Acta Oecologica 37 (2011) 179–186

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

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

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ARTICLE INFO

Article history:
Received 9 October 2009
Accepted 12 January 2011
Available online 26 February 2011

Keywords:
Similarity
Species composition
PERMANOVA
Mediterranean ecosystems
Habitat-heterogeneity hypothesis

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.

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

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doi:10.1016/j.actao.2011.01.011

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 overwintering 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).