



Original article

Natural habitats matter: Determinants of spatial pattern in the composition of animal assemblages of the Czech Republic



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ABSTRACT

Studies that explore species–environment relationships at a broad scale are usually limited by the availability of sufficient habitat description, which is often too coarse to differentiate natural habitat patches. Therefore, it is not well understood how the distribution of natural habitats affects broad-scale patterns in the distribution of animal species. In this study, we evaluate the role of field-mapped natural habitats, land-cover types derived from remote sensing and climate on the composition of assemblages of five distinct animal groups, namely non-volant mammals, birds, reptiles, amphibians and butterflies native to the Czech Republic. First, we used variation partitioning based on redundancy analysis to evaluate the extent to which the environmental variables and their spatial structure might underlie the observed spatial patterns in the composition of animal assemblages. Second, we partitioned variations explained by climate, natural habitats and land-cover to compare their relative importance. Finally, we tested the independent effects of each variable in order to evaluate the significance of their contributions to the environmental model. Our results showed that spatial patterns in the composition of assemblages of almost all the considered animal groups may be ascribed mostly to variations in the environment. Although the shared effects of climatic variables, natural habitats and land-cover types explained the largest proportion of variation in each animal group, the variation explained purely by natural habitats was always higher than the variation explained purely by climate or land-cover. We conclude that most spatial variation in the composition of assemblages of almost all animal groups probably arises from biological processes operating within a spatially structured environment and suggest that natural habitats are important to explain observed patterns because they often perform better than habitat descriptions based on remote sensing. This underlines the value of using appropriate habitat data, for which high-resolution and large-area field-mapping projects are necessary.

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1. Introduction

The most obvious patterns in the distribution of organisms occur in response to variations in the physical environment (Lomolino et al., 2010), which drives species distributions through niche-based processes (Hutchinson, 1957; Chase and Leibold, 2003). In terrestrial animal taxa, distribution patterns of individual species are largely determined by climate, altitude and suitable habitat conditions related to vegetation cover (e.g., Badgley and

Fox, 2000 for mammals; Davies et al., 2007 for birds; Rodríguez et al., 2005 for reptiles and amphibians; Luoto et al., 2006 for butterflies). An important issue in studies that explore species–environment relationships is the quality of available environmental data, particularly of habitat description, an important yet difficult to quantify variable.

Land-cover data, predominantly those based on remote sensing (such as Corine Land Cover or PELCOM), are widely used in various types of studies to explain and model species distributions at broad scales (Storch et al., 2003; Thuiller et al., 2004; Virkkala et al., 2005; Luoto et al., 2006; Reino et al., 2013). In contrast to their easy accessibility and large spatial extent, these data often do not accurately describe fine-scale habitat properties, which may drive

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changes in the composition of local animal assemblages (Storch et al., 2003; Titeux et al., 2004; Reif et al., 2008). Nevertheless, Sizing and Storch (2004) pointed out that the fine habitat variability may be averaged out if coarse spatial grain is used in the analysis of species–environment relationships. Although this may be the case, the coarse description of habitat composition may lead, on the other hand, to underestimating the role of habitat factors, which may be the reason why habitat explanatory power declines towards broader scales (Johnson et al., 2007; MacFaden and Capen, 2002; Rodewald and Yahner, 2001). Moreover, satellite images do not sufficiently differentiate natural habitat patches in intensively managed and fragmented landscapes (Bölöni et al., 2011), whose occurrence may be crucial for species sensitive to habitat quality. Therefore, the relationship between the distribution of natural habitat patches and the composition of animal assemblages is still poorly known.

To reveal the association between fine-scale natural habitats and broad-scale animal distribution patterns, it is necessary to map fine-scale habitat occurrences over a large area with high accuracy and unified methodology. This can be achieved only by extensive field mapping requiring great labour intensity, which is probably the reason that only three field-surveyed, large-area and high-resolution habitat mapping projects have been completed at least in Europe: in Spain (Loidi, 1999), in Hungary (Molnár et al., 2007) and in the Czech Republic (Guth and Kučera, 2005). The survey of natural habitat distribution in the Czech Republic was carried out for implementation of the Natura 2000 network, and it followed the system of habitat classification based on the Habitat Catalogue of the Czech Republic (Chytrý et al., 2001). The Czech classification system contains all major habitat types occurring in the country, and it is compatible with Annex I of the Habitats Directive (92/43/EEC), a European Union legal instrument for the development of the Natura 2000 network. The habitat database of the Czech Republic, thus, contains a precise description of habitat distribution in the common central European landscape, which reliably differentiates natural habitat patches of conservation value across a relatively large area.

Patterns in species distribution may be also ascribed to neutral processes such as dispersal and population dynamics including local immigrations and extinctions (Hanski, 1999; Hubbell, 2001). It is widely acknowledged that these processes produce spatially autocorrelated patterns of species distributions, a so-called distance decay of similarity, meaning that the similarity of composition of species assemblages decreases with increasing geographical distance (Nekola and White, 1999; Soininen et al., 2007). On the other hand, not only species composition, but also environment becomes less similar with increasing distance. Variation partitioning (Borcard et al., 1992) is a tool commonly used to distinguish between environmental control and neutral processes structuring species assemblages. The strength of the neutral processes was traditionally interpreted based on the amount of spatial variation in species distributions, which cannot be explained by the environment (Cottenie, 2005), however, neutral processes contribute also to the amount of variation explained by environmental variables (Smith and Lundholm, 2010). In addition to the effects of neutral processes, spatial variation that cannot be explained by environmental variables may be attributed to the omission of important factors structuring the composition of species assemblages (Dray et al., 2012). Since this study focusses on understanding the environmental influence of spatial patterns in animal assemblages, it is important to quantify all significant spatial variation in species distributions and compare it with the variation explained by the environment to evaluate the extent to which the environmental variables and their spatial structure might underlie the observed patterns in the composition of animal assemblages. Furthermore, if

there is a spatial variation in species composition that cannot be explained by variations in the environment, statistical models including only environmental variables show significant spatial autocorrelation of residuals, which may influence the results of statistical tests of significance of the environmental component (Diniz-Filho et al., 2003). Therefore, it is necessary to account for spatial autocorrelation in residuals of environmental models in order to properly apply statistical tests and correctly evaluate the effects of environmental variables.

In this study, we focus on evaluating the relative effects of natural habitats, land-cover types and climatic variables on the composition of assemblages of distinct animal groups native to the Czech Republic, namely non-volant mammals, birds, reptiles, amphibians and butterflies. We address the following aims: (1) To evaluate the extent to which the environmental variables and their spatial structure underlie the observed spatial patterns in the composition of animal assemblages. (2) To compare the explanatory power of field-mapped natural habitats, land-cover and climatic variables. We hypothesize that the distribution of natural habitats significantly influences the broad-scale composition of assemblages of the considered animal groups and performs better than habitat descriptions based on remote sensing. (3) To test the unique contributions of each environmental variable in order to evaluate their relative importance within the environmental model.

2. Methods

2.1. Species data

We used national distribution atlases of mammals (Anděra and Gaisler, 2012), birds (Štastný et al., 2006), reptiles (Mikátová et al., 2001), amphibians (Moravec, 1994) and butterflies (Beneš and Konvička, 2002) to compile a database of species occurrences (presence/absence records) in a grid of rectangles (hereafter called grid cells) covering the Czech Republic (Fig. 1). Each grid cell spans 10' of longitude and 6' of latitude, which represents ca. 11.1 × 12 km (133.2 km²) on the 50th parallel. Although the area of the country is covered by 679 grid cells in total, we excluded marginal ones and considered only 628 grid cells. Because the above mentioned atlases differ in their methods of data collection and the considered time period, we carefully checked the data for mutual comparability. We considered only records since 1980, and the data on reptiles and amphibians were updated according to records of the Biomonitoring programme organized by the Agency for Nature Conservation and Landscape Protection of the Czech Republic (<http://www.biomonitoring.cz/>). We excluded species that are listed in atlases but their distribution in the Czech Republic is uncertain (e.g., *Emys orbicularis*) and also species that are not native to the country according to Mlíkovský and Stýblo (2006). In the case of mammals, we considered only non-volant mammals. This selection resulted in 46 out of 62 non-volant mammals; 199 out of 215 birds (only records of confirmed and probable breedings were used); 10 out of 11 reptiles; 21 of 21 amphibians and 141 out of 161 butterflies.

2.2. Climatic data

For each grid cell, we calculated the maximal and minimal values of mean annual temperature and annual precipitation according to Tolasz (2007). Note that we prefer maximal and minimal values instead of mean values because, with respect to grid resolution, it provides a more comprehensive characterisation of environmental conditions within each grid cell.

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