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Biodiversity along an elevational gradient of the Bohemian Forest – the BIOKLIM project

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Abstract

To monitor the response of forest biodiversity to environmental changes, the BIOKLIM project collected data on species occurrences along transects covering the elevational gradient within the Bavarian Forest National Park and adjacent areas. The monitoring program was launched in 2006 and repeated in 2016 as a part of the Silva Gabreta Monitoring project. Here we show the potential of such regional monitoring programs for characterizing alpha, beta and gamma biodiversity of 15 groups of organisms along the elevational gradient in forests mainly dominated by European beech and Norway spruce. Overall, we recorded 4,179 species of which 1,918 are common (based on Shannon diversity) and 1,222 dominant (based on Simpson diversity). Asymptotic extrapolation suggested that between 5,340 and 6,100 species might occur in the terrestrial ecosystems of the Bohemian Forest. Most groups showed significant responses in alpha diversity to elevation. However, the relationships varied strongly in strength and shape. Changes in species composition along the elevational gradient were mostly due to turnover and contributed strongly to the overall diversity of the study region. These first analyses show that monitoring schemes as implemented in the Silva Gabreta Monitoring offer the opportunity to study biodiversity along environmental gradients. In the long run resampling of the plots established in 2006 allows characterizing the responses of the communities to changes in forest structure and/or climate.

Key words: biodiversity monitoring, ecology, protected areas, European beech, Norway spruce, Silver fir, Bavarian Forest National Park

Introduction

Following a set-aside strategy, national parks aim at conserving ecosystems in a state as natural as possible and at protecting ecological processes that structure these systems (McNeely & Miller 1983). Nevertheless, national parks are not isolated and therefore biodiversity of the communities occurring within the protected area will change with time, e.g. due to changes in the climate or disturbances (Hannah 2008). One important aim of national parks is therefore also to document such changes and to launch research to understand the processes that underpin fluctuations and trends of biodiversity (Heurich et al. 2010).

Founded in the year 1970, the Bavarian Forest National Park is the oldest national park in Germany. After its expansion in 1997 the national park covers an area of over 24,000 hectares and is part of the Bohemian Forest – the largest contiguous forest area in central Europe. After several consecutive disturbances, mostly due to wind throws and bark beetle outbreaks, the administration of the national park decided to implement a benign-neglect strategy and not to interfere (e.g. by salvage logging) with the natural processes (Müller et al. 2010). Thereby, deadwood availability and structural heterogeneity increased in large areas of the historically managed forest within the park (Lehnert et al. 2013). To monitor environmental changes within the park as well as the response of forest biodiversity to such natural disturbances, the BIOKLIM project was initiated in the year 2006 (Bässler et al. 2009). This project collected data on relevant environmental variables, as well as data on the occurrence and abundance of species of plants, fungi and animals along the elevational gradient of the national park. These groups represent a large proportion of the diversity of central European forests. Such standardized surveys offer baseline data on the biodiversity that are necessary to assess the response of communities to changing environmental conditions and processes that structure these communities. Furthermore, using a space-for-time approach the elevational gradient allowed first insights how the communities will change with global warming (Bässler et al. 2010). As the Bavarian Forest National Park represents only a rather small proportion of the contiguous forest covering the Bohemian Forest, the BIOKLIM survey is now integrated in an interregional monitoring scheme conducted by the Bavarian Forest and Šumava National Parks as part of the Silva Gabreta Monitoring project (Křenová & Seifert 2015, 2018). As part of this monitoring scheme, the survey of the biodiversity inhabiting the forests along the elevational gradient was repeated in the year 2016 (Bässler et al. 2015) and additionally this monitoring was expanded to streams (Bojková et al. 2018).

To show the potential of repeated surveys as implemented here, we present data on the diversity of 15 groups of organisms based on the two surveys conducted in the years 2006 and 2016. The aim of this study is to give a general overview of the biodiversity found in the Bavarian Forest National Park and adjacent areas (gamma diversity) and how biodiversity in terms of alpha and beta diversity is structured along the elevational gradient in the terrestrial ecosystems of the Bohemian Forest. Here, our analyses are based on a harmonized dataset from the two surveys in 2006 and 2016 generated with similar sampling methods conducted on the same study plots.

Material and methods

Sampling area

The surveys were conducted in 2006 and repeated in 2016 in the German part of the Bohemian Forest covering an elevational gradient from 287 to 1420 m a.s.l. Details of these two surveys are described in Bässler et al. (2009, 2015). The original design of 331 study plots was optimized for resampling in 2016 in order to cover the structural gradient across the whole elevational gradient and to maximize the number of plots covered by both surveys (Bässler et al. 2015). The final set of plots with harmonized data of both surveys used in this study consisted of 133 plots ranging from plots at low elevations in the Danube valley to high elevation plots on the mountain ranges of the Bavarian Forest National Park (Fig 1).

Species sampling

Species sampling of both surveys followed the same methods for each taxonomic group on the 133 study plots. Overall 15 groups of plants, fungi, and animals were included in this study (Table 1). The taxonomic rank differed considerably (Table 1). Species were sampled using standard methods suitable for an appropriate sampling of the respective taxon. Higher plants, fungi, and birds were recorded on all 133 plots. Insect samples from flight-interception and pitfall traps of one plot were unfortunately lost in 2016. The other taxa were sam-

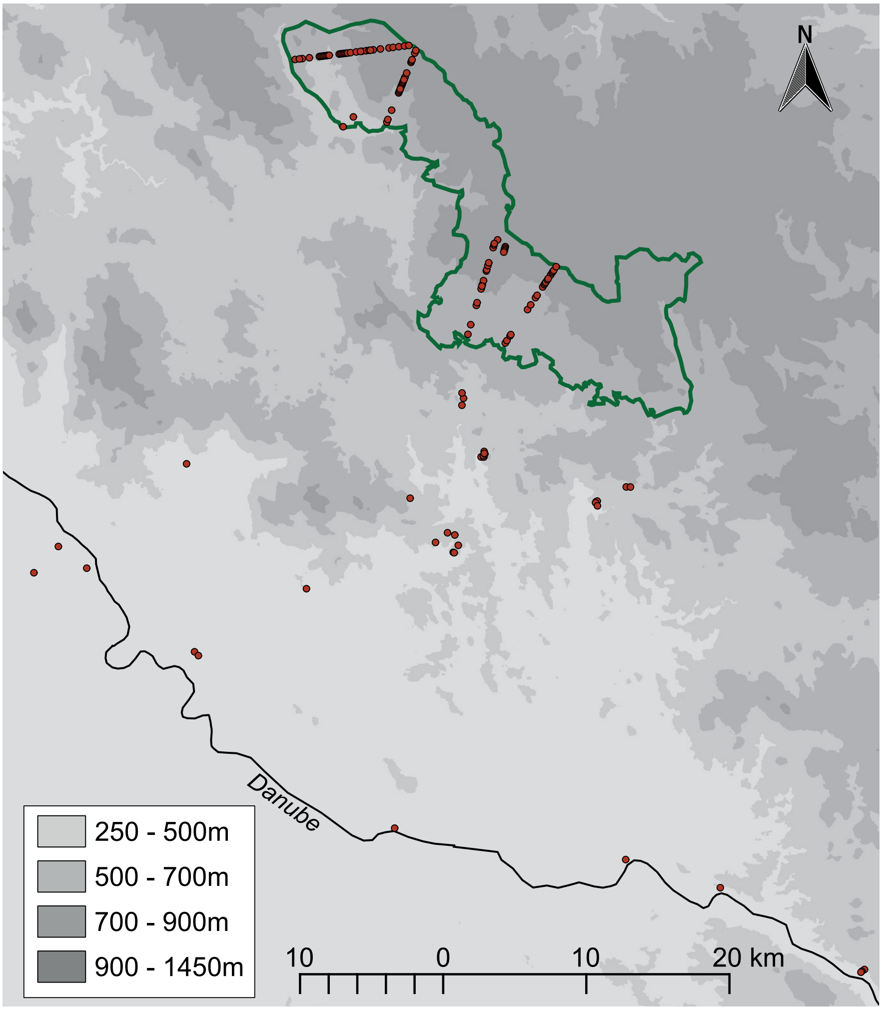

Fig. 1. An overview map of the 133 sampling plots (red points) across the elevational gradient. Main sampling transects are located within the Bavarian Forest National Park (green line). Additional lowland plots (<650 m a.s.l.) outside the NP extended the elevation gradient down to the Danube River representing the gradient from 287–1420 m a.s.l. Some sampling points are not visible (overlaid) due to scaling.

pled on subsets of the study plots due to the constraints imposed by labor-intensive collection methods. We applied hand collections (gastropods, number of the study plots surveyed: n = 108), field mapping (lichens, wood mosses and soil mosses, n = 109), flight-interception traps (beetles, true bugs, spiders and harvestmen, n = 132), pitfall traps (beetles, springtails, spiders and harvestmen, n = 132), malaise traps (bees and wasps, cicadas, hoverflies and true bugs, n = 52), and light traps (moths, n = 33; Table 1). For details of the sampling methods used for different taxa, see Bässler et al. (2009, 2015). All specimens were determined to species by specialists for the respective taxon. For the present communication, the occurrence data of both surveys were aggregated in presence-absence matrices. Thus the results of the present analysis do not distinguish between the two sampling events.

Table 1. Sampling methods for the groups sampled during the BIOKLIM project. FC – field collection, PT – pitfall traps, FIT – flight-interception trap, MT – malaise trap, LT – light trap. Number of species refers to the overall number of species found on the plots during both surveys. Number of plots refers to the number of plots with harmonized data for both survey years.

Group	Taxon	FC	PT	FIT	MT	LT	Number of species	Number of plots
Plants	Spermatophyta	x					297	133
Soil mosses	Bryophyta	x					84	109
Wood mosses	Bryophyta	x					149	109
Lichens	Fungi	x					125	109
Fungi	Fungi	x					562	133
Snails and Slugs	Gastropoda	x					103	133
Birds	Aves	x					51	133
Bees and wasps	Aculeata				x		308	52
Beetles	Coleoptera		x	x			1305	132
Cicadas	Cicadoidea				x		215	52
Hoverflies	Syrphidae				x		185	52
Moths	Lepidoptera					x	272	33
Spiders	Arachnida		x	x			292	132
Springtails	Collembola		x				51	132
True bugs	Heteroptera			x	x		180	52
Sum							4179	

Analysis

All statistical analyses were conducted in the software environment *R* (v. 3.4.3; R Core Team 2017). To estimate metrics of species richness, we used the rarefaction-extrapolation framework suggested by Chao et al. (2014) using the aggregated matrices. We calculated Hill numbers for the aggregated matrices to analyze the diversity of common and dominant species within one framework. Hill numbers represent a family of diversity indices expressed in effective numbers of species that differ among themselves by the exponent q (Hill 1973, Chao et al. 2014). The value of q determines the sensitivity of the diversity measure to rare or common species. Here, Hill numbers with $q = 0$ are equivalent to the species richness of the assemblage which counts species without regard to their prevalence. Hill numbers of orders lower than 1 are sensitive to rare species, while orders higher than 1 are sensitive to the most common or dominant species (Jost 2007). Hill numbers with $q = 1$ conform to the exponential of the frequently used Shannon index and represent the effective number of common species. Hill numbers with $q = 2$ are termed Simpson diversity and discount all but the most common or dominant species (Hsieh et al. 2016). In order to get comparable estimates based on sampling effort we rarified respectively extrapolated the diversity estimates for all groups to 99 sites, which leads to an extrapolation by an factor of three for the group sampled on the fewest number of sites (moths sampled on 33 sites; Hsieh et al. 2016). Additionally, we calculated estimates of the asymptotic richness (i.e. the number of species after extrapolation to the point where an increase in sampling units does not further increase the number of species) for each group separately as an estimate of the lower bound of total species richness, as well as the number of common and dominant species (Chao, 1987). We used

999 replicated bootstraps to calculate confidence intervals around the species-accumulation curves. These methods are implemented in the iNEXT package (Hsieh et al. 2016).

In order to investigate the response of each of the 15 taxa to the elevational gradient on alpha diversity, we modeled the number of observed species for each site using generalized linear models with a Poisson error distribution with elevation above sea level as linear and quadratic predictor. For the analysis of beta diversity, we calculated pairwise Sørensen dissimilarity indices across the assemblages of all 15 groups, based on species-site matrices with varying dimensions depending on the respective group. Beta diversity was partitioned into its additive components of turnover (i.e. dissimilarity due to replacement of species) and nestedness (i.e. dissimilarity due to species loss; Baselga 2010). Subsequently, we calculated generalized dissimilarity models (GDM) on distance matrices for both the turnover and nestedness component including elevation above sea level as predictor variable, while controlling for spatial distance by including the spatial position of the site into the model (i.e. GPS coordinates). GDMs allow the analysis of spatial patterns of community composition under consideration of non-linear relationships between dissimilarity in community composition along environmental gradients (Ferrier et al. 2007). All GDMs were calculated using

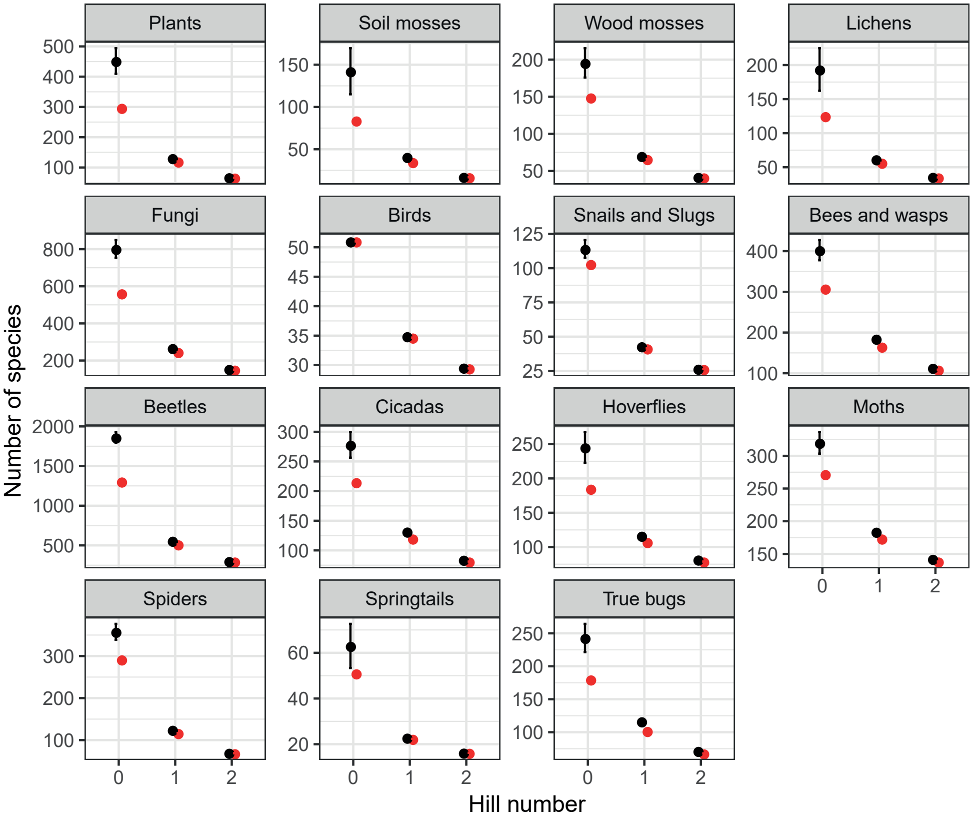

Fig. 2. Observed as well as asymptotic estimates of the number of species of 15 important taxonomic groups. Calculations are based on Hill numbers of the orders 0 (i.e. species richness), 1 (i.e. Shannon diversity representing 'common' species), and 2 (i.e. Simpson diversity representing 'dominant' species). Black circles indicate asymptotic estimations with standard errors. Red circles indicate observed values.

Table 2. Results of the generalized linear models of the number of species of the 15 studied groups. Elevation was included as a linear and quadratic predictor to account for nonlinear relationships. Tables show *z*-values of the predictor together with its statistical significance and the explained deviance of the model. Groups with significant effects of elevation on the number of species are given in bold.

Group	Elevation (z-value)	P-value	Elevation^2 (z-value)	P-value	Explained deviance
Plants	**−6.55**	**<0.001**	**5.53**	**<0.001**	**0.08**
Soil mosses	1.58	0.114	−1.90	0.057	0.03
Wood mosses	**3.51**	**<0.001**	**−3.54**	**<0.001**	**0.04**
Lichens	1.52	0.133	0.17	0.866	0.28
Fungi	3.05	<0.050	−4.62	<0.001	0.20
Birds	0.10	0.918	−0.68	0.494	0.12
Snails and Slugs	**−4.67**	**<0.001**	**1.96**	**<0.050**	**0.43**
Bees and wasps	**−8.10**	**<0.001**	**3.11**	**<0.050**	**0.58**
Beetles	**−9.65**	**<0.001**	**8.28**	**<0.001**	**0.15**
Cicadas	**−7.77**	**<0.001**	**6.56**	**<0.001**	**0.27**
Hoverflies	−0.09	0.928	−0.23	0.817	0.01
Moths	**2.12**	**<0.050**	**−2.61**	**<0.05**	**0.13**
Spiders	**−6.99**	**<0.001**	**7.93**	**<0.001**	**0.29**
Springtails	−0.44	0.661	0.78	0.437	0.07
True bugs	**−5.15**	**<0.001**	**4.49**	**<0.001**	**0.21**

the default of three I-splines. The calculated coefficient for each of the three I-splines represents the rate of change along a third of the gradient of the environmental predictor when keeping all other predictors constant (i.e. high values of the first I-spline indicate a high rate of change along the first third of the gradient). To quantify the contribution of alpha and beta diversity among plots and among elevational zones to the overall gamma diversity in our study system, we used additive diversity partitioning as implemented in the R package vegan, version 2.4-6 (Oksanen et al. 2018). For this analysis, we divided the elevational gradient into five equally spaced zones (1: 287–514 m a.s.l., n = 22; 2: 514–740 m, n = 33; 3: 740–967 m, n = 32; 4: 967–1193 m, n = 37; 5: 1193–1420 m, n = 33). The levels of the sampling hierarchy thus included the alpha diversity at the plot level, beta diversity among plots, beta diversity among elevational zones, and the overall gamma diversity.

Results and discussion

Based on the data from both surveys, we recorded 4,179 species of which 1,918 are common (Shannon diversity) and 1,222 dominant (Simpson diversity). The mean number of species per site and across all sampled taxa was 417±21 species (mean ± standard error). Overall, the sampling effort of our surveys was sufficient to cover most of the common and dominant species of the study system and an increase in sampling effort would only increase the number of rare species for some groups as indicated by the differences between estimated and observed number of species, for the three orders of Hill numbers (Fig. 2). For order 0, which includes also rare species the difference is rather large compared to the other two orders. Beetles and fungi account for more than a quarter of all species and contribute considerably to the overall (gamma) biodiversity (Fig. 3). After asymptotic extrapolation, the expected species richness ranges from 5,340 to 6,100 species for the terrestrial ecosystem of the national park. However, our methods were not able to generate reliable data for the species living in the canopy (especially phytophagous insects), soil or deadwood dwelling species. Thus, the estimate of 6,100 species is only a lower bound for the total terrestrial biodiversity. Furthermore, this study ignored aquatic ecosystems like rivers or bogs, which also host species rich communities and have been the subject of an additional survey as part of the Silva Gabreta Monitoring project (Křenová & Seifert 2015, Bojková et al. 2015, 2018).

Our results show that the elevational gradient forms one of the major gradients of environmental change for biotic communities in the Bohemian Forest. Besides changes in macroclimatic conditions, the elevational gradient is accompanied by several changes in forest types and structures. Our lower sites in the Danube valley range from riparian forests at the most western sites in the river delta of the Isar and the Danube River to a xerothermic forest at the steep southern slope of the Jochensteiner Hänge near Passau. As typical for low mountain ranges in Europe, the higher sites are covered by mountain mixed forests with European beech (*Fagus sylvatica*) as the dominant species at mid elevations and Norway spruce (*Picea abies*) at high elevations (Heurich & Neufanger 2005, Barbati et al. 2014, Hilmers et al. 2018). Thus, it is not surprising that the observed number of species also change with elevation as found for nearly all taxa in our study. However, patterns of these changes vary strongly in strength and shape ranging from more or less linear declines to more complex U- and hump-shaped relationships (Fig. 4, Table 2).

In general, changes in community composition along the elevational gradient are mostly due to species turnover among sites. Nestedness showed no obvious pattern with elevation,

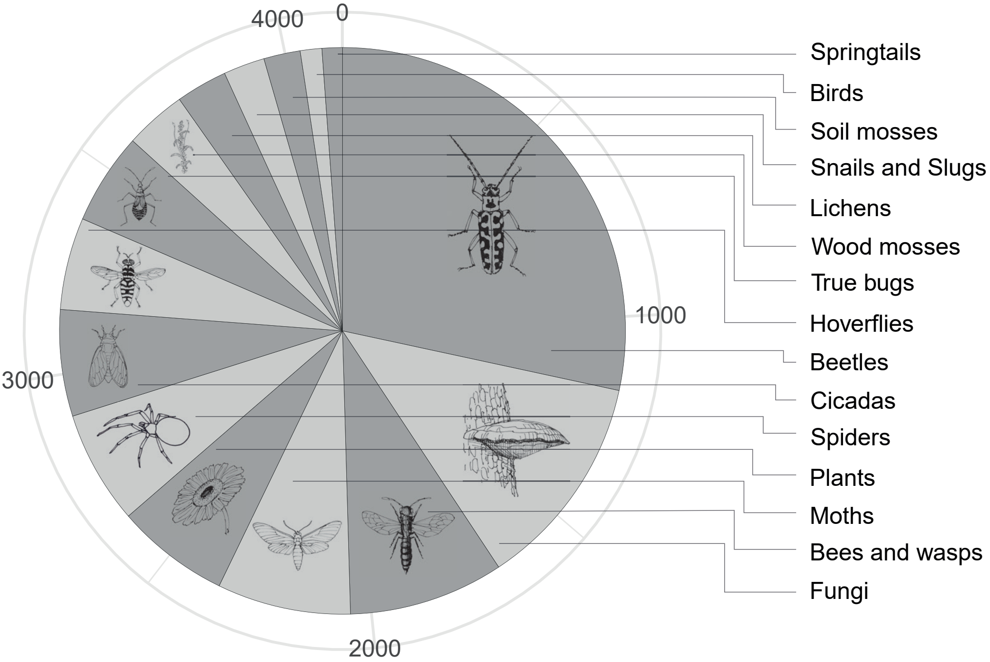

Fig. 3. Relative proportions of the species richness of the 15 groups under study after rarefaction/interpolation on three times the sampling units of the taxonomic group with the lowest number of sampling sites (i.e. 3×33 sites = 99 sites). Segment sizes conform to the number of species of the organism group with an overall estimated number of 4,135 species.

i.e. nestedness of the communities does not increase with elevation (Fig. 5, Table 3). Thus, we do not observe increased rates of species loss as we would expect if environmental conditions get harsher or too harsh for most species at higher elevations. The constant turnover of species along the elevational gradient contributes strongly to the observed gamma diversity of the Bohemian Forest. Additive partitioning showed that for most taxa beta diversity among elevational zones contributed most to the overall observed species pool, exceeding the contributions of local alpha diversity and beta diversity among plots within elevational zones (Fig. 6).

CONCLUSIONS

The implementation of the monitoring scheme generated reliable data for all taxonomic groups under study. This enables upcoming studies to investigate changes in species richness and community composition, as well as changes in the elevational distribution of species in response to a changing climate and changes in forest structure (BODIN et al. 2012). Here, a first study of HILMERS et al. (2018) revealed differential responses of taxonomic and

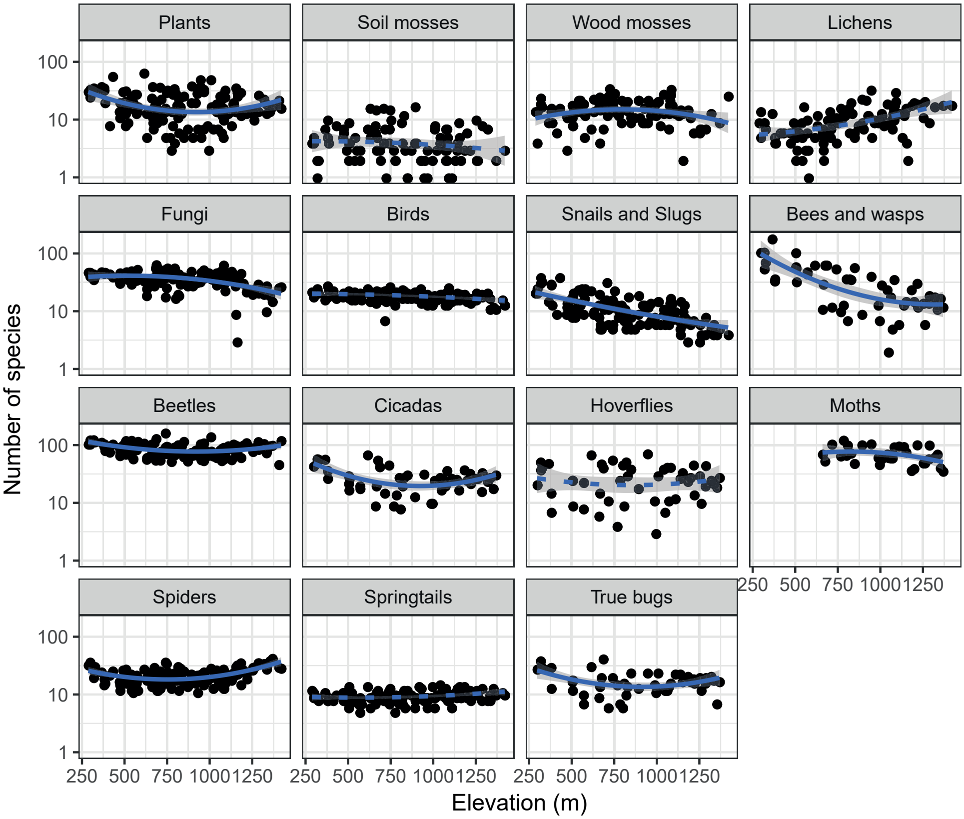

Fig. 4. Relationships of the number of species with elevation above sea level for the 15 groups of sampled organisms. Each point represents the number of species observed at a study site during the two surveys. Blue lines are based on generalized linear models with elevation as linear and quadratic predictor. Shaded areas indicate 95 % confidence intervals. Dashed lines indicate no significant effect of elevation on the number of species.

trophic groups to the stages of forest succession in the study region, which offers a dynamic baseline for assessing the effects of external drivers, such as changes in the temperature regime (Bodin et al. 2012, Thom et al. 2017). To overcome the shortcomings of a space-for-time approach it is necessary to resample the elevational gradient in regular intervals (Bässler et al. 2015). Although urgently needed, long-term regional biodiversity surveys along environmental gradients accompanied by a monitoring of changes in environmental conditions and habitat variables are still rare in ecological research (Lepetz et al. 2009; but see Greenland et al. 2003). Several studies revealed that species might respond to ongoing environmental change by adapting their distributions, including elevational upward shifts due to increasing temperatures (Bässler et al. 2013, Rumpf et al. 2018). Here, species' responses might vary strongly in strength and even direction (Lenoir et al. 2010, Bässler et al. 2013, Alexander et al. 2017). Despite their static nature, protected areas have the potential to buffer negative impacts of climate change on species by improving habitat quality and quantity (Thomas & Gillingham 2015, Betts et al. 2017). Thus, for the successful implemen-

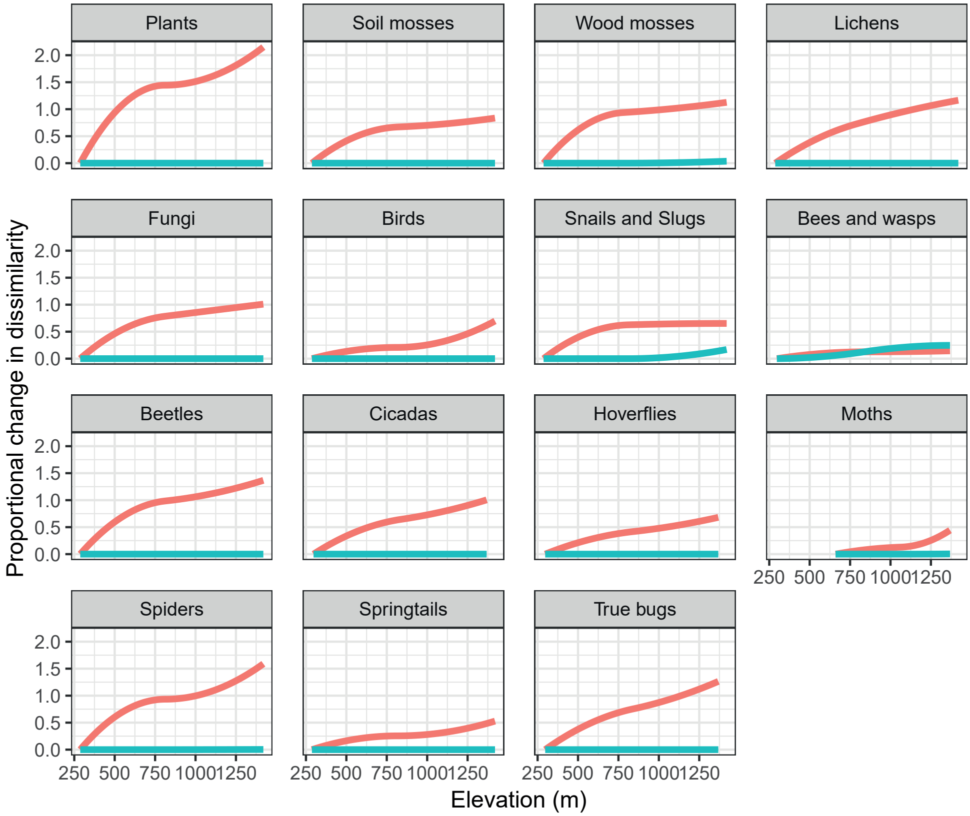

Fig. 5. I-Splines of generalized dissimilarity models after beta diversity partitioning into its turnover and nestedness components. For each group two models were calculated with dissimilarities among sites partitioned in turnover and nestedness as response matrices and dissimilarity among sites in geographic space (i.e. latitude and longitude) and elevation a.s.l. as predictor matrices. Red lines indicate the rate of change in dissimilarity due to turnover along the elevational gradient. Blue lines indicate the rate of change in dissimilarity due to nestedness along the elevational gradient.

Table 3. Percent of explained deviance of the generalized dissimilarity models by dissimilarity in elevation a.s.l. as a predictor for community dissimilarity in terms of turnover or nestedness.

Group	**Explained deviance**	
	Turnover	**Nestedness**
Plants	35.8	0
Soil mosses	5.5	0
Wood mosses	24.7	0.3
Lichens	12.5	0
Fungi	20.7	0
Birds	35.8	0
Snails and Slugs	21.9	4.2
Bees and wasps	1.7	5.6
Beetles	46.6	0
Cicadas	41.1	0
Hoverflies	15.1	0
Moths	25.6	0
Spiders	33.3	0
Springtails	13.6	0
True bugs	26.3	0

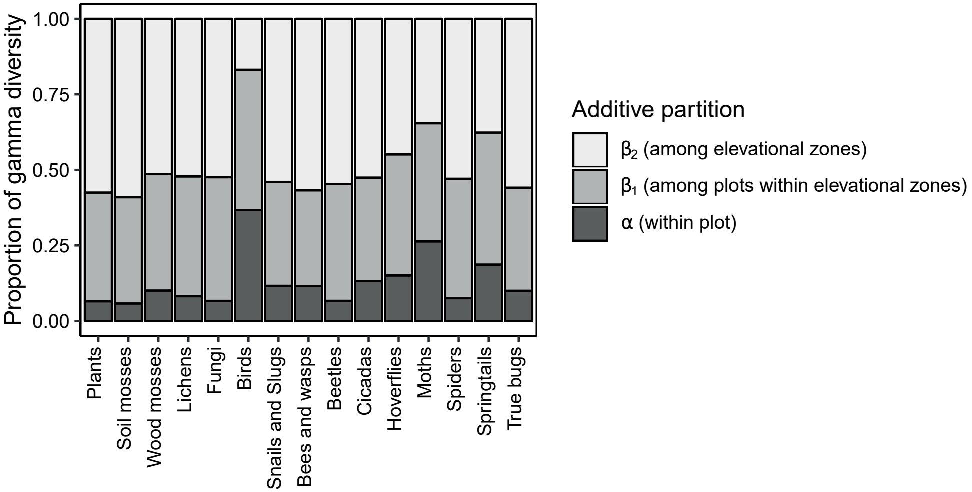

Fig. 6. Results of additive partitioning with three levels of sampling hierarchy including plot-level diversity (i.e. α-diversity), β-diversity among plots within five equally spaced elevational zones, as well as β-diversity among elevational zones. The height of the stacked bar indicates the relative contribution of the respective level of sampling hierarchy to the overall observed diversity (i.e. gamma diversity).

tation of conservation measures, it is crucial to understand how species will respond to changing environmental conditions and which species are most threatened. The BIOKLIM project and its continuation as part of the Silva Gabreta Monitoring will make an important contribution in the endeavor to understand species' responses to global change.

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