable landscape for steppe birds and orthoptera recolonization (Alignan, 2010; Wolff, 2011), the vegetation is mainly species poor but sometimes with interesting community characteristics (especially on restoration treatments topsoil removal and soil transfer; **Chapter 4**); iii) restoration, in the short term, does not allow full restoration of the reference community (less than 50% of the reference community structure for the best restoration treatment, **Chapter 3 and 4**). From a short term perspective, our results are in accordance with Benayas et al.'s review (2009) which shows that restoration does not allow attainment of the reference ecosystem but provides better results than without restoration (Figure D.3).

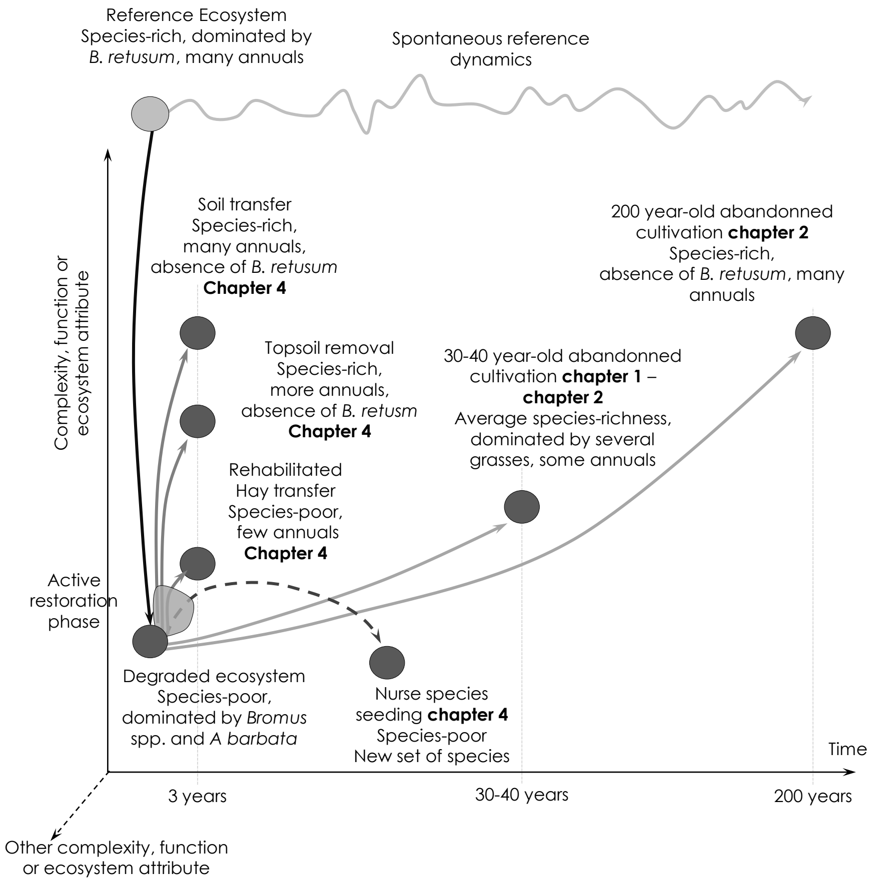


Figure D.3: Ecosystem states observed within the thesis replaced in the general model of restoration trajectories (cf Figure I.2), in a three dimensional plot: time; complexity or ecosystem function characterizing reference ecosystem; and other complexity, function or ecosystem attributes which do not characterize the reference ecosystem.

This third dimension is expressed by dashed lines. Modified from Aronson et al. (1993) and Buisson (2011).Historical contingency is proven to be determinant in plant community assembly (Chase, 2003; Collinge and Ray, 2009). Moreover it has been shown that former events, such as land-use activities, continue to influence long-term composition, structure and function of most ecosystems for decades or centuries after the events (Bellemare et al., 2002; Foster et al., 2003; Henry, 2009). The lack of resilience or lack of complete restoration *sensu stricto* may therefore be explained by the fact that ecological restoration cannot recreate the long-term sequence of events, such as the dispersion sequence (Fukami, 2004) or cycles of endogenous stress or disturbance events (Bartha et al., 2003). While the concept of alternative stable states is increasingly used as a restoration framework (Suding, 2004; Hobbs et al., 2008), it remains difficult to make uncertainty acceptable in restoration projects (Wallington et al., 2005). A major issue is, from now, what will happen in the future?

Will restored areas reach the reference characteristics in the long term? Will non-restored areas reach reference characteristics in the long term? Will both restored areas reach the same endpoint at the same time? Considering these questions, at least six scenarii can be expected (Figure D.4). The final endpoint could be reached before by the restored ecosystem and then by the non restored ecosystem (Figure D.4.A & C) or at the same time (Figure D.4.B & D); the final endpoint could be similar to reference on the long-term(Figure D.4A & B) or be below the reference on the long term (Figure D.4.C & D); the non-restored ecosystem could be at the end closer to the reference than the restored ecosystem (Figure D.4.E).

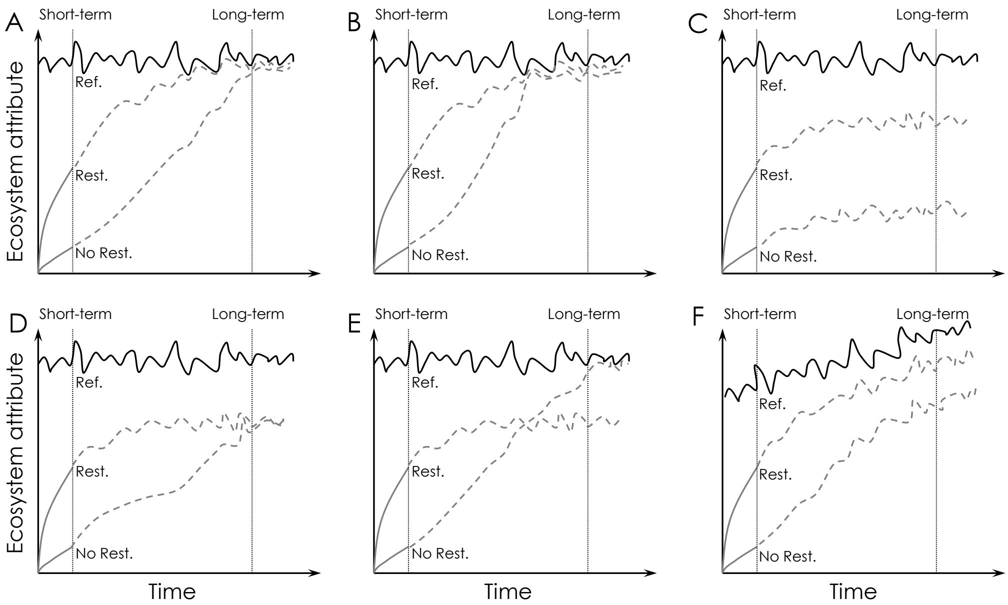


Figure D.4: Potential scenario of future outcomes of restored and non-restored ecosystems compared to the reference. The final endpoint is reached before by the restored ecosystem and then by the non-restored ecosystem (A,C) or at the same time (B,D); final endpoint is similar to reference in the long term (A,B) or is below the reference in the long term (C,D); the E scenario is when the non-restored ecosystem is at the end closer to the reference than the restored ecosystem, the F scenario is when the reference, restored and non-restored ecosystems have no stable endpoint in the long term. Ref. is for reference ecosystem, Rest. is for restored ecosystem and No Rest. is for non-restored ecosystem.

The reference seems currently to be at a sort of equilibrium, with an intrinsic variability attributed to climate variability and traditional land-uses. However, it is also conceivable that it is currently moving with a very slow dynamic, implying that restored or non-restored ecosystems would never be able to reach this moving target (Clewell and Aronson, 2007) (Figure D.4.F). A concept such as the “dynamic reference concept” (Hiers et al., 2012) allows the taking into account of such current dynamics of the reference ecosystem and to adjust both the target and the measurement of restoration success. Such approach is particularly relevant when considering the current global changes (Harris et al., 2006; Maestre, Salguero-Gómez, et al., 2012).

These questions are not only interesting from a theoretical point of view but also from a very applied perspective. Restoration is currently widely used to compensate for impacts on natural ecosystem (cf **Transition to Chapter 3**), and the definition of compensation is based on the equivalence between the loss and the gain obtained from restoration. On which state should the equivalence be based? Several options are available, among others: i) the current restored state; ii) a realistic expected state in the mid-term (e.g. ten years); iii) an uncertain expected state from a long-term perspective (e.g. hundreds or thousands years); iv) an unrealistic goal, even in a the very long-term. Depending on which option is chosen, the real outcome on biodiversity gain or loss is severely affected: if the first option is chosen the natural recovery, even if incomplete, will increase biodiversity with time and thus will lead to an underestimated biodiversity gain whereas if the last option is chosen, the unattained target will lead to an overestimated biodiversity gain (Figure D.5).

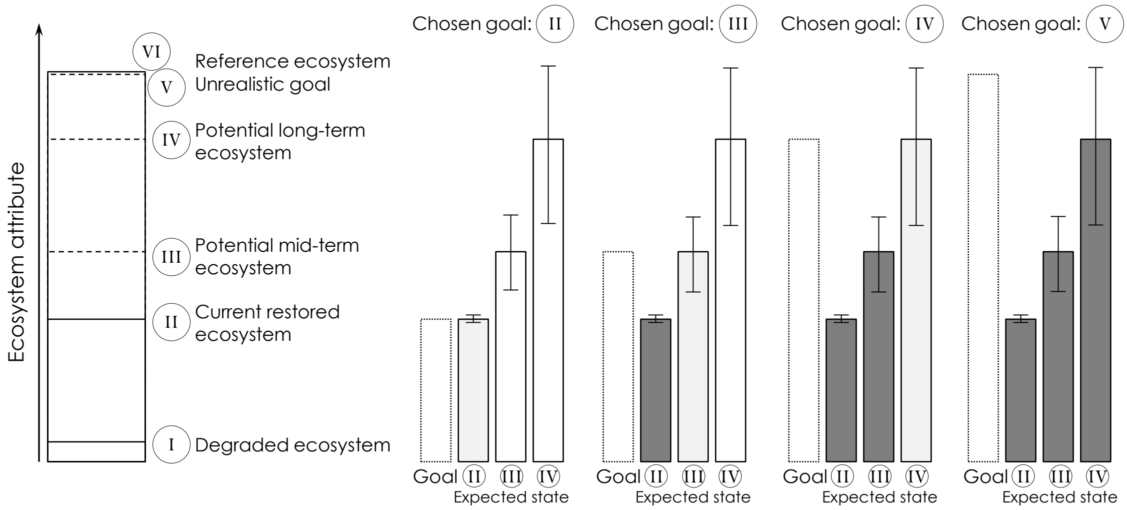


Figure D.5: Goals and realities of biodiversity gain or loss depending on time (Expected state) and on the chosen goal. The biodiversity gain can be well estimated (light grey), underestimated (dark grey) or overestimated (white). Error bars represent the uncertainty which could be attributed to the expected states.

D.2.2. On the notion of restorability

Further reflection should be carried out to clarify the different ecosystem states, whether they are goals, current results, expected results or aims. An idea could be to develop the concept of restorability, which would be a corollary to resilience. If resilience is the potentiality of natural restoration with spontaneous succession (Holling, 1973), the restorability would be the potentiality of restoration after active restoration. This potential depends on several parameters for a given ecosystem: i) obviously on the natural resilience of the ecosystem, but also ii) on the knowledge available about its intrinsic potentialities, its thresholds and about feasibility of restoration techniques to overcome these thresholds, iii) on the time needed to reach a given recovery rate, iv) on the cost of restoration implementation and v) on the severity of the degradation. The assessment of restorability could be based on expectations from current knowledge, but could also be based on real case studies where restoration has already been implemented (e.g. local or ecosystem specific reviews such as (Bullock, 1998; Muller et al., 1998; Fagan et al., 2008). If only one technique is used to restore a given area, and if the restored area obtains a $CSII_{norm}$ index = 0.2 at a given time, then the restorability index R = 0.2. When several techniques are used on a given site, we propose a method to calculate the restorability based on the method used to calculate the *h* index which characterizes the scientific output of a researcher (Hirsch, 2005). The restorability index R would therefore be for a given time the percentage of restored area R with a percentage of restoration ≥ R (e.g. using the $CSII_{norm}$ index, **Chapter 3**). For instance, a R_3=13 would mean that after three years, at least 13% of the restored areas have reached at least 13% of the reference ecosystem. R_3=13 is the restorability found for the Cossure project (Figure D.6), based on the average values for each restoration treatment and their respective areas of implementation. The result is a restorability R_3=13%, which means that concerning plant communities, the current knowledge in the La Crau area allows restoration of at least 13% of areas at 13% of reference community structure for an average cost of 35,000€ per ha.

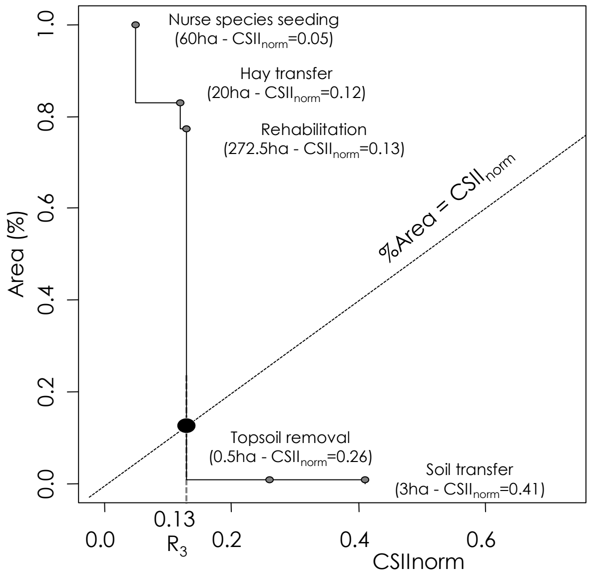


Figure D.6: Representation of restorability for the Cossure project. Each grey point represents one restoration technique and is placed on the plot given its cumulated percentage of total area application and its $CSII_{norm}$. The dashed line represents the line when percentage of area is equal to CSIInorm. The black point represents the intersection between the two lines, which determines the restorability after 3 years.

D.2.3. From restoration ecology to ecological restoration, what would be the best restoration technique to restore the steppe vegetation?

The Cossure project aimed at rehabilitating a steppe-like habitat for steppe birds to return, and restoration ecology research carried out within this project had as an ultimate goal the restoration of steppe vegetation (i.e. **Chapter 4** and (Jaunatre et al., 2012)). Restoration ecology has the role of informing and providing advice for future ecological restoration projects (Falk et al., 2006). From the data provided by our experiment on the former Cossure orchard, none of the assessed techniques seem to provide full satisfactory results in the very short term (3 years) (i.e. successful restoration and low environmental or financial cost). The main conclusion would therefore be to focus on the conservation of remnant steppe areas in order not to have to restore them. If we have to restore, the lowest cost is incurred by the rehabilitation only, but it allows the recovery of only an herbaceous plant community, species-poor and different from the steppe. The nurse species seeding is also a cheap restoration technique. It seems to provide suitable environmental conditions and is expected to be slowly colonized by target species, however uncertainty is for the moment very high. Hay transfer, topsoil removal and soil transfer techniques are more expensive techniques. Although the hay transfer technique has already shown great results on a small-scale on soil disturbed sites (Coiffait-Gombault et al., 2011), it has given only poor results when experimented in the Cossure project, where the transferred propagules seems to have suffered from competition with high grass density. Tospoil removal shows promising results after three years which have to be confirmed in the years to come. Soil transfer is, after three years, the technique which provides the best results. However, this technique has a major drawback which is the necessity to destroy a reference ecosystem area before being applied.

As it has been suggested in **Chapter 4** and in **Transition to discussion**, two methods seem to provide promising ways of restoring the steppe: i) the combination of a nutrient reducing technique with a strengthening dispersion technique seems to provide a promising way of restoring the steppe or ii) delay dispersion strengthening until nutrient availability and vegetation cover and average height all reach low levels more suitable for target species establishment. The dispersion strengthening technique could be the hay transfer, on the condition that the gathering is carried out at the relevant date given target species phenology (i.e. end of June or early July in the La Crau area (Bourrely et al., 1983)). In order to lower nutrient availability, the topsoil removal technique is a conceivable solution which has shown satisfying results in our experiment (**Chapter 4** and **Transition to discussion**). Less energy consuming methods have already been tested to reduce soil nutrients in other ecosystems, such as carbon amendment (e.g. sawdust or sucrose) which allows the decreasing of nutrient availability in the short term but needs to be repeated to exert significant effects on vegetation (Morghan and Seastedt, 1999; Corbin and D'Antonio, 2004). Another technique currently assessed is soil compaction, which at a lower environmental and financial cost than topsoil removal, can decrease soil nutrient availability and space available for roots, and thus decrease the density of potentially competitive species (Bulot, In prep).

Concerning soil transfer, its associated consequence of destroying a reference area has already been stressed in other studies reporting soil transfer results (Bullock, 1998; Box, 2003; Vécrin and Muller, 2003). Nevertheless, in the La Crau area, some steppe areas are still planned to be destroy, especially due to pipeline burying such as the ERIDAN project (GRT gaz, 2012), which is very close to the disturbances studied in Coiffait-Gombault thesis (2011). In this particular case, instead of replacing the steppe soil by ordinary soil after burial, it is conceivable to organize a soil transfer in order to not lose the steppe soil potentiality (Figure D.7). Usually, the soil used to bury the pipeline is either bought or is the steppe soil which has been stock-pilled for weeks or months, and which has therefore lost germinating potential of target-species propagules (Coiffait-Gombault et al., 2012a). The soil removed to dig the hole for the pipeline can be immediately (i.e. less than few days) transferred to another place along the pipeline where it has already been installed (i.e. like in Figure D.7). This would allow the 'rescuing' of some attributes of the steppe plant community and reduction of diversity loss. It seems worth remembering that such reduction of impact, as well as restoration, should be applied only if the project is proven to be unavoidable, and should not become permission for environmental destruction.

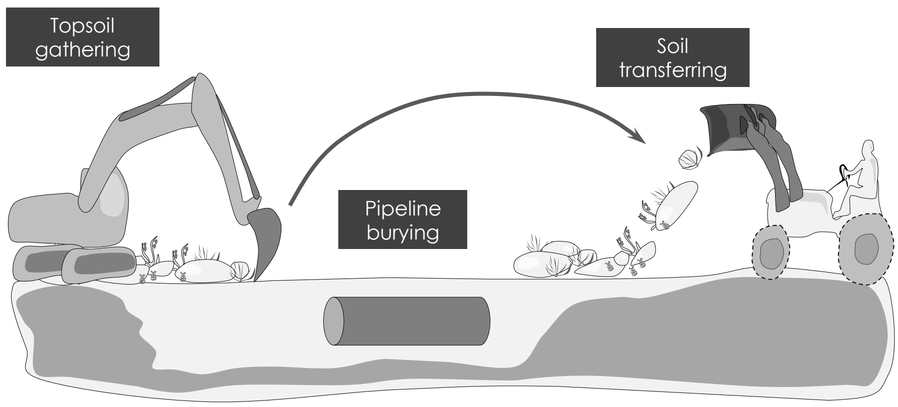


Figure D.7: Proposition of organization of pipeline burying in order to save a part of steppe plant community. This organization should be applied only if the project of destruction has been proved to be unavoidable.

Through the different questions addressed and the experiment implemented, this thesis has provided some insights concerning community ecology, restoration ecology and ecological restoration which are summarized in Table D.1. These contributions are small steps which call for further research of which the questions are exposed as perspectives for this thesis.

Table D.1. Thesis take home messages in community ecology, restoration ecology and ecological restoration.

Contribution of this thesis to **community ecology**
-**Chapter 1** and **2** confirm the low resilience of the steppe plant community both at mid- and long-term.
-**Chapter 1** confirms the role played by the three filters in the plant community recovery and finds that for the La Crau steppe plant community, the recovery is firstly driven by the abiotic filter, then by the dispersion filter and finally by the biotic filter.
-**Chapter 2** finds a better resilience of soil parameters and mycorrhizal infestation than for vegetation, but only in the long term.
-**Chapter 3** develops new indices measuring the recovery or resilience of community structure integrity.
Contribution of this thesis to **restoration ecology**
-**Chapter 3** develops new indices measuring the restoration of community structure integrity.
-**Chapter 4** confirms the difficulty of fully restoring a species-rich old plant community.
-**Chapter 4** confirms that dispersion strengthening techniques have to be combined with reducing competition.
-**Chapter 4** finds that for restoring the La Crau steppe vegetation, the best technique is soil transfer 1:3, followed by topsoil removal, then nurse species seeding and finally hay transfer 1:3.
-**Chapter 4** confirms the already stressed disadvantage of soil transfer that requires the destruction of a part of the reference area.
Contribution of this thesis to **ecological restoration**
-**Transition to Chapter 3** and (Jaunatre et al., 2011) provide advice to further plan a large-scale restoration project
-the thesis work is integrated within the whole restoration project and shows the possibility of transferring restoration ecology knowledge rehabilitating somewhat large areas.

D.3. Perspectives

D.3.1. Science fronts concerning the La Crau steppe vegetation

Before addressing the perspective directly linked to the research carried out in the thesis, I am now going to identify the state of knowledge and science fronts of the study object which could provide further insight into understanding both natural dynamics and restoration outcomes which have been addressed in this thesis (Thompson et al., 2001) (Figure D.8).

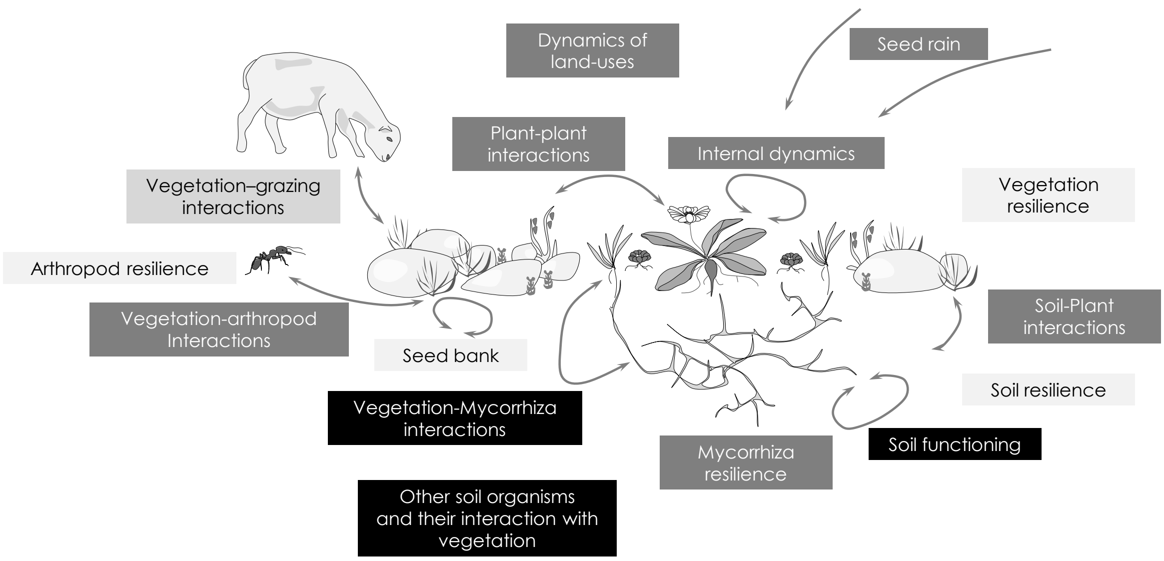


Figure D.8: Representation of advances in and lack of knowledge of the La Crau steppe vegetation. Each box corresponds to a topic which has already been addressed or not: Seed rain (Buisson et al., 2006); Internal dynamics: short time scale (Bourrely et al., 1983) or long time scale (Henry, 2009; Henry et al., 2010); Vegetation resilience (**Chapter 1** and 2, (Buisson and Dutoit, 2004; Römermann, Dutoit, et al., 2005; Coiffait-Gombault et al., 2012a); Soil-plant interactions (**Chapter 1**, (Coiffait-Gombault, 2011)); Soil resilience (**Chapter 1**,2 and 4, (Römermann, Dutoit, et al., 2005)); Soil functioning; Mycorrhiza resilience (**Chapter 2**); Vegetation-Mycorrhiza interactions; Other soil organisms and their interaction with vegetation; Seed bank (**Chapter 4**, (Römermann, Dutoit, et al., 2005; Buisson et al., 2006; Henry, 2009)); Vegetation-arthropod interactions (Bulot, In prep; Fadda, 2006); Arthropod resilience (Alignan, in prep; Fadda, 2006); Vegetation-grazing interactions (Adama, 1994; Henry, 2005); Plant-plant interactions (Masson, In prep; Buisson, 2005; Coiffait-Gombault, 2011); and Dynamics of land-uses (Gaignard, 2003). The color of the box correlates to amount of research already carried out. The lighter the box is, the more the topic has already been studied.

D.3.1.1. Temporal dynamics of vegetation

Some studies have focused on temporal dynamics of the La Crau steppe vegetation on a short-time scale (a year, Bourrely et al. (1983)) or long-time scale (centuries and millenaries (Henry, 2009; Henry et al., 2010)) but not on a mid-time scale (e.g. some years). It could be very interesting to follow permanent plots in order to know more about the internal dynamics of this plant community from year to year in relationship with climate variations. It could both provide insights into plant species coexistence (Maarel and Sykes, 1993) and help with the definition of reference ecosystem variability (Landres et al., 1999).

D.3.1.2. Influence of small abiotic variation on large or very small spatial scale

The fact that abiotic conditions are one of the main drivers of former arable field plant community has been shown in **Chapter 1**. To our knowledge, it is not known how the vegetation is influenced by i) the small variation in soil characteristics across the whole La Crau area or by ii) the microspatial (i.e. a few cm) heterogeneity induced by the long-term degradation of stones issued from different geological sources. However such information could also be relevant to adjust restoration of abiotic conditions.

D.3.1.3. Brachypodium retusum autecology

One of the main black boxes concerning the La Crau steppe vegetation is the poor understanding of the dominant species ecology: *Brachypodium retusum*. Although it is a relatively common species in Mediterranean landscapes, this species seems the most difficult to restore. Neither the hay transfer, nor the excavated soil spreading soil transfer allow the successful translocation of *B. retusum* (Coiffait-Gombault et al. (2011); Jaunatre et al. (2012) and **Chapter 4**). Only the macroturf transfer allows the preservation of some living individuals (**Transition to discussion**). One intriguing fact is that one year after soil gathering, the donor site exhibits a plant community which is again dominated by *B. retusum*. Therefore understanding the physiology and autecology of this species could be very useful for improving restoration techniques.

D.3.1.4. The soil organisms black box

Mycorrhizal infestation resilience has been studied for four species in **Chapter 2**, and as it was stressed in this chapter that it could be relevant to go to the community level to have a more precise view of mycorrhizae resilience. Moreover, it was highlighted that the way mycorrhizae affects individual growth and plant community structure is very complex. It could be relevant to study the effect of mycorrhizae on the La Crau plant communities, especially if certain mycorrhiza species have positive or negative feedback on target or non-target species (Callaway et al., 2001). Such studies on plant-soil organisms should not focus only on mycorrhizae but also on other organisms, such as microorganisms or nematodes, which can exert significant effects on plant communities (Torsvik and Øvreås, 2002; De Deyn et al., 2004; Kardol et al., 2007, 2009; Bever et al., 2010) but remains a black box for the La Crau steppe.

D.3.1.5. The functional trait approach

The use of functional traits is becoming more and more common in community ecology (Cadotte et al., 2011). These traits can contribute to the understanding of where species are able to live (Lavorel et al., 1997) or how species interact (Kissling et al., in press). This approach would mean a significant amount of work as no database is currently implemented on species traits in the La Crau area, of which most of the species are relatively common in Mediterranean landscapes but mostly with dwarf phenotypes (cf Introduction Section I.5.6.). Although needing work beforehand, this approach seems to have the potential to provide insights into the understanding of community dynamics or understanding restoration failure and success. This approach has indeed provided a useful framework for predicting community assembly (Götzenberger et al., in press; Guisan and Rahbek, 2011) or for interpreting either vegetation succession (Dölle et al. (2008)) or ecological restoration (Funk et al., 2008; Helsen et al., 2012).

D.3.1.6. The modeling approach

The modeling approach is being increasingly used to describe ecosystem dynamics and can provide a useful framework for environmental management (Hobbs et al., 2008; Wong et al., 2010). Given the amount of data available after ten years of research focusing on vegetation (Dutoit, Buisson, et al., 2011) and the data base which has been recently implemented (Lorenzetti, 2012), it seems conceivable to try to implement a model describing vegetation patterns, especially since recent modeling advances which allow the integration of more and more complexity (Clough, 2012).

D.3.2. Long-term monitoring of the restoration project

Short-term results of restoration projects are important as i) they provide sponsors, financing large scale restoration projects with indications for further applications, ii) they provide early information which can be used to assess further restoration technique applications, iii) they give an essential base-line which will be used to compare the development of communities following the application of various treatments after several years of monitoring, and iv) they allow managers to adjust their management, in this case grazing, of the site in order to ensure restoration success. Such short-term issues should not occult the need for long-term monitoring of restoration implementations (Block et al., 2001; Prach and Pyšek, 2001). At least for the Cossure project, monitoring should be continued because: i) the restored communities are still highly dynamic and are thus expected to show further changes, ii) to ensure the project success, adaptive management should be carried out regarding the monitoring results. For several reasons it seems unrealistic and unnecessary to continue the same monitoring intensity: i) one size of monitored quadrat (10*10m) is time consuming and did not provided significant additional information (we have not provided results taken from these quadrats in the thesis), ii) some complementary experiments seemed to have the potential for providing useful insights before implementation but ended up not being useful (cf. **Transition to discussion** sections **TD.1.** and **TD.2.**) iii) some complementary experiments (e.g. different methods of soil transfer and combination between topsoil removal and other restoration techniques, cf. **Transition to discussion** sections **TD.1.** and **TD.2.**) show interesting results which seem both scientifically and practically relevant but give more narrowed information and iv) the whole currently used protocol took approximately 12 full days per year to be carried out over a 3-5 week phenological window (Table D.2). That is why we propose a monitoring program which allows results to be compared to previous results and which limits the amount of time needed. It seems that in the context of the Cossure project, monitoring only the treatment applied on a large scale could be enough to adjust adaptive management (in the Cossure case, the main control lever is grazing intensity). The seven modalities are suggested for monitoring: control, rehabilitation, topsoil removal, nurse species seeding, hay transfer, soil transfer, and steppe. We propose two protocols, depending on the time available for doing relevés: normal and light. The normal protocol keeps the same amount of data which has been used for articles such as Jaunatre et al., (2012) or **Chapter 4**. It consists of three 2x2m quadrats in each of the six areas for the seven modalities: the total number of quadrats is 126. If we reckon on between 18 and 24 quadrats per days, it represents 6 days of field works. The light protocol consists of one quadrat in each of the six areas for the seven modalities: the total number of quadrats is 42 and it represents only 2 days of field works (Table D.2). Even if the light protocol can give some insights concerning the succession occurring on the restored areas and useful for management adjustment, the normal protocol is to be preferred in order to draw conclusions which can be statistically supported and to publish the results. Moreover, different soil transfer techniques and combining topsoil with other restoration techniques have shown interesting results that should be monitored carefully at least at a low frequency (e.g. each 5-10 years). As it can lack variation due to variability of climatic events, such low frequency monitoring should be interpreted in view of at least the yearly advocated light protocol.

Table D.2: Current and proposed future monitoring protocol. The quadrat size is 2*2m; the estimated working time is the number of days considering 18 to 24 quadrats per day.

	Currently used protocol	Normal protocol	Light protocol
Number of modalities	18	7	7
Number of replicates	3-18	18	6
Number of quadrats	157 (2*2) - 69 (10*10)	126	42
Estimated working time (days)	12	6	2

D.3.3. Restoration of the whole ecosystem

In this thesis we focused on plant communities although this is only one component of the whole ecosystem. The evaluation of restoration success should also look at other ecosystem characteristics (Tasser et al., 2008). Several guilds are studied in parallel within the Cossure project: birds, Orthoptera, Coleoptera, *Messor* ants, and microorganisms. Birds are monitored by the Reserve co-managers (CEN PACA): results from the first three years are globally positive, most of the species of conservation interest are recorded in the former orchard area during nesting period (*Pterocles alchata*, *Tetrax tetrax*) (Wolff, 2011). Moreover the lesser kestrel (*Falco naumanni*) has been observed hunting in the former orchard since the beginning of restoration works (Wolff, pers. com.), which could be related to the abundance of its prey in the rehabilitated areas. Orthoptera, which constitute 68% of Lesser kestrel diet

(Rodríguez et al., 2010), have indeed recovered in composition and abundance right from the first year (Alignan, 2010). This very positive result could be explained by the good dispersion abilities of grasshoppers and locusts and by the fact that they are only dependant on vegetation structure (Joern, 1982; Fischer et al., 1997; Marini et al., 2008). Coleoptera, which are dependent on vegetation composition (Luff and Rushton, 1989; Perner and Malt, 2003) show less successful recovery than grasshoppers (Gutjahr, 2011). One species of ant (*Messor barbarus*) is also monitored on the Cossure project, and shows a slow but effective natural recolonization of the site (Bulot, 2011). Moreover, root samples of the four species studied in **Chapter 2** have been gathered and prepared in order to count mycorrhizal infestation and to compare rates with or without soil transfer, and in addition soil samples have been lyophilized to be later analyzed with PLFA methods in order to assess microbial communities (Grayston et al., 2004; Ramsey et al., 2006). The mutualisation of the results obtained for different components would provide a better global assessment of the rehabilitation project. Moreover, trying to link the different components and to find how dynamics of restoration of one component could affect the restoration of others would allow the finding of 'limiting components' which could affect, slow down or stop the restoration dynamics of the whole ecosystem (Alard et al., 1998).

The relevés carried out in this study, as well as most of the monitoring carried out within the Cossure project are focused on the former orchard area (albeit always compared with the steppe in the surrounding). Although one of the objectives of the rehabilitation project was to restore the landscape connectivity between steppe patches (Meffre et al., 2011), to our knowledge, no study has been carried out to check if the Cossure rehabilitation had any effect on the landscape scale. In order to validate the benefits, or lack thereof, for biodiversity of the Cossure project, such questions could be of particular relevance, for instance: is the recolonization of the rehabilitated area by steppe birds related to a global steppe bird population increase or is it only related to a spatial displacement of populations? Such larger scale and landscape approaches could provide further insights into birds or other rapidly moving organisms, but also into plants. Lower diversity levels than expected or colonization credit has already been noticed in fragmented landscapes (Cristofoli et al., 2010; Piqueray et al., 2011). Measuring how the design of sheep grazing areas (e.g. in a way that allows the flock to go back and forth between steppe and restored areas or not) can improve connectivity and decrease colonization credit and therefore seems a relevant field of research for the La Crau areas.

D.3.4. Perspectives concerning the use and development of HAI and CSII indices

Chapter 3 presented new indices which provide a new tool for the assessment of restoration success. The presented indices are deliberately very simple, and could be used in their present state (with the script given in Appendix 4). These indices also set a base for further studies such as:

i) a large meta-analyses to assess restoration case studies, such as the study carried out by Rey Benayas et al., (2009). Such meta-analyses should allow the identification of which kinds of ecosystems are showing the most promising results and which are far from their restoration objectives. Moreover it could discriminate the projects according to their needs, either by increasing target abundances or decreasing non-target abundances. It would also certainly emphasize the differences between rehabilitation results and restoration results *sensu stricto*. This study could give arguments in favor of the limitation of ecosystem destruction as we are currently not able to restore it.

ii) the weighting of species in CSII or HAI calculation. All the species have indeed the same weight in the current form of these indices. It could also be relevant to give some weight to species according to their conservation value, indicator value concerning habitat definition, functional importance in the community, invasibility abilities, rarity, *etc.* Such weighting would deviate from the original goal of these indices: measuring in an easily interpretable way the difference from a reference community. Nevertheless it could give a more meaningful sense in some specific conservation purposes.

iii) the comparison of values given by the indices compared to the view environmental experts could have on the restored ecosystem. Such correlation between index-given and expert-given scores would also allow the adjustment weighting suggested in the 2nd perspective.

iv) the modification of CSII index calculation in order not to measure the distance from the target, but the distance from the initial state.

Conclusion

Conservation science plays a determinant role in actual nature conservation and choosing to communicate on the "half-full or the half-empty cup" of the results is a real dilemma (McCauley, 2012). Concerning the Cossure project several positive results can be pointed out:

- ✓ great advances have been made in how to implement such large-scale restoration project;
- ✓ advances have been made about how to restore the La Crau steppe ecosystem;
- ✓ biodiversity has been increased compared to that of the intensive orchard or even of the abandoned orchard.

However such very positive results cannot hide a more negative result: the whole ecosystem has not been fully restored and up to now, current knowledge has not allowed the restoration of the whole complexity and biodiversity of the La Crau steppe. Therefore, considering the results on the very low resilience (**Chapter 1 and 2**) and the incomplete restoration abilities (**Chapter 4**) stressed by the indices developed (**Chapter 3**), if I have only one take home message it would be: stop any destruction to the last remnants of this unique ecosystem. Following the famous sentence of E.O. Wilson (1992) "*The next century will, I believe, be the era of restoration in ecology*", let's hope that he was wrong and that one day restoration ecology becomes a superfluous discipline.

References

Adama, T.Z., 1994. Evaluation des différentes végétation pastorales et fourragères utilisées par des ovins dans une région steppique du sud de la France: La Crau.

Aerts, R., Huiszoon, A., Oostrum, J.H.A.V., Vijver, C.A.D.M.V.D., Willems, J.H., 1995. The Potential for Heathland Restoration on Formerly Arable Land at a Site in Drenthe, The Netherlands. Journal of Applied Ecology 32, 827–835.

Alard, D., Poudevigne, I., 2002. Biodiversity in changing landscapes: from species to patch assemblages to system organisation, in: Application of G.I.S and Remote Sensing in River Studies. Leuven, R.S.W., Poudevigne, I. & Teeuw, R., Backhuys Publishers, Leiden, pp. 9–27.

Alard, D., Poudevigne, I., Dutoit, T., Decaëns, T., 1998. Dynamique de la biodiversité dans un espace en mutation. Le cas des pelouses calcicoles de la basse vallée de Seine. Acta Oecologica 19, 275–284.

Alignan, J.F., In prep. Dynamique d'assemblages d'insectes dans des contextes de restauration écologique en plaine de Crau (Thèse de Doctorat - Université d'Avignon et des Pays de Vaucluse).

Alignan, J.F., 2010. Impact de la réhabilitation et de la restauration écologique d'un verger sur les populations d'orthoptères d'une steppe méditerraénenne (Stage Master 2 - Université d'Aix Marseille III).

Allen, E.B., 1989. The restoration of disturbed arid landscapes with special reference to mycorrhizal fungi. Journal of Arid Environments 17, 279–286.

Allen, M.F., 1982. Influence of Vesicular-Arbuscular Mycorrhizae on Water Movement Through Bouteloua gracilis (HBK) Lag Ex Steud. New Phytologist 191–196.

Allen, V.G., Batello, C., Berretta, E.J., Hodgson, J., Kothmann, M., Li, X., McIvor, J., Milne, J., Morris, C., Peeters, A., 2011. An international terminology for grazing lands and grazing animals. Grass and forage science 66, 2–28.

Allison, M., Ausden, M., 2004. Successful use of topsoil removal and soil amelioration to create heathland vegetation. Biological Conservation 120, 221–228.

Aradottir, A.L., 2012. Turf transplants for restoration of alpine vegetation: does size matter? Journal of Applied Ecology.

Aronson, J., Floret, C., Floc'h, E., Ovalle, C., Pontanier, R., 1993. Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. II. Case Studies in Southern Tunisia, Central Chile and Northern Cameroon. Restoration Ecology 1, 168–187.

Augé, R.M., 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11, 3–42.

Badan, O., Brun, J.-P., Congès Gaetan, O., 1995. Les bergeries romaines de la Crau d'Arles. Les origines de la transhumance en Provence. galia 52, 263–310.

Baer, S.G., Engle, D.M., Knops, J.M.H., Langeland, K.A., Maxwell, B.D., Menalled, F.D., Symstad, A.J., 2008. Vulnerability of Rehabilitated Agricultural Production Systems to Invasion by Nontarget Plant Species. Environmental Management 43, 189–196.

Baeten, L., Jacquemyn, H., Van Calster, H., Van Beek, E., Devlaeminck, R., Verheyen, K., Hermy, M., 2009. Low recruitment across life stages partly accounts for the slow colonization of forest herbs. Journal of Ecology 97, 109–117.

Baize, D., 2000. Guide des analyses en pédologie, 2ème ed. INRA, Paris, France.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution 14, 63–68.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45, 461–490.

Balcombe, C., Anderson, J., Fortney, R., Rentch, J., Grafton, W., Kordek, W., 2005. A comparison of plant communities in mitigation and reference wetlands in the mid-appalachians. Wetlands 25, 130–142.

Balmford, A., Bennun, L., ten Brink, B., Cooper, D., Côté, I.M., Crane, P., Dobson, A., Dudley, N., Dutton, I., Green, R.E., Gregory, R.D., Harrison, J., Kennedy, E.T., Kremen, C., Leader-Williams, N., Lovejoy, T.E., Mace, G., May, R., Mayaux, P., Morling, P., Phillips, J., Redford, K., Ricketts, T.H., Rodríguez, J.P., Sanjayan, M., Schei, P.J., van Jaarsveld, A.S., Walther, B.A., 2005. The Convention on Biological Diversity's 2010 Target. Science 307, 212–213.

Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. Trends in Ecology & Evolution 18, 326–330.

Barbaro, L., Dutoit, T., Cozic, P., 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.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57.

Bartha, S., Meiners, S.J., Pickett, S.T.A., Cadenasso, M.L., 2003. Plant colonization windows in a mesic old field succession. Applied Vegetation Science 6, 205–212.

Beisner, B., Haydon, D., Cuddington, K., 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1, 376–382.

Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography 29, 1401–1420.

Benayas, J.M.R., Newton, A.C., Diaz, A., Bullock, J.M., 2009. Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis. Science 325, 1121–1124.

Benjamin, K., Domon, G., Bouchard, A., 2005. Vegetation Composition and Succession of Abandoned Farmland: Effects of Ecological, Historical and Spatial Factors. Landscape Ecology 20, 627–647.

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society. Series B (Methodological) 57, 289–300.

Bever, J.D., 2002. Negative feedback within a mutualism: host–specific growth of mycorrhizal fungi reduces plant benefit. Proceedings of the Royal Society of London. Series B: Biological Sciences 269, 2595–2601.

Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C., Stock, W.D., Tibbett, M., Zobel, M., 2010. Rooting theories of plant community ecology in microbial interactions. Trends in Ecology & Evolution 25, 468–478.

Bever, J.D., Schultz, P.A., Pringle, A., Morton, J.B., 2001. Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. Bioscience 51, 923–932.

Birks, H.H., Birks, H.J.B., Kaland, P.E., Moe, D., 1989. The Cultural Landscape: Past, Present and Future. Cambridge University Press.

Bischoff, A., 2002. Dispersal and establishment of floodplain grassland species as limiting factors in restoration. Biological Conservation 104, 25–33.

Block, W.M., Franklin, A.B., Ward, J.P., Ganey, J.L., White, G.C., 2001. Design and Implementation of Monitoring Studies to Evaluate the Success of Ecological Restoration on Wildlife. Restoration Ecology 9, 293–303.

Bolan, N.S., 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant and Soil 134, 189–207.

Bonet, A., 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. Journal of Arid Environments 56, 213–233.

Bonet, A., Pausas, J., 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecology 174, 257–270.

Bonnier, G., 1985. Flore complète portative de la France, de la Suisse et de la Belgique. Belin.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73, 1045–1055.

Bossuyt, B., Honnay, O., 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. Journal of Vegetation Science 19, 875–884.

Bourrely, M., Borel, L., Devaux, J.P., Louis-Palluel, J., Archiloque, A., 1983. Dynamique annuelle et production primaire nette de l'ecosystème steppique de Crau (Bouches du Rhône). Biologie-Ecologie méditerranéenne 10, 55–82.

Box, J., 2003. Critical Factors and Evaluation Criteria for Habitat Translocation. Journal of Environmental Planning and Management 46, 839.

Bradshaw, A.., 1987. Restoration: an acid test for ecology, in: Restoration Ecology, A Synthetic Approach to Ecological Research. Jordan III, W.R., Gilpin, M.E. & Aber, J.D., Cambridge university press, Cambridge, pp. 23–29.

Braun-Blanquet, J., Roussine, N., Nègre, R., Emberger, L., 1952. Les groupements végétaux de la France Méditerranéenne. CNRS, Paris, France.

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2006. A unified framework for assessment and application of ecological thresholds. Rangeland Ecology & Management 59, 225–236.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96, 18–34.

Brundrett, M.C., Abbott, L.K., 1994. Mycorrhizal fungus propagules in the jarrah forest. New Phytologist 127, 539–546.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18, 119–125.

Buisson, E., 2005. Ecological restoration of Mediterranean grasslands in Provence and California (Thèse de Doctorat - Université Paul Cézanne Marseille).

Buisson, E., 2011. Community and restoration ecology, importance of disturbance, natural resilience and assembly rules (Thèse d'Habilitation à Diriger les Recherches - Université d'Avignon et des Pays de Vaucluse).

Buisson, E., Dutoit, T., 2004. Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe. Plant Ecology 174, 371–384.

Buisson, E., Dutoit, T., 2006. Creation of the natural reserve of La Crau: Implications for the creation and management of protected areas. Journal of Environmental Management 80, 318–326.

Buisson, E., Dutoit, T., Roche, P., Duhem, C., Campagne, P., Tatoni, T., 2009. The Plain of La Crau, Provence, in: Cultural Landscapes of Europe. Krzywinski, K., O'Connell, M., Küster, H., Bremen, Germany, pp. 96–99.

Buisson, E., Dutoit, T., Torre, F., Römermann, C., Poschlod, P., 2006. The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes. Agriculture, Ecosystems & Environment 115, 6–14.

Buisson, E., Dutoit, T., Wolff, A., 2004. Bilan de trente années de recherches en écologie dans la steppe de Crau (Bouches-du-Rhône, sud-est de la France). Ecologia Mediterranea 30, 7–24.

Bullock, J.M., 1998. Community translocation in Britain: Setting objectives and measuring consequences. Biological Conservation 84, 199–214.

Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in Ecology & Evolution 26, 541–549.

Bulot, A., In prep. Restauration écologique de la plaine de Crau suite à une fuite d'hydrocarbures: de l'ingénierie civile "écologisée" à l'ingénierie écologique par l'utilisation des fourmis. (Thèse de Doctorat - Université d'Avignon et des Pays de Vaucluse).

Bulot, A., 2011. La fourmi Messor barbarus comme ingénieur de la restauration: mise au point d'un protocole expérimental d'implantation (Stage Master 2 - Université d'Aix Marseille III).

Burel, F., Baudry, J., 1999. Ecologie du paysage. Concepts, méthodes et applications Paris, TEC & DOC.

Burrows, R.L., Pfleger, F.L., 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80, 120–130.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of applied ecology 48, 1079–1087.

Cairns, J.J., 2000. Setting ecological restoration goals for technical feasibility and scientific validity. Ecological Engineering 15, 171–180.

Callaway, R., Newingham, B., Zabinski, C.A., Mahall, B.E., 2001. Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbours. Ecology Letters 4, 429–433.

Callaway, R.M., 2007. Positive Interactions and Interdependence in Plant Communities, 1st ed. Springer.

Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4, 765–781.

Cassini, J.D., Cassini, J., Cassini, C.F., Cassini, D., 1778. Carte de Cassini de la région d'Aix en Provence et Légende.

Chabran, F., 2011. Etat de l'art de la compensation écologique par l'offre. Le cas de la première réserve d'actifs naturels: le projet Cossure. (Stage Ingénieur - Isara Lyon).

Chabran, F., Napoléone, C., 2012. Les conditions du développements des banques d'actifs naturels en France. Analyse du régime institutionnel de la première Réserve d'Actifs Naturels française. Développement durable et territoires 3, 1–14.

Champres, J., 2008. Définitions mesures conservatoires, d'évitement, de réduction et de compensation. http://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&ved=0CCIQFjAA&url=http%3A%2F%2Fwww.enjeuxbiodiversite.net%2Ftel%2FCERTU%2520-%2520S%25E9mantique.ppt&ei=H6g7UOzAAsuWhQeByIGYCA&usg=AFQjCNEMyeyy0qDIZIlrwt79jITEIjSh6Q&cad=rja.

Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic Control over the Functioning of Ecosystems. Science 277, 500 – 504.

Charpentier, A., Mesléard, F., Grillas, P., 1998. The role of water level and salinity in the regulation of Juncus gerardi populations in former ricefields in southern France. Journal of Vegetation Science 9, 361–370.

Chase, J.M., 2003. Community assembly: when should history matter? Oecologia 136, 489–498.

Chave, J., 2004. Neutral theory and community ecology. Ecology Letters 7, 241–253.

Chessel, D., Dufour, A.B., Thioulouse, J., 2004. The ade4 package-I- One-table methods. R News 4, 5–10.

Cheylan, G., 1975. Esquisse écologique d'une zone semi-aride: la Crau (Bouches-du-Rhône). Alauda 43, 23–54.

Cheylan, G., Bence, P., Boutin, J., Dhermain, F., Olioso, G., Vidal,, P., 1983. L'utilisation du milieu par les oiseaux de la Crau. Biologie-Ecologie méditerranéenne 10, 83–106.

Cheylan, G., Demandolx-Dedons, J. de, 1998. Patrimoine naturel et pratiques pastorales en Crau pour une gestion globale de la plaine, CEEP. ed. Aix en Provence.

Cheylan, M., Grillet, P., 2005. Statut passé et actuel du lézard ocellé (Lacerta lepida, Sauriens, Lacertidés) en France. Implication en termes de conservation. Vie et Milieu 55, 15–30.

Choi, Y.D., 2004. Theories for ecological restoration in changing environment: Toward "futuristic" restoration. Ecological Research 19, 75–81.

Choi, Y.D., 2007. Restoration ecology to the future: a call for new paradigm. Restoration Ecology 15, 351–353.

Clements, F.E., 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington.

Clements, F.E., 1936. Nature and Structure of the Climax. Journal of Ecology 24, 252–284.

Clewell, A.F., Aronson, J., 2007. Ecological Restoration: Principles, Values, and Structure of an Emerging Profession, 1st ed. Island Press.

Clough, Y., 2012. A generalized approach to modeling and estimating indirect effects in ecology. Ecology 93, 1809–1815.

Coffin, D.P., Lauenroth, W.K., Burke, I.C., 1996. Recovery of Vegetation in a Semiarid Grassland 53 Years after Disturbance. Ecological Applications 6, 538–555.

Coiffait-Gombault, C., 2011. Règles d'assemblage et restauration écologique des communautés végétales herbacées méditerranéennes. Le cas de la Plaine de Crau (Bouches-du-Rhône, France) (Thèse de Doctorat - Université d'Avignon et des Pays de Vaucluse).

Coiffait-Gombault, C., Buisson, E., Dutoit, T., 2011. Hay Transfer Promotes Establishment of Mediterranean Steppe Vegetation on Soil Disturbed by Pipeline Construction. Restoration Ecology 19, 214–222.

Coiffait-Gombault, C., Buisson, E., Dutoit, T., 2012a. Are old Mediterranean grasslands resilient to human disturbances? Acta Oecologica 43, 86–94.

Coiffait-Gombault, C., Buisson, E., Dutoit, T., 2012b. Using a two-phase sowing approach in restoration: sowing foundation species to restore, and subordinate species to evaluate restoration success. Applied Vegetation Science 15, 277–289.
Collinge, S.K., Ray, C., 2009. Transient patterns in the assembly of vernal pool plant communities. Ecology 90, 3313–3323.
Colomb, E., Roux, R.M., 1978. La Crau, données nouvelles et interprétations. Géologie Méditerranéenne 57, 31–42.
Combes, F., 1989. Restauration des terrains en montagne, du rêve à la réalité. Revue Forestière Française 41, 91–106.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111, 1119–1144.
Convention on Biological Diversity, 1992. Convention on Biological Diversity.
Convention on Biological Diversity, 2011. Ways and means to support ecosystem restoration.
Cook, W.M., Yao, J., Foster, B.L., Holt, R.D., Patrick, L.B., 2005. Secondary Succession in an Experimentally Fragmented Landscape: Community Patterns across Space and Time. Ecology 86, 1267–1279.
Coquiot, G., 1925. Renoir. Albin Michel.
Corbin, J.D., D'Antonio, C.M., 2004. Can Carbon Addition Increase Competitiveness of Native Grasses? A Case Study from California. Restoration Ecology 12, 36–43.
Costanza, R., Fisher, B., Mulder, K., Liu, S., Christopher, T., 2007. Biodiversity and ecosystem services: A multi-scale empirical study of the relationship between species richness and net primary production. Ecological Economics 61, 478–491.
Cramer, V.A., Hobbs, R.J., International, S. for E.R., 2007. Old fields: dynamics and restoration of abandoned farmland. Island Press.
Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology & Evolution 23, 104–112.
Cristofoli, S., Piqueray, J., Dufrêne, M., Bizoux, J.P., Mahy, G., 2010. Colonization credit in restored wet heathlands. Restoration Ecology 18, 645–655.
Crutzen, P.J., 2002. Geology of mankind. Nature 415, 23–23.

D'Antonio, C., Bainbridge, S., Kennedy, C., Bartolome, J., Reynolds, S., 2003. Ecology and Restoration of California Grasslands with special emphasis on the influence of fire and grazing on native grassland species.
Daily, G.C., Matson, P.A., 2008. Ecosystem services: From theory to implementation. PNAS 105, 9455–9456.
Davies, D.M., Graves, J.D., Elias, C.O., Williams, P.J., 1997. The impact of Rhinanthus spp. on sward productivity and composition: Implications for the restoration of species-rich grasslands. Biological Conservation 82, 87–93.
Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J., Briggs, J.C., 2011. Don't judge species on their origins. Nature 474, 153–154.

Davy, A.J., 2002. Establishment and manipulation of plant populations and communities in terrestrial systems, in: Handbook of Ecological Restoration. Perrow M.R. & Davy A. J. Cambridge University Press, Cambridge, pp. 223–241.

de Blois, S., Domon, G., Bouchard, A., 2001. Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. Landscape Ecology 16, 421–436.

De Deyn, G.B., Raaijmakers, C.E., Van Der Putten, W.H., 2004. Plant community development is affected by nutrients and soil biota. Journal of Ecology 92, 824–834.

Debussche, M., Escarré, J., Lepart, J., Houssard, C., Lavorel, S., 1996. Changes in Mediterranean plant succession: old-fields revisited. Journal of Vegetation Science 7, 519–526.

Deutschewitz, K., Lausch, A., Kuhn, I., Klotz, S., 2003. Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Global Ecol Biogeography 12, 299–311.

Devaux, J.P., Archiloque, A., Borel, L., Bourrely, M., Louis-Palluel, J., 1983. Notice de la carte phyto-écologique de la Crau (Bouches du Rhône). Biologie-Ecologie méditerranéenne 10, 5–54.

Deverre, C., 1996. La nature mise au propre dans la steppe de Crau et la forêt du Var. Études rurales 141, 45–61.

Dickson, T.L., Busby, W.H., 2009. Forb Species Establishment Increases with Decreased Grass Seeding Density and with Increased Forb Seeding Density in a Northeast Kansas, U.S.A., Experimental Prairie Restoration. Restoration Ecology 17, 597–605.

Dölle, M., Bernhardt-Römermann, M., Parth, A., Schmidt, W., 2008. Changes in life history trait composition during undisturbed old-field succession. Flora-Morphology, Distribution, Functional Ecology of Plants 203, 508–522.

Donath, T.W., Bissels, S., Hölzel, N., Otte, A., 2007. Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. Biological Conservation 138, 224–234.

Donath, T.W., Holzel, N., Otte, A., 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. Applied Vegetation Science 6, 13–22.

Dorland, E., Van Den Berg, L.J.L., Brouwer, E., Roelofs, J.G.M., Bobbink, R., 2005. Catchment Liming to Restore Degraded, Acidified Heathlands and Moorland Pools. Restoration Ecology 13, 302–311.

Douds, D.D., Galvez, L., Janke, R.R., Wagoner, P., 1995. Effect of tillage and farming system upon populations and distribution of vesicular-arbuscular mycorrhizal fungi. Agriculture, Ecosystems & Environment 52, 111–118.

Dray, S., Dufour, A.B., 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. Journal of Statistical Software 22, 1–20.

Dray, S., Dufour, A.B., Chessel, D., 2007. The ade4 package-II: Two-table and K-table methods. R News 7, 47–52.

Dray, S., Legendre, P., Blanchet, G., 2011. packfor: Forward Selection with permutation (Canoco p.46).

Duclos, G., 1994. Atlas des sols de la région Provence-Alpes-Côte d'Azur. Société du canal de Provence et d'aménagement de la région provençale.

Duelli, P., Obrist, M.K., 2003. Biodiversity indicators: the choice of values and measures. Agriculture, Ecosystems & Environment 98, 87–98.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible Impact of past Land Use on Forest Soils and Biodiversity. Ecology 83, 2978–2984.

Dutoit, T., 2010. Restauration d'un verger industriel vers une terre de parcours à moutons. Espaces Naturels 29, 26.

Dutoit, T., Buisson, E., Fadda, S., Henry, F., Coiffait-Gombault, C., Jaunatre, R., 2011. Dix années de recherche dans une pseudo-steppe méditerranéenne: impacts des changements d'usage et restauration écologique. Science et changements planétaires/Sécheresse 22, 75–85.

Dutoit, T., Jaunatre, R., Alignan, J.F., Fontvieille, N., Gariglio, L., 2011. Mise en place d'expérimentations de restauration écologique du site de Cossure (Plaine de Crau): premiers résultats (2010) (Rapport intermédiaire pour la CDC Biodiversité). Avignon.

Dutoit, T., Jaunatre, R., Debras, J.F., Fadda, S., 2009. Diagnostic écologique du verger de Cossure dans la plaine de La Crau (Bouches-du-Rhône): Végétation, Orthoptères et Coléoptères. (Rapport intermédiaire pour la CDC Biodiversité). Avignon.

Dutoit, T., Thinon, M., Talon, B., Buisson, E., Alard, D., 2009. Sampling soil wood charcoals at a high spatial resolution: a new methodology to investigate the origin of grassland plant communities. Journal of Vegetation Science 20, 349–358.

Edwards, A.R., Mortimer, S.R., Lawson, C.S., Westbury, D.B., Harris, S.J., Woodcock, B.A., Brown, V.K., 2007. Hay strewing, brush harvesting of seed and soil disturbance as tools for the enhancement of botanical diversity in grasslands. Biological Conservation 134, 372–382.

Egan, D., 2001. The Historical Ecology Handbook: A Restorationist's Guide To Reference Ecosystems. Island Press.

Egler, F.E., 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio Acta Geobot 4, 412–417.

Ehrenfeld, J.G., Toth, L.A., 1997. Restoration Ecolog y and the Ecosystem Perspective. Restor Ecology 5, 307–317.

Elmore, A.J., Mustard, J.F., Hamburg, S.P., Manning, S.J., 2007. Agricultural Legacies in the Great Basin Alter Vegetation Cover, Composition, and Response to Precipitation. Ecosystems 9, 1231–1241.

Eom, A.H., Hartnett, D.C., Wilson, G.W.T., 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia 122, 435–444.

Eriksson, Å., 2001. Arbuscular mycorrhiza in relation to management history, soil nutrients and plant species diversity. Plant Ecology 155, 129–137.

Fabre, P., 1997. Hommes de la Crau, des coussouls aux alpages. Clergeaud, L. and J.L. Giard, Cheminements, Thoard.

Fadda, S., 2006. Organisation des communautés de coléoptères terricoles en écosysteme multi-perturbé: le cas des écosystèmes de pelouses sèches (Thèse de Doctorat - Université Paul Cézanne Marseille).

Fagan, K.C., Pywell, R.F., Bullock, J.M., Marrs, R.H., 2008. Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. Journal of Applied Ecology 45, 1293–1303.

Falk, D.A., Palmer, M., Zedler, J., 2006. Foundations of Restoration Ecology. The Science and Practice of Ecological Restoration. Island Press Washington, DC.

Fargione, J.E., Cooper, T.R., Flaspohler, D.J., Hill, J., Lehman, C., McCoy, T., McLeod, S., Nelson, E.J., Oberhauser, K.S., Tilman, D., 2009. Bioenergy and wildlife: threats and opportunities for grassland conservation. Bioscience 59, 767–777.

Fattorinni, M., Halle, S., 2004. The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance, in: Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Temperton, V.M., Hobbs, R.J., Nuttle, T. & Halle, S. (eds.) Island Press, Covelo, Washington, US, pp. 96–114.

Fischer, F.P., Schulz, U., Schubert, H., Knapp, P., Schmöger, M., 1997. Quantitative assessment of grassland quality: acoustic determination of population sizes of orthopteran indicator species. Ecological Applications 7, 909–920.

Fitzsimons, M.S., Miller, R.M., Jastrow, J.D., 2008. Scale-dependent niche axes of arbuscular mycorrhizal fungi. Oecologia 158, 117–127.

Forey, E., Dutoit, T., in press. Vegetation, soils and seed banks of limestone grasslands are still impacted by former cultivation one century after abandonment. Community Ecology.

Foster, B.L., Tilman, D., 2000. Dynamic and Static Views of Succession: Testing the Descriptive Power of the Chronosequence Approach. Plant Ecology 146, 1–10.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The Importance of Land-Use Legacies to Ecology and Conservation. BioScience 53, 77.

Foucart, A., Lecoq, M., 1998. Major threats to a protected grasshopper, Prionotropis hystrix rhodanica (Orthoptera, Pamphagidae, Akicerinae), endemic to southern France. Journal of Insect Conservation 2, 187–193.

Fox, J.W., in press. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology & Evolution.

Francis, R., Read, D.J., 1994. The contributions of mycorrhizal fungi to the determination of plant community structure. Plant and Soil 159, 11–25.

Frisch, O., 1965. Beiträg zur Kenntnis des Wirbeltierfauna der Crau (Südfrankreich), Biologie und Oekologie. Bonner Zoologische Beiträge 16, 92–126.

Fukami, T., 2004. Assembly History Interacts with Ecosystem Size to Influence Species Diversity. Ecology 85, 3234–3242.

Fukami, T., 2010. Community assembly dynamics in space, in: Community Ecology, Processes, Models and Applications. Verhoef, H.A.; Morin, P.J., Oxford, UK., pp. 45–54.

Fukami, T., Martijn Bezemer, T., Mortimer, S.R., Putten, W.H., 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8, 1283–1290.

Fukami, T., Nakajima, M., 2011. Community assembly: alternative stable states or alternative transient states? Ecology Letters 14, 973–984.

Funk, J.L., Cleland, E.E., Suding, K.N., Zavaleta, E.S., 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23, 695–703.

Fynn, R.W.S., Morris, C.D., Kirkman, K.P., 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. Journal of Ecology 93, 384–394.

Gaignard, P., 2003. Changements d'usages agricoles et dynamique spatio-temporelle de la stepe de Crau depuis 1955, secteur de ZPS (Zone de Protection Spéciale) (Rapport de DES - Université d'Aix-Marseille III).

Gange, A.C., Brown, V.K., Sinclair, G.S., 1993. Vesicular-Arbuscular Mycorrhizal Fungi: A Determinant of Plant Community Structure in Early Succession. Functional Ecology 7, 616–622.

Gaussen, H., Bagnouls, F., 1957. Les climats biologiques et leur classification. geo 66, 193–220.

Giardina, C.P., Litton, C.M., Thaxton, J.M., Cordell, S., Hadway, L.J., Sandquist, D.R., 2007. Science driven restoration: a candle in a demon haunted world—response to Cabin (2007). Restoration Ecology 15, 171–176.

Gibson, C.W.D., Brown, V.K., 1991. The nature and rate of development of calcareous grassland in Southern Britain. Biological Conservation 58, 297–316.

Gibson, C.W.D., Brown, V.K., 1992. Grazing and Vegetation Change: Deflected or Modified Succession? Journal of Applied Ecology 29, 120–131.

Gibson, D.J., 2009. Grasses and grassland ecology. Oxford University Press.

Gleason, H.A., 1926. The individualistic concept of plant association. Bulletin of the Torrey Botanical Club 53, 7–26.

Gleason, H.A., 1939. The individualistic concept of the plant association. American Midland Naturalist 21, 92–110.

Gómez-Aparicio, L., 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97, 1202–1214.

Good, J.E.G., Wallace, H.L., Stevens, P.A., Radford, G.L., 1999. Translocation of Herb-Rich Grassland from a Site in Wales Prior to Opencast Coal Extraction. Restor Ecology 7, 336–347.

Götzenberger, L., de Bello, F., Anne Bråthen, K., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., Zobel, M., in press. Ecological assembly rules in plant communities—approaches, patterns and prospects. Biological Reviews.

Grace, J.B., 2001. Difficulties with estimating and interpreting species pools and the implications for understanding patterns of diversity. Folia Geobot 36, 71–83.

Graham, D.J., Hutchings, M.J., 1988a. Estimation of the Seed Bank of a Chalk Grassland Ley Established on Former Arable Land. Journal of Applied Ecology 25, 241–252.

Graham, D.J., Hutchings, M.J., 1988b. A Field Investigation of Germination from the Seed Bank of a Chalk Grassland Ley on Former Arable Land. Journal of Applied Ecology 25, 253–263.

Grayston, S.J., Campbell, C.D., Bardgett, R.D., Mawdsley, J.L., Clegg, C.D., Ritz, K., Griffiths, B.S., Rodwell, J.S., Edwards, S.J., Davies, W.J., Elston, D.J., Millard, P., 2004. Assessing shifts in microbial community structure across a range of grasslands of differing management intensity using CLPP, PLFA and community DNA techniques. Applied Soil Ecology 25, 63–84.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 1169–1194.

Grime, J.P., Hodgson,, J.B., Hunt, R., 1988. Comparative plant ecology: A functional approach to common British species, Unwin Hyman. ed. London and Boston.

Grime, J.P., Mackey, J.M.L., Hillier, S.H., Read, D.J., 1987. Floristic diversity in a model system using experimental microcosms. Nature 328, 420–422.

Grinnell, J., 1917. The Niche-Relationships of the California Thrasher. The Auk 34, 427–433.

GRT gaz, 2012. Le projet ERIDAN: développement des capacités de transport de gaz naturel entre Saint-Martin-de-Crau (Bouches-du-Rhône) et Saint-Avit (Drôme). http://www.grtgaz.com/fr/accueil/grands-projets/artere-eridan/le-projet/.

Guisan, A., Rahbek, C., 2011. SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. Journal of Biogeography 38, 1433–1444.

Gustavsson, E., Lennartsson, T., Emanuelsson, M., 2007. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biological Conservation 138, 47–59.

Gutjahr, B., 2011. Etudes des communautés de coléoptères dans le cadre d'un programme de restauration écologique après abandon de cultures intensives dans la plaine de la Crau (Rapport de DUT - Université d'Avignon et des Pays de Vaucluse). Université d'Avignon et des Pays de Vaucluse, Avignon.

Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J., 2006. Ecological restoration and global climate change. Restoration Ecology 14, 170–176.

Harrison, Y.A., Shackleton, C.M., 1999. Resilience of South African communal grazing lands after the removal of high grazing pressure. Land Degradation and Development 10, 225–239.

Hart, M.M., Reader, R.J., Klironomos, J.N., 2003. Plant coexistence mediated by arbuscular mycorrhizal fungi. Trends in Ecology & Evolution 18, 418–423.

Hartnett, D.C., Wilson, G.W.T., 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology 80, 1187–1195.

Hautier, Y., Niklaus, P.A., Hector, A., 2009. Competition for Light Causes Plant Biodiversity Loss After Eutrophication. Science 324, 636–638.

Haywood, J.D., 2009. Eight years of seasonal burning and herbicidal brush control influence sapling longleaf pine growth, understory vegetation, and the outcome of an ensuing wildfire. Forest Ecology and Management 258, 295–305.

Helsen, K., Hermy, M., Honnay, O., 2012. Trait but not species convergence during plant community assembly in restored semi-natural grasslands. Oikos.

Henkin, Z., Seligman, N.G., Noy-Meir, I., 2010. Long-term productivity of Mediterranean herbaceous vegetation after a single phosphorus application. Journal of Vegetation Science 21, 979–991.

Henry, F., 2005. Succession secondaire post-pastorale dans un écosystème herbacé steppique�: le cas de la plaine de la Crau (Bouches-du-Rhône, France) (Rapport de Master 2 - Université d'Aix-Marseille III).

Henry, F., 2009. Origine et dynamique à long terme d'un écosystème herbacé pseudo steppique, le cas de la plaine de Crau (Bouches-du-Rhône, France). (Thèse de Doctorat - Université Paul Cézanne Marseille).

Henry, F., Talon, B., Dutoit, T., 2010. The age and history of the French Mediterranean steppe revisited by soil wood charcoal analysis. The Holocene 20, 25 –34.

Henry, M., Stevens, H., Bunker, D.E., Schnitzer, S.A., Carson, W.P., 2004. Establishment Limitation Reduces Species Recruitment and Species Richness as Soil Resources Rise. Journal of Ecology 92, 339–347.

Heppell, K.B., Shumway, D.L., Koide, R.T., 2002. The effect of mycorrhizal infection of Abutilon theophrasti on competitiveness of offspring. Functional Ecology 12, 171–175.

Herault, B., Thoen, D., 2009. How habitat area, local and regional factors shape plant assemblages in isolated closed depressions. Acta Oecologica 35, 385–392.

Herrera, M.A., Salamanca, C.P., Barea, J.M., 1993. Inoculation of woody legumes with selected arbuscular mycorrhizal fungi and rhizobia to recover desertified Mediterranean ecosystems. Applied and Environmental Microbiology 59, 129–133.

Hiers, J.K., Mitchell, R.J., Barnett, A., Walters, J.R., Mack, M., Williams, B., Sutter, R., 2012. The Dynamic Reference Concept: Measuring Restoration Success in a Rapidly Changing No-Analogue Future. Ecological Restoration 30, 27–36.

Hilderbrand, R.H., Watts, A.C., Randle, A.M., 2005. The Myths of Restoration Ecology.

Hirsch, J.E., 2005. An index to quantify an individual's scientific research output. Proc Natl Acad Sci U S A 102, 16569–16572.

Hobbs, R.J., 2007. Setting effective and realistic restoration goals: key directions for research. Restoration Ecology 15, 354–357.

Hobbs, R.J., Hallett, L.M., Ehrlich, P.R., Mooney, H.A., 2011. Intervention Ecology: Applying Ecological Science in the Twenty-first Century. BioScience 61, 442–450.

Hobbs, R.J., Harris, J.A., 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. Restoration Ecology 9, 239–246.

Hobbs, R.J., Norton, D.A., 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4, 93–110.

Hobbs, R.J., Suding, K.N., International Society for Ecological Restoration (Eds.), 2008. New Models for Ecosystem Dynamics and Restoration, 1st ed. Island Press.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabinski, C., Bever, J.D., Moore, J.C., 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecology Letters 13, 394–407.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4, 1–23.

Hölzel, N., Buisson, E., Dutoit, T., 2012. Species introduction – a major topic in vegetation restoration. Applied Vegetation Science 15, 161–165.

Hölzel, N., Otte, A., 2003. Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. Applied Vegetation Science 6, 131–140.

Hooper, D.U., Chapin Iii, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75, 3–35.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland. Ecology 71, 478–491.

Huston, M.A., 1999. Local Processes and Regional Patterns: Appropriate Scales for Understanding Variation in the Diversity of Plants and Animals. Oikos 86, 393–401.

Huston, M.A., 2005. The three phases of land-use change: implications for biodiversity. Ecological Applications 15, 1864–1878.

Hutchings, M.J., Booth, K.D., 1996. Studies on the Feasibility of Re-Creating Chalk Grassland Vegetation on Ex-Arable Land. I. The Potential Roles of the Seed Bank and the Seed Rain. Journal of Applied Ecology 33, 1171–1181.

Isselin-Nondedeu, F., Rey, F., Bédécarrats, A., 2006. Contributions of vegetation cover and cattle hoof prints towards seed runoff control on ski pistes. Ecological Engineering 27, 193–201.

IUCN, 2010. Species of the Day: Crau Plain Grasshopper. http://www.iucnredlist.org/sotdfiles/prionotropis-hystrix-rhodanica.pdf.

Jacquemyn, H., Brys, R., Hermy, M., 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. Biological Conservation 111, 137–147.

Jansa, J., Mozafar, A., Kuhn, G., Anken, T., Ruh, R., Sanders, I.R., Frossard, E., 2003. Soil tillage affects the community structure of mycorrhizal fungi in maize roots. Ecological Applications 13, 1164–1176.

Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.P., Bekker, R.M., Fillat, F., Oomes, M.J.M., 1998. Relationship between soil chemical factors and grassland diversity. Plant and Soil 202, 69–78.

Jasper, D.A., Abbott, L.K., Robson, A.D., 1989. Soil disturbance reduces the infectivity of external hyphae of vesicular-arbuscular mycorrhizal fungi. New Phytologist 112, 93–99.

Jaunatre, R., Buisson, E., Dutoit, T., 2012. First-year results of a multi-treatment steppe restoration experiment in La Crau (Provence, France). Plant Ecology and Evolution 145, 13–23.

Jaunatre, R., Dolidon, B., Buisson, E., Dutoit, T., 2011. Exemple de restauration de la plaine de la Crau: l'écologie de la restauration face à la restauration écologique. Sciences Eaux & Territoires 5, 36–39.

Jirova, A., Klaudisova, A., Prach, K., 2012. Spontaneous restoration of target vegetation in old-fields in a central European landscape: a repeated analysis after three decades. Appl. Veg. Sci. 15, 245–252.

Joern, A., 1982. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera, Acrididae). The Southwestern Naturalist 197–209.

Johnson, N.C., 1993. Can Fertilization of Soil Select Less Mutualistic Mycorrhizae? Ecological Applications 3, 749.

Jones, M., Norman, K., Rhind, P., 2010. Topsoil inversion as a restoration measure in sand dunes, early results from a UK field-trial. Journal of Coastal Conservation 14, 139–151.

Jongepierová, I., Mitchley, J., Tzanopoulos, J., 2007. A field experiment to recreate species rich hay meadows using regional seed mixtures. Biological Conservation 139, 297–305.

Jordan III, W.R., Gilpin, M.E., Aber, J.D., 1987. Restoration Ecology: A Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge.

Kardol, P., Bezemer, T.M., Putten, W.H.V.D., 2009. Soil Organism and Plant Introductions in Restoration of Species-Rich Grassland Communities. Restoration Ecology 17, 258–269.

Kardol, P., Cornips, N.J., Kempen, M.M.L. van, Bakx-Schotman, J.M.T., Putten, W.H. van der, 2007. Microbe-Mediated Plant-Soil Feedback Causes Historical Contingency Effects in Plant Community Assembly. Ecological Monographs 77, 147–162.

Kardol, P., Souza, L., Classen, A.T., 2012. Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. Oikos.

Keddy, P.A., 1992. Assembly and Response Rules: Two Goals for Predictive Community Ecology. Journal of Vegetation Science 3, 157–164.

Kiehl, K., 2010. Plant species introduction in ecological restoration: Possibilities and limitations. Basic and Applied Ecology 11, 281–284.

Kiehl, K., Kirmer, A., Donath, T.W., Rasran, L., Hölzel, N., 2010. Species introduction in restoration projects - Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. Basic and Applied Ecology 11, 285–299.

Kiehl, K., Pfadenhauer, J., 2006. Establishment and persistence of target species in newly created calcareous grasslands on former arable fields. Plant Ecol 189, 31–48.

Kiehl, K., Thormann, A., Pfadenhauer, J., 2006. Evaluation of Initial Restoration Measures during the Restoration of Calcareous Grasslands on Former Arable Fields. Restor Ecology 14, 148–156.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J., Montoya, J.M., Römermann, C., Schiffers, K., Schurr, F.M., Singer, A., Svenning, J.-C., Zimmermann, N.E., O'Hara, R.B., in press. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography.

Klimkowska, A., Dzierża, P., Brzezińska, K., Kotowski, W., Mędrzycki, P., 2010. Can we balance the high costs of nature restoration with the method of topsoil removal? Case study from Poland. Journal for Nature Conservation 18, 202–205.

Klimkowska, A., Kotowski, W., Van Diggelen, R., Grootjans, A.P., Dzierża, P., Brzezińska, K., 2010. Vegetation Re-development After Fen Meadow Restoration by Topsoil Removal and Hay Transfer. Restoration Ecology 18, 924–933.

Koide, R.T., 1991. Nutrient supply, nutrient demand and plant response to mycorrhizal infection. New Phytol 117, 365–386.

Koide, R.T., Lu, X., 1992. Mycorrhizal infection of wild oats: maternal effects on offspring growth and reproduction. Oecologia 90, 218–226.

Královec, J., Pocová, L., Jonášová, M., Macek, P., Prach, K., 2009. Spontaneous recovery of an intensively used grassland after cessation of fertilizing. Applied Vegetation Science 12, 391–397.

Krebs, C.J., 1972. Ecology; the experimental analysis of distribution and abundance. Harper & Row.

Kulmatiski, A., Beard, K.H., Stark, J.M., 2006. Soil history as a primary control on plant invasion in abandoned agricultural fields. Journal of Applied Ecology 43, 868–876.

Kytöviita, M.M., Vestberg, M., Tuomi, J., 2003. A test of mutual aid in common mycorrhizal networks: established vegetation negates benefit in seedlings. Ecology 84, 898–906.

Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9, 1179–1188.

Lavorel, S., 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. Divers Distrib 5, 3–13.

Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends in Ecology & Evolution 12, 474–478.

Lawton, J.H., 1999. Are There General Laws in Ecology? Oikos 84, 177–192.

Le Houérou, H.N., 1995. Considérations biogéographiques sur les steppes arides du nord de l'Afrique. Sécheresse 6, 167–182.

Le Houérou, H.N., 2001. Biogeography of the arid steppeland north of the Sahara. Journal of Arid Environments 48, 103–128.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Lekberg, Y., Koide, R.T., Rohr, J.R., Aldrich-Wolfe, L., Morton, J.B., 2007. Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. Journal of Ecology 95, 95–105.

Lemaire, S., Tamisier, A., Gagnier, F., 1987. Surface, distribution et diversité des principaux milieux de Camargue: leur évolution de 1942 à 1984. Revue d'écologie 47–56.

Lindborg, R., Eriksson, O., 2004. Historical Landscape Connectivity Affects Present Plant Species Diversity. Ecology 85, 1840–1845.

Lorenzetti, O., 2012. Création d'une base de données botanique et édaphique pour les terres de parcours de la plaine de Crau. Université d'Avignon et des Pays de Vaucluse, Avignon.

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, 433–438.

Luff, M.L., Rushton, S.P., 1989. The ground beetle and spider fauna of managed and unimproved upland pasture. Agriculture, Ecosystems & Environment 25, 195–205.

Luken, J.O., 1990. Directing ecological succession. Springer.

Maarel, E., Sykes, M.T., 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. Journal of Vegetation Science 4, 179–188.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press.

Mackey, R.L., Currie, D.J., 2001. The Diversity-Disturbance Relationship: Is It Generally Strong and Peaked? Ecology 82, 3479–3492.

Mäder, P., Edenhofer, S., Boller, T., Wiemken, A., Niggli, U., 2000. Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic, biological) and high-input (conventional) farming systems in a crop rotation. Biology and Fertility of Soils 31, 150–156.

Maestre, F.T., Castillo-Monroy, A.P., Bowker, M.A., Ochoa-Hueso, R., 2012. Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. Journal of Ecology 100, 317–330.

Maestre, F.T., Salguero-Gómez, R., Quero, J.L., 2012. It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 3062–3075.

Magurran, A.E., 2004. Measuring Biological Diversity, Blackwell. ed. Oxford, UK.

Manchester, S.J., Mcnally, S., Treweek, J.R., Sparks, T.H., Mountford, J.O., 1999. The cost and practicality of techniques for the reversion of arable land to lowland wet grassland: an experimental study and review. Journal of Environmental management 55, 91–109.

Marini, L., Fontana, P., Scotton, M., Klimek, S., 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. Journal of Applied Ecology 45, 361–370.

Marrs, R.H., 1985. Techniques for reducing soil fertility for nature conservation purposes: A review in relation to research at Roper's Heath, Suffolk, England. Biological Conservation 34, 307–332.

Marrs, R.H., 2002. Manipulating the chemical environment of the soil, in: Handbook of Ecological Restoration. Perrow M.R. & Davy A. J. Cambridge University Press, Cambridge, pp. 155–183.

Masip, A.C., 1991. Le peuplement végétal de la Reserve de Peau de Meau: données pour la gestion.

Masson, S., In prep. Restauration écologique des écosystèmes dégradés par pilotage in situ des régimes de perturbations et des ressources trophiques (Thèse de Doctorat - Université d'Avignon et des Pays de Vaucluse).

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

McCain, K.N.S., Baer, S.G., Blair, J.M., Wilson, G.W.T., 2010. Dominant Grasses Suppress Local Diversity in Restored Tallgrass Prairie. Restoration Ecology 18, 40–49.

McCauley, D., 2012. Nature—Half Lost or Half Saved? Science 337, 1455–1455.

McGarigal, K., Cushman, S., Stafford, S., 2000. Multivariate Statistics for Wildlife and Ecology Research, Springer. ed. New York, USA.

McGonigle, T.P., Miller, M.H., Evans, D.G., Fairchild, G.L., Swan, J.A., 1990. A New Method which Gives an Objective Measure of Colonization of Roots by Vesicular-Arbuscular Mycorrhizal Fungi. New Phytologist 115, 495–501.

McIntyre, S., Barrett, G.W., 1992. Habitat Variegation, An Alternative to Fragmentation. Conservation Biology 6, 146–147.

McIntyre, S., Hobbs, R., 1999. A Framework for Conceptualizing Human Effects on Landscapes and Its Relevance to Management and Research Models. Conservation Biology 13, 1282–1292.

McLean, I.F.G., 2003. A Habitats Translocation Policy for Britain.

Medail, F., Quezel, P., 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. Annals of the Missouri Botanical Garden 112–127.

Meffe, G.K., Carroll, C.R., 1997. Principles of Conservation Biology, 2nd ed. Sinauer Associates Inc.

Meffre, B., Wolff, A., Sauguet, F., 2011. Plan de Gestion du site de "Cossure" 2011-2015. Section B: Definition des objectifs et planification des opérations. Saint-Martin de Crau.

Meine, C., 2009. Back to nature at the UW Arboretum. Isthmus.

Meiners, S.J., Pickett, S.T.A., Cadenasso, M.L., 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography 25, 215–223.

Méndez, M., García, D., Maestre, F.T., Escudero, A., 2008. More Ecology is Needed to Restore Mediterranean Ecosystems: A Reply to Valladares and Gianoli. Restor Ecology 16, 210–216.

Mesléard, F., Mauchamp, A., Pineau, O., Dutoit, T., 2011. Rabbits are More Effective than Cattle for Limiting Shrub Colonization in Mediterranean Xero-Halophytic Meadows. Ecoscience 18, 37–41.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative Effects of Grazing on Vegetation and Soils Over a Global Range of Environments. Ecological Monographs 63, 328–366.

Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 87–106.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis, World Resources Institute, Washington, DC. ed.

Miller, A.D., Roxburgh, S.H., Shea, K., 2011. How frequency and intensity shape diversity–disturbance relationships. Proceedings of the National Academy of Sciences 108, 5643–5648.

Mitchley, J., Buckley, G. p., Helliwell, D. r., 1996. Vegetation establishment on chalk marl spoil: the role of nurse grass species and fertiliser application. Journal of Vegetation Science 7, 543–548.

Molinier, R., Tallon, G., 1950. La végétation de la Crau (Basse-Provence). Revue générale de Botanique 56, 1–111.

Morghan, K.J.R., Seastedt, T.R., 1999. Effects of Soil Nitrogen Reduction on Nonnative Plants in Restored Grasslands. Restoration Ecology 7, 51–55.

Muller, S., Dutoit, T., Alard, D., Grevilliot, F., 1998. Restoration and Rehabilitation of Species-Rich Grassland Ecosystems in France: a Review. Restor Ecology 6, 94–101.

Münzbergová, Z., Herben, T., 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. Oecologia 145, 1–8.

Murray, C., Marmorek, D., 2003. Adaptive Management and Ecological Restoration, in: Frederici, P. (Ed.), Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington,CoveloCA, London, pp. 417–428.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nahlik, A.M., Kentula, M.E., Fennessy, M.S., Landers, D.H., 2012. Where is the consensus? A proposed foundation for moving ecosystem service concepts into practice. Ecological Economics 77, 27–35.

Naveh, Z., 1994. From Biodiversity to Ecodiversity: A Landscape-Ecology Approach to Conservation and Restoration. Restoration Ecology 2, 180–189.

Nellemann, C., Corcoran, E., Nellemann, C., Corcoran, E. (Eds.), 2010. Dead planet, living planet: biodiversity and ecosystem restoration for sustainable development., United Nations Environment Programme. ed. Nairobi.

Noss, R.F., 1990. Indicators for Monitoring Biodiversity: A Hierarchical Approach. Conservation Biology 4, 355–364.

Novák, J., Prach, K., 2003. Vegetation succession in basalt quarries: Pattern on a landscape scale. Applied Vegetation Science 6, 111–116.

O'Connor, P.J., Smith, S.E., Smith, F.A., 2002. Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. New Phytologist 154, 209–218.

Oehl, F., Sieverding, E., Ineichen, K., Mäder, P., Wiemken, A., Boller, T., 2009. Distinct sporulation dynamics of arbuscular mycorrhizal fungal communities from different agroecosystems in long-term microcosms. Agriculture, Ecosystems & Environment 134, 257–268.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Henry, M., Stevens, H., Wagner, H., 2008. vegan: Community Ecology Package. R package version 1.13-1.

Olsen, S.R., Cole, C.V., Watanabe, F.S., Dean, L.A., 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate.

Öster, M., Ask, K., Römermann, C., Tackenberg, O., Eriksson, O., 2009. Plant colonization of ex-arable fields from adjacent species-rich grasslands: The importance of dispersal vs. recruitment ability. Agriculture, Ecosystems & Environment 130, 93–99.

Padilla, F.M., Pugnaire, F.I., 2006. The Role of Nurse Plants in the Restoration of Degraded Environments. Frontiers in Ecology and the Environment 4, 196–202.

Palmer, M.A., Ambrose, R.F., Poff, N.L., 1997. Ecological Theory and Community Restoration Ecology. Restor Ecology 5, 291–300.

Palmer, M.A., Bernhardt, E.S., Allan, J.D., Lake, P.S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C.N., Follstad Shah, J., Galat, D.L., Loss, S.G., Goodwin, P., Hart, D.D., Hassett, B., Jenkinson, R., Kondolf, G.M., Lave, R., Meyer, J.L., O'donnell, T.K., Pagano, L., Sudduth, E., 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology 42, 208–217.

Pärtel, M., Kalamees, R., Zobel, M., Rosèn, E., 1998. Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. Ecological Engineering 10, 275–286.

Pärtel, M., Zobel, M., 1999. Small-scale plant species richness in calcareous grasslands determined by the species pool, community age and shoot density. Ecography 22, 153–159.

Pärtel, M., Zobel, M., Zobel, K., Maarel, E. van der, 1996. The Species Pool and Its Relation to Species Richness: Evidence from Estonian Plant Communities. Oikos 75, 111–117.

Patzelt, A., Wild, U., Pfadenhauer, J., 2001. Restoration of Wet Fen Meadows by Topsoil Removal: Vegetation Development and Germination Biology of Fen Species. Restoration Ecology 9, 127–136.

Pausas, J., Bonet, A., Maestre, F., Climent, A., 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. Acta Oecologica 29, 352, 346.

Perner, J., Malt, S., 2003. Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. Agriculture, Ecosystems & Environment 98, 169–181.

Perrow, M.R., Davy, A.J. (Eds.), 2002. Handbook of Ecological Restoration: Volume 2, Restoration in Practice, 1st ed. Cambridge University Press.

Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1, 6–18.

Pickett, S.T.A., Parker, V.T., 1994. Avoiding the old pitfalls: opportunities in a new discipline. Restoration Ecology 2, 75–79.

Pielou, E.C., 1969. An introduction to mathematical ecology. Wiley-Interscience, New York.

Pinke, G., Karácsony, P., Czúcz, B., Botta-Dukát, Z., Lengyel, A., 2012. The influence of environment, management and site context on species composition of summer arable weed vegetation in Hungary. Applied Vegetation Science 15, 136–144.

Piqueray, J., Cristofoli, S., Bisteau, E., Palm, R., Mahy, G., 2011. Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. Landscape Ecology 26, 823–836.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. Biological Conservation 104, 361–376.

Prach, K., Hobbs, R.J., 2008. Spontaneous Succession versus Technical Reclamation in the Restoration of Disturbed Sites. Restoration Ecology 16, 363–366.

Prach, K., Pyšek, P., 2001. Using spontaneous succession for restoration of human-disturbed habitats: Experience from Central Europe. Ecological Engineering 17, 55–62.

Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession. Trends in Ecology & Evolution 26, 119–123.

Primack, R.B., Miao, S.L., 1992. Dispersal Can Limit Local Plant Distribution. Conservation Biology 6, 513–519.

Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J., Warman, E.A., Masters, G., 2007. Enhancing diversity of species-poor grasslands: an experimental assessment of multiple constraints. Journal of Applied Ecology 44, 81–94.

Pywell, R.F., Webb, N.R., Putwain, P.D., 1995. A Comparison of Techniques for Restoring Heathland on Abandoned Farmland. Journal of Applied Ecology 32, 400–411.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raab, D., Bayley, S.E., 2012. A vegetation-based Index of Biotic Integrity to assess marsh reclamation success in the Alberta oil sands, Canada. Ecological Indicators 15, 43–51.

Ramsey, P.W., Rillig, M.C., Feris, K.P., Holben, W.E., Gannon, J.E., 2006. Choice of methods for soil microbial community analysis: PLFA maximizes power compared to CLPP and PCR-based approaches. Pedobiologia 50, 275–280.

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., Vira, B., 2010. Biodiversity Conservation: Challenges Beyond 2010. Science 329, 1298–1303.

Rasran, L., Vogt, K., Jensen, K., 2006. Seed content and conservation evaluation of hay material of fen grasslands. Journal for Nature Conservation 14, 34–45.

Rehounková, K., Prach, K., 2006. Spontaneous vegetation succession in disused gravel-sand pits: Role of local site and landscape factors. Journal of Vegetation Science 17, 583–590.

Řehounková, K., Prach, K., 2008. Spontaneous Vegetation Succession in Gravel–Sand Pits: A Potential for Restoration. Restoration Ecology 16, 305–312.

Ricklefs, R.E., 2008. Disintegration of the Ecological Community: American Society of Naturalists Sewall Wright Award Winner Address. The American Naturalist 172, 741–750.

Riley, J.D., Craft, I.W., Rimmer, D.L., Smith, R.S., 2004. Restoration of Magnesian Limestone Grassland: Optimizing the Time for Seed Collection by Vacuum Harvesting. Restor Ecology 12, 311–317.

Ring, I., Hansjürgens, B., Elmqvist, T., Wittmer, H., Sukhdev, P., 2010. Challenges in framing the economics of ecosystems and biodiversity: the TEEB initiative. Current Opinion in Environmental Sustainability 2, 15–26.

Rio Tinto, 1992. Rio Tinto and biodiversity: Achieving results on the ground. http://www.riotinto.com/documents/ReportsPublications/RTBidoversitystrategyfinal.pdf.

Rodríguez, C., Tapia, L., Kieny, F., Bustamante, J., 2010. Temporal changes in lesser kestrel (Falco naumanni) diet during the breeding season in southern Spain. Journal of Raptor Research 44, 120–128.

Römermann, C., Dutoit, T., Poschlod, P., Buisson, E., 2005. Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. Biological Conservation 121, 21–33.

Römermann, C., Tackenberg, O., Poschlod, P., 2005. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. Oikos 110, 219–230.

Ross, M.A., Harper, J.L., 1972. Occupation of Biological Space During Seedling Establishment. Journal of Ecology 60, 77–88.

Roux, R.M., Colomb, E., 1986. La Crau, histoire Plio-Pléistocène. medit 58, 31–42.

Ruiz-Jaen, M.C., Mitchell Aide, T., 2005. Restoration Success: How Is It Being Measured? Restoration Ecology 13, 569–577.

Ruxton, G.D., Neuhäuser, M., 2010. When should we use one-tailed hypothesis testing? Methods in Ecology and Evolution 1, 114–117.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation biology 5, 18–32.

Schnoor, T., Lekberg, Y., Rosendahl, S., Olsson, P., 2011. Mechanical soil disturbance as a determinant of arbuscular mycorrhizal fungal communities in semi-natural grassland. Mycorrhiza 21, 211–220.

Semelová, V., Hejcman, M., Pavlů, V., Vacek, S., Podrázský, V., 2008. The Grass Garden in the Giant Mts. (Czech Republic): Residual effect of long-term fertilization after 62 years. Agriculture, Ecosystems & Environment 123, 337–342.

Shaish, L., Levy, G., Gomez, E., Rinkevich, B., 2008. Fixed and suspended coral nurseries in the Philippines: Establishing the first step in the "gardening concept" of reef restoration. Journal of Experimental Marine Biology and Ecology 358, 86–97.

Smith, M.D., Hartnett, D.C., Wilson, G.W.T., 1999. Interacting influence of mycorrhizal symbiosis and competition on plant diversity in tallgrass prairie. Oecologia 121, 574–582.

Smits, N.A.., Willems, J.H., Bobbink, R., 2008. Long-term after-effects of fertilisation on the restoration of calcareous grasslands. Applied Vegetation Science 11, 279–286.

Society for Ecological Restoration International Science and Working Policy Group, 2004. The SER International Primer on Ecological Restoration.

Sousa, W.P., 1984. The Role of Disturbance in Natural Communities. Annual Review of Ecology and Systematics 15, 353–391.

Standish, R.J., Cramer, V.A., Hobbs, R.J., 2008. Land-use legacy and the persistence of invasive Avena barbata on abandoned farmland. Journal of Applied Ecology 45, 1576–1583.

Stanley, M.R., Koide, R.T., Shumway, D.L., 1993. Mycorrhizal symbiosis increases growth, reproduction and recruitment of Abutilon theophrasti Medic. in the field. Oecologia 94, 30–35.

Stevenson, M.J., Ward, L.K., Pywell, R.F., 1997. Re-creating Semi-natural Communities: Vacuum Harvesting and Hand Collection of Seed on Calcareous Grassland. Restor Ecology 5, 66–76.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe – A review. Journal of Environmental Management 91, 22–46.

Stroh, M., Storm, C., Zehm, A., Schwabe, A., 2002. Restorative grazing as a tool for directed succession with diaspore inoculation: the model of sand ecosystems. phytocoenologia 32, 595–625.

Suding, K., 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19, 46–53.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications 9, 1189–1206.

Tansley, A.G., 1935. The Use and Abuse of Vegetational Concepts and Terms. Ecology 16, 284–307.

Tansley, A.G., Adamson, R.S., 1925. Studies of the Vegetation of the English Chalk: III. The Chalk Grasslands of Hampshire-Sussex Border. Journal of Ecology 13, 177–223.

Tasser, E., Sternbach, E., Tappeiner, U., 2008. Biodiversity indicators for sustainability monitoring at municipality level: An example of implementation in an alpine region. Ecological Indicators 8, 204–223.

Temperton, V.M., Märtin, L.L.A., Röder, D., Lücke, A., Kiehl, K., 2012. Effects of Four Different Restoration Treatments on the Natural Abundance of 15N Stable Isotopes in Plants. Front Plant Sci 3.

ten Kate, K., Bishop, J., Bayon, R., 2004. Biodiversity offsets: Views, experience, and the business case, IUCN, Gland, Switzerland and Cambridge, UK and Insight Investment, London, UK. ed.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M., Bakker, J.P., 1996. An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. Functional Ecology 10, 144–151.

Thompson, J.N., Reichman, O.J., Morin, P.J., Polis, G.A., Power, M.E., Sterner, R.W., Couch, C.A., Gough, L., Holt, R., Hooper, D.U., Keesing, F., Lovell, C.R., Milne And Manuel C. Molles, B.T., Roberts, D.W., Strauss, S.Y., 2001. Frontiers of Ecology. BioScience 51, 15.

Thompson, K., Grime, J.P., 1979. Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats. Journal of Ecology 67, 893–921.

Tomanek, G.W., Albertson, F.W., Riegel, A., 1955. Natural Revegetation on a Field Abandoned for Thirty-Three Years in Central Kansas. Ecology 36, 407–412.

Török, P., Vida, E., Deák, B., Lengyel, S., Tóthmérész, B., 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. Biodiversity and Conservation 20, 2311–2332.

Torsvik, V., Øvreås, L., 2002. Microbial diversity and function in soil: from genes to ecosystems. Current Opinion in Microbiology 5, 240–245.

Troll, C., 1939. Luftbildplan und ökologische Bodenforschung: Ihr zweckmäßiger Einsatz für die wissenschaftliche Erforschung und praktische Erschließung wenig bekannter Länder. Gesellschaft für Erdkunde Berlin.

Trueman, I., Mitchell, D., Besenyei, L., 2007. The effects of turf translocation and other environmental variables on the vegetation of a large species-rich mesotrophic grassland. Ecological Engineering 31, 79–91.

Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the mediterranean biome. Diversity and Distributions 15, 188–197.

Valladares, F., Gianoli, E., 2007. How Much Ecology Do We Need to Know to Restore Mediterranean Ecosystems? Restor Ecology 15, 363–368.

van de Voorde, T.F.J., van der Putten, W.H., Gamper, H.A., Gera Hol, W.H., Martijn Bezemer, T., 2010. Comparing arbuscular mycorrhizal communities of individual plants in a grassland biodiversity experiment. New Phytologist 186, 746–754.

Van Der Heijden, M.G.A., Boller, T., Sanders, I.R., 1998. Different Arbuscular Mycorrhizal Fungal Species Are Potential Determinants of Plant Community Structure. Ecology 79, 2082–2091.

van der Heijden, M.G.A., Horton, T.R., 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. Journal of Ecology 97, 1139–1150.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396, 69–72.

van der Heijden, M.G.A. van der, Sanders, I.R., 2002. Mycorrhizal Ecology, New Ed. ed. Springer-Verlag Berlin and Heidelberg GmbH & Co. K.

Van Nes, E.H., Scheffer, M., 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. American Naturalist 738–747.

Vécrin, M.P., Muller, S., 2003. Top-soil translocation as a technique in the re-creation of species-rich meadows. Applied Vegetation Science 6, 271–278.

Vellend, M., 2010. Conceptual synthesis in community ecology. Q Rev Biol 85, 183–206.

Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F., Hermy, M., 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. Journal of Ecology 95, 565–573.

Verhagen, R., Klooker, J., Bakker, J.P., Diggelen, R. van, 2001. Restoration Success of Low-Production Plant Communities on Former Agricultural Soils after Top-Soil Removal. Applied Vegetation Science 4, 75–82.

Verhoef, H.A., Morin, P.J. (Eds.), 2010. Community Ecology: Processes, Models, and Applications. Oxford University Press, USA.

Vierheilig, H., Coughlan, A.P., Wyss, U., Piché, Y., 1998. Ink and Vinegar, a Simple Staining Technique for Arbuscular-Mycorrhizal Fungi. Appl Environ Microbiol 64, 5004–5007.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human Domination of Earth's Ecosystems. Science 277, 494–499.

Walker, B., Holling, C.S., Carpenter, S.R., Kinsing, A., 2004. Resilience, adaptability and transformability in social–ecological systems. Ecology and Society 9, [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art5/.

Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., Pywell, R.F., 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation 119, 1–18.

Walker, L.R., Moral, R. del, 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press.

Walker, L.R., Walker, J., Hobbs, R.J., 2007. Linking restoration and ecological succession. Springer.

Wallington, T.J., Hobbs, R.J., Moore, S.A., 2005. Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. Ecology and Society 10, 16.

Wang, B., Qiu, Y.L., 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16, 299–363.

Warner, N.J., Allen, M.F., MacMahon, J.A., 1987. Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. Mycologia 721–730.

Wells, T.C.E., Sheail, J., Ball, D.F., Ward, L.K., 1976. Ecological Studies on the Porton Ranges: Relationships Between Vegetation, Soils and Land-Use History. Journal of Ecology 64, 589–626.

Westman, W.E., 1977. How much are nature's services worth? Science 197, 960–964.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42, 266–274.

Whisenant, S.G., 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge University Press.

White, P.S., Jentsch, A., 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62, 399–450.

White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction., in: The Ecology of Natural Disturbance and Patch Dynamics.

White, P.S., Walker, J.L., 2008. Approximating Nature's Variation: Selecting and Using Reference Information in Restoration Ecology. Restoration Ecology 5, 338–349.

Willems, J. h., Bik, L. p. m., 1998. Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. Applied Vegetation Science 1, 91–100.

Wilson, E.O., 1988. Biodiversity. The National Academies Press, Washington, D.C.

Wilson, E.O., 1992. The Diversity of Life. Harvard University Press.

Wilson, G., Hartnett, D., 1997. Effects of mycorrhizae on plant growth and dynamics in experimental tall grass prairie microcosms. American journal of Botany 84, 478–478.

Wolff, A., 2011. Note sur le suivi ornithologique sur Cossure en 2011.

Wolff, A., Dieuleveut, T., Martin, J.L., Bretagnolle, V., 2002. Landscape context and little bustard abundance in a fragmented steppe: implications for reserve management in mosaic landscapes. Biological Conservation 107, 211–220.

Wolff, A., Fabre, P., Vincent-Martin, N., Paulus, G., Becker, E., 2009. La réserve naturelle des Coussouls de la Crau, plan de gestion 2010-2014. Section A: Diagnostiques et enjeux.

Wong, N.K., Morgan, J.W., Dorrough, J., 2010. A conceptual model of plant community changes following cessation of cultivation in semi-arid grassland. Applied Vegetation Science 13, 389–402.

Yurkonis, K.A., Meiners, S.J., 2004. Invasion impacts local species turnover in a successional system. Ecology Letters 7, 764–769.

Zalasiewicz, J., Williams, M., Haywood, A., Ellis, M., 2011. The Anthropocene: a new epoch of geological time? Phil. Trans. R. Soc. A 369, 835–841.

Zobel, M., 1997. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology & Evolution 12, 266–269.

Zobel, M., Moora, M., 1995. Interspecific competition and arbuscular mycorrhiza: importance for the coexistence of two calcareous grassland species. Folia Geobotanica 30, 223–230.

Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., Grimm, V., 2010. The virtual ecologist approach: simulating data and observers. Oikos 119, 622–635.

Appendices

Appendix 1: Jaunatre, R., Dolidon, B., Buisson, E., Dutoit, T. (2011) Note méthodologique : Exemple de restauration de la plaine de la Crau : l'écologie de la restauration face à la restauration écologique. Sciences, Eaux, Territoires, 5, 36-39.

Note méthodologique

Exemple de restauration de la plaine de la Crau : l'écologie de la restauration face à la restauration écologique

Quel peut être l'apport des recherches en écologie de la restauration pour la réhabilitation d'une communauté végétale unique à forte valeur patrimoniale ? Comment s'intègrent-elles aux opérations de restauration sur le terrain ? Exemple en plaine de Crau pour la réhabilitation des steppes méditerranéennes de Cossure.

De l'expérimental à l'expérimentation

Des solutions techniques issues de la recherche en écologie de la restauration sont utilisées lorsque des écosystèmes à forte valeur patrimoniale ne sont pas ou peu résilients aux perturbations d'origine anthropique. Cependant, le passage de la dimension expérimentale à un projet de restauration écologique à grande échelle constitue plus qu'une simple transposition de techniques et de changements d'échelles. Cette transition nécessite en effet l'implication et la collaboration de nombreux acteurs qui constituent une organisation complexe dont les chercheurs, les financeurs, les gestionnaires d'espaces naturels et les opérateurs de travaux constituent les quatre grandes composantes. Chacun joue un rôle particulier, selon des contraintes et objectifs qui lui sont propres. Les scientifiques ont un rôle de conseil, suivi et d'évaluation. Les financeurs recherchent quant à eux la meilleure réussite sur la plus grande superficie. Garants de leur propre équilibre budgétaire, ils favorisent la qualité du rapport efficacité/coût quitte à réduire le nombre de traitements mis en œuvre. Les gestionnaires du territoire et de la conservation ont pour but la meilleure insertion de l'opération, en lien avec les politiques locales d'aménagement du territoire. Enfin, les opérateurs de terrain, réalisant concrètement le volet travaux, sont avant tout liés à des objectifs contractuels définis par les trois types d'acteurs précédents en amont des opérations comme les surfaces de travail

L'objectif commun à tous est bien la réussite globale de l'opération, c'est-à-dire son effectivité en vue de sa reproduction, qui conditionne l'existence des acteurs eux-mêmes. À cause des objectifs et contraintes parfois divergents, cette réussite nécessite un échange permanent : que ce soit pour mettre en place à grande échelle des techniques originales de restauration écologique ou pour intégrer les contraintes opérationnelles de chacun, qu'elles soient d'ordre scientifique, technique ou financier.

Le projet de réhabilitation de Cossure, débuté en 2008, est un exemple d'opération où la discipline scientifique identifiée comme l'écologie de la restauration, expérimentale, se confronte directement avec la restauration écologique, opérationnelle à grande échelle, celle-ci intégrant pour partie de l'ingénierie écologique basée sur l'application des principes de l'écologie à la gestion de l'environnement.

Mener à bien un projet de restauration écologique : la réhabilitation d'une steppe méditerranéenne

La plaine de Crau constitue l'unique pseudo-steppe méditerranéenne française (photo ❶). Cette communauté végétale exceptionnelle est un habitat pour de nombreuses espèces d'oiseaux steppiques d'intérêt patrimonial (Outarde Canepetière, Ganga cata, etc.) ainsi que pour des insectes endémiques (le Criquet de Crau – photo ❷, et le Bupreste de Crau). Cette vaste plaine d'intérêt écologique majeur a vu sa surface diminuer de 80 % en quatre cents ans, diminution liée en partie à l'implantation de l'arboriculture. Un de ces vergers, Cossure, cultivé de 1987 à 2006, a été abandonné en 2007 et racheté en 2008 par CDC Biodiversité (filiale de la Caisse des dépôts et consignations) avec pour objectif principal la réhabilitation d'un habitat de type steppique visant le retour des oiseaux patrimoniaux. La réhabilitation a consisté en :

- l'arrachage des arbres,
- leur broyage et évacuation
- le nivellement des buttes créées lors de la mise en place du verger.

❷ Le Criquet de Crau (*Prionotropis hystrix rhodanica*, Uvarov), une espèce endémique de la plaine de Crau, aujourd'hui menacée et protégée.

❺ L'*Asphodeletum fistulosii* de Crau est l'une des associations végétales méditerranénnes les plus riches en espèces.

Parallèlement à cette ouverture du paysage nécessaire à la reconnexion écologique de zones steppiques permettant la recolonisation par l'avifaune, des objectifs complémentaires de restauration expérimentale de la végétation ont été fixés : à court terme, minimiser les taxons non caractéristiques et maximiser les taxons caractéristiques, et à long terme restaurer la richesse, la structure et la composition floristique de la pseudo-steppe. La restauration active est nécessaire compte-tenu de la très faible résilience de la communauté végétale de la pseudo-steppe de Crau, servant d'écosystème de référence pour la restauration. Plusieurs facteurs sont à l'origine de cette faible résilience : une quasi-absence d'une banque de graines permanente, une faible production de graines par certaines espèces et la faible dispersion des graines de la plupart des espèces, ainsi qu'une incapacité à la compétition face à la couverture dense d'espèces plus opportunistes favorisées par un sol fertilisé pendant plusieurs années de cultures (Buisson *et al.*, 2004 ; Dutoit *et al.*, 2005).

Les traitements testés pour restaurer la communauté végétale sont :

- le retour du pâturage ovin visant à limiter l'expansion des espèces végétales non désirées ;
- le semis d'espèces dites « nurses » qui vise l'occupation rapide des niches écologiques pour ensuite libérer des sites favorables (*safe sites*) à l'installation d'espèces moins compétitrices une fois le pâturage pérennisé ;
- le transfert de foin qui vise à réintroduire un pool de graines d'espèces locales provenant de la steppe (Coiffait *et al.*, 2008) ;
- le transfert de sol visant la réintroduction d'un pool de propagules d'espèces et leurs micro-organismes associés.

Des exigences environnementales à respecter

En phase travaux, les exigences environnementales liées aux opérations de chantier et à leur contexte écologique se traduisent par des contraintes techniques, spatiales et calendaires. En termes de calendrier, aux contraintes internes liées au phasage d'opérations interdépendantes s'ajoutent des contraintes externes telles que le respect des périodes de reproduction de la faune.

Le respect des enjeux environnementaux, important à la réussite d'une telle opération, s'insère dans un ensemble d'enjeux qu'il est nécessaire de hiérarchiser. Cette classification résulte de la concertation entre les acteurs, et donc entre des disciplines qui se côtoient rarement (opérateurs des travaux publics et ornithologues, par exemple). L'objectif est de trouver le meilleur rapport entre l'efficacité et l'impact des techniques mises en œuvre. Le transfert de foin, par exemple, utilise nécessairement comme source une aire de steppe de référence. Le problème se pose alors de collecter une quantité suffisante de matériel végétal, en impactant au minimum les zones de récolte : la méthode choisie est non destructive, car sans fauchage. La récolte s'effectue par bandes étroites pour préserver la capacité de réensemencement naturel du site de collecte.

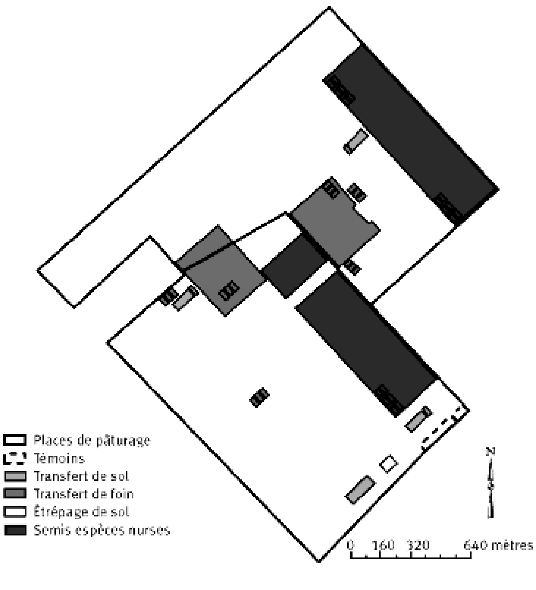
L'ensemble de ces exigences nécessite de travailler sur deux aspects principaux : le phasage et la communication. Un responsable à plein temps de cette tâche de coordination est nécessaire. Si les plans globaux d'avancement sont établis avec les conducteurs de travaux, un accompagnement et un suivi de terrain régulier des opérateurs sont indispensables. C'est le chauffeur de l'engin de terrassement lui-même qui doit avoir vu un individu de la plante à préserver, et non pas uniquement des piquets délimitant la zone mise en défens. S'en tenir à une approche *top down* sans communication directe entre un responsable environnement et les opérateurs de terrain est inefficace.

La bonne réalisation du projet nécessite de faire s'exprimer tous les corps de métier et toutes les sensibilités et de leur permettre d'échanger pour que chacun perçoive les contraintes de l'autre. Le décideur doit se donner les moyens d'entendre chacun pour disposer des éléments nécessaires à une hiérarchisation des priorités selon un ordre acceptable par tous, processus régulièrement enrichi de nouveaux éléments liés au caractère expérimental de la démarche. Aussi, les procédures de mise en œuvre peuvent être réajustées en cours de réalisation. L'importance de cette part d'imprévus étant prévisible, anticipation et adaptabilité sont indispensables.

L'anticipation porte sur les montages techniques et administratifs des opérations. Le montage technique nécessite en amont une large consultation des acteurs du territoire pour la synthèse des connaissances et exigences, qui doivent être transcrites en éléments quantifiés pour la formulation de préconisations opérationnelles. Enfin, un projet est techniquement bien monté lorsqu'on s'est donné les moyens et le temps de réaliser des essais des techniques envisagées, rendus nécessaires par le caractère souvent unique des milieux restaurés, les techniques existantes étant rarement directement transposables. Il faudrait idéalement réaliser les travaux de A à Z à petite échelle, pour affiner les matériels à utiliser, les méthodes et la synchronisation entre les actions. Seul ce test permet d'affiner les rendements, les coûts, et de prendre du recul par rapport aux conséquences des différents phasages possibles.

Le montage administratif, une des clefs d'une réalisation réussie, doit donner une valeur contractuelle aux exigences environnementales. Les délais administratifs (procédure de consultation, par exemple) et la nature du marché doivent respecter les objectifs liés au calendrier écologique des espèces considérées et inclure des réajustements de techniques en cours d'avancement.

❶ Dispositif expérimental des essais de restauration écologique.



Du consensus naît le projet

La délimitation des contours puis des détails d'un projet de cette ampleur se fait en concertation avec les différents protagonistes. Des réunions en cercles d'acteurs, c'est-à-dire avec uniquement les parties concernées par l'objet de la discussion permettent d'optimiser les temps passés par chacun à l'élaboration du projet (Oberlinkels *et al.*, 2010). Un coordinateur a le rôle central de redistribution des informations entre chacune des parties. Ce dialogue nécessaire dans l'élaboration *a priori*, doit se poursuivre pendant la réalisation du projet. Le coordinateur doit donc faire remonter aux personnes concernées les réalités de chantier afin de réagir rapidement et de modifier les consignes si nécessaire. Le projet final est le fruit de l'ensemble de ces dialogues.

Des spatialisations idéales, une réalisation optimale

Le dispositif expérimental

Le dispositif expérimental idéal n'est pas le même selon les acteurs. Pour les scientifiques, il comporte un maximum de répétitions de chacune des modalités sur une même superficie, réparties aléatoirement dans l'espace. Pour les gestionnaires, l'idéal est constitué de grandes superficies homogènes reproduites à l'identique sur chacune des deux places de pâturages afin d'imposer les mêmes contraintes aux deux futurs troupeaux. Le maître d'ouvrage, quant à lui, souhaite un dispositif au moindre coût avec les modalités les plus prometteuses sur des grandes surfaces.

Le dispositif réalisé est le résultat d'un compromis: les modalités comportent chacune au moins trois répétitions réparties plus ou moins aléatoirement, tout en équilibrant leurs surfaces suivant les places de pâturage (figure ❶).

La surface totale des modalités est le rapport optimal entre le coût, l'efficacité attendue et le matériel disponible : le semis d'espèces nurses, au coût moindre, a été réalisé sur soixante hectares, et le transfert de sol (provenant de zones prochainement détruites par des projets d'aménagement), très prometteur mais plus de vingt-cinq fois plus cher que les semis, a quant à lui été réalisé sur seulement trois hectares.

Le calendrier des opérations

Le calendrier effectif résulte finalement d'une priorisation des intérêts : tout d'abord, un évitement des périodes et zones de nidification, ensuite la réalisation dans l'ordre des entrepreneurs, le tout régulé par les aléas du couple terrain/météo qui a pu rendre temporairement inaccessibles certaines surfaces.

L'acceptation de certaines concessions

Pour la réussite globale du projet, il est parfois nécessaire que l'une des parties accepte de faire quelques concessions. Les parcelles témoins du projet Cossure en sont un bon exemple. Les scientifiques ont dès le début du dialogue pointé l'importance de garder des zones témoins, c'est-à-dire avec les arbres laissés morts sur place, importantes pour la validation du protocole mais aussi pour la communication, afin de montrer l'état potentiel en cas de non-intervention. Du point de vue des gestionnaires, de telles parcelles créeraient un obstacle paysager pour l'avifaune et présenteraient des risques d'embroussaillement *via* « l'effet perchoir ». Parallèlement à leur fonction de « témoin », la maîtrise d'ouvrage voit ces parcelles comme une source potentielle de virus et de ravageurs pour les vergers voisins encore en exploitation. Afin de s'affranchir de tout risque phytosanitaire, il a été décidé de ne conserver qu'une parcelle « témoin intermédiaire » où les arbres ont été coupés et exportés mais les buttes non nivelées.

Des opportunités à saisir

Le dialogue permanent est aussi l'occasion de saisir des opportunités. L'un des traitements de restauration possibles était le retrait de la couche superficielle de sol, pour supprimer la banque de graines permanente de l'ancien verger d'une part, et d'autre part, pour diminuer les quantités de nutriments apportés pendant la culture. Ce traitement, non planifié dans le dispositif de restauration expérimentale, a tout de même été mis en œuvre à la faveur d'un besoin en matériaux pour la réalisation d'une butte de terre de sécurité en limite d'une zone accidentée. Ce sont les réunions régulières d'avancement du chantier qui ont permis de saisir l'opportunité de réaliser ce traitement d'étrépage du sol.

Un projet consensuel et pragmatique

Chacun des acteurs d'un projet de restauration écologique à grande échelle s'y insère avec ses propres objectifs, et attentes (figure ❷). C'est à partir de ce champ des possibles que se crée un consensus issu des discussions *a priori*. La poursuite du dialogue est nécessaire à l'éventuelle saisie d'opportunité au cours de la réalisation du projet, mais aussi de manière à faire face aux réalités du terrain. Le projet final est alors le résultat de cette coordination entre les différents acteurs impliqués.

Quelques recommandations

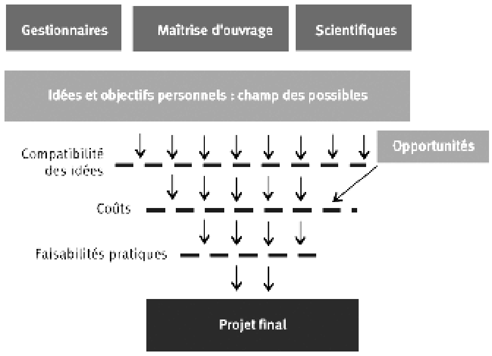
Parmi les principaux enseignements à tirer de la réalisation de ce projet, retenons :

• la nécessité d'intégrer l'ensemble des acteurs du territoire,

• l'intérêt de l'anticipation des modes opératoires et l'importance d'une communication permanente entre tous, techniciens et décideurs

• le besoin de souplesse et de réactivité lors de la phase travaux du projet, le tout maîtrisé par un « coordinateur environnement ». ■

❷ **Schéma conceptuel de la naissance d'un projet final.**



Quelques références clés...

BUISSON, E., *et al.*, 2004, Bilan de trente années de recherches en écologie dans la steppe de Crau (Bouches-du-Rhône, Sud-est de la France), *Ecologia Mediterranea*, n° 30, p. 7-24.

COIFFAIT, C., *et al.*, 2008, Restauration écologique en plaine de Crau. Adaptation de la méthode du transfert de foins, p. 113-119, *in : Actualité de la recherche en écologie des communautés végétales*, Actes du quatrième colloque ECOVEG, Rennes, 12-14 mars 2008, Éditions Tec & Doc, Lavoisier, Paris, 233 p.

DUTOIT, T., *et al.*, 2005, Rémanence des utilisations anciennes et gestion conservatoire des pelouses calcicoles de France, *Biotechnologie, Agronomie, Sociétés et Environnement*, n° 9, p. 125-132.

OBERLINKELS, M., *et al.*, 2010, Le projet de restauration du site de Cossure expérimente un mode de gouvernance, *Espaces Naturels*, n° 29, p. 24-25.

Les auteurs

Renaud Jaunatre, Élise Buisson et Thierry Dutoit
Université d'Avignon, Centre national de la recherche scientifique, UMR CNRS/IRD 6116,
Institut méditerranéen d'écologie et de paléoécologie (IMEP),
IUT, site Agroparc, BP 61207, 84911 Avignon Cedex 9
renaud.jaunatre@yahoo.fr
elise.buisson@univ-avignon.fr
thierry.dutoit@univ-avignon.fr

Baptiste Dolidon
Chambre d'agriculture des Bouches du Rhône,
Maison des agriculteurs,
22 avenue Henri Pontier, 13626 Aix en Provence Cedex 1
b.dolidon@bouches-du-rhone.chambagri.fr

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Appendix 2 : Jaunatre, R., Buisson, E., Dutoit, T. (2012) First-year results of a multi-treatment steppe restoration experiment in La Crau (Provence, France). Plant Ecology and Evolution, 145:1, 13-23.

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REGULAR PAPER

First-year results of a multi-treatment steppe restoration experiment in La Crau (Provence, France)

Renaud Jaunatre*, Elise Buisson & Thierry Dutoit

Université d'Avignon et des Pays de Vaucluse, Institut Méditerranéen d'Ecologie et de Paléoécologie (UMR CNRS/IRD), IUT, Site agroparc BP 61207, FR-84911 Avignon cedex 09, France
*Author for correspondence: renaud.jaunatre@yahoo.fr

Background and aims – Intense agriculture phases on old plant communities, such as Mediterranean steppes, can lead to low resilience. Two main obstacles to the spontaneous recolonization of these plant communities are often the low dispersal of target species and the high dispersal and establishment potential of unwanted species. The aim of the study is to find the most efficient restoration treatments to restore these plant communities.
Methods – After the rehabilitation of an herbaceous sheep-grazed community on a formerly intensively cultivated orchard in the last French Mediterranean steppe (La Crau, Provence, France), four experimental restoration treatments were applied to restore the steppe plant community: (i) topsoil removal to lower ruderal species seed banks and soil trophic levels, (ii) nurse species seeding to rapidly occupy niches, and then to provide safe sites for target species once sheep grazing is reintroduced, (iii) hay transfer to provide local species seeds, and (iv) soil transfer to provide local species propagules with associated microorganisms. One year later, plant species richness, composition and diversity are compared.
Results – Although the communities developing on areas seeded with nurse species and where topsoil was removed differed most widely from the reference ecosystem, i.e. steppe, these restoration treatments succeeded in achieving their goal by significantly lowering the abundance of unwanted dominant species. While hay transfer did not have a significantly higher species richness than that of the rehabilitated area, it showed promising results, as some germinations of target species were observed. One year only after the treatment was applied, soil transfer provided a community richness and composition very close to that of the reference ecosystem, but not with the same vegetation structure.
Conclusion – In order to restore plant community composition, the more the treatment strengthens community dispersal, the more efficient it is. The gain in efficiency is closely linked with the cost of the treatment.

Keywords – Plant community composition, former agricultural land, grassland, hay transfer, nurse species seeding, soil transfer, species richness, topsoil removal.

INTRODUCTION

Ecosystems which have undergone long-term severe environmental constraints, either biotic (e.g. grazing) or abiotic (e.g. dryness), generally exhibit a high species richness, as well as often unique and highly structured communities (Tilman & Pacala 1993, Alard & Poudevigne 2002, Hopper 2009). Intensive agriculture usually induces strong disturbances which are long lasting and/or at large scale; constrained ecosystems which have been cultivated often pass biotic and abiotic thresholds (Whisenant 1999). This is especially true when soil has been enriched, leading to increased competition (Marrs 2002), and when target species propagules are not available anymore: either because the seed bank has been depleted (Hutchings & Booth 1996) or because their dispersion abilities are too weak (Bakker et al. 1996). Such disturbed ecosystems cannot be restored without specific restoration techniques (Cramer et al. 2008), which have to focus on lowering non-target species abundance and on improving target species dispersion (Walker et al. 2004, Baer et al. 2008, Kiehl et al. 2010). Lowering non-target species is achieved either (i) by preventing their emergence: i.e. suppression of seed bank or (ii) by lowering their growth and density: i.e. restoration of low soil nutrient content or suitable disturbance regimes (i.e. grazing, etc.). Among the various techniques available, four are of particular interest: nurse species seeding, topsoil removal, hay transfer and soil transfer.

By changing biotic interactions, the introduction of new species can change the facilitation-competition balance (Gómez-Aparicio 2009). For example, seeding hemiparasitic species of the *Rhinanthus* genus can reduce dominant species density and increase abundance of subordinate species (Davies et al. 1997, Pywell et al. 2007). Seeding species which are not very competitive considering the environmental conditions of the site to be restored, but which show high nutrient consumption and can act as a filter on community composition. The established sown mixture can drive succession from an inhibition to a tolerance model of succession (Connell & Slatyer 1977). In the first years, rapid cover and nutrient consumption can inhibit arable weed species density. Once nutrient level has decreased, environmental stressors like grazing or drought can release safe sites which can be tolerated by target species.

In former agricultural areas, where upper soil layers contain higher nutrient contents (Marrs 1985) and most of the ruderal permanent seed bank (Davy 2002), topsoil removal has been proven to lower nutrient content in soil and to favour low-production plant communities (Aerts et al. 1995, Verhagen et al. 2001).

Where target species do not recolonise rapidly, dispersion improvement is needed to restore plant community composition (Hutchings & Booth 1996, Bischoff 2002). When neither reinforcing natural dispersion processes (Poschlod et al. 1998) nor sowing a commercial regional seed mixture (Jongepierová et al. 2007) can be done, the reintroduction of gathered propagules can be a very efficient solution (Kiehl et al. 2010). Transfering of hay material and soil material were both tested in this study. Hay transfer has been used in several northern Europe species-rich calcareous grassland restoration experiments where a high number of target species were transferred and established (Hölzel & Otte 2003, Kiehl et al. 2006, Rasran et al. 2006). This treatment was however never tested on a large scale in drier ecosystems. Vacuum harvesting of seeds that have already fallen on the ground was used because it has proven to successfully gather species in northwestern Europe (Stevenson et al. 1997, Riley et al. 2004) or in Mediterranean plant communities (Coiffait-Gombault et al. 2011).

Habitat / turf translocation and soil transfer can be used to transfer propagules, either by transferring intact turves, fragmented turves or bulk soil, and have already shown successful results in recreating species rich plant communities (Pywell et al. 1995, Bullock 1998, Vécrin & Muller 2003). Gathering bulk soil is cheaper and easier and the restoration success is similar to whole turf transfer for species richness and composition (Good et al. 1999). Although this technique requires having an area which will be destroyed, it is expected to be very efficient, transferring seeds, but also propagules and associated microorganisms. It is also expected to lower nutrient contents by mixing soil from the donor site with that from the degraded site.

Apart from fire and overgrazing disturbances (D'Antonio et al. 2003), Mediterranean ecosystem restoration issues have been poorly addressed despite the fact that these systems are particularly threatened by anthropogenic disturbances (Underwood et al. 2009). In the present study, we assessed the efficiency of four restoration treatments applied at a large scale with the aim of restoring a Mediterranean species-rich steppe community where the two main barriers identified to the spontaneous recolonisation of plants are the low dispersal potential of target species and the high dispersal and establishment potential of unwanted species, in particular due to increased fertility in the former cultivation area (Buisson et al. 2006). After the rehabilitation of a 357 ha intensively cultivated orchard into an herbaceous sheep-grazed habitat, we applied on a large scale (i) nurse species seeding, (ii) topsoil removal, (iii) hay transfer and (iv) soil transfer to restore a steppe plant community with the last French Mediterranean steppe as a reference ecosystem. We tested the effects of seeding nurse species to inhibit the dense cover of non-target species and to provide food for grazers. To our knowledge, these four treatments were never assessed before at large scale on Mediterranean herbaceous ecosystems. Vegetation characteristics were monitored for the first year in order to compare short-term effects of each treatment regarding the main objectives: increasing target species richness and providing suitable conditions for their recolonization (i.e. low non target species cover and low nutrient content). The first year results are important for four main reasons: (i) they provide sponsors financing large scale restoration projects with indications for further applications, (ii) they provide early information which can be used to assess further restoration technique applications, (iii) they give an essential base-line which will be used to compare the development of communities following the application of various treatments after several years of monitoring, and (iv) they allow managers to adjust their management, here grazing, of the site in order to ensure restoration success.

MATERIAL AND METHODS

Study site

La Crau area is the only French Mediterranean steppe; it has been shaped by millennia of interactions between soil, climatic conditions and sheep grazing (Devaux et al. 1983, Badan et al. 1995, Henry et al. 2010) (fig. 1A). The 40 cm deep soil is made up of 50% of silicaceous stones and lays on a calcareous conglomerate which cannot be penetrated by plant roots (Devaux et al. 1983). The climate is Mediterranean with an average of 540 mm yearly precipitation, mainly in spring and autumn and 110 days per year with a more than 50 $km.h^{-1}$ wind (Devaux et al. 1983). Traditional extensive sheep grazing has taken place in the La Crau area for more than 2000 years (Badan et al. 1995, Henry et al. 2010). This xeric steppe, located in the South of France, is a unique species-rich plant community composed mainly of annuals and dominated by *Brachypodium retusum* Pers. and *Thymus vulgaris* L. Despite the fact that La Crau area is a habitat for numerous steppe birds, such as *Pterocles alcata* and *Tetrax tetrax* and for two restricted-range endemic insects (i.e. *Acmaeoderella cyanipennis perroti* Schaefer (Coleoptera) and *Prionotropis hystrix rhodanica* Uvarov (Orthoptera)), large areas have been destroyed by cultivation since the 1600's and the steppe lost about 80% of its original area (Buisson & Dutoit 2006).

The steppe of La Crau is a unique ecosystem, but insights on restoration technique efficiency in La Crau can provide useful information for other relatively dry ecosystem, restoration like steppes in Spain (Dehesas) and north Africa (Le Houérou 1995).

Restoration goals in a rehabilitation project

All the restoration treatment tested were applied on a larger rehabilitation project: in 2006, an orchard located approximately in the centre of the steppe area (fig. 1A) and adjacent to the largest remnant patch of steppe (6500 ha), was abandoned. The rehabilitation project within which the restoration treatments were applied began in 2009 and aimed at creating an herbaceous steppe-like habitat for steppe birds. Before rehabilitation, vegetation and soil characteristics were studied and the whole area was homogenous (multivariate ordination results not shown). In 2009, fruit trees (200000) and windbreak poplars (100000) were cut down and exported from the abandoned orchard. Soils were then levelled and sheep grazing was reintroduced in spring 2010. As the same rehabilitation procedure was applied on the whole area, it is considered spatially homogenous regarding soil characteristics and potential vegetation. The study focuses on four additional ecological restoration treatments which were applied on this rehabilitated orchard in order to restore the original steppe vegetation that was present before the planting of the orchard in 1987: nurse species seeding, topsoil removal, hay transfer and soil transfer (table 1). The very short-term objectives (one year) of this restoration experiment are to limit the colonisation of unwanted plant species and to improve the establishment of characteristic species just after the end of the rehabilitation phase. The objectives on a longer term (> ten years) are to re-direct the plant community on the desired successional pathway toward the steppe, to reach on a plant community with steppe characteristics: species-richness, composition and structure.

Restoration treatments

A mix of three nurse species (*Lolium perenne* L., *Festuca arundinacea* Schreb. and *Onobrychis sativa* Lam) were sown to compensate for a potential insufficient amount of food for sheep on the rehabilitated area during the first year. These species were chosen for their palatability, their purchase availability, their ability to rapidly cover bare ground, but also for their low competitive ability in Mediterranean environmental conditions and their actual cultivation in La Crau irrigated areas (*F. arundinacea* and *O. sativa*) or their presence in the steppe community (*L. perenne*; Devaux et al. 1983). The topsoil removal treatment consisted in removing the nutrient-rich upper soil layer, down to a depth of 20 cm over a 0.1 ha area at the end of August 2009. In communities with many very small species, seed gathering with conventional hay cutting methods cannot be effective. Therefore, the hay transferred was previously gathered by air-vacuuming (Stevenson et al. 1997, Riley et al. 2004) in summer 2009. The donor site is located less than 5 km away from the restoration site (fig. 1A). The material was then spread with a 1:3 ratio (spreading on 3 ha the seeds gathered on 1 ha) over two 10 ha areas in the rehabilitated orchard (fig. 1B). The material for soil transfer is the 20 cm upper soil layer of a 1 ha steppe patch which was going to be destroyed by construction work, located less than 2 km away from the restoration site. It was gathered on 1 ha

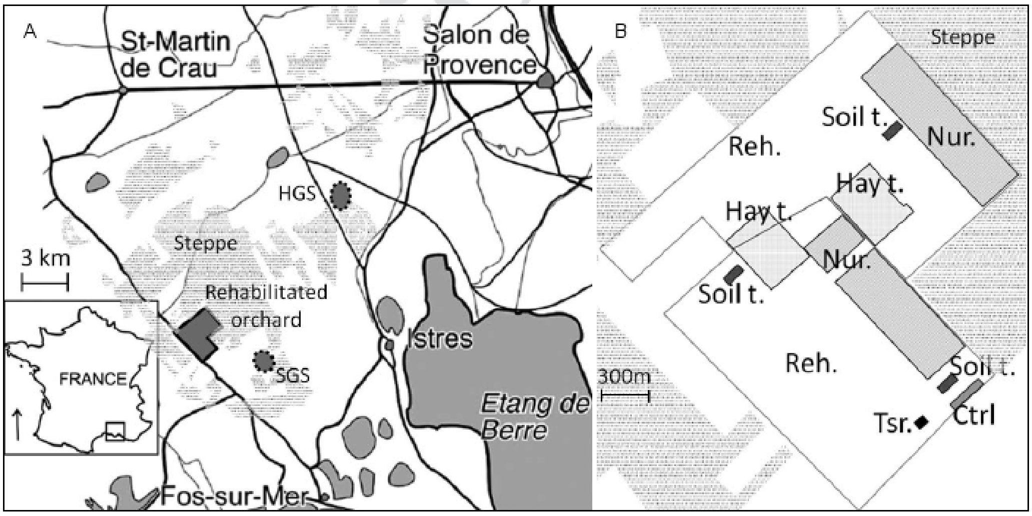

Figure 1 – A, location of the Crau plain in France and location of the rehabilitated orchard (Cossure), the hay gathering site (HGS) and the soil gathering site (SGS); B, experimental design of restoration treatment on former Cossure orchard: Ctrl = Control, Nur. = Nurse species seeding, Ts r. = Topsoil removal, Reh = Rehabilitated areas, Hay t. = Hay transfer and Soil t. = Soil transfer). The light grey color shows remaining steppe patches.

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Table 1 – Description of the actions in each treatment.
A cross means that the action described in the first column was carried out in the treatment named in the first line. The area where each treatment was applied, the number of soil samples collected and number of 2 × 2 m vegetation quadrats are given at the end of the table.

	Reference steppe	Before rehabilitation	Control Area	Rehabilitated Area	Nurse Species Seeding	Topsoil Removal	Hay transfer	Soil transfer
Orchard cultivation (1987-2006)		x	x	x	x	x	x	x
Orchard abandonment (2006)		x	x	x	x	x	x	x
Cutting and removing trees (2008-2009)			x	x	x	x	x	x
Levelling soil (2009)				x	x	x	x	x
Seeding nurse species (2009)					x			
Removing 15 cm topsoil (2009)						x		
Transferring hay (2009)							x	
Transferring soil (2009)								x
Area (ha in 2009)	-	0	2	271.9	60	0.1	20	3
Soil samples (2009 except before rehabilitation in 2008)	10	30	5	5		5		5 (donor site)
Vegetation quadrats (2010)	18	-	18	18	18	3	18	18

in bulk, transported and spread the same day with a 1:3 ratio in early September a few hours before significant rain. The soil was transferred on three 1 ha areas in the rehabilitated orchard (fig. 1B). In order to preserve the genetic integrity of local populations (Sackville Hamilton 2001), hay and soil materials were gathered in areas which used to be connected by sheep grazing from Neolithic times to the establishment of the orchard in 1987 (Fabre 1997) (fig. 1A). Monitoring previous to transfers showed that the species-richness, composition and structure of plant communities on donor sites where similar to those of the reference steppe ecosystem (data not shown). A control area was kept from rehabilitation works. Trees were removed for safety purposes but soils were not levelled on this 2 ha area (fig. 1A, table 1).

As in Hölzel & Otte (2003), the aim was to assess the efficiency of these treatments applied on a large scale for restoration. We thus choose rather to implement techniques on fewer large areas than on many small ones. All techniques have not been applied on the same areas, due to non-scientific constraints imposed by the multiple stakeholders of the project: the treatments had to be applied equally on the two delimited pieces of land for two sheep herds, on surface areas which were a trade-off between costs, expected efficiency and material availability: seeds, hay, soil, etc. (Jaunatre et al. 2011). Nurse species were sown on 60 ha, topsoil were removed on 0.1 ha, hay was transferred on 20 ha and soil was transferred on 3 ha (table 1).

Vegetation survey

On the steppe and for each treatment (i.e. control, rehabilitation and the four restoration treatments), 18 2 m × 2 m quadrats were surveyed, apart from the topsoil removal treatment which covered too small an area for such an extensive survey (n = 3 quadrats) (table 1). Quadrats were all placed at least 20 m from the edge of the area were the treatment was applied. On each quadrat, presence and abundance via the Braun-Blanquet abundance-dominance coefficient of all plant species were recorded (Braun-Blanquet et al. 1952), average vegetation height and vegetation cover were measured in May 2010 one year after treatment applications.

Soil analysis

Soil samples were gathered and analyzed in order to give further information on habitat suitability. Analyses were carried out on 30 samples of soil from the abandoned orchard before rehabilitation phase, ten samples in the reference steppe, and five samples in each of the following: soil transferred from the steppe, control, rehabilitated area, and topsoil removal (table 1). For each sample, three 70 g subsamples of soil were randomly gathered in a 35 m² area before being pooled and sieved with 2 mm mesh sieve for analyses carried out by INRA (Institut National de la Recherche Agronomique). Granulometry: percentage content of clay (< 0.002 mm), fine silt (0.002–0.02 mm), coarse silt (0.02–0.05 mm), fine sand (0.05–0.2 mm) and coarse sand (0.2–2 mm) and nutrient analysis (organic C, total N, P_2O_5 (Olsen et al. 1954), $CaCO_3$, CaO, K_2O) and water pH were measured following standard methods (Baize 2000).

Data analysis

A dissimilarity index was used to measure the distance between the vegetation composition of the restored areas and that of the reference steppe. For each quadrat surveyed in a restored area, the mean Raup-Crick dissimilarity index (Raup & Crick 1979) between this quadrat and the 18 quadrats surveyed in the reference steppe was calculated. This mean varies between zero and one: a zero value means that the vegetation composition is strictly the same on the quadrat surveyed in the restored area and those surveyed on the reference steppe, while a one value means that there are no species in common between the quadrat surveyed in the restored area and those surveyed on the reference vegetation.

As data were not conform to parametric conditions, soil granulometry and nutrient contents, mean vegetation cover, average vegetation height, species richness and mean Raup and Crick dissimilarities were compared between treatments with non-parametric tests: a Kruskal-Wallis test, followed by a pairwise Wilcoxon test with a p-value adjustment according to the Benjamini-Hochberg's method if a significant difference was found (Benjamini & Hochberg 1995).

An ordination of soil data according to their granulometry and nutrient contents was done with a Principal Component Analysis. Correspondence Analysis on Braun-Blanquet abundance-dominance coefficients transformed into absolute cover was used to detect changes in vegetation composition and structure (Guinochet 1973). All analyses were conducted

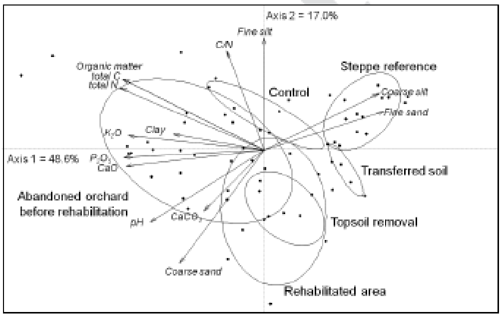

Figure 2 – Ordination plot of the Principal Component Analysis based on soil granulometry and nutrient contents in steppe reference, restoration treatments: topsoil removal, rehabilitated area, control, transferred soil and abandoned orchard. Ellipses are centred on the barycentre and their form is weighted by the distribution of all points corresponding to one treatment.

with R 2.6.1 (R Development Core Team 2007), univariate analyses with its stats package and multivariate analyses with its ade4 package (Chessel et al. 2004, Dray & Dufour 2007, Dray et al. 2007).

RESULTS

Differences in soil properties

Rehabilitation showed significant effects on soil physical and chemical properties (table 2). Rehabilitation and topsoil removal provided a significantly lower content of total carbon, total nitrogen, organic matter and phosphorus P_2O_5 compared to the abandoned orchard and the control but which was still significantly higher than in reference steppe soils. Removing topsoil allowed lowering fine silt and potassium K_2O. When considered together, all nutrient content variables clearly discriminated the soil along a gradient on the first axis (48.6%) from the reference steppe and transferred soil with the lowest nutrient content to the abandoned orchard and the control with the highest values for nutrient contents (fig. 2). The rehabilitated area and topsoil removal were in between these two groups. Transferred soil is discriminated from the reference steppe only on the second axis (17.0%), which is mainly correlated with granulometry variables and not with nutrient variables.

Effect of restoration treatments on vegetation cover and height

Mean vegetation height and cover showed significant differences among treatments ($X^2 = 74.13$, df = 6, $p < 0.001$ and $X^2 = 49.87$, df = 6, $p < 0.001$) (fig. 3A & B). Topsoil removal led to the lowest vegetation cover and height with a mean and standard error of the mean of 16.6 ± 7.2% and 3.33 ± 88.2 cm respectively. Soil transfer and steppe were similar in vegetation height but soil transfer showed a lower vegetation cover. The control and rehabilitated areas and the hay transfer treatment had high vegetation (more than 30 cm) and an extensive vegetation cover (more than 80%).

Effect of restoration treatments on plant species richness

Plant species richness varied significantly according to the various treatments ($X^2 = 66.22$, df = 6, $p < 0.001$) (fig. 3C). Nurse species seeding was the restoration treatment scoring the lowest species richness value (less than fifteen species per 4 m²) but with a significantly higher species richness than the control area (around ten species per 4 m²). Species richness for the topsoil removal and hay transfer treatments was not significantly higher than on the rehabilitated area (between fifteen and twenty species per 4 m²) but lower than on the reference ecosystem (more than 35 species per 4 m²). Only soil transfer, with a mean of 31 species per 4 m², showed no significant difference in species richness with the steppe.

Effect of restoration treatments on community composition

The Correspondence Analysis showed well-discriminated communities according to restoration treatments (fig. 4), confirmed by the Raup-Crick dissimilarity index significant differences ($X^2 = 108.0$, df = 5, $p < 0.001$; fig. 3D). The control area was mainly composed of *Poaceae* species e.g. *Bromus madritensis* L. and *Avena barbata* Pott ex Link, while rehabilitated plots were dominated by the same species with additional dicotyledonous diversity, e.g. *Trifolium stellatum* L., *Diplotaxis tenuifolia* L., etc. The communities the most distant from the steppe were those with topsoil removal and nurse species seeding treatments, which were dominated by ruderal species, e.g. *Stellaria media* L. and *Cardamine hirsuta* L. for the former and by the species sown (*L. perenne*, *F. arundinacea* and *O. sativa*) for the latter. The dominant species of the rehabilitated area showed reduced abundances compared to rehabilitated areas. Hay transfer was close to the rehabilitated area but, here and there, some additional characteristic species of the reference steppe appeared with very low abundances: e.g. *Vulpia bromoides* (L.) Gray and *Plantago lagopus* L. were not found in rehabilitated area. The closest community to the reference steppe was found with the soil transfer, which was characterised by many species from the steppe, e.g. *Bellis sylvestris* Cyrillo, *Taeniaterum caput-medusae* L., *Brachypodium distachyon* L. or *Evax pygmaea* (L.) Brot. Soil transfer is also the treatment which showed the lowest dissimilarity index means (fig 3D). Nevertheless, the steppe plant community was still different in its floristic composition; three of the most frequent species were not recorded in any of the treatments: *Brachypodium retusum* Pers., *Asphodelus ayardii* Jahan. et Maire and *Thymus vulgaris* L.

DISCUSSION

Effect of rehabilitation

Rehabilitation of a flat area dominated by Poaceae species has been successfully carried out through the removal of former orchard peach trees and the levelling of soils. Moreover, vegetation cover and soil nutrient contents were lowered by rehabilitation, which potentially provides better habitat suitability for target species recolonisation (Marrs 2002). However, the rehabilitated community is still very different from the target community in term of richness and composition. The density of Poaceae, especially *A. barbata* and *B. madritensis* may turn out to be an issue as they may inhibit establishment of target species unless sheep grazing pressure is sufficient to reduce their competition (Gibson & Brown 1992, Baer et al. 2008). Such differences between the reference steppe and the rehabilitated area can persist for a long time: in formerly cultivated areas abandoned more than thirty years ago, the difference with reference steppe is still significant (Römermann et al. 2005, Buisson et al. 2006).

Effect of restoration treatments on plant communities

Nurse species seeding and topsoil removal are the treatments on which communities are the most different from the reference one and with the lowest species richness. Nevertheless, even after one year, these treatments succeeded in achieving at least some of their short-term objectives. First year results of the topsoil removal treatment showed that soil

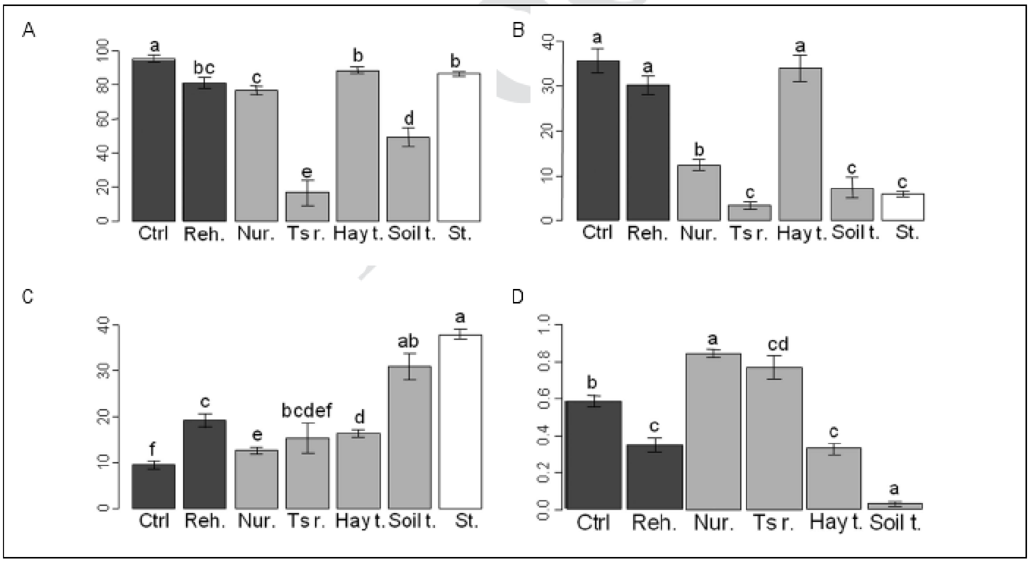

Figure 3 – For each restoration treatment: A, Mean vegetation cover (%); B, average vegetation height (cm); C, species richness; D, Raup & Crick dissimilarity indices. Reference ecosystem in white: St. = steppe, restoration techniques in light grey: Nur. = Nurse species seeding, Ts r. = Topsoil removal, Hay t. = Hay transfer, Soil t. = Soil transfer, and areas without restoration techniques application in dark grey: Ctrl = Control and Reh = Rehabilitated areas on 4 m² plot, error bars represent standard error, bars sharing a common letter are not significantly different (pairwise Wilcoxon test with a p-value adjustment according to Benjamini-Hochberg's method, $p > 0.05$).

Table 2 – Soil granulometry and nutrient contents in abandoned orchard.
(Ab. Orch.), control area (Crtl), rehabilitated area (Reh.), topsoil removal area (Ts r.), transferred soil (T. soil) and steppe reference (St.). df, X^2 and p are respectively the degree of freedom, chi² value and p-value of Kruskal-Wallis test (***: $p < 0.001$, **: $p < 0.01$). Values on a line with a common letter are not significantly different (pairwise Wilcoxon test with a p-value adjustment according to Benjamini-Hochberg's method, $p > 0.05$).

	df	X^2	p	Ab. Orch.		Ctrl		Reh.		Ts r.		T. Soil		St.	
Clay ($g.kg^{-1}$)	5	18.4	**	219.5 ± 3.7	b	216 ± 8	ab	215.2 ± 2.9	ab	220.4 ± 7.7	ab	215.6 ± 11.7	a	195.9 ± 4.1	b
Fine silt ($g.kg^{-1}$)	5	14.7	**	185.5 ± 3.6	a	190 ± 8.4	ab	178.4 ± 2.2	ab	163 ± 4.4	b	181.8 ± 5.4	ab	190.5 ± 4.6	a
Coarse silt ($g.kg^{-1}$)	5	30.8	***	130.5 ± 2.1	b	136.2 ± 4.7	b	136.6 ± 2.5	b	134.6 ± 3	b	141.6 ± 3.4	b	158.7 ± 3.7	a
Fine sand ($g.kg^{-1}$)	5	32.2	***	185.2 ± 3.9	c	226.6 ± 8.5	ab	190.2 ± 5	bc	205 ± 6.5	bc	210.2 ± 5.7	bc	230.2 ± 5.8	a
Coarse sand ($g.kg^{-1}$)	5	29.5	***	279.3 ± 6.7	a	231.2 ± 3.9	bc	279.6 ± 7.7	a	277 ± 7.1	a	250.8 ± 12.7	ab	224.7 ± 6.7	c
Total C ($g.kg^{-1}$)	5	45.1	***	27.99 ± 1.53	a	23.86 ± 1.85	ab	15.01 ± 2.26	cd	15.41 ± 1.81	bcd	13.78 ± 0.75	d	17.47 ± 0.53	c
Total N ($g.kg^{-1}$)	5	48.1	***	2.65 ± 0.13	a	2.23 ± 0.17	ab	1.47 ± 0.2	cd	1.51 ± 0.14	bcd	1.39 ± 0.07	d	1.64 ± 0.04	c
C/N	5	20.9	***	10.48 ± 0.11	a	10.68 ± 0.1	a	10.12 ± 0.44	ab	10.13 ± 0.35	ab	9.87 ± 0.14	b	10.66 ± 0.12	a
Organic matter ($g.kg^{-1}$)	5	44.8	***	48.42 ± 2.65	a	41.26 ± 3.22	a	25.98 ± 3.94	bc	26.68 ± 3.12	bc	23.8 ± 1.32	c	30.22 ± 0.92	b
pH	5	30.7	***	7.53 ± 0.03	a	7.18 ± 0.06	b	7.46 ± 0.12	ab	7.47 ± 0.05	a	7.01 ± 0.04	ab	6.82 ± 0.09	c
$CaCO_3$ ($g.kg^{-1}$)	5	16.8	**	2.18 ± 0.22	a	1.19 ± 0.19	ab	4.42 ± 1.96	ab	1.83 ± 0.7	ab	1 ± 0	ab	1.28 ± 0.15	b
P_2O_5 ($g.kg^{-1}$)	5	50.9	***	0.1 ± 0.01	a	0.1 ± 0.01	a	0.06 ± 0.01	b	0.07 ± 0.01	ab	0.01 ± 0	c	0 ± 0	d
CaO ($g.kg^{-1}$)	5	34.0	***	3.77 ± 0.17	a	3.15 ± 0.18	ab	3.46 ± 0.42	ab	3.46 ± 0.31	ab	2.24 ± 0.04	b	2.05 ± 0.1	c
K2O ($g.kg^{-1}$)	5	51.7	***	0.54 ± 0.04	a	0.31 ± 0.04	b	0.29 ± 0.06	bc	0.13 ± 0.02	cd	0.12 ± 0.01	d	0.15 ± 0.01	c

nutrient contents were not significantly lowered, contrary to what is found in literature (Aerts et al. 1995, Verhagen et al. 2001). Vegetation height and cover were however significantly lowered. As soil seed banks of previously cultivated areas rarely contain seeds from the target community but rather ruderal ones (Thompson & Grime 1979, Hutchings & Booth 1996), this can be attributed to a significantly reduced seed bank associated to removing the topsoil (Verhagen et al. 2001). Removing topsoil, and hence its seed bank, prevents the community from being dominated by non-target species and the remaining free niches may be available for target species (Temperton & Zirr 2004). Despite these advantages, this treatment involves substantial financial and energetic costs if applied over a large area. For instance, removing topsoil on the 357 ha Cossure abandoned orchard would have implied the rotation of 50,000 truckloads of soil. Hence, using more low-input processes to restore habitat settings is preferable in an environmentally sustainable project. Nurse species seeding may fulfil these requirements. Seeded species occupy niches which will thus not be available for early dense colonisation by relatively competitive species (Davies et al. 1997). In our case, the two species with the higher abundances in the rehabilitated area showed lower density and vegetation height was lower where nurse species were sown. Although restoring more suitable habitats for target species germination and growth has been proved to be an essential prerequisite (Marrs 2002), in numerous species-rich communities, recolonisation of target species is seed-limited (Hutchings & Booth 1996, Bischoff 2002, Buisson et al. 2006, Ehrlén et al. 2006). Therefore a wide area of restoration ecology is focused on the dispersion of target species (Hedberg & Kotowski 2010, Kiehl et al. 2010).

Transfer of fresh hay material has been widely used for restoring species-rich meadows in central Europe (Kiehl & Pfadenhauer 2006, Klimkowska et al. 2010). Mowing is not always feasible, so an alternative technique, i.e. air-vacuum material transfer, has also been assessed (Stevenson et al. 1997, Riley et al. 2004), and both these studies have shown that this technique can be very efficient in speeding-up dispersion and persistent establishment of target species. In our study, although with no significantly different results from rehabilitated area, hay transfer showed some promising results with sporadic germination of a dozen of target species. If competition with Poaceae is limited by sheep grazing, these steppe species may be able to increase their abundance in the mid-term. Besides, some species transported with hay material may germinate a few years after having been transferred (Hölzel & Otte 2003). Hay-gathering is a non-destructive method, and the only one which provides seeds from a large species pool, whereas commercial seed mixtures do not provide such large pool. It would be therefore useful to understand how to optimize this method on a large scale, as it has already shown promising results on smaller scales (Coiffait-Gombault et al. 2011). Only one year after soil transfer, the community richness was very close to that of the reference steppe. Almost all the target species have been recorded at least once over the whole areas where soil was transferred. However, community structure is still different. *Brachypodium retusum*, *Thymus vulgaris* and *Asphodelus ayardii*, three species which are well represented in the target community, have not been recorded this first year. On the other hand, some characteristic species but with a very low frequency in the reference ecosystem, such as *Crassula tillaea* Lester-Garland or *Ranunculus paludosus* Poir., have relatively high frequencies and abundances in the soil transfer treatment. Bullock (1998), has reported some soil translocation cases where the transfer leads to species-rich communities although not close to the target community. In our study, the calculated dissimilarity indexes are very close to zero showing that the composition of restored community using soil transfer is very close to that of the target one. The disturbance induced by the transfer has initiated the germination of target species seeds from the seed bank in greater quantity compared to previous experimental *ex situ* studies on the seed bank in such a system (Buisson & Dutoit 2004, Römermann et al. 2005, Buisson et al. 2006). A first explanation is that transferred soil provides soil conditions very close to those of the donor site, even if small nutrient release can occur when soil is transferred (Anderson & Groutage 2003, Trueman et al. 2007). A second and complementary hypothesis may concern the difference of scale. In the standard protocol (Ter Heerdt et al. 1996), less than 0.06 m^3 (30 × 2 L samples) are investigated whereas in such a large scale experiment more than 600 m^3 are transferred (10,000 times more). Hence, the probability of finding viable seeds in the soil is considerably increased. Without questioning the efficiency of the experiment by Ter Heerdt et al. (1996), which assesses viable seed banks, our results suggest an underestimation of the potential seed bank and thus caution is required when interpreting results from this seed bank study method when applied to species-rich dry grassland restoration. Besides, beyond dispersion of both seeds and appropriate substrate, soil transfer allows the pres-

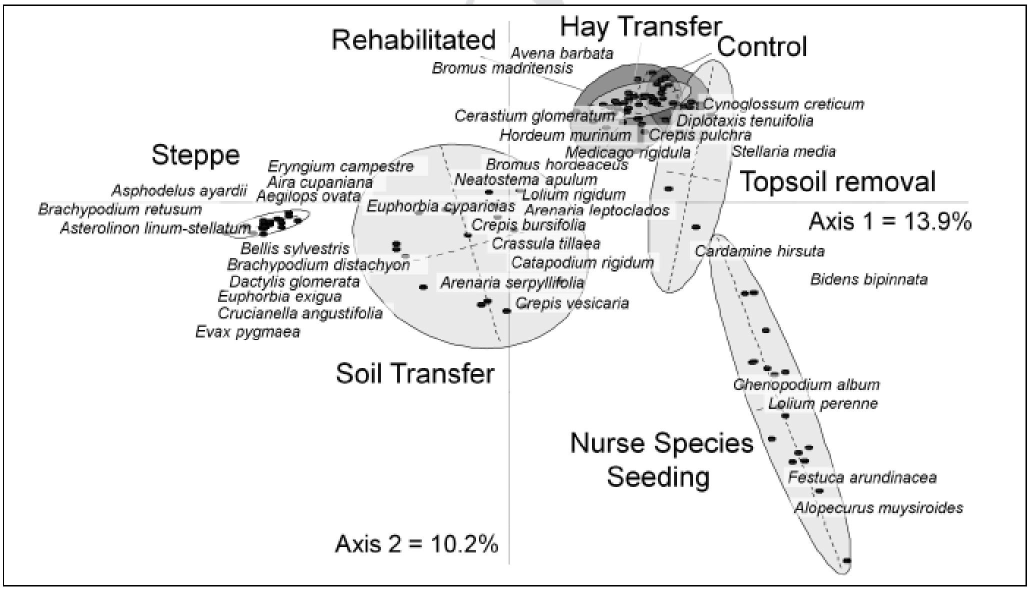

Figure 4 – Ordination plot of the Correspondence Analysis of species abundances on reference steppe (white), restoration techniques (light grey) and treatments without restoration (dark grey). The 37 most discriminant species are shown (out of 195). Ellipses are centred on the barycentre and their forms are weighted by the distribution of all points corresponding to one treatment.

ervation of biotic interactions by also transferring soil fauna (Bullock 1998) and soil microorganisms (Antonsen & Olsson 2005), which can be very important in structuring plant community (Bever et al. 2010, Moora & Zobel 2010). Even if soil transfer techniques are conditioned by the destruction of reference ecosystem areas, the salvage of this potentially wasted soil layer and spreading it for restoration purpose appears to be very promising, although it should be used only if *in situ* conservation cannot be achieved (McLean 2003).

Restoration perspective

Application of a variety of ecological restoration treatments, which achieve their very short-term objectives, is feasible for a large scale project. One year after treatment applications, some treatments have made little headway: topsoil removal and nurse species seeding lowered vegetation height and cover. Others show encouraging results: hay transfer and soil transfer dispersed some target species which can be indicators of the right direction for restoration. The more the treatment strengthens community dispersal, the closer to the target is the resulting community. Further studies should focus on how to lower the environmental and financial cost of restoration projects. One way to proceed is to use ecosystem engineers, such as ants or sheep which can be efficient natural dispersers (Poschlod et al. 1998). Scale issues prevent the use of these species in La Crau area: ants do not disperse more than a few meters (Gomez & Espadaler 1998) and sheep are not present in La Crau when seeds are mature (Bourrely et al. 1983). In the future, sheep grazing, Mediterranean weather and soil conditions will play a determinant role in adjusting successional trajectories for each restoration treatment (Beisner et al. 2003), as they played a major role in creating the reference ecosystem. Nevertheless, our results provide information regarding the interest of using of one treatment or another according to disturbances and short-term objectives. For instance, sowing nurse species just after the abandonment of cultivation can prevent the assembly of a highly competitive community; transferring air-vacuum material on poorly diverse fallows can improve their species-richness in target species; and when the necessary funds and soon-to-be destroyed reference steppe soil are available, transferring this soil can allow conservation of a large part of its diversity at a very short time scale.

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REFERENCES

Aerts R., Huiszoon A., Oostrum J.H.A.V., Van de Vijver C.A.D.M., Willems J.H. (1995) The potential for heathland restoration on formerly arable land at a site in Drenthe, the Netherlands. Journal of Applied Ecology 32: 827–835. http://dx.doi.org/10.2307/2404822

Alard D., Poudevigne I. (2002) Biodiversity in changing landscape: from species to patch assemblages to system organisation. In: Leuven R.S.W., Poudevigne I., Teeuw R. (eds) Application of G.I.S and remote sensing in river studies: 9–27. Leiden, Backhuys Publishers.

Anderson P., Groutage P. (2003) Habitat translocation – a best practice guide. London, Construction Industry and Research Information Association.

Antonsen H., Olsson P.A. (2005) Relative importance of burning, mowing and species translocation in the restoration of a former boreal hayfield: responses of plant diversity and the microbial community. Journal of Applied Ecology 42: 337–347. http://dx.doi.org/10.1111/j.1365-2664.2005.01023.x

Badan O., Brun J.-P., Congès Gaetan O. (1995) Les bergeries romaines de la Crau d'Arles. Les origines de la transhumance en Provence. Gallia 52: 263–310. [Available at http://www.persee.fr/web/revues/home/prescript/article/galia_0016-4119_1995_num_52_1_3152]

Baer S.G., Engle D.M., Knops J.M.H., Langeland K.A., Maxwell B.D., Menalled F.D., Symstad A.J. (2008) Vulnerability of rehabilitated agricultural production systems to invasion by nontarget plant species. Environmental Management 43: 189–196. http://dx.doi.org/10.1007/s00267-008-9167-6

Baize D. (2000) Guide des analyses en pédologie. 2nd Ed. Paris, INRA.

Bakker J.P., Poschlod P., Strykstra R.J., Bekker R.M., Thompson K. (1996) Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45: 461–490.

Beisner B., Haydon D., Cuddington K. (2003) Alternative stable states in ecology. Frontiers in Ecology and the Environment 1: 376–382. http://dx.doi.org/10.1890/1540-9295(2003)001%5B0376:ASSIE%5D2.0.CO;2

Benjamini Y., Hochberg Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society, Series B (Methodological) 57: 289–300. [JSTOR: http://www.jstor.org/pss/2346101]

Bever J.D., Dickie I.A., Facelli E., Facelli J.M., Klironomos J., Moora M., Rillig M.C., Stock W.D., Tibbett M., Zobel M. (2010) Rooting theories of plant community ecology in microbial interactions. Trends in Ecology & Evolution 25: 468–478. http://dx.doi.org/10.1016/j.tree.2010.05.004

Bischoff A. (2002) Dispersal and establishment of floodplain grassland species as limiting factors in restoration. Biological Conservation 104: 25–33. http://dx.doi.org/10.1016/S0006-3207(01)00151-3

Bourrely M., Borel L., Devaux J.P., Louis-Palluel J., Archiloque A. (1983) Dynamique annuelle et production primaire nette de l'ecosystème steppique de Crau (Bouches du Rhône). Biologie-Ecologie méditerranéenne 10: 55–82.

Braun-Blanquet J., Roussine N., Nègre R., Emberger L. (1952) Les groupements végétaux de la France Méditerranéenne. Paris, CNRS.

Buisson E., Dutoit T. (2004) Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe. Plant Ecology 174: 371–384. [JSTOR: http://www.jstor.org/pss/20146662]

Buisson E., Dutoit T. (2006) Creation of the natural reserve of La Crau: Implications for the creation and management of protected areas. Journal of Environmental Management 80: 318–326. http://dx.doi.org/10.1016/j.jenvman.2005.09.013

Roper's Heath, Suffolk, England. Biological Conservation 34: 307–332. http://dx.doi.org/10.1016/0006-3207(85)90038-2

Marrs R.H. (2002) Manipulating the chemical environment of the soil. In: Perrow M.R., Davy A.J. (eds) Handbook of ecological restoration:155–183. Cambridge, Cambridge University Press.

McLean I.F.G., JNCC (Drafted by), on behalf of the Inter-agency Translocations Working Group (2003) A Habitats Translocation Policy for Britain, July 2003. Peterborough, Joint Nature Conservation Committee [Available at: http://jncc.defra.gov.uk/pdf/habitats_policy.pdf]

Moora M., Zobel M. (2010) Arbuscular mycorrhizae and plant-plant interactions: impact of invisible world on visible patterns. In: Pugnaire F.I. (ed.) Positive plant interactions and community dynamics: 79–98. Bilbao, CRC Press.

Olsen S.R., Cole C.V., Watanabe F.S., Dean L.A. (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate. Washington, USDA.

Poschlod P., Kiefer S., Tränkle U., Fischerq S., Bonn S. (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. Applied Vegetation Science 1: 75–91. http://dx.doi.org/10.2307/1479087

Pywell R.F., Webb N.R., Putwain P.D. (1995) A Comparison of techniques for restoring heathland on abandoned farmland. Journal of Applied Ecology 32: 400–411. http://dx.doi.org/10.2307/1479087

Pywell R.F., Bullock J.M., Tallowin J.B., Walker K.J., Warman E.A., Masters G. (2007) Enhancing diversity of species-poor grasslands: an experimental assessment of multiple constraints. Journal of Applied Ecology 44: 81–94. http://dx.doi.org/10.1111/j.1365-2664.2006.01260.x

R Development Core Team (2007) R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Rasran L., Vogt K., Jensen K. (2006) Seed content and conservation evaluation of hay material of fen grasslands. Journal for Nature Conservation 14: 34–45. http://dx.doi.org/10.1016/j.jnc.2005.08.002

Raup D.M., Crick R.E. (1979) Measurement of faunal similarity in paleontology. Journal of Paleontology 53: 1213–1227. [JSTOR: http://www.jstor.org/pss/1304099]

Riley J.D., Craft I.W., Rimmer D.L., Smith R.S. (2004) Restoration of magnesian limestone grassland: optimizing the time for seed collection by vacuum harvesting. Restoration Ecology 12: 311–317. http://dx.doi.org/10.1111/j.1061-2971.2004.00142.x

Römermann C., Dutoit T., Poschlod P., Buisson E. (2005) Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. Biological Conservation 121: 21–33. http://dx.doi.org/10.1016/j.biocon.2004.04.006

Sackville Hamilton N.R. (2001) Is local provenance important in habitat creation? A reply. Journal of Applied Ecology 38: 1374–1376. http://dx.doi.org/10.1046/j.0021-8901.2001.00670.x

Stevenson M.J., Ward L.K., Pywell R.F. (1997) Re-creating semi-natural communities: vacuum harvesting and hand collection of seed on calcareous grassland. Restoration Ecology 5: 66–76. http://dx.doi.org/10.1046/j.1526-100X.1997.09707.x

Temperton V.M., Zirr K. (2004) Order of arrival and availibility of safe sites: an example of their importance for plant community assembly in stressed ecosystem. In: Temperton V.M., Hobbs R.J., Nuttle T., Halle S. (eds) Assembly rules and restoration ecology, bridging the gap between theory and practice: 285–304. Tucson, Society for Ecological Restoration.

Ter Heerdt G.N.J., Verweij G.L., Bekker R.M., Bakker J.P. (1996) An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. Functional Ecology 10: 144–151. http://dx.doi.org/10.2307/2390273

Thompson K., Grime J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893–921. http://dx.doi.org/10.2307/2259220

Tilman D., Pacala S. (1993) The maintenance of species richness in plant communities. In: Ricklefs R.E., Schluter D. (eds) Species diversity in ecological communities: 13–25. Chicago, university of Chicago Press.

Trueman I., Mitchell D., Besenyei L. (2007) The effects of turf translocation and other environmental variables on the vegetation of a large species-rich mesotrophic grassland. Ecological Engineering 31: 79–91. http://dx.doi.org/10.1016/j.ecoleng.2007.05.003

Underwood E.C., Viers J.H., Klausmeyer K.R., Cox R.L., Shaw M.R. (2009) Threats and biodiversity in the Mediterranean biome. Diversity and Distributions, 15: 188–197. http://dx.doi.org/10.1111/j.1472-4642.2008.00518.x

Vécrin M.P., Muller S. (2003) Top-soil translocation as a technique in the re-creation of species-rich meadows. Applied Vegetation Science 6: 271–278. http://dx.doi.org/10.1111/j.1654-109X.2003.tb00588.x

Verhagen R., Klooker J., Bakker J.P., Diggelen R. van. (2001) Restoration success of low-production plant communities on former agricultural soils after top-soil removal. Applied Vegetation Science 4: 75–82. http://dx.doi.org/10.1111/j.1654-109X.2001.tb00236.x

Walker K.J., Stevens P.A., Stevens D.P., Mountford J.O., Manchester S.J., Pywell R.F. (2004) The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation 119: 1–18. http://dx.doi.org/10.1016/j.biocon.2003.10.020

Whisenant S.G. (1999) Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge, Cambridge University Press.

Paper based on results presented during the 7th ECOVEG Congress (Lausanne 2011). Manuscript received 4 Jul. 2011; accepted in revised version 23 Nov. 2011.

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Appendix 3: Survey of indicators used in restoration studies

List of papers used for the survey on indicators used to compare restored communities to their references (Table A3.1). These papers are issued from a search on the ISI web website with the keywords “restoration” in the title and “plant community” OR “vegetation” in the topic. The search performed on the 10th September 2011 resulted in 1283 papers. Only papers published between 2011 and 2007, available with the access provided by Université d’Avignon et des Pays de Vaucluse and which compared vegetation of restored site at the community level to the reference site were used for the survey (82 papers) (Figure A3.1).

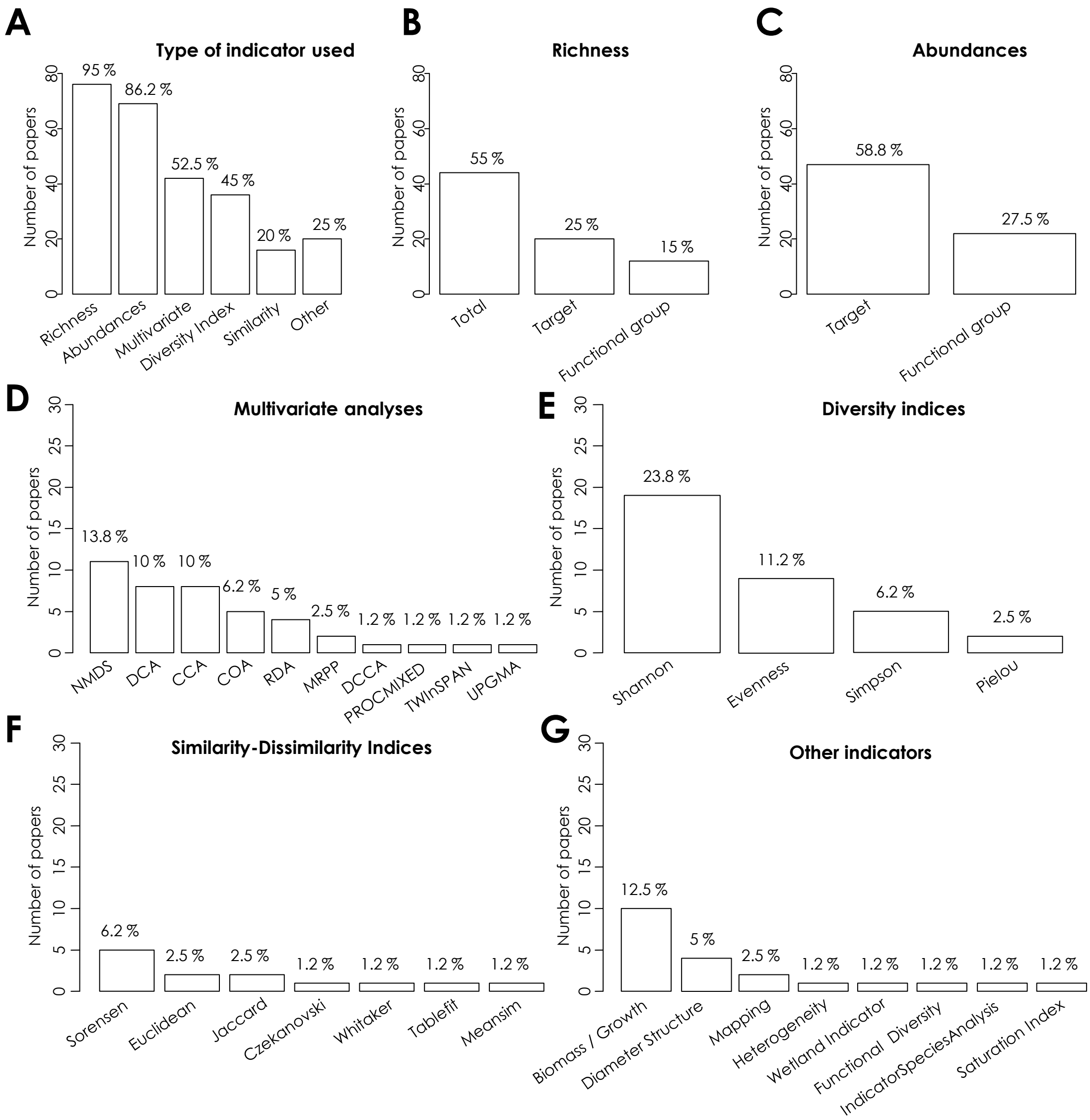

Figure A3.1: Barplots of the number of articles where indicators are used, for each class of indicators (A), richness (B), abundances (C), multivariate analysis (D), diversity indices (E), similarity or dissimilarity indices (F) and other indicators (G). Target is when the richness or abundances are calculated for target species; functional group is when richness or abundance is partitioned between functional groups. Target is when the richness or abundances are calculated for target species; functional group is when richness or abundance is partitioned between functional groups; COA is for Correspondence analysis; DCCA is for Detrended Canonical Correspondence Analysis; DCA is for Detrended Correspondance Analysis; CCA is for Canonical Correspondence Analysis ; NMDS is for Non Metric Multidimensional Scaling; RDA is for Redundancy Analysis; PROCMIXED is the SAS MIXED procedure which fits a variety of mixed linear models to data; Twinspan is a Two Way Indicator Species Analysis; MRPP is for Multiple Response Permutation Procedure and UPGMA is for Unweighted Pair Group Method with Arithmetic Mean.

Table A3.1: Indicators used in ecological restoration scientific papers. Target is when the richness or abundances are calculated for target species ; functional group is when richness or abundances are partitioned between functional groups; COA is for Correspondence Analysis; DCCA is for Detrended Canonical Correspondence Analysis; DCA is for Detrended Correspondence Analysis; CCA is for Canonical Correspondence Analysis; NMDS is for Non Metric Multidimensional Scaling; RDA is for Redundancy Analysis; PROCMIXED is the SAS MIXED procedure which fits a variety of mixed linear models to data; Twinspan is a Two Way Indicator Species Analysis; MRPP is for Multiple Response Permutation Procedure and UPGMA is for Unweighted Pair Group Method with Arithmetic Mean.

Paper	Total	Target	Func. Grp	Target	Func.Grp	COA	DCCA	DCA	CCA	NMDS	RDA	PROC MIXED	TWInSPAN	MRPP	UPGMA	Shannon	Simpson	Evenness	Pielou	Sorensen	Czekanovski	Euclidean	Jaccard	Other	Whitaker	Tablefit	Meansim	Biomass - Growth	Mapping	Heterogeneity	Indicator wetland	Func. Div.	Diameter structure	ISA (indicator species analysis)	SI Saturation index
(Baustian et al., 2009)				x																															
(Bay and Sher 2008)	x	x	x	x																															
(Billeter et al., 2007)	x	x	x																									x							
(Bönsel and Sonneck 2011)	x			x	x																														
(Brockway et al., 2009)	x		x	x																													x		
(Brudvig et al., 2011)	x	x												x			x	x																	
(Brunet 2007)	x			x		x			x																										
(Burmeier et al., 2011)	x	x		x																x															
(Conrad and Tischew 2011)	x	x	x	x	x															x				x											
(Cox et al., 2008)	x			x																															
(Cui et al., 2009)				x																															
(Dazy et al., 2008)	x			x	x											x			x																
(De Deyn et al., 2011)	x																											x							
(Dijk et al., 2007)	x				x											x		x					x												
(Dodson et al., 2007)		x																																x	
(Dodson et al., 2008)	x		x		x					x																									
(Donath et al., 2007)		x		x																															

(Eichberg et al., 2010)		x								x																									
(Firn et al., 2010)				x												x																			
(Foster et al., 2007)		x		x						x				x		x		x													x				
(Freeman and Jose 2009)	x			x	x					x						x		x																	
(Frouz et al., 2009)				x		x																													
(Gaertner et al., 2011)	x			x						x						x		x																	
(Galvánek and Lepš 2008)	x																																		
(García-Palacios et al., 2011)				x		x										x																			
(Godefroid et al., 2007)				x					x																										
(Grant et al., 2011)				x																															
(Gutrich et al., 2009)	x	x	x	x	x																														
(Hellström et al., 2009)				x																															
(Hendrickson and Lund 2010)				x								x																x							
(Huebner et al., 2010)				x																															
(Jacobs et al., 2009)	x			x																															
(Jones et al., 2010)				x																															
(Kardol et al., 2008)						x																						x							
(Klimkowska et al., 2007)																																			x
(Koch et al., 2011)				x																x															
(Kudryavtsev 2007)				x	x																														
(Lencová and Prach 2011)		x						x	x												x														
(Li et al., 2008)	x					x										x		x																	
(Li et al., 2009)	x															x																			
(Liu et al., 2011)	x							x					x			x		x												x					
(Maccherini and Santi)	x										x																								
(Måren et al., 2008)				x	x						x																								
(Matthews et al., 2009)		x			x																														
(McGlone et al., 2009)	x	x		x	x					x																									
(Meira-Neto et al., 2011)	x				x		x																												
(Meng et al., 2011)	x															x	x						x									x			

(Mitchell et al., 2008)				x																															
(Outcalt and Brockway 2010)					x																							x							
(Pavlů et al., 2007)	x				x						x																								
(Piqueray et al., 2011)		x		x				x	x							x																			
(Pretorius et al., 2008)				x	x																												x		
(Pywell et al., 2011a)			x		x																														
(Pywell et al., 2011b)				x																		x													
(Ravenscroft et al., 2010)				x						x																		x	x						
(Rehounková and Prach 2008)		x		x				x	x																										
(Reinecke et al., 2008)	x	x		x	x					x						x	x	x		x															
(Rydgren et al., 2011)	x									x																									
(Sampaio et al., 2007)	x																																x		
(Schaich et al., 2010)	x	x		x	x					x						x	x																		
(Smith et al., 2008)	x										x															x									
(Smits et al., 2008)	x							x	x																			x							
(Stromberg et al., 2007)	x			x												x	x														x				
(Swab et al., 2008)	x			x												x																			
(Toth 2010)	x			x																															
(Tropek et al., 2010)	x			x				x	x																										
(Trowbridge 2007)	x			x	x																						x								
(Tsujino et al., 2010)				x																									x						
(Valkó et al., 2011)	x		x							x																									
(van der Hagen et al., 2008)		x						x																											
(Van Looy 2011)	x	x														x								x											
(Vida et al., 2010)			x		x			x																				x							
(Vogel et al., 2007)				x	x																														
(Wang et al., 2010)	x			x																				x											
(White and Stromberg 2011)			x		x					x										x															
(Wolters et al., 2008)		x		x				x																											

(Woodcock et al., 2008)										x		
(Yoshihara et al., 2010)	x		x									x
(Zhang and Dong 2010)	x	x		x	x	x	x					
(Zhao et al., 2007)	x											x
(Zhu et al., 2009)	x	x				x		x	x		x	

References of Appendix 3

Baustian, J., Turner, R., Walters, N., Muth, D., 2009. Restoration of dredged canals in wetlands: a comparison of methods. Wetlands Ecol. Manage. 17: 445–453.

Bay, R.F., Sher, A.A., 2008. Success of Active Revegetation after Tamarix Removal in Riparian Ecosystems of the Southwestern United States: A Quantitative Assessment of Past Restoration Projects. Restor. Ecol. 16: 113–128.

Billeter, R., Peintinger, M., Diemer, M., 2007. Restoration of montane fen meadows by mowing remains possible after 4–35 years of abandonment. Bot. Helv. 117: 1–13.

Bönsel, A., Sonneck, A.G., 2011. Effects of a hydrological protection zone on the restoration of a raised bog: a case study from Northeast-Germany 1997–2008. Wetlands Ecol. Manage. 19: 183–194.

Brockway, D.G., Outcaltn K.W., Rummer, R.B., 2009. Vegetation Response to Midstorey Mulching and Prescribed Burning for Wildfire Hazard Reduction and Longleaf Pine (Pinus Palustris Mill.) Ecosystem Restoration. Forestry. 82: 299–314.

Brudvig, L.A., Mabry, C.M., Mottl, L.M., 2011. Dispersal, not Understory Light Competition, Limits Restoration of Iowa Woodland Understory Herbs. Restor. Ecol. 19: 24–31.

Brunet, J., 2007. Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. J. Appl. Ecol. 44: 563–572.

Burmeier, S., Eckstein, R.L., 2011. Spatially-restricted plant material application creates colonization initials for flood-meadow restoration. Biol. Conserv. 144: 212–219.

Conrad, M.K. Tischew, S., 2011. Grassland restoration in practice: Do we achieve the targets? A case study from Saxony-Anhalt/Germany. Ecol. Eng. 37: 1149–1157.

Cox, E.S., Marrs, R.H., Pakeman, R.J., Le Duc, M.G., 2008. Factors Affecting the Restoration of Heathland and Acid Grassland on Pteridium aquilinum–Infested Land across the United Kingdom: A Multisite Study. Restor. Ecol. 16: 553–562.

Cui, B., Yang, Q., Yang, Z., Zhang, K., 2009. Evaluating the ecological performance of wetland restoration in the Yellow River Delta, China. Ecol. Eng. 35: 1090–1103.

Dazy, M., Jung, V., Férard, J-F., Masfaraud, J-F., 2008. Ecological recovery of vegetation on a coke-factory soil: Role of plant antioxidant enzymes and possible implications in site restoration. Chemosphere. 74: 57–63.

De Deyn, G.B., Shiel, R.S., Ostle, N.J., McNamara, N.P., Oakley, S., Young, I., Freeman, C., Fenner, N., Quirk, H., Bardgett, R.D., 2011. Additional carbon sequestration benefits of grassland diversity restoration. J. Appl. Ecol. 48: 600–608.

Dijk, J., Stroetenga, M., Bodegom, P.M., Aerts, R., 2007. The contribution of rewetting to vegetation restoration of degraded peat meadows. Appl. Veg. Sci. 10: 315–324.

Dodson, E.K., Metlen, K.L., Fiedler, C.E., 2007. Common and Uncommon Understory Species Differentially Respond to Restoration Treatments in Ponderosa Pine/Douglas-Fir Forests, Montana. Restor. Ecol. 15: 696–708.

Dodson, E.K., Peterson, D.W., Harrod, R.J., 2008. Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. Forest Ecol. Manag. 255: 3130–3140.

Donath, T.W., Bissels, S., Hölzel, N., Otte, A. 2007., Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. Biol. Conserv. 138: 224–234.

Eichberg, C., Storm, C., Stroh, M., Schwabe, A., 2010. Is the combination of topsoil replacement and inoculation with plant material an effective tool for the restoration of threatened sandy grassland? Appl. Veg. Sci. 13: 425-438.

Firn, J., House, A.P.N., Buckley, Y.M., 2010. Alternative states models provide an effective framework for invasive species control and restoration of native communities. J. Appl. Ecol. 47: 96–105.

Foster, B.L., Murphy, C.A., Keller, K.R., Aschenbach, T.A., Questad, E.J., Kindscher, K., 2007. Restoration of Prairie Community Structure and Ecosystem Function in an Abandoned Hayfield: A Sowing Experiment. Restor. Ecol. 15: 652–661.

Freeman, J.E. Jose, S., 2009. The role of herbicide in savanna restoration: Effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. Forest Ecol. Manag. 257: 978–986.

Frouz, J., van Diggelen, R., Pižl, V., Starý, J., Háněl, L., Tajovský, K., Kalčík, J., 2009. The effect of topsoil removal in restored heathland on soil fauna, topsoil microstructure, and cellulose decomposition: implications for ecosystem restoration. Biodivers. Conserv. 18: 3963–3978.

Gaertner, M. Richardson, D., Privett, S., 2011. Effects of Alien Plants on Ecosystem Structure and Functioning and Implications for Restoration: Insights from Three Degraded Sites in South African Fynbos. Environ. Manage. 48: 57–69.

Galvánek, D., Lepš, J., 2008. Changes of species richness pattern in mountain grasslands: abandonment versus restoration. Biodiv. Conserv. 17: 3241–3253.

García-Palacios, P., Bowker, M.A., Chapman, S.J., Maestre, F.T., Soliveres, S., Gallardo, A., Valladares, F., Guerrero, C., Escudero, A., 2011. Early-successional vegetation changes after roadside prairie restoration modify processes related with soil functioning by changing microbial functional diversity. Soil Biol. Biochem. 43: 1245–1253.

Godefroid, S., Monbaliu, D., Massant, W., van der Aa, B., de Vos, B., Q., V., Koedam, N., 2007. Effects of soil mechanical treatments combined with bramble and bracken control on the restoration of degraded understory in an ancient beech forest. Ann. Forest Sci. 64: 321–331.

Grant, A.S., Nelson, C.R., Wsitalski, T.A., Rinehart, S.M., 2011. Restoration of Native Plant Communities after Road Decommissioning in the Rocky Mountains: Effect of Seed-Mix Composition on Vegetative Establishment. Restor. Ecol. 19: 160–169.

Gutrich, J.J., Taylor, K.J., Fennessy, M.S., 2009. Restoration of vegetation communities of created depressional marshes in Ohio and Colorado (USA): The importance of initial effort for mitigation success. Ecol. Eng. 35: 351–368.

Hellström, K., Huhta, A-P., Rautio, P., Tuomi, J., 2009. Seed introduction and gap creation facilitate restoration of meadow species richness. J. Nat. Conserv. 17: 236–244.

Hendrickson, J. R., Lund, C., 2010. Plant Community and Target Species Affect Responses to Restoration Strategies. Rangeland Ecol. Manage. 63: 435–442.

Huebner, C.D., Gottschalk, K.W., Miller, G.W. Brose, P.H., 2010. Restoration of three forest herbs in the Liliaceae family by manipulating deer herbivory and overstorey and understorey vegetation. Plant Ecol. Divers. 3: 259–272.

Jacobs, S., Beauchard, O., Struyf, E., Cox, T., Maris, T., Meire, P., 2009. Restoration of tidal freshwater vegetation using controlled reduced tide (CRT) along the Schelde Estuary (Belgium). Estuar. Coast. Shelf S. 85: 368–376.

Jones, K., Pan, X., Garza, A., Lloyd-Reilley, J., 2010. Multi-level assessment of ecological coastal restoration in South Texas. Ecol. Eng. 36: 435–440.

Kardol, P., van der Wal, A., Bezemer, T.M., de Boer, W., Duyrs, H., Holtkamp, R., van der Putten, W.H., 2008. Restoration of species-rich grasslands on ex-arable land: Seed addition outweighs soil fertility reduction. Biol. Conserv. 141: 2208–2217.

Klimkowska, A., van Diggelen, R., Bakker, J.P., Grootjans, A.P., 2007. Wet meadow restoration in Western Europe: A quantitative assessment of the effectiveness of several techniques. Biol. Conserv. 140: 318–328.

Koch, M.A., Scheriau, C., Schupfner, M., Bernhardt, K-G., 2011. Long-term monitoring of the restoration and development of limestone grasslands in north western Germany: Vegetation screening and soil seed bank analysis. Flora. 206: 52–65.

Kudryavtsev, A., 2007. Vegetation restoration dynamics in the forest-steppe system of the middle Volga region. Russian J. Ecol. 38: 299–305.

Lencová, K., Prach, K., 2011. Restoration of hay meadows on ex-arable land: commercial seed mixtures vs. spontaneous succession. Grass Forage Sci. 66: 265–271.

Li, Y., Wang, W., Liu, Z., Jiang, S., 2008. Grazing Gradient versus Restoration Succession of Leymus chinensis (Trin.) Tzvel. Grassland in Inner Mongolia. Restor. Ecol. 16: 572–583.

Li, Y., Cui, J., Zhang, T., Okuro, T., Drake, S., 2009. Effectiveness of sand-fixing measures on desert land restoration in Kerqin Sandy Land, northern China. Ecol. Eng. 35: 118–127.

Liu, X.Z., Zhang, F., Shao, H.B., Zhang, J.T., 2011. Community succession analysis and environmental biological processes of naturally colonized vegetation on abandoned hilly lands and implications for vegetation restoration strategy in Shanxi, China. African J. Biotechnol. 10: 1133–1145.

Maccherini, S., Santi, E., 2012 Long-term experimental restoration in calcareous grassland: which factors affected species changes? Biol. Conserv. 146(1): 123-135.

Måren, I.E., Vandvik, V., Ekelud, K., 2008. Restoration of bracken-invaded Calluna vulgaris heathlands: Effects on vegetation dynamics and non-target species. Biol. Conserv. 141: 1032–1042.

Matthews, J.W., Spyreas, G., Endress, A.G., 2009. Trajectories of vegetation-based indicators used to assess wetland restoration progress. Ecol. Appl. 19: 2093–2107.

McGlone, C. M., Springer, J.D., Laughlin, D.C., 2009. Can pine forest restoration promote a diverse and abundant understory and simultaneously resist nonnative invasion? Forest Ecol. Manag. 258: 2638–2646.

Meira-Neto, J.A.A., Clemente, A., Oliveira, G., Nunes, A., Correia, O., 2011. Post-fire and post-quarry rehabilitation successions in Mediterranean-like ecosystems: Implications for ecological restoration. Ecol. Eng. 37: 1132–1139.

Meng, J., Lu, Y., Lei, X., Liu, G., 2011. Structure and floristics of tropical forests and their implications for restoration of degraded forests of China's Hainan Island. Trop. Ecol. 52: 177–191.

Mitchell, R.J., Rose, R.J., Palmer, S.C.F., 2008. Restoration of Calluna vulgaris on grass-dominated moorlands: The importance of disturbance, grazing and seeding. Biol. Conserv. 141: 2100–2111.

Outcalt, K.W., Brockway, D.G., 2010. Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. Forest Ecol. Manag. 259: 1615–1623.

Pavlů, V., Hejcman, M., Pavlů, L., Gaisler, J., 2007. Restoration of grazing management and its effect on vegetation in an upland grassland. Appl. Veg. Sci. 10: 375–382.

Piqueray, J., Bottin, G., Delescaille, L-M., Bisteau, E., Colinet, G., Mahy, G., 2011. Rapid restoration of a species-rich ecosystem assessed from soil and vegetation indicators: The case of calcareous grasslands restored from forest stands. Ecol. Indic. 11: 724–733.

Pretorius, M.R., Esler., Holmes, P.M., Prins, N., 2008. The effectiveness of active restoration following alien clearance in fynbos riparian zones and resilience of treatments to fire. S. Afr. J. Bot. 74: 517–525.

Pywell, R.F., Meek, W.R., Loxton, R.G., Nowakowski, M., Carvell, C., Woodstock, B.A., 2011a. Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. Agr. Ecosyst. Environ. 140: 62–67.

Pywell, R.F., Meek, W.R., Webb, N.R., Putwain, P.D., Bullock, J.M., 2011b. Long-term heathland restoration on former grassland: The results of a 17-year experiment. Biol. Conserv. 144: 1602–1609.

Ravenscroft, C., Scheller, R.M., Mladenoff, D.J., White, M.A., 2010. Forest restoration in a mixed-ownership landscape under climate change. Ecol. Appl. 20: 327–346.

Rehounková, K., Prach, K., 2008. Spontaneous Vegetation Succession in Gravel Sand Pits: A Potential for Restoration. Restor. Ecol. 16: 305–312.

Reinecke, M.K., Pigot, A.L., King, J.M., 2008. Spontaneous succession of riparian fynbos: Is unassisted recovery a viable restoration strategy? S. Afr. J. Bot. 74: 412–420.

Rydgren, K. Halvorsen, R., Odland, A., Skjerdal, G., 2011. Restoration of alpine spoil heaps: Successional rates predict vegetation recovery in 50 years. Ecol. Eng. 37: 294–301.

Sampaio, A.B., Holl, K., Scariot, A., 2007. Does Restoration Enhance Regeneration of Seasonal Deciduous Forests in Pastures in Central Brazil? Restor. Ecol. 15: 462–471.

Schaich, H., Rudener, M., Konold, W., 2010. Short-term impact of river restoration and grazing on floodplain vegetation in Luxembourg. Agr. Ecosyst. Environ. 139: 142–149.

Smith, R.S., Shiel, R.S., Bardgett, R.D., Milward, D., Corkhill, P., Evans, P., Quirk, H., Hobbs, P.J., Kometa, S.T., 2008. Long-term change in vegetation and soil microbial communities during the phased restoration of traditional meadow grassland. J. Appl. Ecol. 45: 670–679.

Smits, N.A., Willems, J.H., Bobbink, R., 2008. Long-term after-effects of fertilisation on the restoration of calcareous grasslands. Appl. Veg. Sci. 11: 279–286.

Stromberg, J.C., Beauchamp, V.B., Dixon, M.D., Lite, S.J., Paradzick, C., 2007. Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. Freshwater Biol. 52: 651–679.

Swab, R.M., Zhang, L., Mitsch, W.J., 2008. Effect of Hydrologic Restoration and Lonicera maackii Removal on Herbaceous Understory Vegetation in a Bottomland Hardwood Forest. Restor. Ecol. 16: 453–463.

Toth, L., 2010. Restoration Response of Relict Broadleaf Marshes to Increased Water Depths. Wetlands. 30: 263–274.

Tropek, R., Kadlec, T., Karesova, P., Spitzer, L., Kocarek, P., Malenovsky, I., Banar, P., Tuf, I.H., Hejda, M., Konicka, M., 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. J. Appl. Ecol. 47: 139–147.

Trowbridge, W.B., 2007. The role of stochasticity and priority effects in floodplain restoration. Ecol. Appl. 17: 1312–1324.

Tsujino, R., Fujita, N., Katayama, M., Kawase, D., Matsui, K., Seo, A., Shimamura, T., Takemon, Y., Tsujimura, N., Yumoto, T., Ushimaru, A., 2010. Restoration of floating mat bog vegetation after eutrophication damages by improving water quality in a small pond. Limnology. 11: 289–297.

Valkó, O., Török, P., Tóthmérész, B., Matus, G., 2011. Restoration Potential in Seed Banks of Acidic Fen and Dry-Mesophilous Meadows: Can Restoration Be Based on Local Seed Banks? Restor. Ecol. 19: 9–15.

van der Hagen, H.G.J.M., Geelen, L.H.W.T., de Vries, C.N., 2008. Dune slack restoration in Dutch mainland coastal dunes. J. Nat. Conserv. 16: 1–11.

Van Looy, K., 2011. Restoring river grasslands: Influence of soil, isolation and restoration technique. Basic App. Ecol. 12: 342–349.

Vida, E., Vallkó, O., Kelemen, A., Török, P., Deák, B., Miglécz, T., Lengyel, S., Tóthmérész, B., 2010. Early vegetation development after grassland restoration by sowing low-diversity seed mixtures in former sunflower and cereal fields. Acta Biologica Hungarica 61: 226–235.

Vogel, J.A., Debinski, D.M., koford, R.R., Miller, J.R., 2007. Butterfly responses to prairie restoration through fire and grazing. Biol. Conserv. 140: 78–90.

Wang, Z., Daun, C., Yuan, L., Rao, J., Zhou, Z., Li, J., Yang, C., Xu, W., 2010. Assessment of the restoration of a degraded semi-humid evergreen broadleaf forest ecosystem by combined single-indicator and comprehensive model method. Ecol. Eng. 36: 757–767.

White, J.M., Stromberg, J.C., 2011. Resilience, Restoration, and Riparian Ecosystems: Case Study of a Dryland, Urban River. Restor. Ecol. 19: 101–111.

Wolters, M., Garbutt, A., Bekker, R.M., Bakker, J.P., Carey, P.D., 2008. Restoration of salt-marsh vegetation in relation to site suitability, species pool and dispersal traits. J. Appl. Ecol. 45: 904–912.

Woodcock, B., Edwards, A., Lawson, C., Westbury, D., Brook, A., Harris, S., Brown, V., Mortimer, S., 2008. Contrasting success in the restoration of plant and phytophagous beetle assemblages of species-rich mesotrophic grasslands. Oecologia. 154: 773–783.

Yoshihara, Y. Sasaki, T., Okuro, T., Undarmaa, J., Takeuchi, K., 2010. Cross-spatial-scale patterns in the facilitative effect of shrubs and potential for restoration of desert steppe. Ecol. Eng. 36: 1719–1724.

Zhang, J.T. Dong, Y., 2010. Factors affecting species diversity of plant communities and the restoration process in the loess area of China. Ecol. Eng. 36: 345–350.

Zhao, H-L., Zhou, R-L., Su, Y-Z., Zhang, H., Zhao, L-Y, Drake, S., 2007. Shrub facilitation of desert land restoration in the Horqin Sand Land of Inner Mongolia. Ecol. Eng. 31: 1–8.

Zhu, W., Cheng, S., Cai, X., He, F., Wang, J., 2009. Changes in plant species diversity along a chronosequence of vegetation restoration in the humid evergreen broad-leaved forest in the Rainy Zone of West China. Ecolog. Res. 24: 315–325.

Appendix 4: R scripts for indices calculation

`ComStructIndices`

Description

Calculates indices normalized to community integrity compared to a reference community.

Usage

`ComStructIndices(REF,ASSESS,rar)`

Arguments

REF	is the reference community data matrix
ASSESS	is the assessed community data matrix
rar	(facultative) Minimum number of samples in which species have to be present to be taken into account in the calculation of indices. Default value is 1. It should not be used in the indices calculation, but it can be useful to reduce the number of species with the `structure.plot()` function.

Value

A list containing the following components:

Comb	A combined community data matrix of reference and assessed communities
Nam_Tot	A list of species names corresponding to the Comb matrix
Nam_Tar	A list of the target species names
REF_Tab	Reference community data matrix (with zero values for species which were absent in the reference community)
ASSESS_Tab	Assessed community data matrix (with zero values for species which were absent in the assessed community)
CSII	A list of Community Integrity Index in each assessed community sample
HAI	A list of Higher Abundance Index in each of assessed community sample
CSIInorm	A list of Normalized Community Integrity Index in each assessed community sample
AbMeanREFOnly	A list of mean abundances of target species in reference samples
ASSESSTarOnly_Tab	An assessed community data matrix with target species only
HigherOnly_Tab	An assessed community data matrix with non-target species

The function

```
ComStructIndices<-function(REF, ASSESS, rar=1)
{
  ##------------Combination of the two tables function------------------------
  combin.tab<-function(table1,table2)
  {
    ##-----------Removing of doubles function-----------------
    doubl.rm<-function(list1,list2)
    {
      comb<-c(list1,list2) ## combine
      sort.comb<-comb[order(comb)] ## order
      ## remove doubles
      code<-NULL
      code[1]<-1
      for(i in 2:length(sort.comb))
      {
        code[i]<-ifelse(sort.comb[i]==sort.comb[i-1],0,1)
      }
      comb.wt.db<-sort.comb[code==1]
    }
    #-----------------------------------------------------

    ## Table creation
    liste<-doubl.rm(names(table1),names(table2))
    tabcomb<-data.frame(matrix(0,ncol=length(liste),
                        nrow=nrow(table1)+nrow(table2)))
    names(tabcomb)<-as.character(liste)
    ## Table filling
    for (i in seq(along=liste))
    {
      ## table1
      tabcomb[1:nrow(table1),i]<-
      if(is.numeric(table1[,names(table1)==names(tabcomb)[i]])=="TRUE")
      table1[,names(table1)==names(tabcomb)[i]] else
      rep(0,nrow(table1))
      ## table2
      tabcomb[(nrow(table1)+1):nrow(tabcomb),i]<-
      if(is.numeric(table2[,names(table2)==names(tabcomb)[i]])=="TRUE")
      table2[,names(table2)==names(tabcomb)[i]] else
      rep(0,nrow(table2))
    }
    return(tabcomb)
  }#-------------------------------------------------------------------------

  ## Combine REF and ASSESS tables
  Comb1<-combin.tab(REF,ASSESS)

  ##------Removing rare species function--------------------------------------
  rar.rm<-function(table.AD,n)
  {
    table.PA<-data.frame(apply(table.AD,c(1,2),function(x) if(x>0) 1 else 0))
    occur<-apply(table.PA,2,sum)
    table.AD.wr<-table.AD[,occur>=n]
  }#-----------------------------------------------------------------------

  Comb<-rar.rm(Comb1,rar) ## Removing species which do not occur in Comb1
  Nam_Tot<-names(Comb) ## List of all the species
  ## Removing of species which do not occur in the reference
  REF2<-rar.rm(REF,1)
  REF1<-REF2[,names(REF2) %in% Nam_Tot=="TRUE"]
  Nam_Tar<-names(REF1) ## List of target species
  REF_Tab<-Comb[1:nrow(REF),] ## Reference community table
  ASSESS_Tab<-Comb[(nrow(REF)+1):nrow(Comb),] ## Assessed community table

  ## ----------------------------------------------------------
  AbMeanREF<-apply(REF_Tab,2,mean,na.rm=T) ## Mean abundances in REF
```

```
#Function to calculate the CSII between one ASSESS sample and one REF sample--
CSII.sample<-function(AbSampleREF,AbSampleASSESS)
{
  ## Sum of abundances in the sample of reference community
  SumAbSampleREF<-sum(AbSampleREF)
  ## Sum of Abundances in the sample the assessed community
  SumAbASSESS<-sum(AbSampleASSESS,na.rm=T)
  ## Calculation of differences
  DiffSample<-AbSampleREF-AbSampleASSESS
  ## Sum of positive abudances
  DiffSamplePos<-ifelse(DiffSample>0,DiffSample, 0)
  SumPosSample<-sum(DiffSamplePos)
  ## sample Community Structure Integrity Index
  CSIISample<-(SumAbSampleREF-SumPosSample)/SumAbSampleREF
  return(CSIISample)
}# ---------------------------------------------------------------------------

#Function to calculate the mean CSII between one ASSESS sample and all--------
#REF samples
CSII.All<-function(REF_Tab,ASSESS_Sample)
{
  CSIIn<-apply(REF_Tab,1, function (x) CSII.sample(x,ASSESS_Sample))
  CSIIAll<-mean(CSIIn)
  return(CSIIAll)
}#----------------------------------------------------------------------------

#CSII for all the ASSESS samples
CSII.All.Ass<-apply(ASSESS_Tab,1,function(x) CSII.All(REF_Tab,x))
#CSII for all the REF samples
CSII.All.Ref<-apply(REF_Tab,1,function(x) CSII.All(REF_Tab,x))
# Normalized Community Structure Integrity Index
CSII.All.norm<-CSII.All.Ass/mean(CSII.All.Ref)

#Function to calculate the CSII between one ASSESS sample and one REF sample--
HAI.sample<-function(AbSampleREF,AbSampleASSESS)
{
  ## Sum of abundances in the sample of reference community
  SumAbSampleREF<-sum(AbSampleREF)
  ## Sum of Abundances in the sample the assessed community
  SumAbASSESS<-sum(AbSampleASSESS,na.rm=T)
  ## Calculation of differences
  DiffSample<-AbSampleREF-AbSampleASSESS
  ## Sum of negative abundances
  DiffSampleNeg<-ifelse(DiffSample<0,DiffSample, 0)
  SumNegSample<- -sum(DiffSampleNeg)
  ## Higher Abundance Index
  HAISample<-SumNegSample/SumAbASSESS
  return(HAISample)
}#----------------------------------------------------------------------------

#Function to calculate the mean HAI between one ASSESS sample and all---------
#REF samples
HAI.All<-function(REF_Tab,ASSESS_Sample)
{
  HAIn<-apply(REF_Tab,1, function (x) HAI.sample(x,ASSESS_Sample))
  HAIAll<-mean(HAIn)
  return(HAIAll)
}#----------------------------------------------------------------------------

#HAI for all the ASSESS samples
HAI.All.Ass<-apply(ASSESS_Tab,1,function(x) HAI.All(REF_Tab,x))

## Table with only target species in the references:
AbMeanREFOnly<-AbMeanREF[names(REF_Tab) %in% Nam_Tar=="TRUE"]
## Table with only target species in the assessed communities:
ASSESSTarOnly_Tab<-ASSESS_Tab[,names(ASSESS_Tab) %in% Nam_Tar=="TRUE"]
## Table with only non-target species:
HigherOnly_Tab<-ASSESS_Tab[,names(ASSESS_Tab) %in% Nam_Tar=="FALSE"]
```

```
  ## Output variables-----------------------------------------------------------
  Output<-list(Comb,Nam_Tot,Nam_Tar,REF_Tab,ASSESS_Tab,AbMeanREFOnly,
  ASSESSTarOnly_Tab,HigherOnly_Tab,CSII.All.Ass,CSII.All.norm,HAI.All.Ass)
  names(Output)[[1]]<-"Comb"
  names(Output)[[2]]<-"Nam_Tot"
  names(Output)[[3]]<-"Nam_Tar"
  names(Output)[[4]]<-"REF_Tab"
  names(Output)[[5]]<-"ASSESS_Tab"
  names(Output)[[6]]<-"AbMeanREFOnly"
  names(Output)[[7]]<-"ASSESSTarOnly_Tab"
  names(Output)[[8]]<-"HigherOnly_Tab"
  names(Output)[[9]]<-"CSII"
  names(Output)[[10]]<-"CSIInorm"
  names(Output)[[11]]<-"HAI"
  return(Output)
}#--------------------------------------------------------------------------------
```

`structure.plot`

Description

Performs a barplot of abundances of species in assessed community compared to a reference community.

Usage

```
Structure.plot(FACTOR, MULTI=T, MTITLE="", ABMAX=5, col1="grey60", col2="white", col3="red", col4="orange", noms="T", cex_noms=1,...)
```

Arguments

INDICE	An object issued from `ComStructIndices` function
FACTOR	A factor list, a barplot of species mean abundances will be performed for each factor level. If no factor is specified, `MULTI=F` should be specified.
MULTI	If no factor is specified, `MULTI=F` should be specified
MTITLE	Main title of the plot
ABMAX	Numerical value of the maximum abundance
col1	Colour information for the Reference mean abundances barplot
col2	Colour information for the Reference mean abundances in assessed community barplot, i.e. "missing abundances".
col3	Colour information for the abundances of target species in the assessed community
col4	Colour information for the "higher abundances" in the assessed community
noms	If other than `"T"`, species names are not given
cex_noms	expansion factor for species names

The function

```
structure.plot<-function(INDICE, FACTOR, MULTI=T, MTITLE="", ABMAX=5,
                         col1="grey60",col2="white",col3="red",col4="orange",
                         noms="T",cex_noms=1,...)
{
  ## If there is only one level, creation of the level:
  FACTOR1<-if(MULTI==T) FACTOR else factor(rep("",length(INDICE$HAI)))
  ## target and non-target species tables
  TabCombinASSESS<-cbind(INDICE$ASSESSTarOnly_Tab,INDICE$HigherOnly_Tab)
  TabCombinREF<-c(INDICE$AbMeanREFOnly,rep(0,ncol(INDICE$HigherOnly_Tab)))
  ## Calculation of means
  Means<-as.data.frame(t(apply(TabCombinASSESS,2,
                         function(x) tapply(x,FACTOR1,mean,na.rm=T))))
  MeansALL<-apply(Means,1,function(x) mean(as.numeric(x),na.rm=T))
  ## Ordering the species
  Abundance<-data.frame(INDICE.Nam_Tot=names(TabCombinASSESS),
                         TabCombinREF,MeansALL,Means)
  sort_Abundance1<-data.frame(Abundance[order(-Abundance[,3]),])
  sort_Abundance<-sort_Abundance1[order(-sort_Abundance1[,2]),]

  ## Graphical parameters
  par(mfrow=c(1,length(levels(FACTOR1))+1),mar=c(2.5,0.5,1.5,0.25),
  oma = c(0,0,3,0))
  ## The reference
  ycoo<-barplot(-sort_Abundance$TabCombinREF,xlim=c(-1.4*ABMAX,0),col=col1,
  horiz=T,main="Reference")
  ## names definition
  species.names<-if(noms=="T") sort_Abundance$INDICE.Nam_Tot else ""
  ## names drawing
  text(-0.95*ABMAX,ycoo,species.names,cex=cex_noms)
  ## adding the assessed community barplot
  for (i in 1:length(levels(FACTOR1)))
  {
    ## baseline barplot of reference means
    barplot(sort_Abundance$TabCombinREF,col=col2,xlim=c(0,ABMAX),
    main=levels(FACTOR1)[i],horiz=T)
    ## barplot of higherabundances
    barplot(sort_Abundance[,3+i],col=col4,xaxt="n",horiz=T,add=T)
    # minimum between REF and ASSESS
    MIN<-NULL
    for (j in 1:length(sort_Abundance[,3+i]))
    {
      MIN[j]<-min(c(sort_Abundance[j,3+i],sort_Abundance$TabCombinREF[j]))
    }
    barplot(MIN,col=col3,horiz=T,xaxt="n",add=T) ## barplot of minimum
  }
  ## Adding titles to levels of the factor
  mtext(MTITLE,side = 3, outer = TRUE,font = 2)
  ## Restoring graphical parameters
  par(mfrow=c(1,1),mar=c(5.1,4.1,4.1,2.1),oma = c(0,0,0,0))
}#------------------------------------------------------------------------------
```

ABSTRACT

Ecosystem restoration has been identified as one approach to slow down the loss of biodiversity and to protect all the biodiversity-based goods and services from which humankind benefits. Restoration feeds from knowledge coming from both community ecology and restoration ecology. The objectives of the thesis are to provide insights on both the dynamics of a Mediterranean steppe after changes in land-use and the implementation of techniques which could be applied to restore this ecosystem after severe anthropogenic disturbances. The thesis takes as a study object the La Crau Mediterranean steppe, and especially former cultivated fields to study the recovery after cultivation and the Cossure large scale rehabilitation project to experiment rehabilitation and restoration techniques. Concerning dynamics after severe exogenous anthropogenic disturbances, we confirmed the low resilience of the steppe plant community both at mid- (30-40 years) and long-term (150 years) while the resilience of soil parameters and mycorrhizal infestation rate are effective on the long-term. Moreover we confirmed the role played by the three filters in the plant community recovery and found that for the La Crau steppe, this is firstly driven by the abiotic filter, then by the dispersion filter and finally by the biotic filter. Given this low resilience, we tested several restoration techniques applied at large-scale within the Cossure rehabilitation project: nurse species seeding, topsoil removal, hay transfer and soil transfer. In order to assess the efficiency of restoration techniques we developed indices to measure the community structure integrity, disentangling lower and higher abundances compared to the reference. The best results were obtained with soil transfer, followed by topsoil removal, then nurse species seeding and finally hay transfer. The research conducted for this thesis shows that current knowledge in ecological restoration makes it possible to restore at least partially some La Crau ecosystem components, but ought to lead us to understand the importance of *in situ* conservation of natural habitats as a better alternative to restore them after they were destroyed.

KEY WORDS: Biodiversity – Disturbance – Ecological engineering – Ecological Indicator – Former arable field – Hay transfer – Mediterranean rangelands – Nurse species seeding – Orchard – Plant community – Plant succession – Rehabilitation – Resilience – Restoration ecology – Soil transfer – Species diversity – Species-richness – Topsoil removal

RESUME

La restauration écologique a été identifiée comme une approche permettant notamment de ralentir la perte de biodiversité et de maintenir tous les biens et services issus de cette biodiversité desquels dépend le bien être de notre civilisation actuelle. Cette restauration des écosystèmes se base sur des connaissances provenant à la fois de l'écologie des communautés et de l'écologie de la restauration. Les objectifs de la thèse sont donc de comprendre la dynamique d'une steppe méditerranéenne après changements d'usage ainsi que la mise en œuvre de techniques qui pourraient être appliquées à la restauration de cet écosystème après une perturbation anthropique sévère. La thèse a pour objet d'étude la steppe méditerranéenne de la plaine de Crau, et notamment d'anciennes cultures pour étudier la recolonisation spontanée après perturbation et le projet de réhabilitation à grande échelle de Cossure pour les expérimentations sur les techniques de restauration. En ce qui concerne la dynamique après une perturbation anthropique exogène sévère, nous avons confirmé la faible résilience de la communauté végétale steppique à la fois à moyen (30-40 ans) et long terme (150 ans), tandis que les paramètres du sol et le taux d'infestation des mycorhizes sont résilients sur le long terme. En outre, nous avons confirmé le rôle joué par les trois filtres dans la recolonisation des communautés végétales. En ce qui concerne la steppe de la Crau, la recolonisation est déterminée en premier par le filtre abiotique, puis par le filtre de dispersion et enfin par le filtre biotique. Compte tenu de la faible résilience de la communauté, nous avons testé plusieurs techniques de restauration appliquées à grande échelle au sein du projet de réhabilitation de Cossure: le semis d'espèces nurses, l'étrépage de sol, le transfert de foin et le transfert de sol. Afin d'évaluer l'efficacité des techniques de restauration, nous avons développé des indices pour mesurer « l 'intégrité » de la structure de la communauté permettant de distinguer les abondances inférieures des abondances supérieures par rapport à la communauté de référence. Les meilleurs résultats ont été obtenus avec le transfert du sol, suivi par l'étrépage de sol, puis le semis d'espèces nurses et enfin le transfert de foin. Ces résultats ont toutefois confirmé la difficulté de restaurer totalement la communauté végétale steppique. Les recherches menées au sein de cette thèse montrent que les connaissances actuelles en matière de restauration écologique permettent de restaurer au moins partiellement certaines composantes de cet écosystème, mais suggèrent de mettre un maximum de moyens pour la conservation *in situ* des habitats naturels plutôt que de devoir les restaurer après qu'ils aient été détruits.

MOTS CLES : Biodiversité – Communauté végétale – Ecologie de la restauration – Etrépage de sol – Friches culturales – Indicateurs – Ingénierie écologique – Parcours méditerranéens – Perturbation – Réhabilitation – Résilience – Richesse spécifique – Semis d'espèces nurses – Succession végétale– Transfert de foin – Transfert de sol – Verger