Effects of nitrogen deposition on butterfly species richness on the landscape scale

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Keywords
Deposition model, elevational gradient, Lepidoptera, microclimate, microclimatic cooling, plant insect interactions, trophic interactions, vegetation.

Article Impact Statement
Nitrogen deposition is a further global change driver that negatively affects butterfly species richness.

Data accessibility and reproducibility of results
Data and R-scripts to reproduce the results of this manuscript including figures and tables are provided at https://github.com/TobiasRoth/NDep_butterflies. Raw data for analyses are provided in the folder "data" and the folder "R" contains the R-Script that was used to export the data from the BDM database and to produce the figures and tables of the manuscript.

Acknowledgments
We thank the skilled botanists and entomologists who conducted the fieldwork. The Swiss Federal Office for the Environment (FOEN) kindly provided biodiversity monitoring data and topographic data. This work was supported by the FOEN to L.K., B.R. and T.R. and by the Swiss National Science Foundation (grant no. 156294) to V.A.

Abstract

Nitrogen (N) deposition caused by agriculture and combustion of fossil fuels is a major threat to plant diversity, but the effects on higher trophic levels are less clear. In this study we investigated how N deposition may affect butterfly species richness. We started with reviewing the literature and found that vegetation parameters might be as important as climate and habitat variables in explaining variation in butterfly species richness. It thus seems likely that increased N deposition indirectly affects butterfly communities via its influence on plant communities. We then analyzed data from the Swiss biodiversity monitoring program surveying species diversity of vascular plants and butterflies in 383 study sites of 1 km^2 that are regularly distributed over Switzerland, covering a modelled N deposition gradient from 2 to 44 kg N ha^{-1} yr^{-1}. Using traditional linear models and structural equation models, we found that high N deposition was consistently linked to low butterfly diversity, suggesting a net loss of butterfly diversity through increased N deposition. At low elevations, N deposition may contribute to a reduction in butterfly species richness via microclimatic cooling due to increased plant biomass. At higher elevations, negative effects of N deposition on butterfly species richness may also be mediated by reduced plant species richness. We conclude that in addition to factors such as intensified agriculture, habitat fragmentation and climate change, nitrogen deposition is likely to play a key role in affecting butterfly diversity.

Introduction

The increased flux of reactive nitrogen (N) in the biosphere and its deposition to ecosystems is considered as a major component of global change threatening biodiversity (Weiss 1999; Sala 2000). Increased N availability usually results in increased biomass production, in shifts in species composition (e.g., favoring eutrophic species), and often in a loss of plant species richness through competitive exclusion (Bobbink et al. 2010; Vellend et al. 2017). While the consequences of increased N availability are mainly documented for primary producers such as vascular plants (Bobbink et al. 2010), negative effects of increased N availability may also occur in species groups higher in the food chain, for example in insects.

Because plant and insect communities are closely linked (Zhu et al. 2015), N-induced changes in plant communities are likely to induce changes in insect communities (Sassi et al. 2012). For example, because insects are often specialized on one ore few plant species, the loss of plant diversity may decrease the diversity of insects (Knops et al. 1999; Haddad et al. 2001). Further, increased N availability favoring plant growth and biomass production is likely to alter the structure of the vegetation, thus leading to shifts in microclimatic conditions from open, dry and hot to more dense, humid and cool conditions, which will likely affect insects (Mantilla-Contreras et al. 2011). Further, more direct effects of increased N availability on insects might occur through altered food quality of host plants (Awmack & Leather 2002).

However, our knowledge on how increased N availability affects consumer diversity is rather limited (Humbert et al. 2015). For example, in a recent literature review, only 18 (10%) of the 187 effect sizes on species richness reported from N-addition experiments were about invertebrates (Murphy & Romanuk 2016). Interestingly, the average effect size of

those 18 studies suggest that the effect of increased N availability on local-scale species richness of invertebrates is slightly positive (none of the 18 studies investigated butterflies).

Here, we complement the experimental studies on the effects of N deposition at higher trophic levels with an observational study using multiple field sites representing a large gradient of N deposition (i.e., a gradient study, Roth et al. 2017). The data are from the Biodiversity Monitoring Switzerland program (BDM) and contain information on species richness of vascular plants and butterflies in 383 study sites of 1 km^2 and thus on the landscape scale, covering an N deposition gradient from 2 to 44 kg N ha^{-1} yr^{-1} (Roth et al. 2015). In previous studies, we found that high N deposition in these landscapes was associated with low values of six measures of plant diversity, including species richness (Roth et al. 2015). The BDM data thus provide an opportunity to examine possible direct and indirect effects of N deposition on species diversity of butterflies.

We started with a systematic literature review, searching for published studies investigating how butterfly species richness is related to environmental, land-use and vegetation parameters. The aim of the literature review was to compile a comprehensive list of predictor variables that could be important for explaining the variation in butterfly richness among our study sites. A second aim was to quantify how often N deposition was used as a predictor variable in such studies.

We then compiled the data from the BDM study sites and used traditional linear regression models to investigate how N deposition is correlated with butterfly species richness and how this correlation is affected depending on whether we accounted for all or only a selection of the other predictor variables. Since we assumed that a possible negative effect of N deposition on butterflies would be mediated by plant communities, we predicted that a negative effect would be weaker in models accounting for variables describing plant

communities. We then used structural equation models (SEM) for examining the different paths by which environmental variables could affect butterfly species richness (Grace et al. 2010). In particular, we investigated how N deposition may negatively affect butterfly diversity via a negative effect on plant diversity (Topp & Loos 2018) and, additionally, via microclimatic cooling, for example because the increasingly productive and dense plant canopy may prevent caterpillars from absorbing solar radiation (WallisDeVries & vanSwaay 2006; Klop et al. 2014).

Methods

Literature review

On 12 July 2019 we conducted a literature search in Web of Science to compile a list of possibly relevant predictor variables for explaining butterfly species richness. We searched for original studies that applied some sort of multi-variate regression models, with several predictor variables and the variation in butterfly species richness among sites or grid cells as response variable. We searched for studies with titles that fulfilled the following search criteria: *[(butterfl* OR lepidoptera) AND (diversity OR richness)]*; we excluded studies with *[island OR tropic*]* in the title. Furthermore, the topic needed to contain *["global change" OR driver* OR predictor OR variable]*. See Appendix A1 for a screenshot of the search setting in Web of Science. This search resulted in 95 studies. We excluded off-topic studies and studies that were conducted in habitats clearly distinct from the habitat types available in Switzerland (i.e. research on rain forests or deserts). We found 32 studies that complied with our criteria (Appendix A2).

From the 32 studies, we extracted the predictor variables that were used to model butterfly species richness and assigned them to one of the following categories: (1) broad

environmental category at the landscape level, including climatic gradients (from cool and humid to hot and dry) and variability, and topographic variables (from low to high elevations; from northern to southern expositions; from low to high topographic variability); (2) habitat category at the level of habitat patches, including variables indicating the availability (from low to high total area of suitable habitat patches), configuration (from low to high suitability of habitat patch configuration) and diversity of habitat types (from low to high diversity of habitat patches) as well as land-use intensity (habitat patches with low to high land-use intensity); (3) vegetation category describing the vegetation or the conditions within the vegetation, including resource diversity (from low to high plant or flower richness) and micro-climate (from dense vegetation with cool and humid microclimate to open vegetation with hot and dry microclimate); and (4) other variables that did not fit (1) to (3).

For each of the first three categories (environmental, habitat and vegetation), we then grouped the predictor variables into sub-categories. The idea was that the predictor variables within a sub-category could be used to measure similar underlying processes that may affect butterfly diversity. Assigning predictor variables to categories and sub-categories was an iterative process and was to a certain extend arbitrary.

In Appendix A2 we present the entire list of predictor variables investigated in the 32 studies. For each study we extracted the investigated predictor variables and assigned the reported effect on butterfly species richness using the following coding: 1 = the effect of the category on butterfly diversity as measured by a predictor variable was positive; 0 = there was no obviously important effect; -1 = the effect of the category on butterfly diversity as measured by a predictor variable was negative; "interm" = the effect of the category on butterfly diversity peaked at intermediate level of the predictor variable. We coded an effect as important (1, -1 or "interm") if the authors of the study mentioned in the abstract or

discussion that they considered the reported effect size as important or relevant. If the authors did not make a statement about the importance of the reported effect, we judged the importance and direction of the effect ourselves, based on the reported point estimate and the precision (confidence interval or standard error).

Butterfly and plant data

We analyzed the presence/absence of butterfly and plant species sampled between 2005 and 2009 in the Swiss Biodiversity Monitoring program (BDM, www.biodiversitymonitoring.ch). To monitor species diversity on the landscape scale, a sample grid of 428 equally spaced study sites, each of 1 km^2 size, was selected using a randomly chosen starting cell from the Swiss coordinates system (the total area of Switzerland is 41'285 km^2). From the 428 study sites, seven sites with 100% water surface and 25 sites that were too dangerous for fieldwork because of their exposed alpine terrain were excluded a priori, resulting in 396 study sites.

Within each study site, surveyors walked along a 2.5 km transect that followed existing trails preferably near the diagonal of the grid cell (Plattner et al. 2004); the same transects were used to survey plants and butterflies. If no trails existed, surveyors marked the transect route in the field and plotted it on a map.

The field protocol for butterflies was based on the British butterfly monitoring scheme (Pollard et al. 1995): transects were walked seven times between 21 April and 21 September in the lowlands, and four times between July and August above approximately 2000 m. The difference in numbers of surveys corresponds to the shorter flying season of butterflies at higher elevations; sites at high and low elevations received approximately equal sampling effort per week of the flight season. During each survey, surveyors walked the transects in both directions and recorded all day-flying butterfly species (presence/absence; including

Hesperiidae and *Zygaenidae*) within 5 m to each side of the transects on the way forth and back, respectively. Detectability varied by butterfly species and averaged 88% per survey (Kéry et al. 2009). For more information on the butterfly surveys, see (Kéry & Plattner 2007; Roth et al. 2014).

For the plant surveys, transects were usually walked by qualified botanists once in spring and once in summer, assuring that data collection spanned a large variation in flowering phenologies (Pearman & Weber 2007). At study sites with short vegetation period above approximately 2000 m, only one survey per field season was conducted. During each survey, surveyors recorded all plant species (presence/absence) within 2.5 m to each side of the transects both on the way forth and back, respectively. The overall detection error was relatively small, with an average of 6.6% undetected presences per plant species as estimated in an earlier study using site-occupancy models (Chen et al. 2012). For more information on the plant surveys, see (Plattner et al. 2004; Roth et al. 2014).

Plant and butterfly surveys were usually conducted in the same years; each year, one fifth of the study sites were surveyed. Since we used the N deposition rates modeled for 2007 (see below), we selected the butterfly and plant data from the survey year that was closest to 2007 for each study site; this was the reason why survey data are from 2005 to 2009. In the analyses, we only included study sites for which both the plant and butterfly surveys met our standards of data collection or of weather conditions according to the protocol (Roth et al. 2014). This resulted in omission of 13 study sites and in a final dataset on plant and butterfly data collected in 383 study sites.

Predictor variables

For all categories that were assigned to the predictor variables found in the literature review we included at least one predictor variable that was available for the BDM study sites (Table 1). Climate variables were extracted from the WorldClim database (Fick & Hijmans 2017). The source for the topographic data package was the GEOSTAT data base of the Federal Statistical Office (FSO, version 2006). Habitat data were derived from aerial data and are available on a grid with a 100-m resolution in the land-cover data package, also from the GEOSTAT data base of the FSO (version 2.0, 2013).

Predictor values for land-use intensity and microclimate were derived from the species lists of recorded plants using Landolt indicator values that were developed for the specific situation in Switzerland (Landolt et al. 2010). Landolt values are ordinal numbers that express the realized ecological optima of plant species for different climate, soil or land-use variables. We used the mean Landolt indictor value of the recorded plant species for temperature and moisture as a measure for micro-climatic conditions in vegetation; we used Landolt indicators for nutrients and mowing tolerance as a measure for land-use intensity, and Landolt indicators for light as a measure of vegetation density (Table 1). Additionally, we used the total number of recorded plants as a measure of resource diversity.

N deposition was estimated for the year 2007 in 100x100 m grid cells across Switzerland, using a pragmatic approach that combined monitoring data, spatial interpolation methods, emission inventories, statistical dispersion models, and inferential deposition models (Roth et al. 2015; Rihm & Achermann 2016). For each study site of 1 km^2, we averaged N deposition values from the cells containing parts of the transect used for the BDM surveys.

To obtain meaningful parameter estimates from the statistical models (see below), we centered the predictor variables by subtracting the value of the column "Zero" in Table 1

and standardized the predictor values by dividing them by the value of the column "Relevance". Thus, the estimated intercept of the linear models is the predicted butterfly species richness for the values of the predictor variables as given in the column "Zero". We chose these values to lie within the range of available data. The estimated slopes of the predictor variables in the linear models are in the units that are given in the column "Relevance". The values that we chose for the respective unit reflects the minimum change of the predictor variable that we consider as a relevant change; thus predictor variables become directly comparable among each other, which puts the focus on parameter estimates rather than on significance thresholds (Schielzeth 2010; Amrhein et al. 2019). A matrix with the scatterplots between all centered and standardized predictor variables is given in Appendix A3.

Statistical methods

We used two different approaches for investigating the drivers of the spatial variation in butterfly species richness across Switzerland, with a particular focus on N deposition effects. The first approach is based on linear models, with the square root of butterfly species richness as response variable, and N deposition as focus variable included among the predictor variables in all tested models. Additionally, some of the other variables in Table 1 were included as covariates (i.e., additional predictor variables). We applied the following models: (1) full model that included the linear terms of all predictor variables in Table 1, (2) full model without microclimate variables, because microclimate is rarely considered in other studies on butterfly species richness, and climate and microclimate are usually correlated, (3) topo-climate model that included only the linear terms of the topography and climate-gradient variables, (4) climate model that included only the linear terms of the

climate-gradient variables, (5) land-use model that included only the linear and quadratic term of elevation as a proxy for the climatic variation along the elevational gradient and the variables for habitat configuration, habitat diversity, habitat availability and land-use intensity, and (6) a minimalistic model that included only the linear and quadratic term of elevation as a proxy for climate and land-use intensity. All models assumed normal distribution of the residuals, and we examined this assumption for the full model using residual analyses. Model parameters were estimated in a Bayesian framework using the R-package arm (Gelman & Su 2018).

Our second approach was based on structural equation models (SEM, Hoyle 2012). For our purpose, SEMs have two main advantages over the more traditional linear models used in the first approach: first, SEM allow estimating direct versus indirect links, while linear models only allow separating the effects of two factors if they are mutually exclusive (Menéndez et al. 2007). Many of the variables in Table 1 may have a direct effect on butterfly species richness, but may also indirectly affect butterfly diversity through their effects on vegetation structure or plant diversity. Second, SEM can be used to model constructs that are measured by one or several predictor variables (Hoyle 2012). This is helpful, because we aim to compare the effects of climate, micro-climate and land-use intensity, each of them measured with several predictor variables.

We used the generic model of Fig. 1 as a starting point for the analyses using SEM. In this generic model we assume that butterfly species richness is mediated by vegetation structure and plant diversity (ovals and rectangles with grey background in Fig. 1). Additionally, we assumed that different global change drivers such as climate, atmospheric nitrogen deposition or land-use intensity (white ovals) could each have independent effects on vegetation structure, plant diversity and butterfly diversity. While butterfly and plant species

richness are measured variables in the BDM program (depicted in rectangles in Fig. 1), global change drivers and vegetation structure are latent variables that are measured by one or several of the predictor variables in Table 1. We present the results of different implementations of this generic model that vary in the number of global change drivers considered and in the selection of predictor variables used to measure the latent variables. Parameters of the SEMs were estimated using the R-Package lavaan (Rosseel 2012).

Results

Literature review

From the 32 studies on butterfly species richness that we complied according to our inclusion criteria, we extracted the effect sizes of 252 predictor variables. Predictor environmental variables were included in 75% of studies, habitat variables were included in 84% of studies and vegetation variables were included in 47% of studies. Nitrogen deposition was considered in none of the compiled studies.

While predictor variables for the vegetation category were less likely to be considered in these studies compared to environmental and habitat variables, the importance (as estimated by the proportion of times the variables were considered important) was similar to the importance of the predictor variables for the environmental and the habitat category (Table 2). Furthermore, resource diversity of the vegetation was the variable with the most consistent effect (regarding the direction of the effects) across all variables considered in the reviewed studies (Table 2).

Field study

Based on the linear models that we applied to the BDM data, we found that butterfly diversity decreased with increasing N deposition. The amount of this negative effect of N deposition on butterfly species richness was similar for all considered models (Fig. 2). Except for the climatic variables (annual mean temperature, mean temperature of coldest quarter of the year, and temperature seasonality), N deposition was the variable with the highest absolute effect size in the full model (Table 3).

The results of the structural equation model (SEM) that included climate, N deposition, land-use intensity and habitat availability as global change gradients potentially affecting vegetation structure, as well as plant species richness and butterfly species richness are given in Fig. 3a. Based on the results of this model, butterfly species richness was affected (in descending order of the absolute value of the effect sizes) by climate (highest butterfly richness in warm and dry climate; estimate ± SE: 0.50 ± 0.054), plant species richness (butterfly richness increasing with plant richness; 0.38 ± 0.025), and microclimate (higher butterfly richness in areas with warm, dry and open vegetation than in areas with closed and humid vegetation; 0.13 ± 0.041).

The effects of land-use intensity and habitat availability on butterfly species richness seemed to be rather weak (land-use intensity: -0.035 ± 0.021; habitat availability: 0.026 ± 0.025). However, at sites below 1600 m, where land-use is usually intense, the negative effect of land-use intensity on butterfly diversity was much stronger (-0.19 ± 0.034, Fig. 3b).

The results of applying the SEM to the data of all sites further suggest that higher deposition rates lead to denser, more humid and cooler microclimates within the vegetation (-0.10 ± 0.042) and to lower plant species richness (-0.73 ± 0.15, Fig. 3a). At elevations below 1600 m, N deposition mainly affected vegetation structure (vegetation structure: -0.85 ±

0.097; plant species richness: -0.14 ± 0.17, Fig. 3b), and the negative effect of N deposition at higher elevations was strong both regarding vegetation structure and plant species richness (vegetation structure: -2.43 ± 1.011; plant species richness: -2.11 ± 1.09, Fig. 3c).

Discussion

Drivers of butterfly species richness

In our systematic search for studies that compared different drivers of butterfly species richness, we found that vegetation variables were much less frequently investigated than environmental or habitat variables. However, if the effects of vegetation variables on butterfly species richness were studied, they were usually described as relevant and consistent. The results of our literature review thus suggest that vegetation variables representing microclimate or plant resource diversity are important but underrepresented in published research on the spatial variation of butterfly species richness.

Our results from structural equation models (SEM) applied to the Swiss Biodiversity Monitoring (BDM) data confirm the importance of vegetation variables: butterfly species richness was correlated with plant species richness to a similar degree as with ambient temperature. In contrast, the observed effects of land-use intensity and habitat availability were rather weak. An explanation might be that the available information about land-use intensity at the study plots of the BDM was limited. Our predictor variables are mainly derived from the plant surveys and contain average indicator values per 1-km^2 study plot, therefore hiding within-site variability. Further, land-use intensity is a rather multi-faceted category that includes, for example, the amount of fertilizers and insecticides applied, the mowing frequency of meadows, or the date of the first mowing. The variables for land-use intensity examined in this study might thus be too simplistic to realistically infer effects of

land-use intensity on butterfly and plant diversity, and thus the small effect sizes of land-use intensity need to be interpreted with caution.

Both the literature review and the analyses of BDM data suggest that drivers of butterfly species richness include macroclimatic factors acting on the landscape scale, and microclimatic factors that may vary on the small scale, among layers of vegetation. As a consequence, results of research on butterfly species richness are likely to depend on the investigated scale. In our study, all predictor variables were measured at the scale of 1 km^2. This seems to be an appropriate scale to investigate the effects of larger environmental variation among landscapes on butterfly species richness. In contrast, this scale may be considered too large to reliably infer effects of vegetation structure on butterfly species richness, because variation within the vegetation of a study plot of 1 km^2 may be large. However, on this broad landscape scale, we found on average negative correlations between nitrogen (N) deposition and butterfly species richness, suggesting that N deposition effects mediated by vegetation variables can be even stronger at smaller spatial scales.

Nitrogen deposition effect on butterfly species richness

Given that effects of increased N deposition on plant communities are well established (e.g. reduced plant diversity or increased vegetation density; Bobbink et al. 2010; Vellend et al. 2017), indirect effects of increased N deposition on butterfly diversity through its effects on plant communities are likely to occur. Indeed, several authors argued that increased N deposition has also consequences on species diversity at higher trophic levels (Nijssen et al. 2017; Pöyry et al. 2017; Stevens et al. 2018). However, none of the studies that we compiled in our literature review included N deposition as a predictor variable for butterfly species richness. Note, however, that our literature research was not exhaustive, as the main aim

was to compile a list of predictor variables for butterfly species richness that, based on the literature, should be included in our field study.

Based on the data from the BDM program, our results seem to confirm the importance of N deposition as a driver of butterfly species richness. The different applied models (i.e., multivariate linear models and structural equation models, SEM) that we used to predict the spatial variation of butterfly species richness in Swiss landscapes consistently suggested that butterfly species richness is lower when N deposition is higher. Previous studies have found that N deposition affects butterfly species differently depending on their preferred food plant or other factors (WallisDeVries & vanSwaay 2006). For example, population sizes of butterfly species that depend on nutrient-poor conditions tend to decrease with increasing N deposition, while population sizes of species that depend on nutrient-rich conditions, or N-favored plant species, tend to increase (Öckinger et al. 2006; Betzholtz et al. 2013). Our study complements these results on single species or on species groups with specific traits by suggesting that on the landscape scale, species-dependent N-deposition effects sum up to a net loss of butterfly species richness due to increased N deposition.

At least three main mechanisms have been proposed for explaining how butterfly communities react to increased N deposition: First, reduced plant diversity due to increased N deposition could result in reduced food diversity for butterflies (Zhu et al. 2015). Second, increased N deposition resulting in higher plant biomass and denser vegetation could lead to microclimatic cooling that, for example, may prevent caterpillars from absorbing solar radiation to attain optimal body temperatures (WallisDeVries & vanSwaay 2006; Klop et al. 2014). Third, the chemical composition of plants could change due to increased N deposition, resulting in reduced food plant quality (Fischer & Fiedler 2000; Habel et al. 2016). The results of the structural equation models applied to the BDM data seem to

support the first two pathways: Particularly at higher elevations where the negative effect of land-use intensity on plant species richness was reduced, increased N deposition was correlated with reduced plant species richness, and plant species richness was positively related to butterfly species richness (Fig. 3c). This suggests that at higher elevations, the negative effect of N deposition on butterfly species richness is mediated by its negative effect on plant species richness. At lower elevations, N deposition was mainly correlated with denser vegetation (i.e., with plant indicator values that are associated with less light) and with cooler and more humid vegetation, which was correlated with lower butterfly species richness. This suggests that at lower elevations, microclimatic cooling through increased N deposition contributes to a reduction in butterfly species richness (Fig. 3b).

We do not have data to directly investigate the third explanation stating that reduced butterfly diversity due to N deposition could be caused by reduced food plant quality. However, when we allowed for a direct effect of N deposition on butterfly species richness in the structural equation model (Appendix A4), the results suggested a quite strong negative effect of N deposition on butterfly species richness. This effect is similar to the effect size found based on the traditional linear models (Fig. 2). The direct effect of N deposition on butterfly species richness, which is independent from vegetation structure and plant species richness, might be caused by N deposition resulting in reduced food plant quality. While we are not aware of other explanations that could convincingly explain a direct negative effect of N deposition on butterfly species richness, it seems nevertheless unlikely that high N deposition reduces food plant quality so much that this reduces the number of butterfly species considerably.

Whereas in the published literature, N deposition is usually not considered as a driver of butterfly species richness, we found that in Swiss landscapes, high N deposition was

consistently linked with low butterfly diversity, suggesting a net loss of butterfly diversity caused by increased N deposition. In addition to agricultural intensity, habitat fragmentation and climate change, atmospheric nitrogen deposition might thus play an essential role in reducing butterfly diversity.

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Tables

Table 1: List of the predictor variables used to explain butterfly species richness. The categories are obtained from the literature review and reflect different processes that may affect butterfly diversity. For the statistical analyses we standardized the predictor variables by subtracting "Zero" and dividing it by "Relevance". See main text for details.

Category	Acronym	Description	Unit	Relevance	Zero	Source
Climate-Gradient	amt	Annual mean temperature	degree Celsius	2	5	WorldClim
Climate-Gradient	mtcq	Mean temperature of coldest quarter	degree Celsius	2	0	WorldClim
Climate-Gradient	ap	Annual precipitation	mm	200	1000	WorldClim
Climate-Gradient	pwq	Precipitation of warmest quarter	mm	50	400	WorldClim
Climate-Variability	ts	Temperature Seasonality	degree Celsius (SD)	0.5	6	WorldClim
Climate-Variability	ps	Precipitation Seasonality (Coefficient of Variation)	mm (CV)	5	20	WorldClim
Topgraphy	ele	Elevation (meter above sea level)	m	200	500	GEOSTAT
Topgraphy	ele_SD	Standard deviation of elevation within site	m (SD)	50	100	GEOSTAT
Topgraphy	incli	Inclination	degrees	5	10	GEOSTAT
Topgraphy	cd	Number of the eight cardinal directions	number	2	4	GEOSTAT
Habitat configuration	fe	Forest edges	m	1000	5000	GEOSTAT
Habitat diversity	nlut	Number of land-use types	number	3	10	GEOSTAT
Habitat availability	ah	Available habitat (total area minus sealed areas and open water)	percentage	80	10	GEOSTAT
Habitat availability	agri	Percent of agricultural land	percentage	10	50	GEOSTAT
Land-use intensity	N	Mean Landolt indicator value for nutrients	[1-5]	0.1	3	BDM plant surveys
Land-use intensity	mt	Mean Landolt indicator value for mowing tolerance	[1-5]	0.1	2.5	BDM plant surveys
Atmospheric pollution	ndep	Nitrogen deposition	kg per ha and yr	10	10	Roth et al 2015
Microclimate	T	Mean Landolt indicator value for temperature	[1-5]	0.1	3.5	BDM plant surveys
Microclimate	H	Mean Landolt indicator value for humidity	[1-5]	0.1	3	BDM plant surveys
Microclimate	L	Mean Landolt indicator value for light	[1-5]	0.1	3.5	BDM plant surveys
Resource diversity	PSR	Plant species richness	number (sqrt)	1	-15	BDM plant surveys
Dependend variable	BSR	Butterfly species richness	number (sqrt)	1	-5	BDM butterfly surveys

Table 2: Summary of the literature review. Given are for each subcategory the number of different indicator variables, the number of studies, the proportion of times an "important" effect was identified, and the direction of the important effect size (the mean direction of effects not coded as "zero", excluding effects that peaked at intermediate levels).

Category	Subcategory	Number of variables	Studies	Importance	Direction
Environment	Climate-Gradient	10	18	0.63	0.26
Environment	Climate-Variability	4	8	0.56	0.00
Environment	Topography	3	13	0.45	0.19
Habitat	Habitat configuration	6	7	0.58	-0.10
Habitat	Habitat diversity	4	11	0.64	0.27
Habitat	Habitat-availability	11	20	0.64	0.15
Habitat	Land-use intensity	25	19	0.57	-0.42
Vegetation	Microclimate	3	7	0.64	0.11
Vegetation	Resource diversity	8	13	0.59	0.57
Others	–	4	6	0.29	0.00

Table 3: Parameter estimates of the full model that explains the butterfly species richness with the linear terms of all the variables listed in Table 1.

Predictor variable	Description	Estimate	Std-Error	P-value
amt	Annual mean temperature	-2.179	1.072	0.043
mtcq	Mean temperature of coldest quarter	2.405	1.032	0.020
ap	Annual precipitation	-0.113	0.124	0.364
pwq	Precipitation of warmest quarter	0.236	0.105	0.026
ts	Temperature Seasonality	1.341	0.475	0.005
ps	Precipitation Seasonality (Coefficient of Variation)	-0.081	0.061	0.188
ele	Elevation (meter above sea level)	0.429	0.090	0.000
ele_SD	Standard deviation of elevation within site	-0.193	0.102	0.059
incli	Inclination	0.165	0.064	0.010
cd	Number of the eight cardinal directions	-0.017	0.043	0.690
fe	Forest edges	0.030	0.012	0.018
nlut	Number of land-use types	0.028	0.051	0.580
ah	Available habitat (total area minus sealed areas and open water)	0.058	0.033	0.082
agri	Percent of agricultural land	0.091	0.021	0.000
N	Mean Landolt indicator value for nutrients	-0.198	0.060	0.001
mt	Mean Landolt indicator value for mowing tolerance	0.018	0.054	0.738
ndep	Nitrogen deposition	-0.719	0.094	<0.001
T	Mean Landolt indicator value for temperature	0.200	0.045	<0.001
H	Mean Landolt indicator value for humidity	-0.016	0.043	0.712
L	Mean Landolt indicator value for light	-0.167	0.031	<0.001
PSR	Plant species richness	0.248	0.031	<0.001

Figure-legends

Figure 1: Path diagram of the generic model that we used as a starting point for the analysis using structural equation models. Observed variables are depicted in rectangles; latent variables that were measured using several of the predictor variables are depicted in ovals. Arrows indicate assumed causal relationships between variables.

Figure 2: Effects (with 95%-compatibility intervals; Amrhein et al. 2019) of nitrogen deposition on the square root of butterfly species richness based on linear models that differ in selection of predictor variables. See statistical methods for a description of the different models.

Figure 3: Results obtained from applying the structural equation model to (a) all data from the Swiss Biodiversity Monitoring program, (b) the data of the sites below 1600 m, and (c) the data of the sites above 1600 m. Depicted are presumed effects of different global change drivers and vegetation variables on butterfly species richness at 1-km^2 resolution in Switzerland; the thickness of the arrows is relative to the absolute values of the effect sizes, with arrows in grey indicating positive effects, and arrows in orange indicating negative effects.

Figures

Figure 1: Generic model.

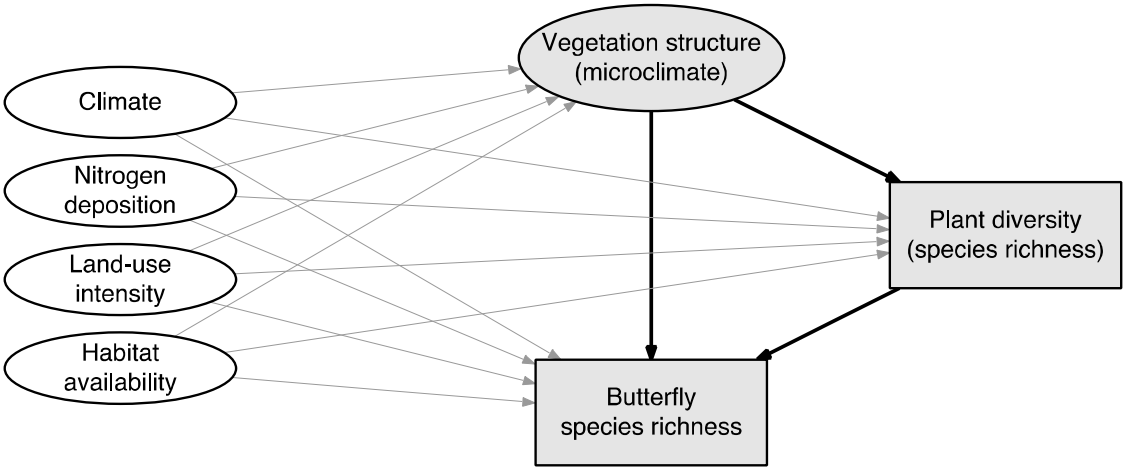


Figure 2: Linear model results

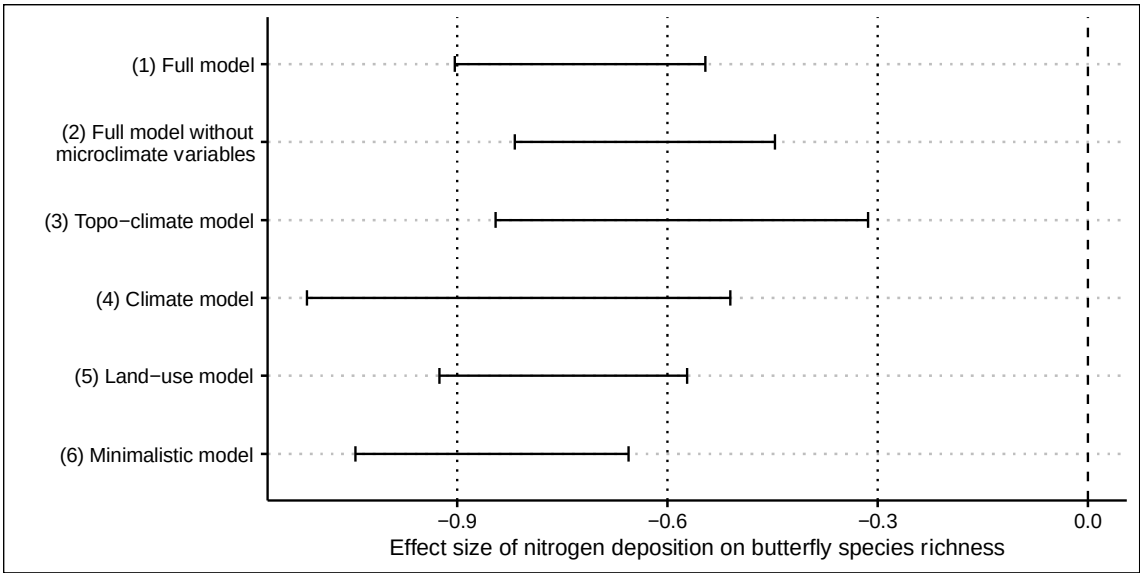
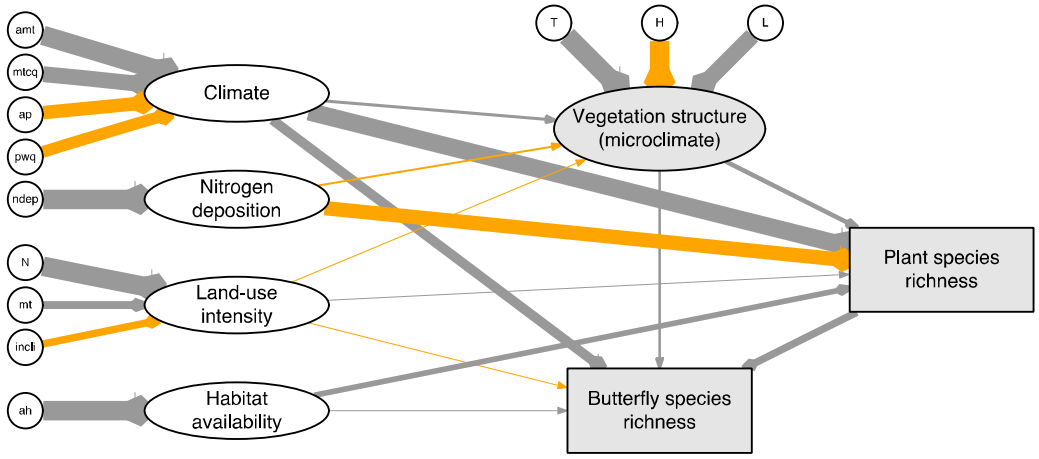
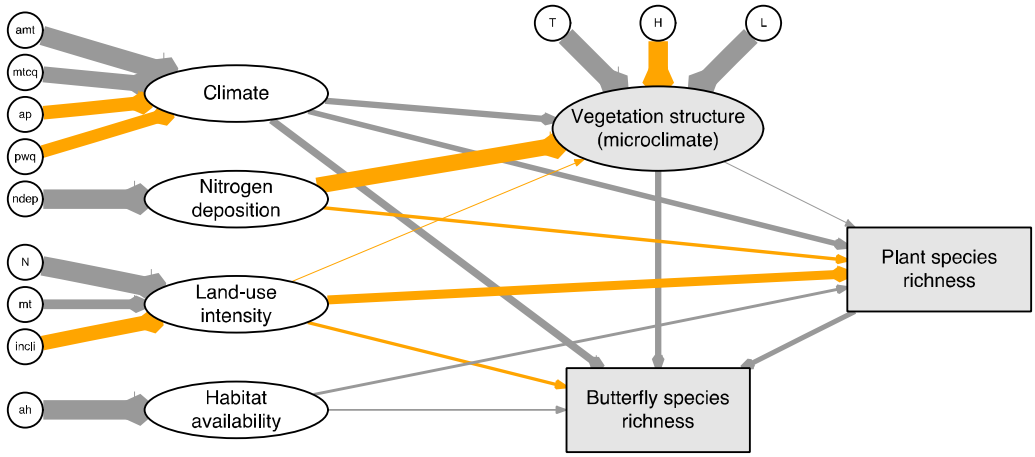


Figure 3: Results obtained from applying the structural equation model.

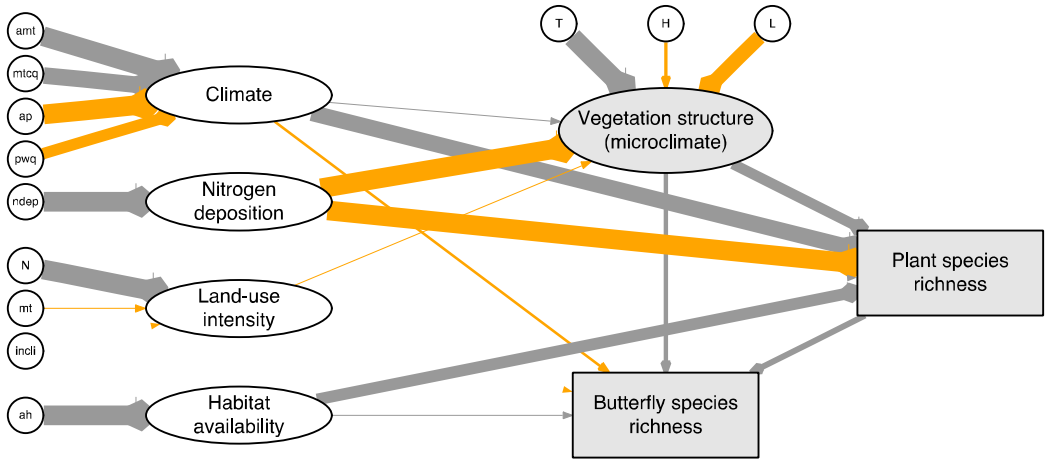
(a) all data



(b) data from sites <1600 m



(c) data from sites >1600 m



Supporting Information

Figure A1: Web of Science search setting used for the systematic literature review.

Webofscience_Search_Setting.png

Table A2: Excel file with one table listing the 32 studies used in the literature review and one table listing the predictor variables extracted from these studies.

Figure A3: Matrix of scatterplots between all predictor variables.

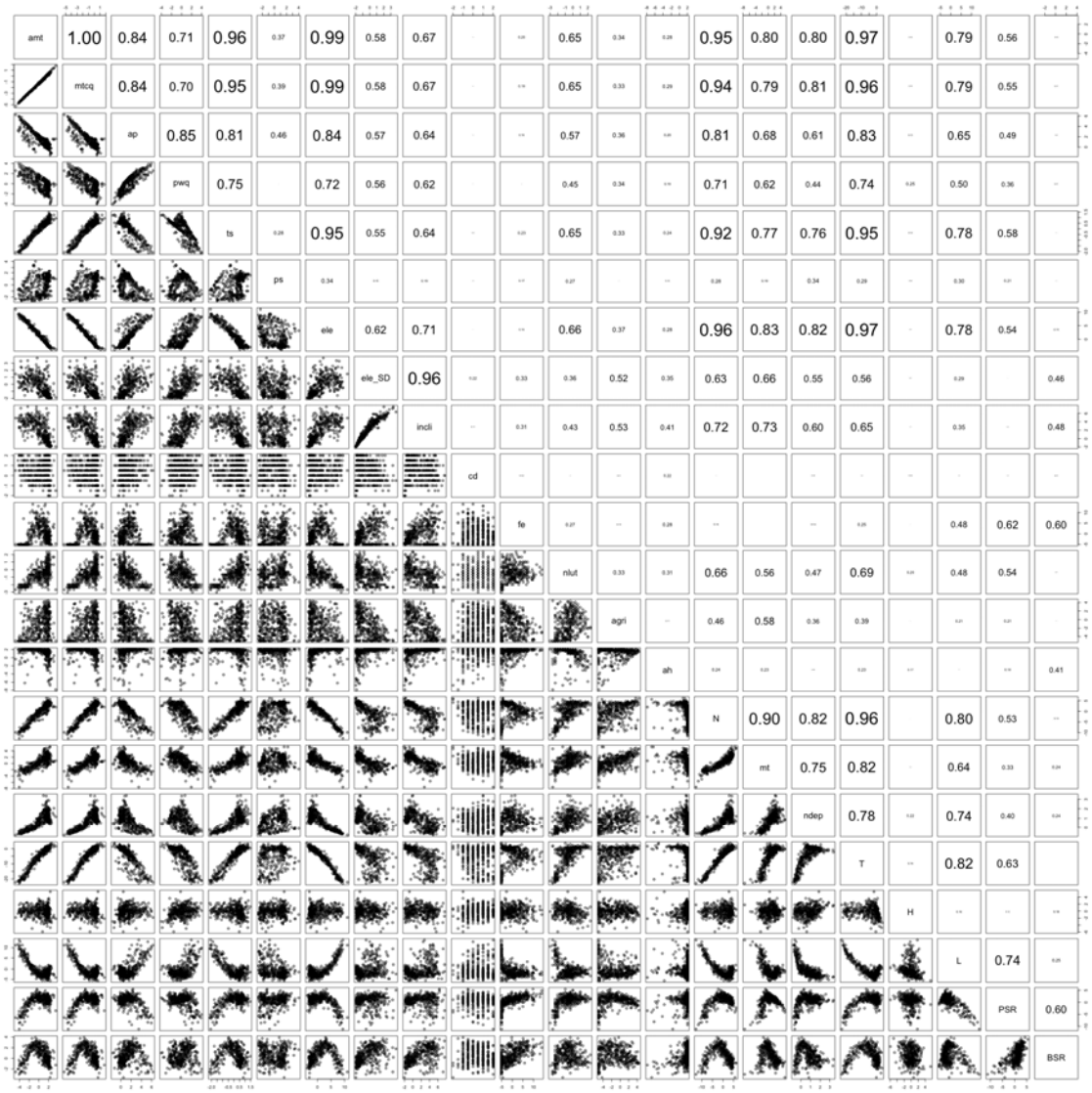
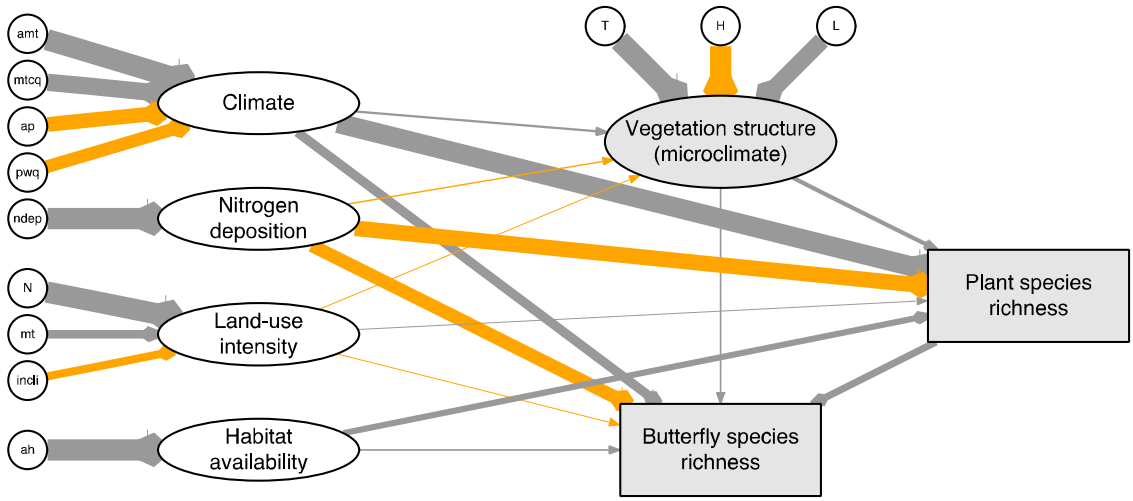



Figure A4: Results of the structural equation model that allows for a direct effect of Nitrogen deposition on butterfly species richness. The thickness of the arrows is relative to the absolute values of the effect sizes, with arrows in grey indicating positive effects, and arrows in orange indicating negative effects.