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To cite this version:

Arne Saatkamp, Frédéric Henry, Thierry Dutoit. Vegetation and soil seed bank in a 23-year grazing exclusion chronosequence in a Mediterranean dry grassland. Plant Biosystems, 2018, Plant Biosystems, 152, pp.1020-1030. 10.1080/11263504.2017.1407375 . hal-01705299

HAL Id: hal-01705299

https://hal.science/hal-01705299v1

Submitted on 7 May 2018

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Vegetation and soil seed bank in a 23-year grazing exclusion chronosequence in a Mediterranean dry grassland

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ABSTRACT

Long-term grazing shaped plant diversity in dry Mediterranean grasslands. Abandonment of grazing affects plant diversity especially in the northern Mediterranean. Considerable efforts are, therefore, under way for grassland conservation and restoration. Yet, we do not know at which temporal scales impacts of grazing abandonment appear and in particular how soil seed banks evolve after longer grazing abandonment. Here, we provide detailed data from one of the very few long-term experiments available. These experiments provide data for up to 23 years (1982–2005) of grazing exclusion built in 1982, 1989, 2000 and 2001. Grazing exclusion decreased species richness, modified vegetation structure and changed soil parameters. Decline in species richness appears in communities that experienced 16 and 23 years of grazing exclusion. Only four to nine plant species of this Mediterranean grassland built persistent soil seed banks appearing after grazing exclusion, compared to 40–50 species in the established vegetation of grazed plots. Hence, similarity between vegetation and soil seed bank decreased with time of grazing exclusion. Even 23 years after abandonment, no woody plants colonised the experiments. We conclude that vegetation will recover fast from grazing abandonment in the short-term. Nevertheless, longer abandonment will impact diversity due to reduced soil seed banks.

ARTICLE HISTORY
Received 2 February 2017
Accepted 26 September 2017

KEYWORDS
Species richness; herbivory; disturbance; sheep; succession

Introduction

One quarter of earth's landscapes is covered by species-rich grasslands (Henwood 1998). Although origins are still controversial, grazing by domestic livestock since the Neolithic has been identified (Vera 2000). Grazing by large mammals modifies vegetation structure, composition and function (Wieren 1995; Peco et al. 2005). A main effect of grazing is the limitation of establishment and development of woody plants (Díaz et al. 2007; Saatkamp et al. 2010). Since grazing creates a high light environment and multiple regeneration niches, grazing maintains a high plant species richness (Milchunas and Noy-Meir 2002). Abandonment of grazing leads therefore to a decrease in plant species richness, a decrease that has been documented for the northern Mediterranean area (Bonet 2004; Peco et al. 2006).

Plant and insect species richness is maximised under intermediate grazing regimes (Fadda et al. 2007; Dutoit et al. 2008). In Mediterranean climates, grazing effects on vegetation are amplified by drought and oligotrophic soils, reducing further standing biomass (Blondel et al. 2010). Therefore, in many Mediterranean areas, this led to species-rich grasslands (Quézel and Médail 2003). Since these grasslands evolved under several thousand years of grazing (Henry et al. 2010), they are excellent models to study the role of grazing and its abandonment on plant composition, richness and structure (Díaz et al. 2007; Saatkamp et al. 2010; Catorci et al. 2012). In order to advice conservation practitioners and to restore species-rich communities, detailed information on how and when dry grassland vegetation structure and diversity change in response to grazing abandonment is needed. In particular, for Mediterranean climates it is still not well-known how soil seed banks contribute to recovery of species richness after low grazing frequency in itinerant systems or low stocking rate in closed pastures (Peco et al. 1998; Saatkamp et al. 2010). Moreover, until now experiments, such as isolated grazing exclosures, have not been evaluated for the importance of dispersal limitation as mechanism limiting plant diversity locally (Turnbull et al. 2000; Poschlod et al. 2013).

The importance of experimental long-term data-sets on vegetation for analysing the effects of land-use changes is now widely recognised (Kahmen and Poschlod 2004; Pei et al. 2008). Unfortunately, very few long-term experimental series are available to study the effect of grazing, due to the difficulty of maintaining such experiments over longer time. Spatial series corresponding to different stocking rates and the study through time of abandoned situations (chronosequences) have been used to analyse long-term effects of grazing (Peco et al. 2005; Yeo 2005; Fırıncıoğlu et al. 2007; Škornik et al. 2010). In this paper, we present data on long-term grazing exclosure experiments with a maximum age of 23 years. These exclosures have been built

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since 1982 and allow the study of a long-term series with precisely known dates which gives important additional information compared to previous spatial chronosequence approaches (Puerto and Rico 1992).

Soil seed banks are of particular importance for recovery after disturbances (Bisteau and Mahy 2005; Forey and Dutoit 2012). However, many Mediterranean dry grassland species have only transient soil seed banks (Saatkamp et al. 2011, 2014; Metzner et al. 2017). This is exacerbated by striking differences in composition between established vegetation and persistent soil seed banks (Peco et al. 1998; Metzner et al. 2017). These differences are much smaller with the transient seed bank (Peco et al. 1998). Persistent seed banks can be used to restore former plant communities after changes in land-use, e.g. abandonment of grazing (Bossuyt and Honnay 2008). Whereas the impacts of grazing abandonment on Mediterranean grassland vegetation has been studied using short-term exclosures (Peco et al. 2006), long-term and different aged exclosures have not yet been used to study the changes in established vegetation and permanent soil seed banks (Witt et al. 2011).

In this context, our aim was to analyse if: (1) diversity of established vegetation and persistent soil seed bank declines after different periods of grazing abandonment and (2) differences between established vegetation and soil seed banks increases with time in terms of species richness, diversity, vegetation composition, within habitat dissimilarity and plant cover. Moreover, we want to know whether: (3) changes in soil physico-chemical parameters are related to species composition in a constrained correspondence analysis. Finally, (4) we also want to compare different sites in order to highlight whether a site effect can alternatively explain the different indices measured. Finally, we discuss our results within the framework of future conservation management plans for Mediterranean dry grasslands.

Methods

Study area

All studied grazing exclosures are in the La Crau plain (Figure 1), which is a particularly well-conserved Mediterranean dry grassland area (Devaux et al. 1983). Although covered by alluvial material, due to tectonic uplift dating back to the Pleistocene, today the La Crau plain is no longer flooded by rivers. Climate is Mediterranean, with dry summers, and rainfall peaks in autumn with annual means of 579.3 mm, and a mean annual temperature of 14.3°C, a mean annual maximal of 18.9°C and a mean annual minimal of 8.9°C (1981–2010 at Salon-de-Provence). Grazing is characterised by itinerant sheep flocks and is documented for at least 2000 years based on Roman archaeological remains and writings by Pliny the elder,[1] but probably existed since the Neolithic (Badan et al. 1995; Henry et al. 2010). Itinerant sheep grazing is heterogeneous and difficult to quantify, stocking rates for the entire plain have been estimated to 1.5–2.5 sheep ha^{-1} $year^{-1}$ since the beginning of the 1980s (Buisson and Dutoit 2006). The plots used in this study have never been ploughed but always been grazed as far as documentation can sustain this point. Wild fires were used for pasture management until the beginning of the 19th but are not longer practice.

Although this steppe-like ecosystem is unique for southern France, many features are representative for dry grasslands in the Mediterranean (Buisson and Dutoit 2006). Vegetation has been described as *Asphodeletum fistulosi* (*Thero-Brachypodietalia*) and *Crassuletum tillaeae* (*Tuberarietalia guttati*) by Molinier and Tallon (1950). It is dominated by *Brachypodium retusum* and *Thymus vulgaris* and is a particularly species rich. Woody plants are extremely rare and 49.4% of all plants species are annuals that mainly germinate in autumn and flower from March to May or in September. Biomass production is highest in spring and autumn, and was assessed to 2.1 t ha^{-1} $year^{-1}$ (Bourrelly et al. 1983). Conservation efforts are underway to preserve intact and restore formerly cultivated parts of this ecosystem (Buisson and Dutoit 2006; Dutoit, Buisson, et al. 2013; Dutoit, Jaunatre, et al. 2013). Today 10 500 ha of the undisturbed steppe plant community still exist in 15 patches. All exclosures were built in large patches that were not affected by past cultivation; some of them were closed to formerly cultivated patches.

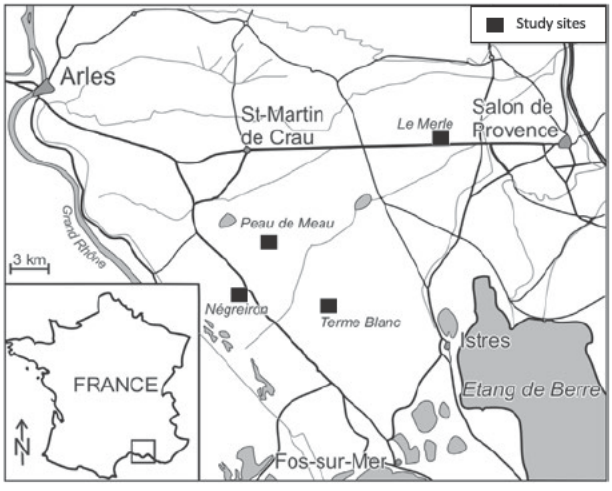

Figure 1. Map of the study area in the plain of La Crau and in Southern France with locations of the four exclosures: Négreiron (N), Terme Blanc (T), Peau de Meau (P), Merle (M).

Sampling design

In 2005, we studied four exclosures of different ages at four sites (Figure 1). Fences were used to exclude sheep from these experimental plots. The precise history of each exclosure was reconstructed in each of the four sites by documentary evidence (references to papers related to the use of the exclosures see Table 1) and aerial photographs from 1979 to 2007. The oldest exclosure of Le Merle was built in the North of the plain. It was set up in 1982 for ecological monitoring purposes on plant community biomass (Bourrelly et al. 1983). The exclosure of Peau de Meau in the centre of the plain was built in 1989, for studying the impact of the absence of grazing (Masip 1991). The two youngest exclosures Terme Blanc and Négreiron in the South of the plain were built, respectively, in 2000 and 2001 to study plant biomass and grasshopper density for the conservation of the Lesser kestrel (*Falco naumanni*), one of their predators (Pilard and Brun 2001). The present itinerant grazing system in the surrounding area of the exclosures was comparable in terms of animals (sheep), intensity and grazed seasons (from February to June) in 2005, but also since the beginning of the 1980s (Bourrelly et al. 1983; Masip 1991; Pilard and Brun 2001).

Table 1. History of the four studied exclosures in the Crau area (Southern France).

Location	Code	Year of creation	Surface	Coordinates	References
Merle	M	1982	0,2 ha	43° 38′ 57.10″ N 5° 00′ 48.81″ E	Bourelly (1984) Molénat et al. (1998)
Peau de Meau	P	1989	0,25 ha	43° 33′ 25.41″ N 4° 49′ 50.37″ E	Masip (1991) Borck (1998)
Terme Blanc	T	2000	3,7 ha	43° 32′ 04.70″ N 4° 52′ 06.09″ E	Pilard and Brun (2001)
Négreiron	N	2001	3 ha	43° 32′ 20.90″ N 4° 49′ 05.66″ E	Pilard and Brun (2001)

Vegetation sampling and analysis

For each of the four exclosures, plant communities were sampled in April–May 2005 in their centre (exclosure treatment), more than 10 metres away from the fences, in order to avoid edge effects already measured for these plant communities (Buisson et al. 2006). In parallel, we studied grazed vegetation outside the exclosures (grazed treatment).

For each treatment (grazed/exclosure) and at each site we studied above-ground vegetation in six quadrates of 2 × 2 m (4 m²) with a distance of 10 m between them, using frequency records in 25 sub-quadrates of 0.16 m². Relevés were done in spring 2005, a year with average rainfall comparable to the 30-year average (Devaux et al. 1983). In total, 24 quadrates were sampled in the grazed areas (600 sub-quadrates) and 24 in the exclosures (600 sub-quadrates).

Additionally, we estimated vegetation cover for three height classes of plants up to 5 cm high, 5–20 cm high and more than 20 cm high in each of the 48 quadrates. The same observer visually estimated stone cover and bare ground cover on a percentage scale. For each exclosure and grazed areas above-ground biomass was collected by clipping all plants in six 50 × 50 cm quadrates after the vegetation survey. Then, the samples were washed and dried until constant weight.

Exclosures size varied from 0.2 to 3.7 ha. Sampling design in terms of distances, number and size of replicates was fitted to the scale of the smallest exclosure at Merle, however, exclosures sizes always exceeded minimal floristic area of 40 m² for these dry grasslands (Loisel et al. 1990) and enabled us to avoid underestimating of plant species richness and diversity. In order to enhance precision of site characteristics, and in order to measure beta-diversity we use pseudoreplication in each exclosure or grazing area. For within-site comparisons, we consider these samples as true replicates. We compared average species richness, diversity and similarity using the Sørensen index for treatments and sites.

Soil sampling and analysis

Parallel to the vegetation study, in 2005, soil samples of 200 g each were taken at each site for five out of six vegetation samples at an average depth of 10 cm. After drying and sieving to 200 µm, soil chemistry (exchangeable calcium, magnesium and potassium) and soil pH (water) were analysed in 2005, by the INRA (*Institut National de la Recherche Agronomique*) using the methods detailed in Baize (1988). Carbon was measured with the Anne method and total nitrogen with the Kjeldahl method. Particle size distribution was measured as 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) using the Robinson method (Baize 1988).

Soil seed bank sampling

The soil seed bank was sampled and analysed in February 2005, before the input of fresh seeds and after the germination of most seeds in the fall and winter corresponding thus to the persistent part of the soil seed bank, i.e. to seeds that persist longer than to the first germination season (Walck et al. 2005). For each exclosure and grazed area, six replicate soil seed bank samples were taken. Classical soil cores could not be used since the soil was extremely rocky. For each replicate, two 1200 cm³ containers, each containing 10 subsamples, were filled with soil using a small trowel, one for the 0–5 cm depth and one for the > 5 cm depth (96 samples in total).

We used the seedling emergence method (Ter Heerdt et al. 1999) to identify species and quantify abundance of seeds in the soil seed bank. Soil samples were reduced by washing through two sieves of 2 mm and 200 µm mesh size. The retained fraction was spread in a thin layer (0.5 cm) in plastic trays filled with 2 cm vermiculite topped with medical compresses of 100 µm mesh size. Trays were covered with fine gauze to prevent contamination and watered every day from below. Emerging seedlings were identified, counted and removed weekly during six months including a cold stratification in a cold chamber at 4°C for one week before and after 3 months. Unidentifiable seedlings were grown in pots and identified at flowering using Jauzein (1995), which also served as nomenclatural reference.

Statistical analyses

We compared vegetation indices of sites, ages and treatments using species richness, Pielou's, Sørensen and Raup–Crick indices. Species richness and Pielou's diversity index were calculated for the established vegetation and soil seed banks. Pielou's index was calculated as: $J' = (-\Sigma_i p_i \log(p_i))/\log(S)$, where p_i is the proportional abundance of species i and S the total species richness. We used this index since it is relatively uncorrelated to species richness. We studied differences between grazed and exclosure plots using the Sørensen index $S = 2a/(2a + b + c)$ for a global comparison of the qualitative plant composition similitude between the two treatments in each site, where a is the number of species in common for two plots, b and c are the numbers of species appearing in only one of the plots. We calculated S and J' according to the above formula using *decostand* and *diversity* functions in the R package *vegan*. We also studied differences in species composition between established vegetation and soil seed bank using the Raup–Crick dissimilarity index. We calculated the Raup–Crick dissimilarity using the R function *vegdist* in the package *vegan* of R (Oksanen et al. 2007). It is a probabilistic index based on presence–absence data and is dependent on the number of species missing in both sites (Legendre and

Legendre 1998). This index gives a dissimilarity reflecting how much fewer species two samples share compared to lists drawn randomly from an overall species pool, a feature particularly interesting for sites with varying species richness as in our data. These diversity parameters as well as vegetation, stone, bare soil cover, soil chemistry (C, N, C:N, MgO, CaO and K_2O content) and particle sizes were compared between grazed plots and exclosures across and within sites. For the across site comparisons, we used linear mixed models (LMM) with maximum likelihood as implemented in the package *nlme* in R (Pinheiro et al. 2009) to analyse the effect of grazed plots *vs*. exclosures coded as binary explanatory variable and including sites as a random effect to account for spatial nesting of samples. When data did not follow a normal distribution (Shapiro–Wilk test) we applied log-transformations. We also wanted to know how grazing/exclosures treatments affected these variables within sites, therefore, we applied *t*-tests for each site, if applicable on log-transformed data, for non-normal data we applied *U*-tests (Sokal and Rohlf 1995).

Multivariate analyses were used to study relationships between vegetation in terms of species composition, soil seed bank composition and environment. We used a correspondence analysis (CA) on plant vegetation frequencies in order to discriminate differences due to sites on the one hand and changes induced by grazing abandonment on the other hand. We then integrated soil seed bank data into the CA space as additional points according to species composition to highlight the evolution of soil seed bank using the *predict* function in the package *vegan* of R (Oksanen et al. 2007).

To identify the factors which influenced the species compositions, we applied a constrained correspondence analysis (CCA) on vegetation composition data as main matrix and soil as well as structural parameters of vegetation as constraining matrix (Legendre and Legendre 1998). All calculations and analyses were done in R.

Results

Plant composition, evenness, α- and β-diversity of established vegetation

We identified 131 different plant species in the soil surface vegetation and the soil seed bank of the studied plots, 119 of which were found in grazed areas and 100 in the exclosures. The total inertia of the CA was 2.25 (Figure 2(a) and (b)). The first two axes of the CA accounted for 19% of the total variation with a contribution of 13% to axis 1 and 6% to axis 2. Samples were clumped by sites and distributed along the first axis from south to north. The CA plot also shows that exclosures are always distributed near the correspondent grazed area; differences in species composition between the two treatments increased with time elapsed for Négreiron, Terme Blanc and Peau de Meau, showing plant communities different in their floristic composition and structure. *Centaurium erythraea, Phlomis lychnitis* and *Lamium amplexicaule* were characteristic species of the oldest exclosure at the northernmost of Merle. Characteristic species of the southernmost site, Négreiron, were *Urospermum dalechampii, Camphorosma monspeliaca* and *Cardamine hirsuta*. The remaining sites – Peau de Meau and Terme Blanc – as well as grazed areas at Merle were clumped and characterised by species like *Vulpia ciliata, Brachypodium distachyon*, *Galium parisiense* and *Taeniatherum caput-medusae*. Axis 2 reflected the opposition between grazed areas and exclosures, with frequent species in exclosures differing among sites but including large plants such as *Centaurea solstitialis* and *Phlomis lychnitis*, as opposed to small annuals, such as *Hypochoeris glabra* and *Asterolinon linum-stellatum* in grazed areas.

Species richness and evenness differed significantly between treatments within sites (Figure 3(a) and (b)) and in the whole study area (Table 2). Nevertheless, only the older exclosures showed a significant decrease in species richness (Terme Blanc, Peau de Meau and Merle) and evenness (Peau de Meau and Merle) (Figure 3(b)). No significant difference was detected between the grazed area of Négreiron and its recent exclosure (Figure 3(a) and (b)).

The floristic similarity between grazed and exclosure decreased as measured by Sørensen index between the youngest exclosure at Négreiron with 67.8–47.6% at Merle the oldest exclosure. Raup–Crick's dissimilarity index increased with increasing age of exclosures between the youngest (N, $d_{rc} = 0.0116$) and the oldest (M, $d_{rc} = 0.1297$) exclosure.

For each site, the above-ground biomass was significantly higher in the exclosures (Table 2) and there was a significant increase of the cover of the highest vegetation layer in the linear mixed model (Table 2), and vegetation cover values decreased for small plants (<5 cm) and increased for high (>20 cm) plants.

Abiotic parameters and vegetation

Linear mixed models including sites as random effect detected significant differences between grazed plots and exclosures (Table 2). The constrained correspondence analysis in Figure 4, shows additionally that the site gradient (axis 1) between more calcareous and mesic sites in the North (Merle) is accompanied by well-known basiphilous mesophytes such as *Dactylis glomerata* and *Vulpia ciliata*, whereas southern sites have more acidiphilous and oligotrophic species such as *Filago gallica* and *Spergula pentandra*.

The coarse sand content in supplementary figure 1 exemplifies a soil parameter that showed no difference among treatments but differences among sites. There are similar site-specific differences for CaO, MgO and K_2O content which are all higher in the northernmost site at Merle. Comparing exclosures to grazed areas using linear mixed models showed that exclosures have higher nitrogen content, higher clay content lower coarse silt content, lower pH and higher magnesium content (Table 2).

Soil seed bank, seed densities and species diversity results

The study of the 96 soil seed bank samples at both depths led to the identification of 1566 seedlings of 55 species. Eight hundred and fifty-eight seedlings were observed in the grazed areas and 708 in the exclosures. Only 187 seedlings were observed in the deeper layer (>5 cm), we therefore excluded these data from all analyses. In the soil seed banks, 38 species were found in the exclosures, 47 in the grazed areas, 29 were shared between in both types. Only 66 seedlings (4% of the total) were not identified.

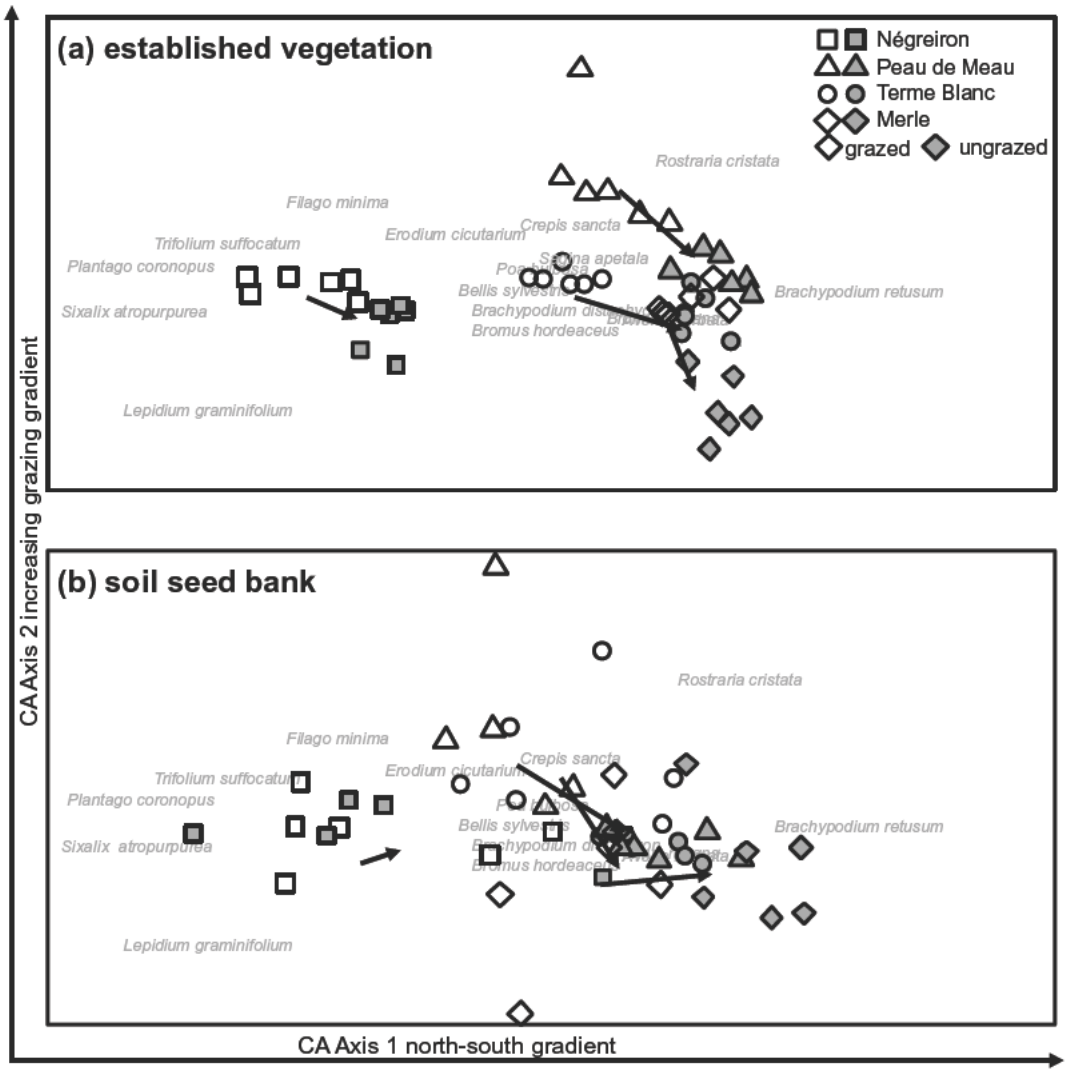

Figure 2. (a) Correspondence analysis (CA) of 48 sampling units of established vegetation in grazed areas (white) and exclosures (grey) for the four studied sites; (b) 48 soil seed bank samples from grazed areas and exclosures have been added according to their species composition in the CA of established vegetation; for visibility we represented only species with CA weight > 0.02; arrows indicate centroids from grazed to exclosure plots.

Conyza canadensis made up more than 32.6% of all emerged seedlings. Frequent species in the seed bank of the grazed areas were *C. canadensis* and *Sideritis romana*. The seed bank of exclosures was dominated by *Senecio vulgaris* and S. *romana.* Only five species were only found in the soil seed bank and in no sample of the established vegetation (*Chenopodium album, Conyza canadensis, Diplotaxis tenuifolia, Portulaca oleracea* and *Solanum nigrum*).

When soil seed bank samples are plotted according to species scores from the CA carried out on the established vegetation samples (Figure 2(b)), there is a much less clear distinction between treatments and sites.

For the richness and evenness of plants in the soil seed bank, there was no overall effect of grazing exclusion (Table 2). However, a significant difference was found in species richness of the whole persistent seed banks between sites ($F = 6.57$, $p < 0.01$). Moreover, there was an increasing evenness at Terme Blanc (Figure 3(d)) when grazing was excluded. There were no significant changes between grazed areas and exclosures for floristic dissimilarities between soil seed bank and established vegetation as measured by Raup–Crick's dissimilarity index (Figure 5). However, there was a site-specific difference in dissimilarity at Merle, yielding a seed bank that more closely resembles the established vegetation than at the grazed part of this area (Figure 5). The differences in species composition within treatments as measured by the Raup–Cricks index did not show a significant trend with time or treatment (Figure 6). When considering floristic differentiation between grazed and exclosure plots, the Raup–Cricks index showed an increase from 5 to 23 years of exclosure (Figure 7).

Measured by emerging seedling number, there was no significant difference between sites and between treatments for the upper seed bank layer. A significant difference appeared only for the number of seedlings in the deeper seed bank layer which was higher in the exclosures ($F = 2.79$, $p < 0.05$).

Discussion

Floristic composition and species richness

Grazing abandonment changes floristic composition and species richness of the established vegetation. Although site and age effects cannot be formally separated in the current experimental setting, the effects of exlosure age on species richness (Figure 3(a))

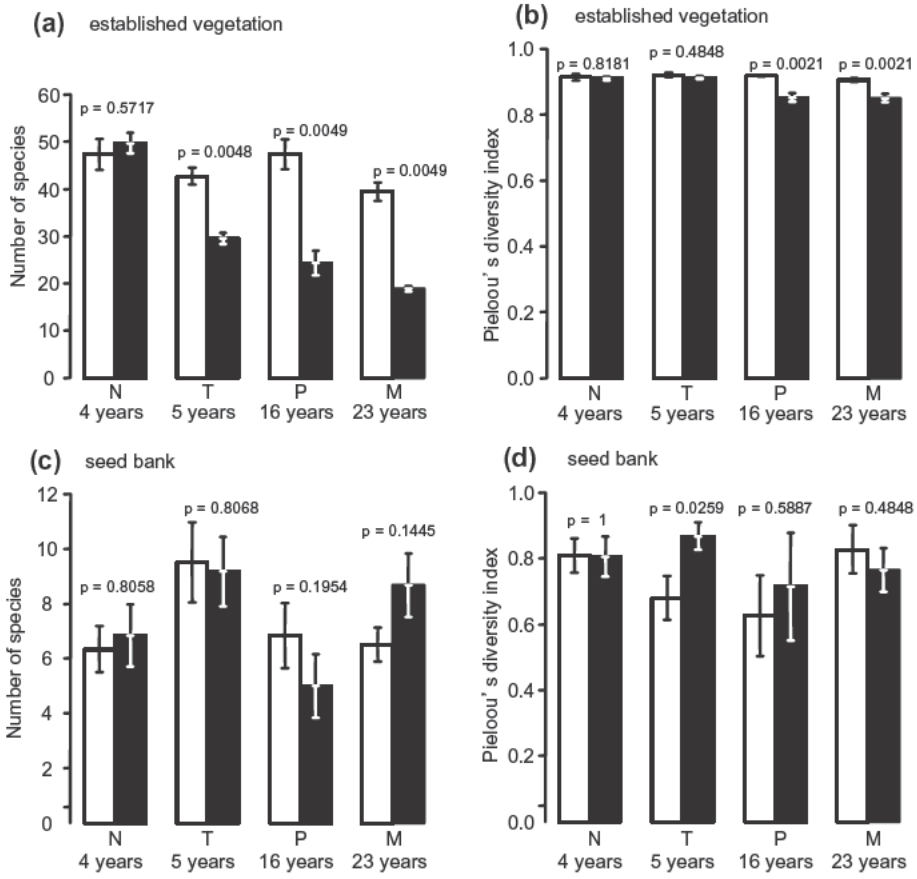

Figure 3. Plant species richness and Pielou's diversity index for established vegetation (a and b, respectively) and soil seed bank (c and d, respectively). Significances from *U*-tests are given in the figure; black = exclosures, white = grazed areas, N = Négreiron, T = Terme Blanc, P = Peau de Meau, M = Merle.

were systematically stronger for older compared to younger exclosures. Nevertheless, floristic dissimilarities between grazed areas and exclosures were still very small five years after the cessation of grazing (Figure 7). These results corroborate locally those of Borck (1998) and Molénat et al. (1998), who have already noticed the absence of significant differences for the species richness and floristic similarity between the grazed and the non-grazed areas in the first years after abandonment. These results confirmed also those of Montalvo et al. (1993) who have shown in a five-year exclosure experiment that the effects of grazing abandonment were very weak. The effects of climate in one particular year on species richness can interfere with the effect of grazing exclosure, especially in grasslands dominated by annual species (Peco et al. 2005). This is also the case for the dry grasslands of the Crau area (Buisson and Dutoit 2006).

In our case, we focused particularly on long-term abandonment (more than 20 years) and it is clear that that the negative effect of exclosure on species richness is more evident in sites that were abandoned between 5 and 16 years even in the absence of colonisation by matorral and forest species which are species confined to natural grazing refuges on the border of the Crau area (Devaux et al. 1983). In his review, Bonet (2004) pointed out that abandoned Spanish Mediterranean grasslands are generally colonised by matorral and forest species after 10 years of grazing abandonment. In our case, even after 23 years, no seedlings of shrub or forest species were identified in the oldest exclosure (Merle). We attribute the absence of woody plant colonisation to dispersal limitation (Turnbull et al. 2000), since seed sources of woody species in remnant patches of forests and matorral are very far from the exclosures, corroborating findings on the effects of woody vegetation patches in other Mediterranean ecosystems (Giarrizzo et al. 2017; Martín-Queller et al. 2017). Moreover, absence of dispersal vectors for tree species e.g. the Eurasian Jay (*Garrulus glandarius*) and the increase of herbaceous cover and standing litter in the older exclosures (Peau de Meau and Merle) can explain the absence in woody species colonisation.

Beside deep changes in species composition, the absence of grazing results in striking changes in vegetation cover and structure. In the oldest exclosure (Merle), there is an increase of height and perennial plant cover superior to 20 cm (e.g. *D. glomerata, B. retusum*). This change in vegetation height and bare soil cover are good predictors of grazing intensity in herbaceous communities, confirming previous works (Peco et al. 2005, 2006; Pueyo et al. 2006). Although we did not quantify litter, the decrease of bare soil and increase of vegetation height suggest that the amount of litter probably also increased in exclosures and in this way added to the differences in composition between grazed plots and exclosures (Loydi et al. 2014).

Soil parameters

The main differences in the soil parameters are linked to a south–north geographical gradient where the northern sites (Merle) are characterised by higher stone cover and soil fertility

Table 2. Differences between grazed and exclosure plots as analysed by linear mixed models (LMM) using sites as a random factor. The sign of the exclosure column indicates the relation between the response variable and the exclusion of grazing.

Dependent variable	Exclosure	*df*	*F*-value	*p*-value	
Species richness – established vegetation	–	1,43	42.62	<0.0001	***
Species richness – soil seed bank		1,43	0.02	0.8676	
Dissimilarity soil seed bank – established vegetation		1,43	2.31	0.1355	
Pielou's diversity index established vegetation	–	1,43	23.77	<0.0001	***
Pielou's diversity index soil seed bank		1,43	0.82	0.3681	
Cover 5 cm (log-transformed)	–	1,35	24.87	<0.0001	***
Cover 5–20 cm (log-transformed)		1,35	0.12	0.7212	
Cover 20 cm (log-transformed)	+	1,35	41.41	<0.0001	***
Biomass (log-transformed)	+	1,35	79.94	<0.0001	***
Clay content	+	1,35	11.29	0.0019	**
Fine silt content		1,35	0.17	0.6756	
Coarse silt content	–	1,35	4.67	0.0375	*
Fine sand content		1,35	2.32	0.1364	
Coarse sand content		1,35	0.60	0.4414	
C content		1,35	1.60	0.2135	
N content	+	1,35	5.74	0.0220	*
C/N ratio		1,35	0.01	0.9263	
pH	–	1,35	3.59	0.0664	
CaO	–	1,35	3.62	0.0653	
MgO	+	1,35	8.23	0.0069	**
K_2O		1,35	0.05	0.8155	
Baresoil cover (log-transformed)	–	1,35	107.69	<0.0001	***
Stone cover (log-transformed)	–	1,35	14.54	<0.0001	***

Notes: Significance levels *$p < 0.05$, **$p < 0.01$, ***$p < 0.0001$.

parameters (mineral contents). This can be linked to the ancient dynamics of the Durance river which deposited more limestone rich material in the northern part of the plain (Colomb and Roux 1978; Molliex et al. 2013).

A significant increase in clay and total nitrogen contents in the oldest exclosure (Merle) could be directly linked to the absence of grazing. Due to important wind erosion in the area, exclosures with their increased plant cover and litter layer accumulate materials which are responsible of the total nitrogen and C:N increases. This is corroborated by abundant soil and detritus material that also accumulates in old sub-shrubs like *Thymus vulgaris* even in grazed areas. We think that the specificities of the Crau area and position of our exclosures are here responsible for differences with previous findings in Mediterranean environments where extensive grazing increases fertility through nutrient redistribution (Peco et al. 2006). The increase in bare ground cover is a direct impact of grazing by plant removal and soil trampling. However, we think that the increase in stone cover is only an observation bias since grazing increases stone visibility simply by reducing plant cover.

Soil seed banks

Previous studies on our study system (Buisson and Dutoit 2004; Römermann et al. 2005; Buisson et al. 2006) and other Mediterranean dry grasslands (Ortega et al. 1997; Peco et al. 1998; Metzner et al. 2017) showed that the soil seed banks of Mediterranean grasslands are mostly transient and that only few species have persistent soil seed banks. Our data (Figure 3(c), (d) and Table 2) indicates that diversity of soil seed bank is not decreasing after grazing abandonment. Differences in species composition as measured by the Raup–Crick index between soil seed bank and established vegetation are only significant in the oldest exclosure. This contrasts with previous works, showing that species richness and density of seed banks generally decreases with successional age and under the same management regime (Donelan and Thompson 1980). Moreover, soil seed bank composition traces the changes in established vegetation to a small extent (Figure 2(b)). Altogether, this indicates that persistent soil seed banks do react only very slowly to grazing abandonment, and that therefore, species that have a persistent soil seed bank are very unlikely to get lost from the system even until 23 years after abandonment. However, much of the variation in the soil seed bank, when grazing and exclosure are compared is inconsistent among sites (Figure 5). Since we essentially sampled the persistent soil seed bank, we think that site-specific disturbance history probably influenced seed bank patterns more than actual vegetation and that exclosures are all relatively recent compared to the date when seed banks were formed. This may explain the contrast to results already revealed by numerous studies on the relation between plant succession and soil seed banks in dry grasslands (Dutoit and Alard 1995; Díaz-Villa et al. 2003) and is probably a result of the very long grazing history in the Crau area (Buisson and Dutoit 2006).

Persistent seed banks usually contain a high proportion of early successional species which rely on long-term viability as part of their opportunistic strategy (Caballero et al. 2003). Here, six species were found in the seed bank only and not in the established vegetation (*Carex* sp., *Chenopodium album*, *Conyza canadensis*, *Diplotaxis tenuifolia*, *Portulaca oleracea* and *Solanum nigrum*). All these species are known to have a persistent soil seed bank (Thompson et al. 1997) and flower in former arable fields close to remnants of dry grasslands (Buisson and Dutoit 2004; Römermann et al. 2005; Buisson et al. 2006). The presence of these species is due to former arable fields (1500 ha) in the surrounding area in the middle of the twentieth century, arable fields did not exist in places where the exclosures have been built (Römermann et al. 2005). Our further investigations on the soil seed banks (Coiffait-Gombault et al. 2012; Jaunatre et al. 2014) suggests that the re-establishment of species richness after long-term abandonement of dry grassland and re-introduction of sheep grazing can fail because ecological target species are unable to colonise from the persistent soil seed bank. This is also consistent with works that show seed rain to be more important than the soil seed bank for the restoration of dry grasslands (Turnbull et al. 2000; Bisteau and Mahy 2005; Poschlod et al. 2013). This depends on remnant patches of undisturbed vegetation in the vicinity and applies especially to plants that form transient soil seed banks (Buisson and Dutoit 2004; Römermann et al. 2005). However, because many dry grassland plants have low seed dispersability, remnant grazed patches cannot act as sources for the dispersal of seeds of sufficiently long distances (Buisson et al. 2006, 2015).

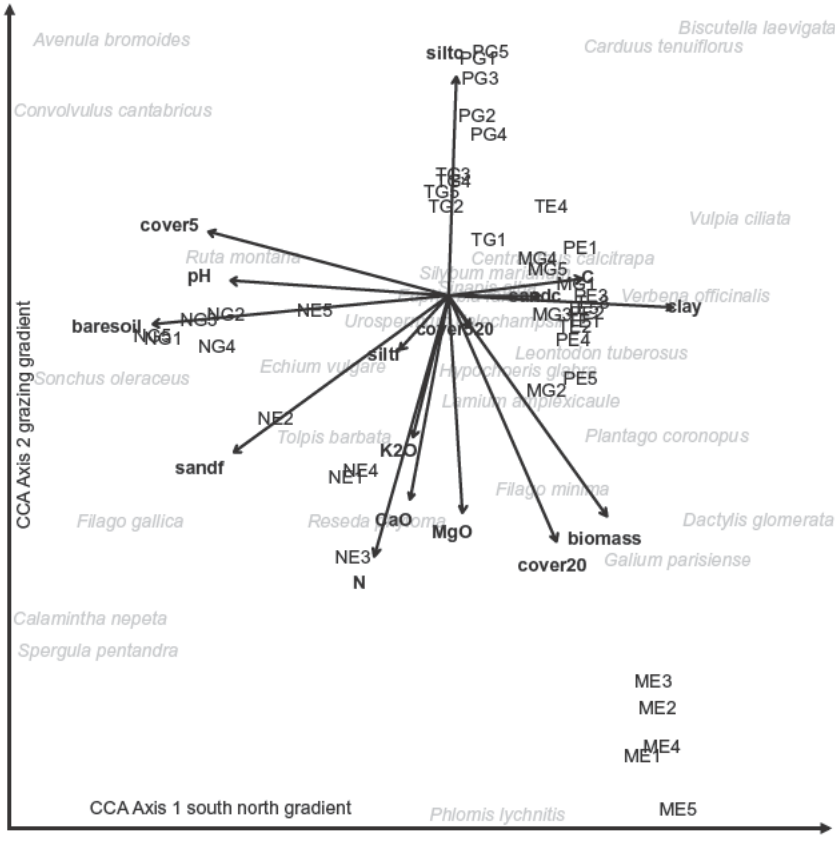

Figure 4. Constrained Correspondence Analysis (CCA) of 40 sampling units of established vegetation showing the site and grazing gradient; and the soil and vegetation features measured in the field (bold); only species with CA scores > 1.2 represented (grey); sites: N = Négreiron; T = Terme Blanc; P = Peau de Meau, M = Merle; G = grazing area; E = exclosure; total inertia was 1.9 with 18% for axis 1 and 9% for axis 2.

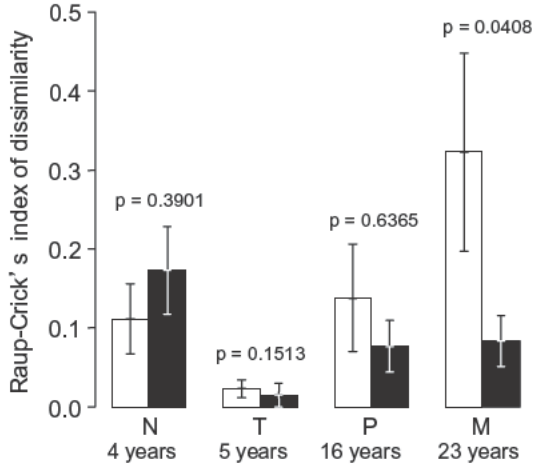

Figure 5. Differences between species composition of established vegetation and soil seed bank as measured by the Raup–Cricks dissimilarity index. Significances from *t*-tests on log-transformed data are given in the figure; black = exclosures, white = grazed areas, N = Négreiron, T = Terme Blanc, P = Peau de Meau, M = Merle.

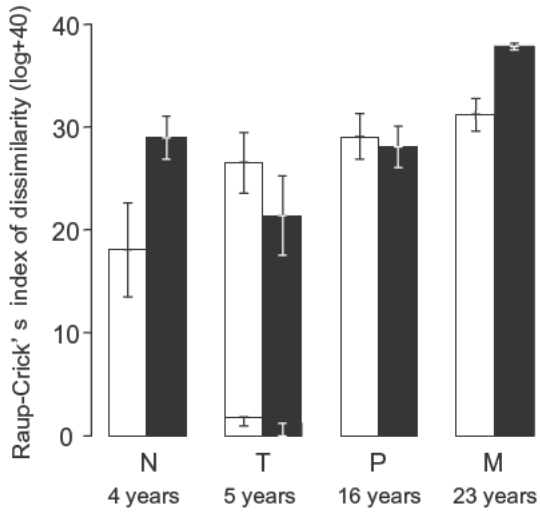

Figure 6. Differences in species composition of plots within treatments for each site as measured by the Raup–Cricks dissimilarity index (log + 40 transformed for visibility) for the established vegetation; G = grazed, E = exclosures, N = Négreiron, T = Terme Blanc, P = Peau de Meau, M = Merle.

Consequences for management of Mediterranean dry grasslands

The results presented here show that the impact of long-term grazing abandonment in Mediterranean grassland affects the composition and species richness of established vegetation but not the composition of the persistent soil seed bank. Persistent soil seed banks still show a strong dissimilarity with the established vegetation whatever the treatment. These effects may have large consequences for conservation of these species-rich ecosystems. If after five years of abandonment the evolution seems to be reversible, this is not the case after 16–23 years where ecological restoration could only be possible if seed sources are still present close to the abandoned areas

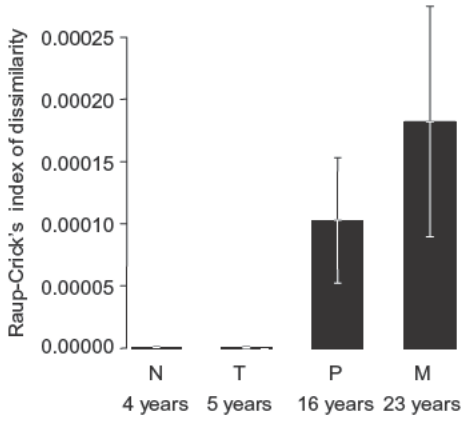

Figure 7. Differences in species composition between treatments for each site as measured by the Raup–Cricks dissimilarity index for the established vegetation; black = exclosures, white = grazed areas, N = Négreiron, T = Terme Blanc, P = Peau de Meau, M = Merle.

(Muller et al. 1998). Long-term grazing abandonment causes the loss of 40% of grassland species in La Crau area, which is not compensated by the invasion of shrub species due to dispersal limitation. This is a major issue for the conservation of plant species richness of short lived and grazing tolerant species, which are an important part of threatened plant species in the Mediterranean (Muller et al. 1998; Peco et al. 2006). The Crau area has strong site specificities such as dry alluvial deposits of pebbles, an ancient weathering, and very extended pasture surfaces. However, species composition is close to other works in Mediterranean pastures (e.g. Ortega et al. 1997; Peco et al. 2006) and also matches with pastures under Mediterranean climate around the world which often harbour plants introduced from Europe that are in our data-set (e.g. *Dactylis glomerata, Brachypodium distachyon, Centaurea solstitialis*). We, therefore, think that our results hold for similar pastures in Mediterranean climate zones.

Our data have shown that little changes occur for short abandonment periods for most measured parameters, with the exception of composition and species richness. Dramatic changes occur only after much more than five years of grazing abandonment. Moderate grazing improves fertility in very poor soils and can promote plant and insect species richness (Peco et al. 2006; Fadda et al. 2007; Blight et al. 2011; Alignan et al. 2014). Therefore, for the very large spatial scale of the Crau area, which exceeds 10 000 ha, it can be suggested that short-time grazing abandonment is tolerable and can even maximise species diversity at higher spatial scales due to increased beta-diversity (Mesléard et al. 2011; Moinardeau et al. 2016). The limited changes occurring after short-term exclosure suggest that flexible grazing management methods might be used with comparatively little impact on species composition, such as rotational grazing.

Note

1. Plinius, Naturalis Historia 21.57.

Acknowledgements

We are grateful to the CEN PACA and Ecomusée de Crau and the Nature Reserve of the Coussouls de Crau for their authorisation to carry out soil samples and access to study sites.

Disclosure statement

No potential conflict of interest was reported by the authors.

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