ORIGINAL ARTICLE

Environmental predictors of species richness in forest landscapes: abiotic factors versus vegetation structure

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ABSTRACT

Aim To investigate the performance and relative importance of abiotic and biotic predictors of species richness of three taxa in forest-dominated landscapes across an environmentally heterogeneous mountain region.

Location Switzerland (central Europe).

Methods We used a broad set of nationally available environmental predictors grouped into (1) climate, (2) topography and soil and (3) 3-D vegetation structure derived from airborne Light Detection and Ranging (LiDAR) data to spatially predict the forest species richness of vascular plants, butterflies and breeding birds. We used presence data of 212 plant, 157 butterfly and 92 bird species from multiple transect samples in > 220 1 km^2 squares at elevations between 261 and 2123 m a.s.l. across 41,248 km^2. We applied an ensemble modelling approach consisting of five modelling techniques and evaluated their predictive performance using the cross-validated percentage of explained variance of each predictor group separately and the combinations thereof. We investigated the relative importance and response of each predictor and partitioned the variation into independent and shared components per variable group.

Results Climate performed best in predicting forest species richness across taxa. Vegetation structure particularly improved the predictions of butterfly and bird species richness, while soil pH was an important predictor for forest plant species richness. Climate appeared to be mainly indirectly related to butterfly species richness, via correlations with habitat type and structure. The strength and direction of the relationships between the predictors and species richness were taxon-specific with low cross-taxon congruence.

Main conclusions The growing availability of LiDAR data offers powerful new tools for describing vegetation structure and associated animal habitat quality across large areas. This will further our understanding of niche-driven assembly processes in forest landscapes. Although climate was the dominant factor controlling species richness across taxa from different trophic levels, the taxon-specific distributional pattern and response to environmental conditions emphasize the difficulty of accounting for a range of taxa in prioritising biodiversity conservation measures.

Keywords

3-D habitat structure, airborne laser scanning, biodiversity, environmental heterogeneity, European Alps, LiDAR, richness, temperate forests

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INTRODUCTION

Investigating the relative importance of abiotic and biotic factors that control the distribution of species diversity is of central interest in ecology and biogeography. Climate and environmental heterogeneity are important predictors of diversity patterns, and there is strong empirical support for the notion that climate and productivity are crucial for

determining species richness at large spatial scales (Currie, 1991; Kerr & Packer, 1997; Hawkins et al., 2003; Field et al., 2009; Stein et al., 2014). However, the relative importance of the various factors explaining diversity patterns remains controversial at smaller spatial scales (Field et al., 2009). This scale effect may be due to (1) the relatively small climatic gradients covered by most studies carried out at small extents, or (2) the fact that climate is usually filtering species at the large scale, while other factors filter species at smaller scales. At small spatial scales, the relevance of habitat structure and complexity for species richness has long been emphasized, especially in forests (MacArthur & MacArthur, 1961). Their effect on diversity patterns is closely related to the environmental heterogeneity hypothesis, which suggests that species richness is promoted through several processes, e.g. by increasing niche availability, which allows more species to coexist (Currie, 1991; Tews et al., 2004; Stein et al., 2014). Moreover, abiotic factors related to topography and edaphic properties such as soil pH have frequently been shown to explain species distributions and richness patterns at regional and local scales (Grime, 1979; Kerr & Packer, 1997; Pausas & Austin, 2001; Rahbek & Graves, 2001). In addition to their scale dependence, the relative importance of environmental correlates of species richness varies between taxa, because different groups of species may respond differently to factors controlling species diversity (Rosenzweig, 1995). This often leads to low cross-taxon congruence and different distributional patterns, which poses difficulties for prioritising locations and actions for biodiversity conservation (Westgate et al., 2014).

Several studies highlighted the importance of complementing climatic variables with land cover and habitat information for improving predictions of species distributions and richness patterns at regional scales (Pearson et al., 2004; Thuiller et al., 2004; Illán et al., 2010). Habitat has usually been described by two-dimensional representations of land cover types, i.e. important aspects of habitat, such as the three-dimensional structure of forests, are overlooked. Indeed, there is growing evidence for a strong relationship between 3-D vegetation and habitat structure and species richness for various taxa (Vierling et al., 2008; Davies & Asner, 2014; Simonson et al., 2014). Bird species richness, in particular, has frequently been shown to respond to the vertical vegetation structure in forests (MacArthur & MacArthur, 1961; Goetz et al., 2007; Lesak et al., 2011), and relationships between vegetation structure and other taxonomic groups, such as invertebrates, are also documented (Vierling et al., 2011; Davies & Asner, 2014). A growing number of such studies apply Light Detection and Ranging (LiDAR) remote sensing data, which is becoming increasingly available across large areas and provides detailed and contiguous information on 3-D vegetation properties and habitat structure (Davies & Asner, 2014). However, the importance of remotely sensed 3-D vegetation structure relative to other environmental predictors of species richness, such as climate, and whether the relationship between vegetation structure and species richness is consistent across different taxa remains poorly investigated. Comparative studies across large spatial extents and climatic gradients were traditionally based on sample plot data of vegetation structure, such that area-wide, spatially explicit predictions of the relationship between vegetation structure and species richness were not feasible. The advent of LiDAR has profoundly changed this and the question thus arises how such data sets can be included into country-wide biodiversity assessments to evaluate large areas in terms of habitat structure and associated quality and quantity.

We used LiDAR-derived vegetation structure to investigate its relative importance compared to climate, topography and soil pH, for predicting the species richness of plants, butterflies and birds in forest-dominated landscapes across an environmentally heterogeneous region in Central Europe, that is, Switzerland. We report on the predictive, as well as the explanatory, power of the environmental variables, and use them to spatially predict species richness at a 1-km^2 resolution. The resulting maps are used for evaluating the degree of spatial covariation between trophically very different taxa and provide essential information for managing landscapes for conservation. Considering the large climatic gradient in our study region, we expect climate to be a strong factor controlling species richness across these taxa. Furthermore, we expected a relatively strong influence of vegetation structure for mobile species such as butterflies and birds, which extensively use the 3-D forest habitat space. We address the following research questions: (1) What is the relative importance of climate, topography and soil pH, and vegetation structure for predicting the number of plant, butterfly and bird species associated with forest landscapes? (2) To what extent can variables related to vegetation structure, topography and soil pH improve climate-based predictions of species richness?

MATERIAL AND METHODS

Study area

The study was carried out in Switzerland, covering 41,248 km^2 of Central Europe (45°49′-47°48′ N, 5°57′-10°30′ E). The country is structured into mountain areas, which cover about 70% of the area (60% Alps, 10% Jura Mountains) and the lowlands (30%). One-third of the country consists of forests, with a larger proportion in the mountain areas. Forty-three per cent of the forests are coniferous, while 33% are mixed and 24% are broadleaved (Brändli, 2010). The elevation ranges from 261 to 2123 m a.s.l., with a mean of 1056 m a.s.l. Within the boundaries of a temperate humid climate, the mean annual temperature and precipitation range from 0.7 to 12.1 °C and 636 to 2149 mm, respectively (Zimmermann & Kienast, 1999).

Species data

We obtained species richness data from surveys conducted within the Swiss Biodiversity Monitoring Program (BDM,

Weber *et al.* (2004)). In 5-year intervals, BDM collects species occurrence data of vascular plants, butterflies and breeding birds on 520 1-km² sample squares, distributed in a systematic national grid. We used the data from the five-year survey period 2004–2008 and filtered out non-forest habitats and taxa later (see below). In each sample square, vascular plant and butterfly species occurrences were recorded along a transect of 2500 m length and 5 m width, following detailed standardized field protocols (BDM Coordination Office (2008), see Appendix S1 in Supporting Information). *Vascular plants* (from now on referred to as 'plants') were sampled twice, in spring and late summer (except in high alpine forest sample squares, which were surveyed once in mid-summer). *Butterfly* surveys were carried out between four (at high altitudes) and seven times (in the lowlands), during April and September. The surveys took place between 10 a.m. and 5 p.m. when specific weather conditions prevailed, that is, an air temperature of at least 13 °C, wind speed not exceeding 19 km/h (Beaufort level 1–2) and more than 80% sunshine. The detectability of butterfly species varied by species and averaged 88% per inspection (Kéry *et al.*, 2009). *Breeding birds* were sampled by the Swiss Ornithological Institute following the procedure of the Common Breeding Bird Survey (MHB, Kéry *et al.* (2005)). During the breeding season (15 April–15 July), each sample square was surveyed three times (sample squares at elevations > 2000 m a.s.l. were surveyed only twice) annually along a sample square-specific route using the territory mapping method (Bibby *et al.*, 1992). Routes aim to cover as large a proportion of a sample square as possible and have an average length of 5 km. Mean detectability of birds was estimated at 89% (Kéry & Schmid, 2006). A more detailed description of the field sampling protocols including further quality measures for the field methods are provided in Appendix S1.

Given our aim to study the relationship between observed species richness (i.e., the total number of observed species per sample squares) and forest/woodland vegetation structure we restricted the analysis to species with an association with forests and woodlands, as well as to sample squares with a forest/woodland cover (from now on referred to as forest cover) of at least 30%. The percentage of forest cover per sample square was calculated based on the aggregated land cover types 'forest', 'open forest' and 'shrubland', as delineated by the Federal Office of Topography (swisstopo, 2014). Our threshold selection is based on Andrén (1994), who found 30% to be the minimum proportion of suitable habitat below which habitat fragmentation starts to negatively affect species richness and density. Furthermore, a relatively low threshold increases the sample size and area for the spatial predictions of species richness (see below).

For classifying *plant* species, we consulted the database of the national species data centre (www.infoflora.ch, accessed 17 October 2014) and selected only species for which 75% of all occurrences were reported in forests. For classifying *butterflies*, we used the habitat profiles listed by van Swaay *et al.* (2006; cf. Appendix 1), who compiled data for butterfly species across Europe based on the CORINE land cover classification. We considered all species that were reported in at least one forest and woodland habitat type (see Appendix S2). While we are aware that the degree of association with forest and woodland varies considerably among species, we hypothesized that the vegetation structure of forests and woodlands influences the habitat quality of these species to some degree, e.g. by determining the availability of food resources or providing shelter (Dover *et al.*, 1997). *Bird* species were selected according to the habitat classification in the species database of the Swiss Ornithological Institute (www.vogelwarte.ch, accessed 6 February 2015). We selected all species whose habitat classification included forest, hedges, forest edge or shrubland. The altitudinal range of the samples was 261 to 2123 m a.s.l., and the sample size was 226 species for plants, 224 for butterflies, and 237 for birds.

Groups of predictor variables

We considered six bioclimatic predictor variables that we assumed to be physiologically relevant to a species' occurrence (Table 1). Monthly mean temperature and precipitation layers were interpolated using DAYMET (Thornton *et al.*, 1997), based on daily measurements of all available recording stations (*c.* 300) during the period 1981 to 2010 (www.meteosuisse.ch), and a digital elevational model with 100 m pixel size (www.swisstopo.ch). Solar radiation was analysed at a finer resolution (25 m) to account for fine-scale availability of radiation and associated energy. We used the standard deviation within the area of each sample square to represent spatial climatic variability.

Topography and its variation were represented by the mean and standard deviation of two complementary variables, topographical position and slope. These variables can be sampled very accurately, and are correlated well with observed patterns of species distribution and richness (Guisan & Zimmermann, 2000). We further used a previously published topsoil pH map (Zellweger *et al.*, 2015) describing edaphic characteristics such as the availability of nutrients and toxic elements.

We used a nationally available set of discrete, first and last return airborne LiDAR data to derive four variables describing different aspects and variation in the 3-D distribution of forest vegetation elements (Table 1). The Swiss Federal Office of Topography acquired the raw data with an average return density of *c.* 1.5 m⁻² in forests during multiple seasons in the years 2000–2008 (Artuso *et al.*, 2003; Zellweger *et al.*, 2013). The nominal footprint size was in the range of small-footprint laser scanning (i.e. several decimetres) and height accuracy varies between ±0.5 m (±1 SD) and ±1.5 m in open and forested areas, respectively. The raw point cloud data were pre-processed using a suite of *LAStools* algorithms (Isenburg, 2013) to derive the normalized vegetation heights above ground. We considered all vegetation return heights above 1 m to calculate the variables described below, and used a national vector data set (swisstopo, 2015) to mask out buildings.

Table 1 Environmental predictor variables for modelling species richness of plants, butterflies and birds in forest landscapes. We analysed the mean and the standard deviation (SD) separately.

Variable name	Description	Resolution [m]
Climate		
t_{min}	Mean monthly minimum temperature (°C) in the coldest month (January)	100
ddeg	Mean and SD of annual degree-days above a threshold of 3 °C (day*°C)	100
sfro	Mean and SD of annual average number of frost days during growing season (Bolliger et al. 2000)	100
swb	Mean and SD of site water balance (cm) (Guisan et al. 2006) (for plants only)	100
P_{veg}	Mean monthly precipitation sum (mm) during growing season (April to September)	100
srad	Mean and SD of potential global clear sky solar radiation (kJ/m^2) in early spring (March)	25
Topography and soil		
tpi	Mean and SD of topographical position index, which measures the exposure of a site in relation to the surrounding terrain. Positive values: Ridges and hilltops; negative values: sinks (Zimmermann and Roberts, 2001)	25
slp	Mean and SD of slope (°)	25
pH	Mean and SD of topsoil pH (see text for details)	25
Vegetation Structure		
CHH	Canopy height heterogeneity (m), i.e. SD of canopy height, which was measured by the 95th percentile of vegetation return heights above 1 m	20
MeanVegH	Mean vegetation height above 1 m (m)	20
VegDens	Mean and SD of vegetation density (%), measured as the proportion of vegetation returns above 1 m relative to all returns	20
UHD	Mean understorey height diversity, expressed as the Shannon–Wiener information index (H′) for the proportion (p) of horizontal vegetation in the ith layer (see text for details). UHD = $H' = -\Sigma p_i \ln p_i$ (MacArthur & MacArthur, 1961; Clawges et al., 2008)	50

Canopy height heterogeneity (CHH) was determined as the standard deviation of the 95th percentile of the vegetation return heights (Næsset, 2002; Simonson et al., 2012). CHH is a frequently used attribute of forest habitat structure, which has been shown to correlate well with species diversity, particularly bird diversity (Davies & Asner, 2014). Average vegetation height and vegetation density represent structural attributes that are related to successional stage and micro-climatic conditions, such as light availability on the forest floor (Müller & Brandl, 2009). CHH, average vegetation height and density rasters were calculated using the *lascanopy* tool (Isenburg, 2013). To this end, we applied a pixel size of 20 m to upscale local forest structure to the stand scale. Inspired by the concept of foliage height diversity proposed by MacArthur & MacArthur (1961), we calculated a measure for the diversity of low vegetation heights, and termed it 'understorey height diversity' (UHD). UHD was defined as the Shannon–Wiener information index $H' = -\sum p_i \ln p_i$, where p_i is the proportion of vegetation returns in the ith height interval. The height intervals were: 1–3 m, 3–6 m, 6–9 m, 9–12 m and > 12 m (cf. Clawges et al., 2008). The proportions within each interval were derived from vegetation density rasters calculated using *lascanopy* (Isenburg, 2013) with a pixel size of 50 m, thus approximating the reference areas that are frequently applied to quantify foliage height diversity (Clawges et al., 2008; Simonson et al., 2012). To account for a minimal amount of overstorey, UHD was only considered for pixels with a tree canopy (i.e. vegetation height > 12 m) whose density exceeded 10%, as calculated from a density raster taking into account all vegetation points

above a height of 1 m (Isenburg, 2013). Because our aim was to analyse the relationship between the 3-D habitat structure and species richness, we did not include any variable directly describing forest fragmentation and edge effects, despite their potential effect on species occurrence and richness.

Ensemble modelling and statistical analyses

To predict species richness and evaluate the relative importance of each predictor variable, we used an ensemble modelling approach consisting of five modelling techniques: three regression methods [generalized linear model (GLM), generalized additive model (GAM) and multivariate adaptive regression splines (MARS)], and two machine-learning methods [gradient boosted model (GBM) and random forest (RF)] (Araújo & New, 2007). We applied different methods because the variability between different modelling techniques has been raised as an important source of uncertainty (Buisson et al., 2010). All parameter settings, including quadratic terms for fitting the GLMs, were adopted from the default settings as implemented by Thuiller et al. (2009). A principle advantage of these methods (except for GLM) is that they account for non-linearities, and, in the case of GBM and RF, automatically consider interactions between variables. Predictive model performance was evaluated based on the percentage of explained variance (R^2) obtained from a threefold cross-validation procedure that we repeated 10 times. Thus, two-thirds of the data were used for model calibration and the remaining third for model evaluation. The final models used for generating maps of species richness

were re-calibrated based on all data. We used the predictive performance of the single modelling techniques to build an R^2-weighted average ensemble. The relative importance of the variables was estimated based on a randomization procedure as described by Thuiller *et al.* (2009). It is reported as one minus the correlation between the standard prediction and the prediction where the considered variable was randomized. We calculated it for each modelling technique separately and averaged it across all techniques. All analyses were performed in R (R Development Core Team 2015).

Within this framework, we built an ensemble model separately for each predictor variable group, as well as for all combinations thereof (i.e. seven ensemble models in total). To reduce the number of variables per group we built an ensemble model with all variables in each variable group and used the three most important variables from each group for building the final ensemble models. In order to have the same number of variables per group combination, the combined model from all three variable groups was built using the six most important variables. This procedure allowed for model comparison without potential bias on model accuracy arising from different numbers of variables. The final sets of variables were tested for multicollinearity using the variance inflation factor (VIF) with a threshold of 10; none of the selected variables had multicollinearity problems. We checked the residuals of each of the seven final ensemble models for spatial independence by calculating correlograms and Morans' I over various lag distances, and found no statistically significant spatial autocorrelation; thus we did not investigate this further.

To analyse the independent versus the shared part of variance explained by the three groups of predictor variables, we partitioned the variation into independent and shared components. To this end, we used the *varpart* function (Oksanen *et al.*, 2015), which computes the adjusted canonical R^2, analogous to the adjusted R^2 in multiple regression (Peres-Neto *et al.*, 2006). Note that this analysis was based on linear regression and serves explanatory purposes, in contrast to the predictive approach based on cross-validation.

RESULTS

Our classified species sets included 212 forest plant species, of which an average number of 48 (range: 10–79) were observed per sample square. For butterflies and birds, we identified 157 and 92 species with an association with woodland or forest landscapes, respectively, with average numbers of 33 (range: 8–68) and 33 (range: 13–46) per sample square, respectively. Below, we refer to plant, butterfly and bird species richness associated with woodland and forest landscapes as PlSR, BuSR and BiSR, respectively. PlSR was moderately and positively correlated with BiSR (Pearson's $r = 0.44$, $P < 0.001$), and negatively correlated with BuSR ($r = -0.42$, $P < 0.001$). BiSR and BuSR were weakly correlated ($r = -0.24$, $P < 0.001$).

Ensemble model predictions of species richness

For all species groups, predictive models using variables from all three variable groups performed best, with R^2 ranging from 67.2% to 44.1% (Table 2). Models based solely on climatic predictors outperformed models solely based on topography and soil pH, or on vegetation structure in the case of plants and birds. Differences in model performance between the single variable group models were less pronounced for butterflies. Adding predictors representing vegetation structure to the climate-based models significantly improved model performance for butterflies and birds.

The spatial predictions showed distinctive richness patterns for each taxon (Fig. 1). Areas of high PlSR were mainly predicted along valley bottoms and in the northern part of the study region. A similar but less distinct pattern was predicted for BiSR. By contrast, BuSR was predicted to be highest in the Rhone valley, i.e. the large valley that is east–west oriented in the south-west of the study region, and in the central Alps in general. Lowest numbers of butterfly species were predicted in the lowlands towards the northern edge of the study region.

Variable importance and relationship with species richness

Degree-days were the most important predictor for PlSR, followed by vegetation height and topsoil pH (Table 3). We found a positive relationship between degree-days and PlSR, with a decreasing slope towards increasing degree-days (Fig. 2). Vegetation height and topsoil pH were also

Table 2 Prediction accuracies (R^2 in %) and the standard deviations (SD) as obtained from 10 times repeated three-fold cross-validated ensemble models predicting species richness in Swiss forested landscapes based on different variable groups and their combinations. Improvements to the models using climate variables only were evaluated with Kruskal–Wallis rank sum tests, and indicated as follows: not significant (n.s.), $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

| Variable group	No. of variables	Plants	Butterflies	Birds
Climate	3	61.8 (5.6)	44.8 (5.5)	37.9 (6.0)
Topography and soil pH	3	24.6 (8.1)	45.0 (7.0)	20.1 (8.0)
Vegetation structure	3	35.6 (5.9)	38.2 (6.7)	28.2 (5.4)
Climate + Topography and soil pH	6	64.3 (5.5)n.s.	48.1 (6.7)**	40.8 (7.8)n.s.
Climate + Vegetation structure	6	63.4 (6.6)n.s.	51.9 (6.4)***	41.8 (5.7)*
Topography and soil pH + Vegetation structure	6	44.1 (6.1)	50.1 (5.5)	31.1 (9.2)
Climate + Topography and soil pH + Vegetation structure	6	67.2 (5.1)**	54.2 (6.9)***	44.1 (5.6)**
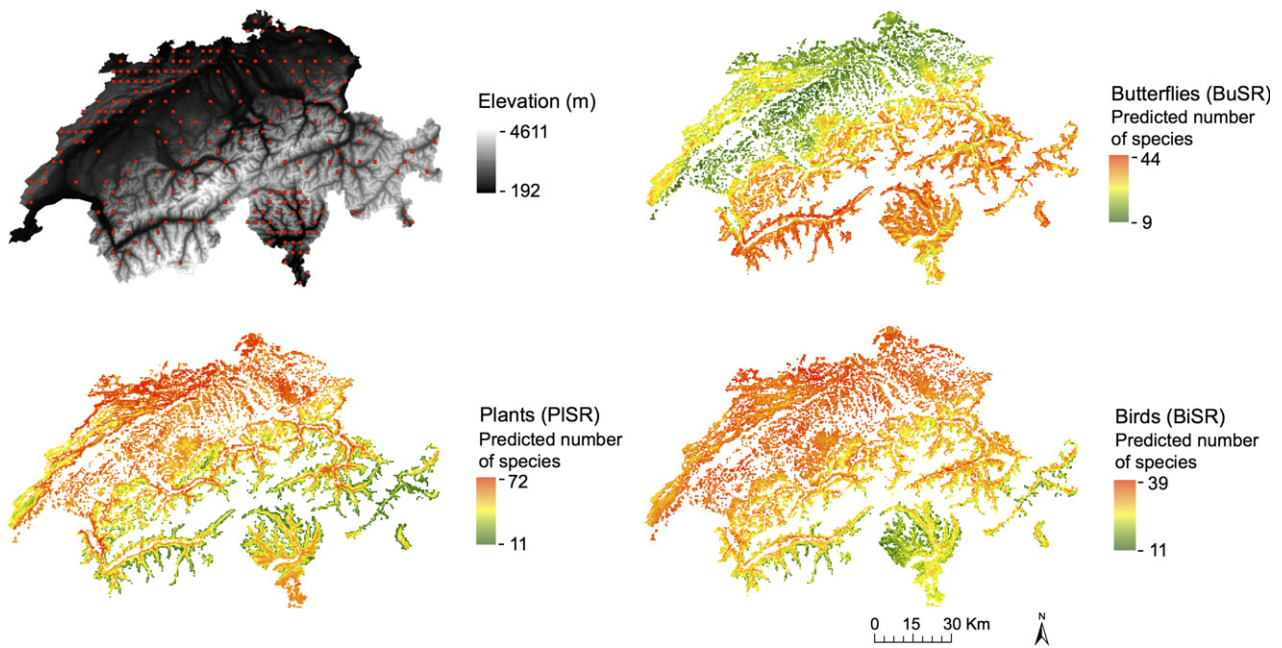
Figure 1 Predicted forest species richness in Switzerland from final ensemble models using environmental variables from all three variable groups. Blank areas represent landscapes with less than 30% forest cover, including lakes and unproductive rocks. The elevational model includes the sampling square distribution (red squares).

Table 3 Variable importance (mean and standard deviation SD) based on permutation tests in the final ensemble model (averaged over five modelling techniques) combining all three variable groups.

	Mean (SD)
Plants (PlSR)	
Degree-days (mean)	0.67 (0.12)
Mean vegetation height (mean)	0.10 (0.02)
pH (mean)	0.07 (0.01)
Topographical position (variation)	0.02 (0.01)
Degree-days (variation)	0.02 (0.01)
Slope (mean)	0.01 (0.01)
Butterflies (BuSR)	
Understorey height diversity (UHD)	0.25 (0.11)
Slope (mean)	0.22 (0.11)
Degree-days (mean)	0.03 (0.02)
Degree-days (variation)	0.02 (0.02)
pH (mean)	0.02 (0.01)
Solar radiation (mean)	0.01 (0.01)
Birds (BiSR)	
Precipitation	0.26 (0.05)
Frost days (variation)	0.17 (0.09)
Topographical position (mean)	0.08 (0.03)
Solar radiation (mean)	0.07 (0.01)
Vegetation density (mean)	0.06 (0.02)
Understorey height diversity (UHD)	0.04 (0.05)

positively related to PlSR, with topsoil pH showing a drop of the curve at the upper end of the pH gradient. BuSR was predicted best by UHD and slope. BuSR increased linearly with increasing UHD but reached an optimum at a slope of *c.* 30°. Precipitation during the growing season and the variability of frost days were the strongest predictors for BiSR, which decreased with increasing precipitation and increasing variability in frost days. The response curve for topographical position on BiSR reached an optimum at values just above zero. Two predictors representing vegetation structure were retained among the six most important variables for BiSR, but their importance was moderate (Table 3).

Variance partitioning

Climate explained the largest independent share of variance for PlSR (22%) and BiSR (12.1%), but only a minor independent share for BuSR (1.6%) (Fig. 3). Among the three variable groups, only vegetation structure consistently explained a considerable amount of independent variance across taxa. The only substantial independent share of explained variance from topography and soil pH was found for PlSR (7.1%). The shared part of explained variance was consistently larger between climate and vegetation structure than between climate and topography and soil pH.

DISCUSSION

Our analysis shows that the relationship between the environment and species richness of plants, butterflies and birds in forest-dominated landscapes across a climatically heterogeneous region is taxon-specific, with evidence for climatic factors performing best in predicting species richness across taxa. This supports the assumption that climate plays a key role in shaping species richness patterns in regions with large climatic gradients (Field *et al.*, 2009).
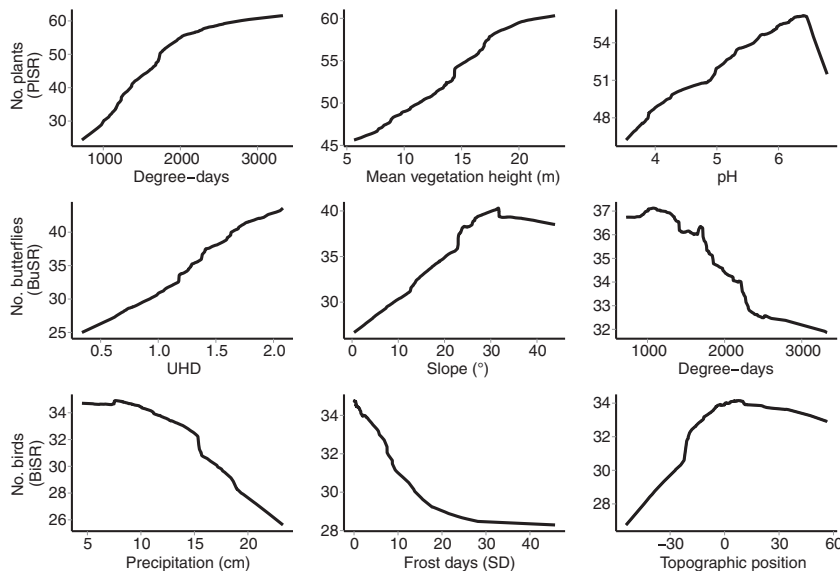
Figure 2 Partial dependence plots showing the effect of the three most important predictor variables on the predicted number of species for each taxon, following the approach proposed by Elith *et al.* (2005).
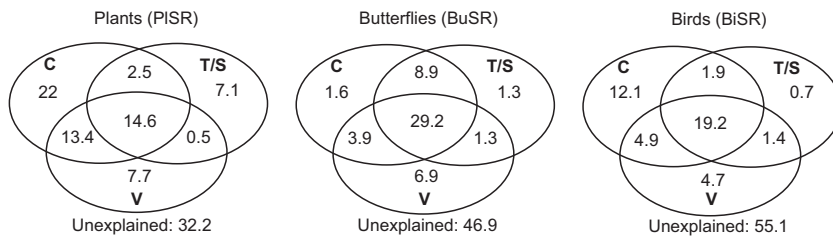

Figure 3 Variation partitioning of species richness per taxon into the independent share of explained variation by climate (C), topography and soil (T/S) and vegetation structure (V), and their overlaps (in %).

Yet, the 3-D vegetation structure derived from LiDAR remote sensing carries additional information, thus it furthers the understanding and prediction of biodiversity patterns (Davies & Asner, 2014). Moreover, vegetation structure and its vertical heterogeneity significantly improved climate-based predictions of species richness of birds and butterflies, which suggests that the structure of the 3-D habitat space in forest-dominated landscapes is particularly important for flying species. Vegetation structure and its heterogeneity are directly associated with the diversity and availability of resources, shelter as well as roosting, breeding or oviposition sites, all of which may qualify as a driver of species richness for flying organisms (MacArthur & MacArthur, 1961; Stein *et al.*, 2014). In fact, vegetation structure was related to species richness of all three focal taxa, indicating that such associations exist consistently at different trophic levels.

Species richness and its relation to environmental variables

Forest plant species richness appears to be controlled most strongly by climate, specifically by the degree-day sum, which is consistent with major syntheses on large-scale climate-richness relationships along latitudinal gradients based on species energy-theory (Francis & Currie, 2003; Hawkins *et al.*, 2003). We confirmed this relationship in our study region as a result of a strong altitudinal gradient. While it has been suggested that historical factors such as post-glacial dispersal

limitation can also strongly affect plant and particularly tree diversity patterns in Europe (Svenning & Skov, 2007), we assume these effects to be of minor importance in our study area, because it is relatively close to glacial refugia. Moreover, butterfly and bird diversity patterns may be even less affected by dispersal limitation, considering their increased dispersive abilities. Apart from climate, our results indicate that further site-specific factors related to vegetation structure, topography and soil pH are important for predicting species richness of forest communities, as discussed below.

Species richness of forest plants responded to the average height of forest vegetation, which is negatively related to the availability of light on the forest floor. Increasing average heights of LiDAR return signals indicate denser and taller canopies, which decrease the availability of light on the forest floor favouring shade-tolerant forest species. A similar relationship was detected by Simonson *et al.* (2012) in a Mediterranean oak forest. However, this relationship may break again under very dense canopies leaving too little light for many species. Average vegetation height may have partially compensated for the missing effect of vegetation density, which is a more direct proxy for canopy cover and associated light conditions. The fact that some of the LiDAR data were recorded during winter may have led to an underestimation of vegetation density in deciduous forests because the LiDAR impulses penetrate deeper into the canopy and more often reach the ground during leaf-off conditions. Because the average forest vegetation height is related to successional stage, the positive relationship with forest plant

species richness may also indicate that processes related to stand age and temporal habitat continuity are important for structuring forest plant communities (Jacquemyn & Brys, 2008). Nevertheless, the ability of LiDAR to measure canopy characteristics and associated light conditions will advance our understanding of the role of light for controlling species distributions and richness patterns.

Topsoil pH is closely linked to the concentration of plant-available nutrients and toxic compounds and the typical response of plant species richness to pH tend to be unimodal (Grime, 1979; Pausas & Austin, 2001). We observed an increasing number of forest plant species with increasing pH values, with a few observations at the upper end of our sampled pH gradient causing a drop of the response curve. The limited representation of the upper boundaries of the pH gradient hampers inference of the exact response along the entire pH gradient, but our results suggest soil pH to be an essential predictor of plant species richness.

Understorey height diversity (UHD) was the most important predictor for butterfly species richness. UHD represents structural heterogeneity in the understorey, which increases in open forests and woodlands as well as along well-structured forest edges with a shrub component. In such forest landscapes the light availability on the forest floor is relatively high, which promotes the occurrence of butterfly host plants and light-demanding shrubs, as well as for the availability of a richly structured lower vegetation profile. These characteristics are important for many butterfly species because they facilitate dispersal along linear habitats, and provide food resources, shelter in unfavourable weather conditions or refuge from heavy disturbance, such as mowing. UHD is thus related to habitat quality, and is likely a crucial factor for species persistence (Thomas et al., 2001). Indeed, the importance of vegetation structure for critical habitat components such as shelter or sites for roosting and mate location has been highlighted earlier (Dover et al., 1997; Dennis, 2004; Marini et al., 2009a), and it is clearly confirmed by our results.

The importance of slope for butterfly species richness may represent an indirect effect of land use intensity, as shown by Marini et al. (2009b). Agricultural intensity tends to decrease with increasing slope, and this affects the occurrence of butterflies through factors such as lower disturbance frequency (e.g. mowing) or increased availability of host plants on less productive soils due to lower fertilization input (Marini et al., 2009b). Surprisingly, climatic factors explained only a minor independent share of variance, and had a large joint share of explained variance with topography and vegetation structure. This indicates that factors related to habitat and land use are important for shaping butterfly species richness patterns in a region that is increasingly human-dominated and suffers from habitat homogenisation in the lowlands. It further implies that climate was mainly indirectly related to butterfly species richness, via correlations with habitat and land use, which exemplifies the difficulty of deriving causalities from correlative models.

Bird species richness was best predicted by climatic factors, with precipitation being negatively correlated with the number of bird species. Although this contrasts with results from large-scale studies (e.g. Rahbek & Graves, 2001), it is consistent with findings from another study across a mountain region with a large climatic gradient (Fitterer et al., 2013). The negative relationship may be due to the adverse effect of increasing precipitation on the availability of food resources such as insects, especially when precipitation tends to increase with increasing altitude, as in our study region. The negative effect of the variability in frost days may indicate that it reduces the availability of areas with a suitable climate. Particularly, migratory birds that spend the winter in warmer regions and are mostly insectivorous may be susceptible to spatially highly variable climatic conditions in their summer habitats, which may partially explain why some of these species are absent in many parts of our study region, particularly those with very steep temperature gradients. Considering this and the relatively large joint share of explained variance by climate and vegetation structure, we propose that the effect of climate on bird species richness may be partly indirect via plants, the associated food resources and the structural complexity of vegetation (Kissling et al., 2008; Ferger et al., 2014). Indeed, we found vegetation structure to be an important predictor for forest-associated bird species richness, and our results compare well with other studies from temperate and boreal forests (Goetz et al., 2007; Zhang et al., 2013).

Implications for ecosystem assessment and conservation

We showed that associations between LiDAR-derived vegetation structure and species richness exist across multiple taxa. We incorporated these associations into spatially explicit modelling to produce nation-wide maps of species richness in forest landscapes. Detailed information about vegetation structure is thus a major asset of national LiDAR campaigns, besides detailed terrain information, and facilitates the integration of biodiversity information into the assessment and monitoring of forest ecosystems. Moreover, repeated data acquisition will allow for analysing forest dynamics and changes in habitat structure, quality and availability. Future challenges include estimating the effects of different times of data acquisition (e.g. leaf on versus. leaf off), as well as of the survey configuration and instrumentation on the consistency of key structural variables.

The maps of multi taxa species richness patterns may help to allocate conservation resources more efficiently because areas with greatest potential diversity can be identified and conservation resources can be targeted to structurally poor areas. Our results suggest that increasing structural heterogeneity in the understorey, for example, along forest edges, is a promising measure to improve the habitat quality for many butterfly species. At the same time, this study also shows that the requirements for specific attributes of vegetation

structure vary considerably between taxa and species, rendering it a key challenge to identify compromises in which undesired effects on other biodiversity attributes are minimized. LiDAR data will thus prove very useful to make conservation actions more effective and to further our knowledge about species-specific habitat requirements.

CONCLUSIONS

We found that species richness of multiple taxa was primarily related to climate and that vegetation structure held unique and complimentary information to improve the prediction of butterfly and bird species richness. For butterfly species, the effect of climate appeared to be mainly indirect, via correlations with habitat type and structure. Low spatial cross-taxon congruence suggests that forest biodiversity conservation should pay attention to the different and partially contrasting demands of various taxa. The predictive performance of vegetation structure derived from LiDAR data suggests that understanding niche-driven assembly processes in forest landscapes will be considerably improved by the growing availability of detailed information of 3-D vegetation structure and associated habitat quality.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Field protocols for vascular plants, butterflies and breeding birds.

Appendix S2 Habitat types used to classify butterfly species.

BIOSKETCH

Florian Zellweger is broadly interested in analysing and conserving biodiversity, particularly in forests. His research focus lies on using remote sensing data to study species-habitat relationships.

Author contributions: K.B. and F.Z. conceived the ideas and designed the study in collaboration with V.B and H.B. A.B. and C.G. provided environmental data and helped analysing them. T.R. provided the species data and valuable method-ological comments. F.Z. conducted the analyses and drafted the manuscript, which was commented and approved by all authors.

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