Impacts of water stress removal and disturbance regimes on Mediterranean dry grasslands diversity and succession

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Abstract Our goal was to disentangle the effects of stress removal and disturbance on plant communities of a Mediterranean rangeland, La Crau (southeastern France). We compared undisturbed reference steppe vegetation with vegetation impacted by changes in land use such as earlier phases of cultivation (dating back 20 years) and/or current water infiltrations (revealed by the presence of *Brachypodium phœnicoïdes*), since the establishment of adjacent hay meadows. We considered plots with and without brambles (*Rubus ulmifolius*), an indigenous shrub species that had colonized the area after the land-use changes. We monitored the composition and measured the taxonomic richness and richness of functional groups, evenness and similarities of plant communities. The species richness of the undisturbed community was significantly higher than that of all disturbed plant communities. Although cultivation led to the dominance of ruderal species, the removal of water stress had a stronger negative impact, enabling the establishment of herbaceous competitor species such as *B. phœnicoïdes*. The dominance of this species resulted in a significant decline in species richness and evenness after water stress removal. The presence of brambles correlating with former cultivation and/or current water infiltration did not have a significant impact on plant species richness in the vicinity of bramble bushes, although it significantly modified the composition of the adjacent herbaceous vegetation. Our study highlights again the low resilience of Mediterranean dry grasslands after disturbance. While both the disturbance and the water stress removal resulted in changes within the plant community, our findings reveal a stronger impact of the water stress removal. Water infiltration led to decreased plant species richness and evenness because the greater availability of water favored competitor species over the stress-tolerant xeric species. Therefore, for restoring the original steppe species richness, the priority will be to control water infiltrations, even before any scrub-clearing is undertaken to control bramble colonization.

Keywords Herbaceous ecosystems · Vegetation dynamics · *Rubus ulmifolius* · Ecological restoration · Alterations · Plant composition

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Introduction

Over the past decades, industrial development, intensification of agriculture, and urban development have resulted in a constant degradation of ecosystems (Chapin et al. 2000). Grasslands, forests, and wetlands in particular have been transformed into agricultural land or urban areas (Chapin et al. 2000). Natural recovery allows some ecosystems to return to their successional pathway in a variable time interval before the disturbance (Holling 1973; Hirst et al. 2003). However, other ecosystems, too severely damaged by events in their history require human intervention (Aronson et al. 1995).

Ecological restoration refers to interventions that aim to re-establish the full functioning, structure, and biodiversity of an ecosystem that has been degraded, damaged, or destroyed, by restoring it to the desired trajectory, the chosen successional pathway (Aronson et al. 1995; SER 2004). Restoration also involves the reconstruction of the plant community, which plays a major role in the ecosystem functioning, the trophic chains, and the biogeochemical cycles in terrestrial ecosystems (Temperton et al. 2004). Ecological restoration, based on successional theory, initiates or accelerates the "assembling" of species (Temperton et al. 2004; Cortina et al. 2006; Cristofoli and Mahy 2010). The simplest way of defining succession is as the evolutionary process of installing species in an environment over time (Clements 1916). While Clements (1916) considered that plant composition tended to reach an equilibrium state ("Climax"), communities are currently rather seen as the result of a non-equilibrium state dependent on history, contingencies, and disturbance regimes (Gleason 1926; Suding et al. 2004; Scott and Morgan 2011). To ensure successful ecological restoration of plant communities, it is therefore necessary to understand ecosystem responses to current or past disturbances and stresses that control vegetation dynamics (Lavorel et al. 1999). According to the criteria of Grime (1979) and of White and Pickett (1985), cultivation can be considered as a major disturbance causing major alterations to the properties of the ecosystem as well as the total destruction of the initial plant community. However, when the degradation of the ecosystem only results in a loss of productivity, this change is termed 'stress.' Then, plant species were differentiated (Grime 1979) on the basis of their strategy of adaptation to stresses and disturbances. In the Mediterranean region, the two main stresses faced by plant communities are lack of water and access to light (Peco et al. 2006).

In the Mediterranean, human activities date back several millennia (Pons and Quézel 1998). Itinerant grazing is one of the most ancient practices. Practiced since the Neolithic Age, it is one of the main factors governing the dynamics of extinction, colonization, and distribution of species (Peco et al. 2006). While it is considered as a disturbance for many ecosystems (Sala et al. 1986; Dutoit and Alard 1995; Rossignol et al. 2011), it is an integral part of Mediterranean rangeland functioning and plays a determining role in vegetation dynamics, with a direct impact on plant community composition and structure (Le Houérou 1981). The centuries of interactions between itinerant grazing, vegetation, and the strong intra/inter-annual variations in the Mediterranean climate (Le Houérou 1981) have favored the development of diversified and locally adapted plant communities (annual plants, sclerophyllous, and thorny ligneous plants) (Noy-Meir et al. 1989; Lavorel et al. 1999).

In addition to this traditional land use, intensive agricultural systems have been added to, or have temporarily replaced, the rangelands, creating a complex mosaic of semi-natural and artificial habitats (Peco et al. 2006). The impact of former intensive farming practices on ecosystems has been the subject of several studies showing that the ploughing and fertilization of Mediterranean rangelands lead to a decline in species richness and changes in floristic composition, even for decades after cessation of cultivation (Römermann et al. 2005).

The plain of La Crau (southeastern France) is an example of a Mediterranean pastoral ecosystem degraded by the development of intensive agricultural practices (Devaux et al. 1983; Dutoit et al. 2013). More than 6000 years of interaction between the Mediterranean climate, in particular weak rainfall (<400 mm/year), itinerant sheep grazing and stone-covered soil, has resulted in a characteristic dry grassland plant community, with more than 50 % of annual species and many stress-tolerant species (Grime 1979; Buisson et al. 2006). This community, often referred to by the term 'steppe' (Myers et al. 2000), can more properly be considered a pseudo-steppe (Devaux et al. 1983; Henry et al. 2010) because the traditional sheep grazing system, rather than the Mediterranean climate, is the driver of grassland maintenance (Fadda et al. 2008).

The plain of la Crau has undergone major degradations since the 16th century: the development of irrigation with the subsequent construction of channels, the planting of orchards, and market gardening (Buisson and Dutoit 2006). The impact of agricultural intensification on this typical vegetation has already been the focus of several studies revealing that the cultivation of the steppe resulted in a decline in species richness and drastic changes in plant and insect community compositions (Dutoit et al. 2013). There is also evidence of very poor resilience even several decades after the abandonment of cultivation and the reintroduction of traditional itinerant sheep grazing (Römermann et al. 2005). Moreover, cultivation led to landscape fragmentation, creating a multitude of patches of variable size and shape (Gaignard 2003). Some of these patches suffer the indirect impact of agricultural practices carried out in neighboring areas, in particular water infiltrations due to the irrigation of hay meadows by submersion and/or leaks from their adjacent irrigation channels (Gaignard 2003). These water infiltrations are already expressed by the presence of a grass tussock perennial species *Brachypodium phœnicoïdes* (L.) Roem. & Schult, which colonized the steppe plant community at the boundaries with irrigated meadows or unmaintained channels (Devaux et al. 1983). *B.phœnicoïdes* possesses high cover capacity and forms dense populations in open habitats (grasslands, pastures or abandoned agricultural fields). This species was also shown to play an important role in plant successions in pastures (Bolòs and Vigo 2001; Domènech and Vilà 2008).

Because of the special status of La Crau plain, assessment of the impact on plant communities of anthropic practices and of their changes is essential in order to prioritize ecological restoration management operations.

The disturbances related to former cultivation and water stress removal affect not only the typical plant community structure of the La Crau area, but also its successional dynamics (White and Jentsch 2004). The elmleaf bramble (*Rubus ulmifolius*), whose colonization is explained by disturbance and stress phenomena separately or correlatively (Mazzorali et al. 2011), is established there. The bramble may not only compete with herbaceous plants for light, but it may also protect them from grazing via its thorny stems that make the herbaceous plants inaccessible (McDowell 2002; Williams et al. 2006; Uytvanck et al. 2008).

The aims of this study were therefore to determine (1) the relative impacts of earlier temporary cultivation phases and water stress removal on the composition, species richness, similarity, evenness, and functional diversity of the local plant community, and (2) the potential impact of colonizing shrub species as a factor aggravating the alteration of the herbaceous vegetation after these changes in land use.

Methods

Study area: the plain of La Crau

The plain of La Crau is situated in southeastern France (4°52′00.84″E–43°33′25.97″N) (See Fig. 7 in Appendix 1 and Table 3 in Appendix 2). This plain is the ancient stony delta of the Durance River, created in the Pleistocene period following fluctuations in the course of the river. Directional changes over time led to large numbers of stones being washed down. Today, the soil is still covered with stones over 40–70 % of its surface area. About 40 cm below the surface, there is a conglomerate formed by calcium carbonates in the runoff waters acting on the stones, which prevents the root systems of plants from reaching the water table (Römermann et al. 2005).

The climate is typically Mediterranean, with a dry, arid summer and a temperate, humid winter, and total insolation of 3000 h/year. The annual temperature range is between 7 °C in winter and 24 °C in summer with a mean of 14 °C. The annual precipitation is 440 mm with a minimum of 285 mm in 2012 and a maximum of 508 mm in 2011. In addition, there is a dominant northeasterly wind reaching more than 50 km/h on 110 days (Devaux et al. 1983). Composed of more than 50 % annual species, this community is also dominated by a few perennial species such as *Asphodelus ayardii*, *Brachypodium retusum*, *Thymus vulgaris*, and *Stipa capillata*. At regional scale, the plant species richness is one of the highest in southeastern France (Devaux et al. 1983; Buisson and Dutoit 2006).

The steppe was converted into hay meadows irrigated by submersion as early as the 16th century. In the course of the 20th century, agricultural intensification and the development of industrial and military buildings accentuated its fragmentation (Devaux et al. 1983; Buisson and Dutoit 2006; Henry et al.2010). From 1960 to 1980, many plots were transformed into irrigated orchards and market gardens (*Solanaceae* and *Cucurbitaceae*), following which new plots were cultivated. The grazed area of La Crau thus drastically declined from initially more than 50,000 ha to 11,500 ha (Buisson and Dutoit 2006; Henry et al. 2010). Gradually, the market gardens were abandoned and traditional sheep grazing was reintroduced on the formerly cultivated fallow lands (Römermann et al. 2004). Today, the remaining steppe fragments are often in direct contact with irrigated orchards and irrigated hay meadows. These changes in land use would appear to have favored some colonizing native species of the Mediterranean region such as the elmleaf bramble, which does not usually occur in the typical steppe vegetation (Jordano 1984).

This species forms networks of clones from the same perennial stock developing on soils with a slightly acid pH (Wehrlen 1985). It also has a well-developed root system (the only perennial part) and the capacity to regulate its water requirements. Its ability to maintain a strong stomatal conductance, low water-resistance, strong transpiration, and high water-potential enables it to adapt to xeric episodes (McDowell and Turner 2002). This species generally not only out-competes herbaceous plants for light, but it can also facilitate the development of certain herbaceous plants and pioneer shrubs, protecting them from over-consumption by domestic and wild herbivores (McDowell 2002).

In the steppe, the presence of brambles is generally limited to stone piles. Around these stone piles, the development of bramble is generally strongly controlled by sheep grazing because of the appetizing nature of its young shoots.

Experimental design

We studied the vegetation of different sites from four different agricultural histories considered as four different treatments applied to vegetation: (1) steppe original vegetation with no history of change in land use, as a reference (C), (2) vegetation of formerly cultivated fields without water infiltration (F), (3) vegetation on fields currently subjected to water infiltration but never cultivated in the past (I) and (4) vegetation on formerly cultivated fields currently subjected to water infiltration (FI). Water infiltrations were detected in the field based on the presence of *B. phœnicoïdes* whose distribution is highly correlated with soil moisture in La Crau (Devaux et al. 1983).

For each of the three agricultural histories involving changes in land use (a disturbance caused by former cultivation and/or a removal of stress caused by water infiltrations), we selected at random three sites using aerial photographs taken between 1945 and 2010 to determine where and when cultivations were created and abandoned and where and when irrigated meadows were created (See Table 3 in Appendix 2).

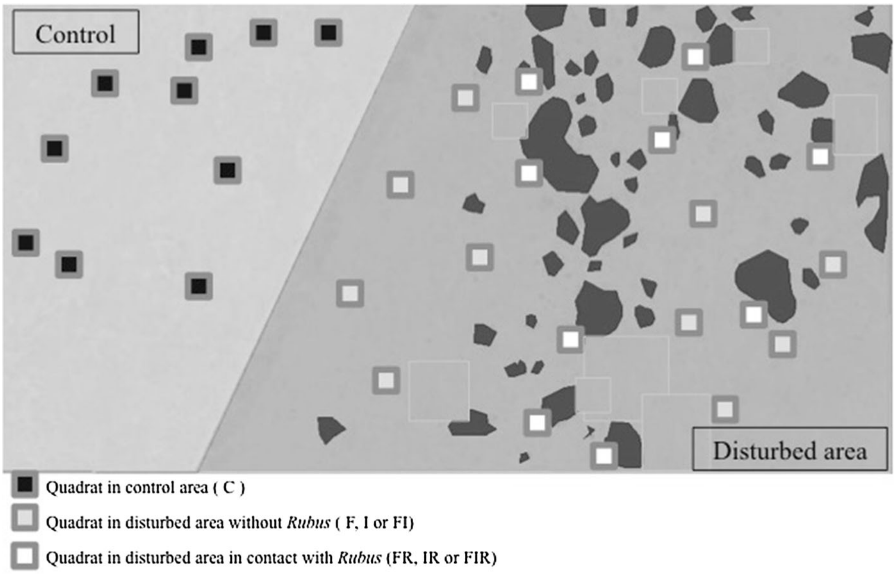
In addition, for each disturbance regime treatment, we examined vegetation growing both in the presence of bramble or its absence (there was no bramble in the reference plots). Thus, we considered a disturbance treatment without bramble (F, I and FI) and a disturbance treatment with bramble (FR = Former cultivation + brambles, IR = Infiltrations + brambles, FIR = Former cultivation + Infiltrations + brambles). Six disturbance treatments and a steppe reference were studied and each was replicated three times.

Because of the heterogeneity of the steppe vegetation at the scale of the La Crau plain (Devaux et al. 1983), the original steppe vegetation immediately surrounding each site was selected as reference. Thus, nine references were studied in addition to the 18 disturbance treatments.

Sampling of the vegetation and habitat measurements were undertaken on 1 m^2 quadrats. Earlier random sampling on 40 m^2 quadrats had enabled us to determine that 10 quadrats were sufficient to find more than 90 % of the species characteristic of the full range of steppe plants, little or no gain in species being achieved by increased sampling (Fig. 1). A total of 270 quadrats were sampled (6 treatments $\times$ 10 quadrats $\times$ 3 replicates and 9 references $\times$ 10 quadrats).

In the study sites with bramble (IR, FR, FIR), we positioned the quadrats in the immediate vicinity of bramble thickets at the southwest but not below the bramble thickets, to detect the influence of brambles on the herbaceous cover in the immediately surrounding vegetation but not beneath the brambles. Under dense bramble thickets, only dead bramble stems, leaves, and spikes cover the soil, herbaceous vegetation being virtually eliminated by the ability of brambles to capture roughly 80 % of the light (De La Fouchardière 1959).

Fig. 1 Example of sampling design for one of the nine study sites in La Crau, southeastern France. A total of 30 quadrats were sampled at random for each treatment, ten references (C), ten disturbed without brambles [Fallow (F), Infiltration (I) and Fallow with Infiltration (FI)] and ten disturbed with brambles (fallow with brambles (FR), Infiltration with brambles (IR) and fallow with infiltration and brambles (FIR)). *Dark gray* patches represent the bramble shrubs



In each 1 m^2 quadrat, an index of abundance was attributed to all the species recorded: 0.5 for cover of less than 1 %, 1 for cover between 1 and 5 %, 2 for cover between 5 and 25 %, 3 for cover between 25 and 50 %, 4 for cover between 50 and 75 % and 5 for cover >75 %. This study was conducted from April to June 2012 during the peak of plant flowering in southeastern France.

In accordance with Grime's classification (1979), we differentiated plant species according to their strategy of adaptation to stresses and disturbances. We determined a number of species per category for each of the 6 treatments and the reference studied using the BASECO database (Gachet et al. 2005).

Statistical analyses

Treatment data (C, F, FR, FI, FIR, I, and IR) were matched with the floristic data recorded on 270 quadrats using a canonical correspondence analysis (CCA) (TerBraak 1986), using treatment as the constrained variable and sites as the conditional variable, with R package Vegan (Oksanen 2011). Floristic data are species occurrences on quadrats; they represent some binary variables which were not transformed. The aim of the CCA was to explain floristic variations in samples by the different treatments. We tested significance of the overall CCA ordination with a permutation procedure using the permute function in the R package Vegan (Oksanen 2011).

To group the sites according to similarity of plant composition, we conducted an agglomerative hierarchical clustering using the complete-link method, based on Euclidian distance.

Plant species richness was measured for each treatment by counting the total number of taxa present spacing 1 m^2 quadrat. Statistical analyses were performed only on taxa, which were identified to species level. Plant diversity was calculated using the Shannon index H' and Evenness (E) and compared between the different treatments. These indices were also compared between quadrats with or without the presence of *B. phœnicoïdes;* the species used as an indicator for the presence of water infiltrations.

Similarity of composition of the different plant communities between treatments (F, FR, FI, FIR, I, and IR) and the reference (C) was calculated by means of the Jaccard index. On each site, the Jaccard index was calculated between one quadrat and references found in the neighborhood ($n = 10$) and mean Jaccard indices were calculated for all treatments ($n = 10$). A The Jaccard index for the references at the same site was also measured by comparing their composition. Therefore, we have compared the mean indices of each treatment to the mean indices for references.

Using a database (BASECO, Gachet et al. 2005), we determined the CSR strategies of each species and compared their distribution between treatments.

Data normality was tested by means of the Shapiro–Wilk test. To assess differences in species richness, evenness, Jaccard index, and adaptative strategies of species (response variables) between treatments, we used a linear mixed effect model with the lmer function, Library Lme 4 (Bates and Sarkar 2007), treating sites as random effects, and treatments as fixed effects. We chose to reduce the estimation of maximum likelihood. A multiple comparison post hoc test was then performed using the glht function with the Tukey test with Library Multcomp (Hothorn et al. 2008).

The statistical analyses were performed using the software R (R Development Core Team 2008).

Table 1 Number of taxa per treatment and number of taxa only found in each of the six different treatments and the reference

Treatment	Number of taxa/treatment	Number of taxa only found on each treatment position
C	137	25
F	94	2
FR	96	4
FI	95	0
FIR	85	7
I	102	12
IR	90	9

C reference; *F* fallow; *FR* fallow and brambles; *FI* fallow; *FIR* fallow with infiltration and brambles; *I* infiltration; *IR* infiltration with brambles in La Crau steppe, southeastern France

Results

We identified two hundred and ten taxa: 198 at the species level, 11 at the genus level, and one at the family level only. Twenty-six taxa were common to all treatments and 25 species were characteristic of references. Two species were only found in the F treatments (Former cultivation, *Campanula erinus* and *Helianthemum salicifolium*), four were only found in the FR treatments (Former cultivation with brambles, *Carex divulsa*, *Celtis australis*, *Prunus* sp., and *Tragopogon porrifolius* L. subsp. *Australis*), seven in the FIR treatment (Former cultivation with Infiltrations and brambles), nine in the IR treatment (Infiltrations with brambles), 12 in the I treatment (Infiltrations, including *Convolvulus lineatus* and *Myosurus minumus*, two wetland species protected in south-eastern France). No species were found only in the FI treatment (Former cultivation with Infiltrations, Table 1; See Table 4 in Appendix 3).

Concerning plant composition and distribution, axis one of the CCA (20.5 % of the inertia) discriminated the quadrats according to the presence of brambles (Fig. 2). Axis two (6.4 % of the inertia) discriminated the quadrats where *B. phœnicoïdes* was present from all the other quadrats. This axis also discriminated treatments under water influence (I, IR, FIR, and FI) with *B. phœnicoïdes* from other treatments. The reference quadrats were characterized by typical steppe species such as *B. retusum*, *Bromus hordeaceus*, and *E. cyparissias*. The quadrats in treatment F were characterized by species such as *Dactylis glomerata* or *Crepis sancta* and were weakly discriminated on this axis. Axis One thus discriminated plots in the references from the quadrats on the basis of the presence of bramble, regardless of whether they were situated on fallow lands, in areas exposed to water infiltration or in the two treatments combined. Axis Two discriminated those extensively covered by *B. phœnicoïdes*, a species occurring in plots exposed to lateral water infiltration, regardless of whether situated on fallow areas.

The descending hierarchical classification (Fig. 3) distinguished three groups. One group consisted of the references (C) and fallow (F) treatments; however, all the reference quadrats were more similar to each other in terms of plant composition than the F treatment quadrats. The second group consisted of the treatments with infiltrations, FI and I. The third group consisted of the quadrats with brambles, namely the FR, FIR, and IR treatments, the FR treatment being distinguished from the FIR and IR treatments.

Species richness per m^2 was significantly higher in the steppe reference treatments (Mean ± SEM; 24 ± 0.77, p value < 0.001, Fig. 4) than in all the other treatments with and without brambles. Species richness of the quadrats situated within the formerly cultivated plots and/or those exposed to lateral water infiltration (F, I and FI) was thus significantly lower than those of the steppe reference quadrats. This was also true for the quadrats situated in the vicinity of the

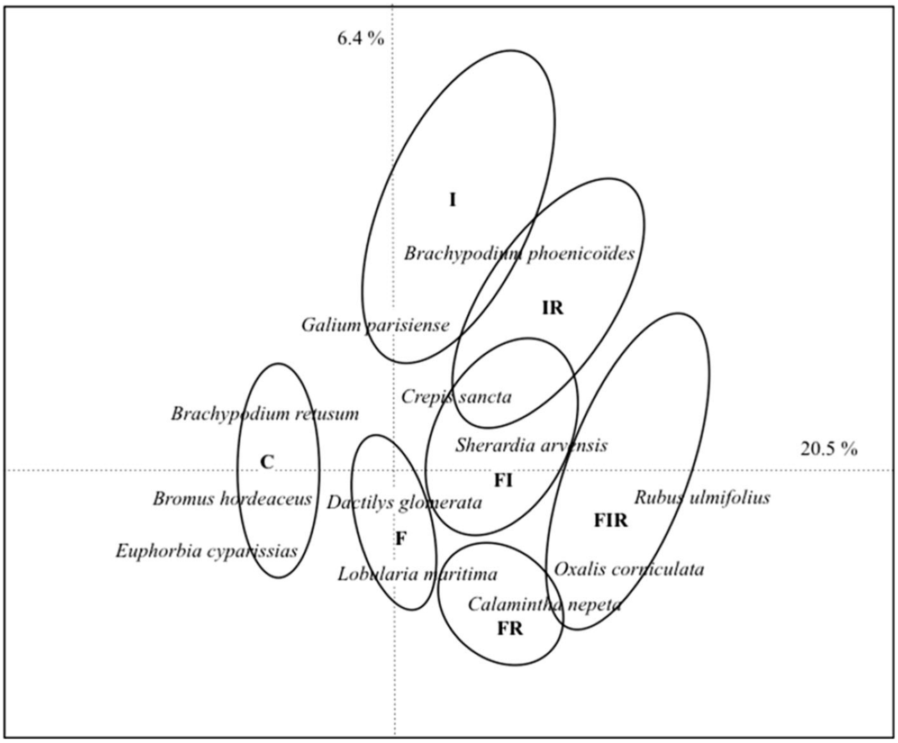


Fig. 2 Species-treatment biplot, presenting the results of the canonical correspondance analysis (CCA). Only species with a high contribution to axis 1 and 2 have been coded. *C* reference; *F* fallow; *FR* fallow and brambles; *FI* fallow with infiltration; *FIR* fallow with Infiltration and brambles; *I* infiltration; *IR* infiltration with brambles; in nine sites on the La Crau plain in south-eastern France

brambles (FR, IR and FIR). Moreover, the overall difference between disturbed treatments with or without brambles (F, I, FI, and FR, IR and FIR) was significant. The sites with lateral water infiltrations (I and IR and FIR) generally had the lowest species richness (respectively, 14 ± 0.99 in I, lower than 12 ± 1.31 in FIR and 12 ± 1.00, p value < 0.001 compared to C) (Table 2).

The quadrats with a high *B. phœnicoïdes* cover showed significantly lower evenness than the quadrats without *B. phœnicoïdes* (respectively, $E = 0.54 \pm 0.15$ and $E = 0.69 \pm 0.10$, p value < 0.001).

The Jaccard index comparing the reference (steppe) plots ($J = 0.39 \pm 0.07$) was significantly higher than the Jaccard indices comparing these reference plots to all the other treatments. Only the index measured in F treatments showed a significantly higher value ($J = 0.198 \pm 0.063$) than in all the other treatments (Fig. 5; Table 2).

The stress-tolerant species were significantly more frequent in the references than in the other quadrats ($\chi^2 = 116.9$, df $= 6$, p value < 0.001, Fig. 6), with the lowest proportions in I, FI, and IR. In contrast, the competitive species were more frequent in IR and poorly represented in C and F ($\chi^2 = 105.56$, df $= 6$, p value < 0.001, Fig. 6.). The ruderal species significantly dominated in F, FIR and the references ($\chi^2 = 81.99$, df $= 6$, p value < 0.001, Fig. 6).

Discussion

The aim of this study was to determine which type of disturbance—water stress removal or previous cultivation phases—has a greater effect on the composition, species richness, diversity, and successional dynamics (colonization by bramble) of a Mediterranean steppe plant community. Like many Mediterranean grasslands, the vegetation of La Crau has highest species richness, with an average of 24 species per 1 m^2; this is comparable with grasslands such as the Spanish "*Dehesa*," where species richness reaches

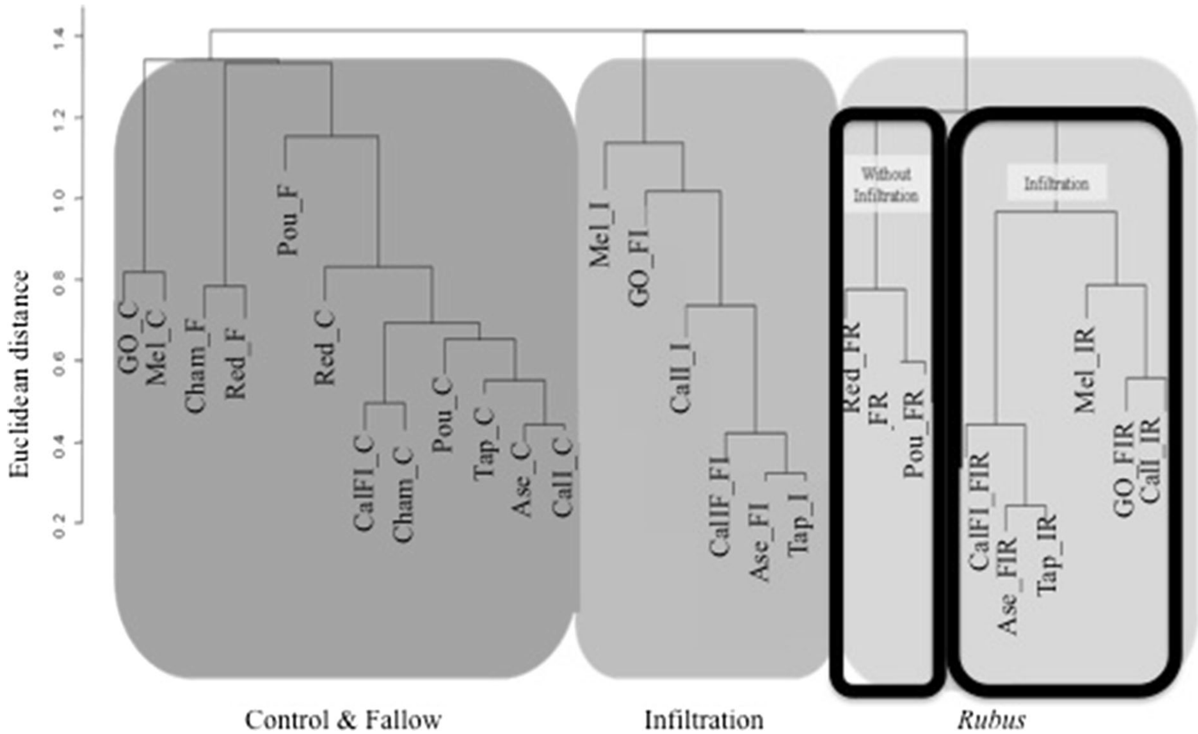


Fig. 3 Similarity dendrogram constructed for the 27 groups of 1 m^2 quadrats (3 sites $\times$ 3 replicates $\times$ 3 treatments). *C* reference; *F* fallow; *FR* fallow and brambles; *FI* fallow with infiltration; *FIR* fallow with infiltration and brambles; *I* infiltration; *IR* infiltration with brambles; in nine sites on the La Crau plain in southeastern France. Euclidean distance was used to measure dissimilarity

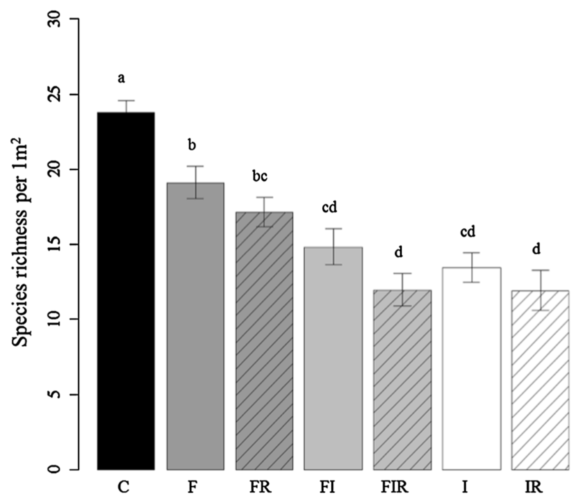


Fig. 4 Average species richness (1 m^2) measured in the six different treatments and the reference. *C* reference; *F* fallow; *FR* fallow and brambles; *FI* fallow with Infiltration; *FIR* fallow with infiltration and brambles; *I* infiltration; *IR* infiltration with brambles in the La Crau steppe, southeastern France ($\chi^2 = 142.31$, df = 6, p value < 0.001). *Error bars* represent standard error; *bars* sharing a common *letter* are not significantly different

Table 2 Results of a multiple comparison (post hoc) test performed using the glht function with the Tukey test on a mixed model which has tested the effect of (1) disturbance; (2) presence of brambles; and (3) disturbance and brambles on species richness

	z value	p value
Controls and disturbed treatments	−9.725	***
Controls and disturbed treatments with brambles	−12.291	***
Disturbed treatments with or without brambles	−2.566	***

Sites were used as random effect

58.8 ± 5.2 species per 100 m^2 and 49.3 ± 3.6 species per 100 m^2 when grazing has been abandoned (Peco et al. 2005). The steppe-type vegetation of La Crau is also very different from that of plots impacted by cultivation—or by the removal of water stress (Lavorel 1999). Here, the steppe plant community is dominated by species such as *B. retusum*, *Aira cupaniana*, *Euphorbia exigua*, *Euphorbia seguieriana*, or *S. capillata,* all fairly stress-tolerant according

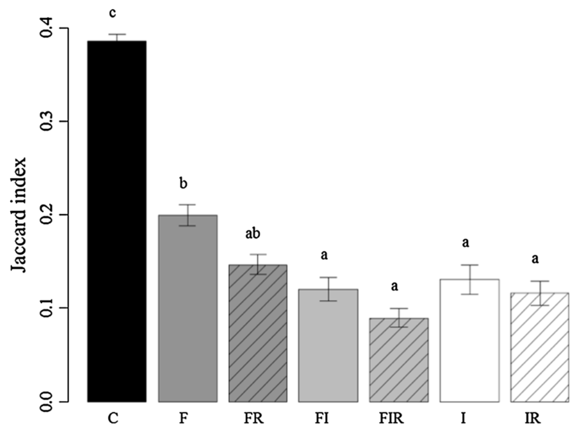


Fig. 5 Jaccard Index measured in the six different treatments and the reference. *C* reference; *F* fallow; *FR* fallow and brambles; *FI* fallow with Infiltration; *FIR* fallow with infiltration and brambles; *I* infiltration; *IR* infiltration with brambles in the La Crau steppe, southeastern France ($\chi^2 = 413.72$, df = 6, p value < 0.001). *Error bars* represent standard error, *bars* sharing a common *letter* are not significantly different

to the criteria defined by Grime (1979). As already shown in previous studies for the impact of previous cultivation but not for water stress removal (Römermann et al. 2005; Jaunatre et al. 2012), when this ecosystem undergoes cultivation disturbances, the subsequent vegetation colonizing the fallow land undergoes changes both in species richness and in composition, evenness, and functional diversity, with a significant decrease in stress-tolerant species in the fallow cultivated areas. Here, the plots with a history of cultivation were characterized by ruderal species such as *Diplotaxis tenuifolia*, *Hordeum murinum*, *Lobularia martitima*, or *Rostraria cristata.* This low resilience of steppe vegetation after a phase of cultivation has already been explained by the poor dispersal and colonization abilities of the typical steppe species, in particular *B. retusum* (Buisson et al. 2006), as well as the absence of a permanent seed bank for these species within the formerly cultivated sites

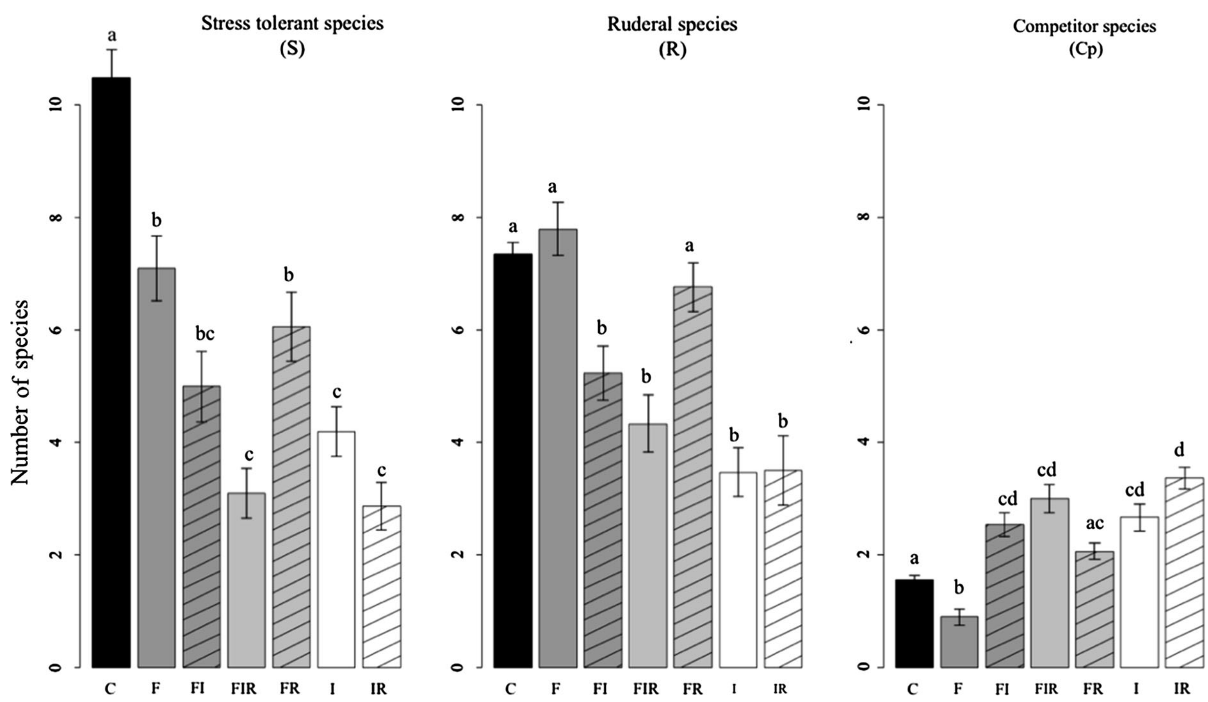


Fig. 6 Functional species richness based on CSR strategies (Grime 1979) for the six different treatments and the reference. *C* reference; *F* fallow; *FR* fallow and brambles; *FI* fallow with infiltration; *FIR* fallow with infiltration and brambles; *I* infiltration; *IR* infiltration with brambles in the La Crau steppe, southeastern France (stress-tolerant species: $\chi^2 = 116.9$, df = 6, p value < 0.001; Competitor species: $\chi^2 = 105.56$, df = 6, p value < 0.001; Ruderal species: $\chi^2 = 81.99$, df = 6, p value < 0.001). *Error bars* represent standard error, *bars* sharing a common *letter* are not significantly different

(Römermann et al. 2005; Buisson et al. 2006). In La Crau steppe, even 150 years after the cessation of cultivation and the restoration of traditional grazing, *B. retusum* and other typical species of the plain have still not re-colonized the fallow cultivated land (Jaunatre 2012). This type of failure by the dominant species to re-colonize has previously been observed in comparable ecosystems. For example, in a steppe in the northern United States, poor dispersal ability of seeds of the dominant species *Bouteloua gracilis,* coupled with soil texture, has been shown to have a major restrictive impact on recruitment, thus limiting re-colonization after disturbance (Coffin and Lauenroth 1994). On Californian coastal prairies, classified as Mediterranean grasslands, the impact of disturbance is still observable 40 years after cereal cultivation: with an enriched soil, the development of invasive species is favored, at the expense of typical species with a low seed bank (Buisson 2006). This poor resilience of the steppe community may be further explained by soil residues from the cultivation phase (e.g., increased soil concentrations of macroelements such as nitrogen, phosphorus, and potassium) which have persisted for more than a hundred years, favoring ruderal species with their rapid growth strategies at the expense of stress-tolerant species (Römermann et al. 2005; Forey and Dutoit 2012).

Our results suggest, however, that water infiltrations, whether they occur in fallow cultivated land or on original steppe vegetation, have a considerably greater impact on the plant communities in ecosystems subjected to high water stress, in particular steppe ecosystems. In dry grasslands, competition should be less intensive, since water stress controls plant growth and drought leads to slow successional processes (Aronson et al. 1995). Removing water stress in La Crau resulted both in changes in composition (homogenization) and in a decline in species richness and evenness, which were higher than the impact of previous cultivation periods. Nevertheless, from a conservation point of view, the unexpected presence of wetland species rare in southeastern France, such as *Convolvulus lineatus* L. and *Myosurus minimus* L. (MNHN 2013), must be underlined. The presence of these species needs to be taken into consideration before undertaking any operations aimed at scrub clearing or re-induction of water stress.

Water availability was found here to favor competitor species, inducing a reduction in the proportion of stress-tolerant steppe species. This competitiveness can be explained in particular by the more rapid uptake of soil mineral resources and light by plants with more highly developed root and aerial systems (Domènech and Vilà 2008). The stress-tolerant species were in this case replaced by *B. phœnicoïdes* which can allow the recruitment of other species such as *Festuca arundinacea* (Bolòs and Vigo 2001; Domènech and Vilà 2008). Nevertheless, despite this facilitating role during the recruitment phase, *B. phœnicoïdes* is also known to be a strong competitor slowing the recruitment of numerous species, as was shown by Tonioli et al. (2001) for *Quercus pubescens*. In our study, the presence of *B. phœnicoïdes* significantly reduced plant community evenness and in the absence of *B. phœnicoïdes,* the plant community subject to water infiltration showed a composition close to those of the formerly cultivated fields and the reference steppe. Thus, water stress removal does not only impact directly individual species, but it also alters the structure of the community by enabling the establishment of more competitive and dominant species. Similar results have already been reported for the Mediterranean grasslands of Spain, where the removal of water stress and greater availability of nutrients altered the size of individuals. The species were dense in productive areas (with high biomass productivity) and in contrast, smaller in the least productive areas (Fernández Alés et al. 1993). The abundance of steppe species would thus appear to be negatively correlated with the presence of competitive dominant species. These results on plant composition and structure confirm that water stress is indeed one of the main filters that explain the richness and the diversity of the herbaceous plant communities of the Mediterranean rangelands (Fernández Alés et al. 1993).

With regard to the successional dynamics of these herbaceous plant communities following water stress removal or cultivation phases, the presence of bramble combined with maintained sheep grazing did not significantly impact plant species richness in the immediate vicinity of bramble thickets, but it did impact botanical composition. Some common steppe species such as *Anagallis arvensis*, *Botriochloa ischaemum*, *B. hordeaceus*, and *Calamintha nepeta* were absent in the vicinity of bramble thickets. Thus, the facilitator role expected of bramble around the plot edges was only confirmed for a few species such as *Galium parisiense* or *Oxalis corniculata,* which were more abundant and better developed under bramble stems than in any other situations (Table 1).

Future work should examine at landscape scale the potential influence of bramble on herbaceous vegetation and seek to predict consequences: these could be an increase in the shrub stratum and the total disappearance of the herbaceous stratum. However, this should be somewhat limited in the plain of La Crau by the persistence of itinerant sheep grazing, which has been demonstrated to prevent brambles from covering the whole herbaceous surface area (Reyneri et al. 1994).

The former cultivation phase, although it significantly modifies the composition, richness, and diversity of the original steppe vegetation, does not lead to the establishment of competitor species, favoring instead ruderal species (seed bank species, stimulated by the cultivation phase (Dutoit and Alard 1995)). Their high density when there are water infiltrations may have the same effect as cover by a competitive and potentially dominant species. In both cases, changes in land use have altered plant successions, allowing colonization by brambles. Colonization by brambles is thus a secondary consequence of changes in land use.

Our results show that water infiltration has a greater impact on the floristic composition, species richness, and diversity of the steppe. Thus, in the plain of La Crau, while there are currently 1500 ha covered by cultivated fallow lands, more than 300 ha are also subject to the impact of water infiltration coming from neighboring irrigated meadows or caused by the poor maintenance of irrigation channels (Devaux et al. 1983). To determine how the re-introduction of water stress might enable the vegetation to return to its initial state, it would be of great interest for the ecological restoration of the steppe plant community to test the consequences of drying out plots via drains or ditches at the edges of irrigated plots or via channel renovation. The resilience of the community that had thus been dried out might then be greater than where there are disturbances linked to formerly cultivated fallow lands (where soils have been reworked, altered, and fertilized). This process could nonetheless be slowed by the presence of silt deposited during phases of infiltration that have enhanced the soil fertility of the plots.

Bramble does not appear to have a major impact on the steppe plant community as long as traditional sheep grazing is maintained: the traditional extensive grazing system is known to limit the spread of shrub species (Carmel and Kadmon 1999). To eradicate bramble thickets, restoration techniques involving annual clearing of the undergrowth and grazing might be a feasible but costly solution (McGregor 1996). In this case, it is essential to take into account the environment surrounding the plot subjected to this colonization. If it is integrated within an agricultural landscape matrix, water infiltrations need to be stopped. Preventing water infiltrations would facilitate clearing and grazing operations to control the brambles, as well as ensuring more rapid recovery of the stress-tolerant annual species typical of the steppe.

Conclusion

On the steppe of la Crau, cultivation and water infiltration significantly affected species richness and plant composition. Due to its low resilience, the herbaceous community is unable to return to the reference state, in this case the undisturbed steppe plant community (Aronson et al. 1995). Our results show that water stress removal is more damaging than a former cultivation phase disturbance or colonization by a colonizing scrub species. With the removal of water stress, the availability of water has led to the spread of more competitive species, such as *B. phœnicoïdes*, at the expense of the stress-tolerant species typical of the steppe. Although the presence of brambles at community scale has a lower impact than infiltrations, at a larger scale, across the landscape, it might have a higher effect. It might lead to the closing-off of the environment, to the disappearance of the herbaceous stratum and thus of the unique steppe vegetation if traditional sheep grazing is totally abandoned. For conservation purposes, it is necessary to find efficient ways to maintain water stress. In addition, a better understanding of bramble dynamics is needed to establish priorities and to apply relevant restoration techniques on the plain of La Crau and more generally in the rangelands encountered throughout the Mediterranean basin.

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Appendix 1

See Fig. 7.

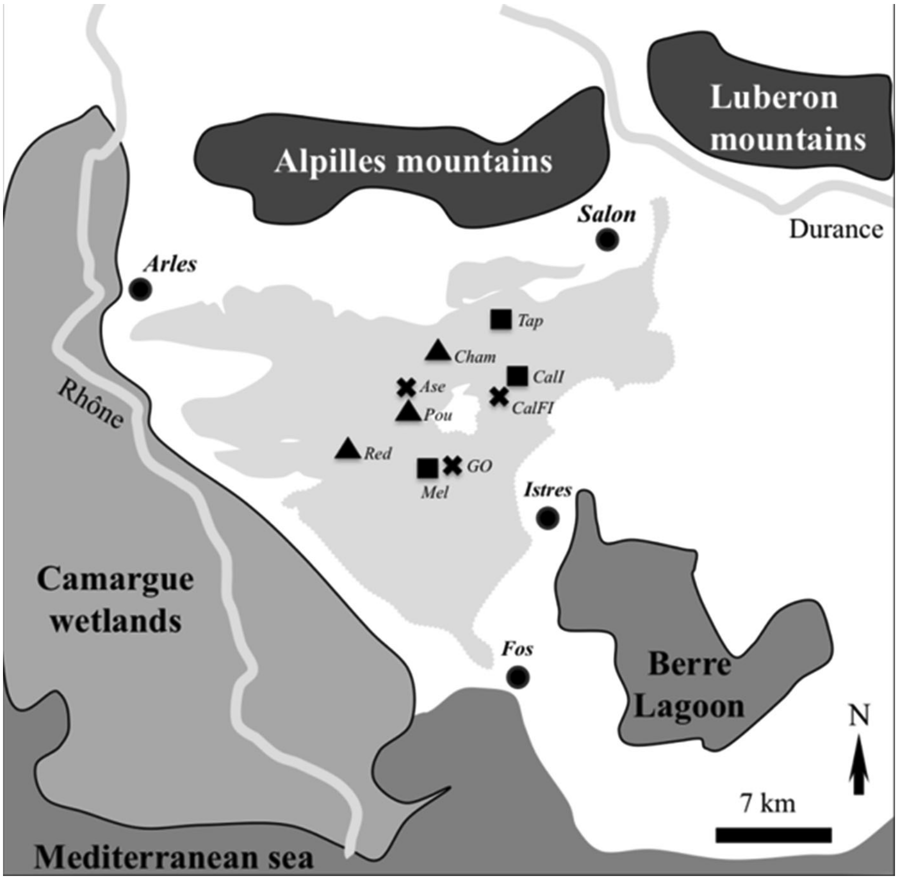

Fig. 7 Geographical position and map of La Crau with the nine study sites represented by: *crosses* for Fallow and Infiltrations sites, *squares* for Infiltrations sites and *triangles* for fallow sites (see Table 1 for abbreviations)

Appendix 2

See Table 3.

Table 3 Main characteristics of the nine study sites in the plain of La Crau, southeastern France: abbreviation; GPS position; treatment applied at each site (F, I and FI)

Site	Abbreviation	GPS Position	Treatment
Ase	Ase	4°52′50.86″E–43°36′57.72″N	FI
Calissane FI	CalFI	4°57′38.48″E–43°36′55.56″N	FI
Calissane I	CalI	4°57′55.33″E–43°37′01.91″N	I
Chambonnet	Cham	4°54′17.49″E–43°38′26.53″N	F
Guillaume orcel	GO	4°54′56.73″E–43°34′11.44″N	FI
La melonnière	Mel	4°53′37.14″E–43°34′07.78″N	I
La tapie	Tap	4°57′36.49″E–43°49′00.40″N	I
Poulagères	Pou	4°52′26.44″E–43°36′34.72″N	F
Redorcarmin	Red	4°49′34.80″E–43°34′56.36″N	F

Appendix 3

See Table 4.

Table 4 Taxa recorded in 9 study sites in the La Crau steppe (south-eastern France)

Taxa	Treatment	C	F	FR	I	IR	FI	FIR
Aegilops ovata L.*		8.9	–	3.3	–	–	–	–
Aira cupaniana Guss.*		50.0	–	13.3	–	6.7	10.0	6.7
Allium sp.		4.4	3.3	–	13.3	10.0	–	–
Anagallis arvensis L. subsp. *Arvensis**		1.1	–	–	6.7	3.3	13.3	3.3
Andryala integrifolia L.*		*10.0*	*23.3*	*13.3*	–	–	*13.3*	–
Anthoxanthum odoratum L.*		1.1	–	–	30.0	23.3	–	–
Arabidopsis thaliana (L.) Heynh.*		–	–	–	–	**10.0**	–	–
Arabis hirsuta (L.) Scop.*		–	–	–	–	**3.3**	–	–
Arenaria leptoclados (Rchb.) Guss.*		4.4	26.7	6.7	–	–	–	–
Asperula cynanchica* L.		**1.1**	–	–	–	–	–	–
Asphodelus ayardii Jahand. &Maire*		11.1	–	3.3	13.3	3.3	3.3	–
Asterolinon linum-stellatum (L.) Duby*		38.9		16.7	–	–	13.3	13.3
Avena barbata Link*		35.6	30.0	23.3	6.7	13.3	3.3	3.3
Avena sterilis L.*		–	–	–	–	**3.3**	–	–
Avenula bromoides (Gouan) H. Scholz*		1.1	–	3.3	–	–	–	–
Bellis sylvestris Cirillo		46.7	16.7	30.0	33.3	33.3	10.0	3.3
Bombycilaena erecta (L.) Smoljan.*		–	3.3	3.3	10.0	13.3	3.3	–
Bothriochloa ischaemum (L.) Keng*		56.7	23.3	16.7	33.3	30.0	20.0	6.7
Brachypodium distachyon (L.) P. Beauv.*		45.6	13.3	16.7	6.7	3.3	3.3	–
Brachypodium phoenicoïdes (L.) Roem. & Schult.*		–	–	–	70.0	63.3	76.7	60.0
Brachypodium retusum (Pers.) P. Beauv.*		78.9	6.7	6.7	20.0	33.3	–	–
Brassicaceae		–	3.3	–	–	6.7	–	–
Bromus diandrus* Roth		**4.4**	–	–	–	–	–	–
Bromushordeaceus L.*		68.9	80.0	50.0	36.7	20.0	30.0	16.7
Bromus lanceolatus Roth*		–	3.3	16.7	23.3	16.7	16.7	6.7
Bromus madritensis L.*		55.6	56.7	46.7	16.7	23.3	36.7	20.0
Bromus rubens L.*		8.9	30.0	20.0	–	–	6.7	–
Bromus sterilis L.*		–	–	–	**3.3**	–	–	–
Calamintha nepeta (L.) Savi*		17.8	86.7	83.3	13.3	20.0	60.0	53.3
Campanula erinus L.*		–	**13.3**	–	–	–	–	–
Camphorosma monspeliaca L.*		**2.2**	–	–	–	–	–	–
Capsella bursa-*pastoris* **(L.) Medik.***		**1.1**	–	–	–	–	–	–
Cardamine hirsuta L.*		–	–	–	3.3	6.7	–	–
Carduus nigrescens Vill.*		22.2	–	3.3	–	3.3	–	–
Carduus pycnocephalus L.*		2.2	10.0	3.3	–	–	6.7	16.7
***Carduus* sp.**		**2.2**	–	–	–	–	–	–
Carex divisa Huds.*		–	–	3.3	10.0	6.7	3.3	6.7
Carex divulsa Stokes*		–	–	**3.3**	–	–	–	–
Carex flacca Schreb.*		–	–	–	–	–	3.3	3.3
Carlina corymbosa L.*		26.7	6.7	–	–	–	–	–

Table 4 continued

Taxa	Treatment	C	F	FR	I	IR	FI	FIR
Carlina lanata L.		1.1	–	–	–	3.3	–	–
Carthamus lanatus L.*		*22.2*	*23.3*	*3.3*	–	–	–	–
Catapodium rigidum (L.) C.E.Hubb.*		*15.6*	*6.7*	*23.3*	–	–	*6.7*	*3.3*
Celtis australis L.		–	–	**3.3**	–	–	–	–
Centaurea melitensis L.*		–	–	–	–	–	6.7	6.7
Centaurium sp.		–	3.3	–	–	–	3.3	–
Centranthus calcitrapae (L.) Dufr.*		–	–	3.3	–	–	3.3	6.7
Cerastium glomeratum Thuill.*		14.4	30.0	20.0	23.3	23.3	16.7	16.7
*Cerastium pumilum Curtis**		*1.1*	–	–	–	–	–	*3.3*
Cerastium semidecandrum L.* *(I)*		–	–	–	**3.3**	–	–	–
Convolvulus arvensis L.*		1.1	3.3	–	26.7	26.7	20.0	20.0
Convolvulus cantabrica* L.		**4.4**	–	–	–	–	–	–
Convolvulus lineatus L.* *(I)*		–	–	–	**3.3**	–	–	–
Conyza sp.		–	–	10.0	10.0	–	26.7	20.0
Cornus sanguinea L.*		–	–	–	–	–	–	**3.3**
***Crassulatillaea* Lest.-Garl.**		**2.2**	–	–	–	–	–	–
Crataegusmonogyna Jacq.*		–	–	–	–	–	–	**6.7**
Crepisfoetida L.*		14.4	20.0	6.7	–	–	3.3	–
Crepis micrantha (Czerep).		1.1	–	–	–	3.3	–	–
Crepis pulchra L.*		4.4	–	6.7	–	3.3	3.3	–
Crepis sancta (L.) Bornm.*		20.0	16.7	20.0	16.7	13.3	30.0	10.0
Crepis vesicaria L.*		2.2	40.0	26.7	6.7	–	–	3.3
Cynodon dactylon (L.) Pers.*		4.4	6.7	–	20.0	20.0	13.3	–
Cynoglossum creticum Mill.*		–	–	3.3	–	13.3	–	16.7
Cynosurus echinatus* L.		**4.4**	–	–	–	–	–	–
Dactylis glomerata L.*		70.0	30.0	46.7	20.0	16.7	10.0	10.0
Daucus carota L.*		3.3	3.3	–	–	–	3.3	–
Diplotaxis tenuifolia (L.) DC.*		–	10.0	6.7	–	–	–	–
Dittrichia viscosa (L.) Greuter*		2.2	–	3.3	–	–	6.7	–
Echium asperrimum Lam.		3.3	3.3	–	–	–	–	3.3
Echium vulgare L.*		–	–	–	3.3	–	–	3.3
Erodiumcicutarium (L.) L'Her.*		18.9	30.0	6.7	–	–	13.3	16.7
Erophila verna(L.) Chevall.*		–	–	–	**3.3**	–	–	–
Eryngium campestre L.*		30.0	16.7	16.7	3.3	–	3.3	–
Euphorbia cyparissias L.*		63.3	63.3	20.0	13.3	10.0	30.0	10.0
Euphorbia exigua L.*		75.6	33.3	10.0	43.3	33.3	16.7	3.3
Euphorbia falcata L.		7.8	–	–	3.3	–	–	–
Euphorbia helioscopia L.*		–	16.7	3.3	–	–	–	–
Euphorbia seguieriana Neck.		24.4	13.3	3.3	–	–	–	–
Festuca sp.		11.1	–	–	30.0	16.7	–	–
Filago gallica L.		51.1	3.3	–	13.3	3.3	16.7	6.7
Filago pygmaea* (L.) Brot.		**8.9**	–	–	–	–	–	–
Filago pyramidata L.*		4.4	3.3	–	–	–	–	–
Filago vulgaris Lam.*		26.7	23.3	10.0	26.7	20.0	30.0	6.7

Table 4 continued

Taxa	Treatment	C	F	FR	I	IR	FI	FIR
Foeniculum vulgare Mill.*		**3.3**	–	–	–	–	–	–
Fumana ericoides (Cav.) Gand.*		–	3.3	–	3.3	–	–	–
Galactites elegans (All.) Soldano*		1.1	3.3	13.3	–	10.0	3.3	–
Galium aparine L.*		–	–	3.3	–	3.3	–	–
Galium murale (L.) All.*		30.0	33.3	26.7	–	10.0	36.7	36.7
Galium parisiense L.*		65.6	26.7	43.3	23.3	16.7	50.0	33.3
***Galium* sp.**		**1.1**	–	–	–	–	–	–
Galium verum L.*		2.2	–	–	6.7	3.3	–	–
Geranium dissectum L.*		–	20.0	13.3	23.3	20.0	3.3	3.3
Geranium molle L.*		57.8	63.3	26.7	6.7	10.0	43.3	30.0
*Geranium robertianum*L.*subsp. *purpureum* (Vill.) Nyman		–	–	–	–	**3.3**	–	–
Geranium rotundifolium L.*		1.1	–	16.7	–	6.7	3.3	3.3
Hainardia cylindrical (Willd.) Greuter		–	–	–	**3.3**	–	–	–
Hedera helix L.*		–	–	–	–	–	–	**3.3**
Hedypnois cretica (L.) Dum.Cours.*		13.3	6.7	3.3	16.7	–	3.3	–
Helianthemum salicifolium (L.) Mill.*		–	**3.3**	–	–	–	–	–
Herniaria glabra L.		–	–	–	**3.3**	–	–	–
Hieracium pilosella L.*		3.3	–	–	50.0	23.3	–	20.0
Hirschfeldia incana (L.) Lagr.-Foss.		–	–	–	–	**3.3**	–	–
Holcus lanatus L.*		–	–	–	–	**3.3**	–	–
Hordeum murinum L. subsp. *leporinum* (Link) Arcang.*		12.2	26.7	–	6.7	6.7	6.7	10.0
Hypericum perforatum L.*		1.1	3.3	16.7	3.3	–	56.7	26.7
Hypochaeris glabra L.*		28.9	10.0	3.3	6.7	–	6.7	–
Hypochaeris radicata L.*		1.1	3.3	–	3.3	–	–	–
Lactuca serriola L.*		–	–	–	–	**3.3**	–	–
Lactuca virosa L.*		–	–	3.3	3.3	–	–	–
Lamium amplexicaule L.*		3.3	–	–	–	–	3.3	–
Lavandula latifolia Medik.*		10.0	–	3.3	3.3	3.3	–	3.3
Leontodon tuberosus L.*		12.2	16.7	20.0	–	–	–	–
Lepidium graminifolium L.*		2.2	43.3	26.7	–	–	16.7	13.3
Linaria arvensis* (L.) Desf.		**5.6**	–	–	–	–	–	–
Linaria pelisseriana* (L.) Mill.		**3.3**	–	–	–	–	–	–
Linum strictum L.*		**2.2**	–	–	–	–	–	–
Linum trigynum L.*		56.7	10.0	23.3	10.0	6.7	6.7	–
Lobularia maritima (L.) Desv.*		46.7	73.3	80.0	–	3.3	50.0	63.3
Lolium perenne L.*		1.1	3.3	3.3	6.7	3.3	–	–
Lythrum hyssopifolia L.		–	–	–	6.7	3.3	–	–
Lythrum thymifolium L.		–	–	–	**3.3**	–	–	–
Marrubium vulgare L.*		–	3.3	–	3.3	–	–	–
Medicago monspeliaca L.		13.3	16.7	–	–	–	–	6.7
Medicago polymorpha L.*		–	–	–	–	**3.3**	–	–
Medicago rigidula (L.) All.*		4.4	3.3	–	–	–	–	–
Medicago truncatula* Gaertn.		**1.1**	–	–	–	–	–	–
Melica ciliata L.*		–	36.7	26.7	10.0	13.3	–	6.7

Table 4 continued

Taxa	Treatment	C	F	FR	I	IR	FI	FIR
Myosotis arvensis Hill.		–	–	–	–	10.0	6.7	–
Myosotis discolor Pers.		–	–	–	16.7	6.7	–	–
Myosurus minimus L.		–	–	–	**3.3**	–	–	–
Myosotis ramosissima Rochel*		–	–	–	–	–	–	**3.3**
Neatostema apulum* (L.) I.M. Johnst.		**3.3**	–	–	–	–	–	–
Ononis sp.		4.4	–	–	3.3	–	–	–
***Onopordon illyricum* L.**		**3.3**	–	–	–	–	–	–
Oxalis corniculata L.*		5.6	20.0	60.0	–	3.3	50.0	53.3
Parapholis incurva (L.) C.E.Hubb.*		–	–	–	10.0	–	10.0	–
Pardoglossum cheirifolium (L.) Barbier & Mathez*		2.2	30.0	16.7	–	–	–	–
Paspalum dilatatum Poir.*		–	3.3	–	3.3	13.3	10.0	16.7
Phillyrea angustifolia L.*		–	–	20.0	–	–	–	10.0
Phleum pratense L.		2.2	–	3.3	26.7	13.3	10.0	3.3
Phlomis lychnitis* L.		**5.6**	–	–	–	–	–	–
Picris hieracioides L.*		–	6.7	3.3	–	–	6.7	16.7
***Plantago bellardii* All.**		**3.3**	–	–	–	–	–	–
Plantago coronopus L.*		–	–	–	3.3	–	–	3.3
Plantago lagopus L.*		37.8	26.7	–	13.3	–	6.7	–
Plantago lanceolata* L.		**1.1**	–	–	–	–	–	–
Poa annua L.*		1.1	6.7	–	6.7	6.7	–	6.7
Poa bulbosa L.*		68.9	10.0	10.0	6.7	3.3	–	3.3
Poa pratensis L.*		–	–	–	3.3	–	16.7	6.7
Poa trivialis L.*		–	–	–	**6.7**	–	–	–
Polycarpon tetraphyllum (L.) L.*		25.6	26.7	10.0	6.7	6.7	36.7	23.3
Polygonum aviculare L.*		–	–	–	–	–	–	**3.3**
Polypogon maritimus Willd. subsp. *maritimus**		–	–	–	3.3	6.7	–	–
Potentilla reptans L.*		–	–	–	**3.3**	–	–	–
Prunus sp.		–	–	**3.3**	–	–	–	–
Psilurusincurvus (Gouan) Schinz & Thell.		48.9	50.0	26.7	–	–	13.3	6.7
Quercus pubescens* Willd.		**1.1**	–	–	–	–	–	–
Ranunculus paludosus Poir.*		13.3	6.7	3.3	13.3	10.0	–	3.3
Reichardia picroides (L.) Roth*		17.8	26.7	16.7	–	–	3.3	–
Rosa agrestis Savi*		–	–	13.3	3.3	6.7	6.7	–
Rostrariacristata (L.) Tzvelev*		15.6	26.7	10.0	3.3	6.7	3.3	–
Rubus ulmifolius Schott*		–	–	100.0	13.3	100.0	40.0	100.0
Rumex crispus L.*		–	–	6.7	3.3	–	6.7	6.7
Rumex pulcher L.*		3.3	6.7	30.0	–	6.7	3.3	3.3
Sagina apetala Ard.*		4.4	6.7	3.3	16.7	10.0	16.7	20.0
Salvia verbenaca L.*		17.8	6.7	–	–	–	–	–
Sanguisorba minor Scop.*		25.6	6.7	36.7	16.7	13.3	26.7	13.3
Scilla autumnalis L.*		–	–	–	**3.3**	–	–	–
Scirpoides holoschoenus (L.) Soják*		–	–	–	36.7	20.0	6.7	–
Scolymus hispanicus L.*		1.1	–	–	–	–	–	6.7
Senecio vulgaris L.*		37.8	26.7	26.7	10.0	10.0	6.7	10.0

Table 4 continued

Taxa	Treatment	C	F	FR	I	IR	FI	FIR
Sherardia arvensis L.*		45.6	16.7	10.0	20.0	10.0	33.3	3.3
Sideritis romana L.*		37.8	–	3.3	10.0	3.3	13.3	6.7
Sixalixa tropurpurea (L.) Greuter&Burdet subsp.*maritima* (L.) Greuter&Burdet*		20.0	30.0	26.7	–	–	–	6.7
Sonchus asper (L.) Hill subsp. *asper**		–	–	–	3.3	6.7	3.3	3.3
***Sonchus bulbosus* (L.) N.Kilian & Greuter.**		**1.1**	–	–	–	–	–	–
Spiranthes spiralis (L.) Chevall.*		1.1	–	–	–	–	3.3	–
Stellaria media (L.) Vill.*		–	3.3	–	–	–	3.3	–
Stipa capillata L.		30.0	–	6.7	–	–	3.3	–
Taeniatherum caput-medusae (L.) Nevski*		1.1	–	3.3	–	–	–	–
Taraxacum sp.		–	10.0	3.3	–	–	6.7	–
Teucrium chamaedrys L.*		8.9	–	–	33.3	20.0	–	–
Teucrium polium L.*		**1.1**	–	–	–	–	–	–
Thymus vulgaris L.*		57.8	36.7	43.3	–	–	–	–
Tolpisbarbata (L.) Gaertn.*		7.8	–	–	–	–	6.7	–
Torilis sp.		5.6	6.7	6.7	10.0	–	3.3	–
Tragopogon porrifolius L. subsp. *australis* (Jord.) Nyman*		–	–	**3.3**	–	–	–	–
Trifolium angustifolium L.*		–	–	–	–	–	–	**3.3**
Trifolium arvense* L.		**1.1**	–	–	–	–	–	–
Trifolium campestre Schreb.*		7.8	6.7	–	3.3	–	3.3	3.3
Trifolium cherleri* L.		**6.7**	–	–	–	–	–	–
Trifolium glomeratum L.*		14.4	3.3	3.3	6.7	3.3	6.7	6.7
Trifolium resupinatum L.		–	–	–	**6.7**	–	–	–
Trifolium scabrum L.*		22.2	–	–	6.7	–	16.7	6.7
Trifolium stellatum L.*		17.8	6.7	–	–	–	–	3.3
Trifolium subterraneum L.*		5.6	3.3	–	–	–	–	–
Trifolium suffocatum L.		10.0	26.7	13.3	3.3	6.7	23.3	13.3
Trifolium tomentosum* L.		**4.4**	–	–	–	–	–	–
Trigonella monspeliaca L.*		–	–	–	–	–	–	**3.3**
Urospermum dalechampii (L.) Scop. ex F.W. Schmidt*		4.4	–	–	3.3	–	–	–
Valerianella sp.		1.1	–	–	3.3	3.3	–	–
Verbascum blattaria L.*		–	–	–	–	**3.3**	–	–
Verbascum sinuatum L.*		14.4	33.3	13.3	–	–	6.7	–
Verbena officinalis L.*		–	–	–	3.3	6.7	6.7	3.3
Veronica arvensis L.*		38.9	30.0	73.3	30.0	36.7	63.3	46.7
Veronica persica Poir.*		1.1	–	–	3.3	–	–	3.3
Vicia parviflora Cav.*		4.4	6.7	3.3	30.0	26.7	20.0	16.7
Vicia sativa L.*		–	3.3	–	–	–	3.3	3.3
Vulpia sp.		73.3	73.3	53.3	53.3	43.3	40.0	43.3

Values correspond to the mean frequency (%) of each one for the 7 different treatments *C* Control; *F* Fallow; *FR* Fallow and *Rubus*; *FI* Fallow with Infiltration; FIR: Fallow with Infiltration and *Rubus*; *I* Infiltration; *IR* Infiltration with *Rubus*. Common species on the 7 treatments are underlined. Species used to functional analysis based on CSR strategies (Grime 1974) are preceded by *(175 species). Species exclusively found in control (steppe) are in bold. Frequencies of species found only in one specific treatment are in bold

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