Contrasting patterns of fine-scale herb layer species composition in temperate forests

Markéta Chudomelová [a, b, *], David Zelený [a, c], Ching-Feng Li [d]

[a] Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czechia
[b] Department of Vegetation Ecology, Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, CZ-657 20 Brno, Czechia
[c] Institute of Ecology and Evolutionary Biology, National Taiwan University, No. 1, Sec. 4, Roosevelt Rd., 10617 Taipei, Taiwan
[d] School of Forestry and Resource Conservation, National Taiwan University, No. 1, Sec. 4, Roosevelt Rd., 10617 Taipei, Taiwan

ARTICLE INFO

ABSTRACT

Although being well described at the landscape level, patterns in species composition of forest herb layer are rarely studied at smaller scales. Here, we examined fine-scale environmental determinants and spatial structures of herb layer communities in thermophilous oak- and hornbeam dominated forests of the south-eastern part of the Czech Republic.

Species composition of herb layer vegetation and environmental variables were recorded within a fixed grid of 2×2 m subplots regularly distributed within 1-ha quadrate plots in three forest stands. For each site, environmental models best explaining species composition were constructed using constrained ordination analysis. Spatial eigenvector mapping was used to model and account for spatial structures in community variation. Mean Ellenberg indicator values calculated for each subplot were used for ecological interpretation of spatially structured residual variation.

The amount of variation explained by environmental and spatial models as well as the selection of variables with the best explanatory power differed among sites. As an important environmental factor, relative elevation was common to all three sites, while pH and canopy openness were shared by two sites. Both environmental and community variation was mostly coarse-scaled, as was the spatially structured portion of residual variation. When corrected for bias due to spatial autocorrelation, those environmental factors with already weak explanatory power lost their significance. Only a weak evidence of possibly omitted environmental predictor was found for autocorrelated residuals of site models using mean Ellenberg indicator values.

Community structure was determined by different factors at different sites. The relative importance of environmental filtering vs. spatial processes was also site specific, implying that results of fine-scale studies tend to be shaped by local conditions. Contrary to expectations based on other studies, overall dominance of spatial processes at fine scale has not been detected. Ecologists should keep this in mind when making generalizations about community dynamics.

© 2017 Elsevier Masson SAS. All rights reserved.

1. Introduction

There seem to be no general rules regarding which particular factors have the most pronounced influence on the ground layer of forest vegetation at a fine-to mesoscale. Indeed, any generalization is difficult, since the combinations of factors and species are peculiar to each site, and different studies focus on different sets of explanatory variables using various sampling designs and statistical analyses. Still, several broadly defined factors appear as important in most settings. These are light (Frelich et al., 2003) and soil conditions (Palmer, 1990; Frelich et al., 2003; Burton et al., 2011), topography (Gazol and Ibáñez, 2010), overstorey characteristics (Beatty, 1984; Scheller and Mladenoff, 2002; Rodríguez-Calcerrada et al., 2011) and, if considered, anthropogenic influences (Fraterrigo et al., 2006) and dispersal (Burton et al., 2011;

Aiba et al., 2012).

It is well recognized that the scale of observation (i.e. grain, lag and extent) influences the relative importance of individual environmental factors and shapes results of vegetation studies (Reed et al., 1993; Siefert et al., 2012). There is a recurring pattern of weakening habitat associations as the scale gets finer, with environmental filtering probably not too important at finer scales, and dispersal or biotic processes (such as plant-plant interactions) gaining influence instead (Legendre, 1993; Richard et al., 2000; Gilbert and Lechowicz, 2004; Laliberté et al., 2009; Gazol and Ibáñez, 2010). There are several reasons why environmental models have reduced predictive power at finer scales. By scaling down, the number of individuals within a given grain or extent is reduced, and individual-based stochastic processes become more important (Chase, 2014). Another reason is less environmental variability at finer scales (Frelich et al., 2003; Chase, 2014), since it is less likely to encounter sharp environmental differences within such a limited space, and also because sampling schemes are often designed to avoid within site heterogeneity.

Another issue associated with fine-scale studies is spatial autocorrelation. As the samples get closer to each other, they are more likely to possess similar properties than those separated by longer distances, representing fewer independent pieces of information than expected from the number of samples. This situation has long been recognized as a problem of pseudoreplication (Hurlbert, 1984). If not treated properly, autocorrelation leads to spurious conclusions in hypotheses testing, with results appearing as more optimistic than they actually should be regarding the number of effective degrees of freedom (Legendre, 1993). Based on such results, one may find significant relationships between response and explanatory variables while the actual cause of these relationships is the spatial autocorrelation (Lennon, 2000).

However, spatial autocorrelation shall not be regarded as a mere threat to ecological inference. Instead, it can serve as a starting point for formulation of further hypotheses (Leduc et al., 1992; Legendre, 1993). We can differentiate between two types of forces generating spatial autocorrelation in the species distribution: external ones like environmental variables or historical events, or internal ones like dispersal (Legendre and Legendre, 2012). From this theoretical background originates the methodology of variance partitioning between environmental and spatial predictors, with the aim to identify determinants of community composition (Borcard et al., 1992). Explained variation in species composition can be separated into three fractions: the fraction representing variation explained solely by the environment, the variation explained both by environment and space, and the variation explained by spatial predictors only. Depending on which fraction prevails, the community is considered to be controlled either by environmental or spatial influence (Cottenie, 2005). Sometimes, the spatial influence is viewed narrowly as dispersal (Karst et al., 2005; Jones et al., 2006; Aiba et al., 2012) or the dichotomy is drawn between niche and neutral community assembly (Gilbert and Lechowicz, 2004).

Although the variation partitioning method is already an established part of ecological statistics toolkit, this methodology has received some criticism. It has been shown that results are dependent on the quality of predictors. The lack of good environmental data may shift the interpretation of results towards the spatial influence model, whereas the choice of spatial predictors may influence the amount of detected spatial variation (Jones et al., 2008; Chang et al., 2013). Simulated data also revealed that the output depends upon the statistical method and sampling design used in the study (Gilbert and Bennett, 2010). Moreover, it is not possible to relate the pure environmental and spatial fractions of variation directly to environmental and spatial processes since both are interdependent (Smith and Lundholm, 2010). Additionally to quantifying the three fractions of variation, spatial filters might as well be used to account for spatial variation in model residuals and to correct the bias in hypothesis testing (Borcard and Legendre, 2002; Diniz-Filho and Bini, 2005; Dormann et al., 2007).

The aim of this study is to quantify to what extent and by which environmental factors it is possible to explain the fine-scale variation of forest herb layer communities. Having spatially explicit data allows for more complex analyses related to this question. We expect that at this scale the environmental control is rather weak, due to prevailing spatial influence and low variance in environmental factors, compared to a considerable proportion of remaining unexplained variation. First, we evaluate whether correcting for spatial autocorrelation will cause changes in significance of the selected environmental factors. Further, we ask whether the spatial variation unexplained by environmental variables more likely represents some important environmental variables which are missing in our dataset, or if it is a result of dispersal processes.

2. Materials and methods

2.1. Study area

The study was conducted in three oak and oak-hornbeam forests located in south-eastern part of the Czech Republic (Fig. 1). All three sites are ancient woods, situated in the warmest and driest region of the Czech Republic, and host rare, species-rich, thermophilous plant communities. Apart from these commonalities, the sites exhibit several contrasting features. They differ in soil properties (i.e. soil texture, soil acidity, amounts of nutrients), topography (flat vs slope), canopy cover and the presence of distinct florogeographical elements (for site photographs and details on site characteristics see Appendix A).

Site 1 (locality Němčičky) is an open thermophilous oakwood, situated on a mild convex slope of SSW aspect, covered with loess deposits, and exhibiting a contrasting pattern in herb layer composition. Site 2 (Dúbrava) is part of a subcontinental oakwood on flat, slightly undulating terrain, built of sands deposited over water-holding clayey sediments. Site 3 (Mokrá) is in a mesic oak-hornbeam wood, on a gentle south-eastern slope, with limestone bedrock partly exposed to the surface.

2.2. Data collection

At each site, we established a square plot of 100 × 100 m, with 100 subplots of 2 × 2 m organized in a regular grid with 10-m lags between adjacent subplots (Appendix B). At each 2 × 2-m subplot, we recorded a list of vascular plant species along with visual estimates of species cover using the nine-degree Braun-Blanquet scale (Westhoff and van der Maarel, 1978). Seedlings and saplings of woody species were later excluded from the analyses. In the center of each subplot, we took a hemispherical photograph of the canopy at the height of 1.3 m (using Nikon Coolpix 4500 camera with FC-E8 fisheye lens). We also measured slope inclination (using Silva ClinoMaster), aspect (using a compass) and relative elevation of each subplot using the Field-Map device (IFER, Ltd., Jílové u Prahy, Czech Republic) with accuracy up to 0.2 m. At four locations within each subplot, we measured soil depth using 30 cm long iron probe, and collected a mixed soil sample from the top 5 cm. All data were collected during three weeks in June and July 2012.

The hemispherical photographs were converted to black and white images in SideLook program (version 1.1, http://www.appleco.ch/) using automatic thresholding algorithm (Nobis and Hunziker, 2005) and further analyzed by Gap Light Analyser (version 2.0, http://www.caryinstitute.org/science-program/our-