



Landscape homogenisation and simplified butterfly community structure go on par across Northern Austria

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Abstract

Context Agricultural intensification has led to strong homogenization of landscapes. Field copses have become larger, the boundaries between habitats became sharper, and land plots have been cultivated more intensively. In parallel, most field copses, ruderal areas and hedgerows were removed. As a result, ecotones and rarely used microhabitats largely disappeared. In consequence, many suitable habitats for species such as butterflies vanished and the permeability of the landscape decreased, with negative effects on biodiversity.

Objective In this study we analyse land-use and habitat configuration, and butterfly diversity for the years 1953 and 2018 for northern Austria.

Methods We assessed land cover and landscape configuration for the years 1953 and 2018 on a field-by-field basis across northern Austria, based on aerial and satellite images. We studied butterfly diversity for these two identical periods of time.

Results Our data show a decrease of the number of field copses over the past decades and a reduction in landscape complexity. The expected number of butterflies per sample unit of an assumed species decreased significantly. Particularly sedentary specialists decreased, while the proportion of mobile generalists increased.

Conclusions Our study underlines the general trend of landscape and faunal homogenization, which specifically leads to the vanishing of extensively used

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micro-habitats and the loss of sedentary specialist species.

Keywords Land cover change · Landscape configuration · GIS · Landscape heterogeneity · Permeability · Micro-habitats · Biodiversity loss · Heterogeneity · Sedentary specialists · Mobile generalists

Introduction

Agricultural intensification is a major driver responsible for the global loss of biodiversity (Maxwell et al. 2016). Especially in Central Europe, agro-environments are suffering under agricultural intensification. Fields have been merged, copses removed and the edges of fields were straightened for intense cultivation with large agricultural machinery. This landscape homogenization has resulted in the disappearance of numerous micro-habitats that often existed along the edges of and between land plots. Especially these micro-habitats are valuable habitats for insects, and valuable stepping stones allowing organisms to migrate throughout landscapes (Emmerson et al. 2016; Fischer et al. 2022). As a result, habitats of high biodiversity have become increasingly fragmented and the remaining ones now exist mostly as small and geographically isolated habitat remnants (Püttker et al. 2020), and subsequently cause the disappearance of many species. These changes in land-cover and landscape configuration have frequently caused dramatic consequences for biodiversity (Flohre et al. 2011).

Landscape homogenization also reduces the permeability of landscapes for many organisms (Dennis et al. 2013; Stein et al. 2014). This trend might have negative consequences for the persistence of organisms that exist today in small and geographically isolated habitat remnants, and tend to vanish in the long run (Tews et al. 2004; Oliver et al. 2010). As proven for various groups of arthropods, species diversity and abundance decreases with landscape homogenization (Habel et al. 2016). Hereby, not all species respond identically (Flohre et al. 2011; Winqvist et al. 2014; Fischer et al. 2022). We expect that sedentary species suffer much stronger under landscape homogenization than mobile generalist species do.

While studies so far have mostly quantified and analysed the degree of land cover change such as the destruction of specific ecosystems (Polus et al. 2007), studies on changes of landscape configuration are still rare (but see Batary et al. 2017). In this study we analyse changes of land-cover and landscape configuration for 50 study plots (2.5 × 2.5 km each) across the federal state of Salzburg (northern Austria). The landscape of this area is characterized by significant changes in land-use and landscape configuration, mainly driven by urbanization and agricultural intensification. Studies showed that this trend might have caused severe reductions of biodiversity, especially in the lowland regions during the past decades (Habel et al. 2022). We digitized each of them by visual identification considering various land cover categories. We hereby consider 2 time periods, one before profound changes of the landscape configuration (1953), and the current situation (2018). For the identical study plots we compiled data on Rhopalocera and Zygaenidae moths (in the following simply termed butterflies). In addition, we used traits on species ecology and behaviour for each of the butterflies observed. Based on these data and results we will answer the following research questions:

1. Did land cover and landscape configuration change when comparing the 2 time periods?
2. Did butterfly diversity and species community composition changed?
3. Which ecological guilds are particularly affected from changes of land-cover and landscape configuration?

Materials and methods

Land cover data

The aerial images of the year 1953 were acquired through the Salzburg Geographical Information System (SAGIS) in MGI/Austria GK M31 projection with a spatial geometric resolution of 0.25 m. These tiles cover 50 study plots (each 2.5 × 2.5 km, 625 ha in total). For the study area selected, aerial imagery tiles were merged to a seamless raster dataset (Fig. 1). For the year 2018, we used the Geoland Basemap Orthofoto web-mapping service (WMTS) interface to QGIS. The Orthofoto Tile Cache of Austria is

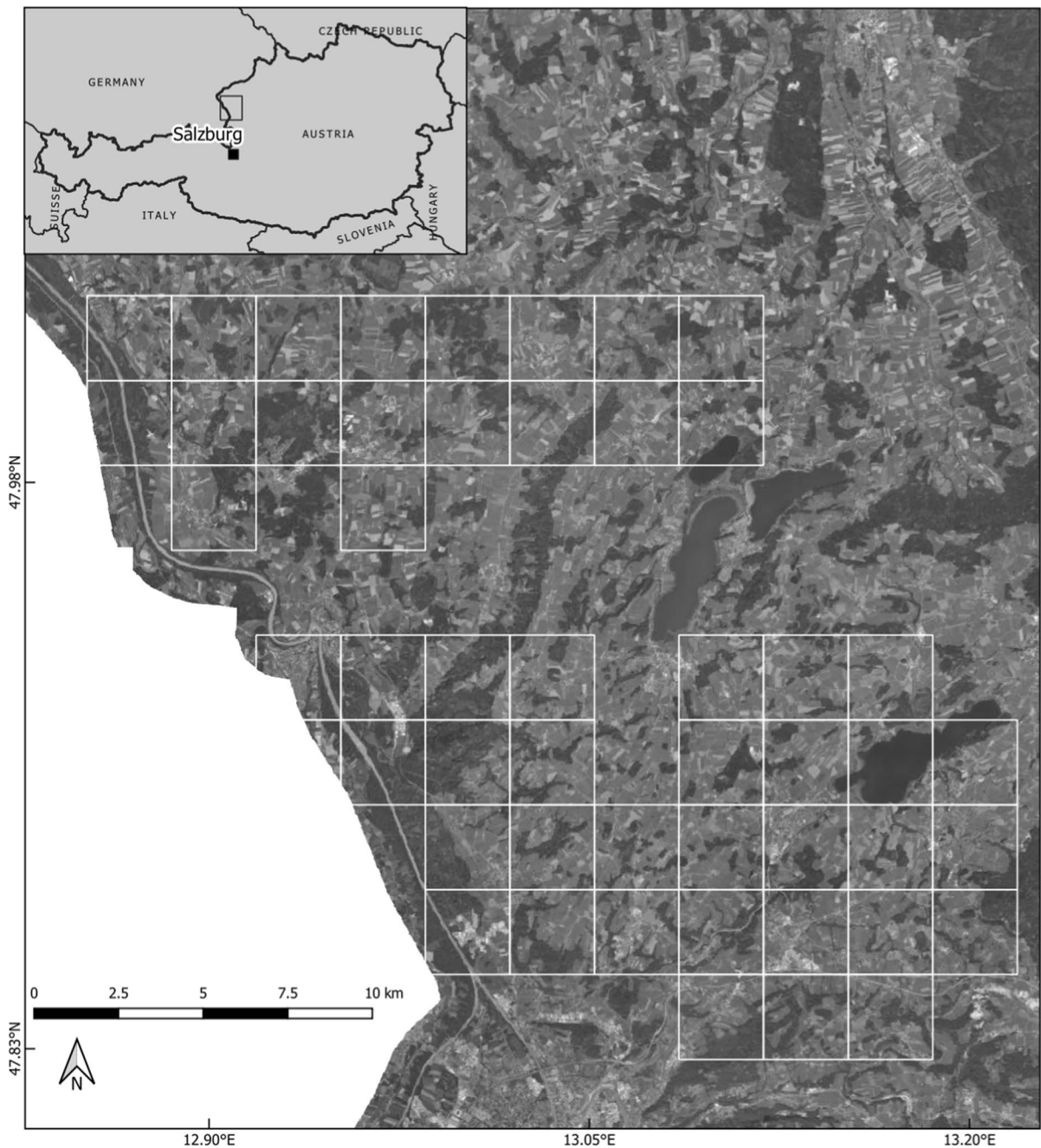


Fig. 1 Study region in northern Austria (small inlet map) and the location of 50 tiles of 2.5×2.5 km used for analysing changes of landscape configuration and the diversity of butterflies and Zygaenid moths

published by geoland at, and the Web Mercator Auxiliary Sphere is used as geographical projection. We subsequently digitized “agricultural land” and “bushes” by visual identification. We measured each individual land plot separately. The two selected land use

categories are of central importance for many open land butterfly species recorded in the lower altitudes of northern Austria. The mapping was restricted to areas below the alpine level and covers areas characterized by intense agricultural production. Raw data

used are given as Supplementary Material Appendix A1.

Butterfly data

In total, we used about 7834 butterfly records. These observations were collected during the respective year, as well as 4 years before and after (time windows 1951–1955 and 2014–2018). For each record, the following basic information was available: Species name, date of observation, exact location of observation (GPS coordinates). Butterfly data were taken from the database of the Haus der Natur museum of natural sciences in Salzburg, Austria (i.e. data from butterfly collections and field observations). Two local entomologists (P. Gros, G. Embacher) recently reviewed the reliability of each record. An overview of all butterfly data used is given as Supplementary Material Appendix A2.

Ecological trait data

To assess temporal shifts in butterfly community composition, we classified all butterfly species into groups according to their ecological requirements. Hereby we considered the following characteristics: Habitat specialisation; Specialist species versus generalist species (specialist are species with monophagous larvae and relying on one specific habitat type, while generalist species are taxa developing on a variety of food plants (polyphagous) and commonly found in a large variety of different habitats); dispersal behaviour. Information for these classifications were taken from various sources (Weidemann 1986, 1988; Bink 1992; Bräu et al. 2013), but were adjusted to regional conditions (WallisDeVries 2014; Habel et al. 2019, 2022). Furthermore we considered information on the degree of endangerment (according to the Red List of Austria (Höttinger and Pennerstorfer 2005, Gros 2021). All traits, categories and species specific classifications are given as Supplementary Material Appendix A2 (see Table A3 and Fig. A2).

Landscape composition analyses

After the digitalization of land cover categories, landscape metrics were calculated to investigate

landscape composition and configuration as proxies for permeability for the selected butterfly species in the respective time window. For the calculation we used the package *landscapemetrics* in R software (Hesselbarth et al. 2019). Squares of 2.5×2.5 km were used as sampling strategy to analyse landscape configuration on patch, land cover category (class) and landscape level. The following metrics were used at patch level. Besides area (AREA) and perimeter (PERIM) values, we used Perimeter-Area ratio (PARA) as a shape metrics to describe patch complexity. As PARA is not scale independent, we used Core area (CORE) as an additional metric to describe patch area and shape simultaneously. At class level, we calculated number of patches (NP), effective mesh size (MESH), Clumpiness index (CLUMPY), mean of core area (CORE_MN) and coefficient of variation of core area (CORE_CV). While NP gives an overview on patch structure, the metrics MESH and CLUMPY are aggregation metrics and allow investigating whether classes are either randomly spread, disaggregated or aggregated throughout the study area. Furthermore, Patch Cohesion Index (COHESION) was included. COHESION belongs to the category of aggregation metrics and characterises the connectedness of patches of the same class and it can be estimated whether patches are dispersed, aggregated or rather isolated throughout a landscape and thus gives information about habitat configuration and landscape permeability (Schumaker 1996). CORE_MN and CORE_CV provide insights in variations of patch shape throughout the land cover categories. Subsequently, the metrics on class level were analysed using Dunn's test for pairwise comparison with Bonferroni correction (Dunn 1964). At the top level (landscape), we used NP, MESH, CORE_MN and CORE_CV. Detailed information and formulas of used metrics are given in McGarigal et al. (2012) and Hesselbarth et al. (2019).

Statistical analyses

The present record data provide a rich source of information on changes in community composition and richness. However, the collected data might be biased because it is assumed that at the beginning of data collection (for private collections) there was an emphasis on rare species, while all species (even very common ones) were considered in the same way in

recent systematic collections. If rare species, possibly being over-represented for the early periods, differ in trait distribution, direct comparisons of these distributions would be biased (see Pellet et al. 2012). In the analysis of long-term trends in butterfly community composition that relied on the same data set, Habel et al. (2022) conservatively used presence–absence data only. For not losing information, we here used two-way ANOVA to check whether species of frequent and occasional records differ in the proportions of each single trait. We arbitrarily divided species placed above the medium number of records as frequent and those below as rare. Naturally, trait distributions differ across study periods and rarity class (not shown). Additionally, the rarity \times period interaction term should be significant if selective sampling would bias the trait distribution in a given study year. This was generally not the case (see Supplementary Material Appendix A4, Table A4). Only ten out of 70 single comparisons were significant and the interaction term accounted for at most 10% of the observed variance (Table A4). Additionally, a Mantel correlation (Bray-Curtis similarity) returned a high positive correlation ($r=0.73$, $P<0.001$) between the trait \times study matrices for numbers of records and species occurrences (raw data in Tables A5, A6). Therefore, we argue that count data might be a valuable source of information on long-term changes in community structure (cf. Gotelli et al. 2021 for a similar result on animal and plant museum records). Below, we present results based on numbers of records (relative abundance) and species occurrence (relative richness) data.

Under the assumption that landscape composition was similar in the years directly before and after 1953 and 2018, we used records from the years 1951 to 1955 and from 2014 to 2018 to assess community composition of the early and the recent time window, respectively. For each trait, we calculated the annual proportion of records and species occurrences. We used the non-parametric Kruskal–Wallis test to compare these proportions across the two study periods. To assess changes in community composition, we fitted lognormal and logseries species models to the observed rank order–abundances distributions (RAD) and used Fisher’s alpha index to quantify diversity. Typically, lognormal RADs are found in closed communities structured by species interactions and filter

processes, while log-series sample distributions are common in communities dominated by dispersal processes (see Magurran and Henderson 2003; Ulrich et al. 2022). Additionally, we applied unconstrained correspondence analysis (seriation) to infer and to visualize changes in community composition across the study periods.

To compare absolute richness values S , we used first order jackknife estimation and applied power function richness accumulation curves of the form

$$S = S_0 N^z \quad (1)$$

where N denotes the sample size (number of records). S_0 is the normalization constant and in samples, the exponent z frequently takes values between 0.1 and 0.2 (e.g. Dembicz et al. 2021). Under the assumption that exponents are similar across the sampling years, differences in S_0 should indicate differences in total richness, as in this case the respective accumulation curves do not intercept. Therefore, we used this range of exponent values to estimate changes in butterfly species richness between the 2 time periods.

Results

Land cover and landscape configuration

The analysis of land cover change revealed that 65.3 ha of former bush patches were converted into agricultural land from 1953 to 2018 (0.5% of the total area). 128.5 ha (1.0% of the total area) were converted from agricultural land into bushes in the same time period. Mean Perimeter-Area ratio (PARA) (metrics for shape complexity without standardization, increase in patch size will cause a decrease in the perimeter area ratio) changed from 0.38 to 1953 to 0.82 in 2018 for bushes (increase of complexity) and for agriculture from 0.31 to 0.18 (trend towards more small and isolated bushes, and bigger homogenous arable fields, decrease of complexity). Core area (CORE) changed from 4263 to 1941 m² in 2018 for bushes and from 31.65 ha to 11.95 ha at the patch level (decrease in core area, decrease in complexity, and a trend towards more homogenous landscape structure).

Concerning landscape configuration, the mean number of patches per 2.5×2.5 km tile for the classes agriculture and bushes changed from 15.1 to 11.2 to 29 and 25.4, respectively. Thus, this is an increase of 192% for agriculture and 227% for bushes. MESH decreased for bushes from 1057 to 174 m² in average from 1953 to 2018. CORE_MN values shifted from 24.77 to 0.48 to 10.34 and 0.26 ha, respectively for agriculture and bushes. According to the performed Dunn's tests, there are significant differences between the years 1953 and 2018 concerning NP ($z=3.77$, $p=0.0002$), and CORE_MN ($z=-3.7$, $p=0.0002$) for agricultural areas. Mean values of COHESION changed marginally from 97.94 to 97.96 for bushes from 1953 to 2018. At landscape level, the metrics NP changed from 996 to 1953 to 2228 in 2018 and MESH decreased from 2194.3 ha to 756.9 ha in 2018 (Fig. 2).

Butterflies

The data for the current study period contained fewer species (139) than the earlier study period (150) despite the much higher total number of records (5669 vs. 2,165, respectively) (Fig. 3a, b). Jack-knife estimates indicated for the earlier study period 155 species and for the later period 148 species. α -diversity decreased from a value of 36.8 (early period) to a recent value of 25.7 (Fig. 4). Species accumulation curves confirmed this trend (Fig. 3c, d). For the assumed range of power function exponents, estimated richness of the later study period was lower than that of the earlier period.

Seriation (Fig. A2) and the analysis of RADs (Fig. 4) indicated major changes in butterfly community composition. The samples from the earlier period were nearly perfectly fitted by a lognormal abundance distribution, while the abundance data from the later period were best mimicked by the log-series sample distribution (Fig. 4). The comparison of the abundance rank orders between the 2 time periods returned a low correlation of $r=0.1$ (Fig. 4b). Thus, abundance in the 1950ies did not forecast abundances in the 2010s. Of the 169 species, nevertheless, 31 (i.e. 22.3%) were recorded in all 10 study years and 56 (40.3%) in at least 9 years (Fig. A2). 18 species were recorded in the earlier period only (Fig. A2). These were mainly associated with oligotrophic habitats (13 species), as well as with alpine and xerothermic grasslands (15) (Fig. A2).

Only three of them are habitat generalists (Fig. A2). Seven species appeared as new in the later study period. Only one of them is xerothermic (Fig. A2) and six are Red List species.

Guild specific analyses of community structure based on relative abundance (Fig. 5, Table A5) and relative richness (Fig. A1, Table A6) demonstrated important temporal changes with respect to each species group. There was a strong decline in the relative abundance of species depending on oligotrophic, xerothermic and alpine habitats (Fig. 5a, c, e). These trends were also visible when using relative richness (Fig. A1a, c, e). In turn, ubiquitous species dependent on eutrophic conditions significantly increased in relative abundance (Fig. 5f) and relative richness (Fig. A1f). Hygrophilic species increased in relative richness but not in relative abundance (Fig. 5d, A1d). Grassland associated species strongly declined and forest and hedges/shrub associated species increased in relative abundance (Fig. 5g–i), while these trends were not visible when using relative richness (Fig. A1g, h, i). Dispersive species increased and habitat specialists decreased in relative abundance (Fig. 5j, k), while these trends were less visible with respect to relative richness (Fig. A1j, k). Despite the decline in typical alpine species, we observed an increase in relative abundance and richness of species observed above 1000 m asl (Fig. 5l, A1l). No clear temporal trends were visible for lowland species (Fig. 5m, A1m).

The observed changes in butterfly community structure had effects on the fraction of endangered species in the records (Fig. 5n, o, Fig. A1n, o). The relative abundance of endangered species strongly decreased in the later period, while the respective proportion of species with IUCN status *least concern* increased to values above 70% (Fig. 5n, o). However, these trends, although qualitatively identical, were not clearly visible when using relative richness data only (Fig. A1n, o).

Discussion

Micro-habitats in agro-environments

Our analyses of land-use change and changes of landscape configuration show a decrease of hedgerows and ecotones, which have been removed from the landscape over the past decades (the remaining ones

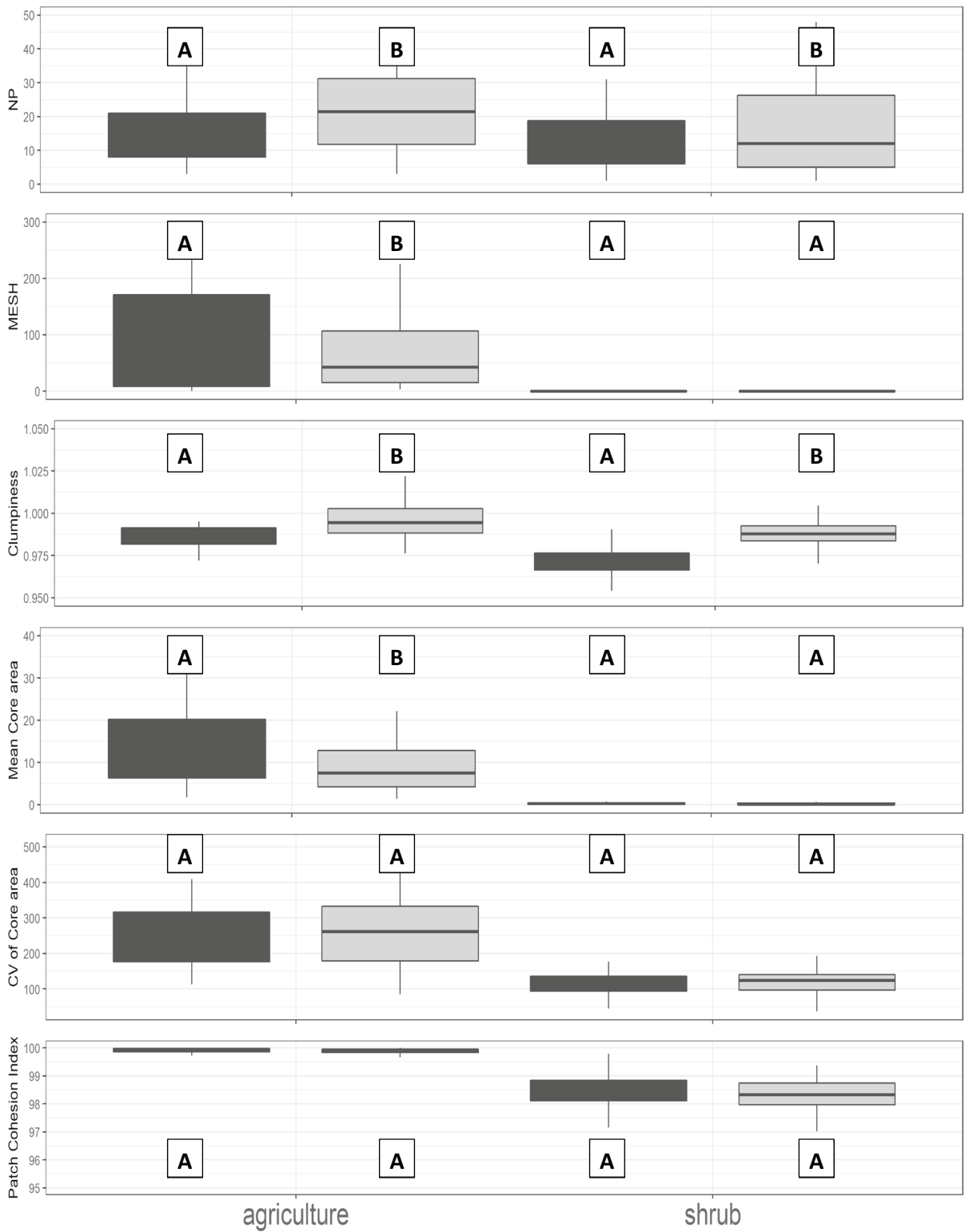


Fig. 2 Boxplot matrix showing the calculated class metrics for the two land cover classes (dark colour: 1953; light: 2018). Letters indicate significant differences

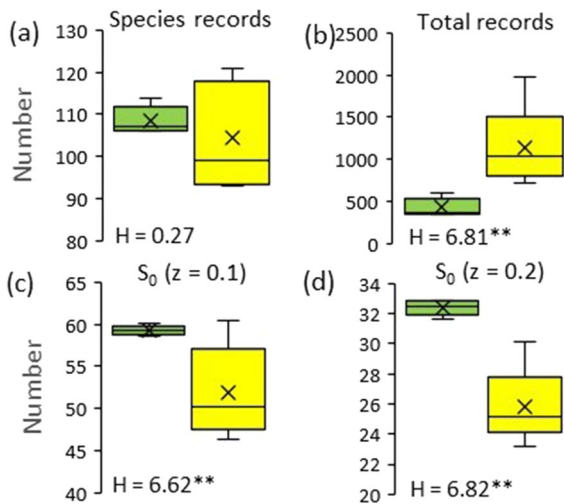


Fig. 3 Box and Whiskers plots showing differences in species richness **a**, total numbers of records **b**, and the expected number of species (S_0) per sample unit of an assumed power function species accumulation curve with slopes $z=0.1$ **c** and $z=0.2$ **d** for the time intervals 1951–1955 (green) and 2014–2018 (yellow). H-values of Kruskal Wallis tests and significance levels: ** $P < 0.01$

exist today rather concentrated, and are less scattered across the landscape). Although the number of bush patches increase, the cohesion and thus connectivity was reduced and in the same time the core area declined as well (reduction of the core area by 50%, reducing of the connectivity). Considering the landscape configuration and metrics, we found a decrease in landscape complexity, evidenced by the decline of PARA and perimeter for agriculture. In consequence, rarely used field margins have become significantly

isolated and smaller over the past decades. In parallel, straight borders of arable land provides the precondition of increasing agricultural intensification, and the disappearance of numerous marginal strips. Such micro-habitats have been farmed only sporadically and hence are valuable refuges for various organisms. The loss of size and connection of such micro-habitats and subsequent negative effects on biodiversity has also been documented for other agro-environments across Central Europe (Cely-Santos and Philpott 2019). Heterogeneous agro-environments including non-crop habitats provide heterogeneous landscapes with a high level of biodiversity, as shown for bees (Cely-Santos and Philpott 2019), butterflies (Konvicka et al. 2016, Körösi et al. 2022). For example, Konvicka and colleagues (2016) reported 2.3 times more butterfly individuals in heterogeneous agro-environments if compared to intensively managed farmland.

In addition to the merging of plots as in our study, the isolation and reduction of hedgerows also destroys valuable habitats that foster ecosystem diversity and landscape heterogeneity. We found that hedgerows became smaller and less connected with halved core area and increased complexity due to reduction in size. Such sites may provide suitable habitats for larvae of butterflies and act as suitable corridors for many organisms (Körösi et al. 2022). Hedgerows also provide very valuable sites for overwintering stages of many insects (Mader et al. 2017; Rischen et al. 2021). And, hedgerows and grassy field margins are known to foster arthropod diversity and support many species, including many endangered and red listed insects (Plath et al. 2021).

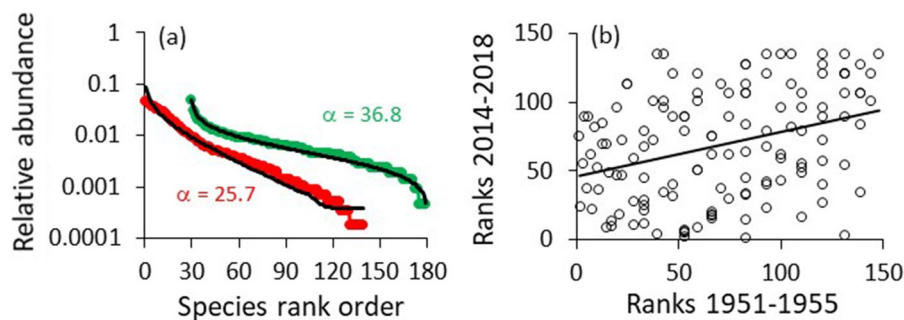
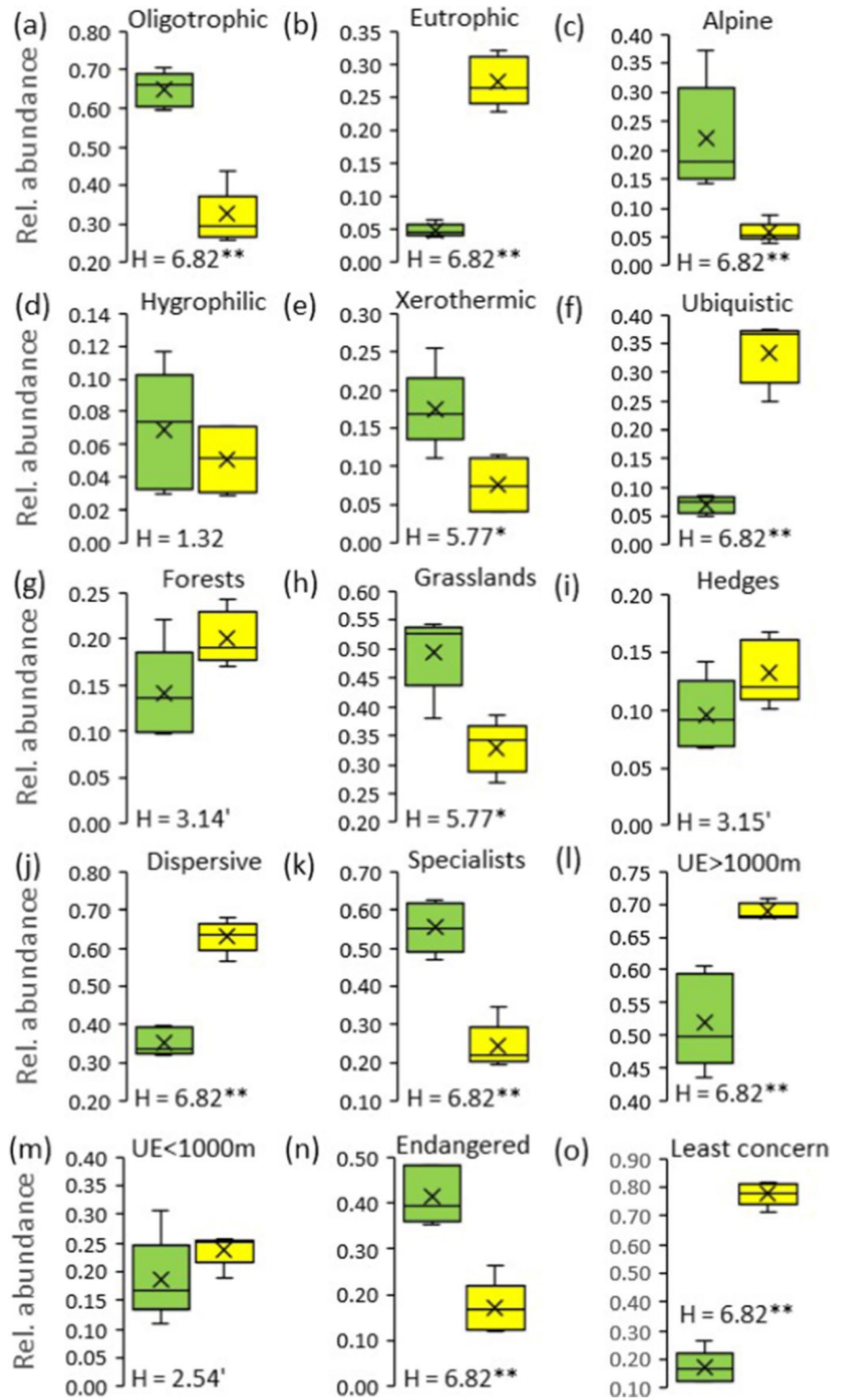


Fig. 4 **a** Fits of a lognormal abundance rank order distribution to the 1951–1955 samples (green data points) and of a log-series series distribution to the 2014–2018 samples (red). Given are also the α -diversity values. **b** Species abundance ranks; both time periods were only weakly correlated (Pearson correlation $r=0.33$)

Fig. 5 Box and Whiskers plots showing differences in relative abundance (given as the proportion of the total annual number of records) of 12 butterfly guilds (based on total numbers of records) for the time intervals 1951–1955 (green) and 2014–2018 (yellow). Oligotrophic **a** and eutrophic **b** habitats; habitat demands: Alpine meadows **c**, hygrophilic **d** and xerothermic **e**; occurrence: ubiquitous **f**, mainly forests **g**, grasslands **h**, hedges and shrubs **i**; dispersive **j** species; habitat specialist **k** species; endangered (threatened, endangered, vulnerable) **l** and least concern **o** species; upper occurrence boundary below **m** and above **n** 1000 m asl. H-values of Kruskal Wallis tests and significance levels: * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$



The changes of landscape configuration becomes reflected by shifts in butterfly community structures and species diversity. Our results show that species composition have been changing in parallel. We found that particularly specialist species such as most *Zygaena* species (except for *Z. filipendulae*, *B. dia*, *G. alexis* and *M. cinxia* even became extinct) and species with restricted dispersal behaviour (all *Zygaena* species, many blues and *Erebia* species) strongly decreased. In parallel, the proportion of mobile ubiquist species increased (*G. rhamni*, *M. jurtina*, *P. napi*, *P. rapae*, *V. atalanta*, *V. cardui*). This trend becomes also approved by other studies showing a filtering towards mobile generalists (Endenburg et al. 2019).

With the data collected and analysed, we are not able to evidence potential changes in habitat quality and to evaluate the decline of extensively used ecosystems such as calcareous grasslands, wet meadows and bogs. However, numerous studies have already shown that the homogenisation of the landscape structure is usually accompanied by an intensification of land management (increase in mowing frequency, increase in nitrogen input, draining of wetlands, levelling of land surfaces). However, our data underline a strong decline of butterflies which are rely on particularly those habitat types (hygrophilic species, species from calcareous grasslands).

Landscape permeability for species persistence

The disappearance of micro-habitats along marginal strips and hedgerows also provide relevant stepping stones and corridors for many organisms, and thus increase habitat connectivity i.e. landscape permeability. Hedgerows and micro-habitats along uncropped field margins often act as important corridors for open-land species that move along such linear structures (Alignier et al. 2020). With the vanishing of these structures, landscape permeability decreases. However, a high level exchange rates of individuals among local habitats is crucial for species persistence at the landscape level (Thomas 2016). Studies showed that mean distance between nearest grasslands is strongly positively correlated with butterfly diversity (Quin and Burel 2002). Furthermore, landscape composition directly impacts the dispersal behaviour of species (DeLattre et al. 2013; Loos et al. 2015; Ehl et al. 2019).

This situation towards small and isolated habitat remnants embedded in an intensively used agricultural

landscape becomes aggravated by the intensification of agricultural management. Numerous species can hardly migrate through such intensively managed fields representing the landscape matrix. This situation increases the likelihood of stochastic extinctions and thus the loss of species diversity at the landscape level (Slanacrova et al. 2014). After extinction of local populations, recolonization of un-occupied habitats is little likely in such an environment (Hanski 1999; Thomas 2016). Thus, enhancing heterogeneity and increasing the proportion of non-cropped areas again may be a valuable tool for conserving farmland biodiversity in intensively farmed landscapes (Rundlöf et al. 2007).

The loss of these habitats as well as of stepping-stones and corridors plays a central role. Thus, for example, Gallé and colleagues (2018) found that small-scale agricultural landscapes have higher overall diversity and densities of arthropods. With the disappearance of these small-scale structures, landscape permeability also decreases substantially, as mirrored in our study by the significant decline of species with low dispersal power. Additionally, this is also supported by the severe losses of species occurring in metapopulation structures in our study region (*A. artaxerxes*, *B. titania*, *E. aurinia*, *M. aurelia*, *M. cinxia*). Today's agricultural landscapes of Salzburg, but also in many other parts of Europe and the world, are more and more intensified and hence homogenous. These novel agricultural landscapes with most of the former stepping stones having vanished are resulting in continuous erosions of diverse butterfly communities and subsequent domination by some few mobile species (Bergman et al. 2004; Thomas 2016).

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Author contributions JCH and MT designed the study, MT and WU did statistical analyses. All authors contributed while writing this manuscript.

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Data availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Not applicable.

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