



Land use and climate change affects butterfly diversity across northern Austria

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Abstract

Context Biodiversity is severely decreasing at a global scale since several decades. There are significant changes in species community compositions, reductions of species richness and abundances of arthropods, as well as of arthropod biomass. Land use intensification and climate change are assumed to be main drivers causing biodiversity change and loss. However, proximate effects of land use, landscape configuration, topography and climate on species richness and species community composition were only rarely analysed.

Objective We study the effects of current land cover, landscape structures and climate on butterfly and burnet moth species diversity and community

composition across northern Austria (i.e. the federal state of Salzburg).

Methods We compiled observation data of butterflies and burnet moths for the past 40 years. We divided faunal data, land cover data and data on climate into 5×5 km² grid cells. We classified all lepidopterans assessed into groups according to their distribution, behaviour, ecology and life-history.

Results We found higher species richness and temporal community shifts in higher elevations, and where topographic heterogeneity is high. Habitat connectivity has a positive impact on ecologically specialised, sedentary, and endangered species. Mean temperature and precipitation positively influenced species richness.

Conclusions Both, land-use and climate strongly shape biodiversity structures. In particular, landscape heterogeneity promotes the diversity of ecological niches, which subsequently accelerates species

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diversity, including specialist species. Agricultural intensification in higher elevations and at steep slopes is more difficult and therefore less attractive, and thus the level of biodiversity is still high. In addition, climate warming might lead to the accumulation of species in higher elevations. Our study further underlines the relevance of habitat conservation at lower elevations, where not all habitat types are conserved sufficiently.

Keywords Land cover · Landscape configuration · Elevation · Slope · Climate · Time series · Butterflies · Zygaenid moths · Community composition · Species diversity · Traits · Endangerment

Introduction

Global biodiversity is severely decreasing (Maxwell et al. 2016). Studies showed significant losses of insects, and reported decreasing species richness over the past decades (Conrad et al. 2006; Thomas 2016), reduction in species abundances (Habel et al. 2019b), and subsequent losses of biomass of flying insects (Hallmann et al. 2017; Seibold et al. 2019). Furthermore, significant changes in community compositions have occurred over the past few decades, towards species assemblies dominated by some few generalist species (Wenzel et al. 2006; Coulthard et al. 2019; Fox et al. 2021; Laussmann et al. 2021). These trends also affect other species groups, beyond insects, and may severely interrupt species interactions. For example, reductions of pollinators such as wild bees caused a significant loss of insect-pollinated plant species across landscapes (Biesmeijer et al. 2006). Furthermore, organisms at higher trophic levels, such as birds or bats, suffer under decreasing insect abundances and thus reduced food availability (Benton et al. 2002; Hallmann et al. 2014).

However, the detailed effects of land use and climate changes on species diversity across landscapes is still insufficiently understood. For example, the seminal work of Hallmann et al. (2017) documented a loss of biomass of flying insects by about 75% over the past 30 years. However, the authors could not determine in more detail the driving forces leading to this biodiversity reduction. Nevertheless, other studies clearly demonstrated that land use intensification

drives changes in species composition and losses in species richness and abundances (Ollerton et al., 2014). Furthermore, Urban (2018) showed that a major proportion of mountain biodiversity is under stress due to climate warming, and thus is expected to partly vanish in the near future. Several of these factors contributing to biodiversity loss are occurring in parallel, and thus may synergise each other.

Several analyses demonstrated the direct negative effects of agricultural intensification on biodiversity (Geiger et al. 2010; Habel et al. 2019a; Zaller and Brühl 2019). Thus, nitrogen influx is modifying habitats by affecting vegetation, hereby diminishing habitat quality, especially in nitrogen-limited ecosystems (such as heathlands, calcareous grasslands and bogs) (Stevens 2004; Wallis de Vries and Van Swaay 2006). This influx also accelerates plant growth with subsequent intensification of mowing regimes (i.e. more frequent mowing). Agricultural intensification also goes in line with changes in habitat configuration. The extensive agricultural systems of the past formed heterogeneous landscapes with generally small field sizes, providing a large number of different ecological niches (Schmitt and Rákossy 2007). Agricultural intensification consequently homogenises landscapes, with subsequent vanishing of small-scale habitats (such as field verges) and a reduction of landscape permeability for most species (Dover and Settele 2009; Öckinger et al. 2012; Thomas 2016). Intensification took place mainly in plains, while regions with strong relief are assumed to be less affected by intensification (Havlíček and Chrudina 2013). At the same time, however, there were also land use abandonments in regions where intensification was not economically possible, mostly due to the topographic relief, with similar negative consequences for ecosystems due to progressive succession (see Erhardt 1985; Colom et al. 2021).

In consequence, today's remaining habitats of high species diversity and richness are mostly small and geographically isolated from each other (Reidsma et al. 2006; Batáry et al. 2017). The loss of habitats and stepping stones in between as well as the ongoing fragmentation of formerly interconnected habitats diminishes species abundance and persistence on the landscape level, especially as negative edge effects are reducing habitat quality and stochastic processes are affecting small and isolated populations more severely than large and interconnected ones (Melbourne and

Hastings 2008). This situation can be exacerbated by stressors related to rapidly occurring climate change.

In this study, we analyse effects of landscape structures including land use and topography as well as climate on the occurrence of butterflies and burnet moths (hereafter simply butterflies). For this purpose, we used an extensive database on the butterflies of the federal State of Salzburg (northern Austria), covering the period from 1980 to the present. As proxies we included details on land coverage, landscape structure (connectivity and diversity of the landscape), and topography (slope, inclination, and terrain roughness) of the landscape. We also considered climate data, such as precipitation and temperature. We compiled butterfly observations collected over the past decades, with detailed information for each record (date, geographic position, observer). We then assigned these data to respective $5 \times 5 \text{ km}^2$ cells. We classified each butterfly species according to its distributional, behavioural, and ecological characteristics. Based on these data, we tackle the following research questions:

Q1: How much of the distribution patterns of the butterfly fauna of the Salzburg region can be explained by natural abiotic factors (geography, climate) and patterns produced by human land use?

Q2: Which of the different traits of butterfly communities is influenced most by these factors?

Q3: Can natural and human induced factors be disentangled?

Q4: What can we learn from our data for nature and species conservation?

Materials and methods

Data set

The data used for this study are taken from the biodiversity database of the “Haus der Natur”, Museum of Natural Science and Technology in Salzburg, and were further completed with records of recent butterfly assessments conducted in our study area, and with data of various literature sources. An overview of all sources used is given in Appendix S1. In total, we included 31,566 butterfly records representing 168 species collected from 1980 to 2019. We selected this recent time period to reconcile faunal observations with current land use and climate information. This time window represents comparatively

stable faunal and land use conditions for our study region if compared with the period of the 1960s and 1970s (P. Gros, pers. comm.). Two local entomologists (P. Gros and G. Embacher) recently performed extensive quality checks of the data used for this study.

Traits

Species performance (such as species behaviour, ecology and life-history) strongly impacts species responses to environmental conditions (Birkhofer et al. 2017). Butterflies are well explored in terms of taxonomy, distribution, behaviour and ecological demands. Based on recently published data bases (Essens et al. 2017; Middleton-Welling et al. 2020), we extracted trait data for all species of this study. The data were taken from the above-mentioned data bases, additional literature, and were subsequently adapted to the regional conditions (according to personal experience of PG). For burnet moth species, we did identical classifications as for butterflies (remark that burnet moths are not part of any of the above-mentioned data bases). We used six traits which characterise species with respect to their behaviour and environmental demands, namely: (i) habitat generalists; (ii) sedentary species; (iii) species of oligotrophic habitats; (iv) forest species; (v) species with monophagous larvae; and (vi) species with their larvae feeding on xerophilic plants. We also assessed the endangerment according to the Red List of Austria (Höttinger and Pennerstorfer 2005). The species' specific classifications are given in Appendix S2.

Land cover and climate

Land cover data were assessed using the Corine Land Cover (CLC) 2018 dataset (EEA 2020) in QGIS version 3.4.10. Land cover classes were used according to the CLC 2018 dataset and overlaid with the observation data. To evaluate landscape parameters, observation data were gridded to quadratic cells with a cell-size of 25 km^2 using QGIS. Quadratic cells with a cell length of 5 km were chosen based on (a) power analyses for observation data covering years from 1980 to 2018 and thus the distribution of these observation data and (b) based on used land cover data and its respective resolution. The CLC2018 dataset provides a spatial resolution of 100 m cell length. Thus, we choose 5000 m cell length for grid

cells to represent a substantial proportion of surrounding landscape of each observation found in the grid cells. Furthermore, aggregating observation data to coarser grid cell size allows more extensive analysis of landscape composition, habitat configuration and connectivity among single grid cells. The following landscape parameters were calculated using the CLC2018 dataset and the user defined grid cells in Fragstat software (McGarigal et al. 2012). On landscape level, we used Percentage of Landscape (PLAND) for each land cover class, as well as Connectance Index (Connectance) as a measure of land cover aggregation, and Simpson's Diversity Index (Diversity) as a measure of landscape diversity. Connectance is defined by the number of functional joining between patches of the same land cover class, where each pair of classes is either connected or not based on a user-specified distance of 500 m. Connectance is low with a minimum of 0 when either the landscape consists of a single class, or none of the patches in the landscape are "connected" and increases when more land cover classes become "connected." Diversity has its minimum of 0 when the landscape contains only 1 class and approaches 1 as the number of different land cover classes increases. To enrich the dataset on landscape composition and configuration for species richness analyses, the parameters slope and aspect were included based on the 5 m geometric resolution digital terrain model from the open government dataset of Salzburg (Land Salzburg—data.salzburg.gv.at). The slope parameter was used to calculate (a) average elevational differences, (b) 75th and c) 90th percentile of slope values within each grid cell using QGIS. 75th percentile was selected to highlight proportion of steep slopes within each grid cell, as 75% of the slope values are below that value. Additionally to slope-based parameters, calculations to incorporate the significance of aspect were performed. Based on 5 m digital terrain model data, the number of north facing cells (Northwest to Northeast, i.e. aspect 292.5° to 67.5° in compass direction) and the number of south facing cells (Southeast to Southwest, i.e. aspect 112.5° to 247.5° in compass direction) were computed. Dividing the number of south facing cells by north facing cells results in a ratio, where values below 1 indicate a dominance of north facing regions in the corresponding grid cell (cooler, shadier) and values above 1 indicate presence of more sun-exposed areas. For the

statistical analyses, we grouped these quotients into four classes < 0.5 (236 cells), 0.5–1.0 (702), 1.0–1.5 (636), > 1.5 (55). Finally, we used the Chelsa climate data (Karger et al. 2017) to link species richness of butterflies and average proportions of habitat and feeding groups to average precipitation and temperature.

Statistical analysis

To relate species richness and composition to land cover characteristics and climate, we arranged all records into a 1629 × 168 grid cell/study year combination × species matrix M (40 study years and 159 grid cells; no butterfly records were available for 4731 grid cell/study year combinations). The matrix contained 31,566 single records and is provided in Appendix S2. Despite of the high number of records, a large part of the annual grid cell records does not reflect the total species richness due to biased sampling and therefore does not allow for a direct comparison of species richness S and composition. Consequently, we used the proportions (relative quantity) of the above mentioned six species traits and two levels of endangerment with respect to species richness ($p_S = S_{\text{trait}}/S_{\text{total}}$), where S_{trait} and S_{total} refer to the numbers of species per trait and endangerment class, respectively, and to the total number of species recorded in a given grid/study year combination. These proportions should well reflect the true species composition in each grid cell. Further, we calculated the dominant eigenvector (53.4% explained variance) of a principle coordinates analysis (Soerensen dissimilarity) that catches the matrix-wide variation in species composition. This eigenvector covers the variability in species composition among grid cells and allows for an assessment of the variability in composition among grid cells in dependence of landscape and climatic factors.

To link compositional changes and variation in the proportions of traits and endangerment (response variables) to landscape and climate (predictor variables), we used factorial analysis of variance and generalised linear modelling (GLM) with identity link function and normal error structure. Log-transformed species richness served in all models as a covariate. To account for the spatial non-independence of grid cells, we calculated the dominant eigenvector (PCoA1) of the Euclidean distance matrix of cells and used PCoA1

as an additional predictor. Predictor and response variables were only moderately correlated (Appendix S3). To avoid model distortions due to different variable scales, all variables were z-transformed ($z = (x - \mu)/\sigma$; x , μ and σ being the variable value and the respective variable mean and standard deviation). Model parameters are therefore β -values that allow for an assessment of respective effect sizes. The full correlation matrix of all variables used in this study is presented in Appendix S3.

According to our starting hypothesis, we were particularly interested in whether and how landscape structures influence the variability in butterfly species richness and composition. To assess these aspects, we used three approaches. First, we estimated the temporal variability (β -diversity) in species composition within each grid cell using Soerensen dissimilarity. Second, we used canonical correspondence analysis to relate variability in grid cell composition to landscape and climate. Respective significances were obtained from 999 residual permutations. Third, the temporal variability (1980–2019) in the annual proportions of the six butterfly traits was quantified by the variance—mean relationship (VMR).

$$VMR = \frac{\sigma^2}{\mu} \quad (1)$$

Because the variance σ^2 of ecological variables generally increases with average variable expression μ according to Taylor's power law ($\sigma^2 = c\mu^z$; Taylor 2019), we followed the approach of Ulrich et al. (2021) and combine Eq. 1 with Taylor's power law and additional environmental variables into the additive model

$$\ln\left(\frac{\sigma^2}{\mu}\right) = \ln(c) + (z - 1) \ln(\mu) + \sum a_j h_j \quad (2)$$

where a_j and h_j denote the parameter and the variable expression, respectively, of the environmental covariates in plot j . Again, we used a GLM with identity link function and normal error structure, this time using raw data. We implemented all GLM and ANOVA models using Statistica 12.0.

Results

Butterfly species richness increased significantly towards higher elevations (parametric $P(\chi^2) < 0.05$), and with average temperature ($P(\chi^2) < 0.001$), and precipitation ($P(\chi^2) < 0.01$) (Fig. 1a). Aspect, quantified by the proportion of south to northward directed habitats did neither significantly influence species richness nor the proportions of the studied butterfly traits, even after accounting for different time periods (Table 1). Similarly, landscape diversity, connectance, and slope had only minor influences on the total species richness per grid cell (Fig. 1). Species-poor grids exhibited proportionally higher degrees of species temporal turnover (β -diversity) than species-richer grid cells (Fig. 1b). Temporal turnover increased with increasing average slope ($P(\chi^2) < 0.05$). Again, landscape diversity and connectance showed no significant influence on temporal species turnover (Fig. 1b). Temporal species turnover and mean elevation were negatively correlated. Importantly, we found a high variability in turnover along the elevation gradient and cell specific patterns in temporal variability as indicated by the high standard error ($SE = 0.23$) for elevation in Fig. 1b.

The temporal turnover in the proportions of the six butterfly groups was well described by the model of Eq. 2 (Table 2). Except for species of oligotrophic habitats, the variance in proportion was linked to mean proportion by a power function according to Taylor's power law formulated in Eq. 2 (Table 2). Higher total species richness was in all cases negatively correlated with temporal turnover (Table 2). Higher connectance increased the temporal variability of species with monophagous larvae, xerophilic plant feeders, and generalist species (Table 2). Cells of higher average precipitation exhibited a decreased variability in the proportion of xerophilic plants feeders (Table 2).

Members of different larval feeding groups and habitat requirements showed specific responses to landscape structure and climatic conditions (Fig. 2, Appendix S3). Higher connectance was positively correlated ($P(\chi^2) < 0.05$) with the proportion of species with monophagous larvae (Fig. 2a), but elevation, slope and landscape diversity did not significantly influence this group (Fig. 2a, Figs. B1, 3, 4). Mean elevation was positively correlated with the proportion of species linked to oligotrophic habitats and with mean precipitation (Fig. 2b, B4). High

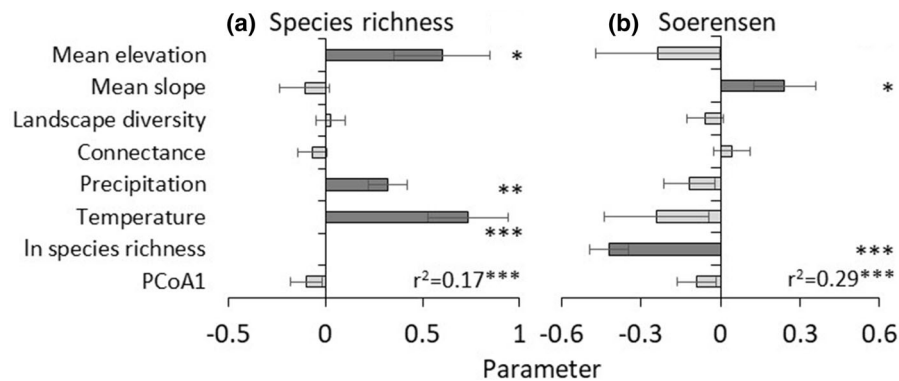


Fig. 1 Generalised linear modelling (identity link function, normal error structure) with mean elevation, mean slope, landscape diversity, and connectance as landscape metric predictors, and average annual precipitation and temperature as metric climate predictors for **a** the butterfly species richness and **b** temporal β -diversity (Soerensen dissimilarity) within

each grid cell. In **b** the ln-transformed species richness and the dominant eigenvector of a Euclidean principle coordinates analysis (PCoA1) entered the model as additional predictors. $N = 159$. AICc selected predictors are shown in dark grey. Given are parametric r^2 values of the whole model and significances: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 1 Factorial two-way ANOVA did not point significant differences between butterfly species richness and traits and habitat proportional aspect and study time period (1980–1989, 1990–1999, 2000–2009, 2010–2019)

Variable	df	Species richness	Oligotrophs	Forest species	Xerophilic plant feeders	Sedentary	Generalists	Endangered
Aspect	3	1.86	4.44*	2.26	2.53	2.73	2.55	1.58
Time period	3	0.95	0.62	2.30	0.30	1.03	1.61	0.77
Aspect \times Time period	9	1.49	0.85	1.02	0.79	1.64	0.67	1.08

Parametric significances * $P < 0.05$

landscape connectance was positively correlated with higher proportions of sedentary species ($P(\chi^2) < 0.05$; Fig. 2c). The proportion of forest species declined along the elevational gradient (Fig. 2d; $P(\chi^2) < 0.05$), while xerophilic plant feeders increased with higher average slope (Fig. 2e; $P(\chi^2) < 0.05$). Connectance and landscape diversity as well as temperature and precipitation were only of minor importance for these two butterfly groups (Fig. 2d, e). In the bivariate comparison, the proportions of generalist butterfly species significantly decreased with elevation (Fig. B4), although the proportions of this group were not significantly correlated in the GLM to any of the landscape and climate predictor variables (Fig. 2f). AICc included connectance and precipitation in the most informative model (Fig. 2f).

The proportions of sedentary and oligotrophic habitat species, as well as of xerophilic plant feeders increased with grid cell richness (Fig. 2), while the

proportion of habitat generalists decreased (Fig. 2). The spatial distance between the grid cells as quantified by the dominant eigenvector of a principal coordinates analysis did not significantly influence any of the single GLMs.

An important finding in this respect is the high observed intercellular variability in the correlations of the different butterfly groups with the environmental and climatic predictors (Fig. 2). This high intercellular variability regards particularly elevation and slope, and the climate variables (Fig. 2). A canonical correspondence analysis (Fig. 3) separated the butterfly species according to the longitude–latitude axis and mainly covered the decrease in richness in the southern Alpine region (Fig. 3a). Furthermore, butterflies were mainly separated along the temperature axis (Fig. 3b), and, with respect to landscape structure, according to average slope (Fig. 3c), while

Table 2 Generalised linear modelling (identity link function, normal error structure) with mean elevation, mean slope, landscape diversity, and connectance as landscape metric predictors, and average annual precipitation and temperature as

metric climate predictors for the temporal variability (ln-transformed variance/mean ratio) in the proportions of important butterfly groups according to Eq. 2

Variable	Monophages			Oligotrophic habitats			Sedentary species		
	Parameter	Standard error	Wald	Parameter	Standard error	Wald	Parameter	Standard error	Wald
Mean elevation	− 0.0003	0.0004	0.53	< 0.001	< 0.001	0.78	< 0.001	0.001	0.56
Mean slope	− 0.0006	0.0119	< 0.01	− 0.003	0.013	0.05	0.006	0.015	0.17
Landscape diversity	− 0.1448	0.5203	0.08	0.469	0.557	0.71	− 0.347	0.650	0.29
Connectance	0.0083	0.0045	3.44*	0.010	0.005	4.49*	− 0.001	0.006	0.01
Precipitation	− 0.0005	0.0003	2.44	− 0.001	< 0.001	2.45	− 0.001	< 0.001	3.01
Temperature	− 0.0506	0.0651	0.61	− 0.064	0.068	0.87	− 0.007	0.082	0.01
ln species richness	− 0.3417	0.0789	18.77***	− 0.226	0.092	6.09*	− 0.252	0.120	4.42*
ln mean	0.2221	0.1201	3.42*	− 0.230	0.126	3.30	0.396	0.106	13.99***
	Forest species			Xerophilic plants feeders			Habitat generalists		
	Parameter	Standard error	Wald	Parameter	Standard error	Wald	Parameter	Standard error	Wald
Mean elevation	< 0.001	< 0.001	0.29	− 0.001	< 0.001	6.59*	< 0.001	0.001	0.53
Mean slope	− 0.006	0.009	0.40	− 0.022	0.011	3.87	− 0.022	0.017	1.65
Landscape diversity	0.103	0.406	0.06	0.300	0.502	0.36	− 0.499	0.725	0.47
Connectance	0.003	0.003	0.87	0.003	0.004	0.54	0.011	0.006	3.15
Precipitation	< 0.001	< 0.001	2.59	− 0.001	< 0.001	9.38*	< 0.001	< 0.001	1.01
Temperature	− 0.066	0.049	1.81	− 0.191	0.055	12.21**	0.043	0.092	0.22
ln species richness	− 0.227	0.087	6.88**	− 0.225	0.092	5.99*	− 0.156	0.118	1.75
ln mean	0.670	0.056	142.62***	0.503	0.052	92.52***	− 2.376	0.288	67.88***

ln-transformed species richness and the ln-transformed mean of the focal variable served as additional covariates. Given are parameter values and the respective standard errors and Wald parameters. N = 159. Statistical significances: *P < 0.05, **P < 0.01, ***P < 0.001

connectance and landscape diversity were of minor importance.

Species classified as being near threatened were not significantly connected to certain landscape types and elevation ranges (Fig. 4a). Their proportion decreased in grids with higher average temperature ($P(\chi^2) < 0.05$). The proportions of vulnerable and endangered species tended to increase in cells with higher landscape connectivity (Fig. 4a; $P(\chi^2) < 0.05$). Additionally, these species were spatially clustered as indicated by the positive correlation with the dominant eigenvector of spatial cell distance (Fig. 4b; $P(\chi^2) < 0.05$).

Discussion

One of the main findings of our study seems contradictory at first glance, namely that the diversity of butterflies is positively correlated with both temperature and altitude (Fig. 1a), because temperature decreases with altitude, which would make an opposite correlation logical. However, these results are sensible because two different systems are apparently overlapping. Thus, it has been clearly demonstrated for the Alps that the number of species potentially present decreases with altitude (Schweizerischer Bund für Naturschutz 1987), supporting a naturally given

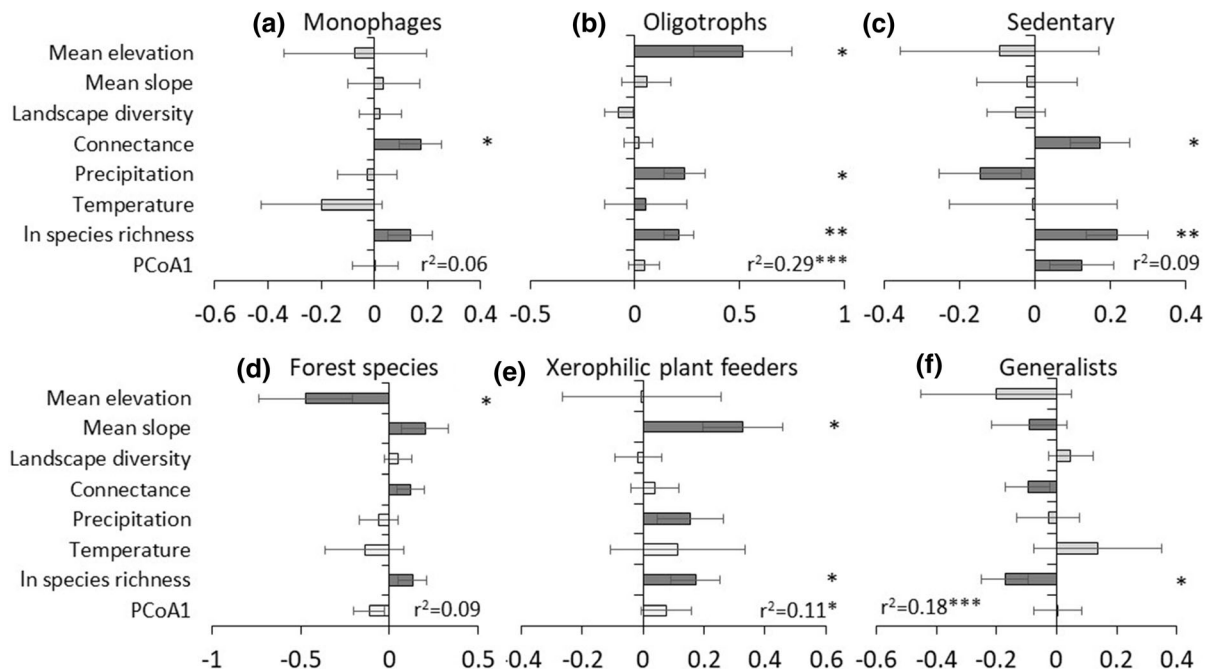


Fig. 2 Generalised linear modelling (identity link function, normal error structure) with mean elevation, mean slope, landscape diversity, and connectance as landscape metric predictors, and average annual precipitation and temperature as metric climate predictors for the butterfly trophic and habitat preferences. The ln-transformed species richness and the

dominant eigenvector of a Euclidean principle coordinates analysis (PCoA1) entered the model as additional predictors. $N = 159$. AICc selected predictors are shown in dark grey. Given are parametric r^2 values of the whole model and significances: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

positive correlation of diversity with temperature (McCain 2007). On the other hand, natural heterogeneity increases and human use intensity decreases with increasing altitude, explaining the positive correlation of diversity with altitude. Thus, our results might show the superimposition of natural factors (here temperature and landscape heterogeneity) by anthropogenic influences (here the intensity of use).

While the increase of butterfly diversity with temperature is intuitively understandable (see Evans et al. 2005), the increase of butterfly diversity with altitude needs to be discussed in more detail. Thus, the increasing landscape heterogeneity with slopes, ridges and valleys is resulting in a higher amount of ecological niches and hence a diverse mosaic of various habitats, consisting of open grassland, wetlands, forests and a high variety of smooth ecotones harbouring high biodiversity. A positive relation between species richness and spatial heterogeneity has been frequently demonstrated on a large array of species and in many regions of the world (e.g. Deutschewitz et al. 2003; Kumar et al. 2006; Stein

et al. 2014; Deák et al. 2021). Additionally, as higher elevations are characterised by more pronounced topographic heterogeneity (including steep slopes and narrow valleys), often accompanied by poor stony soils and harsh climatic conditions, agricultural intensification is becoming increasingly difficult with increasing altitudes (van Vliet et al. 2015). Consequently, the persistence of butterfly species, and in particular of specialists, is favoured by increasing altitude, as testified by the proportional decrease of habitat generalist species towards higher elevations (Fig. B4) because it is mostly the generalists that can survive in the highly intensified agricultural matrix of the lowlands. This finding goes in line with other studies documenting more pronounced trends towards agricultural intensification in lowland regions with soft topographical modulations, fertile soils and suitable climate, which are important preconditions for high agricultural productivity (reviewed in van Vliet et al. 2015).

However, even if significantly more biodiversity is still found at higher altitudes and agricultural

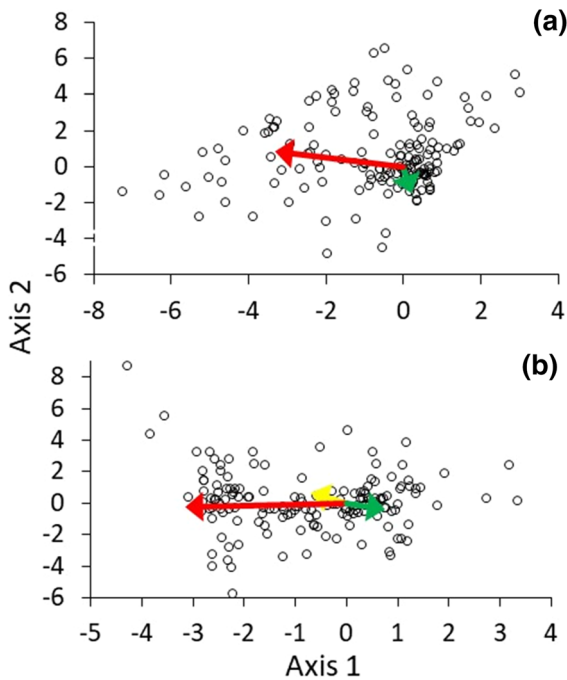


Fig. 3 Biplot of canonical correspondence analysis of **a** climatic and **b** landscape factors. Dots refer to species position. **a** red: annual mean temperature (EV = 0.19, $P < 0.001$), green: annual mean precipitation (EV = 0.001, $P < 0.01$), **b** red: slope (EV = 0.27, $P < 0.001$), green: connectance (EV = 0.04, $P < 0.001$), yellow: landscape diversity (EV < 0.001, $P > 0.05$). For visibility, environmental vector lengths were multiplied by factor 5

intensification is less severe, not everything is better towards higher altitudes because other factors play a decisive and threatening role. One major problem

increasing towards less productive areas is abandonment. Thus, extensively used high-altitude meadows and pastures have frequently turned into fallow land because remote grasslands at steep slopes are of very limited economic interest (Carrer et al. 2020). As a result, these once extensively managed areas with their heterogeneous and often small-scale habitat mosaic, and hence habitat for a large number of species, is gradually replaced by less diverse landscapes (Erhardt 1985). In the meantime, many of these open areas have become covered by shrubs or are already forested in the course of succession; this trend causes a severe loss of biodiversity (Schweizerischer Bund für Naturschutz 1987). However, as the importance of abandonment at high altitudes seems to be less than the one of agricultural intensification in the lowlands, the former seems to be overwritten by the latter so that the negative consequences of abandonment are not detectable in our dataset.

The high relevance of landscape heterogeneity (being more pronounced at higher elevations) for conservation, especially of specialised species, is further supported by our detailed analysis on community assemblies. Thus, higher species richness clearly goes in line with higher proportions of specialist species in the local butterfly communities; vice versa, species poor communities are dominated by generalist species and are mainly found at lower elevations (i.e. in the mostly flat and agriculturally intensified lowlands). Thus, community composition was predominantly driven by the factor slope (Fig. 3b), although the temperature gradient also revealed to be

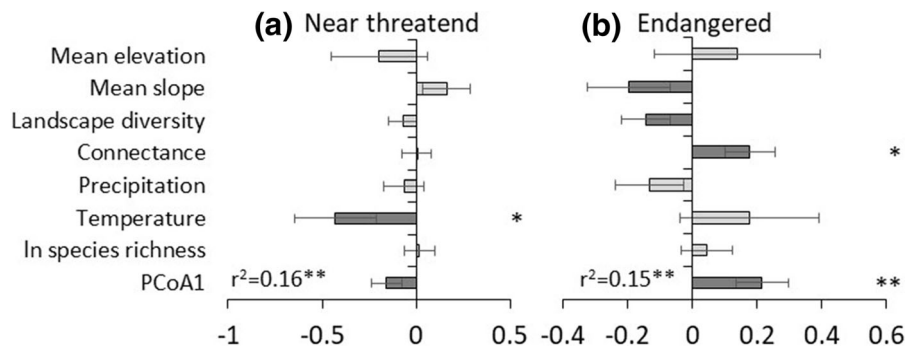


Fig. 4 Generalised linear modelling (identity link function, normal error structure) with mean elevation, mean slope, landscape diversity, and connectance as landscape metric predictors, and average annual precipitation and temperature as metric climate predictors for the butterfly threat status (near threatened, vulnerable/endangered). The ln-transformed species

richness and the dominant eigenvector of a Euclidean principle coordinates analysis (PCoA1) entered the model as additional predictors. $N = 159$. AICc selected predictors are shown in dark grey. Given are parametric r^2 values of the whole model and significances: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

of high importance (Fig. 3a), segregating heat-loving species (e.g. most *Zygaena*) from mountain taxa (e.g. most *Erebia*) (see Appendix 2). In this context, our findings again underline the coherence between topography and the level of agricultural intensification (van Vliet et al. 2015).

Steep slopes are characterised by highly specific and even extreme microhabitats, with broad temperature amplitudes, severe pedological perturbations and disturbances due to erosion. The majority of species occurring in such habitats (like *Parnassius apollo*, *Scolitantides orion*, *Polyommatus dorylas* and *Zygaena transalpina*) are specialists (Stettmer et al. 2007; Bräu et al. 2013a, b; Reinhardt et al. 2020). Furthermore, such steep slopes also provide a large variety of habitat types, with various microhabitats scattered across small spatial scales (Erhardt 1985). These characteristics allow the co-occurrences of many different species occupying rather different ecological niches within a single $5 \times 5 \text{ km}^2$ grid cell (e.g. heat-loving species such as *Colias alfacariensis*, *Lysandra bellargus* and *Melitaea didyma* alongside mountain taxa like several *Erebia* species in close geographic proximity), strongly increasing the local species richness.

In addition to effects from land use change (i.e. intensification, mostly in lower elevations, and progressive abandonment, mostly at higher altitudes), climate change decisively influences the distribution and trends of biodiversity significantly (e.g. Erschbamer et al. 2009; Chhetri et al. 2021). Our results show that temperature positively influences the occurrence of butterfly diversity (Fig. 1a). This is consistent with other studies showing similar trends and an accumulation of species diversity along southern slopes (representing higher mean temperatures) than northern slopes (Hamid et al. 2020). An increase of mean temperature may initially benefit many butterflies (like other arthropods), however might also negatively impact biodiversity on the long run. Numerous studies showed that butterflies migrate to higher altitudes in the course of climate warming, which leads to decreases of habitat size and thus is significantly increasing the probability of extinction (Cerrato et al. 2019; Viterbi et al. 2020). These distribution shifts might also lead to crucial mismatches between interacting species, such as butterflies with their larval food plants, with negative consequences (Schweiger et al. 2008, 2010).

Our data also show that in the Salzburg region specialist species are more frequently encountered at higher elevation (in particular species of oligotrophic habitats, e.g. many representatives of the burnet moths, i.e. genus *Zygaena*; Fig. 2b) and in areas characterized by steep slopes (mainly species whose larvae feed on xerophilic plants such as *Parnassius apollo*, *Scolitantides orion*, *Phengaris arion*; Fig. 2e). However, these correlations are assumed to be produced, at least partly, by human activities due to the negative correlation of land-use intensity on the one hand as well as altitude and relief energy on the other. Therefore, we think that the relation in these cases is not a direct one but an indirect one mediated by differences in human activities. This finding goes in line with other studies on butterflies across altitudinal gradients (Gallou et al. 2017). These coherences support the high conservation value of nutrient poor and extensively used habitats, such as calcareous grassland, oligotrophic bogs, humid meadows, semi-natural forest skirts and alpine meadows, as also highlighted by other studies (cf. Erhardt 1985; Habel et al. 2016, 2019b; Thomas 2016). The strong ecological connection to these habitats is particularly evident for species with limited ecological and behavioural plasticity such as all species of the genera *Phengaris* and *Euphydryas*, but also other species like *Carcharodus floccifera*, *Lycaena helle*, *Hamearis lucina* and *Boloria aquilonaris* (Erhardt 1985; Ebert and Rennwald 1991; Stettmer et al. 2007; Bräu et al. 2013a, b).

Our trait-based analysis also shows that a high level of habitat connectivity (connectance) supports the occurrence of monophagous species (such as *Spialia sertorius*, *Parnassius mnemosyne*, *Cupido minimus*, *Hamearis lucina*, *Melitaea diamina*; Fig. 2a, Appendix S2) as well as sedentary species (e.g. all burnet moth species, the majority of blues; Fig. 2c, Appendix S2). Previous studies also revealed a significant correlation between these two traits, i.e. that increasing specialisation (with respect to larval food plants) goes in line with decreasing dispersal behaviour (Bink 1992; Thomas 2016). Consequently, reduced habitat connectivity (in the wake of habitat destruction and reduced landscape permeability) is particularly negatively impacting specialist species because they are often monophagous and sedentary (Thomas 2016).

These findings are further supported by our results for the vulnerable and endangered species showing a

clear correlation with landscape connectivity (Fig. 4b). As this group of species also has a positive trend with temperature and a negative correlation with slope, these species mostly resemble thermophilic specialists of the lowlands (such as *Carcharodus floccifera*, *Euphydryas maturna*, *Melitaea phoebae*, *Lopinga achine*, *Zygaena ephialtes*), heavily affected by agricultural intensification and hence habitat destruction but without an escape opportunity to higher altitudes (PG pers. observ.). This lack of higher altitude escapes distinguishes these species considerably from many of the group of near threatened species, which also vanished in the intensively used lowlands but still have strong populations in higher altitudes with lower human pressure (such as *Lycaena hippothoe*, *L. virgaureae*, *Lysandra coridon*, *Plebejus argus*, *Erebia medusa*) (PG pers. observ.). This is mirrored in their negative correlation with temperature, but not with connectance (Fig. 4a). These species were formerly common on meadows and grasslands throughout our study region, showing a rather intermediate degree of ecological specialisation (as e.g. many of the more common burnet moths), but meanwhile have lost most of their lowland populations (cf. Habel and Schmitt 2018), similar to the endangered species, but with the difference of higher altitude rescue populations.

More in general, the present study underlines that higher habitat connectance supports the conservation of endangered butterfly species, especially as ecological specialisation and restricted dispersal are coherent with the level of endangerment. This goes in line with the general assumption that landscape permeability (Suter et al. 2007; Thomas 2016) is crucial for nature conservation. Consequently, the (re)connection of habitats via stepping stones (Filz et al. 2013a; Thomas 2016; Habel and Schmitt 2018) and corridors (Hudgens and Haddad 2003; Haddad and Tewksbury 2005; Habel et al. 2020) are central measures in the practical nature conservation toolbox. Habitat connectance is particularly important for endangered species because most of these (such as many *Melitaea* and *Euphydryas* species as well as many of the blues) occur in metapopulation structures (Cizek and Konvicka 2005; Fric et al. 2010; Zimmermann et al. 2011a, b), and thus require vital and balanced population turn-overs, consisting of local extinctions and (re)colonisations through (back)migrations (Hanski 1999a, b).

We would like to conclude by addressing some of the weaknesses of this work. First, the faunistic data used were not recorded in a standardized way and show numerous data gaps over the years—typical characteristics of historical and merged datasets used for such analyses (see Habel et al. 2019b). Second, data on fauna, land use and climate have been assigned to $5 \times 5 \text{ km}^2$ grid cells, which may result in missing the relevance of microhabitats that are highly relevant to insects (see Filz et al. 2013b). Third, our study relates to factors such as climate, topography and landscape heterogeneity. However, there are other very important factors that may affect biodiversity, such as nitrogen influx (Wallisdevries et al. 2012; Filz et al. 2013a; Brunbjerg et al. 2017) as well as pesticides (Heneberg et al. 2018; Main et al. 2020). We have to acknowledge that these are key factors reducing habitat quality, which have to be interpreted to be as relevant as habitat configuration, but which were not considered in our study explicitly.

Conclusion

Our work provides circumstantial evidence that landscape heterogeneity and topography are critical for high species diversity. Southern slopes with steep gradients take a central role. This might be due to the fact that these areas are exposed to less agricultural intensification, and/or that species-rich ecosystems such as calcareous grasslands are mostly found on such areas. Species with a low dispersal behaviour as well as species with specific habitat and resource requirements respond more susceptible on environmental conditions if compared to mobile generalists. Our study underlines the relevance of south-facing slopes and that habitats at lower elevations are not at all conserved sufficiently making specialist species with no up-hill escape option the most seriously affected taxa.

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