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Losses of specialist and expansion of thermophilic generalist macro-moths in nature reserves of Central Europe

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ABSTRACT

Ongoing environmental change has caused significant modifications in the diversity, abundance and community composition of insects across Central Europe. Nocturnal insects, such as macro-moths, are species rich and represent a large part of insect biomass, but are underrepresented in scientific studies. In this study, we analysed long-term changes of macro-moth diversity and community composition across south-western Germany, using records from two time periods: 1970–2000 and 2001–2020 obtained at identical study sites, almost all nature reserves. Total species richness remained constant, while local species composition changed significantly. Endangered and specialized open landscape species, and those adapted to bogs and coniferous forests became less common. Thermophilic species adapted to dry mixed forests became more abundant. The macro-moth communities became considerably more uniform and are increasingly dominated by common habitat generalist species. The decline in specialized open-landscape species seems to be due to losses of formerly extensively used grassland and agricultural intensification. Species with Mediterranean core areas increased in abundance. Likely, climate and land-use change will strengthen the observed trends and continue to reshape macro-moth communities, with the potential for continued compositional homogenisation.

1. Introduction

Worldwide, a variety of anthropogenic activities have caused major changes in environmental conditions leading to decreasing insect diversity and abundances (Thomas, 2016; Hallmann et al., 2017; Montgomery et al., 2020; Wagner et al., 2021a; Harvey et al., 2023). Particularly, the destruction of habitats and the deterioration of habitat quality due to increasing amounts of fertilisers and pesticides have negatively affected plant and insect diversity (Bobbink et al., 2008, Nijssen et al., 2017, Habel et al., 2023b). Insects with specific habitat and resource demands are particularly affected, while generalist species suffer less or sometimes even increase in abundance (Sánchez-Bayo and Wyckhuys, 2019; Didham et al., 2020).

In addition to land-use changes, climate change is starting to impact species diversity and community composition (Harvey et al., 2020; Ulrich et al., 2024). Noteworthy, many insect species show latitudinal and altitudinal shifts, due to increasing temperatures, resulting in gains at higher elevation and higher latitudes (Parmesan and Yohe, 2003; Rödder et al., 2021; Kerner et al., 2023). Thus, on the one hand, cold-adapted species are shifting their distributions poleward and into higher altitudes, and thus disappear from their original habitats in Central Europe. On the other hand, particularly thermophilic species with formerly (sub-)Mediterranean distributions are currently expanding their ranges towards and within Central Europe (Gil-Tapetado et al., 2023). Balancing gains and losses, parts of Central Europe are even experiencing current net gains in insect richness, driven by the expansion of ubiquitous and thermophilic species (Habel et al., 2019b).

Long-term observations are essential for investigating changes in species community composition and diversity. To date, studies have revealed demographic changes in a range of taxa, e.g. population declines in many forest and farmland birds (Böhning-Gaese and Bauer, 1996; Reif et al., 2022) and arthropods (Seibold et al., 2019), but also

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stable or even increasing populations in some taxa (Macgregor et al., 2019; Haris et al., 2025). Most of the long-term studies were conducted with well-studied vertebrates, such as birds (Bowler et al., 2019), but also butterflies (Warren et al., 2021), ground beetles (Pozsgai et al., 2016; Homburg et al., 2019), and dragonflies (Termaat et al., 2019). While these groups contain a rather manageable number of different species, other more species rich taxa, such as macro-moths (Lepidoptera), have received less attention (e.g. Conrad et al., 2006; Macgregor et al., 2019; Fox et al., 2021). At least for Central Europe, macro-moths are taxonomically and ecologically already well understood (Habel et al., 2019b; Roth et al., 2021; Karbiener and Trusch, 2022). Macro-moths are highly sensitive to environmental changes as most species rely on specific conditions during their larval stages (Fox et al., 2014; Coulthard et al., 2019).

Prior studies on macro-moths already revealed considerable decreases in moth diversity in temperate and tropical regions (Wagner et al., 2021a). Using long-term data from the Rothamsted Insect survey, Conrad et al. (2006) reported that more than two-thirds of British moth species declined in abundance. In turn, Yazdanian et al. (2023) found an increasing biomass, particularly of multivoltine species in Finland. Abundances of thermophilic species increased in the UK and Finland (Sparks et al., 2007; Itämies et al., 2011; Fox et al., 2014). Itämies et al. (2011) and Kwon et al. (2024) reported range shifts towards higher latitudes in Finland and South Korea. These results indicate that macro-moth respond to environmental, particularly climate changes, especially because many of them rely on specific habitat conditions during their larval stage (Fox et al., 2014, Coulthard et al., 2019). Furthermore, many macro-moth species are comparatively mobile, making them an excellent study system to test for responses to environmental changes (Conrad et al., 2006; Valtonen et al., 2017; Wagner et al., 2021a, 2021b). So far, moths have been considered only rarely for long-term observations (Yazdanian et al., 2023; Sparks et al., 2007), because data acquisition is more time-consuming and because taxonomic identification is more difficult. The few long-term observations of macro-moths in Central and Northern Europe covered only very restricted areas (Valtonen et al., 2017; Fox et al., 2021).

In our study, we analyse the diversity and community structure of macro-moths across south-western Germany (i.e. the Federal State of Baden-Württemberg). To evaluate the overall changes in macro-moth diversity and community structure, we took advantage of extensive long-term and semi-standardised macro-moth recordings spanning 50 years since 1970. Data collection took place in the framework of the insect monitoring programme of the Landesanstalt für Umwelt Baden-Württemberg (see Karbiener and Trusch, 2022). Based on these data, we analyse the temporal changes in species diversity, abundance, and community composition. We address two major research questions:

1. How did macro-moth richness and community composition change in time?
2. Do changes in richness and community composition differ for species with specific habitat or climatic preferences?

2. Material and methods

2.1. Study area

Our study area is the federal state of Baden-Württemberg (BW in the following) in south-western Germany (Appendix B, Fig. B1). This region covers 35,751 km^2 and is located in the continental region of Central Europe, but shows strong regional differences in climatic conditions (i.e. the warm Upper Rhine Valley in the west (100 m asl), the mountain regions of the Black Forest (up to 1493 m asl), as well as the more continental regions of Swabian Alb and Tauberland). The geology is highly diverse and includes loess-covered lowlands, low mountain ranges with exposed granite, red sand- or limestone, as well as the glacially formed Alpine foothills north of Lake Constance. The excess of precipitation in the Black Forest and Alpine foothills creates the prerequisite for the formation of raised bogs. The climatic and geological diversity across BW results in a variety of habitat types (Karbiener and Trusch, 2022). Most open-land habitats found across BW are extensively farmed meadows, pastures and wetlands. Beeches dominate the natural forest vegetation, accompanied by spruce, fir, and oak (Karbiener and Trusch, 2022).

During the past century, the landscape was highly modified. Mixed forests were transformed into monocultures of spruce, pine and Douglas fir. In the course of land consolidation and urbanisation, wetlands were drained and other habitat types were transformed into settlement areas (mostly during the 1970s). In addition, agricultural intensification caused the destruction of formerly extensively farmed semi-natural ecosystems (Demuth et al., 2021). Rising mean annual temperatures, higher maximum temperatures, and more frequent summer droughts increasingly impact the region (Fischer et al., 2021).

2.2. Collection of data

Our study covers two time periods: 1970–2000 (period I) and 2001–2020 (period II). Data from period I cover a total 81,203 macro-moth records collected in 25 square study plots (Fig. B1), covering 36 km^2 each (in total 2 % of the surface of BW). Sampling in period I was done qualitatively by renowned Lepidoptera collectors and Lepidopterologists, using different methods (light trapping, bait trapping, caterpillar search). These data were compiled as a database at the State Museum of Natural History Karlsruhe, Germany, for the fundamental work for nature conservation 'Die Schmetterlinge Baden-Württembergs' (Ebert, 1991-2005). Plot selection for period II followed four criteria: a) availability of a complete macro-moth checklist for the past (i.e. 1970–2000); b) cover of important natural habitat types, particularly open landscapes; c) cover of landscapes with existing populations of endangered macro-moth species; d) spatially homogeneous distribution across BW (Fig. B1) (Karbiener and Trusch, 2022). Our choice of study periods was due to the different data sources and samples sizes in the single study years that excluded direct comparisons of years and the analysis of temporal trends.

Period II amounted to a total of 50,881 records. Data from 2001 to 2018 came from 20,285 single observations obtained from various entomologists. In the years 2019–2020, every 14 days from March to November two automatic light traps and one light tower (active capture) were run for an average of 4 h (starting from sunset), resulting in a total of 30,596 records. Because all sampling was done in protected areas, comparatively little environmental changes occurred within the plots, while the surrounding landscape underwent significant agricultural intensification. All records from both time periods are contained in Landesdatenbank Schmetterlinge des Staatlichen Museums für Naturkunde Karlsruhe (Germany) (https://www.schmetterlinge-bw.de/Lepi/Default.aspx) and in Ebert (1991-2005). Determination of macro-moths was done by the collecting entomologists, and was verified by O. K., R. T., and Ulrich Ratzel (according to Ebert, 1991-2005, and recent revisions). Raw data used in this study are given as supplementary material in Appendix A (Tables A1 and A2).

2.3. Traits

We compiled information on habitat preference and the distribution range of each single species using Ebert (1991-2005). We distinguished between 13 different habitat types in terms of habitat preference (see Appendix A, Table A1) and counted in how many different habitats a species was recorded. Following Ebert (1991-2005) we classified species into two biogeographic categories Central European (generally also widespread in the Palearctic) and Mediterranean (species with a Mediterranean core distribution).

Furthermore, we considered the threat level for each single species of periods I and II using the BW Red Lists from 2004 (Ebert et al., 2005) and

2024 (Steiner and Trusch, 2025). As these Lists are based on the German classification system (Ludwig et al., 2009; Rote Liste-Team, 2016, 2021), we translated the categories according to the IUCN classification scheme. All raw data are given in Tables A1, A2, and A3.

2.4. Data analysis

Observed species richness increases with the number of records. Due to different numbers of records in periods I and II, we could not directly compare species lists. Further, data from historical sampling campaigns are often biased. In the present case, multiple records of individuals from abundant species in period I might artificially inflate sample sizes with respect to the more standardised sampling in period II. Subsequently, multiple imports into the database also caused duplications of records. Therefore, the effective number of records (the *effective sample sizes*) in period I might be significantly lower than reported, which might bias the estimate of species richness in the samples. To overcome this problem, we compared observed richness across plots and also used individual based rarefaction curves and random resampling to standardise the number of records.

We calculated rarefaction curves separately for all plots combined and for each plot for the period I data, the period with the higher total numbers of records. We then compared the observed species richness in period II with the rarefied richness in period I. Second, we used an equiprobable random sample approach and took 100 random samples of 50,881 individuals (the record number of period II) from the records of period I (81,203 records). We then compared observed richness and trait distributions of period II (*obs*) with the expected ones of period I (*exp*). We focused on differences in species richness S ($\Delta S = S_{obs} - S_{exp}$), and number of occupied plots P ($\Delta P = P_{obs} - P_{exp}$). We also calculated standardised effect sizes (SES) to quantify the observed numbers of records per species (R_{obs}) with those expected from random sampling (R_{exp}) ($SES_R = (R_{obs} - R_{exp}) / \sigma_{\mathrm{exp}}$, where σ_{exp} denotes the standard deviation of the distribution of the random samples). $\mathrm{SES_R}$ values <-1.96 and >1.96 indicate significant deviations from a normally distributed random sample at two-sided error rates of 5 %. Prior to calculations, the expected values of $\mathrm{S_{exp}}$, $\mathrm{P_{exp}}$, and $\mathrm{R_{exp}}$ were rounded to the next integer to avoid biased results at lower values. We used the non-parametric iChao1 estimator and the associated analytic variance as implemented in the iNext package to estimate species richness (Chiu et al., 2014; Hsieh et al., 2016).

In the trait-based approach considering habitat specialisation (number of habitats occupied), biogeographic classification (Mediterranean, continental), and endangerment status, we counted for each trait and each habitat association how often the unbiased random sample returned a number of respective records in period I ($\mathrm{N_{exp}}$) to be larger or smaller than the observed number in period II ($\mathrm{N_{obs}}$). The difference

$$\Delta\pi = \frac{1}{S}\sum_{1}^{S}\left(n\left(N_{obs} > N_{exp}\right) - n\left[\left(N_{obs} < R_{exp}\right)\right]\right) \tag{1}$$

where n $[(\mathrm{N_{obs}} - \mathrm{N_{exp}}) > 0]$ denotes the number of samples of a species where the observed number of records n of a species in period II was larger than expected from the period I sample. Calculated separately for all species of a focal trait, $\Delta\pi$ indicates the proportion of decreasing (negative $\Delta\pi$) or increasing (positive $\Delta\pi$) number of species in the samples from period I to period II with respect to trait membership.

To assess the relative change in the number of records (as a proxy to relative abundances), we calculated for each species the quotient

$$\Delta Q_i = \frac{p_{II} - p_I}{p_I} \tag{2}$$

where $\mathrm{p_I}$, $\mathrm{p_{II}}$ denote the proportions of the total number of records of species i in periods I and II (relative abundances). We note that the absolute numbers of records are poor indicators of species abundances, the relative abundance should largely reflect the true dominance order of the species. A plot of $\mathrm{p_I}$ against ΔQ indicates whether rare or abundant species changed most in abundance. We assessed differences in species composition among plots and study periods using non-metric multi-dimension scaling (NMDS) with Euclidean distances again using the relative abundances as input. The input matrix was a 50 × 868 (plot × species) matrix with plots additionally labelled as period I (25 plots) and II (25 plots).

3. Results

3.1. Diversity and occupancy

In total, we found 868 species of macro-moths (i.e. 91.7 % of all species recorded in BW after 1970). Of the 838 species present in period I, 51 (i.e. 6.1 %) were not recorded in period II, while of the 817 species recorded in period II, 30 (3.7 %) were missing in period I (Table A1), making a net loss of 21 species (2.5 %) in the records (Fig. 1). In period I, 23 species were represented by single records, while 47 such singletons occurred in period II. Rarefaction curves revealed that direct comparison of species lists without considering different sampling intensity might lead to biased conclusions about the decrease in overall richness; this regards the whole BW fauna (Fig. 1), but also the records from each single plot (Fig. B2).

However, after correcting for record number, total macro-moth diversity in the 25 plots (and hence representing nearly the whole of the BW fauna) appeared to be 7 species lower during period II than the rarefied diversity of period I, although this difference was statistically not significant (Fig. 1, *t*-test: $P > 0.1$). The iChao1 estimated total richness in our study plots was 850 species in period I and 862 species in period II, with a wide overlap in the respective standard errors (Fig. 1). The use of a sampling model that accounted for a possible recording bias towards more abundant species did not change this picture: Both periods still did not significantly differ in species richness (Fig. 1). Species rank order distributions and evenness of both sample periods were very similar without any trend towards stronger dominance in period II (Appendix B: Fig. B3). However, local diversities as represented by the 25 plots, showed contrasting and plot specific trends in species richness and turnover over the past five decades (Fig. B2). On average, observed plot richness in period I was 392 species compared to the rarefied average richness of 357 species in period II, making a decrease in average plot richness of 35 species (i.e. 8.9 %) (Fig. B2) despite the

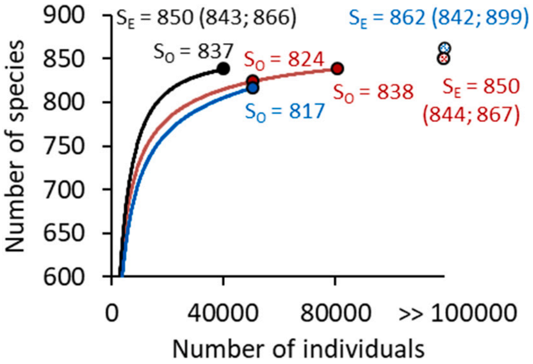

Fig. 1. Rarefaction curves of periods I (red: 1970–2000, 81,203 records) and II (blue: 2001–2020, 50,881 records), all plots combined, 878 species in total. The black rarefaction curve stems from a sample of period I, where all 684 species with more than 10 records have been proportionally downsized to match a total effective record number of 40,000 records. The black, red, and blue data points denote the total numbers of species reported in periods I and II ($\mathrm{S_O}$), as well as the respective iChao estimates ($\mathrm{S_E}$). Lower and upper analytic standard errors are in brackets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temporarily more constant richness across all plots (Fig. 1).

The random sample model revealed that species abundances and average plot occupancy decreased between both time periods (Fig. 2). Ten plots had negative ΔR values from period I to period II while only five were positive, indicating a trend of reduced species abundance (Fig. 2a). These changes caused differences in plot community compositions between both time periods: Composition based on species abundances was more similar among plots in period II, whereas the variability in plot composition was more pronounced in period I (Fig. 2a, inset). As much as 469 species (57.3 %) decreased, while only 256 species (31.3 %) increased in plot occupancy (Fig. 2b). Decreases in abundance were not equally distributed among species. On average, abundant species decreased more than rare species resulting in a significantly negative correlation between relative abundance change (ΔQ, Eq. (2)) and relative abundance (Fig. 2b, inset).

3.2. Community composition

The change in plot occupancy was not clearly related to the number of habitat types used by the species (Fig. 3a). ΔP decreased weakly although statistically significantly with increasing numbers of habitats ($r = -0.09$; $P < 0.01$). Relative abundances decreased on average in specialist species and those with few known habitat types, while abundances increased in ubiquitous species (Fig. 3b). SES_N and number of habitat types used were significantly positively correlated ($r = 0.19$, $P < 0.001$; Fig. 3b). In addition, the range of increases and decreases was more pronounced for specialist species than for ubiquitous species.

Record numbers decreased particularly for species associated with moist habitats and coniferous forests (e.g. species-rich, sparse montane coniferous forests); in turn, species associated with dry forests and bushes increased (Fig. 4a). Least affected were species of agricultural land, which were very poor in their numbers of species already after 1970. Of the habitat specialists, those associated with coniferous forest and moist environments suffered most, while dry forest dwellers increased (Fig. 4b). Several species of lean grasslands and heaths were missing in period II, while fertilised meadows and pastures were not affected from further losses of species richness (Fig. 4c). Particularly those habitat specialist species of extensively used, historical agricultural lands, floodplains, and heathlands were not recorded in period II (Fig. 4d). Thermophilic species of with Mediterranean core areas increased in abundance, while species typical for Central Europe decreased (Fig. 5a).

3.3. Endangerment

The comparison of former (2005) and present (2025) endangerment

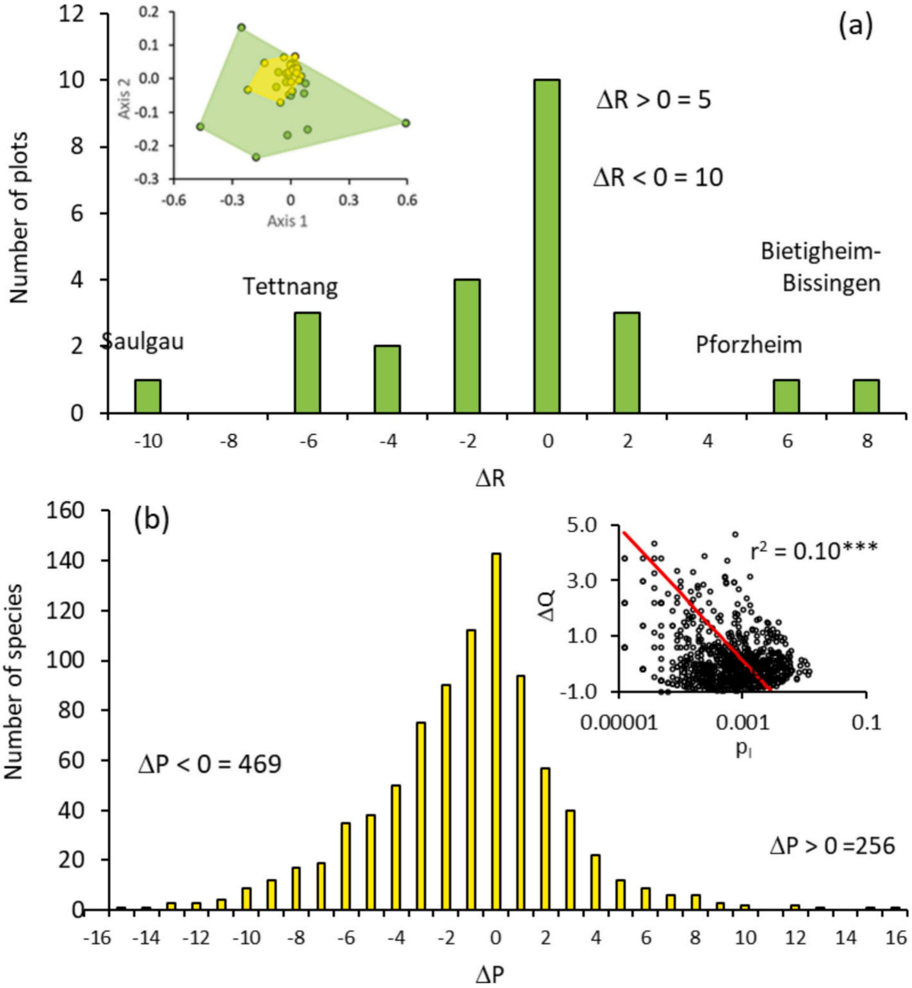

Fig. 2. Histograms of the a) number of plots with average changes in the numbers of records per species (ΔR; 817 species binned into 10 classes of width 2) and b) numbers of species with particular ΔP values (i.e. the change in number of occupied plots) binned into 32 classes of width 1. The inset in a) presents a non-metric multidimensional scaling (Euclidean distances) for period I plots (green) and period II plots (yellow) showing the much wider dispersion of species occurrences in period I. The inset in b) presents the dependence of proportional change in record number (ΔQ, Eq. (2)) against species relative abundance in period I (p_I). The negative logarithmic relationship is parametrically significant at: ***: $P < 0.001$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

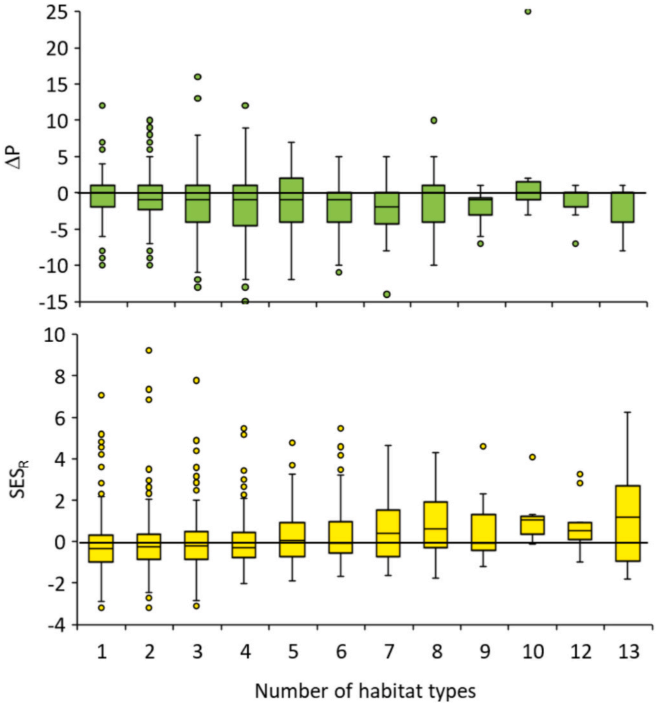

Fig. 3. Difference between study periods I and II in the a) change in number of occupied plots (ΔP) and b) standardised effect sizes (SES_R) of the numbers of records of 818 species recorded in period II according to the number of habitat types they can be encountered in. Box and Whiskers plots show median values, lower and upper quartiles, lower and upper extremes, and outliers.

status of the recorded species revealed severe shifts in IUCN status (Fig. 4b, c). With respect to records, strong positive shifts occurred towards near threatened and endangered species, while least concern, vulnerable and critically endangered species were less recorded (Fig. 4b). Numbers of critically endangered, endangered, vulnerable, and near threatened species increased by 177 species (20.4 %), while the number of least concern species decreased by 192 species (22.1 %) (Fig. 4c).

4. Discussion

4.1. Species richness

Our extrapolation results point to a generally constant species richness in time and across all study plots (Fig. 1). For some specific study plots, we even found significant increases in species richness (Fig. B2). At the first glance, these results contradict other studies recording severe losses of European insect biodiversity and abundance over recent decades (e.g. Hallmann et al., 2017; Seibold et al., 2019), also in central Europe (Valtonen et al., 2017). Recent studies on butterflies and moths showed significant losses of species richness and relative abundances in Central Europe over the past decades, particularly specialist species (Habel et al., 2016, 2019a). The latest Red List from BW (Steiner and Trusch, 2025) indicated local extinctions of at least 24 macro-moth species during the past 20 years. These seemingly contrasting results might stem from several reasons.

First, almost all of the 25 study plots of this study were located in sites of high conservation value, where a rich macro-moth fauna had to be expected. Indeed, the fact that our records contained a total of 868 species (i.e. 91.7 % of all macro-moth species so far recorded for BW since 1970) mirrors this high ecological value and relevance of these locations. Thus, only very rare or even lost species with rather specific habitat requirement or those depending on host plants not present in our plots were missing in our records. This points to an intricate pattern of species loss in diverse environments. Loss occurs in specific habitats not covered by protection or environmental management, and the remaining habitats can no longer guarantee long-term persistence due to decreasing habitat quality and reduced habitat size (Fartmann et al., 2021). Consequently, our results indicate that our study sites with many semi-natural habitats of high conservation value still harbour a diverse macro-moth fauna despite large-scale net diversity loss. They do not represent the common, agricultural landscape in most parts of Central Europe.

Second, our results highlight the common methodological pitfall of whether locally not recorded species are indeed regionally extinct, or whether these species exist in very low densities, below the detection

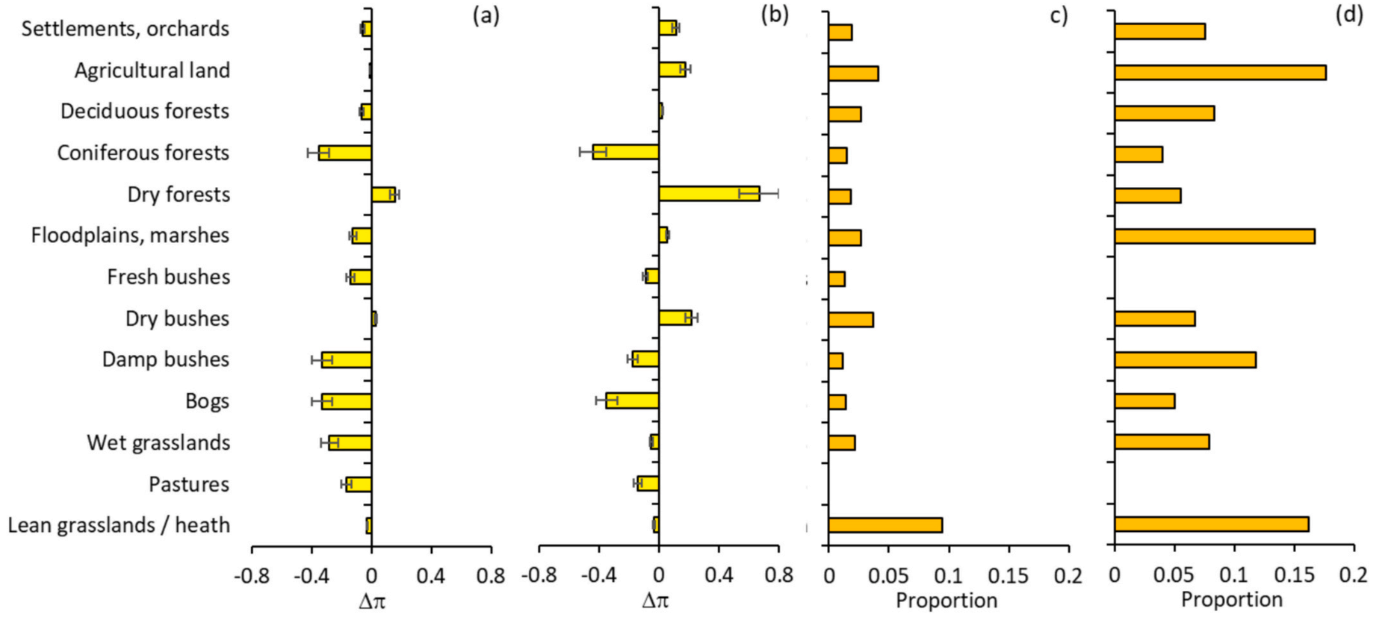

Fig. 4. a), b) Proportions of species (Δπ) associated with different habitat types with lower or higher record numbers in period II compared to the random sample prediction in period I. a) all species, b) habitat specialist species associated with only one or two habitat types. Error bars denote two standard deviations. c), d) Proportions of species (c: all, d: only habitat specialists) in each habitat category recorded in period I but not in period II.

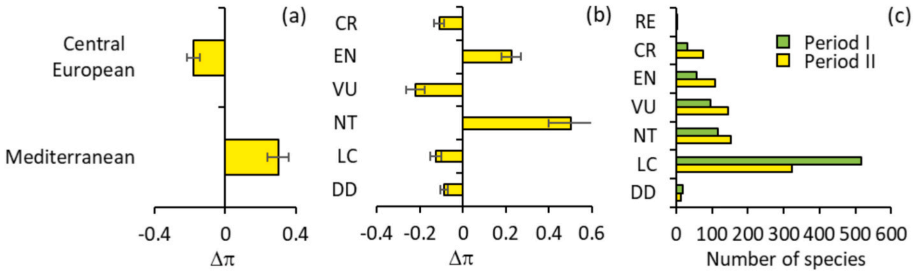

Fig. 5. Proportions of species (Δπ) with Mediterranean or Central European distribution (a) and of 2024 IUCN endangerment categories (b) with lower or higher record numbers in period II compared to the random sample prediction in period I. Error bars denote two standard deviations. C) Numbers of species in each IUCN category in periods I and II according to Ebert et al. (2005) and Steiner and Trusch (2025).

limit. There are iconic examples of so-called Lazarus species believed to be extinct while sighted again after many years, for instance the Miami tiger beetle (Knisley and Brzoska, 2018) or Wallace giant bee (Vereecken, 2018). Of course, at the regional scale, re-colonisation has to be considered and the Lazarus metaphor holds only partially. Particularly larger and mobile insects, like macro-moths, might sustain in very small, although stable local populations of only some few individuals. Therefore, richness differences in local samples, even extensive ones, might not indicate true differences in species numbers. Rather they point to differential effective sample sizes and high demographic stochasticity.

Our assessment of total species richness is based on non-parametric iChao estimates with relative wide error margins that are mirrored by the lack of an asymptotic behaviour of the rarefaction curves. Note that rarefaction might not always provide a statistically adequate adjustment and therefore must be used with care. An example is the ‘Bietigheim-Bissingen’ plot, which in period I (2,600 records) was significantly less intensively recorded than in period II with 6600 records (Fig. B2). Nevertheless, the observed species numbers are similar at 437 (pI) vs. 434 (pII), but 520 macro-moth species are calculated for period I after adjustment with rarefaction. However, such a high species richness is not realistic considering the habitat features of the respective plot. Moreover, it has to be assumed that most of the macro-moths in the respective study plots were recorded, as intensive sampling was carried out over a long period of time (e.g. Bartsch, 2019).

Similarity in community composition among study plots was much higher in period II compared with period I (Fig. 2a, inset). The number of species with reduced regional distribution in period II (i.e. 469) was almost twice the number with increased distribution (i.e. 256) (Fig. 2b). As a consequence, the dominance of common ubiquitous species like *Autographa gamma*, *Apamea monoglypha*, *Noctua pronuba*, *Xestia c-nigrum*, and *Agrotis exclamationis* has considerably increased with time. Hence, our data point to local faunistic impoverishment, which is not reflected by the pure richness data. Our findings go in line with other studies on moth species, showing long-term declines, and composition changes (see Burner et al., 2021).

4.2. *Differences among plots*

Our data revealed high variability in diversity among plots and also in the temporal trends in diversity (Fig. B2). Such site-specific trends might result from regional specificity in land-use such as farming intensity, but also from different conservation efforts, and respective intensity of data collection (Raven and Wagner, 2021; Shipley et al., 2024). Low local numbers of records (<2000) might have affected the results from five plots (Fig. B2). However, these rather low record numbers might indeed reflect the poor habitat conditions. For example, the study plots ‘Rastatt’ and ‘Graben-Neudorf’ are located in the Upper Rhine Valley and ‘Überlingen’ and ‘Tettnang’ in the Lake Constance region, both regions are characterised by severe agricultural intensification. Therefore, due to land use intensity, even the sharp decline in species richness, i.e. 438 to 247 in ‘Rastatt’, 482 to 361 in ‘Graben-Neudorf’, 366 to 240 in ‘Überlingen’ and 414 to 202 in ‘Tettnang’ appear realistic despite low record numbers in period II.

The plots with the most dramatic declines in the numbers of records (less than 30 % of records in the second period compared to the first) are all in regions dominated by rather intensive types of agriculture known for high pesticide input, in all cases accompanied with drastically reduced numbers of observed species (e.g. ‘Lauda-Königshofen’ with abundant viticulture and agriculture (451 to 304 species) or ‘Tettnang’ with intense fruit production (414 to 202)). In addition, the remaining high-quality habitats in both areas are rather small. The study plot ‘Saulgau’ (422 to 277) also must be mentioned with the generally intensive livestock farming practices in Upper Swabia combined with a strong excess of nitrogen.

In contrast, in some plots, species numbers in period II were higher than the record number corrected and estimated values for the first period, hence indicating an increased species richness (e.g. ‘St. Blasien’: 238 increasing to 347 species; ‘Todtnau’: 443 to 474; ‘Elzach’: 308 to 381, or ‘Hohenstein’: 303 to 354). All these plots are located in cool areas of Black Forest and Swabian Alb. These mountain ranges are less intensively farmed than other (lowland) regions in BW and have a significantly larger proportion of nature reserves with more extensively used ecosystems. Further, the diverse topography enables the immigration of thermophilic species to south-facing locations, while at the same time cold-adapted species survive on slopes exposed to the north, while they face population decline in landscapes with less relief. We noticed a particularly strong increase of thermophilic species especially in ‘St. Blasien’ and ‘Elzach’. Such fast range adaptations of Lepidoptera to changing temperature regimes have been reported in a number of studies (Hill et al., 2021; Hällfors et al., 2024).

Areas outside the mountain ranges with constantly high numbers of species (e.g. ‘Bietigheim-Bissingen’, ‘Pforzheim’ or ‘Freiburg’) are particularly characterised by a high diversity of habitats, in particular extensively used dry and moist open-land environments, in combination with sufficient buffer zones (often forests) adjacent to intensive agriculture. We assume that the quality of these habitats has remained high due to a more extensive agricultural, e.g. reduction in pesticides or nitrogen fertilisers (Fartmann et al., 2021). Our study underlines that trends vary strongly among local sites and depend on land-use intensity and habitat composition. These findings go in line with other recently published work on macro-moth assemblages showing different diversity responses depending on ecosystem type (Püls et al., 2025).

4.3. *Winners and losers*

We found that some few generalist species (e.g. *Autographa gamma*, *Apamea monoglypha*, *Noctua pronuba*, *Xestia c-nigrum*, *Agrotis exclamationis*) out of the 30 macro-moth species found in all study plots, tended to dominate local communities in period II (Table A1). On the other side, specialist species adapted to open landscapes, particularly of xerothermic calcareous grasslands (e.g. *Setina irrorella*, *Lasiocampa trifolii*, *Lycia zonaria*), extensively farmed mountain meadows (e.g. *Autographa bractea*, *Cucullia lucifuga*, *Photedes captiuncula*), or species adapted to extensively used wetlands (e.g. *Photedes minima*, *Mesotype parallelolineata*, *Plusia festucae*) have declined sharply (Table A1). This finding is in accordance with other studies that indicated insect communities to become increasingly dominated by some few ubiquitous species, while narrow niched habitat specialist species decline (Fox et al., 2014; Mangels et al., 2017; Gossner et al., 2023; Habel et al., 2023a; Ulrich et al., 2024).

Losers are also species depending on once extensively used meadows, such as *Lemonia taraxaci*, *Horisme aquata*, *Acosmetia caliginosa*, *Actinotia radiosa* (Karbiener and Trusch, 2022; Steiner and Trusch, 2025). These negative trends are consistent with other studies documenting a strong decline of species depending on extensively used grasslands in the same (Habel et al., 2019c) and in adjoining regions (Filz et al., 2013; Habel et al., 2016). In turn, macro-moths depending on forest ecosystems are less affected by habitat fragmentation and habitat destruction, and thus remained stable or even increased in abundance and plot occupancy over time. These findings go in line with Roth et al. (2021) and Schmitt et al. (2024) who also demonstrated mixed forest stands to be more buffered against insect decline than open landscapes. The particular loss of open land species affects not only nocturnal moths, but accounts for many species groups across the federal state of Baden-Württemberg (Lüttgert et al., 2025).

We observed an increase in the number and occupancy of rather thermophilic species (e.g. *Dysgonia algira*, *Aedia funesta*, *Helicoverpa armigera*, *Polyphaenis sericata*, *Mythimna vitellina*, *Eilema caniola* – out of 31 species of Mediterranean origin with a strong increase). In contrast, the number of cold-adapted species decreased (e.g. *Cosmotriche lobulina*, *Falcataria lacertinaria*, *Ennomos autumnaria*, *Mesotype didymata*, *Enargia paleacea* – out of 123 continental macro-moth species with a strong decrease). Similar trends have been found for other macro-moth species in other regions (Fox et al., 2014; Yazdanian et al., 2023). Thus, thermophilic species appear to be the early 'winners' of recent climate change in Central Europe. They are regionally gaining in importance and spatial coverage; those of Mediterranean origin are currently even expanding northwards, while (sub)boreal species, representing a relevant part of the continental species, currently decline or even disappear from Central Europe (Lenoir and Svenning, 2015; Rubenstein et al., 2023).

5. Conclusion

Regional number of macro-moth species remained largely stable in the analyzed high-quality nature reserves during our study period, while community composition increasingly homogenised. Many habitat specialists decreased in abundance, particularly species depending on natural habitats and traditional land-use forms (e.g. extensive pastures and meadows, soft ecotones, wetlands with no or little use). This finding highlights the strong impact of modern agriculture on insect occurrence (Thomas, 2016; Habel et al., 2019a). We hypothesise that the current increase in temperature buffers to a certain degree the trend of declining diversity as it allows the expansion of thermophilic species. Our study also suggests that an increased number of protected areas with high habitat quality could provide a further buffer. We found the best results in nature reserves of sufficient size and with minimized negative external influences to stop the currently ongoing decline of specialised species.

CRediT authorship contribution statement

Jan Christian Habel: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Conceptualization. **Robert Trusch:** Writing – review & editing, Data curation, Conceptualization, Methodology, Resources, Validation. **Oliver Karbiener:** Writing – review & editing, Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Resources, Validation. **Thomas Schmitt:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Werner Ulrich:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

We did not use generative AI at any stage of manuscript preparation.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111646.

Data availability

Data will be made available on request.

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