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High-resolution and large-extent mapping of plant species richness using vegetation-plot databases

Jan Divíšek^{a,b,*}, Milan Chytrý^b

^a Department of Geography, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic
^b Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic

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ABSTRACT

The recent increase in the availability of large vegetation-plot databases has created unprecedented opportunities for analysing and explaining patterns of fine-scale plant species richness across large areas and for individual habitat types. Here we demonstrate how these data can be used to (1) prepare country-wide highresolution maps of species richness and identify national diversity hotspots for grassland and forest vegetation; (2) compare diversity patterns of all, native, alien and Red List species; and (3) identify potential environmental drivers of these patterns. At the same time we examine and quantify the stability of predicted species-richness patterns with respect to the most common biases that are inherent to large vegetation-plot databases. Vegetation-plot records were obtained from the Czech National Phytosociological Database and the Random Forest method was used to map fine-scale spatial diversity patterns of all, native, alien and Red List vascular plant species, separately for grasslands and forests across the Czech Republic. The stability of the predicted species-richness patterns was tested using differently resampled datasets in which we either reduced or increased local oversampling and preferential sampling of more species-rich communities. Models for grassland and forest vegetation explained 40-65% of variation in fine-scale species richness. Spatial patterns of all and native species richness differed considerably between grasslands and forests, whereas alien and Red List species showed a higher congruence between these two vegetation types. Patterns of modelled species richness were highly stable with respect to all resampling strategies applied to the initial datasets. We conclude that vegetation-plot databases are a valuable source of data for high-resolution mapping of the plant species richness of different vegetation types and species groups, because each of them can exhibit a different diversity pattern. The resulting maps provide robust representation of the spatial patterns of fine-scale species richness and can be used both for testing scientific hypotheses about the controls of diversity patterns and for conservation planning.

1. Introduction

The mapping of species-richness patterns is of special importance in biogeography, macroecology and community ecology, because speciesrichness maps provide basic information for studying the history of regional biotas and community assembly mechanisms. Such maps are also important for nature conservation, because appropriate management applied at species-rich sites can ensure protection of a considerable portion of regional biodiversity (Margules and Pressey, 2000; Myers et al., 2000). However, high-resolution maps showing the distribution of plant species richness across large areas are extremely rare, mainly because spatially extensive and detailed field surveys are timeconsuming and expensive.

Information from species distribution atlases (e.g. Jalas and Suominen, 1972 et seq.; Schönfelder, 1999) has been used as the main data source for mapping broad-scale species richness to date (e.g. Araújo et al., 2005; Kalwij et al., 2014; Ronk et al., 2017). However, atlases provide only coarse-grained information on the spatial distribution of species richness, because occurrence records are summed to grid cells of a certain size that usually increases with the extent of the whole mapped area. Moreover, because species counts within grid cells usually represent the whole flora of the cells, species richness cannot be mapped for individual vegetation or habitat types which makes it impossible to address certain ecological questions with atlas data. For example, it has been shown that spatial scale has a crucial effect on the direction of the relationship between native and alien species richness (what is known as the diversity-invasibility paradox; Fridley et al., 2007). If data have a coarse spatial resolution, the relationship tends to be positive due to habitat heterogeneity within large sampling units, whereas at finer scales at which individuals interact the relationship

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^{*} Corresponding author at: Department of Geography, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic. *E-mail addresses:* divisekjan@mail.muni.cz (J. Divíšek), chytry@sci.muni.cz (M. Chytrý).

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Fig. 1. Map of the Czech Republic with geographical names mentioned in this study.

between native and alien species richness may be negative (Melbourne et al., 2007). An advantage of fine-scale data, as opposed to coarse-scale data, is that they show species richness as it develops under the influence of interspecific competition within particular sites.

The lack of both fine spatial resolution and the differentiation of vegetation or habitat types can be overcome by using vegetation-plot databases as a source of fine-scale data for species-richness mapping. These databases, collecting vegetation-plot records (phytosociological relevés; henceforth vegetation plots) from various sources such as local surveys or inventories of protected areas, represent relatively new source of information on plant community diversity (Dengler et al., 2011; Chytrý et al., 2016). Because a considerable proportion of these computerised plots is geographically referenced, they provide an exceptional opportunity for mapping plant species richness at a very fine resolution of a few (or a few dozen) square metres. Vegetation plots can also be classified to vegetation or habitat types and species richness may be mapped for different types separately. A disadvantage of vegetation-plot databases is a spatially uneven sampling intensity and consequently large differences in the density of vegetation plots among regions (Knollová et al., 2005). Species-richness maps based on vegetation plots will therefore inevitably contain regions with no plots available, for which reason effective methods of predicting spatial patterns of species richness across the entire study area are needed (Williams and Gaston, 1994). Spatial modelling has been increasingly used over the past years to relate sparse biological survey or collection data to remotely mapped environmental attributes, thereby allowing distributions of biological entities to be interpolated and extrapolated across the entire study area (Guisan and Thuiller, 2005; Ferrier and Guisan, 2006). Currently, this approach is commonly used to predict distributions of individual species (e.g. Welk et al., 2002; Svenning et al., 2008), communities (e.g. Marage and Gégout, 2009) and species richness (e.g. Steinmann et al., 2009; Revermann et al., 2016), but it has rarely been used for mapping the plant species richness of individual vegetation or habitat types.

Species richness is an important variable in macroecological and biogeographical research, but maps of *total* species richness often have limited value for nature conservation planning. Conservationists need species-richness maps for identifying biodiversity hotspots, but for management planning it is important to know in which habitats these hotspots are found. Even within habitats, it is important to know not only where the hotspots of total species richness are, but also where the hotspots of endangered or potentially harmful (e.g. alien) species are (Genovesi and Shine, 2004; Foxcroft et al., 2013). The spatial patterns of the richness of these specific species groups can differ from the overall patterns of species richness, and the differences in these patterns are of interest from both the theoretical and practical viewpoint.

The aim of this study is to demonstrate the advantages and test the potential caveats of using vegetation-plot data for mapping and understanding fine-scale spatial patterns of vascular plant species richness, using the grassland and forest vegetation of the Czech Republic as a model. The area of the Czech Republic is highly suitable for such a pilot study, because it is well covered by computerised vegetation plots (Chytrý and Rafajová, 2003). Moreover, it is of considerable importance for general biodiversity research, because according to recent studies it hosts grasslands that are among the most species-rich in the world (Merunková et al., 2012; Wilson et al., 2012; Chytrý et al., 2015). Here we focus on characterising the spatial pattern of vascular plant species richness rather than on accurate prediction of actual species numbers at individual sites. In addition to mapping the total species richness of the main vegetation types, we also focus on the richness of species groups that are important for conservation assessment, namely native and alien species and species from the national Red List (Grulich, 2012; hereafter referred to as Red List species). Specific objectives of this study are to (1) prepare country-wide high-resolution maps of species richness and identify diversity hotspots for grassland and forest vegetation using predictive modelling; (2) compare diversity patterns of all, native, alien and Red List species; (3) identify environmental factors potentially driving these patterns; and (4) examine and quantify the stability of predicted species-richness patterns with respect to the most common biases that are inherent to large vegetation-plot databases (uneven sampling intensity and preferential sampling of more speciesrich communities). We hypothesise that (i) spatial patterns of species richness in grasslands and forests will be different, as these two vegetation types respond to environmental factors in a different way; (ii) spatial patterns of richness of all and native species will be different from those of alien and Red List species.

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