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Temporally variable environments maintain more beta-diversity in Mediterranean landscapes

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ABSTRACT

We examined the relationships between different environmental factors and the alpha and beta-diversity of terrestrial vertebrates (birds, mammals, amphibians and reptiles) in a Mediterranean region at the landscape level. We investigated whether the mechanisms underlying alpha and beta-diversity patterns are influenced by energy availability, habitat heterogeneity and temporal variability and if the drivers of the diversity patterns differed between both components of diversity. We defined alpha-diversity as synonym of species richness whereas beta-diversity was measured as distinctiveness. We evaluated a total of 13 different predictors using generalized linear mixed model (GLMM) analysis. Habitat spatial heterogeneity increased alpha-diversity, but contrastingly, it did not significantly affect beta-diversity among sites. Disturbed landscapes may show higher habitat spatial variation and higher alpha-diversity due to the contribution of highly generalist species that are wide-distributed and do not differ in composition (beta-diversity) among different sites within the region. Contrastingly, higher beta-diversity levels were negatively related to more stable sites in terms of temporal environmental variation. This negative relationship between environmental stability and beta-diversity levels is explained in terms of species adaptation to the local environmental conditions. Our study highlights the importance of temporal environmental variability in maintaining beta-diversity patterns under highly variable environmental conditions.

1. Introduction

Changes in ecosystem processes, such as energy and material flows, or biological and abiotic interactions may be indirectly detected by changes in diversity patterns (Chapin et al., 2000). Therefore, changes in diversity patterns may be used as a surrogate to detect ecosystem responses to environmental changes. However, diversity patterns may vary between areas and scales in ways that are not yet completely understood. To gain insight into how diversity is affected by ecosystem characteristics, we can consider diversity to be an emergent consequence of the ecological processes (Brown et al., 2001) and hence we can study how diversity patterns are affected by ecosystem features such as vegetation, climate and other environmental factors (e.g. Stegen et al., 2013). The latter approach is particularly useful for assessing if human induced environmental changes lead to changes in diversity patterns.

Traditionally, three different components of species diversity have been recognized: alpha-diversity which describes the number of species within a place (i.e. species richness); beta diversity which describes the change in species composition between places; and gamma or regional diversity (Whittaker et al., 2001). In recent years, there has been a marked increase in the scientific attention paid to beta-diversity (Anderson et al., 2011; Dornelas et al., 2006; Meynard et al., 2011; Myers et al., 2013; Stegen et al., 2013). A priori, we would expect alpha- and beta-diversity to be related, since the mechanisms associated with richness spatial patterns are also related with changes in species composition among areas (Qian and Ricklefs, 2007). However, different environmental factors may affect both diversity components in different ways (Legendre et al., 2005) and the congruence between diversity within (alpha) and among (beta) areas may differ between taxonomic groups and between different areas (Kessler et al., 2009).

Many competing hypotheses have been proposed to understand the mechanisms that shape and maintain the diversity patterns. Among them, the energy hypothesis, the environmental stability hypothesis and the habitat heterogeneity hypothesis are the most

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often cited in the scientific literature. The energy hypothesis relates diversity to the energy available for ecological processes. Areas with higher solar radiation and precipitation have higher primary production and they favor species co-occurrence, i.e. higher alpha-diversity (Hawkins et al., 2003; Luo et al., 2012). Similarly, increasing productivity is also expected to promote dissimilarity in species composition among sites within a region i.e. beta-diversity (Chase and Leibold, 2002; Chalcraft et al., 2004, 2008; Sandel and Corbin, 2012). The habitat heterogeneity hypothesis assumes that spatial variation (i.e. topographical, landscape, vegetation variability) may provide more niches, thus increase species diversity (Meynard et al., 2011; Stegen et al., 2013). Environmental variation occurs not only in space, but also in time, and spatio-temporal stochasticity has been identified as a major driver of diversity patterns (Dornelas et al., 2006). The environmental stability hypothesis posits that stable environmental conditions can lead to higher diversity (Fjeldsa, 1997). Relatively unchanging physical variables allow more species to co-exist and, consequently, lead to larger alpha diversity. Alternatively, temporally variable environments can maintain species richness via the storage effect (Chesson, 1994; Chesson et al., 2004), a mechanism for the coexistence of competing species (Chesson, 2000). Similarly, moderate disturbance frequencies can maximize species richness by maintaining species with a range of strategies (e.g. competitive vs. weedy species). Regarding beta-diversity, larger differences in species composition (i.e. beta-diversity) are predicted under more stable environmental conditions (Meynard et al., 2011) because environmental stability is predicted to allow for specialization (Currie, 1991). Although it is known that areas with high concentrations of endemic species are characterized by a local reduction in ecoclimatic variability (Fjeldsa, 1997), the opposite might also occur. For instance, very stable conditions can lead to the dominance of one species (i.e. competitive exclusion principle; Levin, 1970). However, the relationship between temporal variation and diversity has only rarely been explored (Fjeldsa, 1997; Luo et al., 2012; Meynard et al., 2011), and there is still a lack of information on how temporal variation generates patterns of biological diversity. On the other hand, patterns of biodiversity may also emerge from neutral processes (Thompson and Townsend, 2006) and these processes, such as dispersal and speciation, may lead to a random variation in species composition that generates spatial autocorrelation.

Environmental conditions under Mediterranean climates are highly variable throughout the year, which can be seen in their high intra-annual variability (Cowling et al., 1996) and in their marked spatio-temporal variation in the availability of resources. In addition, the Mediterranean Basin has been identified as one of the most important biodiversity hotspots in the world (Myers et al., 2000). Its ecosystems are predicted to be some of the most sensitive to global-change drivers and they are projected to experience the greatest biodiversity changes in the next decades.

The local spatial scale of studies on ecological communities is frequently too small for investigating regional processes whereas the biogeographical scale is too large for detecting the local processes. On the contrary, the landscape level, i.e. areas of several hundred to thousands of hectares, may be an adequate scale for measuring alpha- and beta-diversity because this spatial level of analysis enables the detection of both local and regional factors affecting species distribution (Chalcraft et al., 2004).

In this paper, we examine the relationships between different environmental factors and the alpha and beta-diversity of terrestrial vertebrates (birds, mammals, amphibians and reptiles) in a Mediterranean region at the landscape level. We investigated whether the mechanisms underlying alpha and beta-diversity patterns are influenced by energy, habitat heterogeneity and temporal variation at the present time, and if the drivers of the diversity patterns differ between both components of diversity. We evaluated several hypothesis predicting alpha and beta-diversity patterns. First, (1) we predicted that higher energy availability in the ecosystem supports more alpha- and beta-diversity. Second, (2) habitat heterogeneity (i.e., within-patch variation) was expected to promote more alpha- and beta-diversity. (3) We also expected that alpha and beta-diversity levels will be lower in areas with higher degree of temporal variation at the present time. Overall, (4) we expected alpha- and beta-diversity patterns to be related, since the mechanisms associated with richness spatial patterns are also related with changes in species composition among areas. Finally, (5) historical factors affecting diversity distribution (i.e. neutral processes such as dispersal and speciation) were expected to be more important in those vertebrate taxa with moderate dispersal abilities and low colonization capabilities (i.e. reptiles and amphibians; Cody, 2006; Vences and Wake, 2007).

2. Materials and methods

2.1. Study area and data on species distribution

Our study area, the Andalusia Region (southern Spain), is a remarkably diverse area in terms of biodiversity. Its climate is Mediterranean with a marked environmental gradient (annual rainfall varies from 170 mm/year to more than 1800 mm/year) and a wide elevation range (from sea level to approximately 3500 m.a.s.l.). These gradients involve a high degree of spatial and temporal variation in vegetation and landscape conditions. Data on terrestrial vertebrate distribution was obtained from the Atlases of vertebrates in Spain (Palomo, 2002; Pleguezuelos et al., 2002; Martí and Moral, 2003; Ministerio de Medio Ambiente, 2003) which were provided as digital vector files (ArcView format) from the Spanish Ministry of the Environment Web site (http://www.mma.es/portal/secciones/biodiversidad/inventarios/inb/index.htm). Databases cover the distribution of 60 mammalian species, 25 reptiles, 17 amphibians and 206 breeding bird species, all native species, across Andalusia. These databases were mapped at a spatial resolution of 10 × 10 km (940 different squares were taken into account) and contained the distribution of species on the basis of presence/absence data. Data for herptile species were collected between 2000 and 2002 and previous bibliographic information was incorporated, with 70% of the citations registered after 1992. Field work for breeding bird databases was developed between 1998 and 2002, although complementary previous citations since 1985 were added. Mammal presence data belonged to bibliographic information and field collection until 2002.

We defined alpha-diversity as a synonym of species richness (number of terrestrial vertebrate species in each 10 × 10 km square). As far as beta-diversity is concerned, many different indexes using presence-absence data have been proposed (Anderson et al., 2011; Koleff et al., 2003). As an alternative measure to the classical metrics calculated directly from local (alpha) and regional (gamma) diversity, multivariate measures, based on pairwise similarities among sample units, are among the most commonly used (Anderson et al., 2011). The pairwise dissimilarity matrix among a set of sites is in itself an expression of the beta diversity of that set of sites (Whittaker, 1972). In the present study beta-diversity is measured and interpreted as distinctiveness ("differentiation diversity", sensu Jurasinski et al., 2009) and its value measures the "rarity" of each focal cell. Following the recommendation of Lennon et al. (2001), we opted to use Simpson's dissimilarity index (β_{dis}) for all our analyses: