



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



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ARTICLE INFO

Article history:

Received 12 February 2015

Received in revised form 9 April 2015

Accepted 10 April 2015

Available online 27 April 2015

Keywords:

ALS

Forest biodiversity

Site factors

LASSO

NDVI

National forest inventory

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),

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 km² 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 m² 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 dm³ on an area of 10 dm² and were searched for species evidences in the lab following a drying and sieving procedure described by BDM (BDM Coordination Office, 2010).

We analyzed data from 410 plant and bryophyte plots and 406 snail plots containing 749 plant, 336 bryophyte and 116 snail species (Fig. 1). All plots were completely covered by forest and were distributed from 294 to 2235 m a.s.l. For each species group, we calculated two dependent variables: overall species richness (i.e. the total number of species per plot) and forest species richness (i.e. the number of species per plot with a strong association to forest habitats). This enabled us to analyze species richness and biodiversity patterns in general, as well as patterns of forest species communities in particular. For attributing species to the latter group we consulted species experts who were asked to classify a species as a forest species if more than 50% of all occurrences in the national species data center's database (www.infospecies.ch) were reported in forest habitats.

2.3. Area-wide environmental data

2.3.1. Climate and topography

All climatic variables were based on interpolations of daily measurements by the national meteorological network of Switzerland (MeteoSwiss) during the period 1961–1990, using a digital elevation model with 25 m pixel size (computational details are provided in Zimmermann and Kienast (1999)). Together with variables representing topography (Table S1) which were calculated based on the 25 m-digital elevation model (Zimmermann and Roberts, 2001), we used monthly mean temperature and precipitation layers to derive a number of potential predictors (Table S1).

2.3.2. Soil pH

A topsoil pH map was calculated based on the Swiss Soil Suitability Map (SSSM) (FSO, 2001). The SSSM, available at a 1:200,000 scale, contains 144 map units describing geological parent material and topography, such as rate of slope, aspect and position (e.g. ridges or valleys). To model pH, we used 10,865 data points of pH topsoil samples with a sampling depth of approximately 20 cm, taken in forested areas all over Switzerland (Swiss National Forest Inventory LFI, 1984). Median values of the pH measured within a given SSSM unit were assigned to the respective

unit. Map units containing less than 15 soil samples were aggregated to units with similar geological parent material, resulting in 96 final units. The pH map was validated with 1033 independent forest soil profiles taken from Walther et al. (2004), applying ordinary least square regression which resulted in a R^2 of 0.35.

2.3.3. Remotely sensed vegetation data

NDVI – We used published data of the normalized difference vegetation index (NDVI) derived from a mosaic of SPOT-5 satellite images (Mathys and Kellenberger, 2009). The spectral data had a resolution of 10 m, were recorded during the growing season (May–October) in the years 2004–2006 and corrected for shadows, illumination and atmospheric effects. A detailed description of the raw data and the data processing is provided in Camathias et al. (2013) and Mathys and Kellenberger (2009). NDVI indicates the greenness of vegetation canopies and is a frequently used variable for quantifying the productivity and aboveground biomass of ecosystems (Tucker, 1979; Pettorelli et al., 2005). We calculated the mean NDVI value by averaging all pixels within the 30×30 m plot for which vegetation structure based on LiDAR data was analyzed (see below).

Vegetation structure (LiDAR) – We calculated a set of variables from a nationally available set of discrete, first and last return airborne laser scanning (or LiDAR) data, acquired during multiple seasons between 2000 and 2007 (swisstopo, 2011; Zellweger et al., 2013). The nominal footprint size was in the range of small-footprint laser scanning (i.e., several decimeters) and height accuracies were within 0.5 m (one standard deviation) and 1.5 m in open and forest areas, respectively. The raw point cloud data with a mean point density of 1.4 m^{-2} was pre-processed using a suite of LAStools algorithms (Isenburg, 2013) to eliminate duplicates, identify ground returns, classify all returns and calculate the normalized vegetation heights. We calculated a set of forest structural variables describing the distribution of vegetation heights (Table S1). We considered variables indicating important ecological factors such as light condition close to the forest floor (e.g., canopy cover at 1 m, Table 1) and the variation and distribution of vegetation returns along the vertical profile (e.g. standard deviation of vegetation heights, Table 1).

Spatial co-registration of LiDAR data and the species plot centers was based on GPS recordings from the National Forest Inventory (see below). High precision GPS measurements recorded with Trimble GeoExplorer devices with a spatial uncertainty of less than one meter were available for 236 plot centers. All vegetation structure variables were calculated for three plot dimensions: 30×30 m, 50×50 m and 100×100 m. However, correlation analyses with species richness variables revealed highest correlation coefficients for variables based on plot dimensions measuring 30×30 m; thus we restricted further analyses to this variable set.

2.4. Plot-based National Forest Inventory data

The data from the Swiss National Forest Inventory (NFI) were collected from 2004 to 2007 (Brändli, 2010; Keller, 2011). We considered 18 variables that are subject to modifications by forest management (Table 2), thus yielding potential target variables for habitat improvement measures. Beside common variables referring to stand structure such as basal area, diameter at breast height and canopy cover, we calculated compositional variables based on basal area from individual tree measurements. Such variables included the total proportion of a number of alluvial tree species (i.e., from the genera *Fraxinus*, *Tilia*, *Ulmus* and *Acer*), which we expected to provide favorable conditions for snails due to the availability of calcium in a citrate form in their leaves (Wäreborn, 1969). We further considered the availability of deadwood, an often limiting habitat resource in managed forests (Müller and Büttler, 2010), as well as

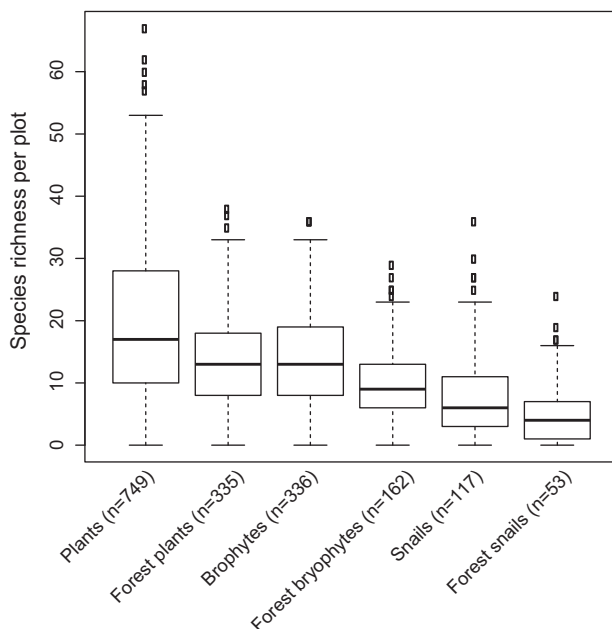


Fig. 1. Boxplots for the species richness per plot. The total number of species sampled is indicated in parentheses.

Table 1

Environmental predictor variables for species richness. Summer months include the period from June to August.

Variable	Description	Resolution (m)
<i>Climate</i>		
Temperature	Mean monthly summer temperature (°C) (Zimmermann and Kienast, 1999)	25
Frost days	Annual average number of frost days during growing season (Bolliger et al., 2000)	25
Precipitation	Mean monthly summer precipitation (mm) (Zimmermann and Kienast, 1999)	25
Site water balance	Estimation of water amount availability (mm) during a year obtained by integrating monthly precipitation and potential evapotranspiration over time, and considering soil storage capacity (Guisan et al., 2006)	25
Solar radiation	Mean monthly potential global clear sky solar radiation (kJ/m ²) during summer (Zimmermann and Kienast, 1999)	25
<i>Topography</i>		
Position	Topographic position index; measures the exposure of a site in relation to the surrounding terrain (radius of 150 m). Positive values: ridges and hilltops; negative values: sinks (Zimmermann and Roberts, 2001)	25
Wetness	Topographic wetness index representing the lateral water flow (Zimmermann and Roberts, 2001)	25
Slope	Slope of terrain (°) (swisstopo, Federal Office of Topography)	25
Eastness	West-east gradient of aspect obtained by cosine function (swisstopo, Federal Office of Topography)	25
<i>Soil</i>		
Topsoil pH	Calculated from the Swiss soil suitability map and field samples (see text for details)	25
<i>Vegetation density and structure</i>		
NDVI	Mean Normalized Difference Vegetation Index derived from SPOT-5 satellite images (Mathys and Kellenberger, 2009)	10
Vegetation height	Mean, standard deviation and coefficient of variation of vegetation heights, calculated from terrain corrected laser return heights (see text for details) (Lefsky et al., 2002; Næsset, 2002)	30
Canopy cover	Canopy cover at 1 m above ground. Expressed as: sum of laser return heights > 1 m/sum of all laser returns * 100. Increasing values represent an increasing canopy cover and thus decreasing light availability on the ground (Næsset, 2002; Müller and Brandt, 2009)	30
Foliage height diversity	Calculated as the Shannon–Wiener information index $H' = -\sum p_j \ln p_j$, where j is proportion of vegetation returns in the j th density quartile (Clawges et al., 2008). The density quartiles are expressed as relative proportions of vegetation returns falling within four equally distributed height classes along the vertical forest profile	30

the presence of wood piles and root plates because we expected such features to increase the range of available micro-habitats.

2.5. Statistics

2.5.1. Spatial predictions of species richness

We used the area-wide available environmental data to spatially predict species richness. Beforehand, all variables were tested for bivariate correlations. From the pairs of highly correlated variables (Pearson's $r > |0.7|$) we retained the ecologically more meaningful variable. This resulted in 16 variables (Table 1) to predict the six response variables (i.e. overall and forest-species richness of the three focal taxonomic groups) which were count data and thus square root-transformed. We used the machine learning method

Table 2

Description of National Forest Inventory variables according to Keller (2011).

Variable	Description
Basal area	Basal area of standing dead and alive trees (m ² /ha)
Basal area alluvial tree sp.	Proportion of basal area from trees of the genera <i>Fraxinus</i> , <i>Tilia</i> , <i>Ulmus</i> and <i>Acer</i> from total basal area (m ² /ha)
Degree of mixture	Proportion of basal area of conifers and deciduous trees. 4 classes: pure coniferous, mixed coniferous, mixed deciduous, pure deciduous
dbh _{avg}	Average diameter at breast height (dbh) (cm)
dbh _{sd}	Standard deviation of diameter at breast height (cm)
Deadwood	Total volume of standing and lying deadwood (m ³ /ha)
Stand layer	Degree of cover per stand layer (%). 3 layers: understory, midstory and overstory
Stand structure	Vertical stand structure defined by the proportion of the different layers. 4 classes: single-layered, multi-layered, all-aged/all-sized, clustered
Stand development stage	Stage of stand development based on the mean dbh of the 100 strongest trees. 6 classes: young growth/thicket, pole wood, young timber, medium timber, old timber, mixed
Shrub layer	Degree of cover of shrub layer (%), consisting of all woody species from 0.5 m to 3.0 m in height. 6 classes: <1, 1–9, 10–25, 26–50, 51–75, 76–100
Ground vegetation	Degree of cover of the ground vegetation (%). 7 classes: 0 (snow), <1, 1–9, 10–25, 26–50, 51–75, 76–100
Root plates	Presence/absence of root plates
Wood piles	Presence/absence of wood piles and heaps of branches
Water bodies	Presence/absence of water bodies such as puddles, ponds and creeks
Pasturing	Presence/absence of pasturing (incl. grazing) by livestock
Last silvicultural treatment	Number of years since last silvicultural treatment
Recreational use	Present/absence of current recreational use based on mean daily frequency of visitors per year
Forest origin	Type of forest origin. 5 classes: always forest, natural reforestation, afforestation, mixed reforestation, unknown

Random Forests (RF) for the predictions (Breiman, 2001). A RF model consists of a large number of decision trees where each tree is constructed using a bootstrapped sample of the data. In addition, each node of the trees is split based on a random subset of independently sampled predictors with the same distribution for all trees in the forest (Breiman, 2001). A key advantage of RF is that it automatically models typical ecological features such as nonlinearities and interactions. Furthermore, the algorithm provides a measure of variable importance, which is calculated based on permutation tests. To determine the predictive accuracy of our models we used a 5-fold cross validation approach and repeated it 10×. Thus, four fifths of the data were used for model training and one fifth for model testing. We evaluated the predictive performance of each model based on the mean percentage of explained variance and its standard deviation calculated over all cross validation replicates. We calculated correlograms and Moran's I coefficients over various lag distances to check whether the residuals of the models were spatially autocorrelated. However, no statistically significant spatial autocorrelation was detected, thus we did not further investigate this. We used the RF models to predict species richness maps in a selected region of ca. 300 km² (Fig. 2). The region was selected based on its strong environmental gradients, including a gradient in tree species composition ranging from broadleaved dominated lowland forests to coniferous dominated mountain forests.

2.5.2. Modeling species richness with NFI data

The data of the National Forest Inventory were used to identify those attributes of forest stand structure and composition that showed a relationship with species richness. Categorical variables

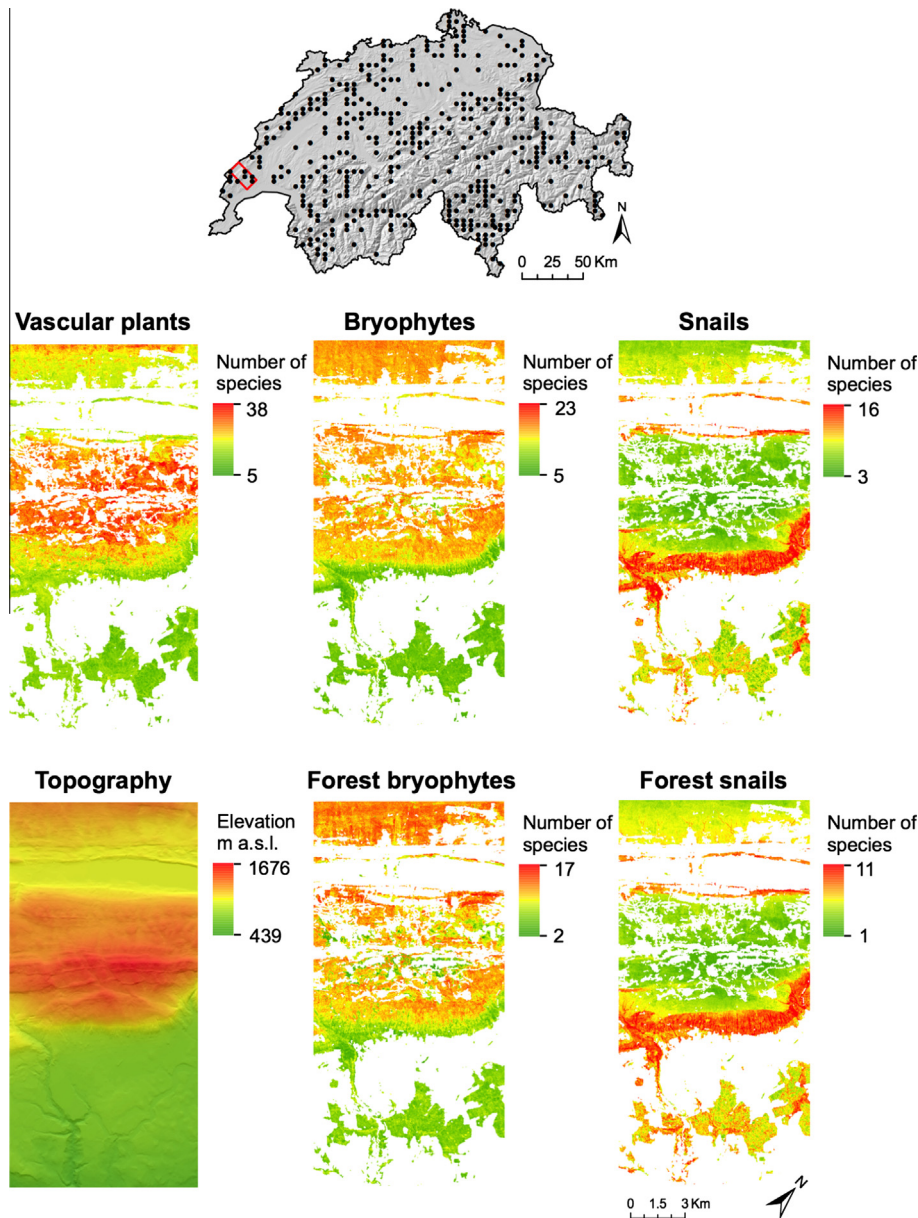


Fig. 2. Spatial predictions of species richness, i.e. the predicted number of species per forest raster cell measuring 30×30 m, for each species group, based on the Random Forest models. Forest plants were not mapped because of the poor model fit. The study area including the sampling plot locations (black dots) and the selected region for the spatial predictions (red rectangle) are shown above.

were included as binary dummy variables and centered to a mean of zero, according to Schielzeth (2010). Continuous variables were scaled (mean = 0, SD = 1) so that their coefficients could be compared as measures of relative importance (Schielzeth, 2010). Variable selection was based on the least absolute shrinkage and selection operator (LASSO, Tibshirani (1996)) method, implemented in the “GLMNET” R package (Friedman et al., 2010). It involves penalized likelihood, which imposes a constraint on model parameter estimates, shrinking many of them to zero (see Hastie et al. (2009) for a detailed description). The optimal LASSO penalty parameter λ was determined by 10-fold cross-validation. We selected all variables with a non-zero coefficient from the most regularized model, i.e. with the largest value of λ such that error was within one standard error of the minimum (Hastie et al., 2009). Due to overdispersion, we fitted negative binomial generalized linear models (GLMs) with the selected variables and

evaluated the parameter estimates. Each model was checked for spatial autocorrelation using Morans’I coefficients over various lag distances, but the residuals of the models were not significantly autocorrelated spatially.

3. Results

3.1. Variation and prediction of species richness

About half of the species in each group showed a close association with forest habitats, and they were thus classified as forest species. The median number of species per plot over all taxa ranged from 4 to 17 (Fig. 1). Species richness of plants and bryophytes was weakly correlated, with the strongest correlation coefficient (Pearson’s r) of 0.41 for forest plant and overall bryophyte richness.

Snail species richness was correlated neither with plant nor with bryophyte species richness.

The prediction accuracy of the six RF models, as evaluated by the percentage of explained variance from 5-fold cross-validation, ranged from 37.2% to 6.8% (Table 3). Snail species richness was predicted best, followed by bryophyte and plant species richness. Species richness of forest snails was modeled more accurately than overall snail species richness, but the opposite was true for plants and bryophytes. While species richness of plants and bryophytes responded positively to decreasing temperature, snail species richness increased with increasing temperatures. Plant and especially snail species richness responded positively to increasing topsoil pH values, while overall bryophyte species richness showed a unimodal relationship with pH. The NDVI was positively related to species richness throughout all forest species groups. Plant species richness increased with decreasing canopy cover, and snail species richness increased with an increasing standard deviation of vegetation heights.

The predictions for the selected region (Fig. 2) illustrate distinctive species richness patterns without a common trend among the groups. Highest numbers of plant species were predicted in the highest elevation belt, where at the same time the models predicted low numbers of snail species. Predictions of bryophyte species richness increased at medium and high elevations.

Table 3

Results from Random Forest models for species richness using area-wide available environmental predictors. Model evaluation was based on percentage of variance explained (R^2) from 5-fold cross-validation (means of 10 runs). The relative variable importance (VarImp, in %) is shown for the six most important predictors, blank entries do not imply that these variables were not important, but that they were not ranked among the six most important ones. Based on visual inspection of the response curves provided by each RF model, we report the response of species richness in relation to the environmental predictors as follows: positive (+), negative (–) and hump-shaped (h).

	Overall species richness	Forest species richness
Plants		
R^2 (SD)	16.8 (1.8)	6.8 (2.2)
Variable name	VarImp	VarImp
Temperature (summer mean)	14.4 (–)	7.2 (–)
Topographic position index	6.2 (–)	7.6 (–)
Eastness	6.4 (+)	8.1 (+)
pH	8.1 (+)	10.1 (+)
NDVI	6.3 (h)	6.7 (+)
Canopy cover at 1 m	7.7 (–)	7.1 (–)
Bryophytes		
R^2 (SD)	24 (3)	20.3 (2.3)
Variable name	VarImp	VarImp
Temperature (summer mean)	16.3 (–)	10.2 (–)
Precipitation (summer mean)		7.3 (h)
Site water balance	6.4 (+)	8.6 (+)
Solar radiation (summer mean)	10.0 (–)	8.4 (–)
Topographic position index	7.3 (–)	
Topographic wetness index	6.4 (+)	
pH	6.1 (h)	
NDVI		8.3 (+)
Canopy cover at 1 m		7.9 (+)
Snails		
R^2 (SD)	31.6 (2.2)	37.2 (1.4)
Variable name	VarImp	VarImp
Temperature (summer mean)	10.6 (+)	14.5 (+)
Precipitation (summer mean)	9.0 (–)	9.7 (–)
Site water balance	5.8 (–)	5.3 (–)
Topographic wetness index	5.6 (+)	
pH	18.0 (+)	16.1 (+)
NDVI		5.6 (+)
SD vegetation height	7.6 (+)	7.7 (+)

Table 4

Coefficients and significance levels from the GLMs for species richness as a function of variables of forest structure and composition from the National Forest Inventory. Continuous variables were scaled (mean = 0, SD = 1) so that their coefficients can be interpreted as variable importance. This does not apply to categorical variables (cat). For bryophytes, the LASSO did not select any variables (see methods for details), thus no GLMs were fitted.

	Overall species richness	Forest species richness
Plants		
(Intercept)	2.933***	2.599***
Overstory cover	–0.205***	–0.085**
Understory cover		0.071**
Basal area alluvial tree species		0.072**
Snails		
(Intercept)	2.054***	1.605***
Overstory cover	0.144**	0.188***
Understory cover	0.077*	0.097**
Ground vegetation cover 76–100% (cat)		–0.324**
Coniferous 91–100% (cat)	–0.294***	–0.310***
Total basal area	–0.114**	–0.138**
Basal area alluvial tree species	0.154***	0.171***
Total volume of deadwood		0.110**
Time since last harvest/intervention	–0.144***	–0.193***

*** Significance level: 0.001.

** Significance level: 0.01.

* Significance level: 0.05.

3.2. NFI variables and their relation to species richness

Stand characteristics significantly explained species richness of plants and snails (Table 4). Plant species richness increased with decreasing overstory cover, and more forest plants were found in plots with a high basal area of alluvial tree species. Increasing overstory and understory cover had a positive effect on snail species richness, yet increasing total basal area was negatively related with snail species richness. Forest composition was also related to snail species richness: while increasing values of total basal area of alluvial tree species were favorable for snails, stands with a very high proportion (91–100%) of conifers harbored fewer snail species. Snail species richness was higher in plots with shorter periods since the last harvesting (or other intervention), and forest snail species richness was positively associated with increasing volumes of deadwood (Table 4).

4. Discussion

Our results show that species richness patterns of plants, bryophytes and snails in central European forests are related to a combination of climate, topography and soil pH as well as forest structure and composition. The relative importance of these determinants, however, varies considerably among the three taxa. Our results further indicate that at least one determinant had a similar effect across all forest species groups (i.e., NDVI), whereas others seem to be taxa-specific (e.g., site water balance, solar radiation, canopy cover at 1 m). This suggests a pronounced differentiation and functional adaptation of the three taxa to micro-habitats at the forest stand scale. In addition, there is no common mechanism for the relationship of these determinants with species richness.

4.1. Species richness along environmental gradients

Among area-wide available predictors, climatic variables were more important for predicting bryophyte and snail species richness than for plant species richness, which depended more on

site-specific factors. In fact, the combination of soil pH, topographic position with variables related to vegetation density (NDVI) and light availability on the forest floor (canopy cover) was more important for predicting local-scale plant species richness patterns than climate, of which temperature was identified as the only important predictor throughout the analysis. This is consistent with other studies of plant diversity in forest ecosystems (Harrison et al., 2006; Wang et al., 2009; Zhang et al., 2013), suggesting that local-scale predictive models of plant species richness should include site-specific predictors representing a range of environmental gradients (Austin et al., 1996; Pausas and Austin, 2001). Soil pH, for instance, is related to the concentration of assimilable nutrient and toxic compounds and therefore constitutes an important environmental variable with a direct physiological impact on plants (Dubuis et al., 2013). Similarly, light availability under the forest canopy, as represented by the LiDAR-based measurement of canopy cover, characterizes an important resource gradient influencing plant species richness patterns (Franklin et al., 2002; Wohlgemuth et al., 2002). Water availability, however, was not a limiting factor for plant species richness. Although this finding contrasts results from broad-scale studies of patterns of plant species richness (Hawkins et al., 2003; Kreft and Jetz, 2007), it is consistent with previous local-scale analyses in temperate forests (Wang et al., 2009) and may be caused by a decreasing importance of water availability as a determinant of plant species richness in regions that are not prone to water deficits. However, several studies from such regions highlighted the importance of soil moisture and hydrologically defined niches for species richness in local plant communities (Moeslund et al., 2013; Silvertown et al., 1999). Thus the interpretation of this result remains difficult and may also be affected by the slight mismatch between the resolutions of our species and environmental data (discussed below).

Bryophyte species richness increased with decreasing temperature. This pattern, which was also visible for plant species richness, can be attributed to the mid-elevation peak of vegetation diversity in our study region (Wohlgemuth et al., 2008). Elevations at the upper end of the elevation gradient (>2235 m a.s.l., i.e. above upper tree line), which are causing the hump-shaped response of species richness to elevation in Wohlgemuth et al. (2008), are not represented in our study with a special emphasis on forest. This explains the linear relationship between temperature and species richness. Besides temperature, increasing solar radiation was related to decreasing bryophyte species richness, a pattern that was probably caused by the limiting effect of higher solar radiation for bryophytes via lower soil moisture (Raabe et al., 2010; Zhang et al., 2014). Indeed, we found that several variables relating to humidity and water availability, such as topographic wetness index or site water balance, were important for predicting bryophyte richness. This result is in line with previous studies highlighting the positive effect of water and moisture availability on bryophyte habitat quality (Mills and Macdonald, 2004; Raabe et al., 2010).

Increasing soil pH values were associated with large numbers of snail species. This relationship has been frequently documented and is likely to reflect the strong correlation between soil pH and calcium availability, which constitutes a vital resource for snails to build their shells (Wäreborn, 1970; Martin and Sommer, 2004). However, snail communities have also been shown to respond differently to soil acidity, irrespective of calcium content (Wäreborn, 1970). Apart from pH, climatic factors were the most important predictors for snail species richness. The positive effect of increasing temperature can be interpreted along the line of evidence that species richness is positively correlated with increasing energy availability (Currie, 1991; Hawkins et al., 2003). We expected a positive influence of factors related to humidity and water availability, but we found a negative effect of precipitation

and site water balance on snail species richness. This can be attributed largely to a regional effect driven by edaphic and climatic factors. The silicate bedrock in the southern part of our study area leads to acidic soils that are unsuitable for many snail species. At the same time, this region receives high amounts of precipitation, and a considerable share of it comes from heavy rainfall events that lead to high surface runoff. Together with frequent drought periods, the resulting highly variable water availability throughout the year may further curtail habitat suitability for many snail species.

4.2. NFI variables for managing species richness

The strongest relationship between species richness and field measurements of forest stand structure and composition was found for snails. The significant correlation of snail, and especially forest snail species richness with the basal area of alluvial tree species, such as the genera *Fraxinus*, *Tilia*, *Ulmus* and *Acer*, suggests that many snail species may benefit from promoting these tree species. This positive relationship has also been documented in other studies (Wäreborn, 1969; Horsak et al., 2010), and Suominen et al. (2003) further pointed out the importance of aspen (*Populus tremula* L.) stands for conserving gastropod diversity in boreal forests. The reason for this positive relationship may be related to the higher content of soluble calcium salts, e.g. calcium citrate, in the litter of these genera (Wäreborn, 1969). Stands dominated by conifers, on the contrary, harbored fewer snail species, which is also related to conifer litter quality, as it is relatively persistent, dries out quickly and promotes soil acidification, thus lowering snail habitat quality. Besides the relationships of snail species richness with the tree species composition, we also found positive associations with stand structural properties. An increasing over- and understory cover, for example, was positively related to snail species richness, which may be explained by favorable microclimatic conditions that are brought about by an increased over- and understory cover, such as buffered temperature ranges or increased topsoil moisture content (Suggitt et al., 2011). Furthermore, our finding that forest snail species richness increased on sites with higher volumes of deadwood confirms results from previous studies (Müller et al., 2005; Kappes, 2006). Increasing the availability of deadwood is thus a promising way to improve habitat quality for many forest snail species because it provides damp sites with lower temperature extremes as well as suitable sites for roosting, oviposition and feeding (e.g. on deadwood-colonizing fungi) (Kappes, 2006).

Contrary to snails, we did not find any relationship between forest inventory variables and bryophyte species richness, and only limited signals for plant species richness. For instance, we found that a decreasing overstory cover promotes plant species richness, which probably relates to the increased availability of light in the lower strata of such stands. However, this effect was weaker in the case of forest plants, which generally tend to be rather shade-tolerant.

4.3. Limitations

Our species data were sampled on 10 m² plots, which were probably not large enough to represent the environmental constraints for the local flora and fauna well. This applies particularly to forests, where local site characteristics such as the availability of light or suitable substrate (e.g., deadwood for bryophytes) may vary over short distances due to micro-topographic heterogeneity. As mentioned by Steinmann et al. (2009), the recognition of ecological patterns is thus likely to be blurred by random effects and non-equilibrium processes (Huston, 1979). To analyze floristic α -diversity in a particular habitat, Crawley and Harral (2001)

recommended using plot areas of at least 100 m². Moreover, the pixel size (i.e. resolution) of our predictor variables ranged from 10 to 30 m, thus they do not exactly correspond to the species survey plots measuring 10 m², and the climate data were derived from interpolations, which may impair their effective level of detail. This implies that our environmental predictors, despite their relatively high resolution, were still limited in representing the exact conditions at the 10 m² plots where the species were recorded. Together, the size of the species survey plots and the respective mismatch with the predictor variables may partially explain the moderate model fits.

5. Conclusions

Our results have implications for the spatial prediction of species richness and its management in forests. The study shows the significance of site-specific factors such as local forest structure and composition as well as soil pH, for complementing topographic and climatic predictors of species richness for multiple taxa in temperate forests. This suggests that local species richness can be positively influenced by appropriate site selection and management of stand structure and tree species composition. Our study further emphasizes the importance of digital, high-resolution environmental data for comparing the relative effects of biotic and abiotic predictors of area-wide species richness in heterogeneous forest landscapes.

Acknowledgements

We would like to thank Michael Jutzi, Norbert Schnyder, Francois Claude, Michael Nobis, Ariel Bergamini and Tamara Schlegel for their help with the species classification and the useful discussions. The Swiss Federal Office for the Environment (FOEN) kindly provided the BDM data. F.Z. was funded by the Swiss National Science Foundation (SNF, Grant number 146786).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.04.008>.

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