Butterfly loss in urban landscapes and nature reserves

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ABSTRACT

Context: Urbanization and landscape homogenization are main drivers causing biodiversity loss across the globe. The transformation of natural and semi-natural habitats into agro-environments and settlement areas causes the reduction of species diversity, and thus faunal homogenization.

Objective: In this study, we analyse changes in land-cover and habitat configuration and test for changes in species richness and community composition of butterflies in an urban area and a nature reserve.

Method: We analysed historical and recent aerial and satellite pictures, and studied the butterfly fauna for two areas in northern Austria, the urban area around Salzburg city and the nature reserve Bluntautal in close geographic proximity. For these analyses we consider the period 1946–2018.

Results: The proportion of settlement area and forest increased in average by about 5%. Size of field copses increased and small-scale connectivity and thus landscape complexity decreased in both areas. In the same time span, we found a decrease in butterfly species richness for both areas, and in the nature reserve Bluntautal particularly for the past two decades by 50%. The species community composition changed significantly, with severe losses of specialist and xerothermophilic species which rely on open and extensively used ecosystems.

Conclusions: The findings underpin that the reduction of landscape complexity and the intensification of land-use including urbanization drives the loss of diversity of butterflies and changes in species composition, today dominated by some few generalist species. This trend is particularly observable for the nature reserve Bluntautal, where a large proportion of species diversity has disappeared in recent years despite nature conservation. This case underlines habitat management in nature reserves is needed to hold a high level of habitat quality and to preserve the entire species diversity.

1. Introduction

In the last years, numerous studies based on long-term population data have demonstrated a decline in insect species diversity (Turvey & Crees, 2019, Didham et al., 2020, Wagner, 2020) and insect abundances and biomass (Hallmann et al., 2017, Seibold et al., 2019). Some other studies also indicate a persistence of species richness and abundance over time (Yazdanian et al., 2023). The decline of insect diversity mostly cause significant changes in species composition, towards losses of specialist species, and a subsequent increase in the proportion of generalist species (Habel et al., 2019,2022, Ogan et al., 2022). Studies showed that organisms relying on extensive land management and nitrogen-limited ecosystems particularly decreased during the past years

(Sánchez-Bayo & Wyckhuys, 2019). These trends seem to be occurring at the local habitat scale (Uroy, Ernoult, & Mony, 2019) as well at the landscape level (Seibold et al., 2019). For example, nature reserves are frequently restricted in size and are geographically isolated and boarder intensively used agro-environments and settlement areas, with negative effects on species diversity living therein (Uroy et al., 2019).

One of the main drivers causing the loss of species diversity, floral and faunal homogenization is urbanization (the transformation of habitats into settlement areas) and agricultural intensification, which includes the application of artificial fertilisers and pesticides (Payne et al., 2017, Raven & Wagner, 2021, Maes, Van Calster, Herremans, & Van Dyck, 2022). Apart from the reduction of habitat quality, habitat configuration is considerably changing. Heterogeneous landscapes

consisting of a mosaic of various partly connected habitats are transformed into homogeneous landscape structures consisting of larger field copses with linear boarders (Gámez-Virués et al., 2015). These trends eliminates numerous small habitats and transition ecosystems, which are stepping stones and corridors for many species (Dennis, Dapporto, Dover, & Shreeve, 2013). In consequence, the availability of habitats and the permeability of the landscape is getting reduced, with negative effects on species diversity (Hodgson, Randle, Shortall, & Oliver, 2022, Rigal et al., 2023). Species respond differently to the destruction of habitats, the reduction of habitat quality, and the progressive fragmentation of the remaining habitats (Gámez-Virués et al., 2015). Species with specific ecological demands and sedentary behaviour suffer particularly under the reduction of habitat quality and habitat fragmentation than mobile generalist species do (Ekroos, Heliölä, & Kuussaari, 2010, Thomas, 2016, Owens, 2020, Merckx et al., 2023).

The current decline of species seems to be not exclusively restricted to intensively used environments such as settlement areas and agro-environments, but may also occur in nature reserves (Habel et al., 2016, Homburg et al., 2019). For example, long-term observations of butterflies underline drastic declines in species diversity and a shift in species community composition in a nature reserve in southern Germany (Habel et al., 2016). This loss of species diversity, even within protected areas, might be due to multiple factors: Most nature reserves are limited in size and geographically isolated and thus local populations may suffer under high population stochastic effects, which frequently cause local extinctions (Melbourne & Hastings, 2008). A recolonization

of these habitats is rather unlikely due to the high degree of habitat isolation and the strong barrier effect landscape matrix (De Ro et al., 2021).

In this study, we analyse changes in land-cover and landscape configuration, butterfly diversity and species community structures for the time period from 1946 to 2018 and in two study areas in northern Austria. Data were collected in a nature reserve and in anthropogenic landscapes around Salzburg city. Land use and land cover analyses are based on aerial photography and satellite imageries. We compiled species-specific trait data on the ecology and behaviour of the butterfly species found. Based on these data we answer the following questions:

1. Do butterfly diversity and landscape structure change over time in the anthropogenic landscape and nature reserve?
2. Are changes of land-use and land-cover, species diversity and community composition identical for both study areas?
3. Which species, with which ecological features and behaviour respond particularly strongly to changes in the landscape?
4. What can we derive from these trends and coherences for practical nature conservation management?

2. Material and methods

2.1. Study regions

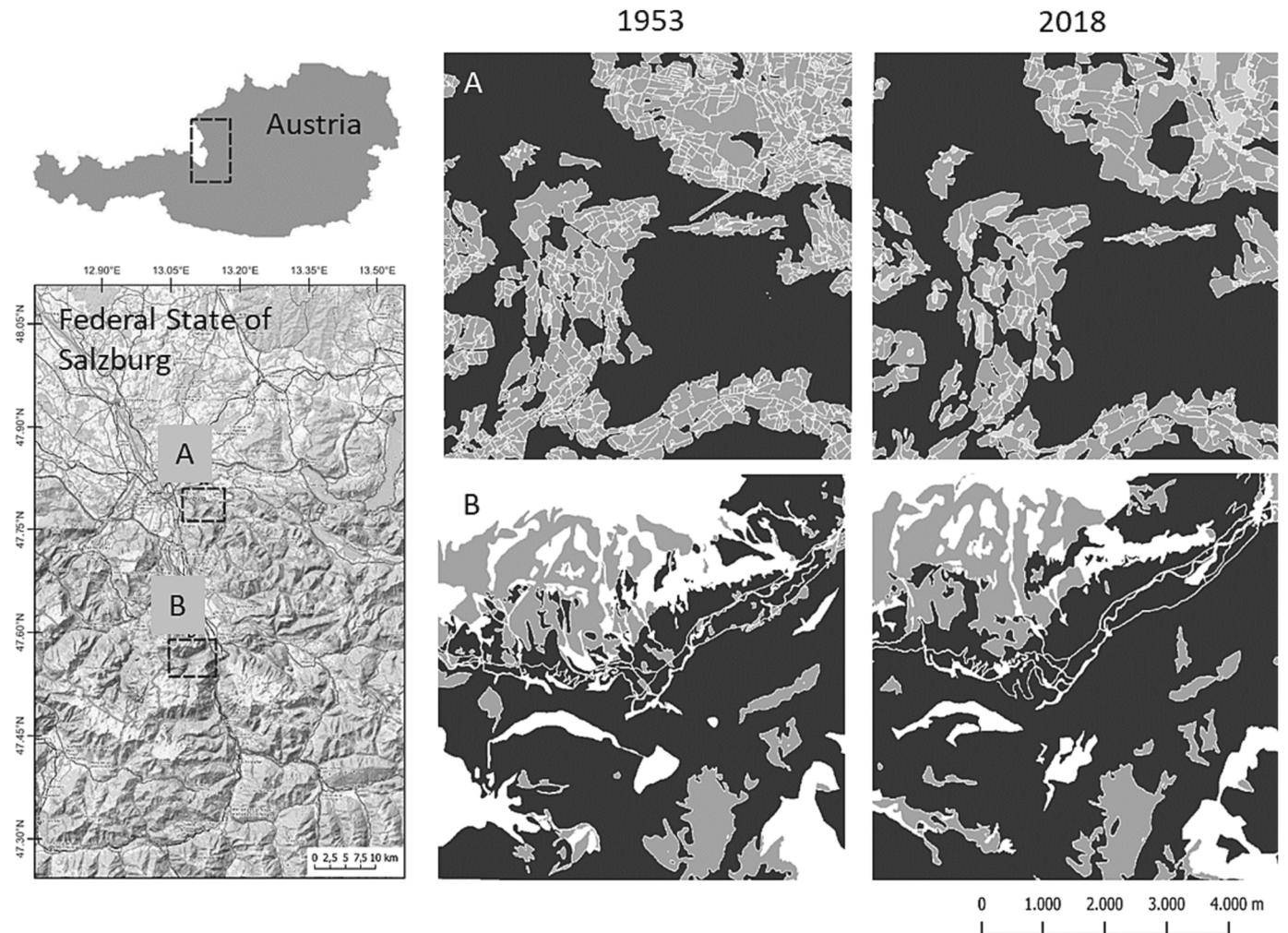The study areas represent two different areas located in the Federal

Fig. 1. Study areas in the Fedral State of Salzburg (small inlet maps on the left), (A) Salzburg area and (B) the Bluntautal nature reserve. Black, grey and light-grey represent the land-use categories forest, grassland and settlement respectively, for the years 1953 and 2018.

State of Salzburg in northern Austria. One area is located at the periphery of Salzburg city and covers an area of 26 km^2 and an altitudinal range from 510 to 1287 m a.s.l (including the Gaisberg Mt.). This area is characterised by settlements, grasslands and meadows, forests, small bogs and rocky slopes (Fig. 1). The natural and semi-natural ecosystems suffer under intense settlement activities accompanied by the growing city of Salzburg (Arming, Nowotny, Eichberger, & Althaler, 2008). The second study area covers the nature reserve Bluntautal, situated in a narrow valley of the limestone high Alps of Salzburg. The area covers 39 km^2 and ranges from 479 to about 1500 m a.s.l. (including parts of the Göll Mts. and Hagengebirge, Kuchler Kamm and the ridges of mountain Hinteres Freieck). This study area represents various natural and semi-natural ecosystems and contains stream ecosystems, forests, grassland and meadows as well as rocks and gravel heaps. Due to the predominantly former occurrence of various EU-protected butterfly species (*Parnassius apollo, P. mnemosyne, Euphydryas maturna, E. aurinia, Lopinga achine, Phengaris* species), this area was designated as an EU nature reserve 25 years ago (Amt der Salzburger Landesregierung, 2013). In the meanwhile, the area is a very popular recreation site for people from the city of Salzburg. Former extensively used grasslands and meadows are today used as intense pastures and some of the original riparian forests have been replaced by pine tree monocultures (PG, pers. comm.).

2.2. Aerial imagery and digitalization

We digitized land-cover data for the two study regions for the years 1953 and 2018, by considering three well distinguishable land-cover categories, settlement, forest, open landscape. Forest comprised all forested and forest-like structures. Settlement areas covered all sites with significant anthropogenic influences and structures, such as at least three small buildings in direct vicinity as well as roads and paths. The remaining landscape matrix was categorized as open landscape, incorporating grasslands, meadows and arable land. Aerial pictures of the year 1953 are in black-white with a resolution of 0.25 m (provided by SAGIS - Amt der Salzburger Landesregierung Referat 7/06 – Geodateninfrastruktur). Digitization was done by visual inspection and delineation using QGIS (vers. 3.10). Land-cover data of the year 2018 are taken from Corine Land Cover 2018 (vers. 2020_20u1 - Eea, 2022). Here we considered identical land-cover categories.

2.3. Butterfly data

Butterflies have been observed intensively in the two study areas over the past decades and occurrence data has been compiled. In total, the data contain 250,108 single records of 2,275 lepidopteran species, collected in the time frame of 1900–2022 across a large altitudinal gradient (380–3105 m asl). These data are provided by Ulrich, Habel, Schmitt, and Gross (2023). All these data are managed in a database at the Haus der Natur museum in Salzburg. Each observation point contains an exact location (GPS coordinate) and the date of the observation. For the present study, we used 9,209 single records from 127 butterfly species collected in the two study areas (all raw data are compiled in Appendix A, Tables A1, A2). Since the data were not collected systematically, this dataset is limited to presence-only data. From this material we extracted data of the two selected study areas. Hereby we also considered a 1 km buffer around each study areas, as occurrences of species might not be restricted to single habitats, but also radiate into the surrounding area (Stevens, Turlure, & Baguette, 2010). The compiled data cover the time period from 1946 to 2018 (in accordance with the time period for which the land use change analysis was conducted).

2.4. Traits

Each species responds differently to environmental changes, according to its ecology and behaviour (Birkhofer et al., 2017). For each species, we compiled information on the use of habitat type, nutrient requirements, feeding preferences, dispersal behaviour. These traits have been shown to be most sensitive to changes in landscape structure and habitat quality (Habel et al., 2016, Seibold et al., 2019). We considered the following traits: Oligotrophic vs. eutrophic habitats (based on the Ellenberg indicator values for the respective larval food plants needed for development, Ellenberg, Weber, Dull, Wirth, Werner, & Paulisen, 1992), woodland vs. grassland species, dispersive vs. sedentary species, and habitat generalist vs. specialist species (based on feeding preference, habitat demands, dispersal). Trait assignments are based on literature sources (Weidemann, 1988, Bink, 1992, Stettmer, Bräu, Gros, & Wanninger, 2022). Cumulative records, details on classifications and respective species specific data are compiled in Appendix A.

2.5. Statistics

2.5.1. Changes in land-cover

Analysis of land-cover change was performed using the R package "raster" and "crosstabs" function to compare areal shifts between 1953 and 2018 in corresponding categories. Based on the assessed land-cover categories an analysis of landscape composition and configuration was done using Fragstat version 4.2. For the landscape analysis the data were rasterized as 16bit integer using 5 m geometric resolution. To consider individual patch boundaries, geometries were corrected with a 2.5 m inner buffer and assigned as background values within Fragstat software. Besides the quantification of mean area in ha for each category, the following landscape metrices were used. Number of Patches (NP) and Patch Density (PD) are simple measures of subdivision by counting the geometries of the corresponding land-cover category (NP) and divided by the area (PD). Percentage of Landscape (PLAND) quantifies the proportional abundance of each land-cover category in the landscape as a relative measure to compare landscapes of different sizes. The metric Euclidean Nearest-Neighbour Distance (ENN) equals the metric distance to the nearest neighbouring geometry of the same category, based on shortest edge-to-edge distance to quantify isolation. The landscape metrices were then used to check for significant differences between the two time stamps. Thus, the metrices AREA and ENN were used to perform the Dunn test for pairwise multiple comparisons of the ranked data using Bonferroni adjustment with R package "rstatix" to find differences between the two time stamps.

2.5.2. Changes in butterfly diversity

We grouped the butterfly records into seven complete decades starting from 1946 (Table 1). This leaves the data from 2016 to 2018 as an incomplete decade. However, due to the larger number of records for the Salzburg area and the fact that the data for both study regions nicely fit into the overall pattern, we included this incomplete decade in the analysis. Table 1 provides the numbers of records and the species richness for both regions and the above-mentioned butterfly guilds.

Separately for both study regions we calculated rarefaction curves (using EstimateS 9.1) to obtain estimates of species richness for different sample sizes. We then compared observed richness values for each decade with the respective rarefied predictions. We also used the first order jackknife method to estimate total species richness for each decade, $S_E = S_O + \frac{S_1(n-1)}{n}$, where S_E and S_O are the expected and observed species richness, respectively, S_1 is the number of singleton species in the sample, and n denotes the sample size. As this and other estimators are known to become increasingly negatively biased at decreasing sample sizes and need unbiased sampling (Chao & Chiu, 2016, Ulrich, Kusumoto, Fattorini, & Kubota, 2020) we treat these estimates as lower boundaries of the true number of species and use them as an additional source of information, only.

We also calculated the relative numbers of species in each guild and compared these proportions between study regions and decades. We

Table 1

Basic data of numbers of records (N) and observed (S_{obs}) and estimated (S_{est}) species richness per decade for butterflies of the Bluntautal and Gaisberg study regions.

Region	Guild	Variable	1946–1955	1956–1965	1966–1975	1976–1985	1986–1995	1996–2005	2006–2015	2016–2018
Bluntautal	Total	S_{obs}	55	89	69	39	60	63	42	24
		S_{est}	81	104	86	50	80	83	44	41
		N	190	635	369	153	227	219	461	43
	Specialists	S	30	43	34	13	21	26	14	8
		N	118	313	211	54	65	79	135	9
	Monophages	S	14	23	18	10	14	16	13	7
		N	60	195	135	47	49	52	143	8
	Polyphages	S	8	23	18	10	14	16	13	7
		N	24	195	135	47	49	52	143	8
	Sedentary	S	11	20	15	3	10	13	6	6
		N	43	157	69	5	19	35	37	6
	Mobile	S	18	32	24	17	22	22	18	10
		N	55	196	123	82	115	89	263	26
	Xerothermophilic	S	14	16	13	6	7	9	7	3
		N	69	141	83	44	36	46	51	5
Gaisberg	Total	S_{obs}	60	97	91	70	77	89	63	56
		S_{est}	84	108	109	84	80	97	72	63
		N	143	916	571	470	878	2345	1013	576
	Specialists	S	27	49	44	31	33	42	21	18
		N	70	476	318	230	320	554	125	88
	Monophages	S	20	26	27	21	22	27	16	14
		N	49	246	155	157	212	584	271	141
	Polyphages	S	5	12	11	5	8	10	7	7
		N	13	78	47	39	91	232	105	62
	Sedentary	S	7	20	22	18	16	22	15	11
		N	23	225	218	158	248	400	130	67
	Mobile	S	27	36	35	26	29	31	26	26
		N	51	264	137	146	314	1064	576	346
	Xerothermophilic	S	15	21	17	13	12	15	6	5
		N	37	226	79	134	104	207	15	18

inferred respective temporal trends of these proportions using ordinary linear regression with parametric error estimates in association with F-tests. Temporal trends in community composition were assessed from non-metric multidimensional scaling (nmds) with Jaccard similarities. nmds was applied separately to the species × decade matrices for Bluntautal nature reserve and Salzburg area. To visualise these trends we used unconstrained correspondence analysis (seriation). This technique sorts the rows and columns of the species × decade matrices in order to maximise the number of occurrences along the matrix diagonal. The degree of compositional change (species turnover) was quantified with multivariate analysis of variance (MANOVA) as implemented in SPSS 29.

The Sørensen coefficient (β_{Soe}) is another measure of species turnover. Applied to the species × decade matrices it can be additively partitioned into a component containing the contribution of species turnover in time (β_{Sim}) and a component containing the ordered loss of species (the nestedness component β_{Nest}; Baselga, 2010). As such partitions cannot be compared directly (Ulrich et al., 2017) we compared the two partitions with a random expectation that accounted for the fact that sample sizes differed between decades. Therefore, we calculated the three partitions from the species × decades matrices of Bluntautal nature reserve and Salzburg area and from 1000 respective matrices where species occurrences were equiprobably resampled with fixed annual numbers of species and equiprobable species occurrences across decades (the equiprobable row – fixed column null model of Gotelli, 2000). We used effect sizes (ES = empirical value – expected value) and confidence limits of the null distribution to assess statistical significance.

3. Results

3.1. Changes in land-cover

Our results show significant land-cover changes for both areas, with an increase of the proportion of forest for the Salzburg area and Bluntautal nature reserve (by 12 %), and an increasing urbanization for the Salzburg area (by 552 %). The landscape configuration changed considerably, with increasing mean size of single arable fields in both regions, Salzburg and Bluntautal nature reserve. In consequence, the number of single patches (polygons) decreased by 60.9 % and 8.3 %, respectively.

In parallel, the complexity (patch density) of the landscape decreased over the past five decades in both study areas. Forest coverage occurred in 177 patches in 1953 and 60 patches in 2018 (66.1 % less) in the Salzburg area. In the Bluntautal nature reserve, forest occurred in 121 patches in 1953 and 95 forest patches in 2018 (21.5 % less). Whereas the mean forest area increased by 43.2 % and patch density dropped from 4.6 to 3.3 in the same time, the proportion of landscape (PLAND) changed only marginally from 70.36 % to 73.13 % in 2018 in the Bluntautal. For the Gaisberg region, the decrease in patches is 66.1 %, while PD changed from 7.1 to 2.4 between 1953 and 2018. Consequently, PLAND changed for the Salzburg area by + 6.72. Concerning the landscape composition, the mean ENN for the Bluntautal nature reserve in 1953 was 51.7 m for grasslands, 21.8 m for forests and 4070 m for settlements. For the latter ones, only 2 patches were found in this year. In 2018 the same categories retrieved 67.2 m, 21.9 m and 52.1 m (Table 2). For the Bluntautal nature reserve only settlement distances changed significantly between 1953 and 2018. In the Salzburg area significant changes occurred in the mean areas and the ENN of grassland and settlement (Table 3).

3.2. Changes in butterfly diversity

In the Bluntautal nature reserve 96 (1946–1955) and 48 (2005–2018) butterfly species where recorded, 50 species were lost between these two time windows, while 2 new species were identified (Appendix B, Fig. B1). At Salzburg area 100 species were recorded during 1946–1955 and 66 species during 2005–2018 Fig. B2). Therefore, 40 species that occurred before have not been recorded since 2005, while 6 new species have been found (Fig. B2). These trends were corroborated by the jackknife richness estimates (Table 1). At Bluntautal nature reserve well above 80 species were expected until the beginning of the 21th century (Table 1). Since then this expectation dropped to less

Table 2
Changes in landscape configuration between 1953 and 2018 for the two study areas. Given are number of plots (NP), patch density (PD), proportion of landscape (PLAND), Mean area (in ha) and Mean Euclidean Nearest-Neighbor Distance (ENN) in m.

Study area	Year	Land-use	NP	PD	PLAND	Mean area in ha	Mean ENN in m
Bluntautal	1953	Forest	121	4.61	70.36	15.27	21.78
		Grassland	170	6.48	23.07	3.56	51.7
		Settlement	2	0.08	0.0002	0.0025	4070.03
	2018	Forest	95	3.35	73.13	21.85	21.94
		Grassland	113	3.98	20.48	5.15	115.18
		Settlement	49	1.73	0.09	0.06	52.13
Gaisberg	1953	Forest	177	7.08	53.42	7.54	28.59
		Grassland	1071	42.85	33.85	0.79	11.82
		Settlement	129	5.16	0.5	0.1	133.86
	2018	Forest	60	2.4	60.14	25.02	35.17
		Grassland	404	16.17	28.5	1.76	14.81
		Settlement	167	6.69	2.74	0.41	75.54

Table 3
Pairwise multiple comparisons of the ranked data using Dunn test between the two study years 1953 and 2018. Shown are mean area (AREA) and Euclidean Nearest-Neighbour-Distance (ENN), with respective p-values.

Metrics	Land-use	Estimate	Statistics	Adjusted p-value	Significance at alpha level 0.05
Bluntautal					
AREA	Forest	23.091	0.912	1	ns
	Grassland	147.664	2.141	0.484	ns
	Settlement	75.316	0.957	1	ns
ENN	Forest	−7.492	−0.306	1	ns
	Grassland	21.626	0.436	1	ns
	Settlement	−301.796	−3.831	0.002	**
Gaisberg					
AREA	Forest	53.576	1.942	0.783	ns
	Grassland	253.777	7.65	3.02E-13	****
	Settlement	61.993	4.848	0.00002	****
ENN	Forest	51.495	1.932	0.799	ns
	Grassland	51.647	2.165	0.456	ns
	Settlement	−46.268	−3.615	0.005	**

than 50 (Table 1). A similar although less severe situation occurred at Salzburg area, where more than 100 species were predicted to be potentially present each decade, while this richness dropped to less than 80 during the last two decades.

Both study areas differed in species richness and temporal trends in community structure. In Salzburg area species richness was consistently higher than at the Bluntautal nature reserve (Table 1). However, the rarefaction curves showed that this difference was partly an effect of the higher sample sizes at Salzburg (Table 1, Fig. 1). On average, the Salzburg area were more depauperated with respect to the rarefaction expectation than the sites in Bluntautal nature reserve (Fig. 1a, b). This pattern was most prominent in the decades since 1980 (Fig. 1c), while before Bluntautal and Salzburg did not significantly differ from another and from the rarefaction expectation (Fig. 1c). Species richness at Salzburg area significantly decreased in time with respect to the rarefaction expectation (Fig. 1c), while the observed respective decrease at Bluntautal was weaker and statistically not significant (Fig. 1c). The changes in diversity were also reflected by changes in community dominance structures (Fig. 1d). We found contrasting temporal changes in evenness between the two study sites (Fig. 1d). Evenness increased at Bluntautal and decreased at Salzburg area. The associated linear regression slopes significantly differ at $P(F) < 0.01$.

The guild specific analysis did not point to significant temporal changes in the proportions of species and records of sedentary species at Bluntautal (Fig. 2a, 4a), while these proportion peaked at intermediate time windows for Salzburg (Fig. 2a, 3a). For both habitat proportions species and record numbers of habitat specialists and of xerothermophilic species significantly decreased in time (Fig. 3b, c, 4b, c). We observed contrasting trends between the two habitats with respect to the proportion of monophagous species and records (Fig. 2a, 3a). At Bluntautal the proportion of monophagous species significantly increased (Fig. 2c).

The analysis of temporal trends in community composition (Fig. 4, B1, B2) revealed an ordered temporal change at Salzburg area, while this change was less ordered at Bluntautal nature reserve (Fig. 4a). At Gaisberg, three pairs of consecutive decades were distinguished (Fig. 5a). MANOVA detected significant composition changes with respect to habitat demands and the degree of specialisation, but not to mobility (Fig. 4b). β-diversity partitioning returned a significantly lower overall ($β_{Soe}$) and partitioned ($β_{Sim}$) temporal species turnover than expected from the null assumption. The observed overall β-diversity (Figs. B1, B2) was mainly driven by an ordered species loss (Fig. 4b).

4. Discussion

Our data on land-cover change and changes in habitat configuration showed a shift towards landscape simplification, consisting of some few large fields and linear and abrupt boundaries between ecosystems. This trend is observable for most parts of Central Europe (Gámez-Virués et al., 2015). Small-scale structures and mosaicking habitats, which made up most of the former Central European anthropogenic agro-environments, are disappearing all across Europe (Amici et al., 2015). Such heterogeneous landscapes are today rather homogeneous and mostly intensively used. This leads to the vanishing of many habitats and transition zones (i.e. ecotones). In consequence, this negatively affects species diversity (Gámez-Virués et al., 2015, Fuller, Williamson, Barnes, & Dolman, 2017). These changes of the landscape structure negatively influence the landscape permeability and thus the abundance and persistence of species and populations. These changes in land-cover and landscape configuration in both study areas are mirrored by significant losses of butterfly diversity and the shift in species community composition. At the beginning of the time period considered here, the two areas hosted similar numbers of butterfly species (96 in the Salzburg area, 100 species in Bluntautal nature reserve). Since then, we observe a dramatic loss of butterfly species richness, with almost 40 % at Salzburg area and 52 % in the Bluntautal nature reserve.

The fact that even more species disappeared in the nature reserve Bluntautal is surprising and needs to be analysed with more caution. The Bluntautal was designated as a nature reserve in the year 1983 as a number of EU-protected butterfly species were found in this valley (*P. nausithous*, *P. teleius*, *E. aurinia*, *E. maturna*, *P. mnemosyne*, *P. apollo* and *L. achine*) (Salzburger Naturschutzgesetz, 1999). However, habitat modifications have taken place even after establishing this nature reserve and deterioration of habitat quality took place in this region (especially during the past 1–2 decades) (Habel, Angerer, Gros, Teucher, & Eberle, 2022). Parts of the once sparse riparian forest have been converted into dense and dark spruce and pine forest, which caused the extinction of light-loving deciduous butterflies (e.g. *E. maturna*). In parallel, most of the bogs and wet meadows were destroyed and
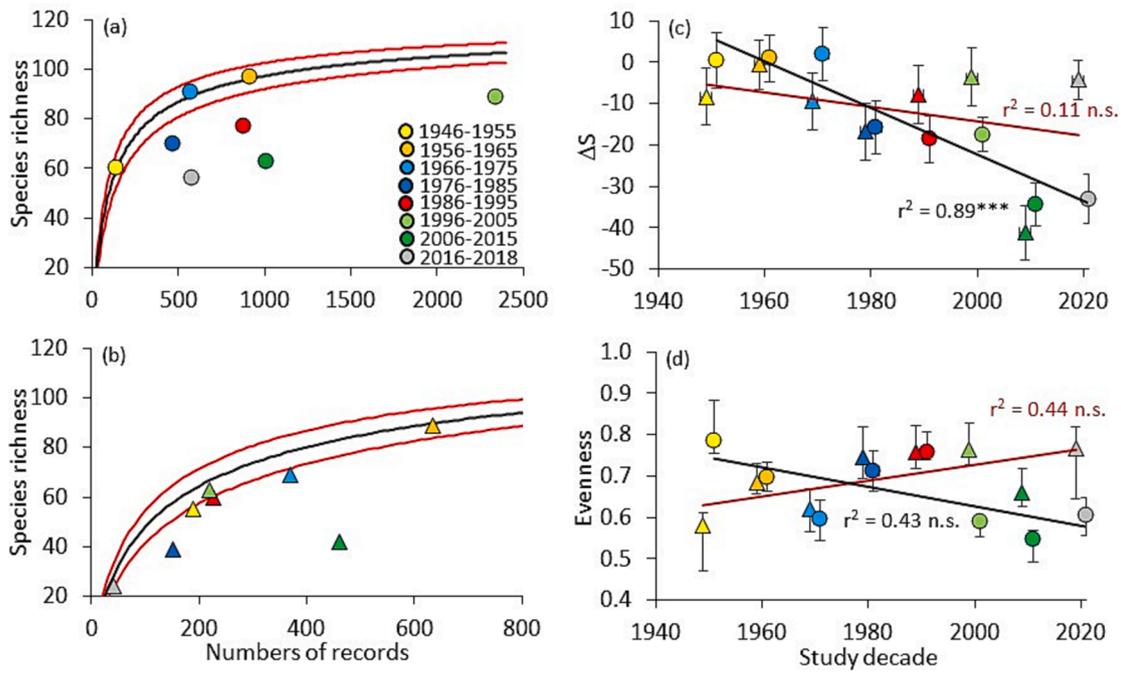
Fig. 2. A) and b) comparisons of observed and rarefied species numbers for the Gaisberg (a, dots) and the Bluntautal (b, triangles) regions in dependences on the number of records for eight study decades. Rarefaction curves (red lines denote two standard errors) were calculated separately for the two study regions. c) Differences ΔS between observed and rarefied species numbers of each sampling decade. Linear regression slopes (Bluntautal: slope = -0.56 ± 0.08; Gaisberg: slope = -0.08 ± 0.20). The black linear regression line for Gaisberg is parametrically significant at ***: $P < 0.001$. d) Evenness values for both study areas in each sampling decade. Linear regression slopes (Bluntautal: slope = +0.002 ± 0.001; Gaisberg: slope = -0.002 ± 0.001). Error bars in c) and d) refer to 95 % bootstrapped confidence limits. Shapes and colours in b), c), and d) as in a). For better visibility, the data points in c) and d) were shifted one year back (Bluntautal) and ahead (Gaisberg).
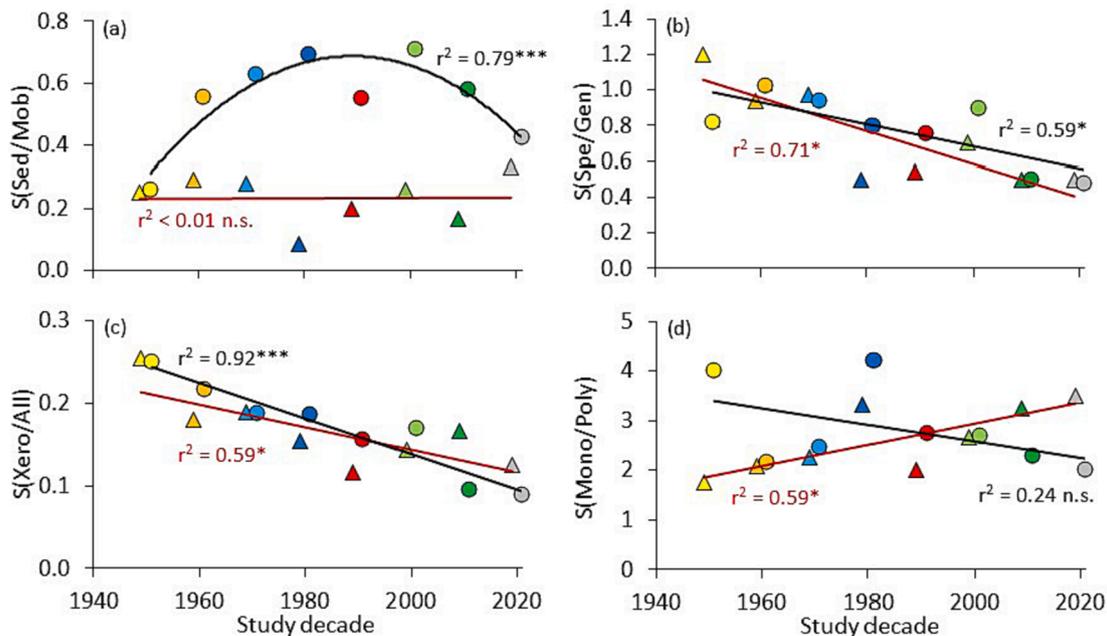

Fig. 3. Temporal trends for the quotients of recorded species numbers of sedentary to mobile species (a: S(Sed/Mob)), of specialist to generalist species (b: S(Spe/Gen)), of monophagous to polyphagous species (c: S(Mono/Poly)), and of the proportion of xerothermophilic species (d: S(Xero/All)). Black linear regression lines refer to Gaisberg, the brown lines to Bluntautal. Regressions are parametrically significant at *: $P < 0.05$ and ***: $P < 0.001$. Shapes and colours as in Fig. 1. For better visibility the data points were shifted one year back (Bluntautal) and ahead (Gaisberg).

converted into lakes and fishponds. In consequence, butterflies relying on such sensitive ecosystems vanished during the early past (e.g. *E. aurinia, P. teleius, P. nausithous*). Most of the open and stony slopes are still present and thus species such as the Near Threatened *P. apollo* still

occurs along the foothills of the Göll Mts. and Hagengebirge. Stocking intensity of cows caused an increase of grazing pressure especially in the lower foothills of the mountain slopes, as also observed in other regions (Homburger, Lüscher, Scherer-Lorenzen, & Schneider, 2015). The
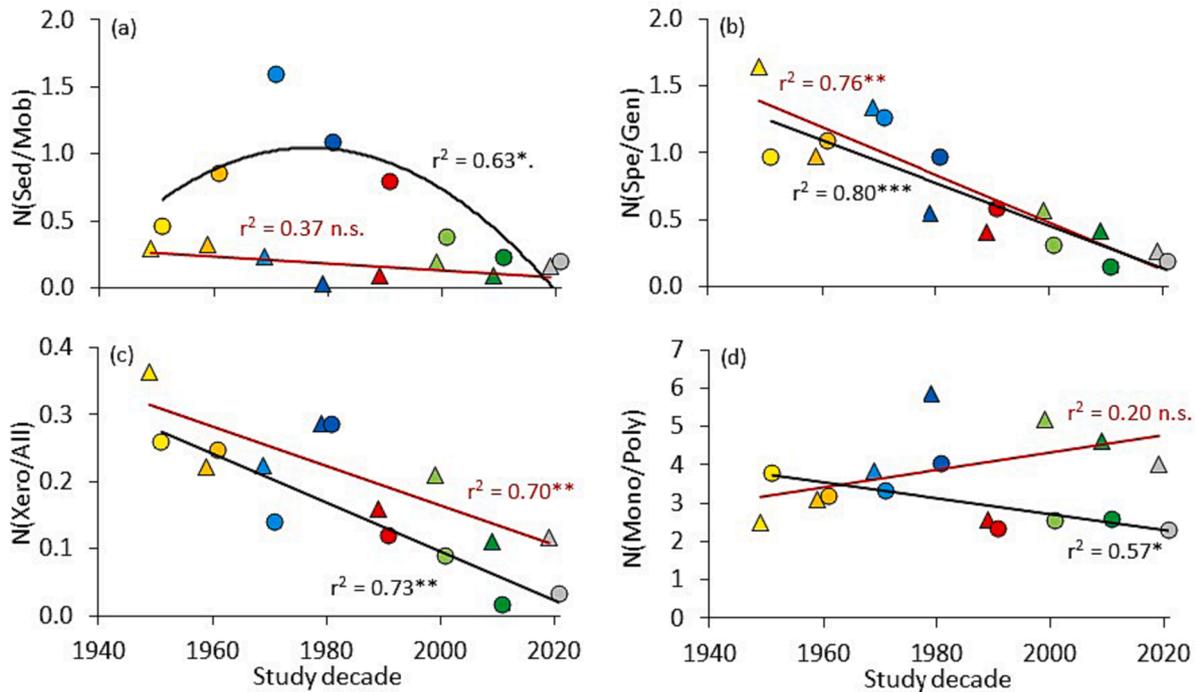
Fig. 4. Temporal trends for the quotients of the numbers of records of sedentary to mobile species (a: N(Sed/Mob)), of specialist to generalist species (b: N(Sed/ Gen)), of monophagous to polyphagous species (c: N(Mono/Poly)), and of the proportion of xerothermophilic species (d: N(Xero/All)). Black linear and quadratic regression lines refer to Gaisberg, the brown linear regression lines to Bluntautal. Regressions are parametrically significant at *: $P < 0.05$, **: $P < 0.01$, and ***: $P < 0.001$. Shapes and colours as in Fig. 1. For better visibility the data points were shifted one year back (Bluntautal) and ahead (Gaisberg).
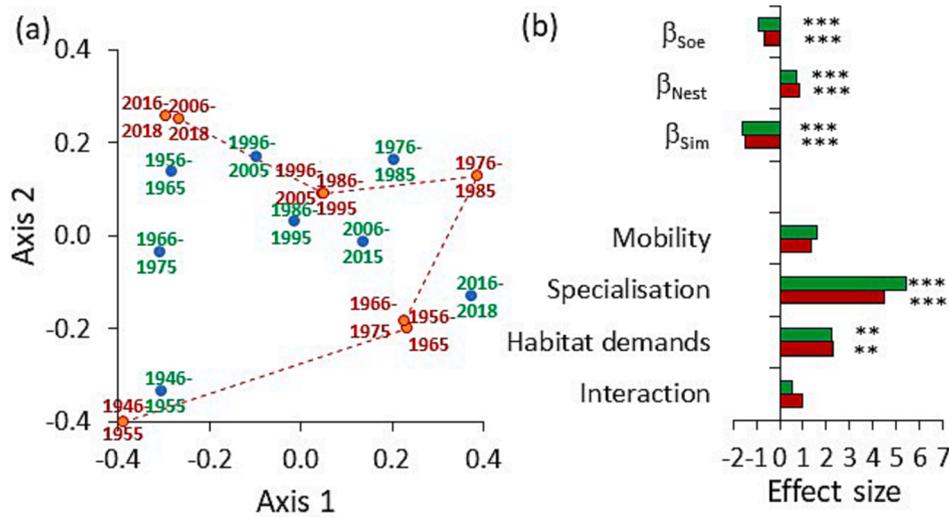

Fig. 5. A) non-metric multidimensional scaling (jaccard similarity) returns an ordered pattern of change in butterfly community composition for Gaisberg (red data), indicated by non-intersecting line connecting along the time gradient. For the Bluntautal (green data) this pattern was more complex (line connecting the decades not shown due to readability). B) Permanova detected specialisation and habitat demands, but not mobility as the main drivers of community composition. β-diversity partitioning indicated significantly lower overall ($β_{Sim}$) and partitioned b-diversity ($β_{Soe}$) than expected by chance, while the degree of ordered species loss ($β_{Nest}$) was significantly higher. Effect sizes refer to F values in case of MANOVA and to the difference of observed and expected β-diversity values in case of the partitioning. Significances: **: $P < 0.01$, ***: $P < 0.001$.

increase in the number of cows causes the influx of nitrogen at specific spots with negative effects on the habitat quality. In consequence, the abundance of the highly endangered *P. mnemosyne* strongly decreased and the successful larval development of species relying on extensively used low nitrogen meadows did no longer exist. These results underline that the designation and administration of nature reserves alone does not stop the vanishing of species. Adapted habitat management is essential here.

Landscape homogenization and decreases of butterfly diversity is also detectable for the Salzburg area. This study area, including the Gaisberg Mts. once provided suitable habitats for alpine specialist butterflies (e.g. *P. apollo, C. phicomone, P. bellargus*). These species went extinct (or strongly decreased in their abundances) over the past years. With the geographical proximity to the city of Salzburg, numerous previously extensively managed grasslands were transformed into settlements and the remaining grasslands have mostly been intensified with

the application of artificial (and organic) fertilizers and increasing mowing frequencies (Zhang, Loreau, He, Zhang, & Han, 2017). This trend causes a reduction of plant diversity as indicated in various previous studies, and subsequently also affects butterfly diversity negatively as successful larval development is no longer possible (see Roth, Kohli, Rihm, Meier, & Amrhein, 2021). The extinction of local populations of species depending on extensively used nitrogen-poor grasslands caused the disappearance and strong reduction in the abundances of species (e.g. *P. arion* and *L. hippothoe*). This result goes in line with trends observed for various grassland ecosystems across Central Europe, which suffer under nitrogen influx and high mowing frequencies (Payne et al., 2017, Roth et al., 2021). In addition to the intensified use of grasslands, part of the former open slopes of the Gaisberg Mt. has been afforested with spruce (PG, pers. comm.). In consequence, sun-loving species relying on open (stony) ecosystems went extinct (e.g. xerothermophilic and light-loving species). Our study approves immediate responses of butterfly diversity on landscape changes.

Particularly specialist species that strongly rely to specific habitat types and microhabitat conditions decreased in both study areas (Fig. 3). We assume that these species are only marginally able to adapt to changes in habitat structures, landscape homogenization and the fragmentation of remaining habitats (Thomas, 2016). Today, most of these species occur mostly in small and geographically isolated remnant populations (Jules & Shahani, 2003). It remains questionable whether such small and isolated populations are able to persist over long time periods, as underlined by the case of Bluntautal nature reserve.

5. Authors' contributions

JCH and MT developed this study, PG compiled data on butterflies, MT and WU analysed data, all contributed while data interpreting data and writing.

CRediT authorship contribution statement

Jan Christian Habel: Conceptualization of the study, writing a first draft, review and editing. **Werner Ulrich:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Patrick Gros:** Writing – review & editing, Writing – original draft, Data curation. **Mike Teucher:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All raw data are provided electronically as supplementary material.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2024.126562.

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