

ORIGINAL ARTICLE

Interactions of land use and climate change disproportionately impact Lepidoptera of the five major insect orders

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Abstract

1. Land use and climate change are two major environmental pressures that interact to impact insect biodiversity.
2. The wide ecological diversity, including life histories, among insects suggests that some groups will be more sensitive to these pressures than others, and it is unlikely that the response of insects in general, as is often assessed in large-scale studies, is representative across insect orders.
3. Using site-level comparisons of insect biodiversity across land uses from a global database, we examine the impact of land use alone and its interaction with climate change on insect richness and abundance. We then compare these results with models that consider varying effects among orders to determine whether some orders are more or less impacted than others.
4. Of the orders assessed, Lepidoptera showed the most extreme differences compared to the average insect response, whereas the Hymenoptera and, in some cases, the Diptera showed dampened responses.

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5. On average, insect species richness and abundance in high-intensity agricultural sites that had also experienced climate change were 33% and 60% lower than in sites of primary vegetation that had not experienced climate change. Compared to this, Lepidoptera had 83% lower species richness and 91% lower total abundance under the same conditions.
6. These results highlight the necessity of exploring the variation within aggregated responses to better identify and protect the most vulnerable groups.

KEYWORDS

abundance, agriculture, biodiversity, climate change, insect declines, interactions, land use, richness, synergistic effects

INTRODUCTION

Anthropogenic land use and associated increases in land-use intensity have been identified as key drivers of insect biodiversity loss (Potts et al., 2010; Schuch et al., 2012; Seibold et al., 2019; Uhler et al., 2021). Agricultural land in particular negatively impacts insects on average (Grab et al., 2019; Seibold et al., 2019; Uhler et al., 2021), with intensification of these areas from pesticide and fertiliser application, mechanisation, reduced plant diversity, invasive alien species and landscape simplification associated with additional declines (Bianchi et al., 2006; Geiger et al., 2010; Hartlieb et al., 2025; Marshall et al., 2003; Millard et al., 2021). A recent global-scale analysis found that high-intensity agriculture was associated with greater reductions in total insect abundance (45% reduction) and species richness (33% reduction) than low-intensity agriculture (19% and 22% reduction, respectively), relative to natural habitats (Outhwaite et al., 2022). Although not all species are negatively impacted by agriculture, with some generalist species increasing in abundance, particularly in low-intensity systems (Chisté et al., 2018; Mangels et al., 2017).

Alongside the impact of land use is the rapidly growing impact of climate change. Shifting temperature maxima and minima and extreme weather events can reduce survival and fecundity (Zhao et al., 2014), reducing insect diversity (Forister et al., 2018; Kerr et al., 2015; Sharp et al., 2025; Soroye et al., 2020). Furthermore, there is mounting evidence that climate change impacts on insects tend to be stronger at sites experiencing other human-driven pressures (Neff et al., 2022; Stefanescu et al., 2011), with recent work identifying interactive effects of land use and climate leading to negative impacts on insect biodiversity globally (Outhwaite et al., 2022). These interactions can work in various ways. For example, human-simplified landscapes can have limited microclimate refugia availability, which would otherwise buffer insects from rising temperatures *in situ* (Hayes et al., 2024; Suggitt et al., 2018). Conversely, the availability of natural habitat surrounding intensively managed cropland has been shown to buffer negative impacts of land use and climate on insects (Fourcade et al., 2021; Outhwaite et al., 2022), likely by providing additional or different habitats, additional resources and increased microclimatic variability.

Insect susceptibility to both individual and synergistic effects of agriculture and climate change will differ both across (e.g., Millard

et al., 2021) and within orders (e.g., Ganuza et al., 2025) since insects display a huge diversity of life-history traits and ecologies. To date, large-scale analyses have generally focused on data combining insect species across multiple taxonomic groups (Neff et al., 2022; Outhwaite et al., 2022) or on well-studied groups like pollinators (Ganuza et al., 2022; Millard et al., 2023). However, which of the different insect groups responds most negatively to the interaction of these two key drivers at the global scale has not been shown. It is therefore unclear whether such responses for insects averaged across large scales are representative of the responses of different clades or whether important differences are being missed. For some insect orders, the impacts of land use and climate change are well documented; however, for other groups, the picture is less clear. Breaking down these responses will ensure that any highly impacted groups are not misrepresented and will allow future research or conservation action to be directed to those groups most at risk. As invertebrates continue to receive a smaller share of conservation funding relative to other taxa (Guénard et al., 2025), ensuring that existing resources are targeted appropriately is of critical importance.

To determine which insect orders are most negatively impacted by land use and its interaction with climate change at the global scale we used mixed-effects models to analyse data from the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) database (Hudson et al., 2016, 2017), assessing change in the species richness and total abundance of five insect orders (Lepidoptera [butterflies and moths], Diptera [flies], Coleoptera [beetles], Hemiptera [true bugs] and Hymenoptera [ants, bees and wasps]). We have tested two hypotheses: (1) agriculture and agricultural intensification reduce insect biodiversity compared to that in natural habitats, but the magnitude of the reduction will vary among orders; and (2) insect biodiversity will be most reduced where climate change interacts with high-intensity agriculture, but again the magnitude of the reduction will vary among orders. Specifically, we expect greater than average responses of Lepidoptera since considerable research has shown strong negative impacts of both land use and climate change at local to national scales (Hill et al., 2021; Martay et al., 2017; Van Deynze et al., 2024; Wagner et al., 2021; Warren et al., 2021). Many butterfly and moth species are particularly sensitive to climate change, as all life stages can be exposed to extreme weather events, from egg through to adult (McDermott Long et al., 2017), and so there

is less opportunity for physical buffering from temperature extremes than for species that spend time underground or within wood, for example. Negative impacts of climate and land use on bees have been shown, indicating a potential for strong negative impacts on the Hymenoptera (de Palma et al., 2015; Soroye et al., 2020). However, some ant species are expected to be tolerant or even benefit from rising temperatures as they are highly thermally responsive, for example, they can regulate nest temperature by changing the depth of chambers or moving it entirely if conditions become unsuitable (Parr & Bishop, 2022). This may lead to a dampened observed effect relative to other groups. The Coleoptera, Diptera and Hemiptera are less well researched, particularly at large spatial scales, although some studies have looked into the responses of certain groups or in specific contexts, for example the negative effect of land use change on rove beetles (Méndez-Rojas et al., 2021), the effect of climate on forest beetles in Japan (Evans et al., 2022), and the response of grassland arthropods (including Coleoptera and Hemiptera) to agricultural intensification in Germany (Hartlieb et al., 2025) have been shown. These studies suggest potential negative impacts of land use and climate change for these groups, but it is unclear whether these will persist at the global scale and how they will compare to other orders. In contrast to the studies showing general negative responses, Diptera have shown positive abundance trends in response to agricultural intensification on Canadian farms (Powell et al., 2024) and increases in diversity over time in the tropics despite climatic changes (Sharp et al., 2025). It is possible that Diptera may therefore respond differently to other orders.

METHODS

Insect diversity data

Insect diversity data were obtained from the PREDICTS Project database (Hudson et al., 2016, 2017), which contains spatial comparisons of local-scale biodiversity between sites of differing land use and/or land-use intensity (Hudson et al., 2014). The complete database contains over 3 million records of 47,044 species from 26,114 sites across 94 countries (Hudson et al., 2017). The database is organised hierarchically. Data from published 'Sources' are split into separate 'Studies' within which data were collected using the same methods. Within Studies, data are organised into spatial 'Blocks' to account for the spatial arrangement of individual sampled 'Sites'. Each Site has associated geographical coordinates.

Here, we used the records for insects (935,078 records): 98% (916,220) of insect records were from five orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera), on which we focus here. For most records (63%), taxon identifications are at the species or genus level, although this does vary by order (Lepidoptera—88%, Hymenoptera—88%, Hemiptera—61%, Diptera—53% and Coleoptera—38%, Table S1). Where sampling effort differed among sampled sites within a study, we followed the approach of previous analyses of PREDICTS to rescale any measurements that may be

sensitive to differences in sampling effort, such as abundance counts. Specifically, effort was rescaled within the study to equal one at the site with the highest effort, with values for all other sites relative to this. We then divided any effort-sensitive abundance measurements by this relative sampling effort, thus assuming a linear relationship between them (Newbold et al., 2014). Sites that included multiple samples taken at the same location, for example, multiple traps along a transect, but that had the same coordinates, were merged into a single record, in that the raw metrics of abundance, occurrence or richness were combined. For abundance and species richness, values were combined using a weighted mean (where the weights were sampling efforts for each site). For occurrence, a taxon was marked as present if it was recorded at any of the merged sites.

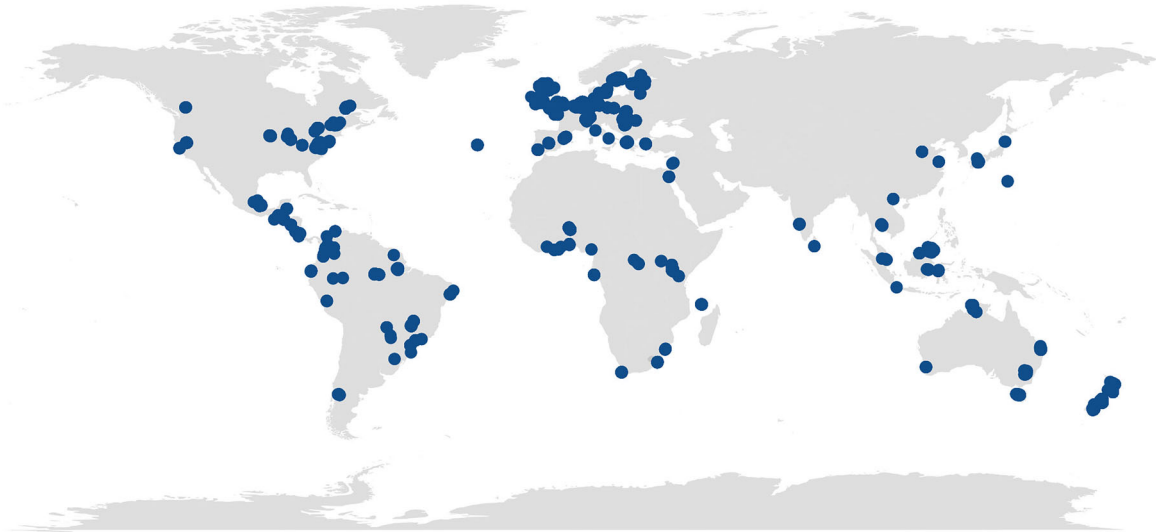
For each site and order combination, records of species abundance, presence or overall species richness were used to determine site-level species richness (the number of unique taxa within each order sampled at a given site, these may be identified to the species level or a coarser taxonomic resolution) and total abundance (calculated as the sum of abundance measurements of all taxa within an order sampled at a given site). Sampled abundances showed huge variation among studies, which could be due to environmental gradients, differences in sampling methods used, or the focal taxa being sampled. To reduce the impact of this variation, for each order, we rescaled abundances within each study so that the highest abundance was 1 and all other values relative to that, following de Palma et al. (2021). Models were also run without rescaling abundance, showing a similar pattern of change, but with wider confidence intervals (CIs) (Supplement 1).

After processing and removal of outliers (see below), the dataset comprised 635,330 records of 16,357 insect taxa (some records were not resolved to species level) with 7845 site-level estimates of order species richness from 5659 unique sites in 250 studies, and 7453 site-level estimates of order total abundance from 5351 unique sites in 232 studies. The number of available site-level samples varied across the five insect orders (Figure 1; Table S2 for breakdown by land-use categories): Coleoptera (N_{sites} richness = 2024, N_{sites} abundance = 2004), Diptera (598, 578), Hemiptera (660, 640), Hymenoptera (3205, 3023) and Lepidoptera (1358, 1208). The dataset contains records for a large range of families within each order: Coleoptera = 101 families (out of 224 described on the Catalogue of Life as of June 2025, <https://www.catalogueoflife.org/>), Diptera = 75 families (out of 231), Hemiptera = 64 families (out of 287), Hymenoptera = 54 families (out of 133) and Lepidoptera = 59 families (out of 143).

Land-use data

The PREDICTS database categorises land use into eight categories based on the habitat description provided in the source publication (described in full by Hudson et al. (2017)). Sites are also categorised into three use intensities—minimal, light and intense use—classified using criteria that vary among land-use types (see Table S2 in Hudson

(a)



(b)

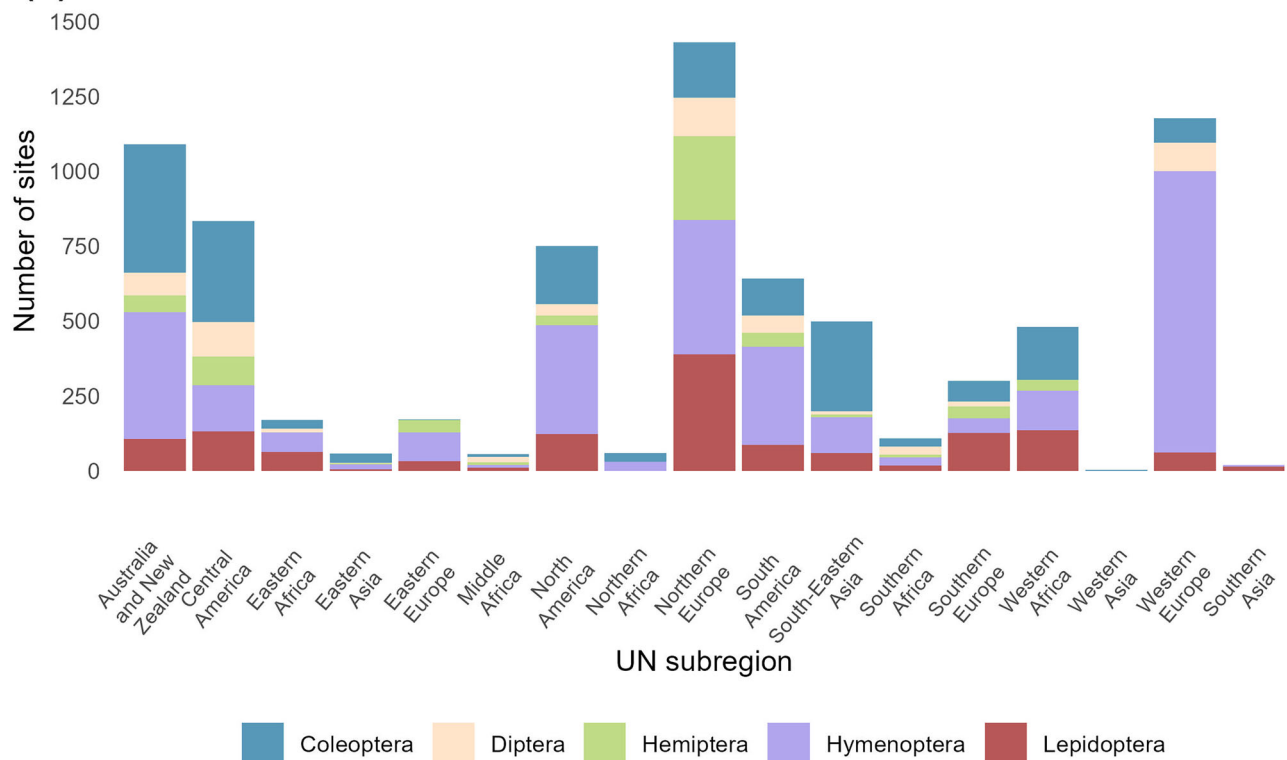


FIGURE 1 Spatial distribution of sampled sites from the PREDICTS database covering the five most sampled insect orders. (a) The location of the sites. (b) The distribution of sites at which each order was sampled among 18 UN subregions (data were lacking for Central Asia, Melanesia, Micronesia and Polynesia).

et al. (2017)). In natural habitats, land use/land-use intensity includes factors such as logging and bushmeat hunting. For cropland, pasture and plantation, it includes management factors such as stocking density, fertiliser application and the extent of monoculture. Following the approach taken by Outhwaite et al. (2022), sites were assigned to one of four aggregate land use/land-use intensity classes: (1) primary vegetation (native vegetation that has not been destroyed) of all use

intensities; (2) secondary vegetation (where native vegetation has been destroyed but is recovering) of all use intensities and stages of recovery; (3) low-intensity agriculture (minimal-use cropland, light- and minimal-use pasture and minimal-use plantation), representing cropland, plantations and pastureland characterised by low chemical input, non-monoculture crops, small to medium field size, absent to low mechanisation and low or medium livestock density; and

(4) high-intensity agriculture (light- and intense-use cropland, intense-use pasture, light- and intense-use plantation), representing cropland, plantations and pastureland characterised by high chemical input, monoculture cropping, large field size, mechanisation and high live-stock density.

Climate data

Following Outhwaite et al. (2022), recent historical climate change was measured by calculating a Standardised Temperature Anomaly (STA) for each site. This metric was calculated using version 4.03 of the Climatic Research Unit Time Series (CRU TS) dataset (Harris et al., 2020). We used the monthly mean temperature estimates available from 1901 at a spatial resolution of $0.5^\circ \times 0.5^\circ$. First, we calculated the absolute temperature anomaly for each site as the difference between the mean of the monthly mean temperatures of the 5-year period preceding data collection and the mean of the monthly mean temperatures during a baseline period (1901–1930). Outhwaite et al. (2022) showed consistent results for baseline lengths of 10 and 20 years, and we do not repeat this sensitivity test here. Changes in mean temperature were calculated using only months during which insects are expected to be active, here, those with an average temperature of 10°C or higher (Johansson et al., 2020), but Outhwaite et al. (2022) also showed consistent results without this restriction. Next, the absolute temperature anomaly was standardised by dividing by the standard deviation of baseline temperatures to account for the fact that some regions of the world experience greater natural variation in temperatures than others (Equation 1). For example, tropical regions experience more stable temperatures compared with seasonal temperate regions.

$$\text{STA} = \frac{T_{\text{mean,presample}} - T_{\text{mean,baseline}}}{\sigma_{T_{\text{mean,baseline}}}} \quad (1)$$

where $T_{\text{mean,presample}}$ is the mean of monthly mean temperatures of insect-active months in the 5 years preceding sampling, $T_{\text{mean,baseline}}$ represents the mean of monthly mean temperatures of the same insect-active months between 1901 and 1930 and $\sigma_{T_{\text{mean,baseline}}}$ represents the standard deviation of the monthly mean temperatures across the baseline period. Thus, an STA of 1 indicates warming equivalent to one standard deviation of the baseline monthly mean temperatures. Maps showing the absolute temperature anomaly and STA are shown in Figure S1. The STA was rescaled before analysis to have a mean of 0 and a standard deviation of 1.

Statistical analysis

All data processing and analyses (Outhwaite & Smith, 2026) were completed using R Version 4.4.2 (R Core Team, 2024). R packages used included brms (Bürkner 2017), cowplot (Wilke, 2025), devtools (Wickham,

Hester, et al., 2026), dismo (Hijmans et al., 2024), dplyr (Wickham, François, et al., 2026), ggplot2 (Wickham, 2016), gridExtra (Auguie, 2017), gridGraphics (Murrell & Wen, 2020), lme4 (Bates et al., 2015), ncdf4 (Pierce, 2025), parallel (R Core Team, 2024), plotly (Sievert, 2020), predictsFunctions (Newbold, 2018), raster (Hijmans, 2025), rasterVis (Perpinan Lamigueiro & Hijmans, 2025), RColorBrewer (Neuwirth, 2022), Rfast (Papadakis et al., 2025), scales (Wickham et al., 2025), sjPlot (Lüdtke, 2025), snow (Tierney et al., 2021), sp. (Pebesma & Bivand, 2005), StatisticalModels (Newbold, 2015), stringr (Wickham, 2025) and viridis (Garnier et al., 2024).

Mixed-effects models were used to determine how the total abundance and species richness of the five insect orders responded to the four land-use/use-intensity categories, and to the interaction of these categories with the STA. Separate models were run for species richness and total abundance using the GLMER function from the StatisticalModels R package (Newbold, 2015), this package calls functions from the lme4 R package (Bates et al., 2015). Species richness was analysed using a generalised mixed-effects model with a Poisson distribution. However, many of the abundance values in the PREDICTS database were not integers (even before rescaling, as they may be measured as density or relative abundance in some cases), so the rescaled total abundance was $\log_e(x + 0.01)$ -transformed and modelled using a linear mixed effects model with a Gaussian distribution of errors. Outhwaite et al. (2022) found very similar results with alternative distributions, including zero-inflated Gaussian and zero-inflated negative binomial models. Fixed effects considered in both the abundance and richness models were insect order (categorical, five levels, with Coleoptera as the reference), land-use class (categorical, four levels, with primary vegetation as the reference) and STA (continuous). Study and block identity were included as nested random intercepts (block nested within study) for both abundance and species richness models to account for differences in sampling methods between studies and the spatial arrangement of sites, respectively. Site (nested within block, nested within study) was included as an additional random effect in the species richness models to account for overdispersion (Newbold et al., 2015).

Specific models were run to address the two hypotheses: (1) agriculture and agricultural intensification reduce insect biodiversity compared to that in natural habitats, but the magnitude of the reduction will vary among orders, and (2) insect biodiversity will be most reduced where climate change interacts with high-intensity agriculture, but again the magnitude of the reduction will vary among orders. To test variation in responses among orders, we included interactions between order and responses to land use/use-intensity (Equations 2 and 3) or responses to the land use/use-intensity/STA interaction (Equations 6 and 7). For comparison, we tested models on the same dataset but didn't include the effect of order (Equations 4, 5, 8 and 9).

Model Set 1: Responses to land use/land-use intensity (LUI).

With order variation:

$$\text{Abundance} \sim \text{order} \times \text{LUI} + (1|\text{Study/Block}) \quad (2)$$

$$\text{Species Richness} \sim \text{order} \times \text{LUI} + (1|\text{Study/Block/Site}) \quad (3)$$

Without order-level variation:

$$\text{Abundance} \sim \text{LUI} + (1|\text{Study}/\text{Block}) \quad (4)$$

$$\text{Species Richness} \sim \text{LUI} + (1|\text{Study}/\text{Block}/\text{Site}) \quad (5)$$

Model Set 2: Responses to the interaction between land use/land-use intensity and STA.

With order-level variation:

$$\text{Abundance} \sim \text{order} \times \text{LUI} \times \text{STA} + (1|\text{Study}/\text{Block}) \quad (6)$$

$$\text{Species Richness} \sim \text{order} \times \text{LUI} \times \text{STA} + (1|\text{Study}/\text{Block}/\text{Site}) \quad (7)$$

Without order-level variation:

$$\text{Abundance} \sim \text{LUI} \times \text{STA} + (1|\text{Study}/\text{Block}) \quad (8)$$

$$\text{Species Richness} \sim \text{LUI} \times \text{STA} + (1|\text{Study}/\text{Block}/\text{Site}) \quad (9)$$

The outputs from all models can be found in Tables S3–S7. Predictions, as presented within the figures, were obtained using the *PredictGLMERRandIter* function from the *StatisticalModels* R package (Newbold, 2015), which works by randomly drawing 1000 estimates of the effects based on the variance–covariance matrix of the model.

Model assumptions were checked using fitted versus residuals plots, observed versus fitted plots and Q-Q plots (Figures S2–S9). Due to the rescaling of abundance, the fitted versus residuals plots for models of abundance presented a box-like pattern. The observed versus fitted plots suggest that the models over-predict both total abundance and species richness for sites with low observed abundance or richness and under-predict for sites of high observed abundance or richness, indicating that models may underestimate true responses. Moran's I tests were used to check for spatial autocorrelation in the residuals from the models associated with each study in the PREDICTS dataset. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies. For our models, there was significant autocorrelation for 11% of the studies for the abundance models and 27–28% of the studies for the richness models.

Comparison with the average response across orders

Models with and without variation in responses among orders were compared using the Akaike information criterion (AIC) and R^2 values (Table S3). Overall, the amount of variance explained by the fixed effects in the models, as assessed by the marginal R^2 values, is low. This is common with studies based on large-scale collations of heterogeneous data, where there is large variation in biodiversity measures among individual datasets in the collated data, including both analyses of the PREDICTS data (Newbold et al., 2015, 2020), as well as other biodiversity databases (Spooner et al., 2018; Williams et al., 2022).

Sensitivity tests

During analysis, four studies were identified as influential outliers when assessed using Cook's distances and sensitivity tests, where we sequentially removed outlier studies (see Supplement 2 for full details). These four studies were removed from the dataset for the main analyses. Since we were interested in the global average responses of the different orders to land use/land-use intensity and its interaction with climate change, it was deemed appropriate to remove this very small number of studies, which overly influenced that global average.

Additional sensitivity analyses were conducted to assess the robustness of the results. First, we ran separate models for each order to assess the effects of land use/land-use intensity and STA, to determine whether model fit was improved due to reduced model complexity (Supplement 3). Second, we assessed correlations between mean temperature at time of sampling, recent absolute temperature change and the STA. We included mean temperature at the time of sampling as a potential confounding effect, given the known strong relationship between average temperatures and overall biodiversity (Supplement 4). Third, we tested whether differences in sampling completeness between studies could bias our species richness estimates using Chao-estimated species richness (Chao et al., 2005) as the response variable instead of sampled species richness (Supplement 5). Chao-estimated species richness could be calculated for only 4058 of the 5659 original sites because it requires counts of the number of individual organisms. Since this test uses only a subset of the data, we chose to include it as a sensitivity test rather than as the main result. Finally, to increase the confidence in the modelled results, we repeated the analysis in a Bayesian framework using the *brms* package in R (Bürkner, 2017), which yielded almost identical results (Supplement 6).

RESULTS

Variation in responses to land use/land-use intensity among orders

For all five orders combined, species richness was on average 30% (CI: –33, –27) lower in low-intensity agriculture and 36% (CI: –39, –33) lower in high-intensity agriculture compared to primary vegetation. Abundance was 34% (CI: –40, –27) lower in low-intensity agriculture and 49% (CI: –55, –43) lower in high-intensity agriculture compared to primary vegetation. However, this average response hides considerable variation (Figure 2). The reduction in species richness between sites of primary vegetation and high-intensity agriculture was much greater for Coleoptera (–45%, CI: –49, –41), Hemiptera (–39%, CI: –47, –28) and Lepidoptera (–67%, CI: –71, –63. Figure 2a) than for Hymenoptera (–13%, CI: –20, –6) and Diptera showed no significant difference (9%, CI: –5, 25). Hymenoptera showed a negative but non-significant difference in abundance between low-intensity agriculture and primary vegetation (–8%, CI: –23, 11), whereas all other orders showed a significant negative difference similar to or greater than the average across orders

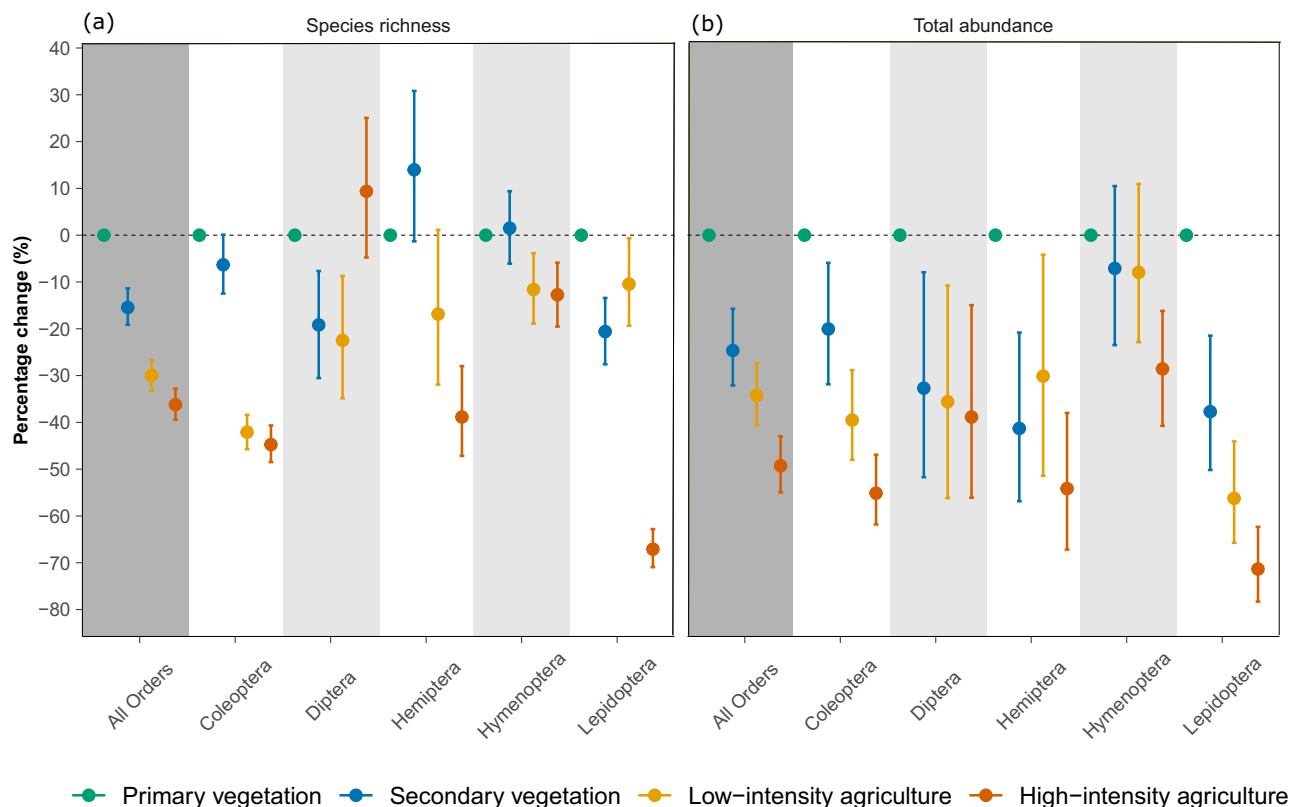


FIGURE 2 Response of (a) species richness and (b) total abundance to land use and land-use intensity. Responses for all five orders combined, predicted from the models excluding the order term, are shown within the darker grey box. order-level responses are then predicted from the models where order was included as an interaction with the land-use/use-intensity category. Responses are presented as relative to biodiversity estimates in primary vegetation within each grouping. Predicted richness/abundance was obtained by randomly drawing 1000 estimates based on the variance-covariance matrix of the model. Points show median model-predicted values, and error bars show 95% confidence intervals.

(Coleoptera: -40% , CI: -48 , -29 ; Diptera: -36% , CI: -56 , -11 ; Hemiptera: -30% , CI: -51 , -4 ; Lepidoptera: -56% , CI: -66 , -44). Responses of abundance to high-intensity agriculture were similar to the average response for Coleoptera (-55% , CI: -62 , -47), Diptera (-39% , CI: -56 , -15) and Hemiptera (-54% , CI: -67 , -38 , Figure 2b), whereas Hymenopterans again showed a dampened but still negative response (-29% , CI: -41 , -16). For Lepidopterans, richness (-67% , CI: -71 , -63) and abundance (-71% , CI: -78 , -62) differences in high-intensity agriculture compared to primary vegetation were the greatest of all the orders, and much greater than the average response across orders (see Table S8 for all model-estimated percentage differences).

Model fit was substantially improved by accounting for varying responses among orders for both species richness and abundance (richness: $\Delta AIC = -4082$; abundance: $\Delta AIC = -141$).

Variation in responses to land use/land-use intensity and climate change among orders

Responses of several orders to the interaction between land use/land-use intensity and climate change differed considerably compared with the average for all insects (Figure 3). For low-intensity

agricultural sites, the average species richness across all orders was 26% (CI: -38 , -10) lower in sites with an STA of 1 compared to primary vegetation with an STA of 0 (hereafter 'the baseline'). Diptera (-81% , CI: -88 , -69) and Lepidoptera (-60% , CI: -71 , -46) showed greater reductions in richness than the average. In contrast, Hymenoptera in low-intensity agricultural sites that have also experienced climate change had a higher species richness than the baseline (87% , CI: 47 , 133).

In sites of high-intensity agriculture, the average reduction in species richness in areas with an STA of 0 was -17% (CI: -23 , -9), and this doubled to -33% (CI: -46 , -19) at sites where the STA was 1, compared to the baseline. For Coleoptera, Diptera and Hemiptera, richness was similar in high-intensity agricultural sites regardless of whether they had experienced climate change or not; however, Hymenoptera richness was higher than in the baseline where there was no climate change impact (20% , CI: 7 , 34) and showed no significant difference compared to the baseline when the STA was 1 (11% , CI: -10 , 39). Reductions in Lepidopteran richness in high-intensity agricultural sites were much greater than the average response across orders, both with (-83% CI: -87 , -76) and without (-62% CI: -68 , -55) climate change, compared with the baseline.

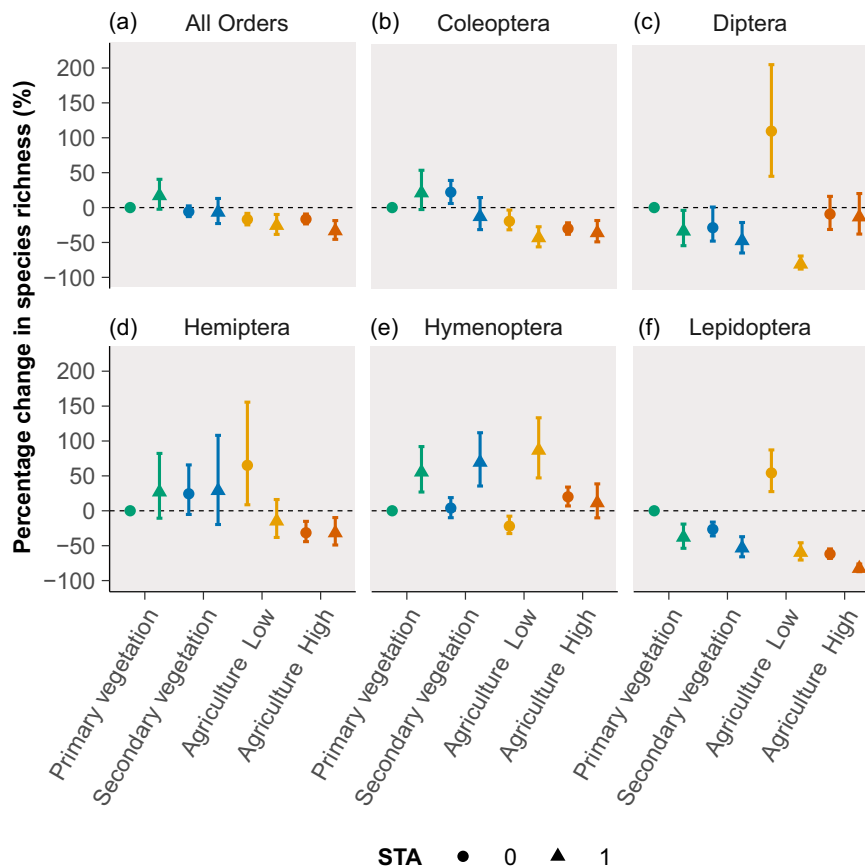


FIGURE 3 Response of species richness to the interaction between land use/land-use intensity and the standardised temperature anomaly. (a) Responses for all five orders combined, based on predictions from the model, excluding order. (b) Coleoptera, (c) Diptera, (d) Hemiptera, (e) Hymenoptera and (f) Lepidoptera are order-level responses predicted from the model, including varying responses among orders. All responses are presented as the percentage change in richness relative to values for sites of primary vegetation with an STA of 0. An STA of 1 indicates warming equal to the standard deviation of temperatures across months in the baseline period, indicating exposure to novel temperatures. Predicted biodiversity was obtained by randomly drawing 1000 estimates based on the variance–covariance matrix of the model. The points show the median model-predicted values, with the error bars showing 95% confidence intervals. Predicted changes in richness and abundance across the range of the STA variable can be seen in Supporting Information Figures S10 and S11.

In primary vegetation, while the average response across orders indicated a potential positive response of species richness to climate change (17%, CI: –2, 41), which was reflected in the responses of Coleoptera and Hymenoptera, our results show that Lepidoptera in primary vegetation sites with an STA of 1 had a species richness 38% lower (CI: –54, –19) than primary vegetation sites with an STA of 0. Richness was also lower for Diptera (–34%, CI: –55, –4).

For total abundance, there were several examples where the order-specific responses differed from the average across orders (Figure 4). In low-intensity agriculture, there was an average 50% (CI: –62, –34) reduction in abundance in sites that have experienced climate warming (STA of 1) compared with the baseline of primary vegetation with no climate warming. For most orders, reductions were greater than this average, including for Coleoptera (–58%, CI: –73, –34), Diptera (–90%, CI: –96, –80), Hemiptera (–64%, CI: –79, –40) and Lepidoptera (–91%, CI: –94, –85). For Hymenoptera, there was no significant difference in abundance between low-intensity agricultural sites with climate change and those of the baseline.

Lower abundances in high-intensity agricultural sites that have experienced climate change were seen for all five orders, compared to the average response across orders (–60%, CI: –69, –49), although for Hymenoptera the difference was not significant (–28%, CI: –47, 4). Coleoptera, Diptera, Hemiptera and Lepidoptera showed much lower abundances than the average would suggest, with reductions of 63% (CI: –75, –48), 71% (CI: –84, –49), 76% (CI: –85, –61) and 91% (CI: –94, –86), respectively, in sites that have also experienced climate warming (STA = 1) compared to the baseline. Diptera, Hemiptera and Lepidoptera also showed lower total abundance in secondary vegetation sites that have experienced climate warming compared to those that have not, with reductions of 91% (CI: –97, –77), 82% (CI: –92, –62) and 87% (CI: –92, –79), respectively.

Model fit was substantially improved by accounting for variation among orders for both species richness and abundance (richness: $\Delta\text{AIC} = -4328$; abundance: $\Delta\text{AIC} = -181$; Table S3). Predictions of responses for all orders in each land-use type across the range of STA values at the sampled sites are presented in

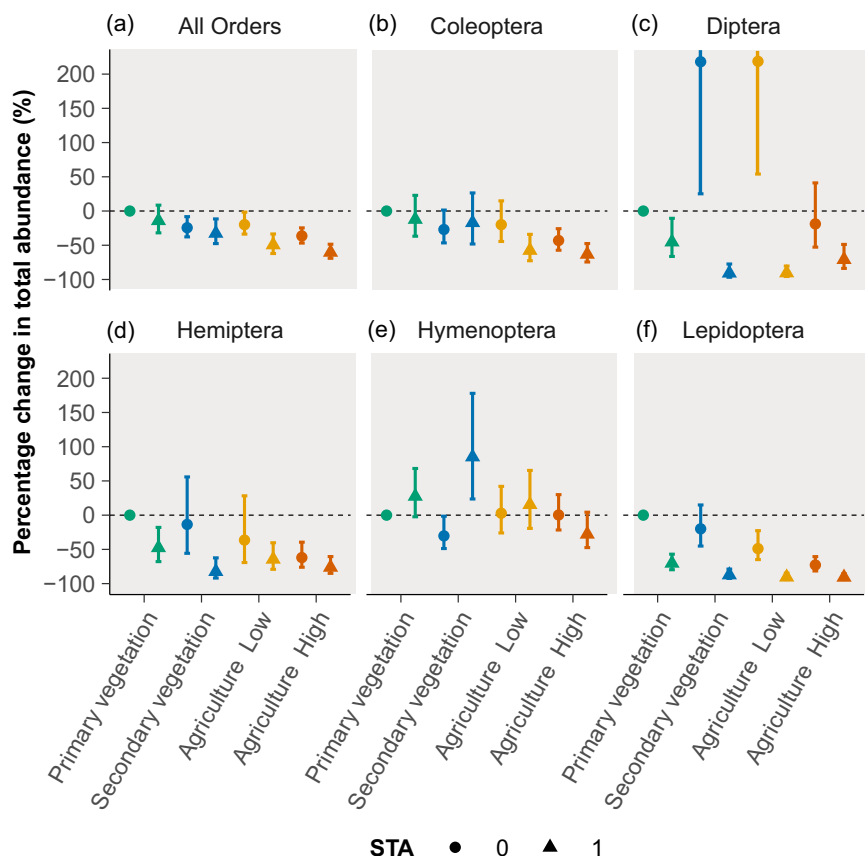


FIGURE 4 Response of total abundance to the interaction between land use and land-use intensity and the standardised temperature anomaly (STA). (a) Responses for all five orders combined, based on predictions from the model without order. (b) Coleoptera, (c) Diptera, (d) Hemiptera, (e) Hymenoptera and (f) Lepidoptera are order-level responses predicted from the model, including the interaction with order. Responses are presented as the percentage change in abundance relative to values for sites of primary vegetation with an STA of 0 within each grouping. An STA of 1 indicates warming equal to the standard deviation of the temperatures in the baseline period, indicating exposure to novel temperatures. Predicted biodiversity was obtained by randomly drawing 1000 estimates based on the variance–covariance matrix of the model. The points show the median model-predicted values, with the error bars showing 95% confidence intervals. Note that the confidence intervals for Diptera have been truncated to aid visibility and comparability of effects within and across orders; see Table S9 for specific values. Predicted changes in richness and abundance across the range of the STA variable can be seen in Supporting Information Figures S10 and S11.

Figures S10 and S11. All percentage changes are presented in Table S9.

DISCUSSION

We show that insect responses to the interactive effects of land use/land-use intensity and climate change vary substantially among orders. Lepidoptera showed much greater negative responses to land use/land-use intensity alone and in interaction with climate change, while dampened responses or even positive differences were observed for the Hymenoptera and, in some cases, the Diptera. Order-level differences are expected given the variation among insect groups in morphology, habitat and dietary preferences, thermal tolerances, dispersal ability, life-history strategy and other traits, which contribute to species' environmental sensitivities (Halsch et al. 2021, Holzmann et al., 2026, Rader et al. 2014). Therefore, although average responses of insect biodiversity to pressures are a useful tool for high-level

assessments and communication of large-scale impacts, they will often mask the considerable variation that is inherent within groups with diverse life histories, which should be explored and considered for conservation planning.

Variation in responses to land use/land-use intensity

High-intensity agriculture led to lower species richness for four of the five orders (not Diptera) and lower total abundance for all five orders relative to the primary vegetation baseline, supporting previous findings (Seibold et al., 2019; Uhler et al., 2021). The consequences of pesticide use can be unpredictable in such systems as a result of the potential for synergistic effects between different chemicals on toxicity, for example, azole fungicides interacting with neonicotinoids (Marshall et al., 2003; Siviter & Muth, 2020), as well as the potential impacts of long-term, low-level exposure on populations (Tosi et al., 2021; Woodcock et al., 2016) are likely mechanisms for change.

Similarly, the prevalence of monoculture crops grown in large areas under simple crop rotation systems and lacking semi-natural habitats and characteristics of high-intensity agriculture, have also been linked to reduced insect diversity (Ghazali et al., 2016; Varah et al., 2020).

Species richness and total abundance of Lepidoptera in high-intensity agriculture showed greater-than-average reductions compared to all other orders. Therefore, relying on the average response of insects would strongly underestimate changes in Lepidopteran richness and abundance. These differences could be due to the number of Lepidopteran species that are dietary specialists in their larval stage (Winfrey et al., 2011), which are often filtered out in landscapes simplified by agricultural intensification (Gómez-Virúes et al., 2015). Additionally, many insecticides are designed to target Lepidopterans, given the role of some species as crop pests (Richardson et al., 2020), likely impacting non-target species.

Responses of Coleoptera and Hemiptera were similar to the global average. Although not commonly studied across large scales, the negative effect of agriculture on the abundance and density of dung beetles has been observed in southeast Germany (Englmeier et al., 2022), more widely for coccinellids across central Europe (Honek et al., 2014), and in a global meta-analysis of rove beetle responses to land use change (Méndez-Rojas et al., 2021). One study that compared responses of four arthropod orders, including Coleoptera and Hemiptera, observed the greatest number of negative impacts for Hemipteran species in response to fertiliser application and mowing (Hartlieb et al., 2025). The greater uncertainty in responses of Hemiptera could reflect more variation in responses; however, the Hemiptera, along with the Diptera, also had fewer sites in the dataset compared to the other orders.

The impact of high-intensity agriculture was not observed for Dipteran richness, although lower abundance was observed. This contrasts with recent studies that found increases in the abundance of Diptera with increasing agricultural intensity of farms in Quebec (Powell et al., 2024) and with increased grassland intensity in the Netherlands (de Vries et al. 2026). The lack of a negative impact in high-intensity agriculture could be due to a higher tolerance of Dipteran species to intensified systems, indeed no decline in hoverfly abundance or diversity was observed in agricultural sites in Belgium (Verboven et al., 2014), or variability in species-level responses leading to a dampened average response. The impact on abundance suggests that although species continue to be present, the number of individuals is generally reduced. Hymenopteran richness and abundance responses were less extreme than the average across orders suggested, although still significantly lower than the baseline, supporting previous studies (de Palma et al., 2015; Verboven et al., 2014).

Variation in responses to land use/land-use intensity and climate change

As opposed to our hypothesis, the greatest relative impact was not always within sites with high-intensity agriculture and climate change. However, there were often strong negative responses in low-intensity

agriculture, which could indicate a filtering out of sensitive taxa. Indeed, for some groups, it has been shown that more specialist species have been filtered out of high-intensity agriculture such that the remaining species are typically generalists with broad climatic and environmental niches (Chisté et al., 2018; Mangels et al., 2017; Redhead et al., 2018). Total abundance was only lowest in sites of high-intensity agriculture that have experienced climate change for Coleoptera and Lepidoptera. For species richness, this was observed for Hemiptera and Lepidoptera. High-intensity agriculture combined with climate change might generally affect insects by reducing the availability of microclimate refugia. Human-dominated habitats are often hotter and drier than natural habitats (Senior et al., 2017), and the lack of potential buffering from high temperatures can limit insects' ability to regulate their body temperature, exposing them to dangerous temperature extremes resulting from ongoing climate change (Ashe-Jepson et al., 2023; Hayes et al., 2024; Suggitt et al., 2018).

Lepidopteran abundance and species richness were much lower in all land use types when sites had also experienced climate change compared with the baseline (primary vegetation and no climate change), and lower than would be suggested by the average response across orders. Anthropogenic land use and climate change have been repeatedly linked to declining abundances of Lepidoptera, particularly moths (Martay et al., 2017; Wagner et al., 2021; Warren et al., 2021), which represented at least 29% of the Lepidopterans in the dataset. The potential phenological or spatial mismatches with host plants as individuals respond to the changing climate and for negative impacts across life stages may explain why Lepidoptera are impacted more than some other groups (Hill et al., 2021). Yet, effects on non-adult life stages are understudied across orders.

For Diptera, low-intensity agriculture interacting with climate change led to the greatest reductions in total abundance and species richness, with no difference or a lower reduction in high-intensity agricultural sites. As mentioned above, this could indicate a filtering out of specialist species with a high abundance of generalists remaining. This is particularly likely if generalist species can use mass-grown flowering crops. Diptera have also been shown to have lower critical thermal maxima relative to other orders (Holzmann et al., 2026), which would explain the greater reductions observed in sites that have experienced climate change compared to sites that have not.

Coleoptera responses were very similar to the average response across insect orders for both species richness and abundance. Local declines in abundance and diversity of beetles have previously been linked to warming temperatures (Evans et al., 2022; Harris et al., 2019). Hemiptera responses were also very similar to the average for richness, but abundance responses were greater in magnitude than the average. To our knowledge, there are no large-scale assessments of this order's response to land use-climate interactions.

The Hymenoptera showed dampened or even positive responses to climate change across land uses. This may be due to species having generally higher thermal limits than other taxa, as has been shown for species in tropical and subtropical regions (Holzmann et al., 2026; López-Urbe et al., 2024). Additionally, this group often had wide CIs,

which could be a result of within-order response variation. The ants (Formicidae) comprise at least 33% of Hymenopterans in our dataset. Ants are highly thermally responsive (Parr & Bishop, 2022) and use behavioural adjustments to adapt to rising temperatures, such as shifting nests within the soil column (Bollazzi et al., 2008; Heller & Gordon, 2006). It has been suggested that ants could benefit from warming temperatures (Parr & Bishop, 2022), possibly leading to generally more stable or positive responses to climate change. Meanwhile, bees (families Apidae, Halictidae, Andrenidae, Megachilidae, Colletidae and Melittidae) represent at least 56% of Hymenopterans in this dataset, and there is accumulating evidence of the negative impacts of land use and climate change on bee populations (Kammerer et al., 2021; Potts et al., 2010; Soroye et al., 2020). Disparate responses among sub-groups of Hymenoptera could explain the dampened responses and demonstrate the need for further analysis into the responses of bees, wasps and ants separately to tease apart the potential differences.

LIMITATIONS

The data used here were collected in the recent past (1992–2012) and mostly from regions with a long history of human pressures (Ellis & Ramankutty, 2008). It is probable that all sites have undergone some degree of human disturbance, and the ‘baseline’ primary vegetation may have already experienced biodiversity change or loss (Newbold et al., 2025). This likely means we have underestimated the effect of historical land-use change on insect diversity. Similarly, using spatial comparisons to infer how biodiversity has changed over time can ignore important temporal processes such as lagged responses of biodiversity to environmental pressures (Lovell et al., 2023).

We were only able to assess variation in responses *among* insect orders in this work because of the relatively limited data. Nevertheless, there is likely considerable variation *within* orders, particularly in those with heterogeneous species ecologies and life histories, as already discussed in relation to Hymenoptera. Further studies assessing within-order differences are needed to explore this. Similarly, our dataset is unlikely to be representative of the true taxonomic spread within each order; that is, the Lepidoptera data are dominated by butterflies, whereas in reality, 90% are moths. Given the likely variation in responses within orders, it is possible that our results would differ if the data more accurately reflected the distribution of diversity within each order. In addition, records are not always identified to the species level (see Table S1); this may impact the effects observed if changes in richness of species per se are not being detected due to this coarse classification. It is possible that the richness responses for Coleoptera and Diptera are underestimated, as these orders have more records at the family level. This will not, however, affect the estimated response of order total abundance. These limitations highlight the need for local to landscape scale studies that can pick apart these responses in a way that is not always possible at the global scale.

To calculate the STA, we used only those months during which insects are likely to be active: that is, where the mean daily

temperature is greater than or equal to 10°C. Insects may also be impacted by temperature changes outside of these months, when overwintering, or when in immature life stages. However, Outhwaite et al. (2022) showed that results based on a STA calculated for all months were very similar.

Within the dataset, the Northern hemisphere is over-represented (Figure 1), which affects the spread of values for the STA index used to define climate change, such that for some land use-order combinations, there was limited climatic variability. Such geographic bias has been highlighted in other studies (van Klink et al., 2020). While addressing this through increased monitoring is important, there is an urgent need for rapid mitigation of the current biodiversity crisis by making the best use of the available evidence (Cooke et al., 2025), and, to our knowledge, the PREDICTS database is the largest global-scale database of biodiversity surveys documenting insect responses to land use.

CONCLUSIONS

Our work shows that although modelling the average response of insects to human-driven pressures can be a useful tool, it often hides substantial variation in responses between different orders. By assuming all insect orders respond to land use and climate change in the same way, we would considerably underestimate impacts on Lepidoptera total abundance (by 31%), for example. It is important to consider this variation to ensure that conservation action is focused where it is most needed, but also to ensure that responses of highly impacted and highly taxonomically variable groups are not underestimated. To maintain insect diversity, there needs to be a strong commitment to the reduction of emissions, the mitigation of climate change impacts, and the implementation of sustainable and regenerative, lower-intensity agricultural practices. Achieving these goals remains complex, involving international co-operation and action across scales.

AUTHOR CONTRIBUTIONS

Kyra Nancie Smith: Conceptualization; formal analysis; methodology; writing – original draft; writing – review and editing. **Tim Newbold:** Conceptualization; methodology; writing – review and editing. **Joseph Millard:** Methodology; writing – review and editing. **Rob Cooke:** Methodology; writing – review and editing. **Andrew J. Bladon:** Methodology; writing – review and editing. **Andy Purvis:** Methodology; writing – review and editing. **Nick J. B. Isaac:** Methodology; writing – review and editing. **John Iwan Iwan Jones:** Methodology; writing – review and editing. **Helen E. Roy:** Methodology; writing – review and editing. **Cang Hui:** Methodology; writing – review and editing. **Charlotte L. Outhwaite:** Conceptualization; formal analysis; methodology; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The 2016 release of the PREDICTS database used in this study can be downloaded from the data portal of the Natural History Museum at <https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database> (Hudson et al., 2016). The CRU TS data used for calculating the temperature anomalies can be downloaded from the CRU data website at <https://crudata.uea.ac.uk/cru/data/hrg/>. The code required to run the analyses presented here can be obtained from the GitHub repository at https://github.com/CharlieOuthwaite/LUCC_ByOrder_paper.

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SUPPORTING INFORMATION

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

Table S1. The percentage of records for each order that are classified at each taxonomic resolution. Lepidoptera and Hymenoptera have the highest percentage of records at the species or genus level, whereas Coleoptera tend to be recorded more frequently at the family level. The total number of records of each order is also presented.

Table S2. A breakdown of the site-level PREDICTS data for the five major insect orders. This includes the number of sites and studies for each insect order in total and by land use/land-use intensity category. The total number of sites where information on total abundance and species richness for each order is also shown.

Table S3. The AIC, delta AIC and conditional and marginal R^2 values for the different model sets, including and excluding order-level effects. Including a main and interaction effect of order results in lower AIC values and small improvements in variance explained by the fixed effects.

Table S4. Model output table for the model of the response of log-rescaled total abundance to the interaction between land use and land-use intensity and insect order. This includes effect sizes, confidence intervals and p-values for each of the modelled variables, the number of levels for each random effect, the total number of observations and the marginal and conditional R-squared.

Table S5. Model output table for the model of the response of species richness to the interaction between land use and land use-intensity and insect order. This includes effect sizes, confidence intervals and p-values for each of the modelled variables, the number of levels for each random effect, the total number of observations and the marginal and conditional R-squared.

Table S6. Model output table for the model of the response of total abundance to the interaction between land use and land-use intensity, the standardised temperature anomaly and insect order. This includes effect sizes, confidence intervals and p-values for each of the modelled variables, the number of levels for each random effect, the total number of observations and the marginal and conditional R-squared.

Table S7. Model output table for the model of the response of species richness to the interaction between land use and land use intensity, the standardised temperature anomaly and insect order. This includes effect sizes, confidence intervals and p-values for each of the modelled variables, the number of levels for each random effect, the total number of observations, and the marginal and conditional R-squared.

Table S8. Percentage changes for all combinations of all insects or orders and each land use category relative to primary vegetation. Percentage changes were calculated based on predicted values from the models.

Table S9. Percentage changes for all combinations of all insects or orders and each land use category for STA values of 0 and 1 relative to primary vegetation with an STA of 0. Percentage changes were calculated based on the predicted values from the models.

Table S10. Parameter estimates for total abundance, where abundance has not been rescaled, as a function of land use in interaction with insect order. Output includes estimates, confidence intervals and

p values for the fixed effects, the number of random effects groups (N_{SS} for studies and N_{SSB} for blocks within studies) and the marginal and conditional R^2 values.

Table S11. Parameter estimates for total abundance, where abundance has not been rescaled, as a function of land use in interaction with the standardised temperature anomaly and insect order. Output includes estimates, confidence intervals and p values for the fixed effects, the number of random effects groups (N_{SS} for studies and N_{SSB} for blocks within studies) and the marginal and conditional R^2 values.

Table S12. The number of sites sampling the different insect orders within the studies that were identified as outliers via Cook's distances. The percentage of sites covering each order that are included in the outlying studies is shown in brackets.

Table S13. Conditional and marginal R^2 values for the separate models for total abundance and species richness run for each insect order. Values have been rounded to two decimal places. Note that for one model, a warning of a singular fit was flagged by the model fitting function.

Table S14. AIC values of the models, including average temperature of the site as a fixed effect, compared to the models of the main text where this is not included.

Table S15. Model output table for the model of the response of log-rescaled total abundance to the interaction between land use and land-use intensity and insect order run using the *brms* package. This includes effect sizes and credible intervals for each of the modelled variables, the number of levels for each random effect, the total number of observations and the Bayes marginal and conditional R-squared values.

Table S16. Model output table for the model of the response of species richness to the interaction between land use and land-use intensity and insect order run using the *brms* package. This includes effect sizes and credible intervals for each of the modelled variables, the number of levels for each random effect, the total number of observations and the Bayes marginal and conditional R-squared values.

Table S17. Model output table for the model of the response of total abundance to the interaction between land use and land-use intensity, the standardised temperature anomaly and insect order using the *brms* package. This includes effect sizes and credible intervals for each of the modelled variables, the number of levels for each random effect, the total number of observations and the Bayes marginal and conditional R-squared.

Table S18. Model output table for the model of the response of species richness to the interaction between land use and land-use intensity, the standardised temperature anomaly and insect order using the *brms* package. This includes effect sizes and credible intervals for each of the modelled variables, the number of levels for each random effect, the total number of observations and the Bayes marginal and conditional R-squared.

Figure S1. Global average absolute and standardised temperature anomalies. a. Absolute change in temperature between the baseline 1901–1930 and 2005 (the median sample year of the insect data). This was calculated as the difference in mean monthly temperatures

of insect-active months between the baseline of 1901–1930 and the period 2004–2006 for each $0.5 \times 0.5^\circ$ grid cell of the terrestrial surface, for which estimates were available. b. The standardised temperature anomaly was calculated as the absolute temperature change between the baseline and 2005, divided by the standard deviation of the baseline temperatures across insect-active months (see the Methods section for more details). For both absolute and standardised temperature changes, we consider only months in which insects are assumed to be active (i.e., monthly mean temperature $\geq 10^\circ\text{C}$). Density plots to the right of each map show the average temperature change at a given latitude. Extreme latitudes and areas of high elevation are blank as they do not have months that meet the assumed temperature threshold for insect activity.

Figure S2. Model checks for the model of rescaled abundance as a function of the interaction between land use and insect Order. a. Fitted versus residuals plot to check for constant variance across the range of fitted values. b. Normal Q-Q plot to check the normality of the residuals. c. Observed values versus fitted values. d. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S3. Model checks for the model of rescaled abundance as a function of land use only. a. Fitted versus residuals plot to check for constant variance across the range of fitted values. b. Normal Q-Q plot to check the normality of the residuals. c. Observed values versus fitted values. d. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S4. Model checks for the model of species richness as a function of the interaction between land use and insect order. a. Normal Q-Q plot to check the normality of the residuals. b. Observed values versus fitted values. c. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each Study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S5. Model checks for the model of species richness as a function of land use only. a. Normal Q-Q plot to check the normality of the residuals. b. Observed values versus fitted values. c. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S6. Model checks for the model of rescaled abundance as a function of the interaction between land use, standardised temperature anomaly and insect order. a. Fitted versus residuals plot to check for constant variance across the range of fitted values. b. Normal Q-Q plot to check the normality of the residuals. c. Observed values versus fitted values. d. Histograms of p values from sets of Moran's tests for

spatial autocorrelation in the residuals of the best models for each Study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S7. Model checks for the model of rescaled abundance as a function of the interaction between land use and standardised temperature anomaly only. a. Fitted versus residuals plot to check for constant variance across the range of fitted values. b. Normal Q-Q plot to check the normality of the residuals. c. Observed values versus fitted values. d. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each Study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S8. Model checks for the model of species richness as a function of the interaction between land use, standardised temperature anomaly and insect order. a. Normal Q-Q plot to check the normality of the residuals. b. Observed values versus fitted values. c. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each Study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S9. Model checks for the model of species richness as a function of the interaction between land use and standardised temperature anomaly only. a. Normal Q-Q plot to check the normality of the residuals. b. Observed values versus fitted values. c. Histograms of p values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for each Study. The red line represents $p = 0.05$. By chance, we expect to detect significant spatial autocorrelation in the residuals associated with 5% of the studies.

Figure S10. Predicted responses of total abundance to the interaction between insect order, land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (i.e., those with monthly mean temperatures $\geq 10^\circ\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use.

Figure S11. Predicted responses of species richness to the interaction between insect Order, land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (i.e., those with monthly mean

temperatures $\geq 10^{\circ}\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use. Note that in some cases, the confidence interval is very wide at high values of STA, and the axes have not been expanded to accommodate them here.

Figure S12. Response of total abundance to land use and land-use intensity, where abundance has not been rescaled within each study/order. Order-level responses are from the model where order is included as an interaction with the land-use/use-intensity category. Responses are presented as relative to biodiversity estimates in primary vegetation within each grouping. The points show the median values as predicted from the models, and the error bars show the 95% confidence interval.

Figure S13. Response of total abundance to the interaction between land use and land-use intensity and the standardised temperature anomaly without rescaling abundance. Order-level responses predicted from the model, including the interaction with insect Order. Responses are presented as the percentage change in abundance relative to values for sites of primary vegetation with an STA of 0 within each grouping. The points show the median values as predicted from the models, with the error bars showing the 95% confidence interval. Note the different y-axis scales for each panel.

Figure S14. Predicted values of the percentage change in species richness for each land use and insect order combination when the STA is 1 relative to that in primary vegetation when the STA is 0. Each point represents the predicted value determined from a model run with a dataset excluding the sites from one study. All studies were sequentially removed, and values were predicted from the resulting model. Four studies had a greater influence on the predicted results than the others. These studies are labelled with the study ID.

Figure S15. The spatial distribution of the sampled sites from four studies in PREDICTS that were identified as highly influential.

Figure S16. Representation of Figure 2 in the main text using the complete dataset, that is, without removing the four influential studies. Response of (a) species richness and (b) total abundance to land use and land-use intensity. Responses for all five orders combined, predicted from the models excluding the order term, are shown first. Order-level responses are then predicted from the models where order was included as an interaction with the land-use/use-intensity category. Responses are presented as relative to biodiversity estimates in primary vegetation within each grouping. The points show median model-predicted values, and the error bars show 95% confidence intervals.

Figure S17. Representation of Figure 3 in the main text using the complete dataset, that is, without removing the four influential studies. Response of species richness to the interaction between land use/land-use intensity and the standardised temperature anomaly. (a) Responses for all five orders combined, based on predictions from the model, excluding the order. (b) Coleoptera, (c) Diptera, (d) Hemiptera, (e) Hymenoptera and (f) Lepidoptera are order-level responses predicted from the model, including the interaction with insect order. Responses are presented as the percentage change in

richness relative to values for sites of primary vegetation with an STA of 0 within each grouping. An STA of 1 indicates warming equal to the s.d. of the temperatures in the baseline period, indicating exposure to novel temperatures. The points show the median values as predicted from the models, with the error bars showing the 95% confidence interval.

Figure S18. Representation of Figure 4 in the main text using the complete dataset, that is, without removing the four influential studies. Response of total abundance to the interaction between land use and land-use intensity and the standardised temperature anomaly (STA). (a) Responses for all five orders combined, based on predictions from the model without Order. (b) Coleoptera, (c) Diptera, (d) Hemiptera, (e) Hymenoptera and (f) Lepidoptera are order-level responses predicted from the model, including the interaction with order. Responses are presented as the percentage change in abundance relative to values for sites of primary vegetation with an STA of 0 within each grouping. An STA of 1 indicates warming equal to the s.d. of the temperatures in the baseline period, indicating exposure to novel temperatures. The points show the median model-predicted values, with the error bars showing 95% confidence intervals.

Figure S19. Predicted responses of Coleoptera total abundance and species richness to the interaction between land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (that is, those with monthly mean temperatures $\geq 10^{\circ}\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use.

Figure S20. Predicted responses of Diptera total abundance and species richness to the interaction between land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (that is, those with monthly mean temperatures $\geq 10^{\circ}\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use. Note that the richness model was flagged as having a singular fit.

Figure S21. Predicted responses of Hemiptera total abundance and species richness to the interaction between land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised temperature anomaly is the difference in mean monthly temperatures

of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (that is, those with monthly mean temperatures $\geq 10^{\circ}\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use.

Figure S22: Predicted responses of Hymenoptera total abundance and species richness to the interaction between land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (that is, those with monthly mean temperatures $\geq 10^{\circ}\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use.

Figure S23. Predicted responses of Lepidoptera total abundance and species richness to the interaction between land use and the standardised temperature anomaly. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardised temperature anomaly of 0). Standardised

temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the 5 years preceding biodiversity sampling, divided by the s.d. of the baseline temperatures across insect-active months (that is, those with monthly mean temperatures $\geq 10^{\circ}\text{C}$). The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use.

Figure S24. Response of Chao-estimated richness to the interaction between insect Order, land use and the standardised temperature anomaly. Values represent the percentage difference compared to primary vegetation with no historical climate warming (a temperature anomaly of 0). Lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval. Results are plotted for the central 95% of modelled anomaly values for each land use.

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