

Conservation of grassland patches failed to enhance colonization of ground-active beetles on formerly cultivated plots

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SUMMARY

The dry grasslands of the Mediterranean Basin have been traditionally managed since ancient times, but have been drastically degraded by recent human activities such as cultivation. Cultivated plots in a dry grassland of Southern France were abandoned more than 20 years ago, but their vegetation and ground-active beetle community structure and composition differ considerably from neighbouring uncultivated grassland plots. Because these formerly cultivated plots are adjacent to an uncultivated grassland area, they constitute a model system for examining beetle recolonization patterns on field margins. No edge effect or ecotone was identified on the margins between two of the formerly cultivated plots and the uncultivated dry grassland; there was no significant peak of beetle species richness in this area. All the most common dry grassland beetle species (mainly saprophagous and predatory species, which are less habitat-specialist than phytophagous species) had already recolonized the formerly cultivated plots. However, although uncultivated dry grassland was adjacent to the formerly cultivated plots it was insufficient for complete regeneration of dry grassland beetle communities on formerly cultivated plots, indicating habitat quality remained lower even after 20 years. Understanding the causes of spatial variation in active-ground beetles at the species level is important before the ecological restoration of habitat quality to its prior state, using the adjacent steppe as a reference.

Keywords: Coleoptera, disturbance, ecocline, ecotone, edge effect, field boundary, Mediterranean grassland, resilience

INTRODUCTION

Herbaceous ecosystems dominated by therophytous, geophytous, hemicryptophytous and chaemephytous species (Poaceae) < 1 m in height (Lacoste & Salanon 1969;

Ozenda 1995), represent more than 25% of the Earth's landscapes (Henwood 1998), and are both flora and fauna rich habitats. In the Mediterranean Basin, from Turkey to Spain and Northern Morocco, herbaceous ecosystems are species-rich steppe formations (Buisson *et al.* 2004) generally found on oligotrophic soils, having evolved through extensive traditional human management for centuries and/or millennia (Quézel & Médail 2003). More recently, herbaceous ecosystems have drastically reduced in extent throughout the world (Jacobs *et al.* 1999), particularly in the Mediterranean basin, owing to housing and industrial development and cultivation intensification (Willems & Bic 1998; Poschold & WallisDeVries 2002; Dutoit *et al.* 2003). While much is known about the effects of agricultural changes on vegetation (in Mediterranean ecosystems: Grove & Rackham 2001; Römermann *et al.* 2005; elsewhere: Austrheim & Olsson 1999[0]) and spontaneous regeneration after abandonment (in Mediterranean ecosystems: Bonet 2004; elsewhere: Wells *et al.* 1976), very few studies have focused on insect communities, particularly their regeneration after land-use changes (Good 1999; Moretti *et al.* 2006; Woodcock *et al.* 2008).

In most areas, remaining dry grassland fragments occur as islands in a sea of intensively farmed or industrialized land. Remnant patches of semi-natural ecosystems constitute a potential source of species for the colonization of abandoned plots, particularly if they are adjacent to one another (Hendrickx *et al.* 2007). Plant and animal colonization processes on the margins of abandoned plots adjacent to remnant patches of undisturbed vegetation need to be studied (Wilson & Aebischer 1995), particularly in Mediterranean and dry areas, where drought greatly slows recovery processes (Blondel & Aronson 1999; Buisson *et al.* 2006; Fadda *et al.* 2007). Colonization processes on field margins are highly dependent on the degree of isolation of the plot, surrounding land uses and the dispersal ability of concerned species (Hendrickx *et al.* 2007). There is little information on the dispersal ability of dry grassland Coleoptera onto former arable fields (Mortimer *et al.* 2002). In large winter cereal fields, diversity and density of carabids decrease from the boundary habitat towards the field interior (Saska *et al.* 2007), but other field types are unstudied and the relationship between field margins and fallow-lands established after crop abandonment is unknown.

Beetles (Coleoptera) are important in successional studies because they represent 40% of the known world insect

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diversity, include a high proportion of rare or endangered species (Erwin 1988; Stork 1991) and occupy almost all types of available habitats and all trophic levels (Crowson 1981; Koch 1989*a, b*, 1992). Moreover, insect communities are very sensitive to ecological changes (Eyre *et al.* 1986) and are thus good indicators of anthropogenic disturbances (Erwin 1997; Orgeas & Andersen 2001; Sieren & Fischer 2002) and of restoration and management success (Mortimer *et al.* 1998).

In the plain of La Crau in southern France (12 000 ha), climate, edaphic constraints and traditional extensive sheep grazing since the Neolithic period (7000 BP) have contributed to the formation of a Mediterranean steppe ecosystem. Human activities considerably modified and fragmented this area (Etienne *et al.* 1998) in the 20th century. This area is a good site at which to study the impacts of land-use changes because the cultivation of melons and cereals from 1965 to 1985 reduced the overall area of the steppe by 1500 ha (to 10 500 ha) (Römermann *et al.* 2005). La Crau is the only steppe ecosystem in France and has many similarities in structure and ecological processes to other Mediterranean steppe-like formations, such as the herbaceous component of *dehesas* in Spain (3 million ha), the herbaceous component of *montados* in Portugal (700 000 ha) and other steppes of North Africa and the Eastern Mediterranean (Grove & Rackham 2001).

In the Nature Reserve of Peau de Meau (160 ha), in the central part of La Crau, cultivated plots were successively abandoned between 1972 and 1985. The current structure and composition of the vegetation which colonized the field after abandonment differ considerably from those of the semi-natural steppe, being mainly composed of ruderal species and consistently poorer in species than the steppe (Buisson & Dutoit 2004; Römermann *et al.* 2005). Steppe vegetation recolonization on the margins of formerly cultivated plots is extremely slow; > 20 years after abandonment, less than 60% of steppe plant species had colonized only a few metres on plot margins (Buisson *et al.* 2006). Ground-active beetle community composition and structure have also been modified in the centre of these formerly cultivated plots (Fadda *et al.* 2007).

With the goal of understanding spatial colonization processes on field margins, this paper aims to determine whether notable changes in the composition, richness and diversity of ground-active beetle communities are observable on the margins of degraded areas adjacent to a large area of semi-natural steppe (6500 ha). We consider recolonization patterns and their implications for the biological management and/or ecological restoration of formerly cultivated plots.

MATERIAL AND METHODS

The study area

The plain of La Crau (Southern France) is the former delta of the Durance River, *c.* 50 km north-west of Marseille. The region has a Mediterranean climate, with long hot summers, mild winters (mean annual temperature 15 °C) and maximal

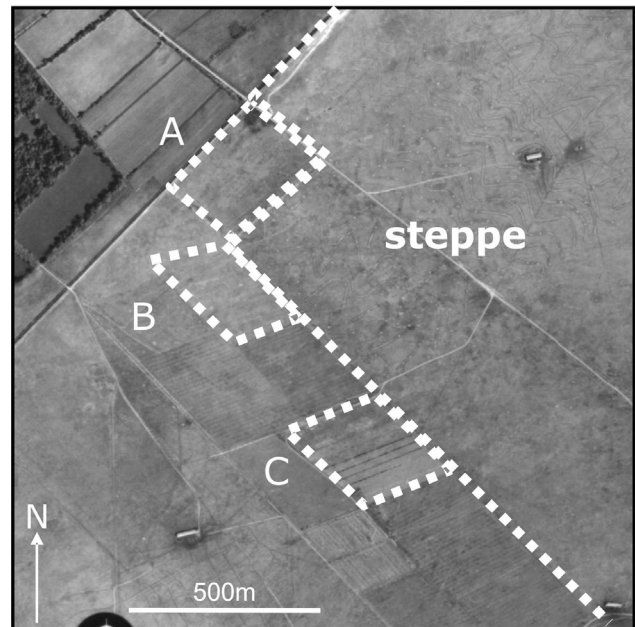


Figure 1 Aerial photograph (Institut Geographique National [France] 1986) of Nature Reserve Peau de Meau with location of the three formerly cultivated plots A, B and C and the steppe.

rainfall in spring and autumn (550 mm per year), with marked interannual variation (see Buisson & Dutoit 2006 for details). The substratum is 5–40 m thick; at the top of this layer is an impermeable conglomerate composed of a calcareous matrix and a mixture of calcareous and silicious stones, which makes groundwater inaccessible to the vegetation (Devaux *et al.* 1983). Grazing maintains the vegetation as a steppe formation, which is currently overgrazed. This steppe hosts a species-rich vegetation characterized by both calcicolous and silicicolous plant species, including locally rare species (Devaux *et al.* 1983).

Three formerly cultivated plots (A, B and C) each *c.* 5 ha in area were selected within the Nature Reserve of Peau de Meau (43° 33' E, 4° 50' N), located in the central part of La Crau. The three plots were adjacent to one large remnant patch (6500 ha) of uncultivated steppe (Fig. 1) in order to avoid confounding changes in plant species composition of steppe patches within the plain (Devaux *et al.* 1983). All plots were currently managed by sheep grazing only. The plots were all cultivated for melons first and then for cereals (see details in Buisson & Dutoit 2004). These types of cultivation are representative of disturbances in this area (20% of the original steppe area) and in the Mediterranean basin as a whole (Römermann *et al.* 2005).

Sampling

Beetles were sampled on the margin of each formerly cultivated plot on three 10 m long transects, set perpendicular to the plot boundary with the steppe and 10 m distant

from each other (see Buisson *et al.* 2006 for details on this experimental set-up). Along these transects, 11 pitfall traps (50 mm × 110 mm plastic containers, half-filled with preservative liquid glycol) were buried flush with the soil surface one metre apart (i.e. 99 traps, 33 per abandoned plot).

The sampling was continuous throughout 204 days April–November 2001, traps being checked and replaced 13 times. Adult beetle species were sorted to morphospecies (Oliver & Beattie 1996) and then identified to species or the closest taxonomic level using the laboratory reference collection. Taxonomic nomenclature followed Fauna Europea (2004). Environmental variables measured included vegetation richness, per cent cover of the dominant steppe plant species *Brachypodium retusum* (Pers.) P. Beauv (Poaceae) and *Thymus vulgaris* L. (Lamiaceae), and per cent cover of stones, bare ground and vegetation in the area surrounding each trap (10 sub-quadrats of 40 cm × 40 cm).

Statistical analysis

We summed all traps sampled at the same spot across all sampling dates. In order to compare the three formerly cultivated plots, we summed the three traps located at the same distance from the boundary for each plot (resulting in a global reduced matrix [33 samples × all species]; based on Fadda *et al.* 2007).

We performed detrended correspondence analysis (DCA) applying the ‘down-weighting of rare species’ option (Canoco 4.5) on this global reduced matrix in order to describe the beetle composition of the formerly cultivated plots. We undertook Kruskal–Wallis tests followed by Mann–Whitney U tests (Statistica 6.0; Statsoft France 2004) on abundance and richness data.

In order to analyse differences with distance from boundaries, each formerly cultivated plot was considered separately, resulting in three matrices [33 traps × species of formerly cultivated plot]. We performed three canonical correspondence analyses applying the ‘down-weighting of rare species’ option (Canoco 4.5) with environmental measurements as covariables. We carried out Kruskal–Wallis tests on abundance and richness data among distances. We compared abundances of the species having a total abundance ≥ 20 among distances from the edge. Then we verified whether any species progressively appeared or disappeared along the distance gradient from the steppe boundary. We tested changes with Spearman rank tests for each formerly cultivated plot, relative abundances with distance (Statistica 6.0; Statsoft France 2004).

We analysed differences in species composition between the steppe and the three formerly cultivated plots with the Sørensen index (presence/absence data) using the $2j/(R_1 + R_2)$ formula, where R_1 and R_2 are species richness in compared areas 1 and 2, and j is the number of species occurring in both areas 1 and 2 (Legendre & Legendre 1998). We calculated the Sørensen indexes for each distance from the boundaries and for each formerly cultivated plot and compared with reference

species lists (Fadda *et al.* 2007) from the centre of the steppe and from the centre of each formerly cultivated plot. We tested changes with increasing distance with Spearman rank tests (Statistica 6.0; Statsoft France 2004).

RESULTS

A total of 2305 individuals belonging to 32 families and 126 species were captured (Appendix 1, see Supplementary material at URL http://www.ncl.ac.uk/icef/EC_Supplement.htm). The dominant species were *Asida sericea* (Olivier) (Tenebrionidae, 1100 individuals, 47.7% of total abundance) and *Longitarsus succineus* (Chrysomelidae (Foudras) 142 individuals, 6.1% of total abundance). Only 17 species had an abundance ≥ 20 (*Acinopus picipes* (Olivier), *Dinodes decipens* (L. Dufour), *Poecilus sericeus* Fischer von Waldheim [Carabidae]; *Protaetia oblonga* (Gory & Percheron) [Cetoniidae]; *Dibolia cryptocephala* (Koch), *Longitarsus obliteratoides* Gruev, *Longitarsus succineus* (Foudras), *Timarcha tenebricosa* (Fabricius) [Chrysomelidae]; *Scymnus frontalis* (Fabricius) [Coccinellidae]; *Coniocleonus nigrosuturatus* (Goeze), *Pseudocleonus cinereus* (Panzer) [Curculionidae]; *Ptomaphagus sericatus* (Chaudoir) [Leiodidae]; *Pelochrus pallidulus* (Erichson) [Malachiidae]; *Onthophagus emarginatus* Mulsant & Godart, *Onthophagus furcatus* (Fabricius) [Scarabaeidae]; *Ocyopus ophthalmicus* (Scopoli) [Staphylinidae] and *Asida sericea* (Olivier) [Tenebrionidae]).

In plot A, 628 individuals were captured in total, which was significantly less than on plots B or C, with respectively 823 and 830 individuals captured (Table 1). However, plot A had greater species richness (89 species) than B (81 species) or C (77 species) (Fig. 2; Table 1). Of the 39 species found in all three formerly cultivated plot margins, 30 were found in the steppe (Fadda *et al.* 2007). Plot C had the greatest vegetation species richness and plot A the lowest (Fig. 2; Table 1).

Axes 1 and 2 of the DCA of the reduced matrix (28.4%) discriminated among the three plots (Fig. 3). Axis 1 also separated the points of plot A further from the boundary (8, 9 and 10 m) from those closer to the boundary. There were no significant peaks or consistent increases or decreases in total

Table 1 Results of Mann–Whitney tests on beetle abundance, beetle richness and vegetation richness data for formerly cultivated plots A, B and C (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant).

		A		B	
		U	p	U	p
Abundances	B	11.5	**		
	C	28.5	*	57.0	ns
Beetle species richness	B	48.5	ns		
	C	30.5	*	39.5	ns
Vegetation richness	B	229.5	***		
	C	175.0	***	383.5	***

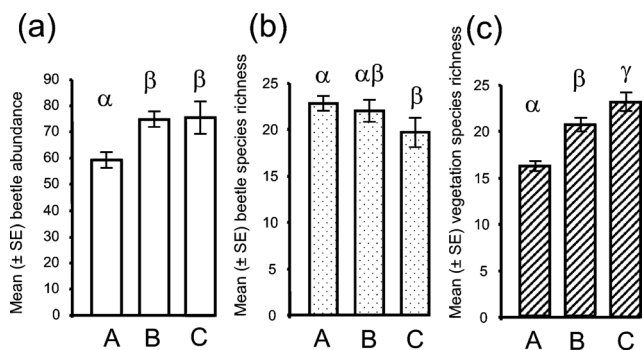


Figure 2 Mean (\pm SE) (a) abundance, (b) species richness of beetles ($n = 11$) and (c) vegetation richness per 4 m² plot (α , β and γ indicate similar groupings based on Mann-Whitney U tests).

beetle abundance or species richness with increasing distance from boundaries on any of the three plots (Fig. 4).

In plot A exclusively, axis 1 of the CCA (32.1%, Fig. 5) discriminated points closer to the boundary, with species such as *Conioleonus nigrosuturatus*, *Dinodes decipens* and *Asida sericea*, correlated with higher *Brachypodium* and *Thymus* cover, from points further from the boundary (8, 9 and 10 m), with species such as *Acinopus picipes*, *Microlestes luctuosus* Holdhaus in Apfelbeck (Carabidae) and *Atheta* sp. (Staphylinidae). Sørensen indices indicating similarity with steppe species decreased with distance from the boundary ($R = -0.78$; $p < 0.01$). Out of all species having an abundance ≥ 20 , only *Acinopus picipes* abundances significantly increased with increasing distance from the boundary ($R = 0.54$; $p < 0.01$; Fig. 6).

DISCUSSION

To develop recommendations for the biological management and/or ecological restoration of former cultivated plots, we studied the spatial colonization processes of beetles on field margins. We found that distance from boundaries did not have any consistent influence on abundance, richness or diversity of beetles on any plot. Margins thus neither possessed an edge effect (Odum 1971; Yahner 1988) where beetle species richness would be greater than those of the two adjacent ecosystems (Magura *et al.* 2001; Magura 2002), nor constituted an ecotone (Frochot 1987) where beetle species not found in the two adjacent ecosystems would appear (Asteraki *et al.* 1995). We were unable to identify any pattern of ground beetle communities on the margins (as observed by Kotze & Samways 2001) in plots B and C.

However, we also found that, for plot A alone, beetle composition changed with distance. The composition of the beetle community seemed to be more similar to that of the steppe closer to the boundary than that further away. As no loss or gain of species was observed, many steppe species disappeared (for example *Conioleonus nigrosuturatus* and *Biopanes meridionalis*) and were replaced by species more typical of formerly cultivated plots (for example

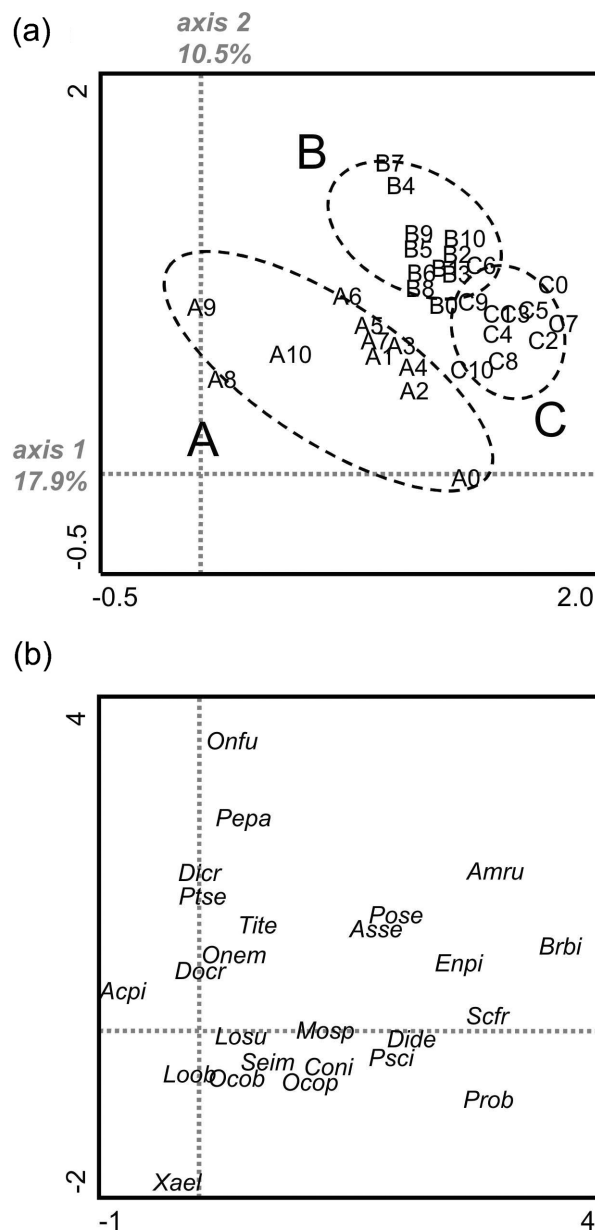


Figure 3 Detrended correspondence analysis ordinations of (a) samples (3-summed-traps), where numbers correspond to distance from boundary, and (b) beetle species where only species contributing more than 1% (i.e. 25 species) are included. Species abbreviations: Acpi = *Acinopus picipes*, Amru = *Amphimallon ruficorne*, Asse = *Asida sericea*, Brbi = *Bruchidius bimaculatus*, Coni = *Conioleonus nigrosuturatus*, Docr = *Donus crinitus*, Enpi = *Enicopus pilosus*, Loob = *Longitarsus obliteratoides*, Losu = *Longitarsus succineus*, Mosp = Mordellidae (G. sp.), Ocop = *Ocypus ophthalmicus*, Onme = *Onthophagus emarginatus*, Onfu = *Onthophagus furcatus*, Pepa = *Pelochrus pallidulus*, Pose = *Poecilus sericeus*, Prob = *Protaecia oblonga*, Psci = *Pseudocleonus cinereus*, Ptse = *Ptomaphagus sericatus*, Scfr = *Scymnus frontalis*, Seim = *Sepedophilus immaculatus*, Tite = *Timarcha tenebricosa* and Xael = *Xantholinus elegans*.

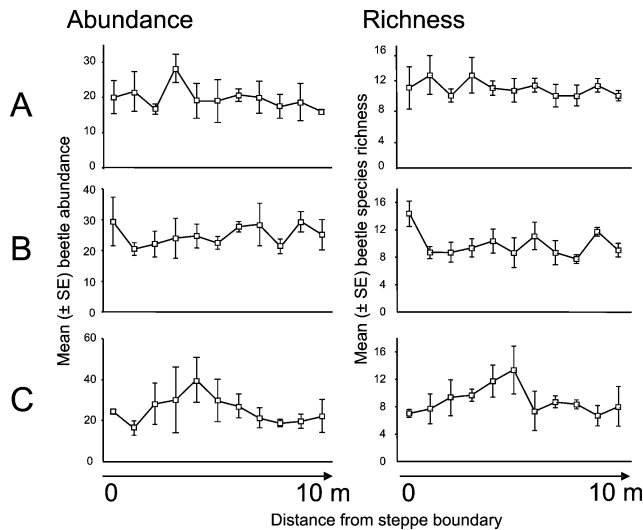


Figure 4 Plots of mean (± SE) abundances and richness against distance from boundaries for each formerly cultivated plot.

Endomia tenuicolis, *Cordicomus instabilis* or *Acinopus picipes*) with increasing distance. This margin therefore constituted an ecocline, defined as a gradient of progressive species appearances and disappearances (Van der Maarel 1976; Gourov *et al.* 1999a, b; Dutoit *et al.* 2007). This ecocline is attributable to changes in plant species composition with increasing distance from boundaries; the plot A margin was characterized by the most visible gradient of *T. vulgaris* and *B. retusum*, mainly found 0–2 m from the boundary. Moreover, a complete study of the vegetation has shown that steppe species progressively disappear with increasing distance from the boundary while arable weeds become more common (Buisson *et al.* 2006). Arable weeds are attractive for beetles (Fadda *et al.* 2007), as they provide food (seeds, herbivorous insects or invertebrates) and may act as a sink (Saska *et al.* 2007) for nearby steppe beetle species. Since the steppe and formerly cultivated plots are grazed, the vegetation gradient may be due to a grazing gradient (Woodcock *et al.* 2005a). Plot A and the steppe do not belong to the same owner, resulting in a less grazed area at their boundary because shepherds modify the sheep access route to avoid grazing on their neighbour’s land (Fig. 7) and this leads to a gradient of sheep grazing pressure (Dureau & Bonnefon 1998).

We also noted that the margin of the plot with the lowest vegetation richness (plot A; Buisson *et al.* 2006) had the highest beetle species richness of all three plots. Conversely, the margin of the plot with the highest vegetation richness (plot C) had the lowest beetle species richness. These results differ from observations in Northern Europe grasslands of a positive relationship between vegetation richness and beetle species richness (Buse 1988). In this study, vegetation richness could not be the factor explaining beetle species richness, supporting the importance of vegetation composition (Perner *et al.* 2005; Woodcock *et al.* 2005a; Fadda *et al.* 2007).

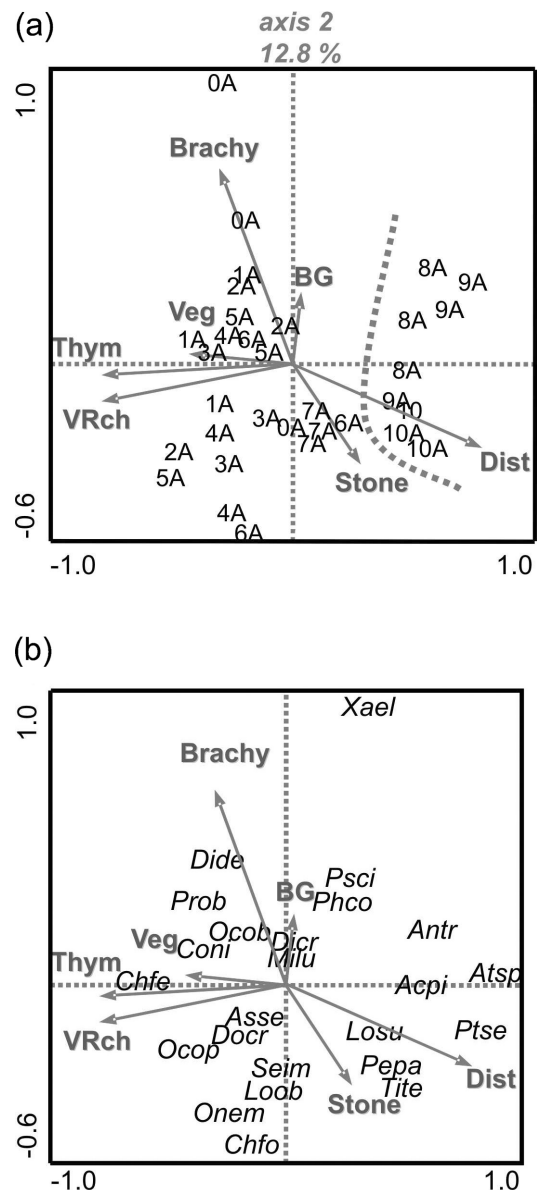


Figure 5 Canonical correspondence analysis ordination of plot A data, of (a) samples (numbers correspond to distance from boundary), and (b) beetle species (only species contributing > 1%, i.e. 25 species, are included). Species abbreviations: Acpi = *Acinopus picipes*, Antr = *Anthicus tristis*, Asse = *Asida sericea*, Atsp = *Atheta* sp., Chfe = *Chrysolina femoralis*, Chfo = *Cholovocera formicaria*, Coni = *Coniocleonus nigrosuturatus*, Dicr = *Dibolia cryptocephala*, Dide = *Dinodes decipens*, Dochr = *Donus crinitus*, Loob = *Longitarsus oblitteratoides*, Losu = *Longitarsus succineus*, Milu = *Microlestes luctuosus*, Ocop = *Ocyopus ophthalmicus*, Onme = *Onthophagus emarginatus*, Pepa = *Pelochrus pallidulus*, Phco = *Phalacrus corruscus*, Prob = *Protaecia oblonga*, Ptse = *Ptomaphagus sericatus*, Seim = *Sepedophilus immaculatus*, Tite = *Timarcha tenebricosa* and Xael = *Xantholinus elegans*. Covariables: BG = % bare ground cover; Brachy = % *Brachypodium retusum* cover; Dist = Distance from steppe boundaries in m.; stone = % stone cover; Thym = % *Thymus vulgaris* cover; Veg = % cover other vegetal species; VRch = vegetation richness.

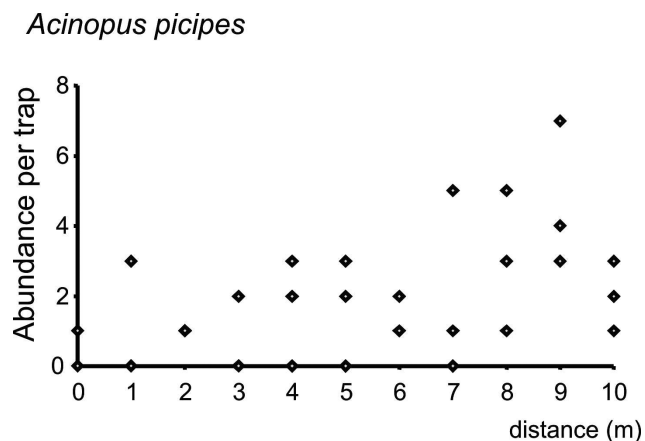


Figure 6 Plot of *Acinopus picipes* abundances against distance from steppe boundary on plot A. (Spearman $R = 0.54$; $p < 0.01$).

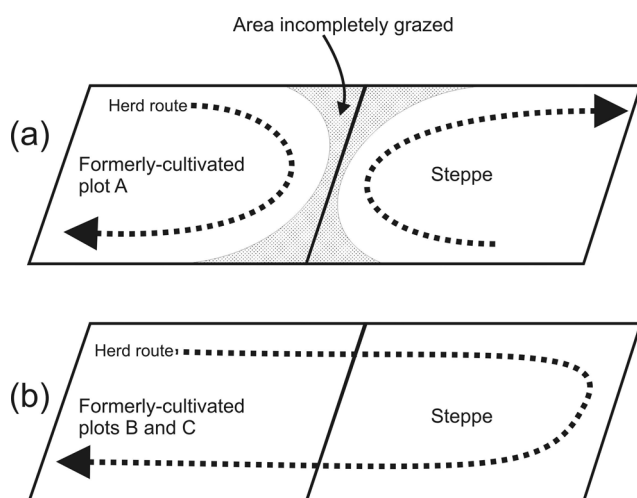


Figure 7 Impact of herd route on grazing intensity when (a) two plots belong to different owners (plot A and steppe) and (b) two plots belong to the same owner (adapted from Dureau & Bonnefon 1998).

Spontaneous colonization of beetle community

The two most abundant beetle species on the steppe were *Poecilus sericeus* and *Asida sericea* (Fadda *et al.* 2007) and these two species occurred in all formerly cultivated plots both in the centres and at the margins. These species disperse in similar ways, are brachypterous and move only along the ground, although *Poecilus* seems to be more active and move more rapidly than *Asida* (S. Fadda, personal observation 2005). As these two species do not have peaks of abundance at the margins, their populations had homogeneous densities across the whole plots whatever the vegetation composition or structure. These species may thus have recolonized the degraded plots in the early years following abandonment of cultivation. However, their abundance differed: *Asida sericea* was less abundant in all formerly cultivated plots than in the steppe and *Poecilus sericeus* was only less abundant on

plot A (Fadda *et al.* 2007). Former cultivation has modified habitats and created new conditions less favourable for these two typical steppe beetle species. Moreover, the responses of the two populations differed from one formerly cultivated plot to another, highlighting the complexity of factors influencing beetle distributions. The environmental variables we tested do not explain these differences and further studies on the influence of the landscape matrix immediately after abandonment of cultivation are necessary. The rove-beetle *Ocyrops ophthalmicus* was the only abundant species occurring in all margins and centres of formerly cultivated plots and steppe in the same proportion; changes in habitat wrought by cultivation do not seem to have affected its distribution.

Fadda *et al.* (2007) found only few individuals of many weevils (such as *Limobius borealis*, *Donus crinitus* and *Cycloderes canescens*) were found in the steppe, while they were found in greater quantity in formerly cultivated plots. They occur on the margins of formerly cultivated plots with no particular variation of abundance with distance and at the same densities as on the plots. These weevils are phytophagous insects with narrow host-plant tolerances (one plant species or genus; Hoffmann 1950, 1954), are already present in steppe and have the highest occurrence in the formerly cultivated plots (Buisson & Dutoit 2004). Formerly cultivated plots have created new habitats where a few common steppe plant species (for example *Plantago* spp., *Erodium* spp. and *Lobularia maritima*) have become established and spread, phytophagous beetles following their host-plants. In contrast, phytophagous beetles were absent when their host plants did not become established or when few individuals colonized formerly cultivated plots. Because species responded differently on margins, understanding the causes of spatial variation in active-ground beetles at the species level is important before agricultural landscape can be successfully manipulated in order to restore the functional diversity of the former arable plots.

CONCLUSIONS

More than 20 years after cultivation abandonment, all the most common steppe beetle species, mainly saprophagous and predator species, had recolonized formerly cultivated plots, albeit at a lower density than in the steppe, because they are less habitat-specialized than phytophagous species (Buse 1988). An adjacent steppe patch is insufficient for complete auto-restoration of steppe beetle communities on the formerly cultivated plots even at the margins while habitat quality remains less favourable in these modified areas, notably with respect to many abiotic factors affecting predator or saprophagous species, and vegetation structure and composition for phytophagous species (Eyre 2006).

Here, restoration measures could accelerate processes. The first possibility, as observed in plot A, would be to decrease grazing pressure on the margins between former cultivated plots and remnant patches of steppe (Fig. 7a). The aim of reorganizing grazing routes would be to create vegetation

gradients which may generate ecoclines (Woodcock *et al.* 2005a). Another option is to restore habitat quality to its prior state using the adjacent steppe as a reference, replacing the 50% stone cover removed for cultivation (Buisson 2006) and combining this stone cover restoration with varying sheep grazing levels, which influence both abiotic and biotic factors in the steppe (Bourrelly *et al.* 1983). Stone cover restoration has already been successfully used in the re-establishment of the two structuring plant species, *Brachypodium retusum* and *Thymus vulgaris*, in the absence of grazing during the initial years after plant reintroduction (Buisson 2006). Seed mixtures have already been sowed to restore Coleoptera assemblages in dry grasslands or field margins on arable farms (Mortimer *et al.* 2002; Woodcock *et al.* 2005b). However these experiments are too recent to draw definitive conclusions as to their success and, in the long-term, an appropriate grazing management regime is required to support the restoration of Coleoptera assemblages of dry grasslands (Woodcock *et al.* 2005a).

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