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Functional trait expression determines contrasting temporal trends of Lepidoptera inside and outside protected areas

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ABSTRACT

The European Biodiversity Strategy for 2030 aims at safeguarding areas that harbour high biodiversity. While such protected areas (PAs) are mainly designated with respect to plants and vertebrates, their ability to conserve invertebrates, in particular insects, is still debated. A central question is, whether PAs are able to sustain the functionality of insect assemblages, that is to preserve a rich space of functional traits. Here, we use a long-term database (1960–2022) on macro-Lepidoptera from northern Austria in combination with a newly compiled large dataset on species traits to compare temporal trends in the distributions of functional traits of butterflies and macro-moths inside and outside selected larger protected areas. We contrast temporal trajectories in the distributions of species body size, numbers of host plants, and dispersal ability. Mean species body weight significantly increased with time inside PAs, while host plant diversity and mobility increased outside PAs. Particularly monophagous species disappeared outside PAs. Total trait spaces did not significantly change in time. Overall, PAs appeared to be more conservative with respect to trait distributions than the surrounding areas and were able to retain the level of functioning as before designation.

Key-words: Environmental change, functional traits, habitat loss, Lepidoptera, protected areas, time series

Running title: Lepidoptera in northern Austrian nature reserves

INTRODUCTION

European landscapes are undergoing a rapid decline in insect abundance and diversity (Blüthgen et al., 2023; Hallmann et al., 2017; Müller et al., 2024; Seibold et al., 2019; Sinclair et al., 2024) although warning signals about insect decline reach back to the 1950th (Taylor, 1974). An increasing number of studies report on the rearrangement of insect assemblage structures towards habitat generalists (Habel et al., 2022; Harpke et al., 2025), a reordering of food webs towards omni- or polyphagous species (Bartley et al., 2019; Roth et al., 2021), and the decline of sedentary species in favour of more mobile ones (Habel et al., 2019). Additionally, climate change starts to favour species of warmer thermal niches (Colom et al., 2026; Habel et al., 2026). These trends together cause a tendency towards increasing faunal homogenisation favouring mobile and often thermophilic habitat generalists (Gonçalves-Souza et al., 2025; Gossner et al., 2023; Lewthwaite and Mooers, 2022; Ulrich et al., 2024), and towards decreasing ecosystem functionality (Polazzo et al., 2022; Zhou et al., 2023).

To counteract these trends, nature reserves and protected areas (PAs) have been established since long (Maxwell et al., 2020). In this respect, the European Biodiversity Strategy for 2030 (EEA, 2024) targets on 30 % of protected areas in the EU by 2030. Major conservation goals include the safeguarding of areas harbouring high biodiversity and the sustainment of sufficient population sizes for long-term species persistence. However, as most PAs, including the majority of European Natura 2000 sites, are rather small and often were established because of public ownership, lack of commercial interest, and low-cost management, it is unclear whether such PAs allow for long-term population persistence necessary to achieve the EEA goals (Habel and Schmitt, 2018; Spiliopoulou et al., 2023; Rodríguez-Rodríguez and Martínez-Vega, 2022; Ulrich et al., 2026a). Furthermore, many European PAs were established with respect to vegetation or to protect larger mammals and birds; their value for insect conservation remains disputed (Chowdhury et al., 2023b; Rodrigues and Rouyer, 2023).

Long-term studies about the value of European PAs for insect conservation are astonishingly rare (Geldmann et al., 2019; Habel et al., 2026; Ulrich et al., 2026a), and short-term comparative assessments are mainly focused on species richness, abundances, and the occurrence of endangered species (Chowdhury et al., 2023a). These studies returned mixed results. The meta-analysis of Coetzee et al. (2014) and work on British PAs by Cooke et al. (2023) demonstrated a generally positive effect of PAs on diversity, also for arthropods. In

turn, Geldmann's et al. (2019) compilation of more than 12,000 global PAs did not indicate convincingly that PAs increase insect diversity. For example, long-term data from seven Czech PAs revealed a loss of about 25 % of the Lepidoptera species since 1938 (Percel et al., 2025). These contrasting results partly arose from different methodology but also from the very limited faunistic knowledge about the vast majority of arthropod species, including insects. Reliable data are mainly available for some taxa, with economic importance (bees, ants, insect pests), but also ground beetles and Odonata (Wagner et al., 2021). Due to their long-lasting sample tradition, butterflies and macro-moths represent another exception (Kristensen et al., 2007).

Changes in species assemblages in general are accompanied by respective changes in the composition of species traits, and consequently of functional diversity (Lewthwaite and Mooers, 2022). Such a trait reassembly should correlate with the magnitude of environmental change, hence being most visible in agricultural and urban landscapes and comparatively low in natural and protected areas (Green et al., 2022). Indeed, some studies have already shown that PAs tend to harbour comparatively higher insect biomasses and numbers of specialist species, while generalist species dominate particularly in agricultural and urban landscapes (Sinclair et al., 2024). However, Percel et al. (2025) reported for the Czech Republic that specialist butterflies with short seasonal flight periods and moths associated with grasslands and with non-feeding adults have decreased significantly inside PAs. In contrast, the so far most comprehensive assessment of temporal trends in insect trait distributions that also included protected areas (Bourhis et al., 2025) only identified weak tendencies for increasing voltinism and decreasing habitat breath. However, both latter studies did not explicitly compare PA and non-PA areas. Thus, it remains unclear whether PAs do better than unprotected areas and which traits are favoured within PAs in comparison to the surrounding matrix.

Here, we try to fill this knowledge gap. We build on a large, long-term database on macro-Lepidoptera from northern Austria (Ulrich et al., 2026b) to compare temporal trends in the distributions of functional traits of butterflies and macro-moths inside and outside protected areas. Prior work with these data has already shown a tendency towards increasing faunal homogenisation (Ulrich et al., 2024) and species specific adaptations to increasing average annual temperatures, in particular uphill shifts of local distributions of mountain taxa (Rödder

et al., 2021), extended annual activity periods (Habel et al., 2024a), and increasing proportions of mobile, habitat generalist species (Habel et al., 2022).

In an accompanying publication, Ulrich et al. (2026c) already indicated that PAs had a comparatively higher species density than the surrounding landscape, but failed to identify PA specific assemblages. Counterintuitively, more than 25 % of mainly rare species occurred only outside of PAs. In this respect we note that most of the respective records have been collected from agricultural, urban, or forested sites. These results leave the questions of what causes this occurrence pattern and which species traits are responsible for diverging Lepidoptera assemblages inside and outside PAs. Here, we try to tackle these questions using a new compilation of important functional traits of northern Austrian Lepidoptera, including body size, feeding and habitat niches, and dispersal behaviour. We ask
1) whether PAs and non-PAs differ in their trait composition,
2) whether PA specific temporal trends in trait frequency exist, and
3) whether functional diversity increased inside PAs in comparison to the surrounding matrix.
Answers to these questions finally allow for a trade-based comparative assessment of the effectiveness of PAs to safeguard species and functional diversity.

MATERIAL AND METHODS

Lepidoptera records

We used an updated long-term data set of Lepidoptera records (butterflies and macro-moths) from the federal state of Salzburg (northern Austria) that is stored in the entomological collection of the "Haus der Natur", Museum of Natural Sciences in Salzburg (https://www.hausdernatur.at/en/; complete raw data in (Ulrich et al., 2026b). This data set contains 306,220 verified records of 1,595 butterfly and macro-moth species (incl. Tortricidae), and also 10,743 records of micro-moths representing 613 species collected at 23,746 single sample sites (Fig. 1). Records span the years 1900–2022 and cover a large altitudinal gradient (380–3105 m asl.). Sampling and verification were performed by trained entomologists (P.G., pers. comm.). Here, we use 207,955 records of the 1,595 butterfly and macro-moth species since 1960. The complete set of raw data and summary tables for each butterfly and macro-moth species is provided in the supplementary material, Appendix A: Tables A1 and A2, and in Ulrich et al. (2026b). Tortricidae are commonly subsumed under the micro-moths. We included this family in our analysis due to its high representation in the records. All other micro-moth families were not considered due to insufficient coverage.

157

158 *Species traits*

159 For all species considered, we compiled species traits, mainly from Shirey et al. (2022), Cook
160 et al. (2022), Lepiforum (https://lepiforum.org/), and diverse public Lepidoptera data bases.
161 We considered the following metric traits: minimum and maximum wing length (males and
162 females), numbers of larval host plants, and numbers of different habitat types. Additionally,
163 we used the categorical traits: dispersal ability (dispersive, intermediate, sedentary), main
164 habitat type (forested or open landscape, or both), and diet breadth (monophagous (single host
165 plant species), oligophagous (2–5 host plants), or polyphagous (> 5 host plants). From
166 minimum and maximum wing length, we calculated the average wing length and used the
167 allometric regressions implicit in Cook et al. (2022) to calculate minimum, maximum, and
168 average dry body weight. For a few missing families, own regression equations were obtained
169 from museum material. A complete list of species traits is contained in Table A3. Weight–
170 wing length regressions for all 22 families considered are provided in Table A4.

171

172 *Protected areas*

173 Austria has several categories of nature protection. Strict protection is guaranteed by Nature
174 reserves (*Naturschutzgebiete*), National Parks (*Nationalparks*), European Protected Areas
175 (*Europaschutzgebiete*), and Special Protection Areas (*Sonderschutzgebiete*). We compiled
176 data from 45 such protected areas from SAGISOnline
177 (https://service.salzburg.gv.at/ogd/client/), all established after 1970. They comprise 20.4 %
178 of the area of the state of Salzburg (Table A5, Fig. 1). About 63 % of PA area covers
179 mountain areas above 2,000 m asl., only 3 % of the area is located below 1000 m asl. (Table
180 S4). The Hohe Tauern National Park (mostly located above 2,000 m a.s.l.) comprise more
181 than half of the total PA area considered in this study (805.5 km^2). As most PAs are small
182 (area < 1 km^2) and were unequally sampled, we used a subset of five larger PAs with areas >
183 3 km^2 from which at least 8,000 records were available (Bluntautal, Hohe Tauern,
184 Kalkhochalpen, Safzachauen, Wallersee-Wenger Moor, Table A5). Summary data of records
185 for these PAs are contained in appendix A2 Tables A1 and A2. We followed Ulrich et al.
186 (2026c) and divided all records into three site categories: records from *outside* any PA,
187 records within the five PAs but *before* PA establishment, and records within a PA but after
188 PA establishment (the *inside* category).

189

190 *Data analyses*

We organised the data into three species × study year matrices, one for each site category (*outside*, *before*, *inside*), with total numbers of records as entries. As study sites were sampled differently, we could not directly use observed record and species numbers. Therefore, to compare temporal trends in species trait distributions, we use a randomisation approach and compared observed values with those obtained from a null model where species identities were reshuffled equiprobably random. Such a model retains the traits expressions and empirical sample sizes across study years but randomises annual occurrences of traits values. To answer our first starting question, we compared observed counts of traits occurrences with those expected from the null distribution obtained from 1,000 randomisations using lower and upper 5 %, 1 % and 0.1 % confidence limits of the random distribution. To answer our second starting question, we compared the observed annual trends in mean species trait expression of the three site categories with those of the random expectation and used the respective effect sizes (Δ_{trait} = observed value – expected value). To assess the magnitude of the trends, we calculated the slopes of ordinary linear regressions of observed and expected trait value and study year. Additionally, we used nested general linear models (glm linear link function, normal error structure), where study year was nested withing site category (*outside*, *before*, *inside*), to study temporal trends in Δ_{trait}. For the categorical trait variables, we used the differences of observed and expected number of occurrences as input. In all models observed, species richness served as covariate.

To answer our third starting question, we first used a 'reversed' logic to link study year as response variable directly to trait expression, site category, and mean altitude of PAs using a glm with Poisson error structure and a linear link. Then, we used Rao's quadratic entropy ρ (Botta-Dukát, 2005) to quantify trait diversity for each metric trait in each study years and again used a nested glm (linear link, normal error structure) to infer the dependence of ρ on study year (nested within site category), site category, and species richness. Study year, richness, and ρ were Z-transformed prior to analysis.

RESULTS

During the 63 years of study inside the protected areas considered here, a total of 1,036 species were recorded (annual average 129 species), outside 1,500 (annual average 542), and before PA erection 1,038 (annual average 190). This results in an average of 3.5 (± 3.0 sd)

223 records necessary to obtain a new species inside PAs, but 3.9 (± 1.9) records outside a PA.
224 Before PA erection, 3.6 (± 1.6 records) were necessary (Tables S2, A1).
225
226 Lepidoptera assemblages inside and outside PAs had contrasting temporal trajectories of trait
227 distributions. Outside of PAs, we found stronger indication for temporarily changing trait
228 distributions, while the respective signals insight PAs were much weaker, although also
229 statistically significant (Fig. 2a). Total functional diversity, in turn, did not show any
230 significant temporal trends although site categories differed ($P_{\chi 2} < 0.05$) in trait diversity with
231 respect to numbers of host plants and dry weight (Fig. 2b). Dry weight was highest inside and
232 range of host plants outside PAs (Fig. 3a, b). Number of habitats was always higher than
233 expected by the null model (Fig. 3c).
234
235 We found significant differences among the site categories with respect to the annual
236 proportions of traits (Figs. 2c, d, 3, 4). Thus, mean species body weight significantly
237 increased with time in PAs, before and after erection. Such a trend was not visible outside
238 PAs (Figs. 2c, 3). Outside PAs, average numbers of species host plants were almost always
239 higher than expected by chance and increased with time, while no such trend was visible
240 inside PAs ($P < 0.001$, Fig. 3). The mean number of species' habitats and therefore the
241 respective proportion of habitat generalist did not show significant temporal trends (Fig. 3c).
242 The number of monophagous species significantly decreased with time outside, but not inside
243 PAs (Figs. 2c, 4). Outside PAs and before PA establishment, this number was always lower
244 than expected by chance, a pattern not seen inside PAs (Fig. 4).
245
246 Outside PAs, the proportion of open landscape species was always higher than expected by
247 chance (Fig. 4a). Inside PAs, we detected a increase in open landscape species although this
248 trend was statistically not significant at the 5% error level(Fig. 4a). The proportion of
249 dispersive species significantly increased with time, outside ($P < 0.001$) and weaker inside (P
250 < 0.01) PAs. In all three categories, proportions of dispersive species were higher than
251 expected by chance (Fig. 4).
252
253 **DISCUSSION**
254 Our data from northern Austria allowed for a unique insight into Lepidoptera diversity in PAs
255 before and after establishment in comparison with non-PA areas. This approach distinguishes
256 our work from previous analyses on the fauna of protected areas (Filz et al., 2013; Habel et

al., 2016; Hallmann et al., 2017; Percel et al., 2025), or from meta-analytical studies without explicit reference to protected and non-protected areas (e.g. Coetzee et al., 2014; Habel et al., 2022). Our study is apparently the first to perform a precise analysis of PA effectiveness with respect to functional traits of insects including a comparison with surrounding areas. This allowed an answer to our starting questions whether protected areas in general, and specifically of our study region, not only safeguard species richness but also functionality, although they were not primarily selected with respect to insects (Chowdhury et al., 2023a). We recall that areas were often chosen because they were not usable otherwise.

Diversity and functional trait distributions before and after PA erection were largely similar but divergent from the pattern in the surrounding landscapes (Figs. 2–4). Locally and regionally, Lepidoptera assemblages of northern Austria are highly variable without detectable overall trends towards lower species diversity (Gros, 2023; Habel et al., 2022; Ulrich et al., 2024). According to the insurance hypothesis (Yachi and Loreau, 1999), such compositional variability is not necessarily accompanied by functional variability shifts if abundance variation is random. However, non-random environmental shifts in land-use and climate caused that compositional variation often translates into temporal trends in functioning, including our study region (Ulrich et al., 2024). Thus, less mobile ecological specialist species, in general, constantly decreased during the last decades, often despite of seemingly constant species richness (Habel et al., 2022; Percel et al., 2025; Ulrich et al., 2024). The observed resistance, not only with respect to species richness but also to functional diversity, demonstrate that the PAs analysed in this publication were apparently able to preserve their level of functioning in comparison to the surrounding non-protected areas that showed significant declines. This supports our first starting hypothesis that PAs differ from the surrounding landscape and do their job in preserving functional diversity. However, this applies only to the larger PAs considered here that, because of their size, should be able to sustain viable populations over larger time periods. In consequence, our hypothesis might not hold true for the majority of PAs in the region because smaller too small PAs might fail with such a task (Köthe et al., 2023).

Answering our second starting question, we found a significant increase in average species dry weight inside PAs, before and after designation, and therefore in the proportion of larger species. Furthermore, the average weight in PAs after designation was significantly higher than expected by chance (Figs. 2, 3). No such trend or difference was obtained outside PAs.

As the overall species richness and species composition of Lepidoptera did not markedly change in our study region during the last century (Gros, 2023), these observed differences are best explained by differential selective forces inside and outside PAs. Dry weight was significantly related to dispersal ability ($P(F_{2,1592}) < 0.001$) and also weaker to phagy ($P(F_{2,1592}) < 0.01$). Consequently, mobility was positively linked with polyphagy ($P(\chi^2) < 0.01$). Dispersive species were on average more than two times larger as sedentary species (361 mg vs. 136 mg) and polyphagous species were on average more than twice as large as monophagous ones (171 mg vs. 69 mg). Freire et al. (2021) and Beck (2008) reported similar relationships in tropical butterflies. However, although a temporal trend towards polyphagous, dispersive species occurred in- and outside PAs (Figs. 3, 4), this trend alone cannot explain the strong tendency towards larger species inside PAs as outside PAs no significant trends of species dry weight appeared (Figs. 2, 3). However, larger insects often need more time for their development, and consequently stable conditions during this period (Beukeboom, 2018), a tendency that might explain why their proportion is higher in the less disturbed PAs compared to outside, where seasonal agricultural practices, cyclic mowing, or tourism lead to increased disturbance regimes. In consequence, the higher dispersal ability inside PAs should not be the causally linked to the differences between inside and outside of PAs but just via the available time for ontogentic development.

Outside PAs, mean numbers of host plants were in most of the study years higher than expected by the null model, and the slope of the number–study year regression was significantly higher than expected by change; neither nor was observed in PAs, neither before implementation nor after (Figs. 2, 3). A similar difference between inside and outside was obtained for the proportion of monophagous species. (Figs. 2, 4). During the study period, the outside category was a mix of very different sample locations, many of them located in agricultural and urban areas. These habitats are characterised by a steady increase in habitat generalists with a high and even increasing percentage of polyphagous species (Habel et al., 2022; Ulrich et al., 2024). In turn, PAs are mostly composed of natural and semi-natural woodland habitats (e.g. mixed forests or bogs) and at higher altitude of alpine grasslands with limited human disturbance. We suspect that this difference in the mix of habitat types safeguards those Lepidoptera, which rely on specific and often rare plant species. Without appropriate habitats outside PAs, the proportion of these plants accumulate in PAs and with them the proportion of monophagous Lepidoptera. The same argument might also explain

why PAs harboured a significantly lower amount of open landscape compared to non-PA areas, where the proportion was significantly higher than expected by chance (Fig. 4).

With respect to our third starting hypothesis, we did not observe significant changes in functional diversity – as quantified by Rao's quadratic entropy, inside and outside PAs (Fig. 2). Only the number of host plants, and therefore polyphagy as an alternative proxy to functional diversity, increased significantly outside PAs. This result strengthens the notion that the Lepidoptera communities inside PAs is rather conserved than changing over time. Further, diversity and trait distributions before and after PA establishment were largely similar (Figs. 2, 4). Apparently, PAs were able to retain the level of functioning before establishment. However, we were surprised to see that outside PAs the level of functioning also remained more or less stable, despite the region-wide tendency to faunal homogenisation (Ulrich et al., 2024). It seems that the studied areas outside PAs are still sufficiently intact to harbour a functionally diverse butterfly and macro-moth fauna at a similar level as half a century before. In this context, we note that the data from outside PAs were often collected in more diverse landscapes and not in highly disturbed areas of intensive agriculture.

Our study did not trace richness and trait distributions for single PAs. The very different sample sizes across the study period in the six PAs considered would make direct richness comparisons and time series analyses challenging. Smaller PAs surely face a considerable species turnover and higher numbers of transient species from the adjacent landscape not developing in the PAs. Nevertheless, we note that an overall constant richness across PAs does not imply stable diversities in single PAs. Thus, in an earlier study, we assessed temporal richness pattern in one of the PA studied here, the Bluntautal (39 km^2), for which sufficient data were available (Habel et al., 2024b). This PA suffered a loss of nearly 50 % of butterfly species richness during the last century. Warren et al. (2021) reported extinction rates between 8 % in Great Britain and up to 29 % in the BeNeLux countries. A recent comparison of butterfly and beetle genetic diversity even reported a lower diversity inside than outside PAs (Baini and De Biase, 2025). However, this study did not control for area effects, and the observed diversities therefore might not be fully comparable. In consequence, local decline might be high despite of regionally stable richness. Metapopulation dynamics allow for a situation that a loss of local α-diversity might be compensated by higher regional species turnover (β-diversity). However, due to the accumulation of random extinctions, such a

dynamic cannot maintain long-term sustainment of diversity, and local losses on the long run also increase the probability of regional extinctions (Hanski, 1998; Yan et al., 2022).

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Statements and Declarations

Author contribution: WU developed the idea of this study, PG compiled and WU and MT analysed the data. TS and JCH gave conceptual input. WU wrote the first draft. All authors contributed to writing and data interpretation.

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Conflict of interest statement

We declare no conflict of interest.

Data availability statement

Raw data of the present study are contained in:

Ulrich, W., Habel, J.C., Schmitt, T. & Gros, P. (2023). Lepidoptera records from Northern Austria 1900-2022. Figshare: https://doi.org/10.6084/m9.figshare.23909694

Ulrich, W., Gross, P., Schmitt, T., Habel, J.C., 2026b. Sampling details for 306,220 Lepidoptera records from the Federal State of Salzburg (Austria). https://doi.org/10.6084/m9.figshare.31569034.

Appendix A1

Ethics declaration

not applicable

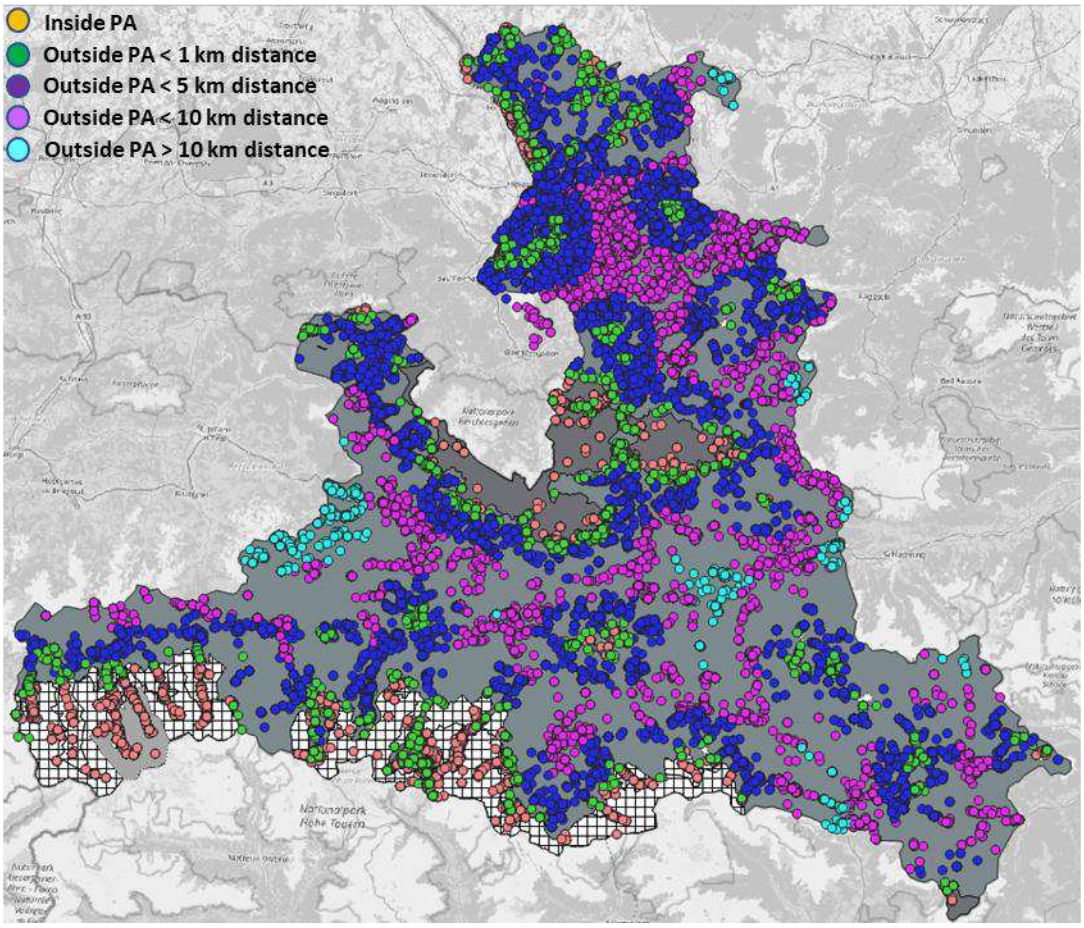
Consent to Publish declaration

not applicable

Consent to Participate declaration

not applicable

578 Figure 1. Distribution of 23,746 single Lepidoptera sample sites in the Federal State of
579 Salzburg (northern Austria) with respect to distance to the nearest protected area (PA). High
580 mountain PAs checkered white, lower altitude PAs in dark grey.
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Figure 2. a) Generalised linear modelling (glm) with time as response variable (Poisson error structure) indicates significant temporal trends in species traits. Brown bars: records outside PAs (N = 140,659), blue: records before PA (N = 33,534), green: inside PA (N = 33,640). b) Wald values of nested glm (linear link function, normal error structure) with functional diversity (Rao quadratic entropy) as response, and Z-transformed study year (nested in site category) and Z-transformed species richness as predictors. c) and d) Nested general linear models (time nested in sample classes outside, before, and inside) with species richness as metric covariate. Dependent variables are given left. Positive and negative values for partial η^2 indicate the temporal direction of response (increasing or decreasing). Maximum likelihood (a, b) and parametric significances (c, d): *: P < 0.05, **: P < 0.01, ***: P < 0.001.

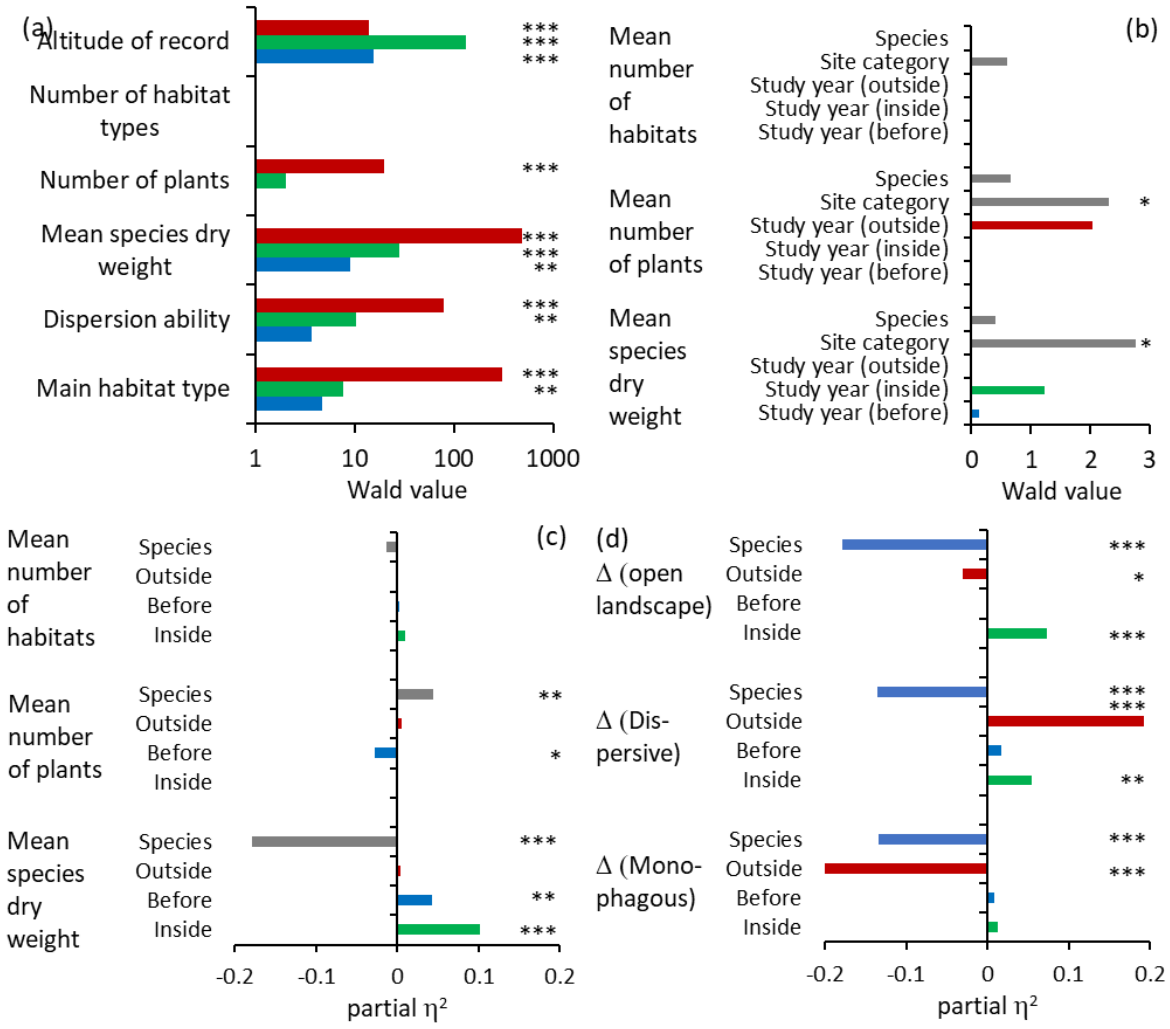


Figure 3. Temporal trends in mean species body weight (a, d, g), mean number of larval host plant species (b, e, h), and mean number of habitat types per species (c, f, i) outside protected areas (PA) (red data points: a, b, c), before PA establishment (blue: d, e, f), and after PA establishment (green: g, h, i). Grey data points denote in all plates an example of the random expectation according to a reshuffling of species identities. Regression lines refer to linear OLS regressions. Permutation significances of differences in regression slopes: ***: $P < 0.001$. Indicated are also significant differences (2×2 contingency table χ^2: $P < 0.001$) in mean traits expressions.

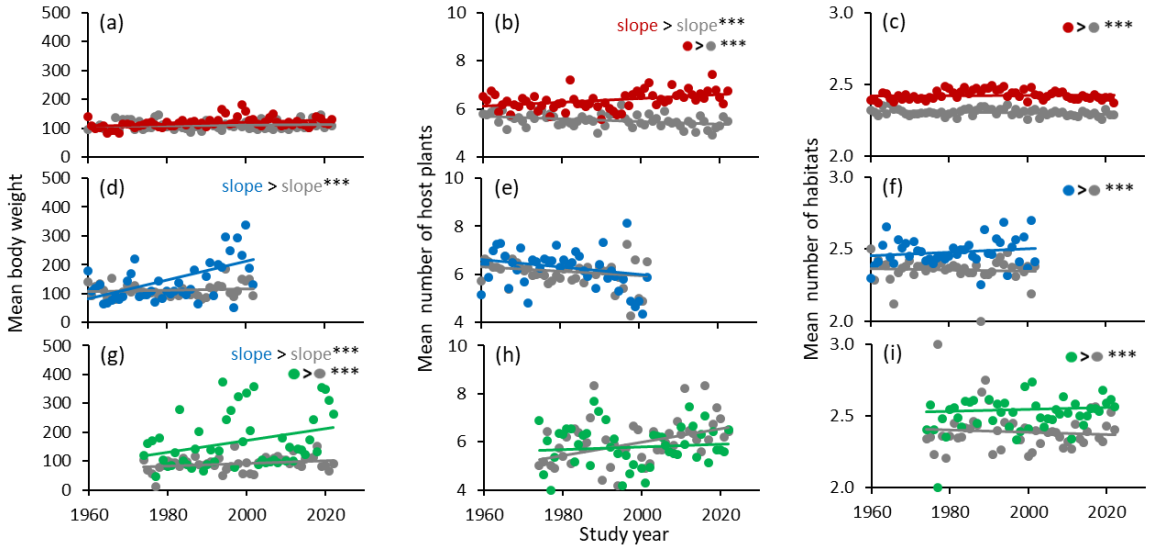
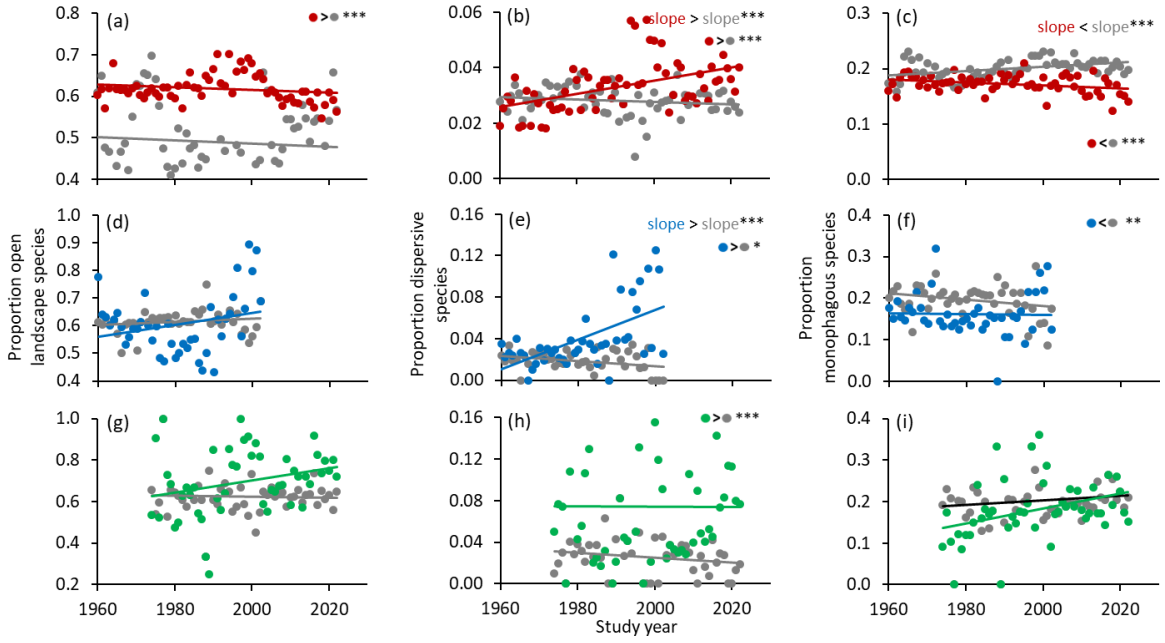


Figure 4. Temporal trends in the proportions of open landscape species (a, d, g), dispersive species (b, e, h), and monophagous species (c, f, i) outside protected areas (PA) (red data points: a, b, c), before PA establishment (blue: d, e, f), and after PA establishment (green: g, h, i). Grey data points denote in all plates an example of the random expectation according to a reshuffling of species identities. Regression lines refer to linear OLS regressions. Permutation significances of differences in regression slopes: *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$. Indicated are also significant differences (2×2 contingency table χ^2: $P < 0.001$) in the respective proportions of species.



Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- AppendixA1.xlsx
- AppendixA2.docx