



Disentangling effects of habitat diversity and area on orthopteran species with contrasting mobility

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ABSTRACT

Loss of semi-natural grasslands and reduction of habitat diversity are considered major potential threats to arthropod diversity in agricultural landscapes. The main aim of this study was to investigate how area and habitat diversity, mediated by shrub encroachment after grassland abandonment, affect species richness of orthopterans in island-like grasslands, and how contrasting mobility might alter species richness response to both factors. We selected 35 isolated patches in landscapes dominated by arable land (durum wheat) in order to obtain two statistically uncorrelated gradients: (i) one in habitat area ranging from 0.2 to 55 ha and (ii) one in habitat diversity ranging from patches dominated by one habitat (either open grasslands or shrublands) to patches with a mosaic of different habitats. Habitat loss due to land-use conversion into arable fields was associated with a substantial loss of species with a positive species–area relationship (SAR), with sedentary species having a steeper and stronger SAR than mobile species. Halting habitat loss is, therefore, needed to avoid further species extinctions. Shrub encroachment, triggered by abandonment, presented a hump-shaped relationship with habitat diversity. An increase in habitat diversity enhanced species richness irrespective of patch area and mobility. Maintaining or enhancing habitat diversity, by cutting or burning small sectors and by reintroducing extensive sheep grazing into abandoned grassland, are suggested as complementary strategies to mitigate further decline of orthopteran diversity in the remnant patches. This would be equally important in both small and large patches.

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1. Introduction

Semi-natural grassland loss (Fahrig, 2003; Tschardt et al., 2002) and abandonment (Marini et al., 2009a) are key drivers of the observed declines of arthropod diversity in agricultural landscape (Stoate et al., 2009). The impact of habitat loss on species richness can be detected in positive species–area relationships (SARs) (Rosenzweig, 1995). They encapsulate the general pattern that larger patches often contain more species than smaller ones (MacArthur and Wilson, 1967). Two suggested mechanisms underpinning these relationships are the area per se and the habitat diversity hypotheses (Connor and McCoy, 1979). The former derives from the island biogeography theory and assumes that the number of species on an island represents an area-mediated equilibrium between extinction and colonisation rates (MacArthur and Wilson, 1967). The latter predicts that larger patches are more likely to contain greater habitat diversity and, therefore, more species as predicted by the niche theory (Rosenzweig, 1995).

In the last decades, there has been a continuous debate on whether area per se or habitat diversity is more important in influencing species richness on true islands or island-like habitats. On a theoretical level, the two hypotheses propose non-mutually exclusive mechanisms and several authors suggest that they are complementary (Kallimanis et al., 2008; Ricklefs and Lovette, 1999; Triantis et al., 2003, 2005). Investigations of spatial variation in species richness are often undermined by the collinearity between these explanatory variables (Johnson et al., 2003; Mac Nally and Watson, 1997) and empirical studies should therefore strive to reduce the correlation between area and habitat diversity (Kallimanis et al., 2008). The very few studies fulfilling this condition have, however, found contrasting results ranging from a dominant effect of area (Nilsson et al., 1988) to an overriding effect of habitat diversity (Báldi, 2008; Jonsson et al., 2009), or mixed effects of both (Kallimanis et al., 2008; Ricklefs and Lovette, 1999).

Recent advances in theoretical ecology have introduced the key role of dispersal limitation in shaping species–area–heterogeneity relationships (Hortal et al., 2009; Hubbell, 2001; Kadmon and Allouche, 2007; Shen et al., 2009). Varying mobility among species might affect how the community species composition shifts in response to both habitat loss (Berggren et al., 2002; Öckinger et al.,

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2009; Thomas, 2000) and habitat diversity (Kadmon and Allouche, 2007; Shen et al., 2009). The importance of immigration and recolonisation from nearby source populations after a local extinction event is likely to increase with decreasing patch size (Hanski, 1999). According to this theory, species with low mobility are predicted to be more strongly affected by reductions in habitat area as compared to more mobile species (Ewers and Didham, 2006). Clear predictions of potential complex interactions between mobility, area, and habitat diversity are still lacking (Shen et al., 2009). Recent empirical studies have found that the positive effects of habitat diversity on species numbers might be stronger in small rather than large islands (Triantis et al., 2003, 2005), while some theoretical models suggest that species with low dispersal might react negatively to increased habitat diversity in small habitats due to increasing stochastic extinctions (Kadmon and Allouche, 2007; but see Hortal et al., 2009).

The main aim of this study was to investigate (i) how area and habitat diversity, mediated by shrub encroachment after grassland abandonment, affect species richness of orthopterans in island-like habitats, and (ii) how contrasting mobility might alter species richness response to both factors. We explored these processes in isolated abandoned grasslands in intensive arable landscapes in a Mediterranean region. Shrub and tree encroachment in grasslands is expected to increase habitat diversity at the beginning of the succession but will decline as the cover of shrubs and trees gradually becomes continuous.

We focused on area and habitat diversity by selecting habitat patches such that no correlation between the two factors was achieved, and where effects of connectivity and matrix quality could be considered and maximally excluded. Specifically, we tested the complementarity of the area per se and habitat diversity hypotheses, i.e. that both area and habitat diversity should enhance species richness monotonically. Furthermore we tested the idea that mobility should modify species richness response to both factors. Firstly, mobile species were hypothesised to be less sensitive to habitat loss than sedentary species (Ewers and Didham, 2006). Secondly, because dispersal ability affects the spatial extent over which species sample the landscape and utilise habitats and resources, we further explored potential interactions between mobility, area, and habitat diversity (Kadmon and Allouche, 2007).

2. Materials and methods

2.1. Study region

The study was located in the southern part of the Siena province in central Italy (43°N–11°E; DATUM: World Geodetic System 84) covering an area of c. 700 km² (Fig. 1a). The climate is temperate sub-Mediterranean with a long summer drought, with a mean annual temperature of 14 °C, and a mean annual rainfall of 750 mm. The landscape was dominated by arable land with scattered isolated patches covered by a mosaic of semi-natural shrubland, forest, and grassland. The patches derive from the erosion of Pliocene claystone resulting in particular forms of erosion ('calanchi', peculiar eroded claystone hill sides, and 'biancane', peculiar claystone domes; see Phillips, 1998). The proportion of remnant semi-natural habitats in the landscape was generally low (<15%). The agricultural matrix was highly homogenous being composed almost entirely of cultivation of durum wheat (*Triticum durum* Desf.). The mean level of fertilization was ~150 kg N ha⁻¹ yr⁻¹ with 25–50 kg P₂O₅ ha⁻¹ yr⁻¹. The average wheat yield was ~4 t ha⁻¹. A herbicide treatment was normally applied in post-emergency while fungal diseases were controlled by seed-coating. Harvest was usually completed in July, causing the complete removal of the crop cover during the rest of the summer.

The main land-use changes occurred between the 1950's and 1970's, when the use of caterpillar-tracked machinery enabled steeper slopes to be cultivated (Guasparri, 1993). Habitat loss causes immediate biodiversity decline, but extinctions can also continue long after the habitat loss has occurred (e.g. Krauss et al., 2010; Sang et al., 2010). Such an extinction debt should not, however, bias our results due to the almost simultaneous historic habitat loss in our studied landscapes. After this area reduction the remaining patches, that were formerly open semi-natural grasslands with scattered shrubs, have undergone shrub and tree encroachment due to suspension of traditional management with sheep grazing and burning (Rocchini et al., 2009).

The typical vegetation covering the patches was a mosaic of dry and wet grasslands, shrubland, forest, bare ground with small claystone domes and hill sides (Maccherini et al., 2000) (Fig. 1b and c). The soil quality was homogenous among patches being composed of primitive soils developed on silty clays with very high clay content (up to 65–70%). All the patches were unmanaged at the time of the sampling but the time since the abandonment differed. The dominant vegetation cover depended on the time at which suspension of management occurred; more recently burnt and grazed areas were dominated by open grasslands while areas abandoned decades ago were increasingly covered by shrubs and trees (Maccherini et al., 2000; Rocchini et al., 2009).

2.2. Sampling design

We selected 35 isolated patches in arable land-dominated landscapes in order to obtain two statistically uncorrelated gradients: (i) one in habitat area ranging from 0.2 to 55 ha and (ii) one in habitat diversity ranging from patches dominated by only one habitat (either open grasslands or shrublands) to patches with a mosaic of different habitats. The selection of the sites could, due to a high image resolution for the study area, be performed using aerial photographs available in Google Earth. The first step was to find a large number of semi-natural isolated remnants surrounded by similar landscapes that were all dominated by arable land for durum wheat cultivation. Possible influences of habitat connectivity were thereby reduced. We quantified two explanatory variables describing each patch: area and habitat diversity (Hab). When calculating area and habitat diversity we omitted the cover of ponds and built-up elements. Closed forest, that was already forest before the abandonment, was also excluded as it is an unsuitable habitat for almost all orthopteran species (Fontana et al., 2002; Marini et al., 2009a). Habitat diversity was quantified with the Shannon index using the following habitat cover: (i) recently encroaching shrubs and trees, (ii) dry grasslands, (iii) wet grasslands, and (iv) bare ground (claystone). These habitat types have been identified as keystone structures (sensu Tews et al., 2004) that determine orthopteran diversity at our spatial scale (Ingrisch and Köhler, 1998). The relatively large habitat areas considered (up to ~55 ha) prevented the estimation of finer measures of habitat diversity such as those employed in small plot studies (e.g. sward architecture). The habitats' cover was obtained with a semi-automatic classification analysis of aerial photographs (1:1000) using the software ImageJ (<http://rsb.info.nih.gov/ij/>). The image classification was performed before the insect sampling. We selected 35 remnant patches keeping as low as possible correlation between Log(area) and habitat diversity ($r_s = 0.24$, $P = 0.18$). Each selected patch was at least 250 m distant from the closest large semi-natural patch. Since the majority of the species have shorter average dispersal distance (Ingrisch and Köhler, 1998), this distance was considered appropriate to avoid high exchange of individuals between patches. Habitat diversity and cover of shrubs and trees were related through a hump-shaped relationship (Fig. 2), i.e. maximum habitat diversity was reached at an intermediate level of

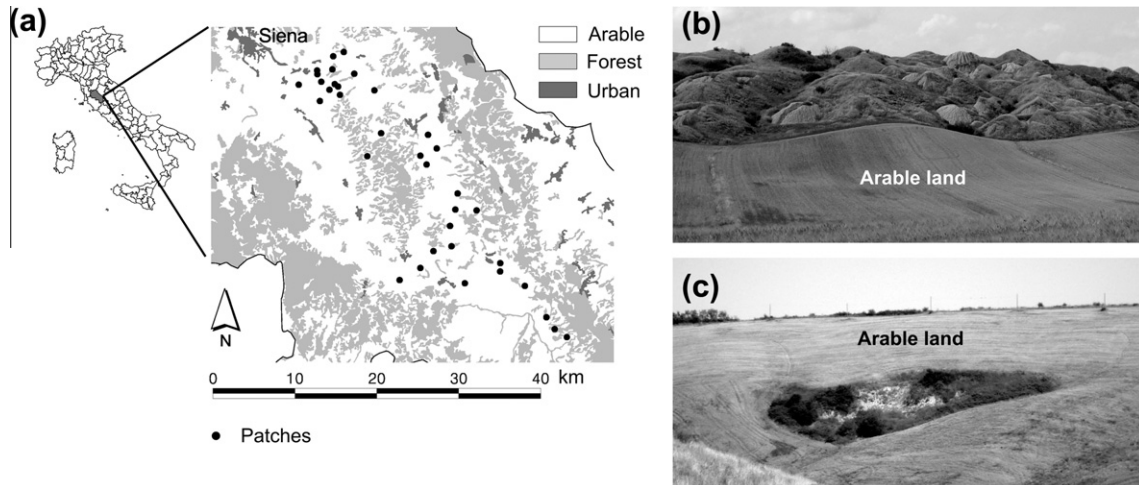


Fig. 1. (a) Study area (Siena province) with the location of the 35 sampled patches (CORINE land cover is also reported) and summer view (14th July 2009) of (b) a large and (c) a small patch.

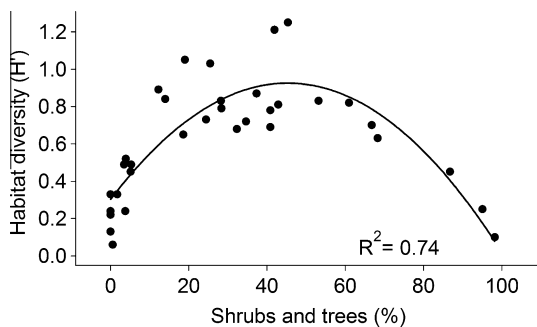


Fig. 2. Relationship between forest encroachment (%) and habitat diversity (Shannon index, H') in the 35 patches. The gradient spanned from open grasslands to shrublands. The fitted line is a significant polynomial regression (linear and quadratic terms, $P < 0.01$).

shrub encroachment. To reduce habitat classification mistakes we performed a coarse survey of the ground cover that was compared to the interpretation of the aerial photographs.

The 35 selected patches had on average 7.1% of semi-natural habitats (minimum: 1.2%, maximum: 17.6%, SD: 4.3%) in the surrounding landscape, quantified within a 1-km radius. This measure can be considered a good proxy for habitat connectivity when investigating the effects of fragmentation on insect diversity (Krauss et al., 2010; Öckinger et al., 2009). The correlation between this connectivity measure and patch area and habitat diversity was 0.18 ($P = 0.39$) and 0.31 ($P = 0.07$), respectively.

2.3. Insect sampling

Orthopteran communities (Ensifera, bush-cricket and crickets, and Caelifera, grasshoppers and pigmy grasshoppers) were sampled in late July (2009) when almost all the species' populations peaked (adults). Due to the very high habitat and topographic variability within the patches we decided to use transect counts. We performed a sampling proportional to habitat area (Báldi and Kisbenedek, 1999) with a time-balancing protocol. Proportional sampling has been demonstrated to be suitable for estimating the SARs (Nufio et al., 2009). First, we defined a transect length linearly proportional to each patch area by dividing the size (m^2) by 200 rendering transect lengths of minimum 10 m and maximum 2850 m. This ratio was selected arbitrarily to keep an appropriate transect

length in both small and large patches. A 4 m wide transect was placed along the main diagonal of the patch. Then, the two operators (L.M. and P.F.) walked the transect actively searching species using both direct inspection with specimen collection and song identification. Both operators surveyed each transect for one hour each, i.e. during a total of 2 h per site. For short transects the sampling was stopped when no new species was found within 15 min. As it was impossible to use either a standardised sweep-netting or box-quadrat method to estimate abundance (Gardiner et al., 2005) due to the highly heterogeneous vegetation structure and very difficult accessibility, we estimated only species richness and not abundance. Nomenclature of orthopterans followed that of Fontana et al. (2005).

During the sampling we also made qualitative observations of the species that were able to disperse into the matrix. In the sites where the wheat harvest was already completed (no crop cover), we observed only a few such individuals of *Oedipoda germanica*. Where the crop cover was still present, we observed individuals of *Decticus albifrons*, *Platycleis* sp., *Tesselana tessellata*, and *Thylopsis liliifolia* venturing into the matrix. The matrix was, therefore, probably not an impervious barrier for certain species which, however, were only found at consistent abundances in a narrow buffer zone around the patches (<20–30 m). Due to the high homogeneity of the matrix and the simultaneous wheat harvesting across the region, the permeability of the matrix was comparable among patches, causing no bias in our analysis (Prugh et al., 2008).

2.4. Mobility classification

The mobility index developed by Reinhardt et al. (2005) was used as measure of dispersal ability. Each species was classified into one of three broad mobility classes: sedentary, intermediate dispersers, and mobile species (Table 1). All apterous and brachypterous species were classified as sedentary, while readily flying species were assigned as mobile. We acknowledge that mobility is not a fixed trait, and that it may differ between and within populations depending on habitat spatial configuration and population history (Merckx et al., 2003; Poniatowski and Fartmann, 2008). For species with wing dimorphism we considered the most common form. By using broad mobility classes, we expect the degree of intra-specific variation to be small as compared to the variation between mobility classes (see also Öckinger et al., 2009). To further reduce potential bias we excluded intermediate dispersers from the analyses, as they were often the species whose allocation

Table 1

List of orthopteran species occurring in the study area. Mobility classes and frequency (proportion of sites where they occurred) of each species are also reported.

Suborder	Latin name ^a	Mobility ^b	Frequency (%)	
Caelifera	<i>Omocestus ventralis</i> (Zetterstedt, 1821)	Sedentary	40.0	
	<i>Dirshius petreus</i> (Brisout, 1855)	Sedentary	31.4	
	<i>Oedipoda germanica</i> (Latreille, 1804)	Sedentary	8.6	
	<i>Calliptamus italicus</i> (Linnaeus, 1758)	Intermediate	80.0	
	<i>Calliptamus siciliae</i> Ramme, 1927	Intermediate	8.6	
	<i>Euchorthippus declivus</i> (Brisout, 1848)	Mobile	82.9	
	<i>Pezotettix giornae</i> (Rossi, 1794)	Mobile	62.9	
	<i>Aiolopus strepens</i> (Latreille, 1804)	Mobile	28.6	
	<i>Glyptothrus brunneus</i> (Thunberg, 1815)	Mobile	28.6	
	<i>Oedipoda caerulescens</i> (Linnaeus, 1758)	Mobile	11.4	
	<i>Chorthippus dorsatus</i> (Zetterstedt, 1821)	Mobile	6.3	
	<i>Aiolopus thalassinus</i> (Fabricius, 1781)	Mobile	2.9	
	<i>Paratettix meridionalis</i> (Rambur, 1838)	Mobile	2.9	
	Ensifera	<i>Tesselana tesselata</i> (Charpentier, 1825)	Sedentary	77.1
		<i>Decticus albifrons</i> (Fabricius, 1775)	Sedentary	71.4
		<i>Racoleis germanica</i> (Herrich-Schaeffer, 1840)	Sedentary	57.1
<i>Pholidoptera femorata</i> (Fieber, 1853)		Sedentary	54.3	
<i>Ephippiger perforatus</i> Rossi, 1790		Sedentary	22.9	
<i>Ephippiger zelleri</i> (Fischer, 1854)		Sedentary	22.0	
<i>Sepiana sepium</i> (Yersin, 1854)		Sedentary	20.0	
<i>Yersinella raymondi</i> (Yersin, 1860)		Sedentary	20.0	
<i>Poecilimon superbus</i> (Fischer, 1854)		Sedentary	11.4	
<i>Pteronemobius concolor</i> (Walker, 1871)		Sedentary	8.6	
<i>Tartarogryllus burdigalensis</i> (Latreille, 1804)		Sedentary	5.7	
<i>Barbitistes</i> sp.		Sedentary	2.9	
<i>Eupholidoptera chabrieri</i> (Charpentier, 1825)		Sedentary	2.9	
<i>Pholidoptera fallax</i> (Fischer, 1854)		Sedentary	2.9	
<i>Platycleis romana</i> Ramme, 1927		Intermediate	48.6	
<i>Platycleis grisea</i> (Fabricius, 1781)		Intermediate	37.4	
<i>Platycleis affinis</i> Fieber, 1853		Intermediate	31.4	
<i>Platycleis falx</i> (Fabricius, 1775)		Intermediate	31.4	
<i>Xiphidion discolor</i> (Thunberg, 1815)		Intermediate	20.0	
<i>Thylopsis liliifolia</i> (Fabricius, 1793)		Mobile	91.4	
<i>Oecanthus pellucens</i> (Scopoli, 1763)		Mobile	45.7	
<i>Phaneroptera nana</i> Fieber, 1853		Mobile	42.9	
<i>Tettigonia viridissima</i> Linnaeus, 1758		Mobile	34.3	
<i>Ruspolia nitidula</i> (Scopoli, 1786)		Mobile	31.4	
<i>Bicolorana bicolor</i> (Philippi, 1830)		Mobile	5.7	

^a Nomenclature of orthopterans followed that of Fontana et al. (2005).

^b Species not included in Reinhardt et al. (2005) were classified using available literature on the single species (Fontana et al., 2002).

was problematic. The species not reported by Reinhardt et al. (2005) were assigned the same values as the most similar recorded species based on information on taxonomic affinities, body size, and wing development (Bruckhaus and Detzel, 1997; Fontana et al., 2002).

2.5. Data analysis

To estimate the relationship between area and species richness, we fitted a linear regression with the log-transformed power function $\text{Log}(\text{species richness}) = \text{Log}(c) + z \text{Log}(\text{Area})$, where c and z are constants. To test the main effect of area and habitat diversity and if the direction of these relationships differed between sedentary and mobile species we used a general linear mixed model with area, habitat diversity, mobility class and their interactions as fixed factors and site as random factor. The latter was included to account for the fact that the numbers of species in each mobility class were quantified at the same sites. First, we fitted the most complicated model including the second-order interaction and the three first-order interactions. Then, we simplified the model by removing one-by-one the least significant interaction terms with $P > 0.05$ starting from the highest order interaction [$\text{Log}(\text{Area}) \times \text{Hab} \times \text{Mobility}$]. We used general linear mixed model assuming normal error distribution using the `aov(stats)` function in R (R Development Core Team, 2008, version 2.8.0). Species num-

bers were log-transformed in all models to approximate normal error distribution.

To evaluate relative importance of area and habitat diversity we performed a variation partitioning analysis (Borcard et al., 1992). First, we built a multiple regression model including both factors. Then, we partitioned the total variation explained by these models into three components: pure area effect, pure habitat diversity effect and a joint component shared between the two. The pure effects were obtained by extracting the adjusted R^2 from a partial regression testing one of the variables as predictor with the other as covariate and vice versa. We did this first for all the species, and then for mobile and sedentary species, separately.

A certain degree of variability in habitat connectivity was found between the 35 sites, although we controlled for such effects. We therefore tested how species richness was affected by the proportion of semi-natural habitat in the surrounding landscape (1-km radius) along with area and habitat diversity and in interaction with mobility. Because connectivity was not significant in any case, we excluded it from further analyses.

3. Results

In total, 38 orthopteran species were found (25 Ensifera and 13 Caelifera) in the 35 investigated patches (Table 1). The most frequent species were *T. liliifolia*, *Euchorthippus declivus*, *Calliptamus*

italicus, *T. tessellata*, and *D. albifrons*. We found 17 sedentary (14 Ensifera and 3 Caelifera), 14 mobile (6 Ensifera and 8 Caelifera) species and 7 intermediate dispersers (5 Ensifera and 2 Caelifera) (Table 1). A Fisher's exact test indicated that the two sub-orders were equally represented only within the intermediate disperser class, while Ensifera were more frequently sedentary and Caelifera more frequently mobile species.

We found a positive linear relationship between species richness and patch area for all the species together (Fig. 3a), and for sedentary and mobile species, separately (Fig. 3b). The test of the interaction between area and mobility showed a difference in slopes between the two mobility classes, where sedentary species had a steeper SAR slope ($z = 0.25$) than mobile species ($z = 0.14$) (Table 2). Increasing habitat diversity also had a positive effect on both mobile and sedentary species (Fig. 4). The slope of these relationships did not differ between the two mobility classes.

The variation partitioning of the separate models for all species, sedentary, and mobile species indicated that the relative importance of area and habitat diversity differed according to the mobility class (Table 3). The total variation explained by the separate models was very similar. However, sedentary species were weakly related to habitat diversity, explaining 3% of the total variation, but strongly related to area (49%). Mobile species, in contrast, presented a stronger relationship with habitat diversity (26%) and a weaker one with area (20%).

4. Discussion

4.1. Habitat area

Orthopteran species richness increased linearly with both area and habitat diversity in our Mediterranean landscape. The effect of area per se was pervasive, irrespective of habitat diversity, while the effect of the latter was less pronounced. The overriding effect of habitat diversity found by Báldi (2008) and Jonsson et al. (2009) was not found in our system, while our findings generally confirmed that habitat diversity and area per se are complementary mechanisms shaping species richness patterns in island-like habitats (Hortal et al., 2009; Kallimanis et al., 2008; Triantis et al., 2003, 2005).

Orthopterans presented strong positive SARs, indicating their sensitivity to habitat loss. The SAR slope ascertained in this study was comparable with that found for orthopterans by Báldi and Kisbenedek (1999) in small steppe patches in Hungary ($z = 0.15$), but smaller than in unmanaged remnant grasslands in urban areas ($z = 0.25–0.31$) (Nufio et al., 2009). A reduction in habitat area is thought to be a major cause of observed species extinctions for several taxonomic groups (Ewers and Didham, 2006; Fahrig, 2003). Reduced habitat area in a landscape leads not only to a de-

Table 2

General linear mixed model testing the fixed effect of area, habitat diversity (Hab), and mobility in the 35 sites. Site was included as random factor to account for the fact that the numbers of species in each mobility class were quantified at the same sites. Species richness was log-transformed. Non-significant interactions were removed one-by-one when $P > 0.05$. In brackets we report the P -value used to remove the non-significant interactions. Variables included in the final model are in bold.

Variables	d.f.	MS	F	P
Log(Area)	1	1.492	69.87	<0.001
Hab	1	0.328	15.38	<0.001
Log(Area) × Hab	–	–	–	(0.811)
Residuals	32	0.021		
Mobility	1	0.030	2.08	0.158
Log(Area) × Mobility	1	0.119	8.28	0.007
Hab × Mobility	–	–	–	(0.158)
Log(Area) × Hab × Mobility	–	–	–	(0.709)
Residuals	33	0.014		

crease in the size of the patches but also to an increase in isolation between remaining fragments, with consequent reductions in population size and colonisation rates that increase the risk of local extinctions (Fahrig, 2003). In our study we kept habitat connectivity constant and relatively low for all the patches and the observed effects of fragmentation was therefore solely related to habitat area.

4.2. Habitat diversity

Although habitat area appeared to be the primary determinant of orthopteran species richness, we also found a positive effect of habitat diversity, conforming to the results of Schouten et al. (2007) who found a positive effect of both factors on orthopteran diversity in the Netherlands. An increase of species richness with habitat diversity is consistent with a large body of empirical evidence that proves the robustness of this pattern across scales and taxa (Hortal et al., 2009; Tews et al., 2004; Triantis et al., 2003, 2005). Large habitat diversity has also demonstrated to promote population stability, reduce extinction risks, and enhance population survival in metapopulations of orthopterans (Kindvall, 1996) and butterflies (Oliver et al., 2010). In our abandoned patches, dominated by a few habitat types, habitat diversity was strongly related to the cover of shrubs and trees in a hump-shaped relationship. At the beginning of the succession, shrub encroachment increased habitat diversity but when the cover became too large (>70%) habitat diversity dropped. Species richness was therefore highest at early to mid successional stages with a mosaic of open grasslands, shrubs, trees, and bare ground (Fig. 5).

High habitat diversity probably offers a greater range of microclimates, and microsites for important phases in the life

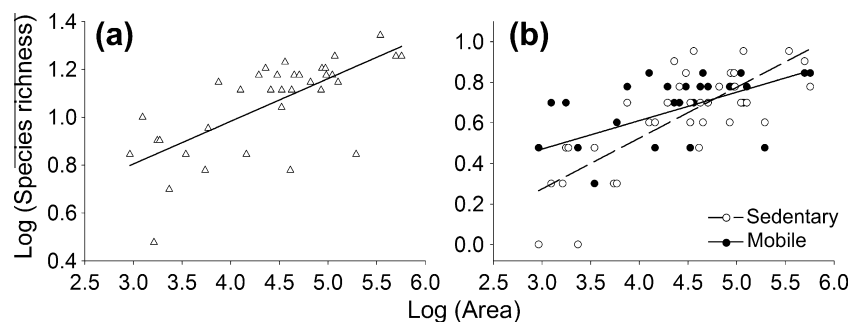


Fig. 3. Relationship of species richness vs. area for (a) all species together ($y = 0.17x + 0.31$; adj. $R^2 = 0.49$), and (b) for sedentary ($y = 0.25x - 0.48$; adj. $R^2 = 0.59$) and mobile species ($y = 0.14x + 0.05$; adj. $R^2 = 0.35$), separately.

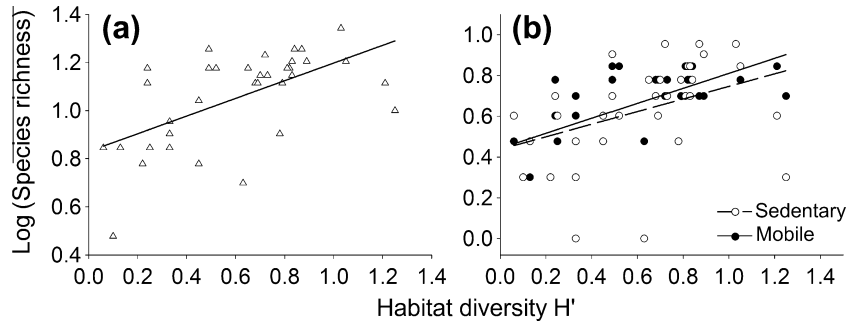


Fig. 4. Relationship of species richness vs. habitat diversity for (a) all species together ($y = 0.37x + 0.83$; adj. $R^2 = 0.33$), and (b) for sedentary ($y = 0.31x + 0.44$; adj. $R^2 = 0.13$) and mobile species ($y = 0.37x + 0.44$; adj. $R^2 = 0.41$), separately.

Table 3

Variation partitioning (% adjusted R^2) of the orthopteran species richness explained in the multiple regression model testing area and habitat diversity (Hab) ($P < 0.01$) vs. the number of (a) all species together, (b) sedentary, and (c) mobile species, separately.

	(a) All species	(b) Sedentary	(c) Mobile
Log(Area) (pure effect)	32.5	48.7	20.0
Log(Area)~Hab (joint effect)	15.5	9.9	15.0
Hab (pure effect)	17.3	2.9	26.0
Total variation explained	65.3	61.5	61.0
Unexplained	34.7	39.5	39.0

4.3. Mobility effect

The capacity of orthopteran species to disperse readily was a major predictor of how species responded to habitat loss. Flightless sedentary species were more strongly related to area than flying mobile species. Low mobility has in several recent studies been linked to increased vulnerability to insect extinctions in fragmented landscapes (Bommarco et al., 2010; Braschler et al., 2009; Driscoll and Weir, 2006; Öckinger et al., 2009, 2010). One reason may be that for sedentary species, the neighbouring habitat patches in our highly-fragmented landscape may be too far away to be reached. This implies that sedentary species strongly responded to patch size (high dispersal mortality or edge effects), while mobile species responded less to habitat area on the spatial scale measured here (Bommarco et al., 2010; Öckinger et al., 2009). The dispersal mortality in the matrix may be reduced for species with a higher re-colonisation ability resulting in lower net losses at the constant level of isolation used in this study. Mobility appears as a strong predictor of widespread success or decline of orthopteran populations, a fact confirmed by the findings of Reinhardt et al. (2005) where this trait to large extent explained nationwide extinctions of orthopterans in Germany.

Positive effect of habitat diversity was consistent across mobility classes and habitat area, and we found no interactions with either habitat area or mobility. However, we did find that the strength of the relationship varied between mobility classes, where sedentary species were only weakly related to habitat diversity whilst mobile species presented a stronger relationship with this factor. This could be related to the fact that almost all the sedentary species were Ensifera (Table 1), such as *Ephippiger* sp. or *Pholidoptera femorata*, that mainly inhabit shrublands and forest edges. They were therefore probably less sensitive to increased cover in

cycle such as mating or oviposition. The large scale focus that we adopted to explore effects of compositional habitat diversity should not downgrade the importance of maintaining heterogeneity at a finer scale (Oliver et al., 2010), e.g. vegetation architecture within-habitat classes, which undoubtedly affects the quality of habitats (Kindvall, 1996; Langellotto and Denno, 2004). This within-habitat heterogeneity has been demonstrated to buffer populations against disturbance and generate more stable population dynamics (Kindvall, 1996), which in the long run can maintain higher species richness within isolated patches. Even if our habitat diversity measure is coarse in comparison to the scale at which insects perceive small-scale habitat heterogeneity, our four habitat classes corresponded well to distinct keystone structures (Tews et al., 2004) for orthopteran species (Ingrisch and Köhler, 1998). In particular, each of the four classes corresponded to different microclimate conditions, food resources, and oviposition sites which are among the most important factors shaping orthopteran communities in Mediterranean areas (Fontana et al., 2002).

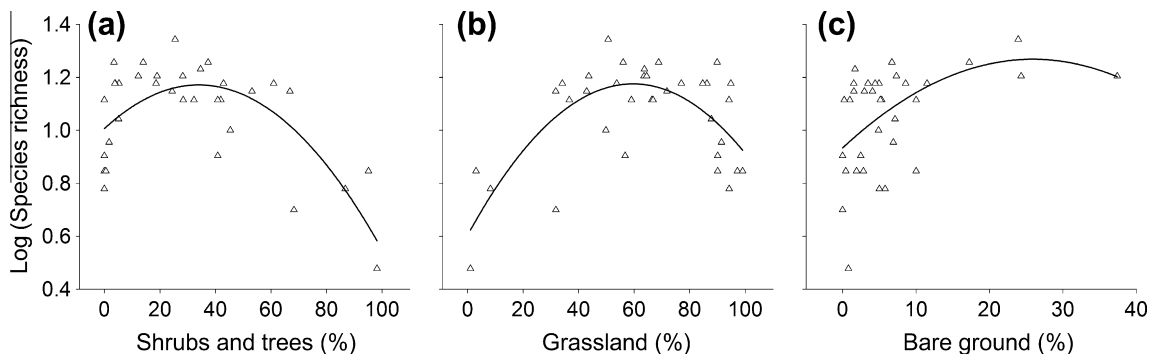


Fig. 5. Relationship between the cover of the three main habitat classes and the log-transformed orthopteran species richness. The fitted line is a polynomial regression (linear and quadratic terms $P < 0.01$).

shrubs and trees (cover > 50%) (see also Marini et al., 2009a). On the other hand, many mobile species were Caelifera, among which several species require the presence of both shrubs and grassland to complete their life cycle (e.g. bare ground for oviposition). The species pool in the current study presented a relatively large overlap between mobility and habitat specialisation, where mobile species probably have more specific habitat requirements, something that can explain the observed response to habitat diversity.

4.4. Implications for conservation

In large parts of the Mediterranean regions these semi-natural remnants are perceived as harsh and infertile landscape elements that hinder agriculture (Phillips, 1998) and piecemeal reclamation for intensive durum wheat cultivation remains as a threat to the biodiversity harboured in these habitats (Clarke and Rendel, 2000). Efforts are, therefore, needed to restrict conversion into arable land in the regions where this still occurs.

Halting habitat loss and providing a static protection status might, however, be an ineffective conservation strategy as the abandonment of traditional agricultural activities causes alteration of habitat quality and diversity (Marignani et al., 2008; Rocchini et al., 2009). This process has probably enhanced species diversity at the beginning of the succession, but it is leading to a loss of species diversity in patches that have reached the stage of closed forest (Fig. 5). The optimal management for orthopteran conservation should aim at maintaining a mosaic of shrubs, grasslands, and bare ground areas (eroded claystone) within the patches at a small spatial scale (Kindvall, 1996; Marini et al., 2009a; Schirmel et al., 2010). Introducing cutting and burning prescriptions associated with the reintroduction of extensive sheep grazing (recurring management) on small sectors of the patches appear as appropriate strategies to protect orthopterans (see also Batáry et al., 2007; Bonte and Maes, 2008). Further research is, however, needed to identify an appropriate grazing intensity due to the high sensitivity of these fragile soils and landforms to erosion (Rossi and Vos, 1993). Alternating different practices on small areas would avoid habitat homogenization, reducing also potential negative effects of specific management options (e.g. burning or grazing) on single species. This mixed management would be also beneficial to maintain diversity of other taxa such as plants (Marignani et al., 2008), butterflies (Marini et al., 2009b; Oliver et al., 2010), bumblebees, and birds (Söderström et al., 2001), which have been found to benefit by a mosaic of scattered shrubs, trees and semi-natural grasslands.

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