ORIGINAL ARTICLE

Similar temporal patterns in insect richness, abundance and biomass across major habitat types

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Funding information
ETH board through the Blue-Green Biodiversity (BGB) Initiative (BGB2020)

Editor: Raphael K. Didham and
Associate Editor: James Bell

Abstract

1. While many studies on insect diversity report declines, others show stable, fluctuating or increasing trends. For a thorough understanding of insect trends and their effects on ecosystem functioning, it is important to simultaneously assess insect richness, abundance and biomass, and to report trends for multiple taxa.

2. We analysed insect richness, abundance and biomass data for all insects and for eight insect taxa (Buprestidae, Cerambycidae, Carabidae, other Coleoptera, Aculeata, other Hymenoptera, Heteroptera and Lepidoptera) from 42 sites across Switzerland from 2000 to 2007, representing three major habitat types in Switzerland (agricultural, unmanaged [open and forested] and managed forest habitats). As potential drivers of temporal patterns, we evaluated weather- and land-use-related factors. As predictors, we included temperature and precipitation as well as the vegetation index and the habitat type, respectively.

3. We found a consistent pattern of stable or increasing trends for richness, abundance and biomass of insects in total and the eight taxa over 8 years. Both overall patterns and six out of eight taxa (except for Cerambycidae and Lepidotpera) showed the highest values in agricultural habitats. However, when accounting for elevation, there was no difference in open habitats regardless of whether they were used agriculturally.

4. Habitat types were the most important predictors, followed by weather- and vegetation-related factors. Modelled responses to mean temperature were unimodal, whereas the standard deviation of temperature showed positive and precipitation negative effects. Longer time series are needed to draw robust inferences and to investigate potential negative effects of future warming.

KEYWORDS
agricultural habitat, climate change, forest habitat, insect decline, insect orders, NDVI, precipitation, temperature, temporal trends, unmanaged habitat

INTRODUCTION

Recently, studies on the state and temporal trends of the insect fauna (e.g., Hallmann et al., 2017; van Klink et al., 2020) have gained much scientific and public attention. While most studies of temporal trends focus on species richness and/or abundance or occupancy of single groups (e.g., Habel et al., 2019; Janousek et al., 2023; Jönsson et al., 2021), other studies focus solely on the biomass of overall

patterns without further taxonomic classification (Hallmann et al., 2017; Müller et al., 2023). The simultaneous assessment of temporal trends in species richness, abundance and biomass is rare (but see Fürst et al., 2022; Seibold et al., 2019). However, evaluating insect diversity trends and their potential consequences for ecosystem functioning and service provisioning is only possible with the joint analysis of richness, abundance and biomass data (Hallmann et al., 2021). Furthermore, to draw comprehensive conclusions, it is crucial to assess multiple groups of insects since there is little evidence for one indicator taxon, reflecting the trends of all insect taxa (van Klink et al., 2022).

As potential drivers for insect trends, climate- and land-use related factors are the most prominent (Outhwaite et al., 2022). Substantial ambiguity persists regarding the significance of drivers, their interactions and the variations in their intensity over space and time (Wagner et al., 2021). Because of their ectothermy and small size, insects are especially vulnerable to changes in ambient temperatures and humidity. Therefore, weather plays an important role in determining insect habitat use and distribution (Wilson et al., 2007). As a response to climate change, species may alter their distribution in space and/or time. The most common changes due to climate change are shifts in geographic ranges of species and a modified phenology (Wilson et al., 2007). Changes in the distribution or phenology of insects may also impact on species interactions, either leading to spatial and temporal mismatches between species, possibly involving several trophic levels, or resulting in the emergence of novel interactions between species formerly isolated across space or time (Harvey et al., 2022).

Land-use change entails habitat loss, fragmentation, agricultural intensification and abandonment of traditional land-use practices (Wagner, 2020). The intensity of land-use has been reported to strongly influence insect richness and abundance (e.g., Méndez-Rojas et al., 2021). In particular, farming practices are negatively affecting insects due to repeated mechanic disturbances and the use of fertilisers and pesticides (Wagner, 2020). Forestry practices are less detrimental because they only happen in a multi-year frequency, but they can strongly alter tree species composition and stand structure from natural states (Grove, 2002). Unmanaged habitats in the general sense or habitats in which the vegetation management is directed towards conservation goals should support high insect diversity (Frenzel et al., 2021). In general, it is expected that responses to climate and land-use change will be specific for different species. Generalist and specialist species will be affected differently, and there will be winners and losers of global change (Habel et al., 2019; Neff et al., 2022).

We considered the orders Coleoptera, Hymenoptera, Heteroptera and Lepidoptera. To obtain more nuanced patterns, we divided Coleopterans into the families Buprestidae, Cerambycidae and Carabidae and pooled the results for the remaining beetles. For Hymenopterans, we evaluated patterns for the suborder Aculeata and remaining Hymenopterans separately. We chose these taxa since they represent the major functional groups that can be found in insects, namely pollinators (all but Carabidae, Heteroptera), herbivores (all but Carabids, Aculeata), carnivores (Carabids, Aculeata, other Hymenoptera) and decomposers (Buprestidae, Cerambycidae). To explore the effects of temperature and precipitation as well as the main habitat types on insect diversity in Switzerland, we analysed annual data from 42 study sites from 2000 to 2007. The 42 sites were distributed across three habitat types: 15 agricultural and managed habitats each and 12 unmanaged habitats. The unmanaged study sites were composed of six unstocked, open study sites and six sites in unmanaged forests. Since patterns in insect trends have been shown to differ between habitats (Seibold et al., 2019), the analysis was conducted separately for the three habitat types. We considered temperature and precipitation as weather-related factors while we employed the normalised difference vegetation index (NDVI) as a land-use related factor. The latter served as a measure of vegetation cover and vegetation activity (Pettorelli et al., 2011; Weber et al., 2018).

We addressed the following questions:

1. Are there differences in the patterns of temporal trends in insect morphospecies richness, abundance, and biomass from 2000 to 2007?
2. Do patterns differ between the three habitat types agriculture, managed forest and unmanaged habitats—consisting of unmanaged open and unmanaged forested habitats?
3. Are trends similar for pooled data and for the eight different taxa?
4. Which environmental predictors are influencing trends?

MATERIALS AND METHODS

Study area and sampling

We analysed data from the Rapid Biodiversity Assessment (RBA) Switzerland (Obrist & Duelli, 2010). In this programme, insects and other arthropods were sampled on 42 study sites for a duration of 8 years from 2000 to 2007. The 42 sites represent the three major habitat types across Switzerland: 15 sites in agricultural habitats, 12 in natural unmanaged habitats (hereafter unmanaged; consisting of six open and six forested habitats) and 15 in managed forested habitats (Figure 1). Agricultural habitats were composed of arable fields ($N = 7$, including two wildflower strips) and grasslands ($N = 8$, including one hedgerow and one orchard). Unmanaged habitats were comprised of protected areas such as grasslands ($N = 4$, including one alpine meadow and a xeric grassland), wetlands (one bog and one reed habitat) and forest reserves (deciduous forest [$N = 1$], coniferous forest [$N = 1$] and mixed forest [$N = 4$]). Managed forest habitats consisted of deciduous ($N = 6$), coniferous ($N = 7$) and mixed forest stands ($N = 4$; Table S1). The sites were not distributed randomly across Switzerland with the agricultural habitats located on the Swiss Plateau and the managed forest and unmanaged habitats distributed more broadly across Switzerland (Figure 1).

Sampling was standardised across all sites. On each study site, arthropods were collected with a pitfall trap and a combination of a flight interception and a yellow pan trap (Obrist & Duelli, 2010). Arthropods were sampled weekly for 7 weeks, starting in week 24 of
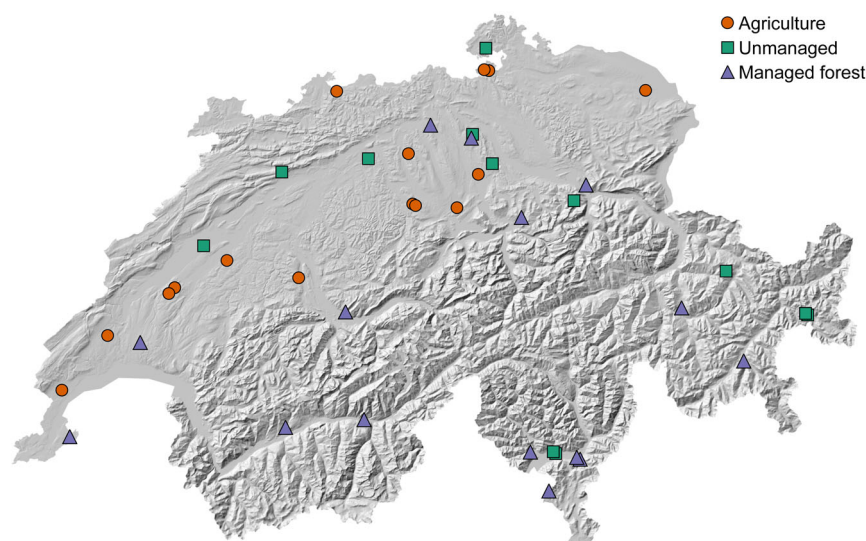
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FIGURE 1 Distribution of the 42 study sites across Switzerland. Modified from Obrist and Duelli (2010). GIS layers were obtained from the Swiss Federal Office of Topography (DHM25 copyright 2010 swisstopo, 5704 000000).

each year. The method of choosing the 'best seven weeks' is based on the results of a large sample campaign conducted in various landscapes of Switzerland (Duelli et al., 1999). Out of these 7 weeks, the samples of 4 weeks were selected for analysis to further curtail identification costs. Normally, the first and last weeks of sampling were selected so that samples comprised the whole season. Of the 5 weeks left, the two with most content were chosen to maximise the number of specimens and species. The approach of choosing 4 weeks also allowed for accounting for bad weather—if 1 week of sampling was not successful, the neighbouring week could be chosen for analysis (Obrist & Duelli, 2010). Samples were stored in 70% ethanol.

Morphospecies data

In the RBA, parataxonomic units were identified instead of species, so called morphospecies. A morphospecies consists of specimens that do not show external morphological differences. Morphospecies were sorted by entomologically trained non-specialists. For every study site, specimens were first sorted into the eight target taxa. For every taxon, specimens identified to the same morphospecies were grouped together. These groups were then counted to represent the morphospecies richness of the respective taxon on the respective study site. However, these morphospecies groups were not given identifiers, so it was not possible to compare the identity of morphospecies between the sites. Compared with traditional identification of invertebrates to species level, the morphospecies approach is more cost- and time-efficient and opens the opportunity to include insects and other arthropods in monitoring schemes without having to consult expert taxonomists. A caveat of this approach is that species with sexual

dimorphism will be counted as two morphospecies, whereas cryptic species will be considered as a single morphospecies. However, it was shown that the splitting and lumping of species averaged out and that morphospecies richness and species richness were highly correlated ($r = 0.92$) (Obrist & Duelli, 2010). Therefore, the morphospecies approach can be considered as a robust indicator of species richness. While the morphospecies approach precludes inferences about single species and the calculation of community metrics such as beta and gamma diversity since single species cannot be named, this approach is still of ecological importance as alpha diversity and functional diversity can be assessed.

Before sorting specimens into morphospecies, insects were divided into the orders Coleoptera, Hymenoptera, Heteroptera and Lepidoptera. Coleopterans were further divided into the families Buprestidae, Cerambycidae and Carabidae. All remaining beetles were lumped together into the group 'other Coleoptera'. Hymenopterans were divided into Aculeata and remaining Hymenopterans ('other Hymenoptera'). Morphospecies richness was calculated separately for these taxa. For more methodological details and a thorough discussion of the morphospecies approach, see Obrist and Duelli (2010).

Abundance and biomass data

Biomass was estimated from size calculations based on photographs of liquid samples. For each study site, photographs were taken separately for each of the eight taxa Buprestidae, Cerambycidae, Carabidae, other Coleoptera, Aculeata, other Hymenoptera, Heteroptera and Lepidoptera. All specimens of a taxon were transferred into a Petri dish that was filled with ethanol. It was ensured that specimens

were spread so that they did not overlap, and their silhouettes were clearly visible. Back light photographs were taken in a fixed photo station with a Petri dish holder (Figure S1). If a taxon consisted of many specimens, it was necessary to photograph multiple Petri dishes. For processing photographs, an application called 'Insect weight estimation tool' is being developed (Obrist et al., in preparation), which is based on the free image analysis software ImageJ (Schneider et al., 2012). With this tool, it is possible to calculate the biomass of wet samples. For each insect specimen, length, width and area were calculated and biomass was estimated with the formula

$$m = 10^{\wedge}(c + b_l * \log_{10}(l) + b_w * \log_{10}(w) + b_a * \log_{10}(a))$$

(Sohlström et al., 2018), where m is the estimated biomass, c is the intercept, b_l is the slope of the length, b_w the slope of the width, b_a the slope of the area and l, w and a the length, width and area of a single specimen, respectively. For each of the eight taxa, we used the temperate data and group-specific parameters for c, b_l, b_w and b_a were selected (supporting information 1 in Sohlström et al., 2018 and Table S2).

Environmental predictors

We considered both weather- and landscape-related predictors for morphospecies richness, abundance and biomass, which were estimated for each of the 42 study sites. As weather-related predictors, we chose temperature and precipitation. For both predictors, the mean and standard deviation (SD) across the vegetation period (March–July) of the sampling year were calculated from monthly data. The NDVI was employed as a landscape-related predictor to have a measure of the distribution of vegetation and the vegetation activity (Pettorelli et al., 2011; Weber et al., 2018). The NDVI was calculated for buffers of 50 and 200 m, and the yearly mean, median, minimum, maximum and SD were calculated for each buffer. In total, this amounted to two predictors each for temperature and precipitation and 10 predictors for NDVI, respectively. We analysed correlation plots between these predictors and morphospecies richness, abundance and biomass. For each group of predictors (temperature, precipitation, and NDVI), we chose the one that correlated best with morphospecies richness, abundance and biomass, respectively. We performed this analysis for all insects in total and for each of the eight taxa (Figures S2–S4). A more detailed description of the environmental predictors can be found in Table S3.

Data analysis

All statistical analyses were conducted in R v. 4.2.2 (R Core Team, 2022). The distribution of total morphospecies richness, abundance and biomass as well as the distribution of the eight taxa over time were analysed with generalised linear models (GLMs), employing a Poisson error distribution for count data and the Gaussian family for logarithmic data.

When overdispersion was detected for count data, we used a negative binomial error distribution. To account for extreme variation in the data, abundance and biomass data were log-transformed ($\log(x + 1)$) prior to analysis. For abundance and biomass, data were missing for the taxon 'other Coleoptera' in the years 2000 and 2001 and for Aculeata and 'other Hymenoptera' in the year 2005. To compute trends for these groups, we, therefore, calculated linear equations without these years and then estimated the missing values. For calculating total abundance and biomass trends, these missing values were included as data points. To check whether there were differences between the trends in agricultural, managed forested and natural unmanaged open and forested habitats, the Tukey post hoc test was computed with the 'glht' function of R package 'MULTCOMP' (Hothorn et al., 2008).

For modelling, missing years were handled as missing data. The relationship between morphospecies richness, abundance and biomass (pooled for all insects and separately for the eight taxa) was analysed with correlation plots. Correlation analyses were also used as a first step to explore the relationship between the response variables morphospecies richness, abundance and biomass and the environmental predictors. For each group of environmental predictors, we selected the predictor with the highest correlation with the respective response variable. Correlation plots for morphospecies richness, abundance and biomass including all predictor and response variables can be found in the supplement (Figures S2–S4). To determine the environmental drivers behind trends, we conducted multivariate analysis. Environmental predictors were assessed for total morphospecies richness, abundance and biomass data, and for the eight different taxa, respectively. All environmental predictors as well as the study year and the habitat—a categorical variable with the three levels 'agriculture', 'unmanaged' (consisting of open and forested habitats) and 'managed forest', where 'agriculture' was used as the intercept—were included as fixed effects in the models, whereas the study sites were included as a random effect. In addition to linear terms, we also added quadratic terms of mean and maximum temperature and mean, maximum, median and minimum NDVI to our models to also account for possible unimodal relationships between these predictors and the response variables. All explanatory variables were standardised with the 'scale' function by subtracting the mean and division by the SD prior to analysis. Models were computed with the 'glmmTMB' package (Brooks et al., 2017), and the full models were documented. In addition, we also tested for a unimodal effect of the year variable by computing GAMs (generalised additive models) instead of GLMs. For illustrating effect sizes of predictors, joint forest plots for morphospecies richness, abundance and biomass were calculated with the 'plot_summs' function of the 'jtools' package (Long, 2022). We calculated response curves for each significant predictor by inserting its coefficients of the quadratic and linear terms in the parabolic equation $f = ax^2 + bx$, with a being the coefficient of the quadratic term and b the coefficient of the linear term, respectively. Response curves were computed along the range of the respective predictor. For morphospecies richness, where we employed a Poisson or negative binomial error distribution, f was a logarithmic function, which was exponentiated to facilitate interpretation.
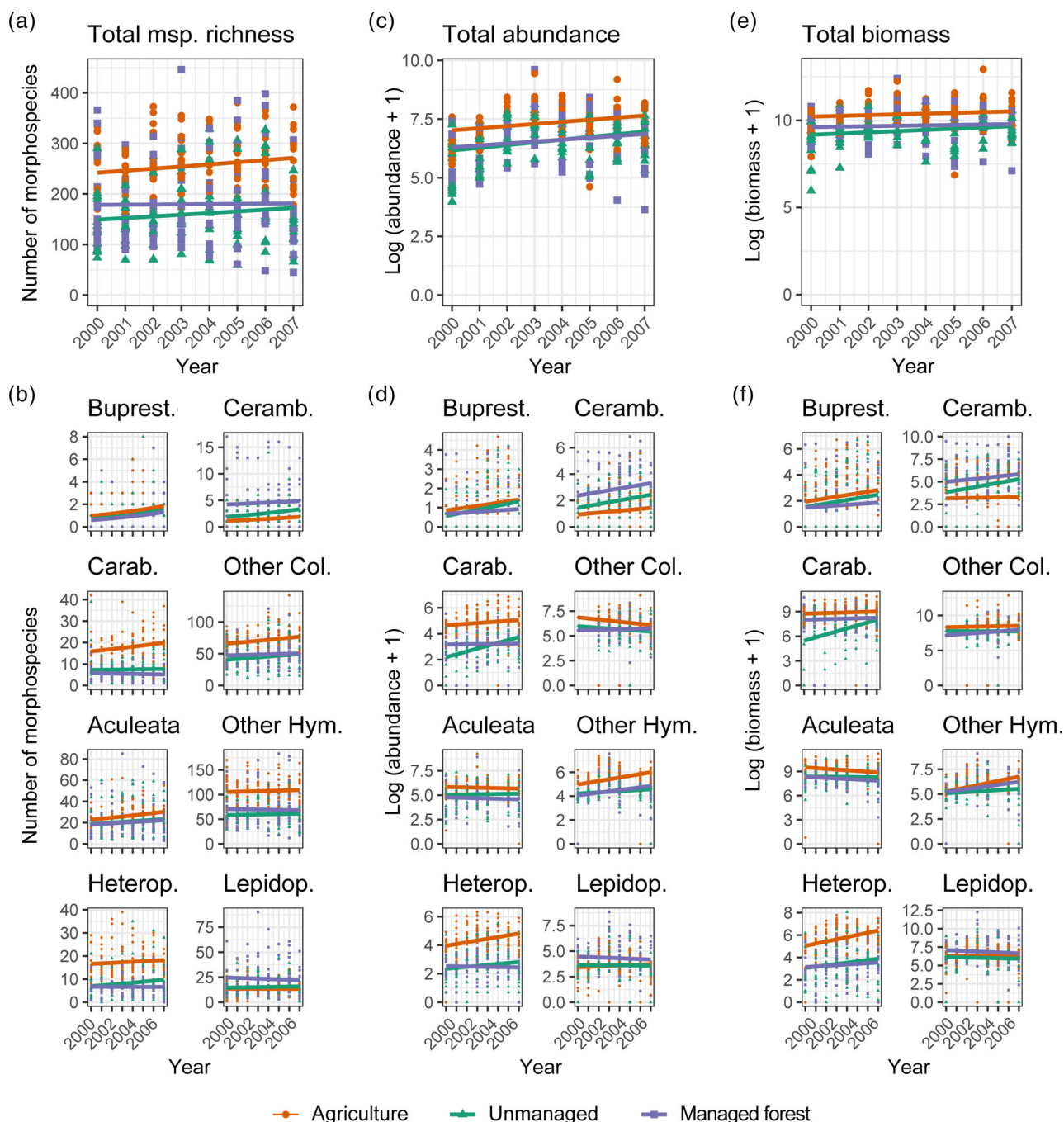
FIGURE 2 Patterns of insect morphospecies richness, abundance and biomass in the three habitats 'agriculture', 'unmanaged (open and forest)' and 'managed forest' for the years 2000–2007. (a) Total number of morphospecies; (b) number of morphospecies for different taxa; (c) total abundance; (d) abundance for different taxa; (e) total biomass and (f) biomass for different taxa. Colours denote the three different habitats 'agriculture' (red), 'unmanaged' (green) and 'managed forest' (purple). Dots represent original measurements for each study site. Trend lines were computed with GLMs. Buprest., Buprestidae; Carab., Carabidae; Ceramb., Cerambycidae; Heterop., Heteroptera; Lepidop., Lepidoptera; Other Col., Other Coleoptera; Other Hym., Other Hymenoptera.

RESULTS

Morphospecies richness, abundance and biomass of insects showed stable or increasing trends with time across agricultural, unmanaged (open and forested) and managed forested study sites from 2000 to 2007, both pooled for all insects and on the level of individual taxa (Figure 2 and Table S4). Total morphospecies richness showed increasing trends in agricultural habitats. For total abundance, increases occurred across all three habitat types, while biomass showed an increasing trend in unmanaged habitats ($p < 0.05$, Table S4). Trends in the remaining habitats were stable (morphospecies richness: managed forest: $p = 0.89$, unmanaged: $p = 0.25$; biomass: agriculture: $p = 0.173$, forest: $p = 0.452$, Table S4).

Overall, the highest richness, abundance and biomass were found in agricultural habitats compared with unmanaged habitats and managed forest habitats (Tukey post-hoc test, agriculture compared with unmanaged: $p < 0.05$; agriculture compared with managed forest: $p < 0.05$, Figure 2a,c,e and Table S5). Carabids, other Coleopterans, Aculeate Hymenopterans, other Hymenopterans and Heteropterans mirrored the overall pattern of highest morphospecies richness, abundance and biomass in agricultural habitats (Figure 2b,d,f and Table S4 and S5). For Buprestidae, richness, abundance and biomass were higher in agricultural habitats compared with forested habitats, whereas there was no difference between the other habitat types (Figure 2b,d,f and Table S5). Cerambycids and Lepidopterans deviated from this pattern: both groups showed the highest morphospecies richness and abundance in forested habitats (Figure 2f and Table S5).

A minority of single taxa had negative year coefficients, implying negative trends over time (Table S4). However, none of these trends were significant and were thus labelled as stable trends (Table S4). In general, spatial variation between the study sites within years was larger than temporal variation among years (Figures 2 and S5). Within-year variation was more pronounced for morphospecies richness (mean = 202, SD = 81) than for abundance (mean$_{\log(\text{abundance}+1)}$ = 6.85, SD$_{\log(\text{abundance}+1)}$ = 0.99) and biomass (mean$_{\log(\text{biomass}+1)}$ = 9.86, SD$_{\log(\text{biomass}+1)}$ = 0.91; Figure S5). When unmanaged closed and unmanaged open habitats were considered as two separate habitat types, morphospecies richness was higher in unmanaged open than in unmanaged closed habitats, whereas there was no difference between these two habitat types for abundance and biomass (Figure S6 and Table S6). Morphospecies richness, abundance and biomass were consistently higher in agricultural habitats compared with unmanaged open and unmanaged closed habitats and when comparing agriculture with managed forest (Figures S6 and S7 and Table S6). The elevational distribution of the habitat type agriculture, unmanaged open, unmanaged closed and managed forest showed that study sites in agricultural habitats were on average located at lower elevations and had the narrowest, whereas unmanaged open habitat displayed the widest elevational extent, spanning the whole elevational gradient (Figures S8 and S9). When only considering the elevational extent where both agricultural and unmanaged open habitats overlapped, there was no difference between the two habitat types (Figure S9). Temperature and elevation were strongly correlated (mean temperature $\sim$ elevation: $r = -0.79$). Furthermore, we looked at the two main types of agricultural habitat—arable land and grassland—separately. Trends did not differ between these two categories for total morphospecies richness, abundance and biomass (Figure S10). When we grouped the habitat types into open (agriculture and unmanaged open) and closed habitats (unmanaged closed and managed forest), open habitats mostly showed higher morphospecies richness, abundance and biomass than closed habitats, except for Cerambycids and Lepidopterans where metrics were higher in closed habitats. The biomass of Carabids and other Hymenopterans did not differ between the open and closed habitats (Tables S7 and S8 and Figure S11). Moreover, when we grouped the habitat types into managed (agriculture and managed forest) and unmanaged habitats

(unmanaged open and unmanaged closed), managed habitats either displayed higher values than unmanaged habitat, or there was no difference between management types (Tables S9 and S10 and Figure S12). All trends were stable or increasing with time.

Total abundance and biomass were more strongly correlated ($r = 0.71$, $p < 0.05$) than morphospecies richness and abundance ($r = 0.41$, $p < 0.05$) and morphospecies richness and biomass ($r = 0.35$, $p < 0.05$), respectively (Figure S13a). Single taxonomic groups also consistently showed stronger correlations between abundance and biomass than between morphospecies richness and the two other metrics (Figure S13b–i).

For total morphospecies richness, abundance and biomass, different predictors were significant in the models (Figures 3 and 4). Predictors related to temperature and precipitation as well as habitat types were consistently significant across the three metrics. For total morphospecies richness, the relationship with mean temperature was unimodal, whereas for total abundance and biomass, the SD of the temperature was more strongly correlated than mean temperature and showed a positive relationship. For total morphospecies richness, agricultural habitat displayed the highest optimum temperature ($T = 14.4°C$), followed by managed forests ($T = 13.3°C$) and unmanaged habitats ($T = 11.1°C$, Figure S14). Total morphospecies richness and total abundance displayed a negative relationship with mean precipitation and total biomass with the SD of precipitation, respectively. The year effect was positive, both for total morphospecies richness and for total abundance (Figures 3 and 4). In comparison to agricultural habitats, lower morphospecies richness, abundance and biomass were found in unmanaged habitats and managed forest habitats. NDVI was not significant for all three metrics (Figure 3).

When predictors were compared among total morphospecies richness, abundance and biomass and the eight different taxonomic groups, a common pattern emerged (Table 1 and Figures S15–S30): Weather-related predictors were more often significant than vegetation-related predictors. With regard to the former, the effects of the mean temperature showed an optimum between 10 and 12°C across the vegetation period (March–July) and the effects of the SD of temperature were always positive. The effects of the mean or the SD of precipitation were always negative, except for biomass of Cerambycids, where the effect of mean precipitation was positive. The habitat variables were negative—that is, a lower morphospecies richness, abundance and/or biomass were found in unmanaged and managed forest habitats compared with agricultural habitats—for all taxa but Cerambycids and Lepidopterans. Different parameters of NDVI had a positive effect on morphospecies richness of other Coleopterans (max NDVI in 200 m Buffer), morphospecies richness and abundance of Aculeata (SD NDVI in 50 m Buffer) and abundance and biomass of Heteropterans (SD NDVI in 200 m Buffer), respectively. The year variable was the most common predictor and positive in most cases except for abundance and biomass of Aculeate Hymenopterans and for all three metrics of Lepidopterans (Table 1). The year variable was still positive after controlling for temperature. The year variable and temperature were not strongly correlated (year $\sim$ mean T: $r = 0.2$). When using a GAM instead of a GLM to allow for
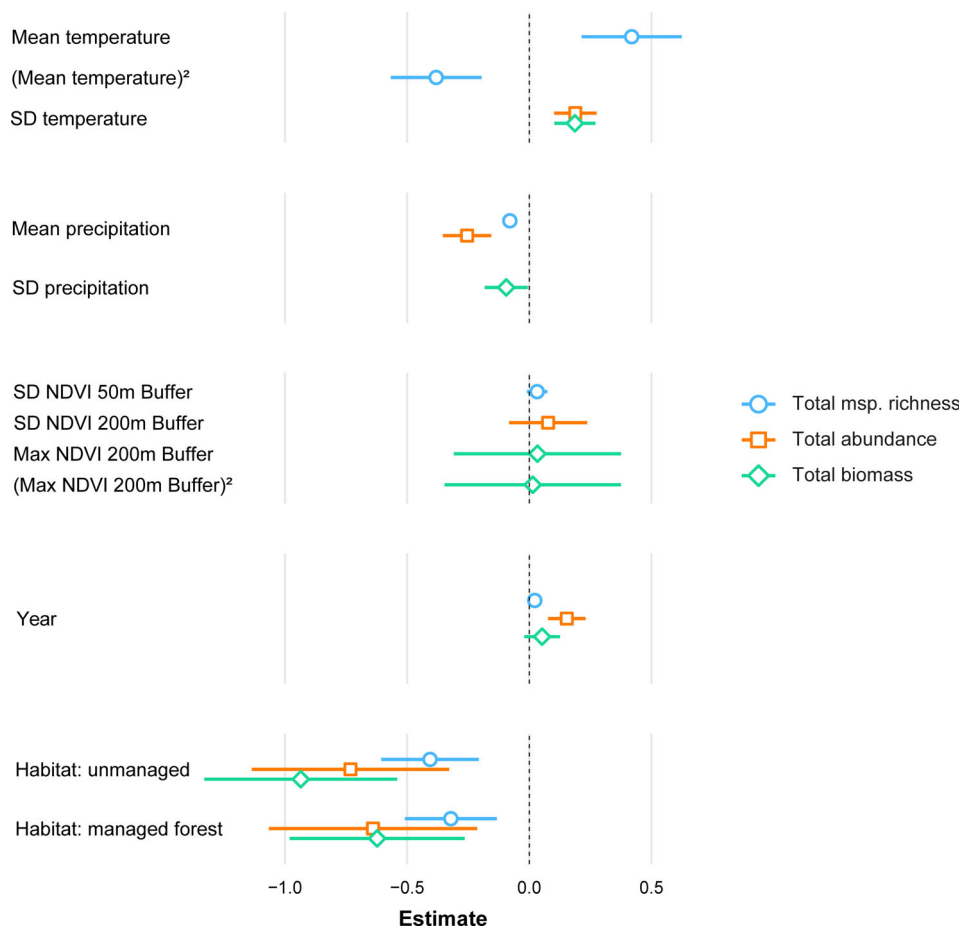
FIGURE 3 Effect sizes of scaled predictors for total insect morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor, the coefficient and its 95% confidence interval are shown.

more flexible responses, we found that a unimodal effect of year fitted the data better than GLMs (Figure S31). Especially for abundance, the GAMs reflect that the highest values were found in the heat year of 2003 (Obrist & Duelli, 2010). However, the smoothing term s(year) was never significant. GAMs yielded the same results as GLMs: the highest morphospecies richness, abundance and biomass were found in agricultural habitats (Figure S31).

DISCUSSION

In this study, we compare patterns in morphospecies richness, abundance and biomass of insects, both pooled for all insects and separately for eight different taxonomic groups, from 2000 to 2007. We found stable or increasing trends for total morphospecies richness, abundance and biomass as well as across the taxonomic groups Buprestidae, Cerambycidae, Carabidae, other Coleoptera, Aculeata, other Hymenoptera, Heteroptera and Lepidoptera. For the pooled data and for most taxa, the highest richness, abundance and biomass occurred in agricultural habitats. Only taxa that are known to be forest dwellers, such as Cerambycids (Linsley, 1959), showed highest values in forested habitat. Unexpectedly, also Lepidopterans predominantly

occurred in forested habitats, which is most likely due to the preponderance of forest moths.

While a time series of 8 years is not long enough for an extrapolation into the future, it allows us to compare the temporal variation in morphospecies richness, abundance and biomass and their dependence on weather- and land-use related environmental predictors. The simultaneous assessment of the three metrics richness, abundance and biomass and the consideration of multiple taxa are rare, although called for (Seibold et al., 2021).

Our findings seem to contradict the common finding of declining insect richness with time (e.g., Hallmann et al., 2021; Homburg et al., 2019; Powney et al., 2019). For both overall diversity patterns (Hallmann et al., 2017; Seibold et al., 2019) and for different insect taxa, declining patterns are common, also during the 8 years we covered (Habel et al., 2019; Halsch et al., 2021; Janousek et al., 2023). Across beetle families (Hallmann et al., 2020; Harris et al., 2019), and more specifically for Carabids (Brooks et al., 2012; Homburg et al., 2019) and a Cerambycid (Baur et al., 2020), declining patterns with time have been reported. The same was true for Hymenopterans (Bartomeus et al., 2019; Ollerton et al., 2014) and Lepidopterans, especially for moths (Bell et al., 2020; Fox, 2013; Fox et al., 2014; Habel et al., 2019; Macgregor et al., 2019). However, temporal trends
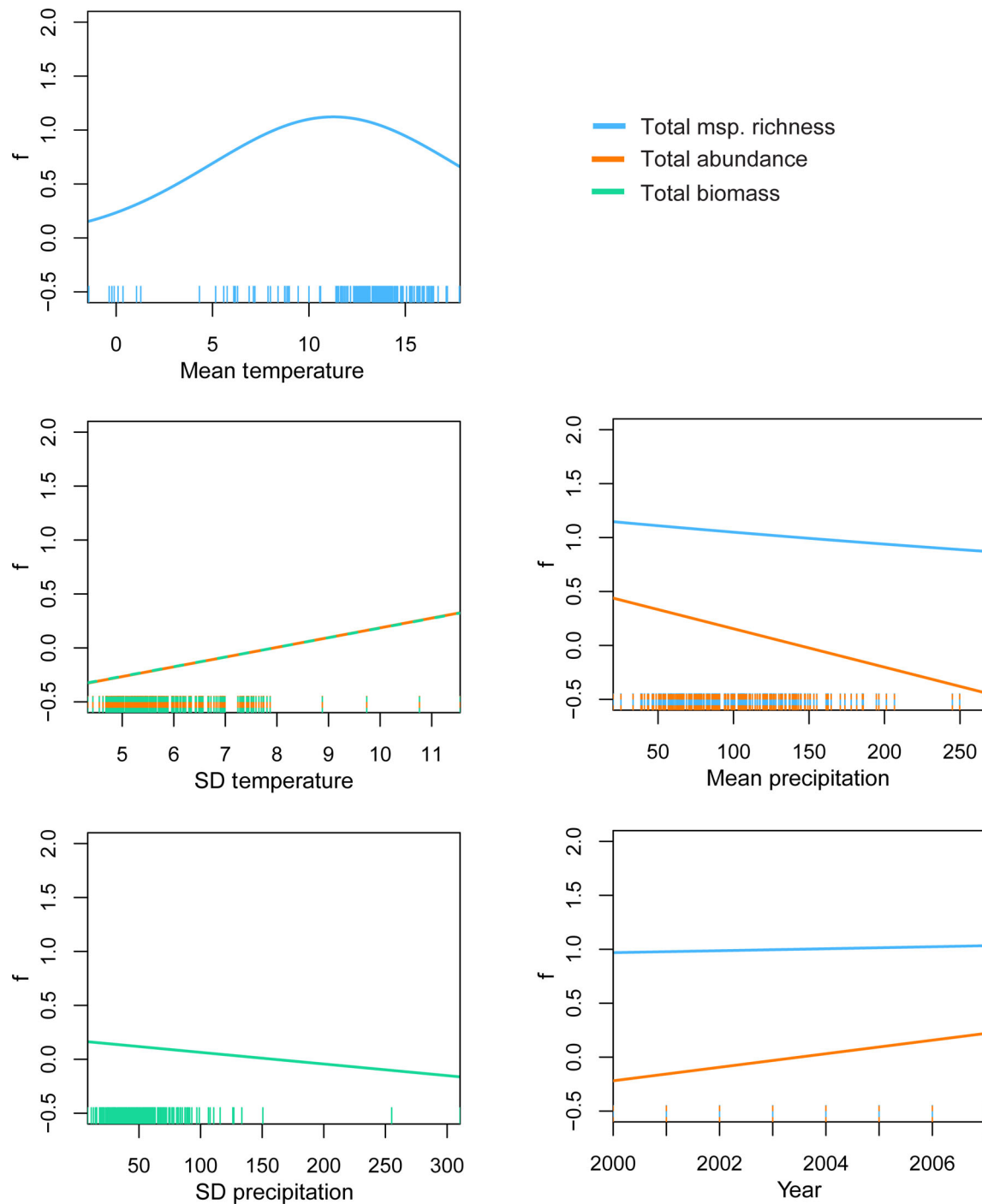
FIGURE 4 Response curves of significant predictors for total morphospecies richness (blue), abundance (orange) and biomass (green). f shows the response curve of the predictor. If quadratic terms are included it follows the form $f = ax^2 + bx$, where a and b signify the coefficients of the quadratic and linear terms of the predictor, respectively. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines in colour indicate the distribution of data points across the range of each predictor. Total msp. richness = total morphospecies richness. The response to the categorical habitat variables is not shown. Mean and standard deviation of temperature (°C) and precipitation (mm) refer to the vegetation period (March–July).

are context- and taxon-specific, and cannot be generalised—there are multiple examples of complex patterns of insect diversity change with time (Engelhardt et al., 2022; Macgregor et al., 2019; Outhwaite et al., 2020). For example, Heteropterans have been shown to display stable and increasing trends with time (Ewald et al., 2015; Hallmann et al., 2020). Interestingly, also in studies mainly reporting declines, there are exceptions to this finding, particularly when multiple habitats are considered. For example, moths across Great Britain declined in coastal, urban and woodland habitats, whereas trends fluctuated around zero in farmland and parkland habitats (Bell et al., 2020).

TABLE 1 Overview of predictors and direction of effects; positive (+), negative (−) or unimodal (∩) for total morphospecies richness, abundance and biomass as well as for different taxa.

Predictor	Total			Bupres.			Ceram.			Carab.			Oth. Co.			Aculeat.			Oth.Hy.			Hetero.			Lepido.		
	M	A	B	M	A	B	M	A	B	M	A	B	M	A	B	M	A	B	M	A	B	M	A	B	M	A	B
Temperature																											
SD		+	+	+	+	+	+	+	+								+	+		+	+				+	+	+
Mean	∩									∩			∩						∩			∩					
Maximum ∩	11.3									10.8			10.5						11.4			11.9					
Precipitation																											
SD			−						+		−	−		−	−		−							−			−
Mean	−	−											−			−	−	−	−			−			−	−	−
NDVI																											
Max 200 m													∩														
Maximum ∩													−1.8														
SD 50 m																+	+										
SD 200 m																+	+										
Year	+	+		+	+	+	+	+		+	+	+	+			+	+	−	+	+	+	+	+	+	−	−	−
Habitat																											
Agric:unmang.	−	−	−				+			−	−	−	−	−		−	−	−	−	−		−	−	−			
Agric:forest.	−	−	−				+	+	+	−					−	−	−	−	−	−		−	−	−	+	+	+

Note: The rows 'Maximum ∩' give the optimum value for unimodal relationships. For the eight individual taxa, this table summarises Figures S15–S30.

Abbreviations: −, negative effect size; +, positive effect size; A, abundance; Agric:forest., agricultural habitat in comparison to managed forest; Agric:unmanaged, agricultural habitat in comparison to unmanaged habitat; B, biomass; Bupres., Buprestidae; Ceram., Cerambycidae; Hetero., Heteroptera; Lepido., Lepidoptera; M, morphospecies richness; NDVI, normalised difference vegetation index; Other Co., other Coleoptera; Other Hy., other Hymenoptera; total, total morphospecies richness/abundance/biomass.

Another study on British moths found no declines in arable land compared to declines in woodland and in grassland (Macgregor et al., 2019). Similarly, for Carabid beetles, in contrast to moorland and pasture, trends in woodland and hedgerow habitats were increasing (Brooks et al., 2012). For Buprestidae, studies on temporal trends are missing so far.

Other recent studies from Switzerland show no overall increases or decreases in insect occupancy over 40 years (Neff et al., 2022) and increases in an agricultural landscape when three points in time (1987,1997 and 2019) were compared (Fürst et al., 2022). Furthermore, we also found stable and increasing trends when looking at aquatic insects in Switzerland (Gebert et al., 2022). The finding that the highest richness, abundance and biomass were found in agricultural habitats was surprising. Apparently, Swiss agricultural landscapes can sustain high levels of taxa predominantly occurring in open habitats, such as Carabid beetles and most other beetles, the pollinators among Aculeata and other Hymenopterans as well as Heteropterans. In international comparison, Swiss agricultural landscapes are characterised by relatively small fields and a heterogenous landscape mosaic, which could have positive impacts on insects (Groher et al., 2020; Outhwaite et al., 2022). Moreover, the higher average temperatures in open habitats compared with closed habitats could have positive effects on insects (Figures S32–S34, Matuszewski et al., 2013). When we separated sampling sites in unmanaged habitat into unmanaged open and unmanaged closed habitats and thus considered four habitat types (agriculture, unmanaged open habitat, unmanaged forest habitat and managed forest), we still consistently found higher values for morphospecies richness, abundance and biomass in agricultural compared with unmanaged open habitats. This result is most likely a consequence of the diverging elevational distributions and the concomitant different temperature ranges of agricultural versus unmanaged open study sites. While agricultural study sites were consistently located at the Swiss Plateau at elevations between 285 and 818 m asl, unmanaged open study sites spanned elevations from 199 to 2549 m asl. While morphospecies richness, abundance and biomass were thus stable across elevations for agricultural habitats, values decreased with increasing elevation and accompanying decreasing temperatures for unmanaged habitats (Hodkinson, 2005). When comparing sites from the same elevation, there was no difference between the agricultural and open unmanaged habitats. It is, therefore, important to consider elevation in comparisons across habitats. In addition, we pooled the habitat types into open (agricultural and unmanaged open habitats) and closed (unmanaged closed and managed forest habitats) as well as into managed (agricultural and managed forest habitats) and unmanaged habitats (unmanaged open and closed habitats). We mostly found higher morphospecies richness, abundance and biomass in open and managed habitats, respectively, mirroring the highest diversity metrics in open, agricultural habitats. Unlike Uhler et al. (2021), we did not find different patterns when we looked at the two main categories of agricultural habitats separately, that is, arable fields and grasslands, which may be due to similar abiotic conditions in these two open habitat types.

Regarding the drivers behind trends for both total patterns and the eight taxa, weather-related factors were more important than vegetation-related factors. While we found positive effects of temperature variability, as indicated by the SD, responses to the mean value showed an optimum between 10 and 12°C. This indicates that increasing global warming as well as long periods with stable temperatures can be expected to have negative effects on the investigated taxa (Deutsch et al., 2008). Responses to the mean or SD of precipitation were, with one exception, consistently negative. Negative effect sizes of precipitation could indicate that wetter conditions during the collection period might reduce insect activity and increase larval mortality (Roy et al., 2001). Max NDVI is a proxy for landscape productivity (Parviainen et al., 2010), which is mainly influenced by climate in Switzerland, whereas SD NDVI is a proxy for agricultural intensity (Weber et al., 2018). SD NDVI was higher on study sites dominated by agriculture and could thus reflect the general positive impact of open habitat on insect morphospecies richness, abundance and biomass. In addition to testing for the existence of linear trends with the GLMs, we also tested GAMs that can describe more flexible temporal responses. The higher flexibility leads to a better fit to the data. The resulting models exhibit a unimodal effect of year, especially for abundance, with an optimum around the year 2003, which was especially warm (Obrist & Duelli, 2010). We decided to use GLMs to better reflect the trends across the whole time period without putting too much emphasis on this rather exceptional year.

When we compared the relationship between richness, abundance and biomass, abundance and biomass were the most strongly correlated, a pattern also found by Vereecken et al. (2020) when assessing multiple biodiversity metrics for wild bees. In contrast, context-specific relationships between richness and biomass have been reported (Uhler et al., 2021). Of all three metrics, abundance is most useful in a conservation context as an early warning indicator of population changes, whereas species richness is more robust to short-term disturbances, since, usually, declines happen before a species' absence (Beever et al., 2013). Even though, so far, only few studies simultaneously assessed insect richness, abundance and biomass patterns (Fürst et al., 2022; Seibold et al., 2019), it is paramount to move beyond exclusive richness or biomass studies to contribute to a better understanding of insect diversity trends and how they will impact on ecosystem functioning and service provisioning (Seibold et al., 2019).

A limitation of our study is that we only had data covering a time series with eight time points (Didham et al., 2020). There is wide consensus that a time series of at least 10 time points is necessary to observe population trends (White, 2019). However, especially for insects, even such a 'ten-year rule' might not be sufficient to mirror true population trends because of their high population variability (Fox et al., 2019). Nevertheless, for a short time series with eight time points, we found consistent patterns of stable or increasing trends across taxonomic groups. However, our findings cannot be generalised or extrapolated beyond the 8-year study period. Furthermore, the morphospecies richness approach does not allow for species identification. Therefore, community composition, gamma diversity and the robustness of trends could not be assessed (Wauchope

et al., 2019). However, with the morphospecies approach, the number of species and thus alpha diversity can be obtained in a cost-effective and reliable manner (Obrist & Duelli, 2010), and sampling was conducted in a rigorously standardised way (Seibold et al., 2021). Even though the morphospecies richness approach is restricted to mainly common, generalist taxa, these taxa are functionally important, probably more so than rare specialist taxa (Obrist & Duelli, 2010). We cannot preclude that there might be different patterns if true species richness and thus rare taxa were included in the analysis. However, this is not possible with the chosen methodology.

In conclusion, our study highlights the value of multi-annual, multi-taxa insect surveys across different habitats. We show general differences among main habitats and that mainly weather variables explain the stable and increasing trends for overall insect morphospecies richness, abundance and biomass, as well as for the different taxa. Warming ambient temperatures because of climate change seem to be obvious drivers of increasing insect trends, which has recently been confirmed in other studies from Switzerland in aquatic (Gebert et al., 2022) and terrestrial habitats (Fürst et al., 2022; Neff et al., 2022). However, further warming in combination with frequent drought events may have negative effects on insects, as shown by Scherber et al. (2013) and indicated in the unimodal response of morphospecies richness to temperature in this study. Within the climate range of our study area, already nowadays most study sites are located above the optimum temperature and thus can be expected to lose morphospecies richness with future warming. Conversely, abundance seems to be promoted by higher temperature variability and less precipitation. However, we cannot rule out different responses in other climates or across more extended gradients. Furthermore, the relative importance of different habitats for the insect fauna may change in the future as land-use is strongly influenced by local climate conditions. The highest morphospecies richness, abundance and biomass in agricultural habitats may surprise at first glance but seems to be mainly related to the lower elevational extent and accompanying higher temperatures compared with the two other habitat types, which may both be beneficial to insects in general. However, when correcting for elevation, agricultural habitats still had similar richness compared to unmanaged habitats, which could be related to the relatively small field sizes and heterogeneous landscape mosaic typical for Switzerland. Nevertheless, the era of agricultural intensification is still ongoing and may lead to lagged effects on the insect fauna or to further biotic homogenisation with detrimental effects on the functionality and resilience of the insect community and its associated ecosystem services. Thus, more investigations and longer time series studies are needed to assess how insect richness, abundance and biomass have developed in recent decades. Studies of these metrics and of the impact of the main landscape habitats on insect richness and biomass should be conducted within the framework of climate and land-use change, as both processes show interacting effects (Neff et al., 2022).

AUTHOR CONTRIBUTIONS

Friederike Gebert: Conceptualization; data curation; formal analysis; investigation; visualization; writing – original draft; writing – review and editing; methodology; software; validation. **Kurt Bollmann:** Conceptualization; Project administration; resources; supervision; writing – review and editing; funding acquisition; methodology. **Nele Schuwirth:** Conzeptualization; Writing – review and editing; funding acquisition; methodology; supervision. **Peter Duelli:** Investigation; writing – review and editing; methodology; conceptualization. **Dominique Weber:** Data curation; formal analysis; investigation, writing – review and editing. **Martin K. Obrist:** Conceptualization; methodology; data curation; investigation, supervision; writing – review and editing; formal analysis; resources.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.24551695.

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13

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information.

Table S1: Overview of study sites. # Site = ID of study site. Habitat = more detailed information on habitat for each of the three habitat types; Habitat type = rough separation of habitats into agriculture, unmanaged and managed forest. Succ. = Succession state. Steady = late successional stages, near steady state. Early = early successional stages, pioneer stages. Elev. = elevation.

Table S2: Overview of taxon-specific coefficients used to calculate the best regression model for biomass (m) using the formula $m = 10^{\wedge}(c + b_l * \log_{10}(l) + b_w * \log_{10}(w) + b_a * \log_{10}(a))$, c = intercept, b_l is the slope of the length, b_w the slope of the width (of abdomen $b_w\_Abdomen$) and b_a the slope of the area. l, w and a are the length, width, and area of a single specimen. Coleoptera_Rest includes Buprestidae, Cerambycidae and other Coleopera. Hymenoptera-All includes Aculeata and other Hymenoptera.

Table S3: Environmental predictors used to model morphospecies richness, abundance, and biomass.

Table S4: Model outcomes for GLMs to calculate figure 1. Models have the form response ∼ monitoring year. The estimate, standard error, z and p values refer to the predictor monitoring year. Man. Forest = managed forest; Std. error = standard error. For GLMs, the t value is given and for GLM.NBs, the z value. p values < 0.05 are marked with "*" and models with p < 0.1 are shown in bold. For abundance and biomass, the log of the response is used.

Table S5: Results of Tukey post hoc tests to check for differences between the three habitats agriculture, unmanaged and managed forest. Models have the form response ∼ habitat (factorial, with three levels agriculture, unmanaged, managed forest) + monitoring year. p values < 0.05 are marked with "*" and values p < 0.1 are shown in bold. Man. forest = managed forest; Msp. = morphospecies; Ab. = abundance; Bio. = biomass; Oth. Hymenopera = other Hymenoptera.

Table S6: Results of Tukey post hoc tests to check for differences between the four habitats agriculture, unmanaged open, unmanaged closed and managed forest. Models have the form response ∼ habitat (factorial, with three levels agriculture, unmanaged, managed forest) + monitoring year. p values < 0.05 are marked with "*" and values p < 0.1 are shown in bold. Msp. = morphospecies; Ab. = abundance; Bio. = biomass. This table is corresponding to Figure S7.

Table S7: Model outcomes for generalised linear models used to calculate trends for open versus closed habitats (see corresponding Figure S11). Models have the form response ∼ monitoring year. The estimate, standard error, z, and p values refer to the predictor monitoring year. Std. error = standard error. For GLMs, the t value is given and for GLM.NBs, the z value. p values < 0.05 are marked with "*" and models with p < 0.1 are shown in bold.

Table S8: Results of Tukey post hoc tests to check for differences between open and closed habitats. Models have the form response ∼ openness (factorial, with two levels open, unmanaged) + monitoring year. p values < 0.05 are marked with "*" and values p < 0.1 are shown in bold. Msp. = morphospecies; Ab. = abundance; Bio. = biomass; Oth. Hymenopera = other Hymenoptera.

Table S9: Model outcomes for generalised linear models used to calculate trends for managed versus unmanaged habitats (see corresponding Figure S12). Models have the form response ∼ monitoring year. The estimate, standard error, z and p values refer to the predictor monitoring year. Std. error = standard error. For GLMs, the t value is given and for GLM.NBs, the z value. p values < 0.05 are marked with "*" and models with p < 0.1 are shown in bold.

Table S10: Results of Tukey post hoc tests to check for differences between managed and unmanaged habitat. Models have the form response ∼ habitat (factorial, with two levels (managed, unmanaged) + monitoring year. p values < 0.05 are marked with "*" and values p < 0.1 are shown in bold. Msp. = morphospecies; Ab. = abundance; Bio. = biomass; Oth. Hymenopera = other Hymenoptera.

Figure S1: Fixed photo station with Petri dish holder. Pictures were taken in a fixed distance between camera and Petri dish.

Figure S2: Correlations between all variables for morphospecies richness. TotalMSP = overall morphospecies richness; Temp_mean = mean temperature; Temp_sd = standard deviation of temperature; Precip_mean = mean precipitation; Precip_sd = standard deviation of precipitation; NDVI_B200_max = maximum NDVI (normalized difference vegetation index) in 20m buffer; NDVI_B200_mean = mean NDVI in 200m buffer; NDVI_B200_median = median NDVI in 200m buffer; NDVI_B200_min = minimum NDVI in 200m buffer; NDVI_B200_sd = standard deviation of NDVI in 200m buffer.

Figure S3: Correlations between all variables for abundance. TotalAB = overall abundance; Temp_mean = mean temperature; Temp_sd = standard deviation of temperature; Precip_mean = mean precipitation; Precip_sd = standard deviation of precipitation; NDVI_B200_max = maximum NDVI (normalized difference vegetation index) in 20m buffer; NDVI_B200_mean = mean NDVI in 200m buffer; NDVI_B200_median = median NDVI in 200m buffer; NDVI_B200_min = minimum NDVI in 200m buffer; NDVI_B200_sd = standard deviation of NDVI in 200m buffer. Overall abundance and abundance of all taxa (Buprestidae, Cerambycidae, Carabidae, other Coleoptera, Aculeata, other Hymenoptera, Heteroptera and Lepidoptera) was log (x+1) transformed.

Figure S4: Correlations between all variables for biomass. TotalWeight = overall biomass; Temp_mean = mean temperature; Temp_sd = standard deviation of temperature; Precip_mean = mean precipitation; Precip_sd = standard deviation of precipitation; NDVI_B200_max = maximum NDVI (normalized difference vegetation index) in 20m buffer; NDVI_B200_mean = mean NDVI in 200m buffer; NDVI_B200_median = median NDVI in 200m buffer; NDVI_B200_min = minimum NDVI in 200m buffer; NDVI_B200_sd = standard deviation of NDVI in 200m buffer. Overall biomass and biomass of all taxa (Buprestidae, Cerambycidae, Carabidae, other Coleoptera, Aculeata, other Hymenoptera, Heteroptera and Lepidoptera) was log (x+1) transformed.

Figure S5: Patterns of intra annual variation in insect morphospecies richness, abundance and biomass for the three habitats agriculture, unmanaged and Managed forest over time from 2000 to 2007. Boxes represent the mean plus and minus the standard deviation. The vertical lines show the extent of data from minimum to maximum values. Colours denote the three different habitats agriculture (red), unmanaged (green) and Managed forest (purple). Symbols represent original measurements on study sites.

Figure S6: Patterns of intra annual variation in insect morphospecies richness, abundance and biomass for the four habitats agriculture, unmanaged open, unmanaged closed and Managed forest over time from 2000 to 2007. Boxes represent the mean plus and minus the standard deviation. The vertical lines show the extent of data from minimum to maximum values. Colours denote the three different habitats agriculture (red), unmanaged open (light green), unmanaged closed (dark green) and Managed forest (purple). Symbols represent original measurements on study sites.

Figure S7: Patterns of total insect morphospecies richness, abundance, and biomass in the four habitats "agriculture", "unmanaged open", "unmanaged closed" and "managed forest" for the years 2000 to 2007 (corresponding to Table S6). Dots represent original measurements for each study site. Trend lines were computed with GLMs.

Figure S8: Elevational distribution of the four habitat types agriculture, unmanaged open, unmanaged closed, and managed forest. Boxes

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15

represent the mean plus and minus the standard deviation. The vertical lines show the extend of data from minimum to maximum values. Colours denote the four different habitats agriculture (red), unmanaged open (light green), unmanaged closed (dark green) and managed forest (purple). Symbols represent original measurements on study sites.

Figure S9: Elevational distribution of the four habitat types "agriculture", "unmanaged open", "unmanaged closed" and "managed forest" for total morphospecies richness, abundance and biomass. Symbols represent original measurements on study sites. Trend lines were computed with GLMs.

Figure S10: Patterns of total insect morphospecies richness, abundance, and biomass for agricultural habitats, divided into the habitat types arable field and grassland, for the years 2000 to 2007. Dots represent original measurements for each study site. Trend lines were computed with GLMs.

Figure S11: Patterns of insect morphospecies richness, abundance, and biomass in open (agricultural and unmanaged open habitats) and closed (unmanaged closed and managed forest) habitats for the years 2000 to 2007 (corresponding to Tables S7, S8). Dots represent original measurements for each study site. Trend lines were computed with GLMs. Buprest. = Buprestidae; Ceramb. = Cerambycidae; Carab. = Carabidae; Other Col. = Other Coleoptera; Other Hym. = Other Hymenoptera; Heterop. = Heteroptera; Lepidop. = Lepidoptera.

Figure S12: Patterns of insect morphospecies richness, abundance, and biomass in managed (agricultural and managed forest habitats) and unmanaged (unmanaged closed and unmanaged open) habitats for the years 2000 to 2007 (corresponding to Tables S9, S10). Dots represent original measurements for each study site. Trend lines were computed with GLMs. Buprest. = Buprestidae; Ceramb. = Cerambycidae; Carab. = Carabidae; Other Col. = Other Coleoptera; Other Hym. = Other Hymenoptera; Heterop. = Heteroptera; Lepidop. = Lepidoptera.

Figure S13: Correlation plots between morphospecies richness, abundance and biomass pooled for all insects (a) and for the eight taxonomic groups (b-i). Abundance and biomass data was not log-transformed. MSP = morphospecies richness; AB = abundance; Bio = biomass; Bupr. = Buprestidae; Ceram. = Cerambycidae; Carab. = Carabidae; oth. Col. = other Coleoptera; Acul. = Aculeata; Hym. = other Hymenoptera; Hetero. = Heteroptera; Lepi. = Lepidoptera.

Figure S14: Response curves of mean temperature for total morphospecies richness separately for the habitats agriculture (red), unmanaged (green) and managed forest (purple). f shows the response curve of the predictor. Note that f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S15: Effect sizes for Buprestidae, separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S16: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of Buprestidae. f shows the response curve of the predictor. Note that

for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S17: Effect sizes for Cerambycidae separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S18: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of Cerambycidae. f shows the response curve of the predictor. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S19: Effect sizes for Carabidae separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S20: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of Carabidae. f shows the response curve of the predictor. If a quadratic term is included, it follows the form $f = ax^2 + bx$, where a and b signify the coefficients of the quadratic and linear terms of the predictor, respectively. Note that for morphospecies richness f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S21: Effect sizes for other Coleoptera, separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S22: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of other Coleoptera. f shows the response curve of the predictor. If a quadratic term is included, it follows the form $f = ax^2 + bx$, where a and b signify the coefficients of the quadratic and linear terms of the predictor, respectively. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S23: Effect sizes for Aculeata, separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S24: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of Aculeata. f shows the response curve of the predictor. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S25: Effect sizes for other Hymenoptera, separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S26: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of other Hymenoptera. f shows the response curve of the predictor. If a quadratic term is included, it follows the form $f = ax^2 + bx$, where a and b signify the coefficients of the quadratic and linear terms of the predictor, respectively. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S27: Effect sizes for Heteroptera, separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S28: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of Heteroptera. f shows the response curve of the predictor. If a quadratic term is included, it follows the form $f = ax^2 + bx$, where a and b signify the coefficients of the quadratic and linear terms of the predictor, respectively. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S29: Effect sizes for Lepidoptera, separately for morphospecies richness (blue), abundance (orange) and biomass (green). For each predictor retained in the best model, the coefficient and its 95% confidence interval are shown. Man. Forest = managed forest.

Figure S30: Response curves of significant predictors for morphospecies richness (blue), abundance (orange) and biomass (green) of Lepidoptera. f shows the response curve of the predictor. Note that for morphospecies richness, f is a logarithmic function, which was back-transformed to make interpretation easier. Vertical lines indicate the distribution of data points across the range of each predictor.

Figure S31: Patterns of insect morphospecies richness, abundance, and biomass in the three habitats "agriculture", "unmanaged" and "managed forest" for the years 2000 to 2007. Colours denote the three different habitats "agriculture" (red), "unmanaged" (green) and "managed forest" (purple). Dots represent original measurements for each study site. Trend lines were computed with GAMs.

Figure S32: Correlations between total morphospecies richness (totalMSP) and the significant predictors of the model. Correlations and density plots are shown for agricultural (red), unmanaged (green) and managed forest (blue) habitats.

Figure S33: Correlations between total abundance (TotalAB) and the significant predictors of the model. Correlations and density plots are shown for agricultural (red), unmanaged (green) and managed forest (blue) habitats.

Figure S34: Correlations between total biomass (TotalWeight) and the significant predictors of the model. Correlations and density plots are shown for agricultural (red), unmanaged (green) and managed forest (blue) habitats.