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Disentangling the effects of climate, topography, soil and vegetation on stand-scale species richness in temperate forests

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ABSTRACT

The growing awareness of biodiversity by forest managers has fueled the demand for information on abiotic and biotic factors that determine spatial biodiversity patterns. Detailed and area-wide environmental data on potential predictors and site-specific habitat characteristics, however, are usually not available across large spatial extents. Recent developments in environmental data acquisition such as the advent of Light Detection And Ranging (LiDAR) remote sensing provide opportunities to characterize site-specific habitat conditions at a high level of detail and across large areas. Here, we used a dataset of regularly distributed local-scale records of vascular plant, bryophyte and snail (Gastropoda) species to model richness patterns in forests across an environmentally heterogeneous region in Central Europe (Switzerland). We spatially predicted species richness based on a set of area-wide environmental factors representing climate, topography, soil pH and remotely sensed vegetation structure. Additionally, we investigated the relationship between species richness and field measures of forest stand structure and composition obtained from National Forest Inventory (NFI) data to identify potential target variables for habitat management. The predictions for species richness were most accurate for snails, followed by bryophyte and vascular plants, with R^2 values ranging from 0.37 to 0.07. Besides climate, site-specific factors such as soil pH, indices of topographic position and wetness as well as canopy structure were important for predicting species richness of all three target groups. Several NFI variables were identified as potential target variables for managing snail species richness. Stands with tree species from the genera *Fraxinus*, *Tilia*, *Ulmus* and *Acer*, for example, showed a positive relationship with snail species richness, as did an increasing overstory cover or higher volumes of deadwood. However, only weak relationships were found between NFI variables and species richness of vascular plants, and none for bryophytes. Our findings support the assumption that besides climate, site-specific habitat factors are important determinants of spatial variation of species richness at the local scale. The strength and direction of the determinants vary with taxa, thus indicating a functional relationship between site conditions and the respective species community.

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1. Introduction

Understanding the relationships between species richness patterns and environmental conditions is a key issue in ecology and biodiversity conservation. While climate is considered to be one of the main large-scale abiotic factors controlling the distribution of organisms and community composition (Hawkins et al., 2003),

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the importance of habitat properties is expected to increase at regional and particularly local scales (McGill, 2010). At these scales, which are most relevant for management, forest biodiversity and habitats are strongly associated with forest structure and composition (Hunter, 1999; Lindenmayer and Franklin, 2002; Zhang et al., 2013). Thus, management activities to maintain or restore biodiversity in forests often include measures to enhance structural and compositional characteristics (Lindenmayer et al., 2006; Bauhus et al., 2009; Gustafsson et al., 2012). However, spatial conservation planning and management often suffer from the lack of area-wide, fine-scale information on attributes describing site-specific habitat quality. Such information would be particularly useful for a number of sessile and immobile species groups in order to gauge the potential impacts of stand-level management on their communities.

The increasing availability of high-resolution digital environmental data, e.g. downscaled climate or remote sensing data pave the way for fine-scaled predictions of habitat properties of increasing accuracy and across broad spatial extents. Forest habitat structure, for example, can now be quantified and predicted at a high level of detail using Light Detection And Ranging (LiDAR) data, which capture the three-dimensional structure of forest canopies and vegetation (Næsset, 2002; Vierling et al., 2008; Davies and Asner, 2014; Simonson et al., 2014). Canopy structure is a dynamic habitat property, and variation in it will prompt changes in other habitat attributes such as light availability on the ground, air and ground temperature, humidity or wind speed (Franklin et al., 2002; Kimmins, 2004). Quantifying canopy structure thus allows for deriving site-specific indicators of microclimatic conditions in forests. The occurrence of plant species, for example, is related to light availability on the forest floor, with some plants being tolerant of shade and others requiring intermediate or high light conditions (Ellenberg, 1988; Alexander et al., 2013). Habitat quality for other species groups, such as land snails, is related to the moisture content in the stratum close to the ground, which is influenced by canopy structure as well (Horsák et al., 2010). Valuable remotely sensed predictors for site quality and forest species communities also include vegetation indices such as the normalized difference vegetation index (NDVI), which has been widely used as surrogate of primary productivity and vegetation density both at global and local scales (Pettorelli et al., 2005; Goetz et al., 2007; Levin et al., 2007). Other spatially detailed and extensive environmental data that are increasingly sought for comprise edaphic characteristics such as soil pH, which is related to the concentration of assimilable nutrient and toxic compounds and thus constitutes an important factor influencing species distributions and habitat quality (Gobat et al., 2004; Martin and Sommer, 2004; Dubuis et al., 2013).

The increasing availability of detailed digital environmental data thus allows for describing important environmental correlates of species distributions and richness patterns (Guisan and Zimmermann, 2000). Based on niche theory and gradient analysis (Hutchinson, 1957; Austin, 2002), predictive spatial models frequently referred to as species distribution models (SDM) combine such data with species occurrence records to produce maps of habitat suitability (Franklin, 1995; Guisan and Thuiller, 2005; Peterson et al., 2011), based on the principle to infer areas where environmental conditions are similar to those where the species were found.

Despite the practical value of habitat suitability maps for spatial conservation planning, they are less informative when it comes to specifying particular measures required for targeted forest management. Relating field-based measurements of stand structure and composition to species occurrence data is a promising way to inform forest managers about the potential benefits for biodiversity that could be brought about by modifying stand structure and composition. However, information on the target variables that would be important to consider is rare and often derived from plot-based inventories, which hampers their integration into area-wide predictive models. Moreover, many attributes of forest structure and composition, such as the availability of deadwood or the occurrence of particular tree or shrub species, remain difficult to predict in space. Thus, a combination of maps depicting habitat suitability for spatial priority setting with field-based evidence of the relationship between species richness and forest stand characteristics would provide a promising way to integrate novel environmental datasets into a consistent framework for forest biodiversity management.

In this study, we used nationwide, high-resolution data of abiotic and biotic parameters to spatially predict local scale species richness of vascular plants, bryophytes and snails in Swiss forests. Further, we tested the capacity of National Forest Inventory field data of stand structure and composition to explain the differences in species richness. We focused on these sessile and immobile species groups because of their association to local site conditions and complimentary habitat requirements. Specifically, we investigated the following research questions: (1) What is the relative importance of climate, topography, soil pH, and vegetation structure for predicting stand-scale species richness of vascular plants, bryophytes and snails in temperate forests? (2) What field-based measurements of forest structure and composition can be used as target variables for habitat improvement measures at the stand scale?

2. Material and methods

2.1. Study area

This study was carried out in Switzerland, covering 41,248 km^2 in Central Europe (45°49′–47°48′N, 5°57′–10°30′E). The landscape consists of mountain areas, covering about 70% of the country (60% Alps, 10% Jura Mountains) and the lowlands (30%) (Brändli, 2010). Forests cover about one third of the total area of the country, with a larger proportion in mountain areas. Elevations range from 193 to 4634 m a.s.l., with a mean of 1300 m a.s.l. Within the generally temperate humid climate, the mean annual temperature and precipitation range from −10.5 to 12.5 °C and 438 to 2950 mm, respectively (Zimmermann and Kienast, 1999).

2.2. Species data

Species richness data were obtained from species recordings conducted by the Swiss Biodiversity Monitoring Program (BDM) during the years 2004–2008 (Weber et al., 2004). The BDM performs local-scale species surveys at intervals of five years within circular plots distributed on a regular national sampling grid with a mesh size of 6 km × 4 km covering all landscape types. Plots in forests were spatially aligned with the National Forest Inventory (NFI) grid to allow joint analyses of species data and forest inventory data (BDM Coordination Office, 2014). Vascular plant, from now on referred to as plant, and bryophyte species numbers were recorded within 10 m^2 circular plots (r = 1.78 m). All species present in the space from the ground up to 150 cm in height were recorded (BDM Coordination Office, 2008). The number of snail (Gastropoda) species was assessed from eight samples regularly distributed on the edge of a circle with r = 2.28 m around the center of the plots for the plant and bryophyte surveys. Both the soil and habitat structures up to 150 cm (including e.g. tree trunks, walls, rocks and plants) were surveyed for species presences. Together, all soil samples per plot had a volume of 5 dm^3 on an area of 10 dm^2 and were searched for species evidences in the lab following a drying and sieving procedure described by BDM (BDM Coordination Office, 2010).

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