Agriculture and climate change reshape insect biodiversity worldwide

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In recent years, several studies have investigated changes in insect biodiversity, some highlighting declines, while others have shown turnover in species composition without net declines[1–5]. Biodiversity changes are driven primarily by land-use change, and increasingly by climate change[6,7], but no study has assessed the potential for interactions between these drivers on insect biodiversity globally. Here, we show that the interaction between indices of historical climate warming and intensive agricultural land use is associated with a reduction of almost 50% in abundance and of 27% in numbers of species within insect assemblages, compared to 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 are seen in non-tropical regions in natural habitats. A high availability of nearby natural habitat often buffered reductions in insect abundance and richness associated with agricultural land use and substantial climate warming, but only in low-intensity agricultural systems. In low-intensity agriculture, where high-levels (75% cover) of natural habitat were available, abundance and richness were reduced by 7% and 5% respectively, compared to reductions of 63% and 61% when little natural habitat was available (25% cover). Our results show that insect biodiversity will likely 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 their biodiversity in recent decades[2–4,8,9]. Insects play important roles within ecosystems, from pollination and pest control, to soil quality regulation and decomposition[10]. Therefore,

alterations to insect assemblages could have important implications for both biodiversity conservation and human well-being[10,11]. Although 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], 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[2,6,14–16]. Evidence suggests that these drivers may interact synergistically, leading to greater responses than would be expected if they acted independently[17]. For example, human land use alters local climatic conditions, reducing the availability of suitable microclimates, altering the heterogeneity, and buffering capacity of these microclimates, and changing the permeability of landscapes for species tracking climate change[17–20]. Synergistic interactions between the effects of land use and climate change have been shown to be important drivers of biodiversity in regional studies of vertebrates, and a few insect groups[17,21–23].

The impact of land-use-climate interactions is likely to vary spatially. In general, tropical species are considered to be more sensitive to climate change than temperate species[24,25]. Due to the relative stability of temperatures in the tropics compared to the temperate realm, tropical species have experienced a much narrower range of past climatic conditions and, as a result, tend to have narrower thermal niches than temperate species[24,26]. When warming does occur, species with narrower thermal niches are the most likely to be pushed towards or beyond their thermal limits, by regional climate change or by the microclimatic changes caused by land-use change[24]. It is therefore likely that the effects of the 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, recent studies have shown that climate-driven losses of bird diversity are reduced or even reversed in landscapes with more natural habitat[23,27,28]. The presence of nearby natural

habitat can moderate changes in biodiversity by providing alternative habitats and resources for local biodiversity[29]. Additionally, natural habitat provides microclimates that offer shelter from the more extreme temperatures experienced in agricultural areas[30].

We assessed the effects of interactions between land use and climate warming on insect abundance and species richness across the global land surface using a spatial analysis of differences in biodiversity among land uses. To do so, we analysed site-level comparisons of local insect biodiversity across land uses from the PREDICTS database[31]. 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. While the data spanned a total of 20 years (1992 to 2012), the individual studies within which biodiversity comparisons were made were generally collected over a very short time span (99.7% of locations were sampled over no more than two years). Our dataset contained 756,879 records for 17,889 insect species (6,037 beetles, 4,528 hymenopterans, 3,874 butterflies/moths, 1,477 flies, 1,302 true bugs, 237 grasshoppers/crickets/locusts, 95 dragonflies/damselflies, and 339 species from other Orders), from which we were able to determine site-level estimates of species richness, and for a subset of sites total abundance (see Figure 1 for sample sizes). These data were derived from 264 published studies and sampled 6,095 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 most reduced where historic climate warming interacts with agricultural land use, particularly higher-intensity agriculture and in tropical regions; 3. Natural habitat in the surrounding landscape can buffer against the detrimental effects on insects of agricultural land use and climate warming. To assess these hypotheses, sites were grouped into four major land-use and land-use-intensity classes (primary vegetation, secondary vegetation, low-intensity agriculture,

and high-intensity agriculture), using the classifications from the PREDICTS database, which are based on information in the original source publications[31]. For each site, we calculated changes in both mean and maximum temperatures between a 1901-1930 baseline period and the five years preceding biodiversity sampling, based on the Climatic Research Unit Time Series dataset Version 4.03[32]. For the anomaly based on mean temperatures, we use only those months where insects can be considered active. Following a previous study[33], we assume insects to be active when the monthly mean temperature is 10°C or higher, but we also test the sensitivity of our results to different temperature thresholds (see Supplementary Information S1). The anomaly based on maximum temperatures uses the three hottest months of each year, during which we assume insects to be active. We standardised temperature differences to account for the range of temperature conditions typically experienced by species (Extended Data Figure 1), by dividing the raw change in temperature between the baseline period and sampling period by the standard deviation of temperatures across insect-active months in the baseline period for the anomaly based on mean temperatures, and by the standard deviation of temperatures of the three hottest months for the anomaly based on maximum temperatures. Although insects may respond to daily variations in climatic conditions, it was not possible to standardise the anomaly by variation in temperatures at a finer than monthly temporal resolution owing to the availability of historical climate reconstructions. We further examined whether the amount of natural habitat surrounding sampled sites altered the responses of insects to land use-climate change interactions. We derived estimates of the fractional cover of natural habitat within radii of 1, 3, 5 or 10 km of sampled sites, based on a 1-km map of modelled land use for the year 2005[34].

We show that in high-intensity agriculture (typically characterised by chemical inputs, low crop diversity, large field size, mechanisation, or high livestock density), insect total abundance was reduced by 45% and species richness by 33% compared to levels in primary vegetation

(note that these models did not consider the effects of historical temperature change), whereas in low-intensity agriculture there was a 19% and 22% reduction in abundance and species richness respectively (Fig. 1b, c). This loss of insect biodiversity in agricultural systems will likely 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 (e.g., from extreme climatic events)[11,37].

The aforementioned average reduction of 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 have experienced substantial climate warming. Warming equivalent to 1 standard deviation of baseline temperature variation (a standardised temperature anomaly of 1.0) led to a 49% reduction in insect abundance and a 27% reduction in species richness in intensive agriculture, compared to sites in primary vegetation with no climate warming (Fig. 2). With the same level of climate warming, low-intensity agriculture experienced a 30% reduction in insect abundance and a 23% reduction in species richness. Overall, this suggests that sensitive species are filtered out in areas exposed to recent climate change under any level of land-use modification. In contrast, abundance is somewhat buffered in lower-intensity agriculture, but declines steeply with further intensification. Similar patterns were observed when assessing climate warming based on maximum monthly temperatures, although the difference in response of species richness between agricultural land-use intensities was greater, suggesting that biodiversity in lower-intensity agricultural systems is partially buffered against the negative impacts of increases in extreme temperatures (Extended Data Figure 2). Results were robust to using baseline periods of differing length (Methods – Model Testing; Supplementary Information S2), and generally

robust to the removal of potentially influential studies (Extended Data Figures 3 and 4, Supplementary Information S7), although in one case the removal of influential studies containing a very large number of sites (650) altered responses slightly (Extended Data Figure 3). Model diagnostics including fitted versus residual plots, observed versus fitted plots, Q-Q plots and tests for spatial autocorrelation were carried out for all models. The observed versus fitted plots suggest that responses from the abundance models may be conservative, underestimating the strength of differences in abundance (see Methods – Model Testing).

Insect biodiversity is particularly sensitive to climate warming since thermoregulatory behaviour is used to access thermally buffered microhabitats (e.g., shade) to survive the warmest parts of the year[38]. As land-use change reduces the availability of these buffered microhabitats[19], particularly in intensively used systems, insects are likely to be more exposed to the effects of climate warming[30,38]. This may be particularly important for tropical species, which have narrower thermal niches[24,26]. Furthermore, there are other features of tropical species, such as relatively smaller range sizes and a higher degree of specialism, that may render them more sensitive to land-use change and climate change[25]. To explore tropical-temperate differences, and to check that our reported association between land-use responses and temperature anomalies was not caused by sensitivity of tropical biodiversity unrelated to climatic mechanisms, we repeated our analyses separately for the tropical and non-tropical realms.

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 Figure 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 at least in part be because the most climate-sensitive species have already been filtered out of non-tropical regions by a long history of land-use change[39]. Similarly, these historical changes in land use have resulted in increases in microclimatic temperatures, which have allowed southern species to colonise more northerly regions while cold-adapted species are lost[12].

Our analyses also showed that natural habitat buffers against the detrimental impacts of climate warming on both total abundance and species richness, but only in low-intensity agriculture (Fig. 4). In low-intensity agriculture with a climate anomaly of 1 and surrounded by a high fractional cover of natural habitat (75%), insect abundance was reduced by 7% and species richness by 5% compared to primary vegetation with no climate warming. In contrast, we observed a reduction in abundance of 63% and in species richness of 61% when only 25% natural habitat cover was present. In high-intensity agriculture, the buffering effect was smaller or non-existent. No buffering effect was seen for total abundance or species richness in response to the standardised temperature anomaly based on maximum temperatures ($p > 0.05$; Extended Data Figure 6). It is possible that the benefits insects gain from nearby natural habitat availability, including more suitable microclimates, are not able to buffer against the effects of extreme maximum temperatures.

Previous local-scale studies have shown that incorporating natural habitat into agricultural landscapes can promote the maintenance of local insect biodiversity[40–43]. We go further by showing that natural habitat cover is associated with a buffering of the reductions in insect biodiversity otherwise seen where low-intensity agriculture coincides with substantial recent climate warming. The fact that no buffering effect of natural habitat was seen for the anomaly based on maximum temperatures suggests that natural habitat cannot buffer against increases in the most extreme temperatures, the occurrence of which is 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 habitat within production landscapes, or a move toward higher-intensity agriculture, our results suggest there will be large declines in insect biodiversity, especially as climate warming accelerates.

Insect biodiversity in substantial portions of the world has likely already been exposed to detrimental levels of climate change (Extended Data Figure 7). In much of the tropics, as well as some high northerly latitudes, insect communities are experiencing novel high temperatures during the months they are active, with many regions already experiencing temperature increases that exceed historic variability. In most non-tropical regions, average warming is still within the range of typical natural variability (standardised temperature anomaly < 1), and thus communities are less likely yet to have been exposed to novel temperatures. Nevertheless, temperate regions are now experiencing new extremes of temperature (e.g., heatwaves)[44]. As climate warming continues into the future, the risk to insect biodiversity from land use-climate change interactions will become much more widespread, including in much of the world's temperate area (Extended Data Figure 7).

Regional-scale studies have linked insect declines to land use[45,46] and climate change[2,24]. Ours is the first quantitative, global-scale analysis explicitly to link global insect biodiversity changes to the interactions between land use, land-use intensity, and climate change. A recent meta-analysis describing global insect declines[9] was unable to find a link between insect population changes and local temperature changes, possibly because they did not consider the potential for land-use-climate interactions, or because temperature change was not standardised to historical variability, as it was here. Additionally, the data in this meta-analysis were drawn predominantly from non-tropical regions, where populations are more likely to be limited by cold temperatures, and so have a greater potential to respond positively to climate change.

Furthermore, these data consisted of short time series, over which it will be difficult to detect impacts of climate change.

As with any correlative study, we cannot infer causal effects, and 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 changes on biodiversity. Additionally, since the data underlying our study were mostly collected since 2000, our biodiversity estimates, particularly within primary vegetation in non-tropical systems, may not be fully representative of a true baseline since these systems have a long history of land use, which will have filtered out some species from natural habitats. Although the biodiversity data span a large proportion of the terrestrial surface of the world, as with most biodiversity studies[47], there are relatively fewer data for the tropics and for high latitudes. A number of sensitivity tests were carried out to check the robustness of the results. These include 1. Assessing the impact of climate estimates based on more recent climatology, 2. Comparing these models to those including other climatic variables, and 3. Testing the potential influence of incomplete sampling on the species richness results (see Methods: Model Testing for more information).

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 aspects of microclimate between land uses and use-intensities in locations undergoing different rates of climate warming could identify the mechanistic basis for observed changes in insect biodiversity. We did not include other aspects of climate here, such as precipitation. 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/use-intensity data might be able to reveal further insights.

Conclusions

Studies aiming to understand recent change in insect biodiversity have increased in recent years, however, there has not been a quantitative analysis of the impacts of major drivers on global insect diversity. Here, we show that reductions in both insect abundance and richness are greatest in areas of intensive agricultural land use, where the climate has warmed most relative to background seasonal and inter-annual variation, particularly in the tropics. The ability of natural habitat availability to buffer against 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 extreme high temperatures. Insect biodiversity is essential for many ecosystem functions and services, including key services for agriculture. Ensuring these services remain available in agricultural landscapes will benefit both people and nature. Under the highest-emissions scenarios, the majority of the terrestrial surface will be exposed to novel temperatures by 2070. To reduce the magnitude of changes in insect biodiversity will require strong climate mitigation alongside the implementation of land-management strategies that increase the availability of natural habitats.

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Figure Legends

Figure 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. Here, agricultural land uses in PREDICTS (cropland, plantation, pasture) have been combined into a single agriculture class and divided according to their use

intensity into two groupings: low and high (see Methods for details). Number of sites included in the analyses (abundance model, richness model) were: Primary n = 1,410, 1,516; Secondary n = 1,338, 1,483; Agriculture Low n = 1,294, 1,317; and Agriculture High n = 1,717, 1,779.

Figure 2: Response of a. insect total abundance and b. species richness to the interaction between land use and the standardised temperature anomaly (Likelihood-ratio test: abundance: $\chi^2_{3,11} = 47.4$, $p =$ <0.001, richness: $\chi^2_{3,11} = 124$, $p =$ <0.001)**.** Values represent the percentage difference compared to primary vegetation with no historical climate warming (a 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 five years preceding biodiversity sampling, divided by the standard deviation of baseline temperatures across insect-active months (i.e., monthly mean temperature $\geq$ 10°C). 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. The 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.

Figure 3: Response of insect total abundance (a & b) and species richness (c & d) to the interaction between land use and the standardised temperature anomaly in non-tropical (a & c) and tropical (b & d) realms (Likelihood-ratio tests: abundance: non-tropical $\chi^2_{3,11} = 17.5$, p <0.001, tropical $\chi^2_{3,11} = 20.4$, $p < 0.001$; richness**:** non-tropical $\chi^2_{3,11} = 99.2$, $p < 0.001$, tropical $\chi^2_{3,11} = 23.1$, $p < 0.001$)**.** 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 Figure 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 within each realm. The number of sites included in the analyses (abundance model, richness model) were: Primary vegetation (Primary) Non-tropical: n = 857, 902, Tropical: n = 552, 613; Secondary vegetation (Secondary) Non-tropical: n = 941, 1034, Tropical: n = 384,435; Low-intensity agriculture (Agriculture_Low), Non-tropical: n = 1031, 1047, Tropical: n = 258, 265; and High-intensity agriculture (Agriculture_High), Non-tropical: n = 1317, 1344, Tropical: n = 395, 429.

Figure 4: Response of insect total abundance (a & b) and species richness (c & d) to the interaction between the standardised temperature anomaly, land-use intensity, and availability of nearby natural habitat (Likelihood-ratio tests: abundance: $\chi^2_{3,19} = 23$, $p = {<}0.001$, richness: $\chi^2_{3,19} = 30$, $p = {<}0.001$)**.** a & c. Low-intensity agriculture. b & d. High-intensity agriculture. Values represent the percentage difference compared to primary vegetation with no historical climate warming (a standardised temperature anomaly of 0), and with 100% nearby natural habitat. % NH (Natural Habitat) describes the potential availability of primary and secondary vegetation surrounding an agricultural site. Note that these plots show model predictions, and do not necessarily represent in all cases plausible combinations of land use/land-use intensity and surrounding natural habitat. Details of the calculation of the standardised temperature anomaly are given in the legend of Figure 2. 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. The number of sites included in the analyses (abundance model, richness model) were: Low-intensity agriculture (Agriculture_Low): n = 1,289, 1,312; and High-intensity agriculture (Agriculture_High): n = 1,712, 1,773.

Methods

Biodiversity data - PREDICTS

The PREDICTS database is an aggregation of spatial comparisons of local biodiversity across land uses and contains data from all 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 species richness for a wide range of taxa, including vertebrates, invertebrates, and plants. The data within PREDICTS are organised hierarchically: 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[51].

For this study, we extracted PREDICTS data for the insects Class for all land uses, except Urban, where use intensity was known, a total of 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 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, while total abundance was the sum of all abundance measurements at a site, where available. Where sampling effort differed among Sites within a Study (affecting 2% of the non-zero measurements), 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 recorded abundance scales linearly with sampling effort[6]. The abundance values in our insect data subset had a highly right-skewed distribution, caused in part by the variety of different ways of measuring abundance in the underlying studies, as well as the variation that would be seen from measuring abundances across many different

taxonomic groups. To reduce this skew, following a previous study, we rescaled abundance values between 0 and 1 within each study, such that the highest abundance value was set to 1 and remaining values rescaled relative to this maximum value. This ensured that samples still remained independent of each other. Differences in sampling effort among studies were not accounted for beyond fitting 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, a method of estimating species richness that accounts for incomplete sampling effort[52]. Chao-estimated richness could not be determined for all sites with species richness data since its calculation requires an integer measure of abundance, however results using those sites for which it could be estimated were very similar to the main results for species richness (see Supplementary Information S4 for more on this test). 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 S5-S8.

The PREDICTS database recognises 8 land-use categories, classified based on the description of the habitat as given by the authors of the original source publications: primary vegetation (forest or non-forest native vegetation that is not known to have ever been destroyed), young secondary vegetation, intermediate secondary vegetation, mature secondary vegetation (secondary vegetation is where the primary vegetation has been completely destroyed and now recovering, age classifications are based on the complexity of the vegetation), cropland (lands planted with herbaceous crops), pasture (where livestock are known to be regularly or permanently grazing), plantation forest (previously cleared areas planted with crop trees or shrubs) and urban (areas with human habitation or buildings). Each of the broad land-use categories are further sub-divided into three use intensities based on factors describing the level of human disturbance (such as: selective logging and bushmeat extraction in natural habitats;

or crop diversity, chemical inputs, rotation length, irrigation, and livestock density in agricultural classes): minimal, light, and intense. For this study, sites were pooled into four land-use/use-intensity classes based on combinations of these original PREDICTS classifications so that there were enough sites to investigate interactions between land use, use intensity, climate change and the amount of nearby natural habitat. These classifications were: primary vegetation, secondary vegetation, low-intensity agriculture, and high-intensity agriculture. For the agricultural sites (including Cropland, Pasture and Plantation), PREDICTS definitions that had high pesticide input were deemed high-intensity agriculture, if pesticide input was uncertain, sites that were in monoculture were deemed high-intensity agriculture. If the site was unlikely to have significant inputs of pesticides and was not monoculture, then it was deemed low-intensity agriculture (See Supplementary Table S4 for PREDICTS definitions and reclassification). These use-intensity criteria were chosen because both pesticide input and monoculture are likely to influence insect biodiversity[53,54]; pesticide use will either directly (in the case of insecticides) or indirectly (in the case of other forms of pesticide) reduce insect biodiversity and monoculture will likely be lacking in the variety of habitats needed for a diverse insect community.

Temperature anomaly data

The standardised temperature anomaly metrics were based on monthly mean and maximum annual temperature estimates from the Climatic Research Unit Time Series (CRU TS) v4.03[32]. This dataset provides monthly mean and maximum temperature estimates for every month since 1901, at a $0.5 \times 0.5°$ spatial resolution. These estimates are interpolated from monthly climate anomalies based on a global network of weather stations and are bias-corrected using the WFDEI dataset[55]. It should be noted that this dataset makes extensive use of an older version of CRU TS.

The standardised temperature anomaly was calculated, at each PREDICTS site, as the difference between the mean of the monthly mean temperatures of the 5 years preceding the end sample date of the PREDICTS site, and the mean of the monthly mean temperatures across months from 1901 to 1930, our chosen baseline. For any location, we only considered those months during which insects can be assumed to be active. Specifically, we followed the approach recommended by Johannsen *et al*[33], and considered all months with a mean temperature greater than or equal to 10°C to be insect-active months. A general threshold for all species was used because data on the lifecycles and temperature preferences of all insect species is currently unavailable. Alternative thresholds of 6 and 8°C were also tested, and results remained consistent (see Supplementary Information S1). The temperature anomaly was then standardised by dividing the absolute change in temperatures by the standard deviation of the monthly mean temperatures for all insect-active months between 1901 and 1930 (Eq. 1). Locations with an anomaly of 1 have experienced warming since the baseline equal to the standard deviation of active month, mean temperatures of 1901 to 1930, indicating substantial exposure to novel temperatures.

$$STA = \frac{\overline{T_{mean.presample}} - \overline{T_{mean.baseline}}}{s(T_{mean.baseline})} \qquad \text{Eq. 1}$$

Where STA is the Standardized Temperature Anomaly, $T_{mean.presample}$ are the monthly mean temperatures for all insect-active months for the five years preceding biodiversity sampling, and $T_{mean.baseline}$ are the monthly mean temperatures for all insect-active months in the baseline period (1901-1930).

We also used an anomaly based on maximum temperatures to test whether maximum temperatures, which better reflect extreme weather events such as heatwaves, have a similar impact on insect biodiversity. This metric was determined in the same way as 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, (Eq. 2).

$$SMTA = \frac{\overline{T_{max.presample}} - \overline{T_{max.baseline}}}{s(T_{max.baseline})} \qquad \text{Eq. 2}$$

Where SMTA is the Standardized Maximum Temperature Anomaly, $T_{max.presample}$ are the mean maximum temperatures for the three hottest months (in which we assume insects to be active) for the five years preceding biodiversity sampling, and $T_{max.baseline}$ are the mean maximum temperatures for the three hottest months per baseline year (1901-1930).

To determine the projected standardised temperature anomaly for the year 2070 under a business-as-usual scenario, as presented in Extended Data Figure 7, we used projections of future climate from the Inter-Sectoral Impact Model Intercomparison 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 future climate for the years 2069 to 2071[56]. These datasets are daily-resolution, bias-corrected data estimating annual mean temperature anomalies at a $0.5° \times 0.5°$ resolution. Here, we use the data for the Representative Concentration Pathway (RCP) 8.5 scenario[57], 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 of the years 2069-2071. Anomalies were then added to 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 in the years 2069-2071, one for each GCM, relative to the CRU baseline at $0.5° \times 0.5°$ resolution. We then took the mean across the four individual GCM projections to give ensemble estimates of the future climate for the time period 2069-2071. These estimates were then used to calculate the projected standardised 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. Rather than having missing data, the missing observations are replaced by more recent climatology[58] which will reduce the amount of variation in the temperature data[32]. This could result in a reduced standard deviation in our anomaly calculations, particularly in the tropics where weather station data are particularly 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 over-estimation of the standardised temperature anomaly. To investigate the potential effect of this on our results, we assess the number of stations that support the CRU data (recorded as the "stn" variable in the data files and varies between 0 (climatology inserted) and 8 stations (maximum station count)) for the baseline period 1901-1930, where data support is particularly low. We rerun the models for Hypothesis 2, dropping sites that are supported by few weather-stations. Our global results, as well as results for the non-tropical realm, were qualitatively consistent and generally very similar when we removed sites supported by the fewest weather stations (see Supplementary Information S3). In the tropical realm, results were quantitatively very similar when removing sites supported by zero, one or two weather stations (Supplementary Figures S12 and S13). However, when more restrictive cut-offs were applied, while overall qualitative patterns were very similar for total abundance (i.e., with steep declines in intensive agriculture), abundance responses for low-intensity agriculture and natural habitats, as well as all responses for species richness, were more positive. It is important to note though that with these more restricted tropical datasets, the range of temperature anomaly values sampled was much reduced. More detail on this test can be found in Supplementary Information S3.

Percentage Natural Habitat data

Percentage natural habitat estimates were obtained from an openly available dataset[34]. This dataset has global maps of fractional cover for primary and secondary vegetation at 30-arc-second resolution (1 x 1 km at the equator) for the year 2005 (the same as the median sample year for sites that sampled insects in PREDICTS). 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 drivers (see ref [34] for more detail). 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 either 1, 3, 5 or 10 km was created around the coordinates of each sampling location, using the *buffer* function in the *raster* R package version 3.0-12[59]. 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. Results using varying buffer size were quantitatively similar, and interactions were consistent across the range of buffers tested, (1 km, 3 km, 5 km, and 10 km), although interactions were generally strongest for the 3 and 5-km buffers (results not shown).

Statistical analysis

Mixed-effects models were used to determine the response of both insect species richness and scaled total abundance to land use/use intensity classes, climate anomalies and natural habitat in the surrounding landscape. Random effects considered were: 1) Study, to account for differences in sampling methods between studies; and 2) Block, as a nested effect within Study, to account for the spatial arrangement of sites within studies. For the species richness models, Site (which is nested within Block) was also included as an observation-level random effect to account for overdispersion[6,60]. All nesting is defined within the data. Fixed effects considered were: 1) the standardised temperature anomalies; 2) the land use/use intensity classification;

and 3) the proportion of natural habitat in the landscape surrounding sites. Following previous analyses of the PREDICTS database[6], species richness was analysed within a generalised linear mixed-effects model assuming Poisson-distributed errors, while $\log_e$-transformed, scaled abundance was modelled using linear mixed-effects models assuming normally-distributed errors. Scaled abundance was $\log(x+0.01)$ transformed prior to analysis. Abundance values are analysed using a log-normal distribution rather than a distribution better suited to count data, due to the high proportion of non-integer values in the PREDICTS database. Nevertheless, we tested 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 very similar results to the main models (See Supplementary Information S5). We present the results for the log-normal model of total abundance and Poisson model of species richness in the main text because these are better suited to the often non-integer data in the PREDICTS database, and because the residual distribution conformed better to model assumptions (Supplementary Information Figs. S23-S31). Continuous fixed effects were rescaled to have a mean of 0 and standard deviation of 1. Models were run using the *lme4* R package, version 1.1-21[61]. Separate models were run for the standardised temperature anomaly based on mean temperatures and the anomaly based on maximum temperatures.

Models were run with three combinations of fixed-effect structures in order to test three explicit hypotheses:

1. Conversion to agriculture, and intensification of agriculture reduces insect biodiversity

   Scaled abundance ~ Land Use-Intensity + (1|Study) + (1|Block)

   Species richness ~ Land Use-Intensity + (1|Study) + (1|Block) + (1|Site)

2. Insect biodiversity will be most reduced where historic climate warming interacts with agricultural land use, particularly higher-intensity agriculture, and in the tropics. This reduction in biodiversity will be greater for tropical sites compared to non-tropical sites.

Scaled abundance ~ Land Use-Intensity × Standardized Temperature Anomaly + (1|Study) + (1|Block)

Species richness ~ Land Use-Intensity × 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. Any site located between latitudes of -23.44 and 23.44 were classed as tropical, and outside of this region as non-tropical. We had to fit separate models rather than fitting realm as an interacting term in the global model, since the latter approach resulted in high multicollinearity for some terms. This is likely due to the tropical realm having generally higher anomaly values than the non-tropical realm.

3. Natural habitat in the surrounding landscape can buffer against the detrimental effects on insects of agricultural land use and climate warming.

Scaled abundance ~ Land Use-Intensity × Standardized Temperature Anomaly × Percentage Natural habitat + (1|Study) + (1|Block)

Species richness ~ Land Use-Intensity × Standardized Temperature Anomaly × Percentage Natural habitat + (1|Study) + (1|Block) + (1|Site)

Outputs for all models can be found in Supplementary Tables S9-22

Model testing

Checks were carried out on each of the final models for Hypotheses 2 and 3 above to test the degree to which model assumptions were met. Specifically, we generated fitted versus residuals plots, observed versus fitted plots, and Q-Q plots to check for a normal distribution of residuals. Moran's tests were used to check for residual spatial autocorrelation (Supplementary Information S8).

The fitted versus residuals plots for abundance exhibit 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 strong skew in the residuals, and rapid increases in prediction confidence intervals for higher model fitted values (results not shown). Another recent study using the PREDICTS database also found that a rescaling approach improved model behaviour[62]. Plots of observed values versus fitted values for the total abundance models suggest that for sites with low observed total abundance the model overpredicts, while for sites with high observed total abundance the model underpredicts (Figures S23d, S25d, S27d, S29d). This suggests that our models underestimate the strength of differences in abundance, and so our results are likely to be conservative if anything. Plots of model residuals as a function of land use and the standardised temperature anomaly (Figure S31) show little bias with respect to the explanatory variables, indicating that the patterns we observe should be robust.

To determine whether the length of the baseline period used to calculate the standardised temperature anomaly influenced our results, we tested three alternative baselines of different 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 original baseline, 1901-1930 (Supplementary Figs. S6-7). See Supplementary Information S2 for more detail on this test.

It is also possible that our results reflect an association with contemporary climate or absolute changes in temperature, rather than our standardised temperature measure, but among the models comparing these three climatic measures, models fitting the standardised anomaly fit the best, and fitting current mean temperature in the main models did not change the results (see Supplementary Information S6). We also tested for the potential influence of outliers on our analysis, see Supplementary Information S7 for detail on the approach used.

Data availability statement

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.

Code availability statement

The code required to run the analyses presented here is available from the following GitHub repository: https://github.com/timnewbold/LanduseClimateInsects

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Author contributions

TN and PM conceived the study, all authors processed and analysed the data, and wrote and edited the manuscript.

Competing interest declaration

There are no competing interests.

Additional information

Supplementary Information is available for this paper.

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Extended Data Figure Legends

Extended Data Figure 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 $0.5 \times 0.5°$ 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 $\geq 10°C$). 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 Figure 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 historical 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 Figure 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 Figure 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.

Extended Data Figure 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 Figure 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 Figure 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 Figure 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.

Extended Data Figure 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: $\chi^2_{3,13} = 77.3$, $p < 0.001$). 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 Figure 2. The interaction was non-significant for total abundance ($p > 0.05$) and is thus not presented here.

Extended Data Figure 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 $0.5 \times 0.5°$ 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 $\geq 10°C$).