Vol. 37 • N° 3 • May–June 2011 • ISSN 1146-609X

ELSEVIER

ACTA
OECOLOGICA
INTERNATIONAL JOURNAL OF ECOLOGY

Original article

Spatio-temporal change in the relationship between habitat heterogeneity and species diversity

Adela González-Megías [a],[*], José María Gómez [b], Francisco Sánchez-Piñero [a]

[a] Dpto de Biología Animal, Facultad de Ciencias, Universidad de Granada, C/ Fuentenueva s/n, E-18071 Granada, Spain
[b] Dpto de Ecología, Facultad de Ciencias, Universidad de Granada, C/ Fuentenueva s/n, E-18071 Granada, Spain

ABSTRACT

Beta diversity plays an important role in mediating species diversity and therefore improves our understanding of species-diversity patterns. One principal theoretical framework exists for such patterns, the "habitat-heterogeneity hypothesis (HHH)", which postulates a positive relationship between species diversity and habitat heterogeneity. Although HHH is widely accepted, spatial and temporal variability has been found in the relationship between diversity and heterogeneity. Species turnover has been proposed as the main factor explaining spatial variation in the relationship between species diversity and habitat heterogeneity. In this study, we tested the role of species turnover in explaining spatial and temporal variability on diversity–heterogeneity relationship in a Mediterranean ecosystem, using beetles as the study organisms. A hierarchical design including different habitats and years was used to test our hypothesis. Using different multivariate analyses, we tested for spatial and temporal variability in beta diversity, and in the beetle diversity–heterogeneity relationship using two diversity indices. Our study showed that beetle composition changed spatially and temporally, although temporal change was evident only between sampling periods but not between years. Notably, there was spatial and temporal change in the relationship between habitat descriptors and beetle diversity. Nevertheless, there was no correlation between the changes in beetle composition with the changes in the habitat-heterogeneity relationships. In this Mediterranean system, spatial and temporal changes in the diversity–heterogeneity relationships cannot be predicted by species turnover, and other mechanisms need to be explored to satisfactorily explain this variability.

© 2011 Elsevier Masson SAS. All rights reserved.

1. Introduction

Numerous studies examined the effect of space and time in species richness at fine and coarse scales, but only recently has the scientific community focused on the effect of space and time on species turnover, or beta diversity (Crist and Veech, 2006; Krasnov et al., 2006; Beck and Chey, 2007; Gaston et al., 2007; McKnight et al., 2007; Numa et al., 2009; Sobek et al., 2009a,b; Barton et al., 2010). As a general idea, the greater the spatial differences in environmental conditions, the more species turnover increases and consequently the fewer the species shared (Gaston et al., 2007; McKnight et al., 2007). Associated with this idea, temporal species turnover will increase with greater temporal differences in environmental conditions on any time scale. Beta diversity reflects not only environmental changes but also differences in ecological interactions, and dispersal limitation due to geographical barriers (Gaston et al., 2007; McKnight et al., 2007). Consequently, beta diversity plays an important role in mediating species alpha diversity, and therefore in increasing our understanding of alpha-diversity patterns (Beck and Chey, 2007; Gaston et al., 2007).

One major theoretical framework exists for alpha-diversity patterns, the "habitat-heterogeneity hypothesis" (HHH, hereafter), suggesting that habitat heterogeneity modulates the outcomes of ecological processes, influences the way species coexist in space and time, and affects the functioning of the whole ecosystem (García-Charton and Pérez-Ruzafa, 1999; Cardinale et al., 2000). HHH postulates a consistently positive relationship between species diversity and spatial heterogeneity (Davidowitz and Rosenzweig, 1998; Wettstein and Schmid, 1999; Romero-Alcaraz and Avila, 2000; Tews et al., 2004 and references therein). Although HHH is widely accepted, some studies have found spatial and temporal changes in the relationship between diversity and habitat heterogeneity at the same and at different spatial and temporal scales (Hill et al., 1995; Wilby and Shachak, 2000; Stewart

et al., 2000; Sullivan and Sullivan, 2001; Hamer et al., 2003; Tews et al., 2004; De Mas et al., 2009). Species turnover has been proposed as the main factor explaining spatial changes in relationships between alpha diversity and habitat heterogeneity (Levin, 1992; Niemelä, 1997; Lassau et al., 2005; Zamora et al., 2007). Hypothetically, this occurs because species respond differently to habitat characteristics due to their intrinsic characteristics, and consequently a change in species composition would imply that the relationship between habitat heterogeneity and alpha diversity varies. Additionally, there are temporal changes (within and between years) in species composition (Palmer and White, 1994; Adler and Lauenroth, 2003; Beck and Chey, 2007), which may affect the relationship between alpha diversity and habitat heterogeneity. Indeed, seasonality is one of the main causes of species turnover for insects due to species traits such as over-wintering stage or host−plant phenology (Sobek et al., 2009b), but also for migratory mammals and birds (Huston, 1994).

The Mediterranean basin is characterized by dramatic spatial heterogeneity and a strong seasonality (Blondel and Aronson, 1999). This spatial heterogeneity is the consequence of many factors including topographical and climatic variability, and human influence (Blondel and Aronson, 1999; Lobo et al., 2001; Baselga and Jiménez-Valverde, 2007). As a result, the Mediterranean basin is a hotspot of biodiversity, with levels of endemism approaching 20% in many plant and animal groups (Blondel and Aronson, 1999; Médail and Quézel, 1999; Myers et al., 2000). Indeed, it is estimated that about 75% of European insect species are found in the Mediterranean basin (Balletto and Casale, 1991). Among insects, beetles are one of the most abundant and diverse organisms in most ecosystems, responding to spatial and temporal heterogeneity in many different ways (Speight et al., 1999). Beetles, especially epigeal beetles, are highly sensitive to the effects of landscape changes, and have proved to be a useful tool for monitoring and detecting changes in the environment (Bohac, 1999; Rainio and Niemelä, 2003; Hodkinson and Jackson, 2005). Higher values of beta diversity are therefore expected even at small spatial and temporal scales in these types of habitats, making beetles in Mediterranean ecosystems useful as organisms for which to study the HHH.

The aim of this study is the spatial (and temporal) changes in the HHH in a Mediterranean ecosystem which can be explained by beta diversity. Although there are many studies that have examined the HHH, no study available has tested this hypothesis. To do so, we explore the relationship between habitat heterogeneity and alpha diversity, and their spatial and temporal changes in two habitats. Additionally, we measure spatial and temporal beta diversity, and we tested the relationship between beta diversity and the number of diversity−heterogeneity relationships that changed. We predict significant changes in the diversity−heterogeneity relationship associated with higher beta diversity (higher differences in species composition).

2. Methods

2.1. Sampling design

In 1997 we selected the two most abundant habitats in the high mountain of Sierra Nevada National Park (Granada, SE Spain) above the treeline between 2100 and 2300 m a.s.l. One habitat, with a community dominated by *Astragalus granatensis* Lam. and *Juniperus* spp. (*Astragalus* habitat hereafter), occurred on calcareous soils, whereas the other habitat had a community associated with siliceous soils, and dominated by the shrub *Genista versicolor* Boiss. (*Genista* habitat hereafter). In addition, these areas were similarly grazed by domestic (sheep and goats) and wild ungulates

(Spanish ibex, *Capra pyrenaica* Schinz; González-Megías et al., 2004).

In each habitat we randomly established three zones of approximately 2500 m^2, and more than 500 m apart: in the *Astragalus* habitat (A1, A2 and A3) and in the *Genista* habitat (G1, G2 and G3). In each zone, 10 plots were installed (of 25 m^2). In total, we thus studied 2 habitats × 3 zones × 10 plots = 60 plots (see González-Megías et al., 2007 for a detailed description).

2.2. Beetle sampling

Arthropods were sampled using pitfall traps partly filled with water with soap to break the surface tension. The use of pitfall traps has been found to give an adequate representation of relative abundance of epigeal fauna (Sutherland, 1996). In each of the 60 plots, 5 traps were placed at least 2 m from each other (see Ward et al., 2001 for inter-trap effects). Traps operated for three days in June and August in both 1997 and 1998, the minimum time estimated to collect a representative sample of the arthropod community (Digweed et al., 1995), while avoiding the vacuum effects over the local assemblages. Traps were covered to avoid arthropod collection for the rest of the time. The possible disturbance caused by placing the pitfall traps was minimized by digging carefully and removing all the extra soil. Additionally, the vegetation around the traps was not cleared to minimize the "digging-in" effect (Digweed et al., 1995). Collected samples (60 plots × 5 traps × 2 seasons × 2 years = 1200 in total) were analysed in the laboratory, where individuals were counted and identified to the family level. Beetles were sorted and sent to specialists for identification to the species level or for characterization of the morphospecies when identification was not possible. Some of the 1200 traps were excluded due to severe damage by wild animals, nine from the *Astragalus* habitat and 21 from the *Genista* habitat.

2.3. Beetle-community indices

Beetle alpha diversity was assessed by two indices: i) Richness (S_{obs}); and ii) Hulbert's probability of intraspecific encounter (HP), which is the probability that two randomly sampled individuals from the community belong to two different species (Gotelli and Entsminger, 2004). This index is one of the few that is unbiased by sample size (Magurran, 2004). Both indices were generated using EcoSim® (Gotelli and Entsminger, 2004). Beetle alpha-diversity indices were generated for each small plot by pooling the individuals collected from all traps located inside each small plot over the study period.

Similarity in beetle-assemblage composition (beta diversity) between habitats and sampling periods was calculated using the Bray−Curtis similarity coefficient (Magurran, 2004). This index ranges between 0 (indicating no similarity in community composition between sites) and 1 (indicating complete overlap), and it is considered one of the most robust measures of community similarity (Magurran, 2004).

Rarefaction curves were calculated for each habitat (*Astragalus* and *Genista*) to estimate the efficiency of the methods used in capturing beetle species (Magurran, 2004). Curves were generated using the program EstimateS v 7.5 (Colwell, 2005). Additionally, the Chao1 species-richness estimator was applied to sample data (Colwell, 2005). This non-parametric method is based on the concept that rare species carry the most information about the number of missing ones, using the singletons and doubletons to estimate the number of missing species (Colwell, 2005).

2.4. Habitat heterogeneity

Habitat was described by the following variables: Percentage of bare soil, percentage of cover by the dominant plant species, plant alpha diversity (plant diversity hereafter), and vertical complexity. Plant diversity and vertical complexity are widely used as estimators of habitat heterogeneity (Lassau et al., 2005; and references therein). To determine these variables, we used a modification of the method described by Wiens and Rotenberry (1981). Three transects (5 m long) were established in each small plot. Together with each of these transects, three points (one in the centre of the transect, and two points situated 1 m right and left of the transect) were taken at 1-m intervals (15 points per transect × 3 transects = 45 points/small plot).

Using a graduated stick (two m high) the contact points were categorized as shrubs (identified to species level), herbs, bare soil or stone. Vegetation cover was measured as the percentage of points of any category. Vertical complexity was estimated recording plant height every 10-cm intervals, and calculating the coefficient of variation $(100 \times SD/mean)$ of vegetation height. This method allowed us to determine one value of each habitat-heterogeneity variable per small plot. Plant diversity was estimated as species richness.

2.5. Statistical analysis

To analyse spatial and temporal changes in species composition (species turnover), we used the permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001). This method analyses the variance of multivariate data explained by a set of explanatory factors on the basis of any distance or dissimilarity measure of choice, providing *p*-values by permutations (Anderson, 2001). To perform the PERMANOVA, the FORTRAN computer program PERMANOVA was used (Anderson, 2005). Each term in the model was put through permutation tests based on 9999 permutations of residuals under a reduced model to determine *p*-values. Analyses were made on Bray–Curtis distances. The spatial model was a two-way design with habitat as a factor and zones as a nested factor on habitat/year. The temporal model was a two-way design with year as a factor and sampling periods (S1 and S2 for 1997; and S3 and S4 for 1998) as a nested factor on year. PERMANOVA allows pair-wise *a posteriori* comparisons using the *t*-statistic. Among zone and sampling periods pair-wise comparisons were made based on 9999 permutations.

Nonmetric Multidimensional Scaling (NMDS) plots were used to help interpret the results found with the PERMANOVAs (see Anderson, 2001 for similar procedure). The NMDS ordination technique was performed using the autopilot routine in the PC-Ord v. 5 package (McCune and Mefford, 1999) to select the best dimensional solution. NMDS assumes that dissimilarity is monotonically related to ecological distance and provides a robust and easily interpretable ordination method (Quinn and Keough, 2002). The method maximizes rank-order correlation between distance measures and distance in an ordination space. Points are moved to minimize "stress", i.e. the mismatch between the two kinds of distance. Analyses were made on Bray–Curtis distances.

To analyse the spatial and temporal variation in the relationship between species alpha diversity (Richness and HP indices) and habitat heterogeneity, we used an ANCOVA with an interaction term (Zar, 1996; Edwards, 1985). Each spatial model included the habitat-heterogeneity variable as a factor, habitat (or zone) as a covariate, the interaction between the two variables, and the alpha-diversity index as a response variable. Each temporal model included the habitat-heterogeneity variable as a factor, year (or sampling periods) as a covariate, the interaction between the two

variables, and the alpha-diversity index as a response a variable. In this case the null hypothesis was that no spatial or temporal variation occurred, and it was rejected when the interaction term was significant (Dowdy and Wearden, 1985).

When spatial or temporal variation was detected in the ANCOVA models, the relationship between the diversity indices and the habitat-heterogeneity variables was determined by simple regressions. For the problem of a reduced sample size in zones ($n = 10$ plots/zone), we solved the problems of reduced sample size by means of permutation tests using Permute! ver. 3.4 (http://www.bio.umontreal.ca/casgrain/en/labo/permute/index.html). Permutation tests assess the probability of the regression coefficients and the associated R^2 using a permutational method described in Legendre et al. (1994). For data with non-normal error structure, permutation tests had a type I error closer to the nominal significance level alpha and greater power than the normal-theory *t*-test. The variables were log-transformed or arccosine square-root transformed when necessary to normalize the data (Zar, 1996). Homogeneity of variance was checked by means of Levene's test.

To analyse the relationship between the Bray–Curtis similarity index (beta diversity) and the percentage of relationships that spatially and temporally changed, we used the spearman rank correlation coefficient (Zar, 1996). We calculated the percentage of relationship that spatially and temporally changed from the results obtained by the ANCOVA models (see description above).

3. Results

3.1. Abundance and diversity

A total 97 species of beetles were found in the *Astragalus* habitat (1477 individuals) and 81 species in *Genista* habitat (835 individuals). Rarefaction curves showed that both habitats were well sampled although the curve reached an asymptote only for the
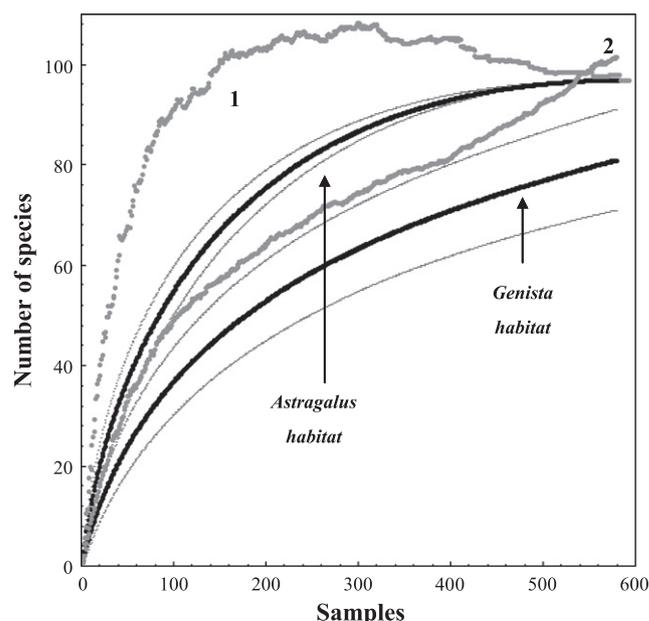

Fig. 1. Rarefaction curves for the *Astragalus* and *Genista* habitats showing the number of species for both habitats (thick black lines) and the 95% confidence limit for each location (thin black lines). Grey lines represent 1) Chao1 for *Astragalus* habitat and 2) Chao1 for *Genista* habitat.

Astragalus habitat (Fig. 1). The Chao1 species-richness estimator showed that almost all species where captured in the *Astragalus* habitat (97 species) according to this estimator, and most species in *Genista* habitat (101.65 species).

3.2. Spatio-temporal species turnover

Beetle-assemblage composition varied significantly between habitats (0.35 for Bray—Curtis similarity coefficient; Fig. 2). Zones within habitats also significantly differed in species composition (0.49 ± 0.03 for *Astragalus* zones, and 0.46 ± 0.05 among *Genista* zones; Table 1). Pair-wise comparisons showed that all zones significantly differed in species composition in both habitats (Table 1, Fig. 2).

No significant differences were detected between years in beetle composition (0.62 for Bray—Curtis similarity index) but highly significant differences appeared in similarity between sampling periods (Table 1, Fig 2). Species composition also significantly varied between sampling periods in both study years (Table 1, Fig. 2).
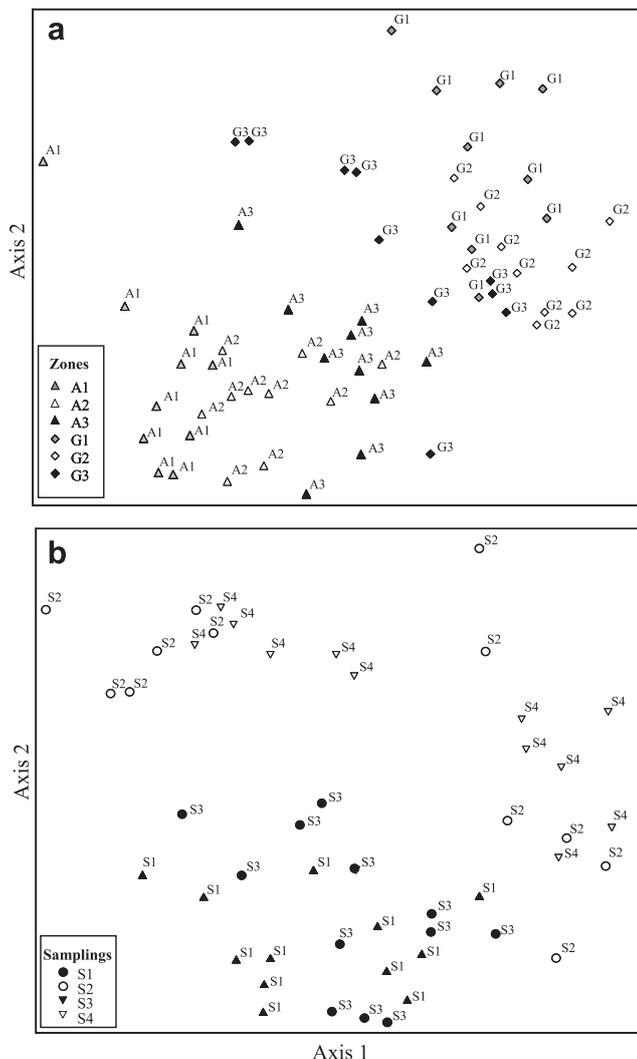
Table 1
A) Results of the PERMANOVA analyses for beetle assemblage, testing spatial (Habitat and zone) and temporal variability (year and sampling) on beetle composition. B) Pair-wise comparisons between A) zones (A1, A2 and A3 within the *Astragalus* habitat: G1, G2, and G3 within the *Genista* habitat), and B) sampling periods (S1 and S2 within 1997; S3 and S4 within 1998) for beetle-assemblage composition. Similarity = Similarity of beetle-assemblage composition based on Bray—Curtis similarity coefficient. $**p < 0.01$, $***p < 0.001$.

	d.f.	F
Panel A)		
Spatial		
Habitat	1	125.49***
Zone [Habitat]	4	14.15***
Error	54	
Temporal		
Year	1	1.97
Sampling [Year]	2	47.79***
Error	116	

	t	Similarity		t	Similarity
Panel B)					
Spatial					
A1—A2	2.53**	0.54	G1—G2	2.54**	0.54
A1—A3	3.16***	0.49	G1—G3	3.97***	0.38
A2—A3	3.77***	0.44	G2—G3	3.17***	0.47
Temporal					
S1—S2	10.19***	0.16	S3—S4	4.56***	0.27

3.3. Spatial changes in the relationship between alpha diversity and habitat variables

3.3.1. Between habitats
Beetle diversity was significantly related to % bare soil and vertical complexity at least for one of the habitats (Appendix A). Only the relationship between Richness and HP with vertical complexity significantly changed between habitats (Richness: $F_{\text{Verticalcomplexity} \times \text{Habitat}} = 4.77$, d.f. = 1, 56, $p = 0.03$; HP = $F_{\text{Verticalcomplexity} \times \text{Habitat}} = 6.98$, d.f. = 1, 56, $p = 0.01$; Appendix A).

3.3.2. Among habitats
HP was significantly related to vertical complexity, the % of the dominant plant species, and % bare soil in the *Genista* habitat (Appendix A), but only the relationship between HP and % bare soil significantly changed among zones within the *Genista* habitat ($F_{\text{\%baresoil} \times \text{Zone}} = 3.46$, d.f. = 1, 28, $p = 0.04$, Appendix A).

3.4. Temporal changes in the relationship between alpha diversity and habitat variables

3.4.1. Between years
The relationship between beetle richness and dominant plant species ($F_{\text{Dominatplant} \times \text{Year}} = 7.89$, d.f. = 1, 236, $p = 0.005$), plant diversity ($F_{\text{Plantdiversity} \times \text{Year}} = 8.24$, d.f. = 1, 236, $p = 0.005$), and % of bare soil ($F_{\text{\%baresoil} \times \text{Year}} = 10.46$, d.f. = 1, 236, $p = 0.001$) changed between years (Appendix A). Similarly, the relationship between HP and plant diversity ($F_{\text{Plantdiversity} \times \text{Year}} = 3.75$, d.f. = 1, 236, $p = 0.05$) and dominant plant species ($F_{\text{Dominantplant} \times \text{Year}} = 3.16$, d.f. = 1, 236, $p = 0.07$) also changed between years (Appendix A).

3.4.2. Between sampling periods
In 1997, Richness was significantly related to dominant plant species and plant diversity but only the relationship with dominant plant species significantly changed between sampling periods ($F_{\text{Plantdiversity} \times \text{sampling}} = 15.31$, d.f. = 1, 116, $p = 0.0002$, Appendix A). In 1998, the relationships between beetle richness and dominant

Fig. 2. Nonmetric multidimensional scaling ordination of assemblage composition for A) the different habitats (A = *Astragalus* habitat, G = *Genista* habitat), and zones within each habitat. B) The different years, and the two sampling periods within each year (1997 = S1 + S2, and 1998 = S3 + S4). S = Sampling period.

plant species ($F_{\text{Dominantplant} \times \text{sampling}} = 9.60$, d.f. = 1, 116, $p = 0.008$), plant diversity ($F_{\text{Plantdiversity} \times \text{Sampling}} = 15.31$, d.f. = 1, 116, $p = 0.0002$), and % bare soil ($F_{\text{\%baresoil} \times \text{Sampling}} = 4.70$, d.f. = 1, 116, $p = 0.03$) differed between sampling periods (Appendix A). Beetle HP relationships with dominant plant species ($F_{\text{Dominantplant} \times \text{sampling}} = 6.25$, d.f. = 1, 116, $p = 0.01$) and plant diversity ($F_{\text{Plantdiversity} \times \text{sampling}} = 2.25$, d.f. = 1, 116, $p = 0.03$) also differed between sampling periods (Appendix A).

3.5. Relationship between beta diversity and spatial/temporal changes in the HHH

The percentage of relationships between beetle alpha diversity and habitat descriptors that change spatially (see Appendix A) varied between 0% and 100%, and the percentage of the relationships that change temporally between 50% and 100% (Table 2). However, there was no correlation between the values of similarity in species composition (Bray–Curtis index) and the percentage of relationships that remain stable in space and time (Fig. 3; $r_s = -2.67$, $p = 0.49$; Table 2, Fig. 3).

4. Discussion

An increase in habitat heterogeneity was associated with greater species diversity of beetles, conforming to previous patterns reported for many different groups of animals, and particularly arthropods (Wettstein and Schmid, 1999; Humphrey et al., 1999; Magura et al., 2000; Kumar et al., 2008). However, we found exceptions to this rule with negative relationships between alpha diversity and habitat heterogeneity. Other studies have also found non-significant relationships (Hamer et al., 2003)
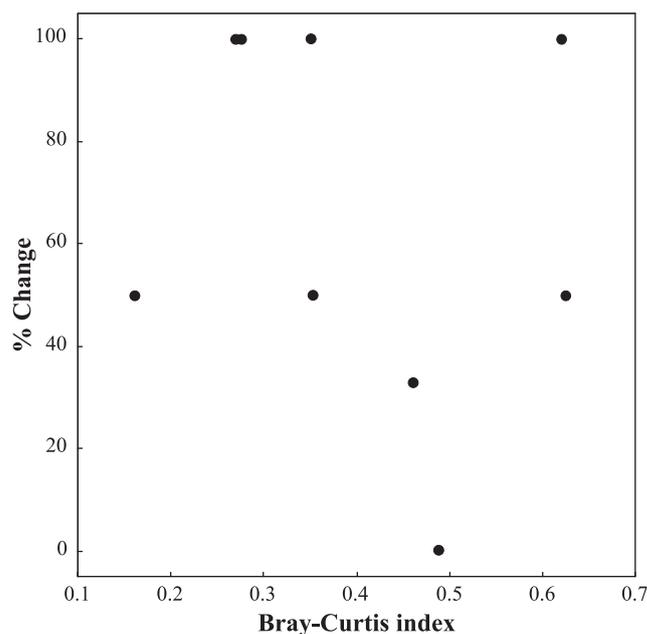

Fig. 3. Relationship between Bray–Curtis similarity indices obtained for each spatial and temporal scales and the percentage of diversity–heterogeneity relationships that changed spatially and temporally (columns 5 and 6 in Table 2).

or negative heterogeneity–diversity relationships for other insect groups (Hill et al., 1995; Sullivan and Sullivan, 2001). There were spatial and temporal changes in the relationship between habitat descriptors and beetle alpha diversity in our system. As pointed out by Tews et al. (2004), the relationship between alpha diversity and habitat heterogeneity might vary depending on the spatial and temporal scale. In our study, both spatial and temporal scales are inherent to our design (a hierarchical design), and its effect on the HHH previously discussed (González-Megías et al., 2007).

Changes in species composition, and therefore high spatial and temporal beta diversity, were also apparent in our study. Spatial beta diversity was high between habitats but also among zones within habitats. In fact, zones shared less than 50% of beetle species. A low similarity in species composition within habitats has also been found in other systems, where for example there are high levels of spatial species turnover even between individual plants of the same species (Sobek et al., 2009a,b; Barton et al., 2010). Small shifts in altitude, usually implying changes in climate, soil properties and plant diversity, usually entails high beta diversity in tropical (Novotny et al., 2007) and non-tropical environments (see Hodkinson, 2005 for a review). High beta diversity in the Mediterranean basin, even at a small scale, has been found for beetles (Verdú and Galante, 2002; Baselga and Jiménez-Valverde, 2007; Zamora et al., 2007; González-Megías et al., 2007). Differences in beetle-species composition in an altitudinal gradient in the same area were related to plant richness and vegetation structure (González-Megías et al., 2008), which might explain high values of beta diversity even between zones inside the same habitat. Temporal species turnover was also great in our system, with higher values of beta diversity between sampling periods than between years. Less than 30% of the species were shared between sampling periods, supporting the idea that temporal changes proved to be one of the main factors causing heterogeneity, and therefore affecting species alpha diversity (Huston, 1994; Wiens, 2000; Adler and Lauenroth, 2003; Tews

Table 2
Summary of the significant diversity–heterogeneity relationships that spatially and temporally changed (Change) and those that remained equal (No Change). Values of the beta diversity (Bray–Curtis similarity index) found between habitats, zones, years, and sampling periods, and the percentage of relationship that changed for each diversity index and spatial and temporal level. Vertical com. = Vertical complexity, Dominant pl. = % of the dominant plant.

	No change	Change	Bray–Curtis index	% Change
Between habitats	Richness	% bare soil Vertical com.	0.35	50%
	HP	Vertical com.	0.35	100%
Within habitats *Astragalus*	HP	Vertical com.	0.49	0%
Within habitats *Genista*	HP	Vertical com. Dominant pl.	% bare soil	0.46	33.33%
Between years	Richness		% bare soil Dominant pl. Plant diversity	0.62	100%
	HP		Dominant pl. Plant diversity	0.62	100%
Within years 1997	Richness	Plant diversity	Dominant pl.	0.16	50%
1998	Richness		% bare soil Dominant pl. Plant diversity	0.27	100%
	HP		Dominant pl. Plant diversity	0.27	100%

et al., 2004; Sobek et al., 2009a,b). This is evident mainly in Mediterranean ecosystems affected by strong seasonality, with species turnover occurring drastically between seasons (Zamora et al., 2007).

Our study shows no correlation between beta diversity and the changes in alpha diversity–heterogeneity relationship. Therefore, species turnover did not explain the observed spatial and temporal changes in the heterogeneity–diversity relationships. Indeed, although similarity in beetle-species composition between years was higher than between sampling periods, all significant relationships found between richness and habitat heterogeneity changed across years. On the contrary, similarity between sampling periods was very low in 1997 but only 50% of the relationship between habitat descriptors and alpha diversity changed that year. Other factors, rather than differences in species composition, should then help to explain this variability. For example, epigeal arthropod relationship with plant cover was less evident or even opposite during the winter period as a consequence of changes in soil temperature and moisture (Crist et al., 1992; Honek, 1997). Therefore, some species may have different spatial distributions in the same habitat according to microclimatic preferences (Crist et al., 1992; Niemelä et al., 1996; Atauri and de Lucio, 2001). Species richness and abundance might also vary between habitats or years due to differences in the presence of predators (Spiller and Schoener, 2001; Ives et al., 2005). Many animal species, including insects, change their behaviour in the presence of predators, for example avoiding open areas or remaining more time under leaf litter or leaves, trying to avoid predators (Head and Lawton, 1985; Resetarits, 2001; Thomson et al., 2006). Therefore, epigeal beetle preferences in the same habitat but in different areas might differ according to the abundance of their predators. In general, communities are structured by two non-mutually exclusive factors: environmental and biotic factors (Quinn and Dunham, 1983); therefore both factors should be explored to solve changes in alpha diversity–heterogeneity relationship in the Mediterranean basin rather than species turnover.

5. Conclusions

In this Mediterranean system, spatial and temporal changes in the diversity–heterogeneity relationships cannot be predicted by species turnover. This is a striking outcome suggesting that other mechanisms need to be explored to satisfactorily explain this variability. Species microhabitat selection or even predators pressure appears as alternative hypotheses to explain changes in alpha diversity–heterogeneity relationships. Our study also suggests that alpha and beta diversity patterns at the same and different spatial and temporal scales may respond to different factors.

Acknowledgements

Appendix A

The results of the linear regressions between habitat characteristics and the diversity indices (Richness and HP) between a) habitats and zones, B) years and samplings. In bold the relationships that varied between habitats/years or among zones within habitats/sampling within years. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Vertical com. = Vertical complexity, Dominant pl. = % of the dominant plant.

		Habitat		Zone					
		Astragalus	Genista	Astragalus			Genista		
				A1	A2	A3	G1	G2	G3
A) Spatial									
Richness	Vertical com.	$t_{1,28} = -0.39$	$t_{1,28} = 3.26^{**}$	$t_{1,8} = 0.35$	$t_{1,8} = -0.72$	$t_{1,8} = 0.36$	$t_{1,8} = 0.93$	$t_{1,8} = 1.15$	$t_{1,8} = 2.24$
	% bare soil	$t_{1,28} = 0.41$	$t_{1,28} = 3.53^{**}$	$t_{1,8} = 1.68$	$t_{1,8} = -0.35$	$t_{1,8} = -0.31$	$t_{1,8} = 2.18$	$t_{1,8} = 0.16$	$t_{1,8} = 2.12$
	Dominant pl.	$t_{1,28} = -0.63$	$t_{1,28} = -1.63$	$t_{1,8} = 0.06$	$t_{1,8} = -0.72$	$t_{1,8} = -1.54$	$t_{1,8} = 0.58$	$t_{1,8} = 0.58$	$t_{1,8} = -0.52$
	Plant diversity	$t_{1,28} = 1.68$	$t_{1,28} = 0.03$	$t_{1,8} = 1.18$	$t_{1,8} = -0.95$	$t_{1,8} = 1.97$	$t_{1,8} = -1.27$	$t_{1,8} = -0.51$	$t_{1,8} = 1.38$
HP	Vertical com.	$t_{1,28} = -2.47^{*}$	$t_{1,28} = 2.74^{**}$	$t_{1,8} = -2.08^{*}$	$t_{1,8} = -1.18$	$t_{1,8} = 0.52$	$t_{1,8} = 0.12$	$t_{1,8} = 0.38$	$t_{1,8} = 2.65^{*}$
	% bare soil	$t_{1,28} = 0.04$	$t_{1,28} = 0.89$	$t_{1,8} = 0.89$	$t_{1,8} = -0.12$	$t_{1,8} = -1.23$	$t_{1,8} = -0.16$	$t_{1,8} = -0.77$	$t_{1,8} = 3.24^{*}$
	Dominant pl.	$t_{1,28} = -1.53$	$t_{1,28} = -0.37$	$t_{1,8} = 0.54$	$t_{1,8} = -0.78$	$t_{1,8} = -2.06$	$t_{1,8} = -0.47$	$t_{1,8} = 2.68^{*}$	$t_{1,8} = -0.24$
	Plant diversity	$t_{1,28} = 0.24$	$t_{1,28} = 1.46$	$t_{1,8} = -0.99$	$t_{1,8} = 0.68$	$t_{1,8} = 1.34$	$t_{1,8} = 0.12$	$t_{1,8} = -0.57$	$t_{1,8} = 0.50$
		Year		Sampling			
		1997	1998	S1	S2	S3	S4
B) Temporal							
Richness	Vertical com.	$t_{1,118} = -0.04$	$t_{1,118} = -0.10$	$t_{1,58} = -0.59$	$t_{1,58} = 1.12$	$t_{1,58} = -1.64$	$t_{1,58} = 0.91$
	% bare soil	$t_{1,118} = -1.13$	$t_{1,118} = 4.99^{***}$	$t_{1,58} = -1.40$	$t_{1,58} = -0.80$	$t_{1,58} = 2.03$	$t_{1,58} = 5.10^{***}$
	Dominant pl.	$t_{1,118} = -2.76^{*}$	$t_{1,118} = 0.88$	$t_{1,58} = 3.58^{**}$	$t_{1,58} = -1.68$	$t_{1,58} = -0.89$	$t_{1,58} = 2.78^{**}$
	Plant diversity	$t_{1,118} = 1.97^{*}$	$t_{1,118} = -2.29^{*}$	$t_{1,58} = 2.48^{*}$	$t_{1,58} = 1.45$	$t_{1,58} = 0.64$	$t_{1,58} = -4.60^{***}$
HP	Vertical com.	$t_{1,118} = 0.90$	$t_{1,118} = 0.16$	$t_{1,58} = -0.76$	$t_{1,58} = 1.29$	$t_{1,58} = -0.54$	$t_{1,58} = 0.39$
	% bare soil	$t_{1,118} = -0.35$	$t_{1,118} = 1.39$	$t_{1,58} = 0.27$	$t_{1,58} = -0.57$	$t_{1,58} = 0.40$	$t_{1,58} = 1.40$
	Dominant pl.	$t_{1,118} = 0.53$	$t_{1,118} = -2.26^{*}$	$t_{1,58} = -2.03$	$t_{1,58} = 0.13$	$t_{1,58} = 0.09$	$t_{1,58} = 2.85^{**}$
	Plant diversity	$t_{1,118} = 0.57$	$t_{1,118} = -2.49^{*}$	$t_{1,58} = 1.52$	$t_{1,58} = 0.11$	$t_{1,58} = -0.47$	$t_{1,58} = -2.80^{*}$

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral. Ecol. 26, 32–46.

Anderson, M.J., 2005. PERMANOVA: A FORTRAN Computer Program for Permutational Multivariate Analysis of Variance. Department of Statistics, University of Auckland, New Zealand.

Adler, P.B., Lauenroth, W.K., 2003. The power of time: spatiotemporal scaling of species diversity. Ecol. Lett. 6, 749–756.

Atauri, J.A., de Lucio, V., 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Land. Ecol. 16, 147–159.

Balletto, E., Casale, A., 1991. Mediterranean insect conservation. In: Collins, N.M., Thomas, J.A. (Eds.), The Conservation of Insects and Their Habitats. Academic Press, London, pp. 121–142.

Barton, P.S., Manning, A., Gibb, H., Lindermayer, D.B., Cunningham, S.A., 2010. Fine-scale heterogeneity in beetle assemblages under co-occurring *Eucalyptus* in the same subgenus. J. Biogeogr. doi:10.1111/j.1365-2699.2010.02349.x.

Baselga, A., Jiménez-Valverde, A., 2007. Environmental and geographical determinants of beta diversity of leaf beetles (Coleoptera: Chrysomelidae) in the Iberian Peninsula. Ecol. Entomol. 32, 312–318.

Beck, J., Chey, C.V., 2007. Beta-diversity of geometrid moths from northern Borneo: effects of habitat, time and space. J. Anim. Ecol. 76, 230–237.

Blondel, J., Aronson, J., 1999. Biology and Wildlife of the Mediterranean. Oxford University Press, Oxford.

Bohac, J., 1999. Staphylinid beetles as bioindicators. Agric. Ecosyst. Environ. 74, 357–372.

Cardinale, B.J., Nelson, K., Palmer, M.A., 2000. Linking species diversity to the functioning of ecosystems: on the importance of the environmental context. Oikos 91, 175–183.

Colwell, R.K., 2005. Estimates – Statistical Estimation of Species Richness and Shared Species from Samples Version 7.5. User's guide and application published at: http://purl.oclc.org/estimates.

Crist, T.O., Veech, J.A., 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying alpha, beta, and gamma diversity with sample size and area. Ecol. Lett. 9, 923–932.

Crist, T., Guertin, D., Wiens, J., Milne, B., 1992. Animal movement in heterogeneous landscape: an experiment with *Eleodes* beetles in shortgrass prairie. Funct. Ecol. 6, 536–544.

Davidowitz, G., Rosenzweig, M.L., 1998. The latitudinal gradient of species diversity among North American grasshoppers (Acridiidae) within a single habitat: a test of the spatial heterogeneity hypothesis. J. Biogeogr. 25, 553–560.

De Mas, E., Guillem, C., Pretus, J.L., Ribera, C., 2009. Spatial modelling of spider biodiversity: matters of scale. Ecography 19, 1945.

Digweed, S.C., Currie, C.R., Carcamo, H.A., Spence, J.R., 1995. Digging out the "digging-in effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia 39, 561–576.

Dowdy, S., Wearden, S., 1985. Statistics for Research, second ed. Wiley Interscience, New York.

Edwards, A.L., 1985. Multiple Regression and the Analysis of Variance and Covariance, second ed. W.H. Freeman and Company, New York.

García-Charton, J.A., Pérez-Ruzafa, A., 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fish. Res. 42, 1–20.

Gaston, K.J., Davies, R.G., Orme, C.D.L., Olson, V.A., Thomas, G.H., Ding, T., Rasmussen, P.C., Lennon, J.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M., 2007. Spatial turnover in the global avifauna. Proc. R. Soc. Ser. B 274, 1567–1574.

González-Megías, A., Gómez, J.M., Sánchez-Piñero, F., 2004. Effects of ungulates on epigeal arthropods in Sierra Nevada National Park (SE Spain): The importance of temporal variability. Biodivers. Conserv. 13, 733–752.

González-Megías, A., Gómez, J.M., Sánchez-Piñero, F., 2007. Diversity–habitat heterogeneity relationship at different spatial and temporal scales. Ecography 30, 31–41.

González-Megías, A., Gómez, J.M., Sánchez-Piñero, F., 2008. Factor determining beetle richness and composition along an altitudinal gradient in the high mountains of Sierra Nevada National Park (Spain). EcoScience 15, 429–441.

Gotelli, N.J., Entsminger, G.L., 2004. EcoSim: Null Models Software for Ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear, Jericho, VT 05465. http://garyentsminger.com/ecosim/index.htm.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M., Chey, V.K., 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. J. Appl. Ecol. 40, 150–162.

Head, P.A., Lawton, J.H., 1985. Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. Ecol. Entomol. 10, 29–42.

Hill, J.K., Hamer, K.C., Lace, L.A., Banham, W.M.T., 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. J. Appl. Ecol. 32, 754–760.

Hodkinson, I.D., 2005. Terrestrial insects along elevational gradients: species and community responses to altitude. Biol. Rev. 80, 489–513.

Hodkinson, I.D., Jackson, J.K., 2005. Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. Environ. Manag. 35, 649–666.

Honek, A., 1997. The effect of plant cover and weather on the activity and density of ground surface arthropods in a fallow field. In: Honek, A. (Ed.), Entomological Research in Organic Agriculture. AB Academic Publishers, Oxford, pp. 203–210.

Humphrey, J., Hawes, C., Peace, A., Ferris-Kaan, R., Jukes, M., 1999. Relationships between insect diversity and habitat characteristics in plantation forests. Forest Ecol. Manag. 113, 11–21.

Huston, M., 1994. Biological Diversity. The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

Ives, A.R., Cardinale, B.J., Snyder, W.E., 2005. A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. Ecol. Lett. 8, 102–116.

Krasnov, B.R., Shenbrot, G.I., Mouillot, D., Khokhlova, I.S., Poulin, R., 2006. Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographical distance or faunal similarity? J. Biogeogr. 32, 633–644.

Kumar, S., Simonson, S.E., Stohlgren, T.J., 2008. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. Biodivers. Conserv. 18, 739–763.

Lassau, S.A., Hochuli, D.F., Cassis, G., Reid, C.A.M., 2005. Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? Divers. Distrib. 11, 73–82.

Legendre, P., Lapointe, F.J., Casgrain, P., 1994. Modeling brain evolution from behavior: a permutational regression approach. Evolution 48, 1487–1499.

Levin, S., 1992. The problem of pattern and scale in ecology. The Robert H. McArthur Award Lecture. Ecology 73, 1943–1967.

Lobo, J.M., Lumaret, J.P., Jay-Robert, P., 2001. Diversity, distinctiveness, and conservation status of the Mediterranean coastal dung beetle assemblage in the Regional Natural Park of Camargue (France). Divers. Distrib. 7, 257–270.

Magura, T., Tóthmérész, B., Molnár, T., 2000. Spatial distribution of carabids along grass-forest transects. Acta Zool. Acad. Scient. Hung. 46, 1–17.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Malden, Massachusetts.

McCune, B., Mefford, M.J., 1999. PC-ORD-Multivariate Analysis of Ecological Data, Vers. 5.0. MjM Software, Gleneden Beach, Oregon.

McKnight, M., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S., Stuart, S.N., 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. Plos Biol. 5, 2424–2432.

Médail, F., Quézel, P., 1999. Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. Conserv. Biol. 13, 1510–1513.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Niemelä, J., 1997. Invertebrates and boreal forest management. Conserv. Biol. 11, 601–610.

Niemelä, J., Haila, I., Punttila, P., 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19, 352–368.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M., Setliff, G.P., Darrow, K., Stewart, A.J.A., Auga, J., Isua, B., Molem, K., Manumbor, M., Tamtiai, E., Mogia, M., Weiblen, G.D., 2007. Low beta diversity of herbivorous insects in tropical forests. Nature 448, 692–695.

Numa, C., Verdú, J.R., Sánchez, A., Galante, E., 2009. Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. Divers. Distrib. 15, 489–501.

Palmer, M., White, P.S., 1994. On the existence of ecological communities. J. Veg. Sci. 5, 279–282.

Quinn, J.F., Dunham, A.C., 1983. On hypothesis testing in ecology and evolution. Am. Nat 122, 602–617.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers. Conserv. 12, 487–506.

Resetarits, W.J., 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). Oecologia 129, 155–160.

Romero-Alcaraz, E., Avila, J.M., 2000. Landscape heterogeneity in relation to variation in epigaeic beetle diversity of a Mediterranean ecosystem. Implications for conservation. Biodivers. Conserv. 9, 985–1005.

Sobek, S., Steffan-Dewenter, I., Scherber, C., Tscharntkel, T., 2009a. Spatiotemporal changes of beetle communities across a tree diversity gradient. Divers. Distrib. 15, 660–670.

Sobek, S., Goßner, M., Scherber, C., Steffan-Dewenter, I., Tscharntkel, T., 2009b. Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera). Ecol. Entomol. 34, 772–782.

Speight, M.R., Hunter, M.D., Watt, A.D., 1999. Ecology of Insects. Concepts and Application. Blackwell Science, Oxford.

Spiller, D.A., Schoener, T.W., 2001. An experimental test for predator-mediated interactions among spider species. Ecology 82, 1560–1570.

Stewart, A.J.A., John, E.A., Hutchings, M.J., 2000. The world is heterogeneous: ecological consequences of living in a patchy environment. In: Stewart, A.J.A., John, E.A., Hutchings, M.J. (Eds.), The Ecological Consequences of Environmental Heterogeneity. Blackwell Science, Oxford, pp. 1–8.

Sullivan, T.P., Sullivan, D.S., 2001. Influence of variable retention harvest on forest ecosystems. II. Diversity and population dynamics of small mammals. J. Appl. Ecol. 38, 1234–1252.

Sutherland, W., 1996. Ecological Census Techniques. A Handbook. Cambridge University Press, Cambridge.

Tews, J., Brose, U., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, M., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Thomson, R.L., Forsman, J.T., Sardá-Palomera, F., Mönkkönen, M., 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. Ecography 29, 507–514.

Verdú, J.R., Galante, E., 2002. Climatic stress, food availability and human activity as determinants of endemism patterns in the Mediterranean region: the case of dung beetles (Coleoptera, Scarabaeoidea) in the Iberian Peninsula. Divers. Distrib. 8, 259–274.

Ward, D.F., New, T.R., Yen, A.L., 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. J. Insect Conserv. 5, 47–53.

Wettstein, W., Schmid, B., 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J. Appl. Ecol. 36, 363–373.

Wiens, J.A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: Stewart, A.J.A., John, E.A., Hutchings, M.J. (Eds.), The Ecological Consequences of Environmental Heterogeneity. Blackwell Science, Oxford, pp. 9–31.

Wiens, J.A., Rotenberry, J.T., 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecol. Monogr. 51, 21–41.

Wilby, A., Shachak, M., 2000. Harvester ant response to spatial and temporal heterogeneity in seed availability: pattern in the process of granivory. Oecologia 125, 495–503.

Zamora, J., Verdú, J.R., Galante, E., 2007. Species richness in Mediterranean agro-ecosystems: Spatial and temporal analysis for biodiversity conservation. Biol. Conserv. 134, 113–121.

Zar, J.H., 1996. Biostatistical Analysis, third ed. Prentice-Hall, Englewood Cliffs, New Jersey.