

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

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**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 (Poschold 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). Transferring 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 north-western 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 siliceous 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<sup>-1</sup> 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).

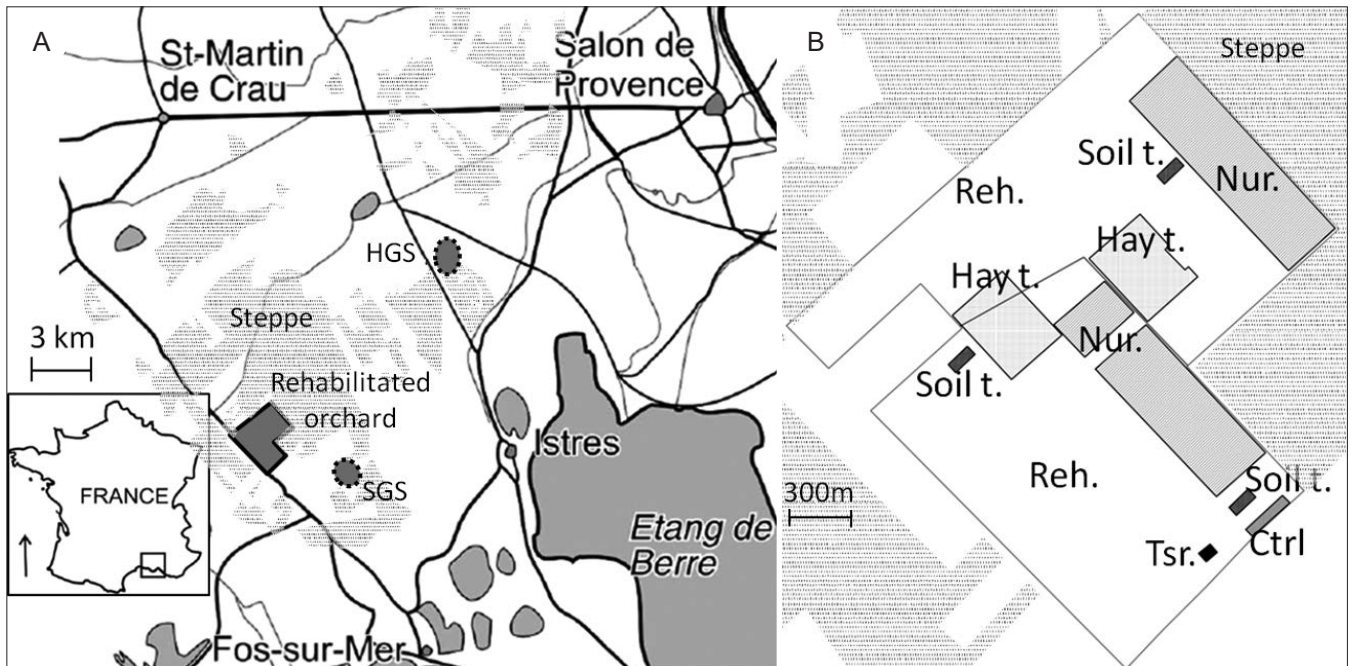
### Restoration goals in a rehabilitation project

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.

**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 were 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 where 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 m<sup>2</sup> 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<sub>2</sub>O<sub>5</sub> (Olsen et al. 1954), CaCO<sub>3</sub>, CaO, K<sub>2</sub>O) 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

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<sub>2</sub>O<sub>5</sub> 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<sub>2</sub>O. 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

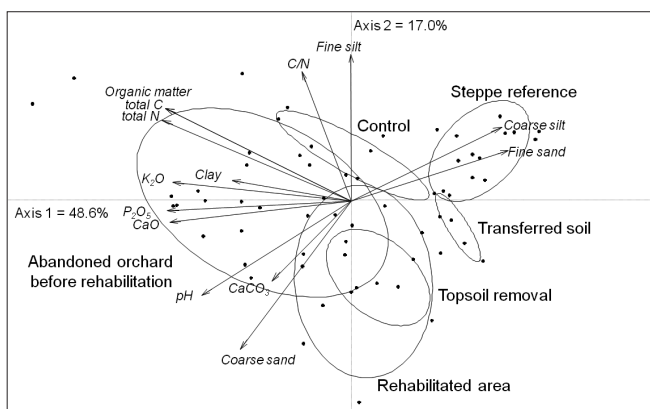
Mean vegetation height and cover showed significant differences among treatments ( $X^2 = 74.13$ ,  $df = 6$ ,  $p < 0.001$  and  $X^2 = 49.87$ ,  $df = 6$ ,  $p < 0.001$ ) (fig. 3A & B). Topsoil removal led to the lowest vegetation cover and height with a mean and standard error of the mean of  $16.6 \pm 7.2\%$  and  $3.33 \pm 88.2$  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 m<sup>2</sup>) but with a significantly higher species richness than the control area (around ten species per 4 m<sup>2</sup>). 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 m<sup>2</sup>) but lower than on the reference ecosystem (more than 35 species per 4 m<sup>2</sup>). Only soil transfer, with a mean of 31 species per 4 m<sup>2</sup>, 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),



**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.

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.

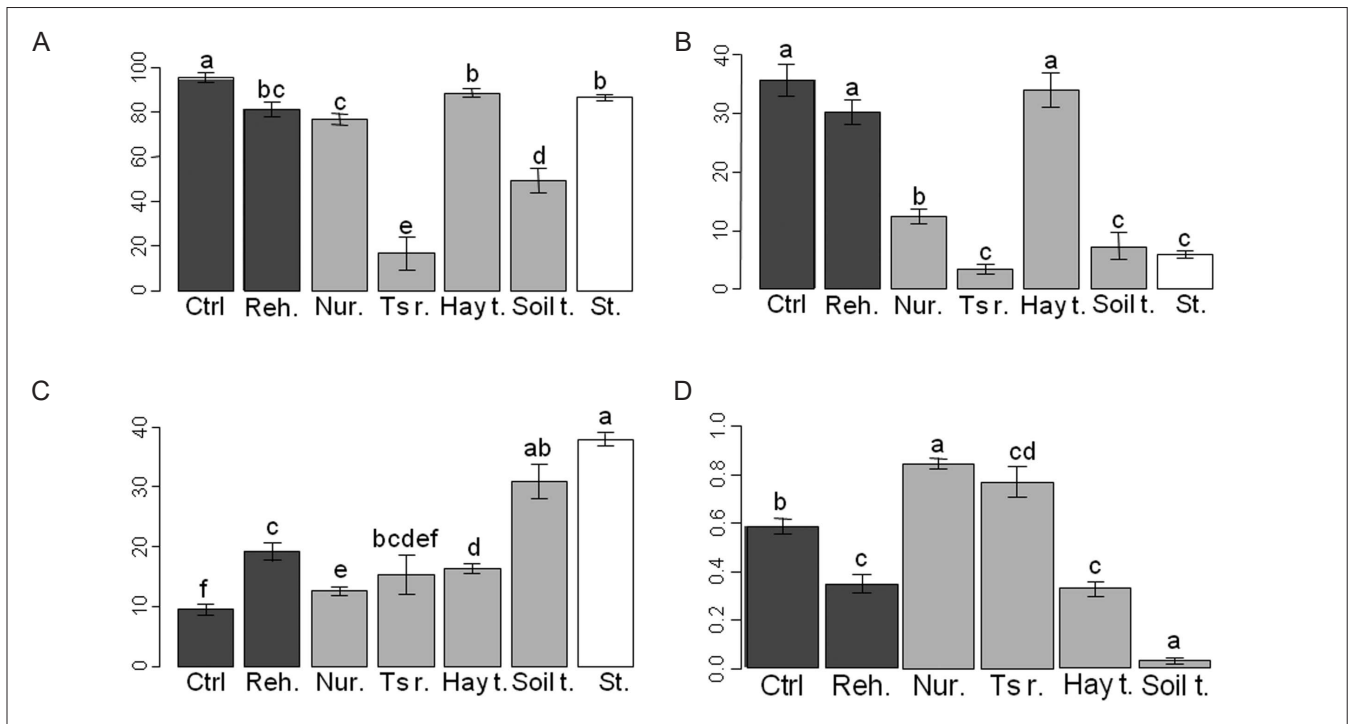
## DISCUSSION

### 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 m<sup>2</sup> 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 (Ctrl), rehabilitated area (Reh.), topsoil removal area (Ts r.), transferred soil (T. soil) and steppe reference (St.). df, X<sup>2</sup> and p are respectively the degree of freedom, chi<sup>2</sup> 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).

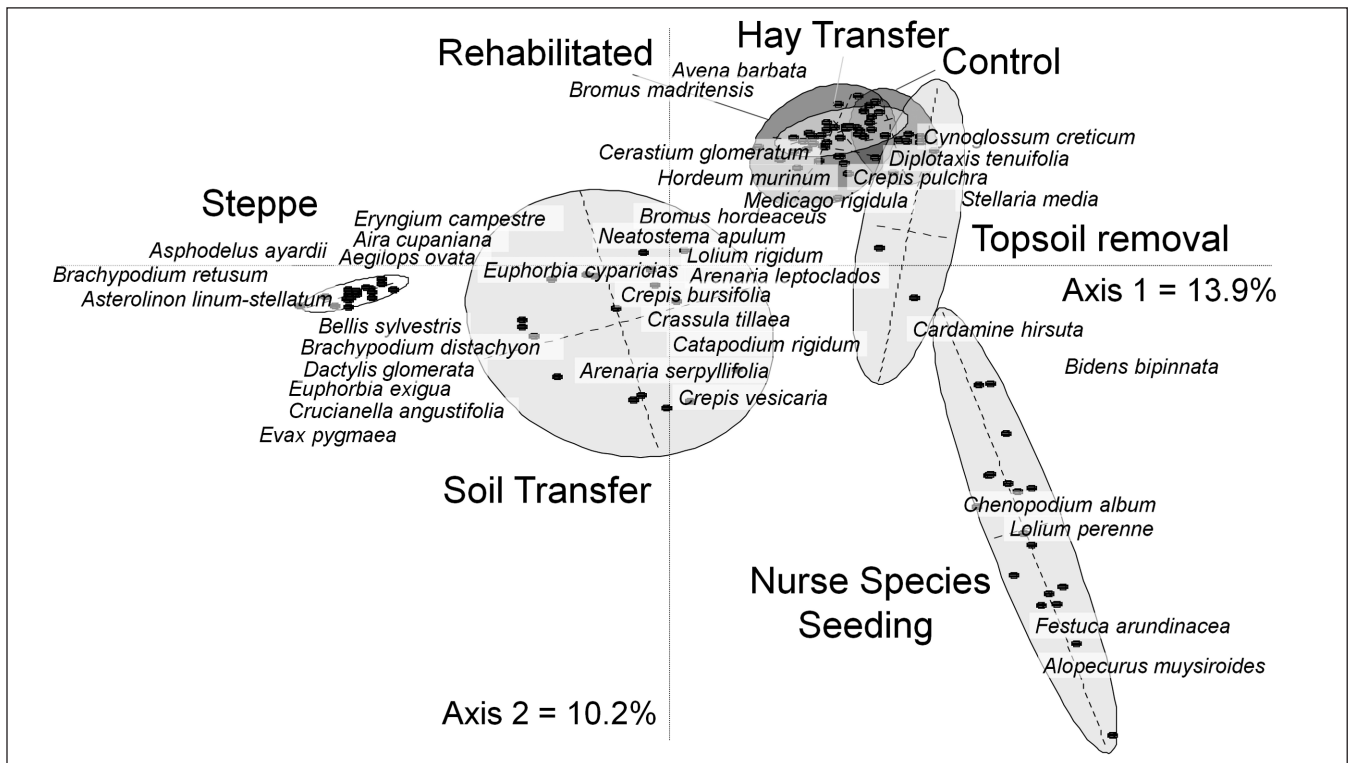
	df	X <sup>2</sup>	p	Ab. Orch.	Ctrl	Reh.	Ts r.	T. Soil	St.
Clay (g.kg <sup>-1</sup> )	5	18.4	**	219.5 ± 3.7 b	216 ± 8 ab	215.2 ± 2.9 ab	220.4 ± 7.7 ab	215.6 ± 11.7 a	195.9 ± 4.1 b
Fine silt (g.kg <sup>-1</sup> )	5	14.7	**	185.5 ± 3.6 a	190 ± 8.4 ab	178.4 ± 2.2 ab	163 ± 4.4 b	181.8 ± 5.4 ab	190.5 ± 4.6 a
Coarse silt (g.kg <sup>-1</sup> )	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 <sup>-1</sup> )	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 <sup>-1</sup> )	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 <sup>-1</sup> )	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 <sup>-1</sup> )	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 <sup>-1</sup> )	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 <sub>3</sub> (g.kg <sup>-1</sup> )	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 <sub>2</sub> O <sub>5</sub> (g.kg <sup>-1</sup> )	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 <sup>-1</sup> )	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
K <sub>2</sub> O (g.kg <sup>-1</sup> )	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 & Kottowski 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 Heerd et al. 1996), less than 0.06 m<sup>3</sup> (30 × 2 L samples) are investigated whereas in such a large scale experiment more than 600 m<sup>3</sup> 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 Heerd 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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