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Original article

Climate and landscape explain richness patterns depending on the type of species' distribution data

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ABSTRACT

Understanding the patterns of species richness and their environmental drivers, remains a central theme in ecological research and especially in the continental scales where many conservation decisions are made. Here, we analyzed the patterns of species richness from amphibians, reptiles and mammals at the EU level. We used two different data sources for each taxon: expert-drawn species range maps, and presence/absence atlases. As environmental drivers, we considered climate and land cover. Land cover is increasingly the focus of research, but there still is no consensus on how to classify land cover to distinct habitat classes, so we analyzed the CORINE land cover data with three different levels of thematic resolution (resolution of classification scheme → less to more detailed). We found that the two types of species richness data explored in this study yielded different richness maps. Although, we expected expert-drawn range based estimates of species richness to exceed those from atlas data (due to the assumption that species are present in all locations throughout their region), we found that in many cases the opposite is true (the extreme case is the reptiles where more than half of the atlas based estimates were greater than the expert-drawn range based estimates). Also, we detected contrasting information on the richness drivers of biodiversity patterns depending on the dataset used. For atlas based richness estimates, landscape attributes played more important role than climate while for expert-drawn range based richness estimates climatic variables were more important (for the ectothermic amphibians and reptiles). Finally we found that the thematic resolution of the land cover classification scheme, also played a role in quantifying the effect of land cover diversity, with more detailed thematic resolution increasing the relative contribution of landscape attributes in predicting species richness.

1. Introduction

Large-scale species distributional maps are fundamental for understanding macroecological patterns, such as the spatial patterns and drivers of species richness (e.g. Rodríguez et al., 2005; Jetz et al., 2008), or even for applied conservation issues such as species' extinction risk and conservation status (e.g. IUCN, 2013). There is considerable variation in how such species distribution maps are generated, depending on the availability of knowledge concerning the species (e.g. habitat preferences of species) and concerning the environmental variation (e.g. availability and resolution of environmental datasets). Maps of richness patterns are usually constructed from (i) expert-drawn species range maps and (ii) occurrence data (e.g. field survey data, museum records, point observations, interpolated or modelled distribution maps) (Graham and Hijmans, 2006).

Over broad scales, survey data collection is rare, thus most continental and global biodiversity analyses have been based on expert-drawn range maps. Hawkins et al. (2003) reviewed 85 such analyses where 69% used expert-drawn range maps at global and continental scales despite their limitations (Hurlbert and Jetz, 2007). Expert-drawn range maps are a drawn outline encompassing all recorded occurrences of a species (Gaston, 1996). This type of data may be prone to commission errors, assuming that species are distributed across the entire area of their ranges (which often includes areas of unfavorable habitat) (Gaston, 2003). Thus, 'expert-

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drawn range overlap maps' might overestimate species richness because they include areas where species do not occur (Gaston, 2003; Cantú-Salazar and Gaston, 2013). However, atlas data are also not perfect, since they may be prone to omission errors. In atlas data presence is based on records, so presences are quite reliable, but absence is based on lack of observations which may be due to true species absence but may also be due to other causes, e.g. inadequate or spatially biased sampling, etc. (Pulliam, 2000).

What is clear is that both approaches are approximations of species distribution and try to represent where the species actually occur. All methods are prone to errors and imperfections (none of them give us "exactly" where a species is distributed) which might affect any conclusions driven by them (La Sorte and Hawkins, 2007). This mismatch has been attributed to an inherent difference in the spatial resolution at which expert-drawn range maps and atlases capture distributional information (expert-drawn range map data are more coarse grained while survey data more fine grained) (Hurlbert and Jetz, 2007).

Species richness patterns are often driven by different environmental variables across different scales (Rahbek and Graves, 2001). A substantial discrepancy between atlas and expert-drawn range map diversity patterns would have important implications on the inference regarding the explanatory power of environmental predictors (Hurlbert and White, 2005). Climate (e.g. temperature, precipitation and their seasonalities) and productive energy (e.g. net primary productivity, actual evapotranspiration) are often considered as the major determinants of biodiversity patterns (Rodríguez et al., 2005), while the role of landscape attributes (e.g. landscape diversity: number of landscape classes) remains unclear. Climatic variables account for more than 60% of the variation in species richness patterns (Hawkins et al., 2003). The explanatory power of landscape attributes for biodiversity patterns strongly improves the power of climate (e.g. for birds, Reino et al., 2013; for terrestrial vertebrates, Xu et al., 2014). However, other studies argue that landscape configuration variables did not contribute significant to climatic factors (Thuiller et al., 2004; Triviño et al., 2011). One possible explanation for these contradictory findings is the difficulty of classifying landscape in ecologically meaningful schemes (Herold et al., 2008; Tuanmu and Jetz, 2014).

In many landscape ecology studies, land cover is classified in only few (10 or fewer) classes while many studies reclassify preexisting data sets of higher thematic resolution to only a few classes (e.g. Reino et al., 2013; Xu et al., 2014). However, a number of studies at continental scales have used land cover classification with more than 80 land cover classes (e.g. Belmaker and Jetz, 2011; Tuanmu and Jetz, 2014). Moreover, thematic resolution significantly affected the value of landscape metrics (Buyantuyev and Wu, 2007; Kallimanis and Koutsias, 2013). There is a tradeoff implied in the thematic resolution. Few classes mean few variables needed to quantify the landscape composition, but it also means losing information on the landscape heterogeneity and diversity. So, it remains unclear if and how the thematic resolution of land cover affects the predictive power of land cover diversity to explain the diversity spatial patterns.

Several studies concluded that diversity patterns are influenced by data sources (Hurlbert and White, 2005; Graham and Hijmans, 2006; Hurlbert and Jetz, 2007; Pineda and Lobo, 2012) but few examined how the different sources of species distribution data affect the inference regarding the environmental drivers of biodiversity (Hurlbert and White, 2005). Still, there is little evaluation at continental scales of how estimates of species richness from expert-drawn range maps correlate with those based on atlases, and how these differences affect the inferences regarding the environmental drivers of biodiversity.

Here, we use species richness data from atlas and expert-drawn range maps for terrestrial vertebrates (amphibians, reptiles and mammals) at intermediate grain size (50×50 km^2) and at continental extent to explore discrepancies in species richness patterns. We also assess how these discrepancies may affect the relative ranking and explanatory power of environmental predictors (climate and landscape attributes, all of which have been shown to have substantial effects on richness e.g. Xu et al., 2014). We use landscape attributes which reflect both natural and human land-uses, since the latter are also important predictors especially for the distribution of threatened species (e.g. Davies et al., 2006), and quite likely for the biodiversity of non-threatened species (Xu et al., 2014). We go one step further and examine if the thematic resolution of land cover diversity provides more information to understand these patterns, and examine how the landscape diversity estimated at different levels of land cover thematic resolution is associated with species richness.

2. Methods

2.1. Species richness maps

We compiled distributional data for 68 amphibian species, 102 reptile species and 160 mammal species (all terrestrial) native to EU (European Union) from two atlases, 'The Atlas of European amphibians and reptiles' (Sillero et al., 2014) and 'The Atlas of European Mammals' (Mitchell-Jones et al., 1999). From these data, we derived maps of species richness for EU within 50×50 km^2 grid cells. We excluded grid cells with less than 50% land area and analyzed 2488 cells. We estimated species richness from digitized geographical range vector maps (expert-drawn range maps) for the same species of amphibians, reptiles and mammals (IUCN, 2013) and constructed a biodiversity map based on the same grid as the atlas maps. To avoid mismatches due to differences in the species nomenclature between the databases (atlases vs IUCN species ranges) we followed the atlas taxonomy as atlases were more recently updated.

2.2. Environmental variables

The environmental data were reprojected and resampled to the same projection and resolution as the atlases. Climate data were based on the WorldClim climate database (Hijmans et al., 2005). We used mean annual temperature (MAT), mean annual precipitation (MAP), and the seasonality of temperature and precipitation (TS and PS, respectively) as climatic predictor variables. We also used as estimates of landscape attributes: ANTHROPRESS (anthropogenic surface area in km^2) as a measure of anthropogenic effects, AGRILAND (area in km^2) to account for the influence of agriculture, and land cover diversity (LC) (number of land cover classes). All information provided by the land cover dataset CLC2000 (CORINE land cover technical guide – Addendum, 2000; Bossard et al., 2000). The CLC2000 classification scheme is hierarchical and consists of 3 levels: I, II and III (which represent three thematic resolutions), these levels comprise of 5, 15 and 44 classes respectively. The classification scheme gives equal weight to human land use classes and natural or semi-natural land cover classes. Thus, to examine the importance of landscape attributes we analyzed two aspects the area covered by key land cover classes of the first CLC level (using ANTHROPRESS, AGRILAND) as well as the land cover diversity (LC) in all three CLC levels to examine the effect of thematic resolution (e.g. level I consists of fewer classes than level III). As a result, we used LC I, LC II, LC III to see how the different levels of quantifying landscape heterogeneity affect diversity patterns. Land area (LANDAREA) of each cell was used as a covariate to control for