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Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure

Florian Zellweger[1,2] 🄳 | Tobias Roth[3,4,5] | Harald Bugmann[2] | Kurt Bollmann[1]

[1]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[2]Forest Ecology, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland

[3]Zoological Institute, University of Basel, Basel, Switzerland

[4]Hintermann and Weber AG, Reinach, Switzerland

[5]Research Station Petite Camargue Alsacienne, Saint-Louis, France

Correspondence
Florian Zellweger, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.
Email: florian.zellweger@wsl.ch

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Abstract

Aim: The aim was to investigate the relationship between climate, topography and soil pH, as well as vegetation structure and the beta diversity of plants, butterflies and birds; and to investigate the correlations of (woody) plant beta diversity with animal beta diversity.

Location: Switzerland (central Europe).

Methods: We used pairwise Sørensen dissimilarity as measure of total beta diversity and partitioned it into its turnover and nestedness components. Variation partitioning was used to assess the independent and cumulative effects of environmental predictors, with vegetation structure being derived from airborne light detection and ranging (LiDAR) data. We also checked for independent effects of plant and woody plant beta diversity on butterfly and bird beta diversity, respectively, and for independent effects of spatial distance on beta diversity.

Results: Climate emerged as the strongest statistical predictor of beta diversity across taxonomic groups, with large independent effects on species turnover. Climate effects were most pronounced for plants, followed by butterflies and birds. We also found large independent effects of vegetation structure on total beta diversity and its turnover component across taxonomic groups, particularly for birds. Plant and woody plant beta diversity substantially improved the predictions of butterfly and bird beta diversity, respectively. Spatial distance had hardly any independent effect on beta diversity.

Main conclusions: Climate is a stronger filter for plant communities than for butterfly and bird communities, which are more affected by vegetation structure, probably owing to associated resources and niches. Vegetation structure is a crucial predictor of beta diversity, and therefore contiguous and detailed 3-D habitat structure data are highly relevant to further our understanding of niche-based community assembly. Plant and animal beta diversity appear to be non-independent, suggesting that differences in the response times of interacting taxa should be accounted for in environmental change impact assessments on biodiversity.

KEYWORDS
Airborne laser scanning, biodiversity, biotic interactions, community ecology, ecological networks, environmental filtering, habitat complexity, LiDAR

1 | INTRODUCTION

Understanding the processes that lead to variation in species composition among sites (i.e., beta diversity) remains a fundamental challenge for ecologists (Ricklefs, 2004). Niche-based processes, such as environmental filtering and biotic interactions, drive community assembly through selective forces on traits that allow a species to occupy a niche, resulting in spatial heterogeneity in community composition (Belyea & Lancaster, 1999; Chase & Myers, 2011). Environmental filtering assumes that the establishment and persistence of a species at a particular location is driven by the species' physiological tolerances to abiotic environmental conditions (Weiher & Keddy, 1999).

In general, studies addressing environmental effects on beta diversity rely on rather coarsely resolved climatic and topographical predictor variables, whereas effects of biotic interactions on beta diversity are often not considered (but see, e.g., Trojelsgaard, Jordano, Carstensen, & Olesen, 2015). As a consequence, the effects of site and habitat factors related to vegetation structure and composition on beta diversity remain elusive, particularly for taxa other than plants. Such effects may emerge particularly at local and regional scales, where habitat attributes are expected to influence diversity patterns strongly (e.g., Baldeck et al., 2013; Zellweger et al., 2016). Thus, using a comprehensive set of abiotic and biotic predictors of beta diversity might provide a more complete picture of how communities are structured by abiotic and biotic filters (Kraft et al., 2015).

An important but only poorly understood filter is 3-D habitat structure. Habitat structure provided by vegetation and topography affects the available niche space and provides a variety of essential animal habitat elements, such as nesting sites, shelter and cover (Dennis, 2004; MacArthur & MacArthur, 1961). Moreover, canopy structure drives microclimatic conditions and light availability on the forest floor, thus affecting habitat suitability for plants and the small-scale distribution of temperature extremes (Alexander, Moeslund, Bøcher, Arge, & Svenning, 2013; Suggitt et al., 2011). Habitat structure should therefore be related to beta diversity of both plants and animals.

Gathering data about habitat structure in the field is not only tedious but, more importantly, suffers from strong restrictions in extent and resolution. Emerging remote sensing data sets, such as those acquired with light detection and ranging (LiDAR) instrumentation, overcome many limitations of conventional, field-based habitat structure measurements. These data sets allow for high-fidelity 3-D habitat structure mapping, offering new opportunities to explore the effect of habitat structure on community assembly (Simonson, Allen, & Coomes, 2014). Thus, complementing the growing body of literature using LiDAR for investigations of alpha diversity (e.g., Davies & Asner, 2014; Goetz, Steinberg, Dubayah, & Blair, 2007) by studies addressing the effect of habitat structure on beta diversity constitutes an important step forward to make comprehensive use of this promising data source for ecology and biogeography.

Another recurring question is to what extent diversity patterns are congruent among different taxa. Although this can be expected along the same environmental gradients as a result of the same environmental filters having similar consequences for diversity patterns (e.g., Hawkins & Porter, 2003), it is interesting to investigate whether plant beta diversity is related to animal beta diversity after environmental effects have been controlled for. Additional explanatory power of plant on animal beta diversity could be indicative of biotic interactions, because plants provide resources that many animals depend on directly. The provision of food and foraging opportunities by plants is thus frequently interpreted as an important determinant of the relationships and associations between consumer and producer assemblages in trophic networks (e.g., Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Kissling, Field, Korntheuer, Heyder, & Böhning-Gaese, 2010; Lee & Rotenberry, 2005; Ponisio, M'Gonigle, & Kremen,

2016). However, such associations are difficult to quantify within entire ecological networks. Yet, as long as such trophic relationships are important for shaping the community structure of higher trophic levels, it should be possible to detect effects of producer (plant) on consumer (animal) beta diversity independent of environmental effects.

The main purpose of our study was to elucidate the relative and cumulative relationships between climate, topography and soil pH, as well as vegetation structure and the beta diversity of vascular plants, butterflies and birds in an environmentally heterogeneous and diverse mountain region. Analysis of these taxonomic groups allowed us to investigate how the effects of statistical predictors vary between taxa with different ecological requirements, covering three trophic levels. We were thus able to test for trophic relationships between plants and animals (i.e., by analysing whether plant beta diversity improves the model for butterfly and bird beta diversity after controlling for environmental effects). Likewise, we were interested in potentially unique effects of spatial distance.

Given that our study area is characterized by a steep climatic gradient, we expect climatic filtering effects to prevail across all studied taxa. Such effects should be most obvious for plants, because climate drives critical niche dimensions of plants (Ellenberg, 1988). Climate is expected to influence beta diversity of butterfly and bird species directly, for instance by influencing survival at the cold end of the temperature gradient, and indirectly, for instance through factors that are themselves driven by climate, such as food resources (Gaston, 2003). Topography influences water availability and soil biogeochemical processes and should thus filter communities based on limiting soil resources, such as water and nutrient availability (e.g., Baldeck et al., 2013; Legendre et al., 2009). Similar effects can be expected from soil pH, as it is related to the abundance of toxic elements and nutrients. Among the three taxa studied, topography and soil pH should thus primarily affect plant beta diversity. Vegetation structure should be most important for predicting bird beta diversity, considering the prominent niche partitioning of birds along the vertical gradient of vegetation structure (MacArthur, 1958). Butterfly distributions may also be affected by vegetation structure, because it constitutes critical habitat components, such as refuges, and drives microclimatic conditions that affect the spatial distribution of temperature extremes and the availability of resource plants (Dennis 2004; Suggitt et al., 2011; Zellweger et al., 2016). If plant beta diversity improves the environmental predictions for animal beta diversity, this would indicate that the environmental predictor variables do not capture all ecological dimensions affecting beta diversity, potentially missing trophic interactions between producer and consumer communities. The same applies to spatial distance, whereby improved predictions attributable to spatial distance may suggest that dispersal limitation or unmeasured environmental conditions affect species assemblages.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area encompasses Switzerland, covering 41,248 km² of Central Europe (45°49′–47°48′ N, 5°57′–10°30′ E). The area has

mountains covering *c.* 70% (60% Alps, 10% Jura Mountains) and lowlands (30%). Human population density and land-use intensity are higher in lowlands compared with mountain areas. One-third of the country is forested, with a larger proportion in the mountain areas. Approximately 43% of the forests are coniferous, 33% are mixed and 24% are broadleaved (Brändli, 2010). Elevation ranges from 193 to 4634 m above sea level (a.s.l.), with a mean of 1300 m a.s.l. Within the boundaries of a temperate humid climate, the mean annual temperature and precipitation range from −10.5 to 12.5 °C and from 438 to 2950 mm, respectively.

2.2 | Species data

We used species compositional data from surveys conducted by the Swiss Biodiversity Monitoring Program (BDM; Weber, Hintermann, & Zangger, 2004). BDM collects species occurrence data of vascular plants, butterflies and breeding birds on 520 1-km^2 sample squares (subsequently referred to as 'plots') that are regularly distributed on a systematic grid covering all of Switzerland. Field surveys were carried out between 2004 and 2008. In each plot, the occurrences of vascular plant and butterfly species were recorded along a 2.5 km transect, using detailed standardized field protocols (Appendix S1 in Supporting Information and references therein). Vascular plants (subsequently referred to as 'plants') were sampled twice (i.e., in spring and late summer), except for high-elevation alpine plots that were surveyed once in mid-summer. Butterfly surveys took place during April and September, between four (at high elevations) and seven times (in the lowlands). The butterfly surveys were carried out between 10 a.m. and 5 p.m. when certain 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 > 80% sunshine during the survey. Breeding birds were sampled by the Swiss Ornithological Institute according to the protocol of the common breeding bird survey (see Supporting Information Appendix S1 for details). Each plot was surveyed three times (plots at elevations > 2000 m a.s.l. were surveyed only twice) during the breeding season (15 April–15 July), along a plot-specific route. The routes have an average length of 5 km and aim to cover as large a proportion of a plot and its habitats as possible. Further details and references concerning the species sampling, including detection probability estimates, are provided in Supporting Information Appendix S1.

Woody plants were classified according to the species list of the National Forest Inventory (NFI; Keller, 2011).

The elevation of the BDM plots included in our sample ranged from 249 to 3125 m a.s.l., and the number of sampled plots was as follows: plants 452; butterflies 426; birds 449. The differences in sample size among taxa are attributable to taxon-specific environmental requirements for valid field surveys.

2.3 | Data analyses

2.3.1 | Beta diversity

We used pairwise dissimilarity matrices to measure the spatial variation in species composition. For each taxon (plants, butterflies and birds), we calculated the Sørensen dissimilarity (β_{SOR}) and partitioned it into its turnover (Simpson dissimilarity, β_{SIM}) and nestedness (β_{SNE}) components using the package *betapart* (Baselga & Orme, 2012) in R (R Core Team, 2015). The value of β_{SIM} represents a richness-independent measure of replacement differences in species composition, whereas β_{SNE} represents a measure sensitive to species gains or losses (Baselga, 2010, 2012). This resulted in 101,926, 90,525 and 100,576 pairwise comparisons for plants, butterflies and birds, respectively. Following the same methodology, we also calculated β_{SOR} for woody plant species and used it as a predictor for bird beta diversity (see below). It should be noted that beta diversity metrics are affected by the size of the regional species pools (Kraft et al., 2011), which are not considered here. We thus do not elaborate on beta diversity differences between taxa but focus on biotic and abiotic factors associated with beta diversity.

2.3.2 | Predictor matrices

Climate was represented by the number of degree-days above a threshold of 3 °C and the precipitation sum (in millimetres) during the growing season (from April to September). Temperature and precipitation layers with a 100 m resolution were interpolated using DAYMET (Thornton, Running, & White, 1997) based on mean daily measurements of all available recording stations (*c.* 300; www.meteosuisse.ch) and a digital elevation model (www.swisstopo.ch). We averaged the temperature and precipitation data using all data of the years 1981–2010 (for details, see Zellweger et al., 2016; Zimmermann et al., 2009).

Potential effects of topographical and edaphic features were represented by slope, topographical position and soil pH. Topographical position measures the exposure of a site relative to the surrounding terrain (Zimmermann, Edwards, Moisen, Frescino, & Blackard, 2007). Slope and topographical position represent habitat features that are frequently correlated with observed patterns of species diversity and distributions (Zellweger et al., 2016), but they describe indirect environmental gradients without direct physiological relevance for biota (Guisan & Zimmermann, 2000). Topsoil pH affects the occurrence of plant species because it is related to edaphic characteristics, such as the availability of nutrients and toxic elements. The topography and topsoil pH rasters had a pixel size of 25 m and were adopted from Zellweger et al. (2015).

The 3-D vegetation structure was derived from a national airborne LiDAR data set. LiDAR is an active remote sensing technology that depicts the 3-D structure of ecosystems at an unprecedented level of detail (Lefsky, Cohen, Parker, & Harding, 2002). The contiguous spatial coverage and high level of detail offered by LiDAR data provide clear advantages over traditional vegetation structure surveys in the field, which are often limited in precision and spatial extent. We used airborne LiDAR to calculate the mean and standard deviation of canopy height (in metres) for each 20 × 20 m raster cell, representing spatial habitat heterogeneity and complexity. Canopy height was defined as the 95th percentile of the terrain-corrected vegetation heights. The discrete, small-footprint LiDAR raw data were acquired during multiple seasons in the years 2000–08, with an average return density of 0.5 and 1.5/m^2 in open and forested areas, respectively. Further details about the raw data processing and variable extraction are provided by Zellweger et al. (2016). Environmental filtering effects on beta diversity

and its turnover and nestedness components were investigated using the pairwise differences of the standardized environmental variables.

To test whether plant beta diversity provides additional predictive power for animal beta diversity after having controlled for the above-mentioned environmental effects, we used plant beta diversity (plant β_{SOR}) as a predictor of butterfly beta diversity, and woody plant beta diversity (woody plant β_{SOR}) as a predictor of bird beta diversity. Plant beta diversity is likely to be correlated with additional environmental effects that are not captured by our environmental variables, and thus plant beta diversity could serve as a proxy to account for additional environmental variation. However, plant beta diversity could also qualify as a potential predictor of butterfly beta diversity because of the co-evolution of butterflies and plants and the resulting strong associations between them (Ehrlich & Raven, 1964). Woody plant beta diversity is expected to predict bird beta diversity because of widespread associations between birds and particular food and foraging resources, as well as the functional relationships modulated by vegetation structural complexity (Jankowski et al., 2013; Kissling, Field, & Böhning-Gaese, 2008; MacArthur & MacArthur, 1961).

Finally, we tested for effects of spatial distance on beta diversity of each taxonomic group. Spatial distance might be correlated with other environmental effects that are not captured by our variables. Thus, we added spatial distance to test how well our variable set captures the relevant environmental information. Spatial distance might also serve as a proxy for dispersal limitation, simply because emigrants of a source population might re-colonize nearby habitat patches but not distant sites (Tuomisto, Ruokolainen, & Yli-Halla, 2003).

2.3.3 | Statistical analyses

We used permutational distance-based multivariate analysis of variance (PERMANOVA; Anderson, 2001), as implemented in the *adonis* function in the R package *vegan* (Oksanen et al., 2015), to examine the individual relationships between each of the environmental predictor matrices and the beta diversity metrics (β_{SOR}, β_{SIM} and β_{SNE}) of each taxon. We thus analysed whether plots with more dissimilar species communities were associated with increasing environmental distances. The strengths of these relationships were analysed based on the partial R^2, and the significance was estimated using 999 permutations.

To assess the independent and shared effects of climate, topography and soil pH, and vegetation structure on beta diversity, we applied distance-based redundancy analysis (db-RDA; Legendre & Anderson, 1999) and variation partitioning based on the adjusted R^2 (Borcard, Legendre, & Drapeau, 1992).

To test for independent effects of producer (plant) beta diversity on consumer (animal) beta diversity and of effects of spatial distance on beta diversity, we performed variation partitioning based on db-RDA with the respective variables or groups thereof, namely (a) all environmental variables, (b) producer beta diversity and (c) spatial distance. For plants, we thus partitioned the variation between all environmental variables and spatial distance, whereas for butterflies and birds we partitioned the variation between all environmental variables, producer beta diversity and spatial distance. Producer beta diversity was represented by the principal co-ordinates of a db-RDA for plant

and woody plant β_{SOR}, respectively. Spatial distance was represented by principal co-ordinates of neighbour matrices (PCNMs), whereby only PCNMs with significant effects on the dependent variable entered the models (Dray, Legendre, & Peres-Neto, 2006). db-RDA, variation partitioning and PCNM analyses were performed using the *capscale*, *varpart* and *pcnm* functions, respectively, all implemented in the R package *vegan* (Oksanen et al., 2015). All analyses were done in the R statistical programming language (R Core Team, 2015).

3 | RESULTS

The species assemblages that we analysed had 1765 plant, 185 butterfly and 144 bird species, with the number of species per plot ranging from 15 to 395 for plants, from 2 to 78 for butterflies and from 1 to 55 for birds. Total beta diversity (pairwise β_{SOR}) ranged from 0.552 for birds to 0.622 and 0.631 for butterflies and plants, respectively (Table 1). The species turnover (β_{SIM}) component of β_{SOR} was substantially larger than the species nestedness (β_{SNE}) component, with values ranging from 0.441 to 0.571 and from 0.060 to 0.164, respectively (Table 1).

3.1 | Environmental filtering effects

We found that the number of degree-days predicted β_{SOR} and β_{SIM} best across taxa, but there was no effect of climate on β_{SNE} (Table 2). Topographical slope was related to beta diversity of all taxa and also to butterfly β_{SNE}. Vegetation structure emerged as a strong predictor for β_{SOR} and β_{SIM}, especially for birds. In general, the bivariate models revealed that the strongest environmental effects were on the turnover component of beta diversity (β_{SIM}), followed by total beta diversity (β_{SOR}), which included differences in community composition caused by species gains or losses (i.e., nestedness, β_{SNE}). Variation in β_{SNE} alone, however, could not or only marginally be explained by the environmental variables, and we thus did not investigate models for β_{SNE} any further.

The cumulative environmental effects on β_{SIM} were larger than on β_{SOR}, with R^2 values ranging from 0.59 to 0.72 and from 0.44 to 0.60, respectively (Figure 1). Variation partitioning based on db-RDA revealed a central role of climate for plant β_{SIM} and plant β_{SOR}, with large independent effects compared with the other environmental factors. Across taxa, climate independently explained relatively large fractions of the variation in species turnover (β_{SIM}), but this effect

TABLE 1 Total beta diversity expressed as Sørensen dissimilarity (β_{SOR}) and its two components, turnover (Simpson dissimilarity, β_{SIM}) and nestedness (β_{SNE}), in plant, butterfly and bird assemblages

	β_{SOR}	β_{SIM}	β_{SNE}
Plants	0.631	0.571	0.060
Butterflies	0.622	0.458	0.164
Birds	0.552	0.441	0.111

Note. We report the means of pairwise dissimilarity (i.e. our dependent variable), but we acknowledge that pairwise dissimilarity might not represent the overall compositional heterogeneity within the species pool (Baselga, 2013).

TABLE 2 Explained variation (R^2) of distance matrices representing effects of climate, topography and soil pH, as well as vegetation structure on total beta diversity (Sørensen dissimilarity, β_{SOR}) and its turnover (Simpson dissimilarity, β_{SIM}) and nestedness (β_{SNE}) components of plants, butterflies and birds

	Plants			Butterflies			Birds		
	β_{SOR}	β_{SIM}	β_{SNE}	β_{SOR}	β_{SIM}	β_{SNE}	β_{SOR}	β_{SIM}	β_{SNE}
Climate									
Degree-days	0.356***	0.473***	–	0.278***	0.472***	–	0.384***	0.520***	–
Precipitation	0.096***	0.121***	–	0.068***	0.092***	–	0.089***	0.096***	–
Topography/soil pH									
Topographical position	0.016***	0.016***	–	0.014***	0.016***	–	0.025***	0.035***	–
Slope	0.207***	0.266***	–	0.193***	0.207***	0.156***	0.194***	0.242***	–
pH	0.040***	0.047***	–	0.022**	0.035***	–	0.018***	0.008*	0.054***
Vegetation structure									
Canopy height	0.126***	0.138***	–	0.132***	0.206***	–	0.233***	0.305***	–
Canopy height variation	0.217***	0.255***	–	0.189***	0.324***	–	0.323***	0.335***	0.070***

– = no effect. *$p < .05$. **$p < .01$. ***$p < .001$.

decreased for total beta diversity (β_{SOR}), especially in the case of butterflies and birds. For these, vegetation structure had the largest independent effects, which was especially evident for birds. Interestingly, we found that relatively large independent effects of vegetation structure occurred in all taxa, whereby these effects were larger for β_{SOR} than for β_{SIM}. In fact, the cumulative independent effect of vegetation structure on β_{SOR} across all taxa (54.7) was higher than that of climate (48.6). Topography and soil pH showed independent effects on both plant β_{SOR} and β_{SIM} as well as butterfly β_{SOR}, whereas such effects were marginal for butterfly β_{SIM} and bird β_{SOR} and β_{SIM}. It should be noted that for all taxa, relatively large shares of the variation in β_{SOR} and β_{SIM} were explained by shared environmental effects or environmental covariation (Figure 1).

3.2 | Plant–animal relationship and spatial distance

Including plant beta diversity (plant β_{SOR}) as a predictor of butterfly beta diversity (butterfly β_{SOR}) improved the model substantially [i.e., plant β_{SOR} independently explained 19.2% ($p < .001$) of the total variation in butterfly β_{SOR}]. The same applied when adding woody plant β_{SOR} as a predictor to bird β_{SOR}; woody plant β_{SOR} independently explained 10.9% ($p < .001$) of the total variation in bird β_{SOR} (Figure 2). The woody plant species assemblages encompassed 146 species. It is worth noting that the shared effects between plant as well as woody plant beta diversity and the environmental predictor variable set were very large, being 44 and 55.5% in the models for butterfly β_{SOR} and bird β_{SOR}, respectively (Figure 2).
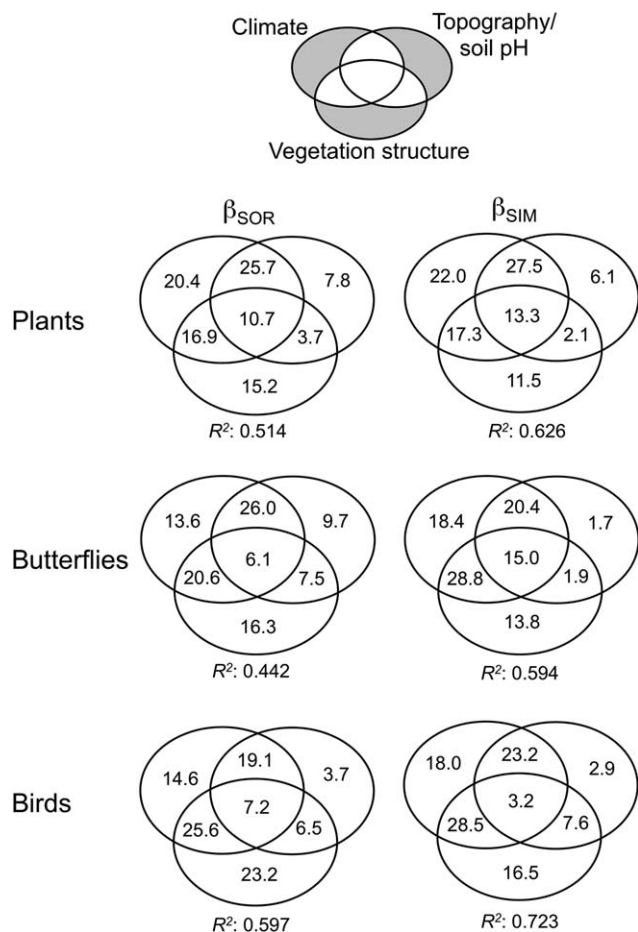
Spatial distance had hardly any independent effect on beta diversity of any taxonomic group; the variance explained in β_{SOR} increased by 3.9% ($p < .001$) for plants, 0.2% ($p < .05$) for butterflies and 0.7% ($p < .001$) for birds. Independent effects of plant β_{SOR}, woody plant β_{SOR} and spatial distance on β_{SIM} were very similar to but weaker than

those on β_{SOR}, and we thus report and discuss the results for total beta diversity β_{SOR} only.

4 | DISCUSSION

We showed that plant, butterfly and bird communities are mainly structured by environmental filtering in a heterogeneous temperate region with steep climatic gradients. Species turnover contributed much more to total beta diversity than community dissimilarity due to nestedness, which is in line with the expectation that environmental filtering effects on community structure along environmental gradients mainly reveal turnover (Anderson et al., 2011). Climate emerged as the strongest filter across taxa, with large independent proportions of explained variance in species turnover and total beta diversity. In line with predictions from niche theory, this suggests that species are sorted along climatic gradients, either directly, because of their physiological tolerance to climatic conditions, or indirectly, via factors that are themselves driven by climate, such as food resources (Ellenberg, 1988; Gaston, 2003; Wiens, 2011).

Climatic filtering effects were more pronounced in plant than in butterfly and bird assemblages. This is in accordance with the assumption that plant species are filtered according to their physiological tolerance to climatic conditions, which directly affect plant community structure (Ellenberg, 1988). However, the mechanism underlying the relationship between climate and butterfly community structure, as well as between climate and bird community structure, remains elusive. The substantial proportion of shared environmental effects between climate and habitat on butterfly and bird beta diversity makes it difficult to gauge the relative effect strength of climate and habitat filtering. Empirical evidence suggests that climate may affect bird assemblages indirectly via effects on food resources and the structural complexity of vegetation (Ferger et al., 2014; Kissling et al., 2008). However, climate also limits animal species distributions directly by influencing

that modulates the effects of climate warming on terrestrial ectotherms (Deutsch et al., 2008; Woods, Dillon, & Pincebourde, 2015). Thus, both climate and habitat filtering may act in concert to determine beta diversity, and disentangling their relative and interactive effect strengths on animal beta diversity warrants further research.

Interestingly, our analysis revealed a strong independent filtering effect of vegetation structure on community assembly for all taxa, with canopy height and its spatial heterogeneity emerging as key predictors of beta diversity. In line with the expectation that vertical vegetation structure affects bird assemblages, for instance through vertical niche partitioning in forests (MacArthur, 1958; MacArthur & MacArthur, 1961), the largest independent effect of canopy height and its spatial heterogeneity on beta diversity was found for birds. Irrespective of taxa, however, the positive relationship between habitat heterogeneity and beta diversity is plausible in the light of the environmental/habitat heterogeneity hypothesis and the available niche space (Stein, Gerstner, & Kreft, 2014). Habitat heterogeneity derived from remotely sensed land cover variation, for example, has been found to predict community similarity of butterflies (Kerr, Southwood, & Cihlar, 2001). Moreover, plants are expected to be sorted along the gradient of light availability (Ellenberg, 1988). Canopy height and heterogeneity are directly related to the light conditions experienced by plants, and we thus represented this critical niche dimension. Our results suggest that landscapes that are complex in terms of 3-D vegetation structure provide more habitats and niches and may thus harbour not only more (Stein et al., 2014) but also different species than structurally simpler landscapes (e.g., Ponisio et al., 2016), thus increasing total beta diversity.

Estimating such filtering effects of vegetation structure on community assembly across entire landscapes and biogeographical regions has not been feasible until the recent advent of contiguous high-fidelity 3-D ecosystem structure data sets. LiDAR thus offers a powerful new approach to gain insights into the processes leading to the spatial variation of community composition. For example, we showed that across all taxa, the cumulative independent effect of vegetation structure on total beta diversity (including nestedness) was larger than the cumulative independent effect of climate, whereas the opposite was true for species turnover. This may be explained by the dependence of many forest species and other habitat specialists on the availability of niches and food resources that are mediated by vegetation structure. Particularly in regions where vegetation structure is increasingly subject to human modification, the use of large-area LiDAR data to map this dynamic habitat attribute better constitutes an important step forward to quantify and monitor beta diversity, a primary determinant of the total species diversity of a landscape (Flohre et al., 2011).

As expected, plant beta diversity was affected more strongly by topography and soil pH than animal beta diversity. Although not very pronounced, plant beta diversity was related to topography and soil pH, which suggests that plant distributions are affected by edaphic resources, which themselves are driven by the topography and soil pH, such as water and nutrient availability. The rather low independent effect of soil properties on plant beta diversity is likely to be related to the fact that our set of variables describing soil properties across the entire

FIGURE 1 Results from variation partitioning based on distance-based redundancy analysis (db-RDA) relating climate (degree-days and precipitation), topography/soil pH (topographical position, slope and topsoil pH) and vegetation structure (canopy height and canopy height variation) to plant, butterfly and bird total beta diversity (Sørensen dissimilarity, β_{SOR}) and its turnover component (Simpson dissimilarity, β_{SIM}). Community dissimilarity due to nestedness alone could not or only marginally be explained by db-RDA; we thus do not elaborate on these models. Following the structure outlined in the inset, we report the independent (grey) and shared (white) proportions (expressed as percentages) of explained variation by climate, topography/soil pH and vegetation structure, respectively. The R^2 values for the total model are shown outside circles
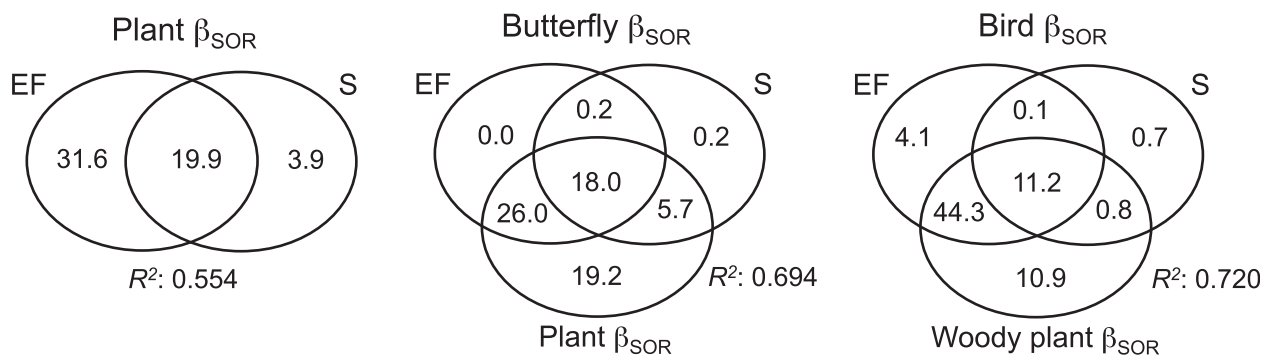
survival and fecundity at the cold, upper end of environmental gradients (Gaston, 2003), which were better represented in our sample than the warm, lower end, where drought may be a principal limiting factor for species occurrence. Furthermore, butterfly community turnover through space and time across Canada was found to be associated with temperature differences (Lewthwaite, Debinski, & Kerr, 2017). The physiological sensitivity and performance of ectotherms such as butterflies is directly related to temperature and their thermal tolerances (Huey & Stevenson, 1979). The local variability and distribution of temperature extremes is in turn influenced by habitat structure, for instance through microclimatic buffering mediated by vegetation structure. This affects critical temperatures that drive the performance of butterflies and constitutes an important but not well-studied subject

FIGURE 2 Results from variation partitioning based on distance-based redundancy analysis (db-RDA) relating all variables associated with environmental filtering (EF) (climate, topography/soil pH and vegetation structure), spatial distance (S) and plant and woody plant beta diversity to total beta diversity (Sørensen dissimilarity, β_{SOR}) of the respective taxonomic groups. The numbers in the circles represent independent and shared effects expressed as proportions (as percentages) of explained variation. The R^2 values for the total model are shown outside the circles

study area is rather limited, and including a more comprehensive set of soil variables would probably lead to an increase of the independent effect of the soil on plant beta diversity (cf. Baldeck et al., 2013).

Bird beta diversity was only weakly related to topography and soil pH, but total beta diversity of butterflies was clearly affected by topography and soil pH. Such effects are likely to be connected to topographical slope, which in human-dominated mountain regions is often negatively correlated with land use intensity (e.g., Marini, Fontana, Klimek, Battisti, & Gaston, 2009). This leads to preserved habitats for many habitat-specialist butterfly species in landscapes on steep slopes, thus causing community differences due to nestedness, a finding that is further supported by species richness patterns (Marini et al., 2009; Zellweger et al., 2016).

We showed that plant and woody plant beta diversity substantially improved the environmental predictions of butterfly and bird beta diversity, respectively. This suggests that our set of environmental predictors lacks important ecological information explaining beta diversity of animals. Such information may be related to historical factors and large-scale topographical features (e.g., mountain ranges) affecting the formation of biogeographical regions, as these factors have been shown to improve biodiversity predictions (Graham, Moritz, & Williams, 2006; Svenning, Fløjgaard, & Baselga, 2011). However, it could also be indicative of trophic associations between plant (producer) and animal (consumer) communities. Strong correspondence between vegetation composition, particularly tree species composition, and bird species composition has been documented widely (e.g., Fleishman & Mac Nally, 2006; Jankowski et al., 2013; Lee & Rotenberry, 2005), and often such associations are interpreted as the result of different food and foraging opportunities provided by different vegetation communities. Similar effects could be expected for associations between plants and butterflies, whereby beta diversity patterns of specialist species are likely to be more affected by such associations than those of generalists. Our correlative framework and the fact that many of the temperate butterflies studied here are generalist species thus make it difficult to address the effects of trophic interactions clearly. Nevertheless, our results support the assumption that plant and animal beta diversity patterns are not independent from each other, implying that differences in the

response times of interacting taxa need to be accounted for in impact assessments of environmental change on beta diversity (Kissling et al., 2010).

We hardly found any additional predictive power in spatial distance. Although this suggests that our set of predictor variables captures spatially structured environmental conditions, it also implies that post-glacial dispersal limitation plays a minor role in driving species assemblages in the study region and at the scale of the study. This is supported by the fact that the study region is relatively close to glacial refugia, which, in addition to the relatively long time span since the last glacial maximum (i.e., *c.* 24,000 years), may help to explain the low nestedness components of beta diversity (cf. Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012). However, in mountain areas with many potential dispersal barriers, spatial distance may be a rather weak predictor for dispersal limitation. A more meaningful way to address dispersal effects on beta diversity would be to include cost distances (Weinstein et al., 2014).

We conclude that the main mechanisms for community assembly in our study region relate to niche-based filtering processes. Among those, climate and vegetation structure emerged as key environmental filters driving the community structure of plants, butterflies and birds. Climate appears to filter plant assemblages more strongly than butterfly and bird assemblages, for which effects of vegetation structure play a more important role. The growing spatial and temporal availability of contiguous and detailed LiDAR data describing 3-D habitat structure thus offers new opportunities to further the understanding of niche-based community assembly mechanisms. Such data will help to provide a better gauge of the relative effects of changes in biotic and abiotic environmental drivers of beta diversity. Together with accounting for differences in response times of interacting taxa, this will be useful for improving the predictions of global change effects on biodiversity.

AUTHOR CONTRIBUTION

F.Z. and K.B. conceived the ideas and designed the study in collaboration with T.R. and H.B. T.R. provided the species data and valuable methodological comments. F.Z. conducted the analyses and drafted the manuscript, which was commented on and approved by all authors.

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BIOSKETCH

Florian Zellweger focuses on the ecological dimensions of latest developments in remote sensing. His current interests are centred on biodiversity dynamics, particularly in forests.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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