

Agriculture and climate change are reshaping insect biodiversity worldwide

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Several previous studies have investigated changes in insect biodiversity, with some highlighting declines and others showing turnover in species composition without net declines^{1–5}. Although research has shown that biodiversity changes are driven primarily by land-use change and increasingly by climate change^{6,7}, the potential for interaction between these drivers and insect biodiversity on the global scale remains unclear. Here we show that the interaction between indices of historical climate warming and intensive agricultural land use is associated with reductions of almost 50% in the abundance and 27% in the number of species within insect assemblages relative to those in less-disturbed habitats with lower rates of historical climate warming. These patterns are particularly evident in the tropical realm, whereas some positive responses of biodiversity to climate change occur in non-tropical regions in natural habitats. A high availability of nearby natural habitat often mitigates reductions in insect abundance and richness associated with agricultural land use and substantial climate warming but only in low-intensity agricultural systems. In such systems, in which high levels (75% cover) of natural habitat are available, abundance and richness were reduced by 7% and 5%, respectively, compared with reductions of 63% and 61% in places where less natural habitat is present (25% cover). Our results show that insect biodiversity will probably benefit from mitigating climate change, preserving natural habitat within landscapes and reducing the intensity of agriculture.

Increasing evidence shows that many insect assemblages have undergone changes in biodiversity in recent decades^{2–4,8,9}. Insects are important for ecosystems, including for pollination and pest control as well as for soil quality regulation and decomposition¹⁰. Therefore, alterations in insect assemblages could have important implications for both biodiversity conservation and human well-being^{10,11}. Recent studies have quantified trends in insect biodiversity, and the drivers of insect declines have been assessed for some regions and species groups^{12,13}; however, little research has addressed the impact of drivers at the global scale. Human land use and climate change have emerged as key determinants of changes in the biodiversity of well-studied species groups (insects and non-insects) and regions (such as the UK and Europe)^{2,6,14–16}. Evidence suggests that these drivers may interact synergistically, leading to greater responses than would be expected had they acted independently¹⁷. For example, human land use alters local climatic conditions, which reduces the availability of suitable microclimates, alters the heterogeneity and the buffering capacity of microclimates and changes the permeability of landscapes for species to track climate change^{17–20}. Synergistic interactions between the effects of land use and climate change are important drivers of biodiversity in regional studies of vertebrates and a few insect groups^{17,21–23}.

The impact of land-use–climate interaction is likely to vary spatially. In general, tropical species are considered to be more sensitive than temperate species to climate change^{24,25}. Owing to the relative stability of temperatures in the tropics compared with those in the temperate

realm, tropical species have experienced a much narrower range of past climatic conditions and thus tend to have narrower thermal niches than temperate species^{24,26}. When warming does occur, those with narrower thermal niches are the most likely species to be pushed towards or beyond their thermal limits by regional climate change or by microclimatic changes caused by land-use change²⁴. It is therefore likely that the effects of interaction between land use and climate change will be strongest in the tropics.

The negative effects of climate change may be reduced through conservation management. For example, previous studies have shown that climate-driven losses of bird diversity are reduced or even reversed in landscapes with large amounts of natural habitats^{23,27,28}. The presence of nearby natural habitats can moderate changes in biodiversity by providing alternative habitats and resources for local biodiversity²⁹. Furthermore, natural habitats provide microclimates that offer shelter from the more extreme temperatures in agricultural areas³⁰.

We assessed the effects of the interaction between land use and climate warming on insect abundance and species richness across the global land surface using a spatial analysis of the differences in biodiversity among land-use types. To do so, we analysed site-level comparisons of local insect biodiversity across land-use types from the Projecting Responses of Ecological Diversity in Changing Terrestrial Systems (PREDICTS) database³¹. The database includes snapshot samples of terrestrial biodiversity from different locations across the globe, enabling spatial comparisons of sites under differing land-use and climatic conditions.

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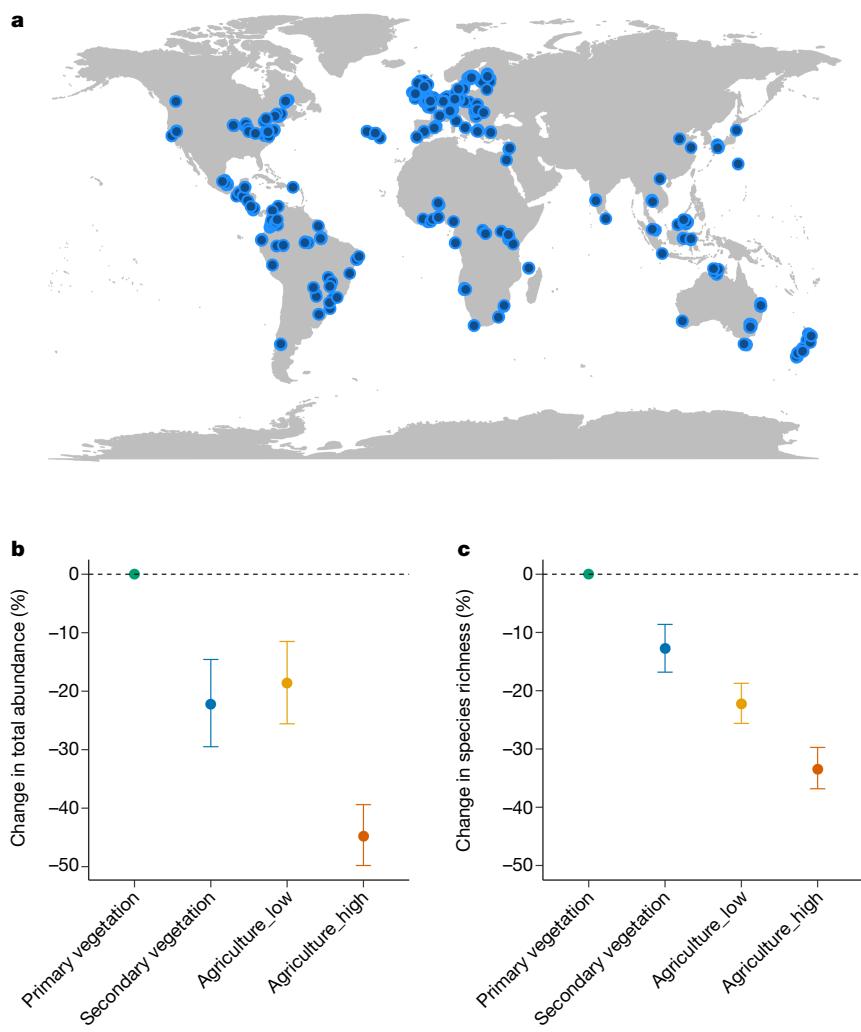


Fig. 1 | Locations of sites and responses of insect total abundance and species richness to land use and land-use intensity. **a**, Location of PREDICTS sites that include insect data. **b**, Response of insect total abundance to land use (likelihood ratio test: $\chi^2_{3,7} = 132, P < 0.001$). **c**, Response of insect species richness to land use ($\chi^2_{3,7} = 243, P < 0.001$). Error bars show 95% confidence intervals. The agricultural land-use types in PREDICTS (cropland, plantation,

pasture) were combined into a single agriculture class that was divided into two groups according to use intensity: low and high. The number of sites included in the analyses for the abundance and richness models are primary vegetation, $n = 1,410, 1,516$; secondary vegetation, $n = 1,338, 1,483$; low-intensity agriculture (agriculture_low), $n = 1,294, 1,317$; and high-intensity agriculture (agriculture_high), $n = 1,717, 1,779$, respectively.

Although the data span 20 years (from 1992 to 2012), the individual studies within which the biodiversity comparisons were made were generally collected over a very short time span. Specifically, 99.7% of the locations were sampled within a two-year period. Our dataset contained 756,879 records for 17,889 insect species including 6,037 beetles, 4,528 hymenopterans, 3,874 butterflies or moths, 1,477 flies, 1,302 true bugs, 237 grasshoppers/crickets/locusts, 95 dragonflies/damselflies and 339 species from other orders. From these, we obtained site-level estimates of species richness and, for a subset of sites, total abundance (Fig. 1). These data were derived from 264 published studies and 6,095 sampled locations in 13 out of 14 of the world's terrestrial biomes, all except tundra (Fig. 1a). We conducted our analysis using mixed-effects models specified to explore three main hypotheses: (1) conversion to agriculture and intensification of agriculture reduces insect biodiversity; (2) insect biodiversity will be reduced the most where historical climate warming interacts with agricultural land use, particularly in higher-intensity agriculture and tropical regions; and (3) natural habitat in the surrounding landscape can mitigate the detrimental effects of agricultural land use and climate warming on insects. To assess these hypotheses, the sites were grouped into the four major land-use and

land-use-intensity classes of primary vegetation, secondary vegetation, low-intensity agriculture and high-intensity agriculture using a subset of the classifications from the PREDICTS database, which are based on information in the source publications³¹. For each site, we calculated the changes in the mean and maximum temperatures that occurred between a baseline period of 1901–1930 and the five-year period preceding the biodiversity sampling using version 4.03 of the Climatic Research Unit Time Series (CRUTS) dataset³². For the anomaly based on mean temperature, we used only months with insect activity, which a previous study³³ determined to occur when the monthly mean temperature is 10 °C or higher. We also tested the sensitivity of our results to different temperature thresholds (Supplementary Information section S1). The anomaly based on maximum temperature used the three hottest months of each year, during which time we assumed insects to be active. We standardized the temperature differences to account for the range of temperature conditions typically experienced by species (Extended Data Fig. 1) by dividing the raw change in temperature between the baseline and sampling periods by the s.d. of temperatures across insect-active months in the baseline period for the anomaly based on mean temperature and by the s.d. of temperatures of the three hottest

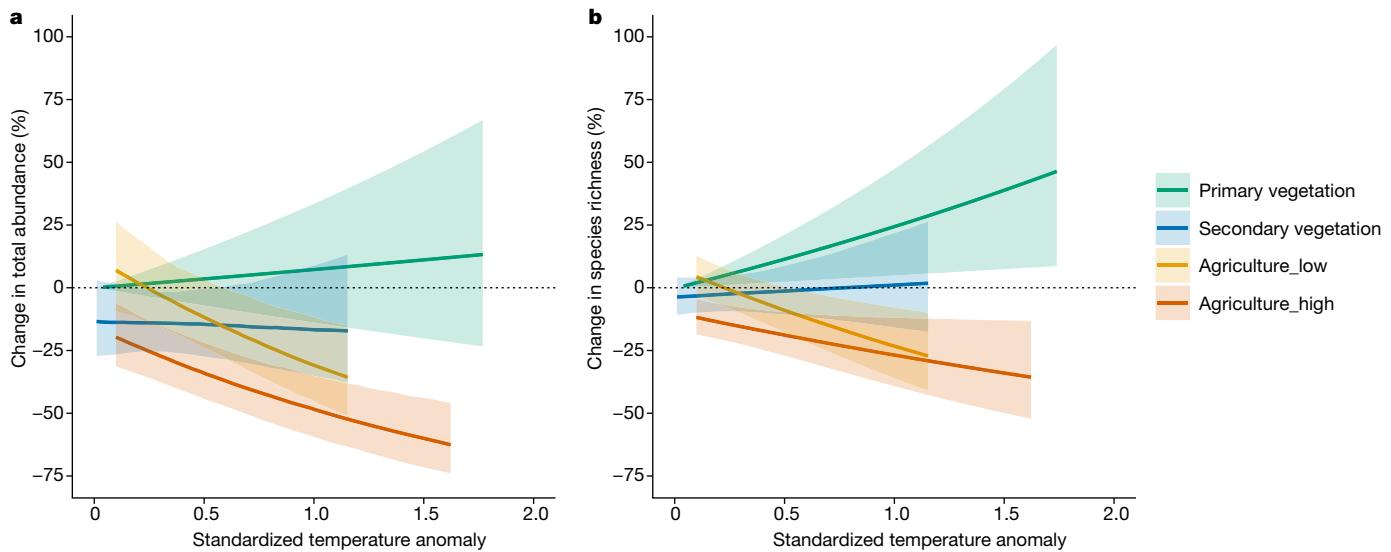


Fig. 2 | Response of insect total abundance and species richness to interaction between land use and standardized temperature anomaly.

a, b, Insect total abundance (a) and species richness (b). Likelihood ratio tests: abundance, $\chi^2_{(3,11)} = 47.4, P < 0.001$; richness, $\chi^2_{(3,11)} = 124, P < 0.001$. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardized temperature anomaly of 0). Standardized temperature anomaly is the difference in mean monthly temperatures of insect-active months between the baseline of 1901–1930 and the five 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 shaded area represents the 95% confidence interval. The results are plotted for the central 95% of modelled anomaly values for each land use. The number of sites included in the analyses for the abundance and richness models are primary vegetation, $n = 1,458, 1,563$; secondary vegetation, $n = 1,338, 1,471$; low-intensity agriculture, $n = 1,479, 1,499$; and high-intensity agriculture, $n = 1,717, 1,775$, respectively.

months for the anomaly based on maximum temperature. Although insects may respond to daily variations in climatic conditions, it was not possible to standardize the anomaly by variation in temperatures at a temporal resolution finer than monthly owing to the availability of historical climate reconstructions. We further examined whether the amount of the natural habitat surrounding the sampled sites altered the responses of insects to land-use–climate-change interactions. We derived estimates of the fractional cover of natural habitats within radii of 1 km, 3 km, 5 km or 10 km of the sampled sites on the basis of a 1-km map of modelled land use for the year 2005³⁴.

We show that in high-intensity agriculture, which is typically characterized by chemical input, low crop diversity, large field size, mechanization or high livestock density, the insect total abundance and species richness were reduced 45% and 33% compared with those in primary vegetation, whereas those in low-intensity agriculture were reduced 19% and 22%, respectively (however, these models did not consider the effects of historical temperature change) (Fig. 1b, c). This loss of insect biodiversity in agricultural systems will probably reduce the provision of ecosystem services essential to agriculture such as pollination and pest control^{35,36}. Moreover, theory suggests that declines in biodiversity could reduce the resilience of natural and agricultural ecosystems to future shocks such as those from extreme climatic events^{11,37}.

The aforementioned average reduction in both insect abundance and richness concealed strong variation in responses depending on the level of past climate change. Synergistic interactions between land use and climate change were associated with large reductions in insect biodiversity within intensively used agricultural systems that experienced substantial climate warming. Warming equivalent to 1 s.d. of baseline temperature variation (standardized temperature anomaly of 1.0) led to 49% and 27% reductions in insect abundance and species richness in intensive agriculture, respectively, compared with those in primary vegetation with no climate warming (Fig. 2). Under the same level of climate warming, low-intensity agriculture experienced 30% and 23% reductions in insect abundance and species richness, respectively. Overall, these results indicate that sensitive species are

filtered out in areas exposed to recent climate change under any level of land-use modification. By contrast, insect abundance was buffered slightly in lower-intensity agriculture but declined steeply with further intensification. Similar patterns were observed when assessing climate warming based on maximum monthly temperature, although the difference in species richness was greater between agricultural land use-intensities. This indicates that biodiversity in lower-intensity agricultural systems is partially buffered against the negative impacts of increases in extreme temperature (Extended Data Fig. 2). These results were robust to using baseline periods of differing length (Methods and Supplementary Information section S2) and were generally robust to the removal of potentially influential studies (Extended Data Figs. 3, 4 and Supplementary Information section S7). In one case, however, the removal of influential studies containing a very large number of sites (650) altered the responses slightly (Extended Data Fig. 3). Model diagnostics including fitted versus residual plots, observed versus fitted plots, Q–Q plots and tests for spatial autocorrelation were conducted for all models. The observed versus fitted plots indicate that responses from the abundance models may be conservative, underestimating the strength of the abundance differences (Methods).

Insect biodiversity is highly sensitive to climate warming because thermoregulatory behaviour is used to access thermally buffered microhabitats such as shady conditions to survive the warmest parts of the year³⁸. Because land-use change reduces the availability of these buffered microhabitats¹⁹, particularly in intensively used systems, insects are likely to be more exposed to the effects of climate warming^{30,38}. This may have greater importance for tropical species, which have narrower thermal niches^{24,26}. Furthermore, other features of tropical species, such as their relatively smaller range size and higher degree of specialization compared to temperate species, may render them more sensitive to changes in land use and climate²⁵. To explore the tropical–temperate differences and to verify that our reported association between land-use response and temperature anomaly was not caused by sensitivity of tropical biodiversity unrelated to climatic mechanisms, we repeated our analyses separately for the tropical and non-tropical realms.

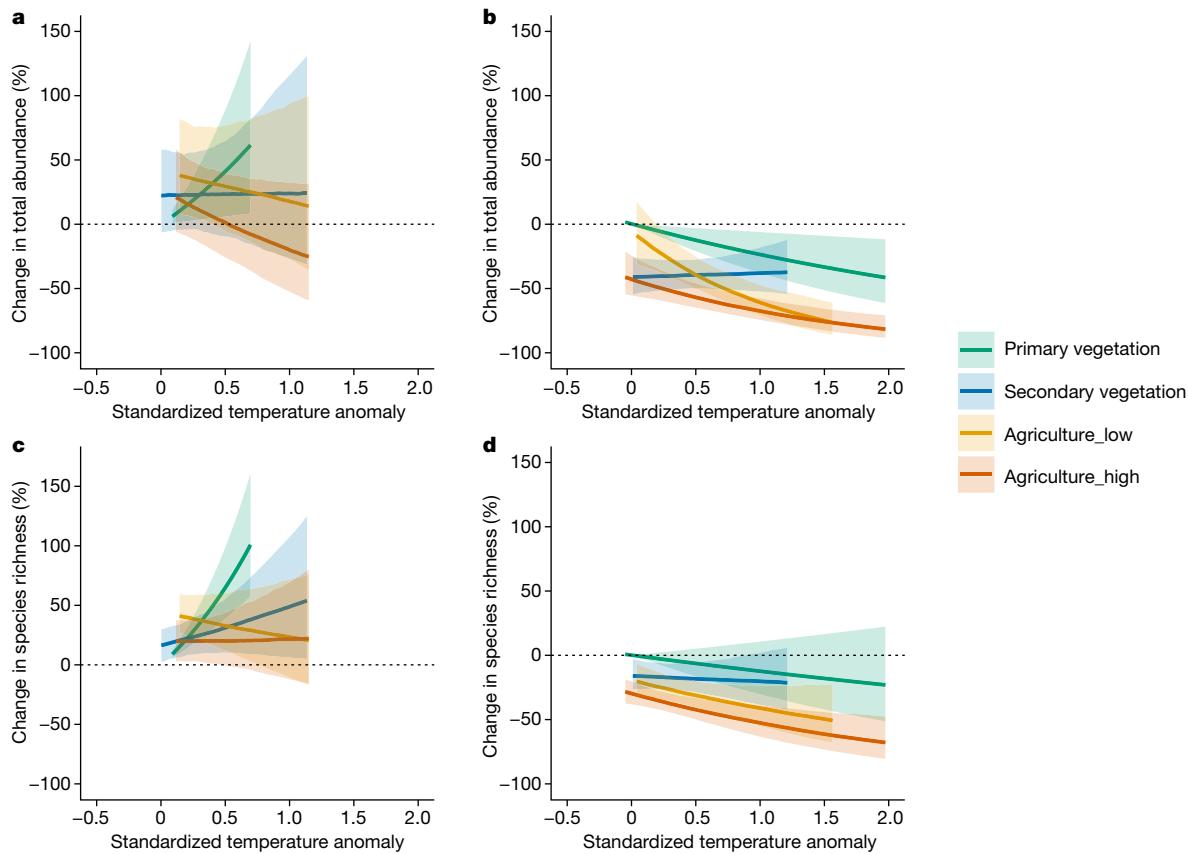


Fig. 3 | Response of insect total abundance and species richness to the interaction between land use and standardized temperature anomaly in different realms. **a–d**, Insect total abundance (**a, b**) and species richness (**c, d**) in the non-tropical (**a, c**) and tropical realms (**b, d**). Likelihood ratio tests: abundance, non-tropical, $\chi^2_{3,11} = 17.5, P < 0.001$; abundance, tropical, $\chi^2_{3,11} = 20.4, P < 0.001$; richness, non-tropical $\chi^2_{3,11} = 99.2, P < 0.001$; and richness, tropical, $\chi^2_{3,11} = 23.1, P < 0.001$. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardized temperature anomaly of 0). Details of the calculation of the standardized temperature anomaly are given in the legend of Fig. 2. 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 within each realm. The number of sites included in the analyses for the abundance and richness models are primary vegetation non-tropical, $n = 857, 902$; primary vegetation tropical, $n = 552, 613$; secondary vegetation non-tropical, $n = 941, 1,034$; secondary vegetation tropical, $n = 384, 435$; low-intensity agriculture non-tropical, $n = 1,031, 1,047$; low-intensity agriculture tropical, $n = 258, 265$; high-intensity agriculture non-tropical, $n = 1,317, 1,344$; and high-intensity agriculture tropical, $n = 395, 429$, respectively.

The interaction between land use and climate anomaly was present within both the tropical and non-tropical realms except when modelling total abundance as a function of the maximum anomaly in non-tropical sites (Extended Data Fig. 5). Consistent with expectations, the negative associations of abundance and richness with climate change and land use were greater in the tropical realm, whereas positive associations were observed in natural habitats (primary and secondary vegetation) in the non-tropical realm (Fig. 3). This positive relationship with climate change may have occurred at least in part because the most climate-sensitive species have already been lost in non-tropical regions through a long history of land-use change³⁹. Similarly, these historical changes in land use have resulted in increases in microclimatic temperatures that have enabled southern species to colonize more northern regions, whereas cold-adapted species have been lost¹².

Our analyses also show that natural habitat mitigates the detrimental impacts of climate warming on total abundance and species richness but only in low-intensity agriculture settings (Fig. 4). In areas of low-intensity agriculture with a climate anomaly of 1 surrounded by a high fractional cover of natural habitat (75%), insect abundance and species richness were reduced by 7% and 5%, respectively, compared with that in primary vegetation with no climate warming. By contrast, we observed reductions of 63% and 61% in insect abundance and species richness, respectively, when only 25% natural habitat cover was present.

In high-intensity agriculture areas, the buffering effect was smaller or non-existent. No buffering effect was observed for total abundance or species richness in response to the standardized temperature anomaly based on maximum temperature ($P > 0.05$; Extended Data Fig. 6). It is possible that the benefits insects gain from nearby natural habitat availability, such as more suitable microclimates, are not able to mitigate the effects of extreme maximum temperature.

Previous local-scale studies have shown that incorporating natural habitat into agricultural landscapes can promote the maintenance of local insect biodiversity^{40–43}. We further show that natural habitat cover is associated with buffering against the reductions in insect biodiversity otherwise present in places in which low-intensity agriculture coincides with substantial recent climate warming. The fact that no mitigation by natural habitat was observed for the anomaly based on maximum temperature suggests that natural habitat cannot mitigate increases in extreme temperatures, the occurrences of which are likely to become more frequent in the future. As the global demand for food increases, it is likely that the expansion of agricultural systems will continue. If this agricultural expansion is associated with a reduction in the availability of natural habitats within production landscapes or a move toward higher-intensity agriculture, our results indicate that large declines in insect biodiversity will occur, particularly as climate warming accelerates.

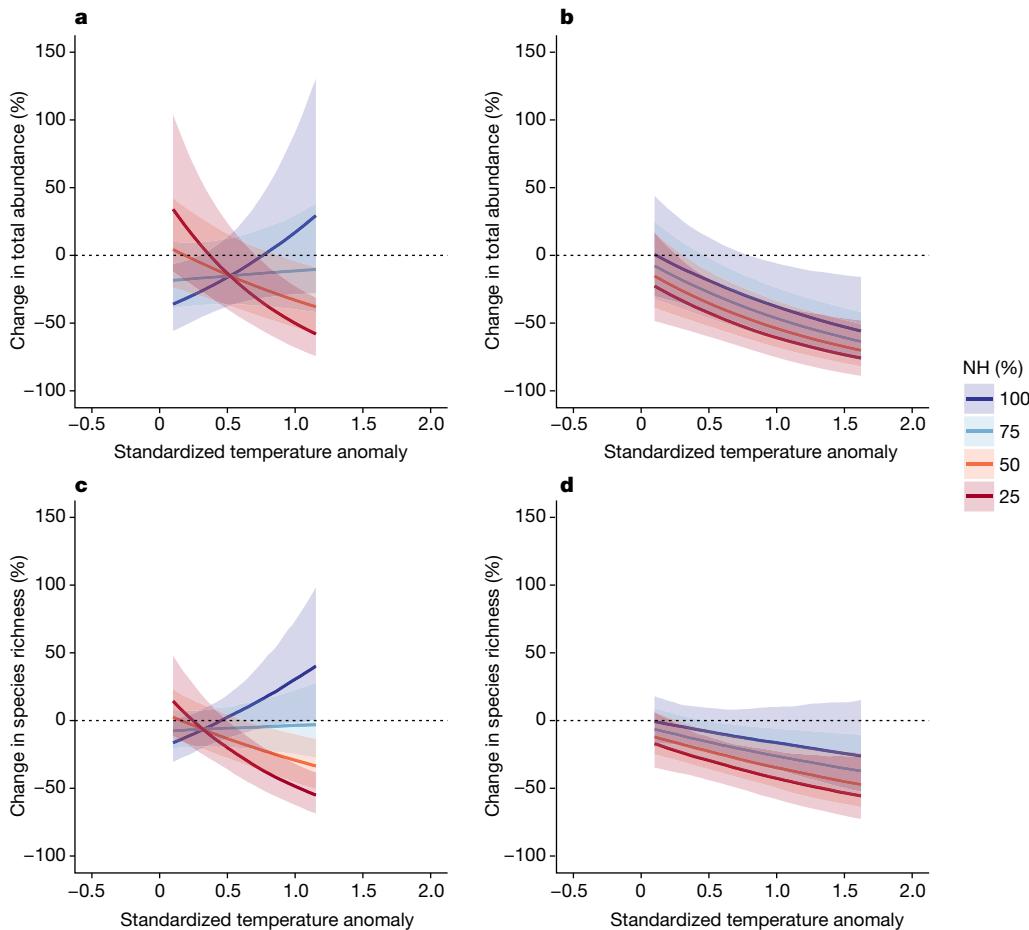


Fig. 4 | Responses of insect total abundance and species richness to the interaction between the standardized temperature anomaly, land-use intensity and availability of nearby natural habitat. **a–d,** Insect total abundance (**a, b**) and species richness (**c, d**) in areas of low-intensity agriculture (**a, c**) and high-intensity agriculture (**b, d**). Likelihood ratio tests: abundance, $\chi^2_{3,19} = 23, P < 0.001$; richness, $\chi^2_{3,19} = 30, P < 0.001$. These values represent the percentage difference compared with primary vegetation with no historical climate warming (standardized temperature anomaly of 0) and with 100% nearby natural habitat. The percentage of natural habitat (NH) describes the potential availability of primary and secondary vegetation surrounding an

agricultural site. These plots show model predictions and do not necessarily represent plausible combinations of land use/land-use intensity and surrounding natural habitats in all cases. Details of the calculation of the standardized temperature anomaly are given in the legend of Fig. 2. The lines correspond to the median predicted values, and the shaded area represents the 95% confidence interval for sites with differing cover of natural habitat within a 5-km radius of the sampled site. The number of sites included in the analyses for the abundance and richness models are low-intensity agriculture, $n = 1,289, 1,312$; and high-intensity agriculture, $n = 1,712, 1,773$, respectively.

Insect biodiversity has probably been detrimentally affected by high levels of climate change worldwide (Extended Data Fig. 7). In much of the tropics and in some high northern latitudes, insect communities are exposed to novel high temperatures during their active months. Moreover, many regions are currently affected by temperature increases that exceed historical variability. In most non-tropical regions, average warming is still within the range of typical natural variability (standardized temperature anomaly < 1); thus, communities in such areas are less likely to have been exposed to novel high temperatures. Nevertheless, temperate regions are currently experiencing new temperature extremes such as heatwaves⁴⁴. As climate warming continues in the future, the risk to insect biodiversity from land-use–climate-change interactions will become much more widespread, including in temperate areas (Extended Data Fig. 7).

Regional-scale studies have linked insect declines to land use^{45,46} and climate change^{2,24}. Our quantitative, global-scale analysis explicitly links global insect biodiversity change to the interaction of land use, land-use intensity and climate change. A recent meta-analysis describing global insect declines⁹ was unable to find a link between changes in insect populations and local temperature changes possibly because the authors did not consider the potential for land-use–climate interactions or because temperature change was not standardized to historical variability, as it was

in our study. Furthermore, the data in this meta-analysis were obtained predominantly from non-tropical regions, where populations are more likely to be limited by cold temperatures and thus have greater potential to respond positively to climate change. Those data also consisted of short time series, which may not enable the detection of climate change impacts.

As with any correlative study, we cannot infer causal effects; moreover, because this study uses a spatial rather than temporal analysis, we cannot address changes in insect biodiversity over time. An important limitation of using spatial analysis is that we cannot consider the possibility of time lags in the effects of environmental change on biodiversity. Furthermore, because most of the data underlying our study were collected after 2000, our biodiversity estimates—particularly for primary vegetation in non-tropical systems—may not be fully representative of a true baseline. This is because such systems have a long history of land use, which will have led to the loss of some species from natural habitats. Although the biodiversity data span a large proportion of the world's terrestrial surfaces, as with most biodiversity studies⁴⁷, relatively few data are available for the tropics and for high latitudes. Several sensitivity tests were conducted to verify the robustness of our results. These include (1) assessing the impact of climate estimates based on more recent climate estimates; (2) comparing these models to those that

include other climatic variables; and (3) testing the potential influence of incomplete sampling on the species richness results (Methods).

Despite the limitations of correlational analyses of observational biodiversity data, we showed a clear and consistent association between insect biodiversity (both species richness and abundance) and the interaction between land use and climate change. Future work that directly measures the aspects of microclimate between areas under different land-use regimes in locations with different rates of climate warming could identify the mechanistic basis for the observed changes in insect biodiversity. We did not include other aspects of climate such as precipitation here. However, temperature is thought to be a key climatic variable for insect species^{48,49}. Nevertheless, future studies that include additional climate variables and finer-scale land-use and/or land-use-intensity data might be able to offer further insights.

Studies aiming to understand recent change in insect biodiversity have increased in recent years; however, a quantitative analysis of the impacts of major drivers on global insect diversity has been lacking. Here we show that reductions in insect abundance and richness are greatest in areas of intensive agricultural land use, where the climate includes the warmest temperatures relative to background seasonal and inter-annual variation, particularly in the tropics. The ability of natural habitats to mitigate the negative impacts of agriculture and climate change in low-intensity agriculture presents a management option that could help to maintain insect populations, although our results suggest that this buffering is less effective against extremely high temperatures. Insect biodiversity is essential for many ecosystem functions and services, including key services for agriculture. Ensuring that these services remain available in agricultural landscapes will benefit people and nature. Under the highest-emissions scenarios, most of the terrestrial surface will be exposed to novel high temperatures by 2070. Reducing the magnitude of changes in insect biodiversity will require strong climate mitigation and implementation of land-management strategies that increase the availability of natural habitats.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-022-04644-x>.

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Methods

Biodiversity data from the PREDICTS database

The PREDICTS database is an aggregation of spatial comparisons of local biodiversity across land-use types and contains data from all major terrestrial regions of the world^{31,50}. These samples are taken from published sources (or unpublished datasets, provided the methodology was published) and include measures of species abundance, presence/absence and richness for a wide range of taxa, including vertebrates, invertebrates and plants. The data within PREDICTS are organized hierarchically: the published sources contain one or more studies, encompassing data that were collected using the same methodology. Such studies contain one or more spatial blocks, within which the data were collected from sites with associated geographical coordinates⁵¹.

For this study, we extracted PREDICTS data for insects for all land-use types where use intensity was known, except urban, comprising 756,879 records. This subset contained 732,394 records with an associated measure of abundance (although not always a true count), 2,997 records of density, 21,355 records of occurrence or occurrence frequency and 133 records of species richness. Within-sample species richness was calculated as the total number of species sampled at a site, whereas total abundance was the sum of all abundance measurements at a site, where available. Where the sampling effort differed among sites within a study (affecting 2% of non-zero measurements), the effort was scaled for each study so that the highest sampling effort had a value of 1. The abundance measurements were then divided by this measure of relative sampling effort, assuming that the recorded abundance scaled linearly with the sampling effort⁶. The abundance values in our insect data subset had a strong right-skewed distribution caused in part by the variety of methods for measuring the abundance in the underlying studies and by variation in measuring the abundances across many different taxonomic groups. To reduce this skew, following a previous study⁵², we rescaled the abundance values between 0 and 1 within each study such that the highest abundance value was set to 1; the remaining values were rescaled relative to this maximum value. This ensured that the samples still remained independent of each other. Differences in sampling effort among studies were not accounted for beyond fitting the study identity as a random effect. To assess the effect of incomplete sampling on our results, we ran a set of models using Chao-estimated species richness, which is a method of estimating species richness that accounts for incomplete sampling effort⁵³. The Chao-estimated richness could not be determined for all sites with species richness data because its calculation requires an integer measure of abundance. However, the results using those sites for which it could be estimated were very similar to the main results for species richness (Supplementary Information section S4). The final dataset consisted of data on insect abundance from 5,759 sites from 244 studies and for insect species richness from 6,095 sites from 264 studies. More information on the composition of the dataset can be found in Supplementary Tables 5–8.

The PREDICTS database recognizes eight land-use categories classified according to the description of the habitat as given by the authors of the source publications.

- (1) Primary vegetation, consisting of forest or non-forest native vegetation that is not known to have ever been destroyed.
- (2) Young secondary vegetation, where the term ‘secondary vegetation’ describes primary vegetation that has been destroyed and is now recovering; age classifications are based on the complexity of the vegetation.
- (3) Intermediate secondary vegetation.
- (4) Mature secondary vegetation.
- (5) Cropland, consisting of land planted with herbaceous crops.
- (6) Pasture, where livestock are known to be regularly or permanently grazing.

- (7) Plantation forest, consisting of previously cleared areas planted with crop trees or shrubs.

- (8) Urban, consisting of areas with human habitation or buildings.

Each broad land-use category is further subdivided into three use intensities of minimal, light or intense according to factors describing the level of human disturbance such as selective logging and bushmeat extraction in natural habitats, or crop diversity, chemical input, rotation length, irrigation and livestock density in agricultural classes. For this study, the sites were pooled into four land-use/use-intensity classes consisting of combinations of the original PREDICTS classifications to ensure sufficient sites for investigating the interactions between land use, use intensity, climate change and the amount of nearby natural habitat. These new classes were primary vegetation, secondary vegetation, low-intensity agriculture and high-intensity agriculture. For the agricultural sites (including cropland, pasture and plantation), PREDICTS definitions with high pesticide input were deemed high-intensity agriculture. If the pesticide input was uncertain, sites that were in monocultures were also considered high-intensity agriculture. Sites unlikely to have considerable inputs of pesticides and that were not monoculture were deemed low-intensity agriculture (see Supplementary Table 4 for PREDICTS definitions and reclassification). These use-intensity criteria were chosen because both pesticide input and monoculture are likely to influence insect biodiversity^{54,55}. Pesticide use will either directly (insecticides) or indirectly (other forms of pesticide) reduce insect biodiversity, and the monocultures will probably lack the variety of habitats and diversity of flowering plants needed for a diverse insect community.

Temperature anomaly data

The standardized temperature anomaly metrics were based on monthly mean and maximum annual temperature estimates from CRUTS version 4.03³². This dataset provides monthly mean and maximum temperature estimates for every month since 1901 at a spatial resolution of $0.5^\circ \times 0.5^\circ$. These estimates were interpolated from monthly climate anomalies based on a global network of weather stations and are bias-corrected using the WFDEI dataset⁵⁶. It should be noted that the WFDEI dataset makes extensive use of an older version of CRUTS.

The standardized temperature anomaly was calculated at each PREDICTS site as the difference between the mean of the monthly mean temperatures of the five years preceding the end sample date of the PREDICTS site and the mean of the monthly mean temperatures across months from 1901 to 1930, which is our chosen baseline. For all locations, we considered months only with assumed insect activity. Specifically, we followed the approach recommended by ref.³³ and considered all months with mean temperatures $\geq 10^\circ\text{C}$ to be insect-active months. A general threshold for all species was used because data on the life-cycles and temperature preferences of all insect species are currently unavailable. Alternative thresholds of 6°C and 8°C were also tested, and the results remained consistent (Supplementary Information section S1). The temperature anomaly was then standardized by dividing the absolute change in temperature by the s.d. of the monthly mean temperatures for all insect-active months between 1901 and 1930 (equation (1)). Locations with an anomaly of 1 experienced warming since the baseline equal to the s.d. of the active months in the baseline period, indicating substantial exposure to novel temperatures.

$$\text{STA} = \frac{\bar{T}_{\text{mean.presample}} - \bar{T}_{\text{mean.baseline}}}{s(\bar{T}_{\text{mean.baseline}})} \quad (1)$$

In equation (1), STA is the standardized temperature anomaly, $\bar{T}_{\text{mean.presample}}$ represents the monthly mean temperatures for all insect-active months for the five years preceding biodiversity sampling and $\bar{T}_{\text{mean.baseline}}$ represents the monthly mean temperatures for all insect-active months during the baseline period (1901–1930).

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We also used an anomaly based on maximum temperatures to test whether maximum temperatures, which better reflect extreme weather events such as heatwaves, had a similar impact on insect biodiversity. This metric was determined in the same way as that for the mean temperature anomaly, except that the mean present and baseline values were estimated using the maximum temperatures of the three hottest months per year (equation (2)).

$$\text{SMTA} = \frac{\bar{T}_{\max,\text{presample}} - \bar{T}_{\max,\text{baseline}}}{s(\bar{T}_{\max,\text{baseline}})} \quad (2)$$

In equation (2), SMTA is the standardized maximum temperature anomaly, $\bar{T}_{\max,\text{presample}}$ represents the mean maximum temperatures for the three hottest months (in which we assumed insects to be active) for the five years preceding biodiversity sampling and $\bar{T}_{\max,\text{baseline}}$ represents the mean maximum temperatures for the three hottest months per baseline year (1901–1930).

To determine the projected standardized temperature anomaly for the year 2070, as presented in Extended Data Fig. 7, we used projections of future climate from the Inter-Sectoral Impact Model Inter-comparison Project (ISIMIP). Specifically, we used the bias-corrected ISIMIP2b input data from the MIROC-ESM-CHEM, IPSL-CM5A-LR, GFDL-ESM2M and HadGEM2-ES global climate models (GCMs) to project the future climate for the years 2069–2071⁵⁷. These datasets are daily resolution, bias-corrected data estimating annual mean temperature anomalies at a $0.5^\circ \times 0.5^\circ$ resolution. Here we used the data for the Representative Concentration Pathway 8.5 scenario⁵⁸ as a worst case should current ambitions to reduce emissions be unsuccessful. Within-GCM annual climatic anomalies relative to a respective GCM baseline (1979–2013) were calculated for each year from 2069 to 2071. Anomalies were then added to the mean monthly temperatures across the same baseline period (1979–2013) as in the CRU data. The result of this process was a set of annual projections of mean temperature for each month during 2069–2071, one for each GCM, relative to the CRU baseline at $0.5^\circ \times 0.5^\circ$ resolution. We then took the mean across the four individual GCM projections to obtain ensemble estimates of the future climate for 2069–2071. These estimates were then used to calculate the projected standardized temperature anomaly, as described above, for the year 2070.

It should be noted that the CRU TS data used here to calculate the temperature anomalies are not always supported by the same number of weather stations across all spatial and temporal points. To avoid missing data, the missing observations were replaced by more recent climate estimates⁵⁹, which will reduce the amount of variation in the temperature data³². This could have resulted in a reduced s.d. in our anomaly calculations, particularly in the tropics where weather station data are sparse for the baseline period. As a result, the estimated variation in temperatures across the baseline period is likely to have been underestimated owing to spatial and temporal smoothing, leading to overestimation of the standardized temperature anomaly. To investigate the potential effect of this on our results, we assessed the number of stations that support the CRU data for the baseline period 1901–1930, in which data support is low. These stations are recorded in the data files using the variable stn, which varies between 0 (climatology inserted) and 8 (maximum station count). We reran the models for hypothesis 2, dropping sites that are supported by few weather stations. Our global results, as well as those for the non-tropical realm, were qualitatively consistent and were generally very similar when we removed sites supported by the fewest weather stations (Supplementary Information section S3). In the tropical realm, the results were quantitatively very similar when we removed sites supported by zero, one or two weather stations (Supplementary Figs. 12 and 13). However, when more restrictive cutoffs were applied, the overall qualitative patterns were very similar for total abundance, showing steep declines in intensive agriculture, although the abundance responses for low-intensity agriculture and

the natural habitats, as well as all responses for species richness, were more positive. It is important to note that the increased restrictions on the tropical datasets resulted in substantial reductions in the range of temperature anomaly values sampled. Further details on this test can be found in Supplementary Information section S3.

Natural habitat percentage data

Estimates for the percentage of natural habitat were obtained from an openly available dataset³⁴ that includes global maps of fractional cover for primary and secondary vegetation at a resolution of 30 arc-sec (1×1 km at the Equator) for the year 2005, which is the same as the median sample year in PREDICTS for sites that sampled insects. These data were derived by statistically downscaling land-use data using the modelled relationships with various other datasets including climate, land cover, landform and anthropogenic drivers³⁴. To calculate the fractional cover of primary and secondary vegetation (natural habitat) around each sampling location in PREDICTS, a circular buffer with a radius of 1 km, 3 km, 5 km or 10 km was created around the coordinates of each sampling location using the buffer function in the raster R package version 3.0-12⁶⁰. The mean fractional cover of primary and secondary vegetation from all grid cells within these buffers was extracted and summed to calculate the proportion of natural habitat. Analyses in the main text show results using the 5-km buffer. Those using varying buffer sizes were quantitatively similar, and the interactions were consistent across the range of buffers tested, although they were generally strongest for the 3-km and 5-km buffers (results not shown).

Statistical analysis

Mixed-effects models were used to determine the responses of insect species richness and scaled total abundance to land-use and use-intensity classes, climate anomalies and natural habitat in the surrounding landscape. Random effects considered were study, which accounted for differences in sampling methods between studies, and block, as a nested effect within the study effect to account for the spatial arrangement of sites within studies. For the species richness models, site, which is nested within the block effect, was also included as an observation-level random effect to account for overdispersion^{6,61}. All nesting is defined within the data. Fixed effects considered were standardized temperature anomalies, land-use/use-intensity classification and the proportion of natural habitat in the landscape surrounding the sites. Following previous analyses of the PREDICTS database⁶, we evaluated species richness within a generalized linear mixed-effects model assuming Poisson-distributed errors; log_e-transformed, scaled abundance was modelled using linear mixed-effects models assuming normally distributed errors. Scaled abundance was log(x + 0.01) transformed before the analysis. Abundance values are analysed using a log-normal distribution rather than a distribution better suited to count data owing to the high proportion of non-integer values in the PREDICTS database. Nevertheless, we tested the models assuming alternative data distributions; specifically, zero-inflated Gaussian and Poisson models for abundance and richness, respectively, and a zero-inflated negative binomial model for abundance, yielding results very similar to those of the main models (Supplementary Information section S5). We presented the results for the log-normal model of total abundance and the Poisson model of species richness in the main text because these are better suited to the non-integer data often present in the PREDICTS database and because the residual distribution conformed better to the model assumptions (Supplementary Figs. 23–31). Continuous fixed effects were rescaled to have a mean of 0 and a s.d. of 1. The models were run using the lme4 R package, version 1.1-21⁶². Separate models were run for the standardized temperature anomaly based on mean temperature and the anomaly based on maximum temperature.

The models were run with three combinations of fixed-effect structures to test the three explicit hypotheses given below.

- (1) Conversion to agriculture and intensification of agriculture reduces insect biodiversity.

Scaled abundance ~ land use class + (1|study) + (1|block)

Species richness ~ land use class + (1|study) + (1|block) + (1|site)

- (2) Insect biodiversity will have the highest degree of reduction where historical climate warming interacts with agricultural land use, particularly in higher-intensity agriculture and in the tropics. This reduction in biodiversity will be greater for tropical sites than for non-tropical sites.

Scaled abundance ~ land use class
 × standardized temperature anomaly
 + (1|study) + (1|block)

Species richness ~ land use class
 × standardized temperature anomaly
 + (1|study) + (1|block) + (1|site)

To test for differences in insect responses to climate change and land use between the tropical and non-tropical realms, we ran separate models on subsets of the global dataset. All sites located between or outside latitudes of -23.44 and $+23.44$ were classified as tropical or non-tropical, respectively. We fit separate models rather than fitting the realm as an interacting term in the global model because the latter approach resulted in high multi-collinearity for some terms. This probably occurred because the anomaly values are generally higher in tropical realm than in the non-tropical realm.

- (3) The natural habitat in the surrounding landscape can mitigate the detrimental effects of agricultural land use and climate warming on insects.

Scaled abundance ~ land use class
 × standardized temperature anomaly
 × natural habitat percentage
 + (1|study) + (1|block)

Species richness ~ land use class
 × standardized temperature anomaly
 × natural habitat percentage
 + (1|study) + (1|block) + (1|site)

Outputs for all models can be found in Supplementary Tables 9–22.

Model testing

Checks were done for each of the final models for hypotheses 2 and 3 to test the degree to which the model assumptions were met. Specifically, we generated fitted versus residuals plots, observed versus fitted plots, and Q–Q plots to check for normal distribution of residuals. Moran's I test was used to check for residual spatial autocorrelation (Supplementary Information section S8).

The fitted versus residuals plots for abundance exhibited a box-like pattern due to the rescaling of the abundance data. When abundance was not scaled in this way, our model behaved even more poorly, showing a strong skew in the residuals and rapid increases in prediction confidence intervals for higher model fitted values (results not shown). A recent study using the PREDICTS database also found that a rescaling approach improved model behaviour⁶². The plots of observed versus fitted values for the total abundance models indicate that the model overpredicts and underpredicts for sites with low and high observed total abundance, respectively (Supplementary Figs. 23d, 25d, 27d and

29d). This suggests that our models underestimated the strength of abundance differences; thus, our results are likely to be conservative. Plots of model residuals as a function of land use and the standardized temperature anomaly (Supplementary Fig. 31) showed little bias with respect to the explanatory variables, indicating that the patterns observed should be robust.

To determine whether the length of the baseline period used to calculate the standardized temperature anomaly influenced our results, we tested three alternative baselines of different period lengths: 1901–1905, 1901–1910 and 1901–1920. The models for hypothesis 2 were rerun using each of these baseline periods. In all cases, the patterns observed were very similar to those produced using the 1901–1930 original baseline (Supplementary Figs. 6 and 7). See Supplementary Information section S2 for more detail on this test.

It is possible that our results reflect an association with contemporary climate or absolute changes in temperature rather than our standardized temperature measure. However, among the models that compare these three climatic measures, those fitting the standardized anomaly showed the best fit; fitting current mean temperature in the main models did not change the results (Supplementary Information section S6). We also tested for the potential influence of outliers on our analysis, which is detailed in Supplementary Information section S7.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

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>. 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 data from ref.³⁴, including the primary and secondary vegetation layers that were combined into the natural habitat layer, can be downloaded from the Commonwealth Scientific and Industrial Research Organisation data access portal at <https://doi.org/10.4225/08/56DCD9249B224>.

Code availability

The code required to run the analyses presented here can be obtained from the GitHub repository at <https://github.com/timnewbold/LanduseClimateInsects>.

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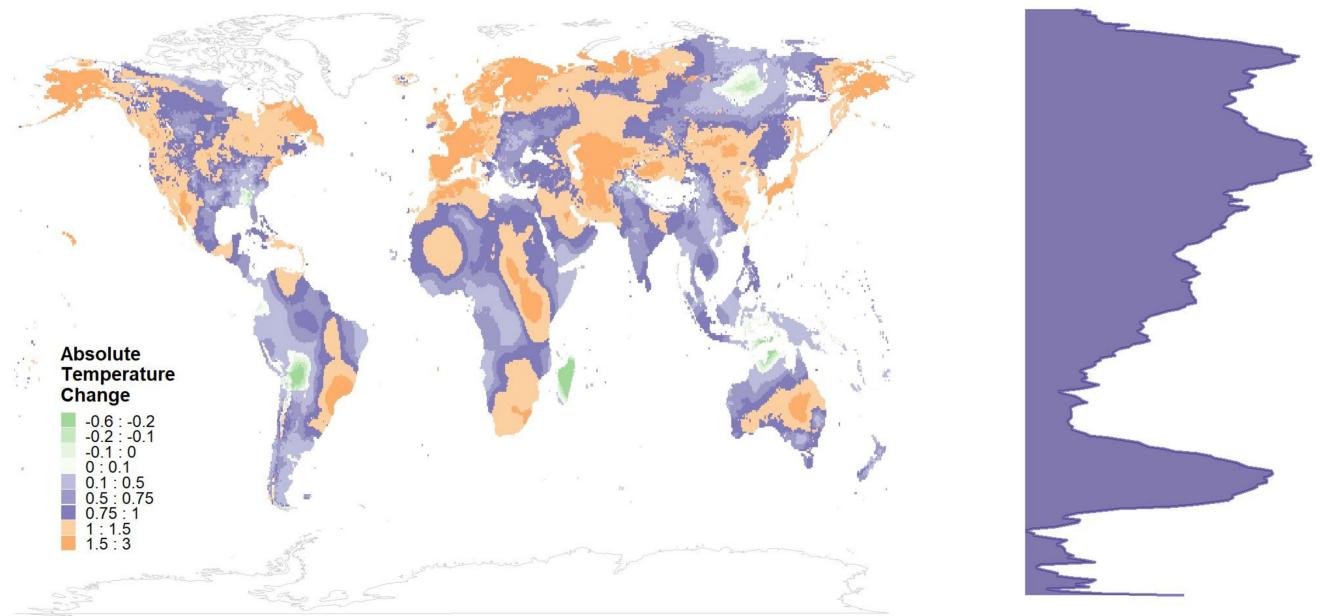
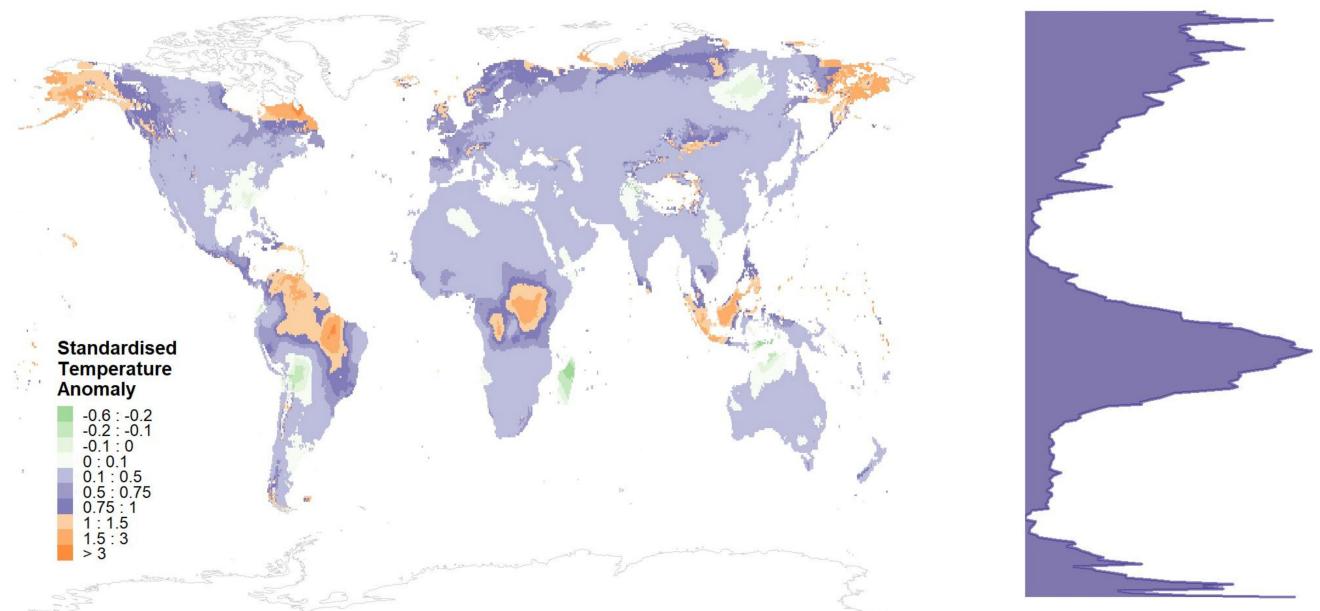
Competing interests The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-022-04644-x>.

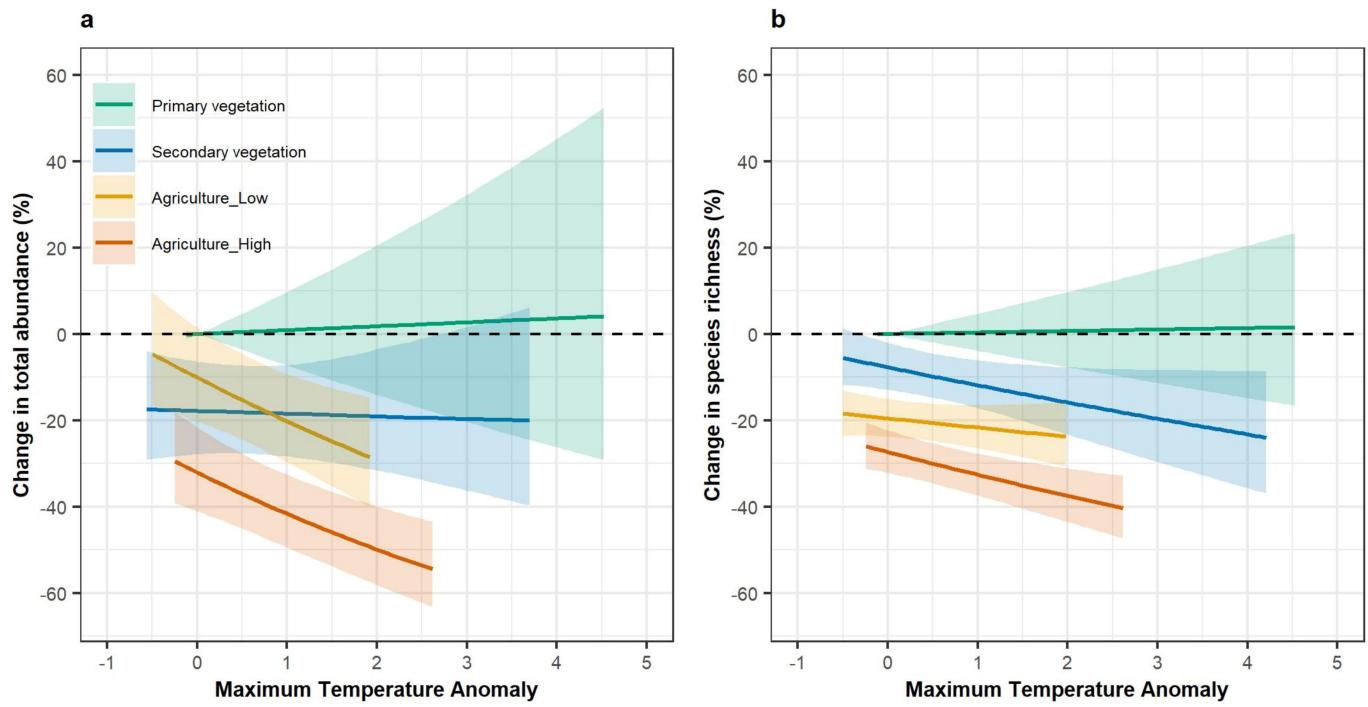
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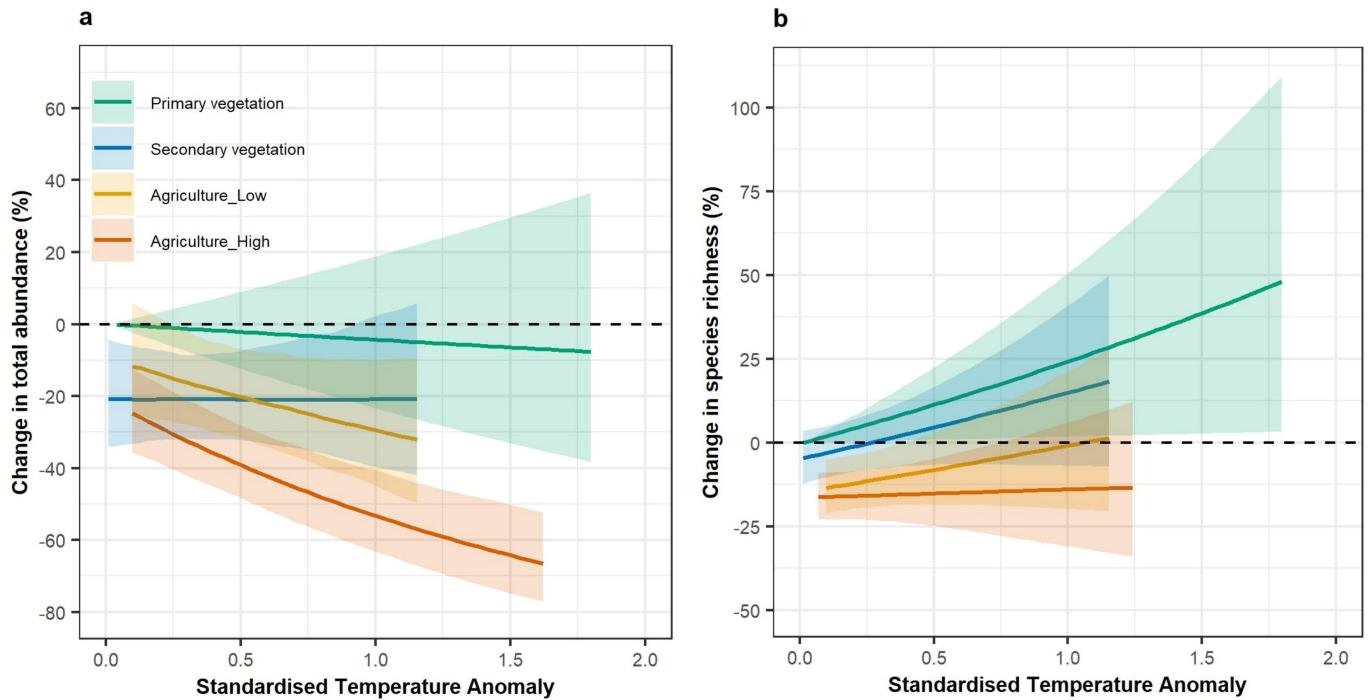
Extended Data Fig 1 | Global average changes in absolute and standardised temperatures. a. Absolute change in temperature between the baseline 1901–1930 and 2005 (the median sample year of the insect data). This was calculated as the difference in mean monthly temperatures of insect-active months between 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 temperate change between the baseline and 2005, divided by the standard

deviation of the baseline temperatures across insect-active months (see Methods for more detail). 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.



Extended Data Fig 2 | Response of insect total abundance (a) and species richness (b) to the interaction between land use and the maximum temperature anomaly. (Likelihood-ratio tests: abundance: $\chi^2_{3,11} = 29, p < 0.001$; species richness: $\chi^2_{3,11} = 21, p < 0.001$). Values represent the percentage difference compared to primary vegetation with no historic climate warming (a maximum temperature anomaly of 0). The maximum temperature anomaly is the difference in the average of the maximum temperatures in the three hottest months each year between the baseline of 1901–1930 and the five years preceding biodiversity sampling, divided by the standard deviation of the

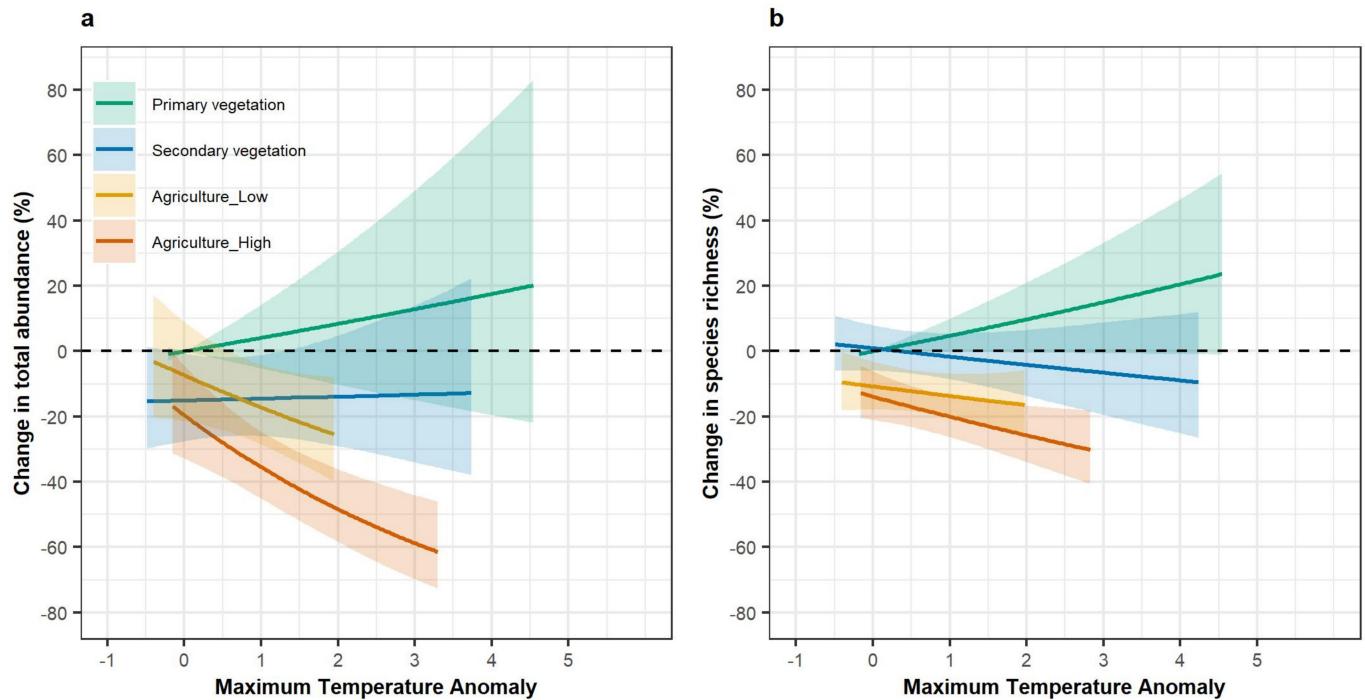
baseline monthly maximum temperatures (for the three hottest months per baseline year). Lines correspond to the median predicted value and shaded area represents the 95% confidence interval. Results are plotted for the central 95% of modelled anomaly values for each land use. Number of sites included in the analyses (abundance model, richness model) were: Primary vegetation (Primary) n = 1,458, 1,563; Secondary vegetation (Secondary) n = 1,338, 1,471; Low-intensity agriculture (Agriculture_Low) n = 1,479, 1,499; and High-intensity agriculture (Agriculture_High) n = 1,717, 1,775.



Extended Data Fig 3 | Response of insect total abundance (a) and species richness (b) to the interaction between land use and the standardised temperature anomaly after influential studies were removed from the dataset. Values represent the percentage difference compared to primary vegetation with no historical climate warming (a standardised temperature

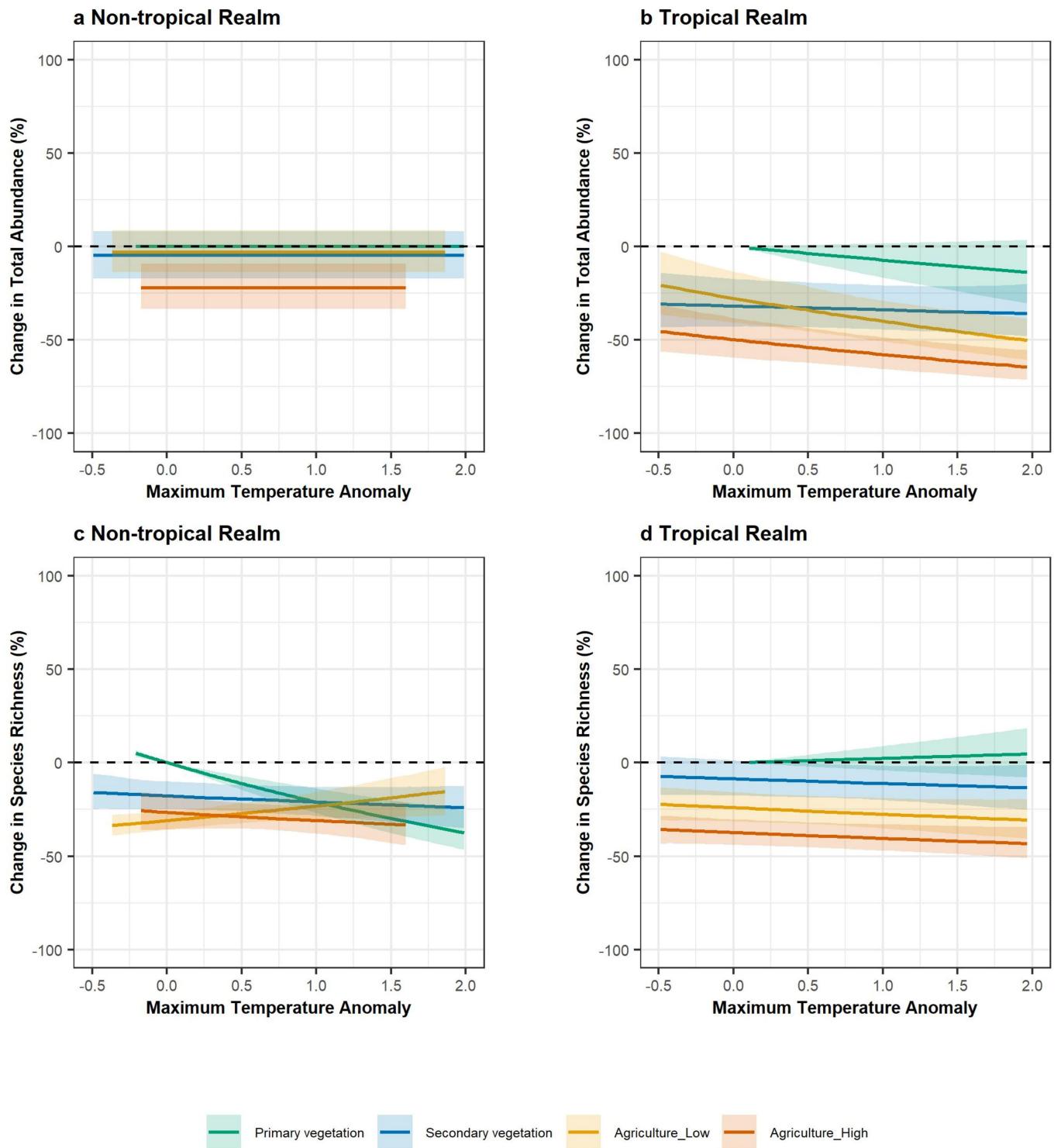
anomaly of 0). Details of the calculation of the standardised temperature anomaly are given in the legend of Fig. 2. Lines correspond to the median predicted value and shaded area represents the 95% confidence interval. Results are plotted for the central 95% of modelled anomaly values for each land use. Number of sites removed: abundance, 361 sites; richness, 650 sites.

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Extended Data Fig 4 | Response of insect total abundance (a) and species richness (b) to the interaction between land use and the standardised maximum temperature anomaly after influential studies were removed from the dataset. Values represent the percentage difference compared to primary vegetation with no historical climate warming (a maximum temperature anomaly of 0). Details of the calculation of the maximum

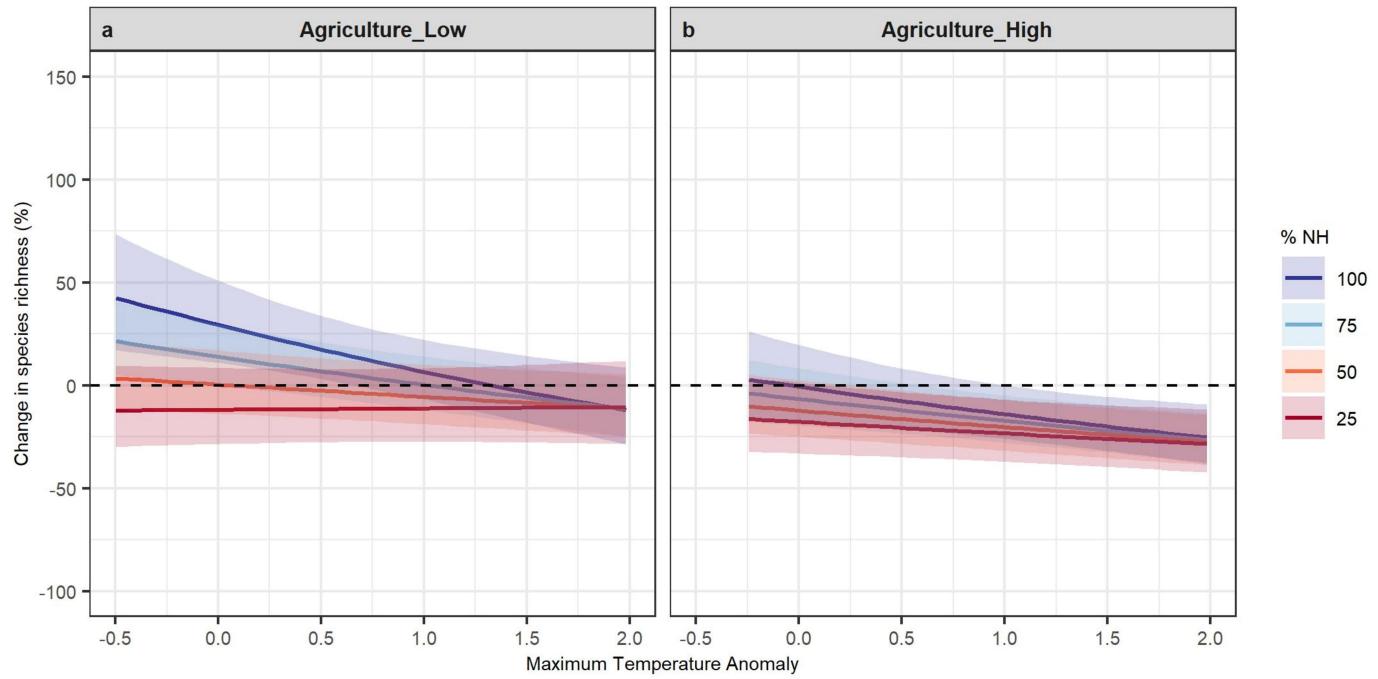
temperature anomaly are given in the legend of Extended Data Fig. 2. Lines correspond to the median predicted value and shaded area represents the 95% confidence interval. Results are plotted for the central 95% of modelled anomaly values for each land use. Number of sites removed: abundance, 409 sites; richness, 698 sites.



Extended Data Fig 5 | Response of insect total abundance (a & b) and species richness (c & d) to the interaction between land use and the standardised maximum temperature anomaly in non-tropical (a & c) and tropical (b & d) realms. (Likelihood-ratio tests: abundance: non-tropical $\chi^2_{3,11} = 8, p = 0.05$, tropical $\chi^2_{3,11} = 24, p < 0.001$; richness: non-tropical $\chi^2_{3,11} = 68, p < 0.001$, tropical $\chi^2_{3,11} = 8.5, p < 0.05$). Values represent the percentage difference compared to

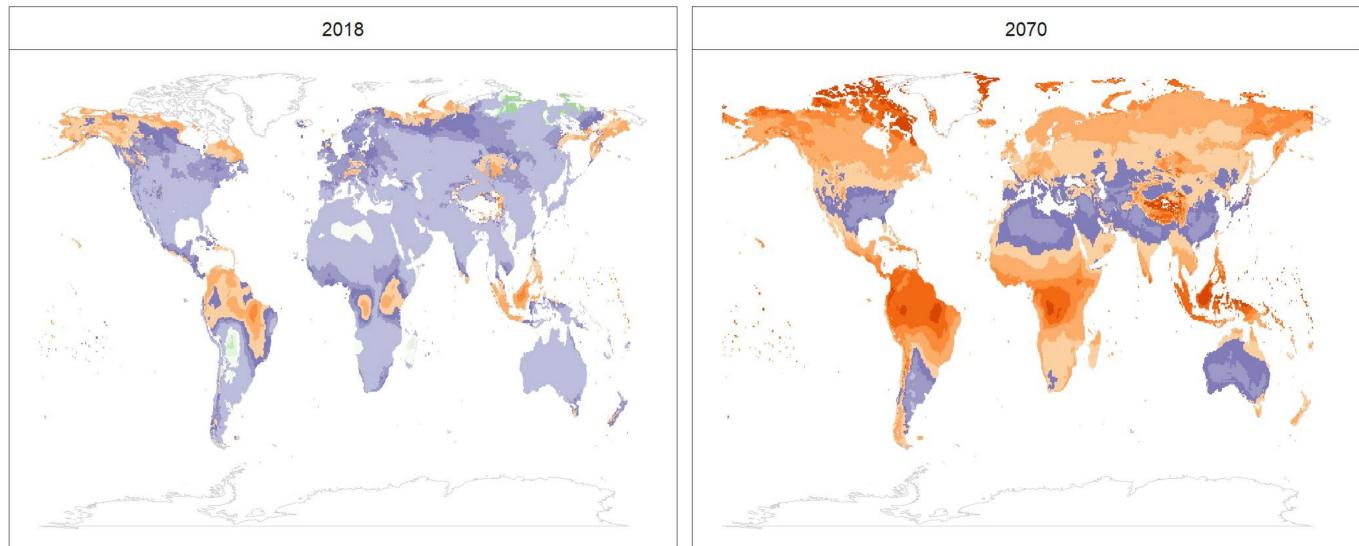
primary vegetation with no historical climate warming (a maximum temperature anomaly of 0). Details of the calculation of the maximum temperature anomaly are given in the legend of Extended Data Fig. 2. Lines correspond to the median predicted value and shaded area represents the 95% confidence interval. Results are plotted for the central 95% of modelled anomaly values for each land use.

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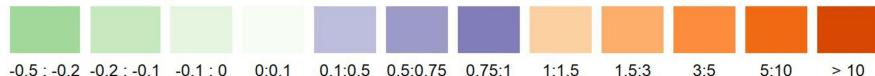


Extended Data Fig 6 | Response of insect species richness to the interaction between the standardised maximum temperature anomaly, land-use intensity, and the amount of nearby natural habitat. (Likelihood-ratio test: richness: $\chi^2_{3,12} = 77.3, p < 0.001$). a. Low-intensity agriculture and b. high-intensity agriculture. Lines correspond to the median predicted value and shaded area represents the 95% confidence interval, for sites with differing

cover of natural habitat within a 5-km buffer. Values represent the percentage difference compared to primary vegetation with no historical climate warming (a standardised maximum temperature anomaly of 0), and with 100% nearby natural habitat. Details of the calculation of the maximum temperature anomaly are given in the legend of Extended Data Fig. 2. The interaction was non-significant for total abundance ($p > 0.05$) and is thus not presented here.



Standardised Temperature Anomaly



Extended Data Fig 7 | Maps of the standardised temperature anomaly for the years 2018 and 2070 under RCP 8.5. The standardised temperature anomaly was determined for each $0.5 \times 0.5^\circ$ grid cell of the global terrestrial land area. Based on data on monthly mean temperatures for 2016–2018, and projected temperatures for 2069–2071 under RCP 8.5 as a worst-case scenario should current ambitions to reduce emissions be unsuccessful (see Methods).

Negative values indicate a decrease in temperature compared to the historical baseline, while positive values indicate an increase in temperature. A value of 1 indicates warming equivalent to 1 standard deviation of monthly variation during the baseline period 1901–1930 (for insect-active months, i.e., monthly mean temperature $\geq 10^\circ\text{C}$).

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- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection No code was used for data collection. All datasets were downloaded from publicly available repositories.

Data analysis All code for data analysis is available from the following Github repository: <https://github.com/timnewbold/LanduseClimateInsects>. The following R packages were key to this analysis: raster (version 3.3-13), lme4 (version 1.1-23), influence.ME (version 0.9-9) and glmmTMB (version 1.1.2.2). The R packages StatisticalModels and predictsFunctions are available from the following GitHub repositories: (timnewbold/predicts-demo and timnewbold/StatisticalModels).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

The 2016 release of the PREDICTS database, as used in this study, can be downloaded from <https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database>. The CRU data for calculating the temperature anomalies can be downloaded from <https://crudata.uea.ac.uk/cru/data/hrg/>.

The data from Hoskins et al including the primary and secondary vegetation layers, which are then combined into a "natural habitat" layer can be downloaded from <http://doi.org/10.4225/08/56DCD9249B224>

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description

This study is a quantitative analysis of the effects of climate change and land use interactions on insect biodiversity globally. It uses a subset of a freely available dataset, the PREDICTS database, alongside freely available temperature and natural habitat data. These data are analysed using mixed effects models. Within the mixed effects models, interactions between land use and a climate anomaly are assessed as well as a three way interaction between land use, climate anomaly and availability of nearby natural habitat. The main dataset consists of 756,879 species records. The insect subset analysed here included information from 6095 sites across 264 studies. Sites are nested within Blocks which are nested within Studies.

Research sample

The PREDICTS data is a publicly available dataset of local biodiversity estimates compared between sites of differing land use or use intensity. The data are organised hierarchically, whereby published Sources contain one or more Studies, encompassing data that were collected using the same methodology. Studies contain one or more spatial Blocks, within which data are collected from Sites with associated geographical coordinates. Since we were only interested in insect responses in this study, we subset the database to information on insects only. This covered 17,889 insect species. Sample sites were spread across all major biomes except one (tundra), representing global insect populations although there are some taxonomical and geographical biases. The 2016 release of the PREDICTS database, as used in this study, can be downloaded from <https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database>. The CRU TS data for calculating the temperature anomalies can be downloaded from <https://crudata.uea.ac.uk/cru/data/hrg/>. The data from Hoskins et al including the primary and secondary vegetation layers, which are then combined into a "natural habitat" layer can be downloaded from <http://doi.org/10.4225/08/56DCD9249B224>.

Sampling strategy

All records within the database for insects that we were also able to extract data for the climate and habitat variables of interest were used. This covered 6095 sites across 264 studies.

Data collection

All datasets used a freely available online, these were collated by the authors and used as described in the accompanying methods and code. No new data was collected as a part of this study.

Timing and spatial scale

The PREDICTS database includes sample from across the globe. Sites were available for all terrestrial biomes except tundra. The analysis carried out here was a spatial analysis however, 2005 was the median sampling year for the insect data used in this analysis.

Data exclusions

No data were excluded from this study.

Reproducibility

All datasets are freely available online and the code to run the analyses and produce the figures from these datasets has been provided. The results are fully reproducible using this code and datasets.

Randomization

Randomization is not possible for this study, all data are from previously collected and published datasets. Differences due to study design etc are accounted for using random effects in the analysis.

Blinding

It is not possible to carry out blinding in this analysis.

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

- | | |
|-------------------------------------|--|
| n/a | Involved in the study |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Human research participants |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data |
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Methods

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|-------------------------------------|---|
| n/a | Involved in the study |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |