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The unusual suspect: Land use is a key predictor of biodiversity patterns in the Iberian Peninsula

Inês Santos Martins [a, b, *], Vânia Proença [c], Henrique Miguel Pereira [a, b, d]

[a] Center for Environmental Biology, Faculty of Sciences of the University of Lisbon, Edifício C2, Campo Grande, 1749-016 Lisboa, Portugal
[b] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[c] IN+, Center for Innovation, Technology and Policy Research, Energy and Environment Scientific Area, DEM, Instituto Superior Técnico, University of Lisbon, Av. Rovisco Pais n° 1, 1049–001 Lisbon, Portugal
[d] Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany

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ABSTRACT

Although land use change is a key driver of biodiversity change, related variables such as habitat area and habitat heterogeneity are seldom considered in modeling approaches at larger extents. To address this knowledge gap we tested the contribution of land use related variables to models describing richness patterns of amphibians, reptiles and passerines in the Iberian Peninsula. We analyzed the relationship between species richness and habitat heterogeneity at two spatial resolutions (i.e., 10 km × 10 km and 50 km × 50 km). Using both ordinary least square and simultaneous autoregressive models, we assessed the relative importance of land use variables, climate variables and topographic variables. We also compare the species–area relationship with a multi-habitat model, the countryside species–area relationship, to assess the role of the area of different types of habitats on species diversity across scales. The association between habitat heterogeneity and species richness varied with the taxa and spatial resolution. A positive relationship was detected for all taxa at a grain size of 10 km × 10 km, but only passerines responded at a grain size of 50 km × 50 km. Species richness patterns were well described by abiotic predictors, but habitat predictors also explained a considerable portion of the variation. Moreover, species richness patterns were better described by a multi-habitat species-area model, incorporating land use variables, than by the classic power model, which only includes area as the single explanatory variable. Our results suggest that the role of land use in shaping species richness patterns goes beyond the local scale and persists at larger spatial scales. These findings call for the need of integrating land use variables in models designed to assess species richness response to large scale environmental changes.
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1. Introduction

Explaining the spatial patterns of species richness is a central goal in ecology (Rosenzweig, 1995). Several explanatory factors have been identified, including energy availability, habitat heterogeneity, area, evolutionary history, and geometric constraints, that is, physiographical and physiological boundaries (Rahbek and Graves, 2001).

Land use change has a direct effect on some of these factors, namely on habitat heterogeneity and area, and was the main direct driver of biodiversity loss and change in terrestrial systems at regional and global scales during the past century (Pereira et al., 2012). While the role of land use in shaping species richness patterns at local scales is well described (Atauri and de Lucio, 2001; Tews et al., 2004), there is still a knowledge gap regarding its effect at regional and global scales.

On the other hand, climate is often reported as the main predictor of species richness at large spatial extents (Hawkins et al., 2003; Field et al., 2009). Climate affects species richness, from variations in productivity to establishing physiological limits (Clarke and Gaston, 2006). However, given current and predicted rates of land use change, modeling approaches largely based on climate will be limited in their predictive power (Thuiller et al., 2004). For example, species that are highly sensitive to habitat change and degradation may be absent from areas with potentially suitable climate conditions. In addition, it has been reported that the interacting effects of climate change and land use change may

* Corresponding author. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.
E-mail addresses: ines.martins@idiv.de (I.S. Martins), vania.proenca@ist.utl.pt (V. Proença), hpereira@idiv.de (H.M. Pereira).

have a greater impact on biodiversity than their individual effects (Clavero et al., 2011; Mantyka-pringle et al., 2012).

In addition to the relative effect of land use and climate on species richness patterns, there is an ongoing debate about the concurrent role of habitat composition or heterogeneity (i.e., number of habitats in an area) and habitat area, both land use related variables, in determining species richness in a particular region or scale (MacArthur and Wilson, 1967; Rosenzweig, 1995; Tjørve, 2002; Tews et al., 2004; Desrochers et al., 2011). However, disentangling the individual effect of each factor is not straightforward because the two factors tend to be correlated, that is, larger spatial areas also tend to encompass a larger number of habitats (Ricklefs and Lovette, 1999; Triantis et al., 2003; Desrochers et al., 2011).

The response of species richness to habitat area loss is often assessed using species—area relationship (SAR) models (Arrhenius, 1921; Brown and Lomolino, 1998). The classic SAR or power model (Arrhenius, 1921) assumes that the number of species is mainly determined by habitat area, and that the habitat is uniform and continuous. Hence, when using the classic SAR, only the responses to changes in habitat area are captured, leaving out the responses to changes in habitat composition. This is particularly relevant in those situations where land use change causes habitat modification instead of real habitat loss (Guilherme and Pereira, 2013; Proença and Pereira, 2013). A possible approach to this issue is the use of multi-habitat SARs (Tjørve, 2002; Triantis et al., 2003; Pereira and Daily, 2006; Koh and Ghazoul, 2010).

Moreover, though area and habitat heterogeneity tend to be positively correlated, their combined effect on species richness may generate a unimodal relationship between species richness and habitat heterogeneity, due to a trade-off between species pool size and the probability of stochastic extinctions of species with low population sizes (Allouche et al., 2012), or in other words, between average habitat size and population size. Therefore, the shape of the relationship will vary depending on the niche width of species in the community, that is, specialist species (narrower niche) will be more affected by declining habitat size as habitat number increases than generalist species (wider niche). Still, more research is needed regarding the shape of this relationship, and in particular, there is still a lack of studies that consider multiple spatial scales and taxa (Tews et al., 2004).

Finally, the relative importance of explanatory factors in shaping species richness patterns may vary with the scale of analysis (Rahbek and Graves, 2001; Willis and Whittaker, 2002; Luoto et al., 2007; Hortal et al., 2008). Therefore, when modeling species richness distribution the choice of spatial scale (i.e., grain size or resolution and extent of the data or overall size of the study area) can directly affect results and limit their comparison with similar studies (Rahbek, 2005).

Here, we examine the relationship between land use related variables, and the species richness distribution of terrestrial vertebrates in the Iberian Peninsula. We investigate the added value of land use variables to models incorporating well accepted predictors, namely climate, topography and area, when explaining species richness patterns. We start by testing the association between habitat heterogeneity and species richness of amphibians, reptiles and passerines, at two different spatial resolutions (i.e., 10 km × 10 km and 50 km × 50 km). We then analyze the individual effects of sets of climate, topography, and habitat variables on the richness of these taxa, and proceed to explore their joint effects using a multimodel approach, at a spatial resolution of 10 km × 10 km. Finally, we investigate the contribution of land use variables to species-area models, by comparing the fit of the countryside SAR model that considers species affinity to different land uses, with the fit of the classic SAR model. We predict that species richness will show a unimodal response to habitat heterogeneity as predicted by the area-heterogeneity trade-off hypothesis (Allouche et al., 2012) at 10 km × 10 km resolution, but also that this pattern will be less perceptible at the 50 km × 50 km resolution, due to weaker area effects on population size. Moreover, we hypothesize that land use related variables play a role in shaping species richness patterns beyond local scales.

2. Methods

2.1. Study area

We selected the Iberian Peninsula as the study area. The environmental context of the Iberian Peninsula, between two biogeographic regions (the Mediterranean and the Atlantic) and featuring several mountain chains, grants this region a high diversity of habitats and species communities. The Mediterranean region encompasses almost the entire surface of Spain and Portugal and is characterized by warm to hot, dry summers with a lengthy period of drought. The Atlantic region includes the north and northwest coastland of the peninsula, and is characterized by cold winters and lack of a distinct dry season. The elevation ranges from sea level to 3478 m, and the mean annual air temperature ranges from below 2.5 °C in areas at highest altitude, namely in the Pyrenees, to temperatures higher than 17 °C in southeast Spain. Mean annual precipitation shows a large spatial variability, with the highest values above 2200 mm and usually in mountain areas, and the lowest values being below 300 mm in the southeast of Spain (AEMet and IM, 2011).

2.2. Data sources

We retrieved species distribution data in 10 km × 10 km UTM cells in the Iberian Peninsula from published atlases for 182 vertebrate species (Fig. 1): 87 passerines (Martí and del Moral, 2003; Equipa Atlas, 2008), 64 reptiles and 31 amphibians (Pleguezuelos et al., 2002; Loureiro et al., 2008). These taxa were selected due to the availability of high quality data on their distribution at the Iberian scale. We excluded marine and aquatic species.

We merged two land cover datasets (Fig. 2, for more detail see Table A.1 in Supplementary Information): the Portuguese land cover map, COS'90 (IGP, 1990), and the land cover map of the Second Spanish National Forest Inventory, IFN2 (MARM, 1998). Water bodies, rocky areas, human-dominated areas (e.g. urban fabric, quarries, green urban areas, etc.) and unclassified land cover were excluded from both datasets. We intersected the land cover maps with the 10 km × 10 km UTM grid and selected grid cells with at least 25% cover, resulting in a final set of 5885 cells. The percentage cover of each habitat in each cell was calculated using ArcGIS 9.3 (ESRI, 2009). We derived climatic variables from the WorldClim dataset on a 1 km resolution (Hijmans et al., 2005), and collected topographic data from the United States Geological Survey HYDRO 1 km digital terrain model for Europe (USGS, 2000). Slope inclination and aspect variables were combined in a Radiation Index (RI = ƒ(aspect + inclination + latitude); Oke, 1987). We then aggregated these variables in a 10 km × 10 km UTM grid using ArcGIS 9.3 (ESRI, 2009), to match the resolution of species and land cover data.

To avoid multicollinearity between the independent variables, we performed pairwise correlations tests using the Spearman's rank correlation coefficient. Variables strongly correlated (i.e., rho > 0.7) were identified and the variables explaining less variance overall were removed from the analysis (Elith et al., 2006; Wisz and Guisan, 2009).