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Past cultivation is a factor driving organization of dry grassland ground-active beetle communities

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SUMMARY

The steppes of the Mediterranean Basin, traditionally managed since ancient times, have been drastically degraded by recent human activities, and are a valuable model to study the impact of present and past anthropogenic disturbances. Climate and edaphic constraints and free sheep grazing have contributed for over 6000 years to the development of a steppe unique to France, but similar to many others in the Mediterranean Basin. This steppe is increasingly threatened by both industrialization and cultivation, and formerly-cultivated plots developed less species-rich vegetation than the steppe. Here, sampling with pitfall traps showed that formerly-cultivated plots hosted more diverse beetle assemblages owing to the presence of ruderal plants, which had greater nutritional value and hosted more phytophagous insects, beetles or other groups, enhancing prey diversity. The steppe had a less species-rich assemblage, but included many species typical of arid areas, some of which are threatened. Former disturbances led to the settlement of ubiquitous species, which increased the overall species richness, but decreased the biological value for conservation. Conservationists have to decide whether they would rather maintain beetle species diversity or biological value.

Keywords: *Brachypodium* grasses, Coleoptera, disturbance, grazing pressure, ruderal vegetation

INTRODUCTION

Herbaceous ecosystems constitute more than 25% of the Earth's landscapes (Henwood 1998). They are widespread habitats, rich in floral and faunal species, but have been drastically reduced throughout the world (Jacobs *et al.* 1999), owing to settlement and industrial development, agricultural intensification and changes in fire and grazing regimes. In the Mediterranean Basin, from Turkey to Spain and Northern Morocco, steppe-like formations are species-rich (Quézel & Médail 2003), are found on oligotrophic soils with slow plant succession processes and have evolved with extensive traditional human management. Thus these dry grasslands are a particularly valuable model in which to study the impact of present and past anthropogenic disturbances.

Climate, edaphic constraints and traditional extensive sheep grazing since the Neolithic period (6000 years before present [BP]) have widely contributed to the character of the steppe of the 60 000 ha plain of La Crau (south of France). Grazing maintains the vegetation as a steppe-like formation with typical plant species such as *Brachypodium retusum* (Pers.) P. de Bauv., *Thymus vulgaris* L. and *Asphodelus ayardii* Jahand & Maire (Devaux *et al.* 1983). Currently, the steppe is overgrazed. This steppe hosts diverse vegetation characterized by a mixture of calcicolous and silicolous plant species, including locally rare species, such as *Taeniatherum caput-medusae* (L.) Nevski, *Hyssopus officinalis* L., *Plantago holosteum* Scop. and *Bufonia tenuifolia* L. (Devaux *et al.* 1983), and many protected or endangered animal species, such as the pin-tailed sandgrouse (*Pterocles alchata* L.), the little bustard (*Tetrax tetrax* [L.]), the lesser kestrel (*Falco naumanni* Fleischer) and an endemic grasshopper (*Prionotropis rhodanica* Uvarov). Unique in France, La Crau has many similarities of structure and ecological processes with other Mediterranean steppes like the dehesa in Spain (three million ha), montado in Portugal (700 000 ha) and those of North Africa and the Eastern Mediterranean (Buisson & Dutoit 2006).

Human activities have considerably modified and fragmented the plain of La Crau (Etienne *et al.* 1998). The cultivation of melons and cereals from 1965 to 1985 caused a large reduction in the overall area of the steppe, from an original 60 000 ha to its present area of 10 000 ha (Römermann *et al.* 2005). In our study site (Peau de Meau) in the central part of La Crau, cultivated plots were successively abandoned between 1972 and 1985 and included in a nature reserve created in 1989. Their current vegetation structure and composition are considerably different from those of the natural steppe because of past agricultural practices, duration of cultivation and date of abandonment, and they are always floristically less species-rich than the steppe (Buisson & Dutoit 2004; Römermann *et al.* 2005). These formerly-cultivated plots are currently grazed, as the steppe has been for centuries. The recolonization of formerly-cultivated plots by steppe plants is extremely slow; after approximately 20 years of abandonment, steppe plants have colonized only a few metres

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from field margins (Buisson & Dutoit 2004; Buisson *et al.* 2006).

While the impacts of these disturbances on vegetation and on birds (Wolff *et al.* 2001, 2002) are well known in La Crau, the impacts on other groups are still poorly understood. Apart from species inventories (Bigot *et al.* 1983) and Orthoptera-focused studies, especially on *Prionotropis* (Foucart & Lecoq 1996; Foucart 1997; Foucart *et al.* 1999), there has been little interest in the disturbance ecology of insect groups in this area. Yet, insects have an important role in food webs (Paulian 1988; Gullan & Cranston 1994; Lawrence & Britton 1994) and ecosystem functioning (Lovejoy 1997). Moreover, insects are very sensitive to fine ecological changes and are thus good indicators of anthropogenic disturbances (Erwin 1997; Orgeas & Andersen 2001; Samways 2004).

Beetles (Coleoptera) represent 40% of the known world entomological diversity, and include a high proportion of rare and endangered species (Erwin 1988; Stork 1991). They occupy almost all types of habitats available and are present at all levels of food webs (Crowson 1981; Koch 1989*a*, *b*, 1992). Moreover, beetles have a high density and diversity in La Crau (Bigot *et al.* 1983; Fadda *et al.* 2004).

The effects induced by changes in land use on arthropods, and more particularly on beetles, are well known for calcareous grasslands (Morris & Rispin 1988; Eyre *et al.* 1990; Morris 2000; Woodcock *et al.* 2005). These studies emphasize the importance of vegetation structure, defined as the interplay between succession and management, in maintaining beetle diversity. However, almost all of these studies were conducted in northern Europe and/or solely on the Carabidae family, the ecology and taxonomy of which are well known (Lövei & Sunderland 1996; Raino & Niemelä 2003). Very few studies consider all beetle families or have been undertaken in the dry grasslands of the Mediterranean basin.

This study aimed to quantify the impacts of former cultivation on beetle communities, with a view to informing management of abandoned fields in the Mediterranean Basin.

METHODS

The study area

The plain of La Crau (Southern France) is the former delta of the Durance River, an approximately triangular area between the cities of Salon-de-Provence, Arles and Fos-sur-Mer (*c.* 50 km north-west of Marseille). The region has a Mediterranean climate, with long hot summers, mild winters (mean annual temperature 14°C) and maximum rainfall in spring and autumn (500 mm yr^{-1}), with marked inter-annual variation. On average, in La Crau, there are 3000 h yr^{-1} sunshine and the wind blows for 334 days yr^{-1}, notably the strong and cold northern *Mistral* wind. The substratum is an impermeable 5–40 m thick conglomerate layer, with a calcareous matrix containing a mixture of calcareous and siliceous stones, which makes groundwater inaccessible to vegetation (Devaux *et al.* 1983).

Three formerly-cultivated plots (A, B and C) were selected in the Peau de Meau Nature Reserve (43°33′E 4°50′N, altitude 10 m, area 160 ha), located in the central part of La Crau and managed only by sheep grazing. The three fields were adjacent to one large remnant patch (6500 ha) of non-cultivated steppe (Ste) in order to avoid confounding changes in plant species composition of steppe patches within the plain (Buisson *et al.* 2006). The fields were all cultivated for melons first and then for cereals (Buisson *et al.* 2006). Melon cultivation is representative of disturbances in this area (20% of the original steppe area) and in the Mediterranean Basin (Römermann *et al.* 2005). The main features of the steppe are high cover of stones deposited by the Durance River, a vegetation richness twice as high (31.1 species m^{-2}) as neighbouring formerly-cultivated plots (15.75 species m^{-2}; Römermann *et al.* 2005) and > 50% of plant biomass constituted by the perennial plants *Brachypodium retusum* and *Thymus vulgaris* (Bourelly *et al.* 1983). The plant-species list of the formerly-cultivated plots and of the steppe can be found in Buisson and Dutoit (2004) and Römermann *et al.* (2005).

Beetle sampling

In order to avoid edge effects and spatial autocorrelation, we set 11 sampling units, one each metre along a 10-metre transect, in the central zone of each of the four studied plots. Each sampling unit was composed of three pitfall traps aligned 10 m to one another (plastic containers 50-mm × 100-mm, half-filled ethylene glycol). The experimental design was that of Fadda *et al.* (2004).

In each pit, traps were changed five times over a continuous sampling period from April to November 2002 (44 sampling units, 132 traps). Adult beetle species were sorted into morpho-species (Oliver & Beattie 1996) and then identified to species or the lowest taxonomic level using the laboratory reference collection. Taxonomic nomenclature follows Fauna Europaea (2004). Species were classified into four basic functional groups, namely phytophagous, predators, saprophagous and coprophagous, based only on the imago diet.

Environmental measurements were carried out on percentages covered by *Brachypodium retusum*, *Thymus vulgaris*, stones and 'other' (bare ground and annual plants) in 1-m × 1-m quadrats, each with a trap at its centre. Measured variables had very low annual and seasonal variations (Bourrelly *et al.* 1983) and can be considered as constant over the sampling period. *Brachypodium*, *Thymus* and stones were the most important factors for vegetation structure in the steppe (Buisson *et al.* 2006).

Analyses

All statistical treatments (except the Spearman rank tests) were based on the 44 sampling units: all five traps sampled at the same spot at the five sampling dates were summed and the three traps of each sampling unit were also summed (Fadda *et al.* 2004).

To describe beetle composition in the steppe and in the formerly-cultivated plots, correspondence analyses (CAs) using Canoco 4.5 were performed on the [sampling units × species] matrix. Evenness (E; Barbault 1992) was calculated on the data of each of the four plots, and beta diversity or differences in species composition were analysed using Sørensen (presence/absence data) and Steinhaus (abundance data, measured as the density of each species) indexes (Legendre & Legendre 1998). The Steinhaus index was calculated using the formula: $S_t = (2 \times \sum \min(n_{i1}; n_{i2}))/(n_1 + n_2)$, where n_{i1} and n_{i2} = abundances of species i in plots 1 and 2, respectively, and n_1 and n_2 = total beetle abundance of plots 1 and 2 respectively; diversity is compared in between plot 1 and 2. Kruskall-Wallis tests, followed by Mann-U Whitney tests (R Statistical Computing version 2.0.1.; The R Project 2005) were carried out on abundance and richness data after testing for normality and variance homogeneity. Finally, the correlations between abundance and environmental data and between richness and environmental data were tested with non-parametric Spearman rank tests (Statistica version 6.0; Statsoft 2004). This was done for the 33 traps of the steppe only as the measured variables were mainly representative of the steppe (% cover of perennial species and % cover of stones).

RESULTS

A total of 3890 individuals belonging to 36 families and 144 species were captured (see Supplementary material at http://www.ncl.ac.uk/icef/EC_Supplement.htm, Appendix 1). The dominant species were *Poecilus sericeus* Fisher von Apfelbeck (Carabidae 1401 individuals, 36% of total abundance), *Asida sericea* (Olivier) (Tenebrionidae, 461 individuals, 11.9%) and *Sepedophilus immaculatus* (Stephens) (Staphylinidae, 317 individuals, 8.1%). The abundances of all 141 other species did not exceed 44%. On plot A, 628 individuals were captured in total, which was less than on B, C and Ste (respectively 1134, 1034 and 1094 individuals). However, it was on plot A that the highest species richness was found (89 species in total), followed by B, C and Ste (81, 77 and 65 species) (Kruskal-Wallis: abundance $\chi^2 = 21.2974$, df = 3, $p < 0.001$; richness $\chi^2 = 13.2146$, df = 3, $p < 0.005$). Plot A had the lowest abundance of all plots and steppe (Ste) the lowest species richness (Fig. 1; Table 1).

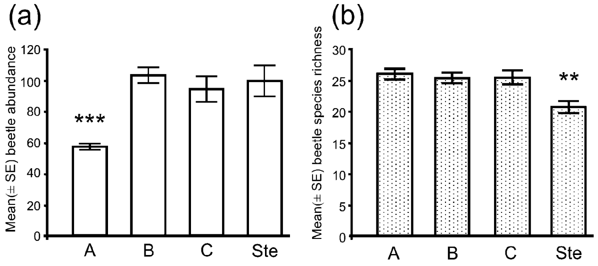

Figure 1 Mean (± SE) (*a*) abundance and (*b*) species richness of beetles per sampling unit for each plot. $^{***}p < 0.001$; $^{**}p < 0.01$.

Table 1 Results of Mann Whitney tests on abundance and richness data for formerly-cultivated plots A, B and C and steppe (Ste). $^{**}p < 0.01$; $^{***}p < 0.001$, ns = not significant.

	A		*B*		*C*	
	U	*p*	*U*	*p*	*U*	*p*
Abundance						
B	0	***				
C	1.5	***	83	ns		
Ste	2.5	***	78.5	ns	56.6	ns
Richness						
B	69	ns				
C	76	ns	65	ns		
Ste	108.5	**	101	**	101.5	**

Plot A had the highest richness of phytophagous species (38 species). All formerly-cultivated plots had a higher richness of predators and saprophagous species than the steppe (Fig. 2).

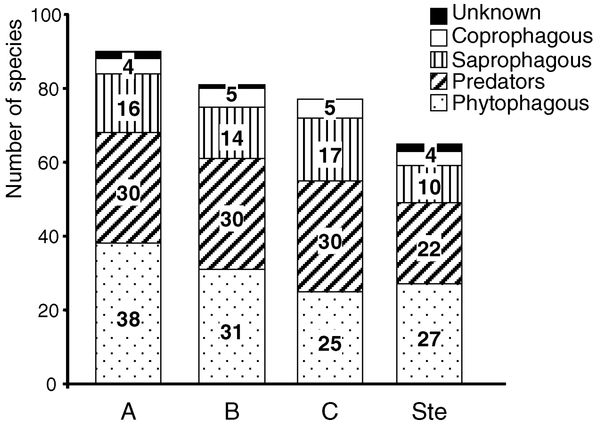

Figure 2 Richness of each functional group of species in each plot, A, B and C = formerly-cultivated plots and Ste = steppe. Values for 'Unknown' group are not indicated.

Axis 1 of the CA (10.7%) separated plot A, which was associated with species such as *Harpalus dimidiatus*, *Coccinella septempunctata* and *Aphthona cyparissiae*, from plot B and from both plot C and Ste (Fig. 3). Axis 2 (6.7%) separated Ste, which was associated with species such as *Harpalus sulphuripes*, *Pseudocleonus cinereus* and *Longitarsus obliteratoides*, from plots B and C. The two-dimensional space covered by the steppe plot was much smaller in area compared to the former-cultivated plots, especially plot A (Fig. 3), thus showing that the steppe has a more homogeneous species distribution.

Plot A had the highest evenness ($E_A = 0.79$) compared to other plots (B 0.63, C 0.59 and Ste 0.54). For both the Sørensen (Table 2) and the Steinhaus indexes (Table 3), the plots that were the most different from each other were Ste and plot A. Plots A and C had the highest Sorensen index, and Ste and C had the highest Steinhaus index (Tables 2 and 3).

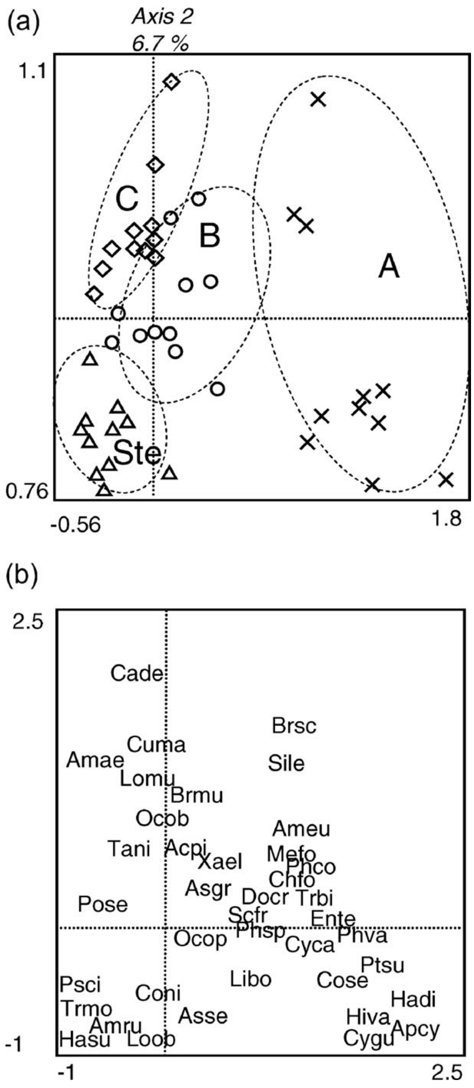

Figure 3 Correspondence analysis ordination of (*a*) 44 sampling units (× = the sampling units of formerly-cultivated plot A, ○ = B, ◇ = C and △ = Ste) and (*b*) 144 beetle species, only species contributing >14% (i.e. 39 species) included. Species abbreviations: Acpi = *Acinopus picipes*, Amae = *Amara aenea*, Ameu = *Amara eurynota*, Amru = *Amphimallon ruficorne*, Apcy = *Aphtona cyparissiae*, Asgr = *Astenus gracilis*, Asse = *Asida sericea*, Brmu = *Brachycerus muricatus*, Brsc = *Brachinus sclopeta*, Cade = *Cartodere delamarei*, Chfo = *Cholovocera formicaria*, Coni = *Coniocleonus nigrosuturatus*, Cose = *Coccinella septempunctata*, Cuma = *Curimopsis maritima*, Cyca = *Cycloderes canescens*, Cygu = *Cycloderes guinardi*, Docr = *Donus crinitus*, Ente = *Endomia tenuicollis*, Hadi = *Harpalus dimidiatus*, Hasu = *Harpalus sulphuripes*, Hiva = *Hippodamia variegata*, Libo = *Limobium borealis*, Lomu = *Lobrathium multipunctatum*, Loob = *Longitarsus obliteratoides*, Mefo = *Merophysia formicaria*, Ocob = *Ocypus obscuroaenus schatzmayeri*, Ocop = *Ocypus ophtalmicus*, Phco = *Phalacrus corruscus*, Phsp = *Phrydiuchus spilmani*, Phva = *Phyllotreta variipennis*, Pose = *Poecilus sericeus*, Psci = *Pseudocleonus cinereus*, Ptsu = *Ptomaphagus subvillosus*, Scfr = *Scymnus frontalis*, Sile = *Sitona lepidus*, Tani = *Tachyporus nitidulus*, Trbi = *Trachyphloeus bifoveolatus*, Trmo = *Trachyploeus monspeliensis* and Xael = *Xantholinus elegans*.

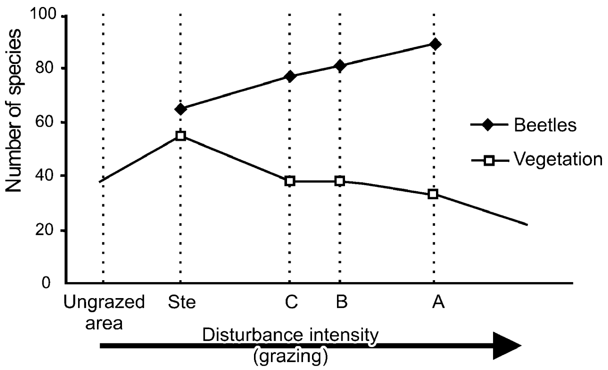

Figure 4 Comparison of observed species richness of beetles and vegetation (Buisson & Dutoit 2004; Römermann *et al.* 2005) in each studied plot ordered by increasing disturbance intensity (grazing pressure). A, B and C = formerly-cultivated plots and Ste = steppe. The vegetation trends for extreme disturbance intensities are extrapolated from the literature (Bonet 2004; Peco *et al.* 2006).

Table 2 Sorensen similarity index between formerly-cultivated plots (A, B and C) and steppe (Ste).

	A	*B*	*C*	*Ste*
A	1	0.55	0.68	0.52
B		1	0.63	0.59
C			1	0.58
Ste				1

Table 3 Steinhaus similarity index values between formerly-cultivated plots (A, B, C) and steppe (Ste).

	A	*B*	*C*	*Ste*
A	1	0.51	0.44	0.36
B		1	0.64	0.64
C			1	0.69
Ste				1

Beetle species richness decreased as *Brachypodium* per cent cover increased in the steppe ($R_s = -0.39$, $p < 0.05$). Other measured variables did not correlate with beetle abundance or richness.

DISCUSSION

The steppe

The steppe has been maintained by recurrent grazing during the last 3000 years (Badan *et al.* 1995); half of the vegetation biomass consists of *Brachypodium retusum* (Bourelly *et al.* 1983). The Spearman rank tests indicated that this Poaceae cover has negative effects on beetle richness. High leaf contents of cellulose and silica (Cherel 1988; Buisson 2005) may lower the nutritional quality of this plant for beetles (Tscharntke & Greiler 1995). In La Crau, *Brachypodium* produces few flowers and fruits since most of its ears are eaten by sheep (Cherel 1988), reducing food resources for beetles still further. This is illustrated by the low numbers of the common ground beetle *Acinopus picipes*, a granivorous species feeding on Poaceae seeds; only three specimens, out of a total of 85, were found in the steppe. Moreover, *Brachypodium* is not the most palatable species for sheep (Cherel 1988), which means that other plant species are more intensively grazed (Römermann *et al.* 2005), again lowering food resources for beetles.

The other plant species of the steppe are mainly therophytes (50%), hemicryptophytes (25%) and geophytes (5%) that all have a modified phenology, developing earlier or later in the season than elsewhere, and have a reduced vegetative part (Bourelly *et al.* 1983). These adaptations to grazing and drought contribute to reduced food resources and may explain the lower beetle diversity in the steppe. However, some species have succeeded in using available resources. The lower beetle species evenness of the steppe showed that a small number of species account for the majority of beetle abundance. Conversely, the vegetation evenness of the steppe is higher than that of the formerly-cultivated plots (Römermann *et al.* 2005), indicating a better species distribution in steppe plant assemblages. The beetle assemblages thus seem to be more sensitive to age-old disturbances, such as grazing in the steppe, than vegetation.

The beetle assemblages were more typical of oligotrophic and arid dry grassland biotopes. The curculionid *Coniocleonus nigrosuturatus* and the chrysomelid *Longitarsus obliteratoides* are *Thymus*-associated species, while the carabid *Harpalus sulphuripes*, tenebrionid *Asida sericea* and *Bioplanes meridionalis* and the curculionid *Pseudocleonus cinereus* are found on calcareous, dry and arid grassland (Hoffmann 1950; Caillol 1954; Thérond 1976).

Formerly-cultivated plots

The richer beetle assemblages in the formerly-cultivated plots than in the steppe can be partly explained by the fact that the vegetation of these plots is mainly composed of more ruderal species (*sensu* Grime 2001). Most of these plants are pioneer species, whose short lifespan is devoted to fast and efficient growth leading to high seed production (Grime 2001), and are thus an attractive food source for insects (Fraser & Grime 1999). Therefore, the formerly-cultivated plots represent a more attractive food source than the steppe, which could also explain the presence of some phytophagous beetle species such as the generalists *Longitarsus succineus* and *Acinopus picipes*, the Geraniaceae-specialized *Limobius borealis* or plantain-specialized *Cycloderes guinardi*. In addition, more predatory beetle species, such as the Coccinellidae, Carabidae and Staphylinidae, were found in the formerly-cultivated plots. This is supported by the occurrence of the coccinellids *Coccinella septempunctata* and *Hippodamia variegata*, both found only in the formerly-cultivated plots. Since these two species feed exclusively on aphids, which are phytophagous sap-suckers, they may indirectly indicate that aphids are much more abundant on formerly-cultivated plots (Magagula & Samways 2001) because of the higher nutritional value of plants.

Past ploughing has modified the soil granulometry and chemistry, leading to a lighter better-aerated soil with increased humidity (Römermann *et al.* 2005). These changes in the habitat may have allowed more species to shelter, since burrowing is easier in soft or moist soils. The presence of two Carabidae species associated with moist soils *Harpalus dimidiatus* and *H. distinguendus*, on formerly-cultivated plots A and C, may indicate that moisture is higher on these plots.

Plot A is also distinguishable from the others by the presence of rabbits, which selectively graze on certain species (Watt 1962), and favour repellent or toxic plants such as *Geranium* spp., *Lobularia maritima*, *Diplotaxis tenuifolia, Euphorbia cyparissias* or the spiny *Carduus tenuiflorus*. All these plant species are known to host many beetle species (Hoffmann 1950; Doguet 1994): six curculionids and three chrysomelids on *L. maritima*, at least 11 species of chrysomelid on *E. cyparissias*, three curculionids and one chrysomelid on *C. tenuiflorus*. Some of the representatives of these specialized species were found during the present study (i.e. *Aphthona cyparissiae*, *Aphthona euphorbiae*, *Phyllotreta foudrasi*, *Phyllotreta variipennis* and *Limobius borealis*). Paradoxically, plot A had the lowest plant richness compared with that of all other formerly-cultivated plots (33 species; Buisson & Dutoit 2004) and the highest beetle richness (89 species).

The whole Nature Reserve is grazed; sheep are preferentially fed on formerly-cultivated plots in spring, because of the higher nutritional value of the fallow-like vegetation (Dureau & Bonnefon 1998), and plot A is overgrazed by wild rabbit, reducing vegetation species richness (Buisson 2005). These different grazing pressures can be considered an indirect effect of past cultivations. The disturbance is null in an ungrazed steppe area, moderate on the grazed steppe (Ste), higher on cultivated plots B and C, and maximum on plot A. Thus, vegetation species richness is probably low on ungrazed steppe (Bonet 2004; Peco *et al.* 2006), higher on Ste, low on plots B and C, and at a minimum on plot A (Buisson & Dutoit 2004; Römermann *et al.* 2005; Buisson *et al.* 2006). Vegetation species richness will decline under increasing grazing pressure (Gibson *et al.* 1987). Conversely, beetle species diversity increased along the increasing disturbance gradient and was thus higher at the highest disturbance level, which led to the lowest plant species richness. These findings are similar to those of other studies of beetles (Niemelä *et al.* 2002; Magura *et al.* 2004), where species richness was not highest in the moderately disturbed area, in contrast to predictions of the intermediate disturbance hypothesis (IDH; Connell 1978). There are two potential explanations for this: (1) beetle data do not follow the IDH, or (2) beetle data follow the IDH, but for a similar level of disturbance, there is a difference in the responses of plant and beetle communities; plant species richness reacts to lower levels of disturbance and beetle species richness will eventually decrease at levels of disturbance higher than observed in this study (Fig. 4).

CONCLUSIONS: CONSEQUENCES FOR THE MANAGEMENT OF STEPPES AND FUTURE STUDIES

More than 20 years after abandonment, the formerly-cultivated plots had beetle communities with composition and structure that still differed from those of the steppe. If we consider only species richness, former cultivation practices seem to have a positive effect on beetle communities, since their diversity increased; formerly-cultivated plots hosted different beetle communities that were always richer than the adjacent steppe plot. These results are unexpected, since a reverse effect on the vegetation was recorded. Even if the steppe is less species rich, its beetle community is more characteristic of oligotrophic and dry grasslands and, like the vegetation, constitutes a threatened original assemblage. In addition, among all the collected species, 16 can be considered as having a particular biological value (See Supplementary material at http://www.ncl.ac.uk/icef/EC_Supplement.htm, Appendix 1), because they are rare, their distribution area is limited, they are endemic or their ecology is poorly known (Hoffmann 1950; Caillol 1954; Thérond 1975, 1976; Villiers 1978; Paulian & Baraud 1982). While the present data cannot quantify the impact of past cultivation on these species, as they were found in both steppe and formerly-cultivated plots, on-going studies in this area suggest that they are more dependent on steppe habitat (S. Fadda, unpublished data).

Conservationists need to decide whether they would rather maintain species diversity, with more common species in the assemblage, or maintain biological value, with the original assemblage including rare and endemic species. As it is, the mosaic constituted by the formerly-cultivated plots and the natural steppe favours high beetle diversity, but remaining areas of uncultivated steppe should be protected in order to preserve typical steppe species.

Contrasting the impacts of disturbance on vegetation and beetles highlights the importance of studying more than one group to assess ecosystem effects of a disturbance. Moreover, in the study of dry Mediterranean ecosystems, it seems to be more pertinent to consider all beetle families instead of considering only Carabidae or predators. Compared to other studies with similar sampling methods carried out on Carabidae alone in northern grasslands and agricultural fields or degraded fields (Luff 1996; Desender & Bosmans 1998; Eyre *et al.* 2003), 19 is a very low number of species of Carabidae. Here, although Carabidae were the most abundant mainly owing to one species, *P. sericeus*, Staphylinidae and Curculionidae contributed more to the overall species richness.

Sheep grazing has been the traditional land use for several centuries and thus the main disturbance within the system. It is the only management advocated to maintain the steppe (Buisson & Dutoit 2006), but has been based only on vegetation studies. Effects of grazing on vegetation are well known for Northern (Hansson & Fogelfors 2000; Moog *et al.* 2000) and Southern Europe (Sternberg *et al.* 2000) as well as those on some invertebrate groups for Northern Europe (Morris 2000). Except for dung beetles (Verdù *et al.* 2000), few data are available on the impact of grazing on the entomofauna of Mediterranean herbaceous ecosystems. Further studies should now be carried out on the effects of various grazing rates on all beetles and other invertebrates.

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