

# ECOGRAPHY

## Research

### Insect occurrence in agricultural land-uses depends on realized niche and geographic range properties

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Geographic range size predicts species' responses to land-use change and intensification, but the reason why is not well established because many correlates of larger geographic ranges, such as realized niche breadth, may mediate species' responses to environmental change. Agricultural land uses (hereafter 'agroecosystems') have warm, dry and more variable microclimates than do cooler and wetter mature forests, so are predicted to filter for species that have warmer, drier and broader fundamental and realized niches. To test these predictions, we estimated species' realized niches, for temperature and precipitation, and geographic range sizes of 764 insect species by matching GBIF occurrence records to global climate layers, and modelled how species presence/absence in mature forest and nearby agroecosystems depend on species' realized niches or geographic ranges. The predicted species niche effects consistently matched the expected direction of microclimatic transition from mature forest to agroecosystems. We found a clear signal that species with preference for warmer and drier climates were more likely to be present in agroecosystems. In addition, the probability that species occurred in different land-use types was predicted better by species' realized niche than their geographic range size. However, niche effects are often context-dependent and varied amongst studies, taxonomic groups and regions used in this analysis: predicting which particular aspects of species' realized niche cause sensitivity to land-use change, and the underpinning mechanisms, remains a major challenge for future research and multiple components of species' realized niches may be important to consider. Using realized niches derived from open-source occurrence records can be a simple and widely applicable tool to help identify when biodiversity responds to the microclimate component of land-use change.

Keywords: agroecosystems, climate niche, environmental filtering, geographic range size, land-use change, species distribution



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## Introduction

The rules governing assembly of species communities have a long history in ecology (MacArthur 1958, Tilman 1977, Leibold et al. 2004). Species in an assemblage are expected to be filtered by their local environment based on their properties and traits (e.g. their fundamental niche). Filtering occurs when aspects of species' environment (e.g. temperature) interacts with organismal properties and traits (i.e. physiological tolerance or fundamental niche) to affect demographic rates, population dynamics, local species' occupancy rates and community composition (Webb et al. 2010, Salguero-Gómez et al. 2018). The lens of environmental filtering – here considered as the interaction between a species-level property and the local environment – is expected to enable clearer predictions of how local environmental change will affect local biodiversity.

An emerging paradigm is that species' sensitivity and assemblage responses to land-use change depend on species' range size, ecological generality and niche limits (Williams and Newbold 2019, Staude et al. 2020). One often-supported prediction is that local communities in agroecosystems are largely comprised of species with wider geographic ranges (Cleary and Mooers 2006, Scott et al. 2006, Cofre et al. 2007, Nowakowski et al. 2017, Newbold et al. 2018). For example, a recent analysis of 19 000 species demonstrates human-dominated land uses filter for wide-ranged species leading to an assemblage with an average range size far exceeding those in primary habitats (Newbold et al. 2018). These 'emergent' properties of species can be simpler to quantify than the many trait combinations that facilitate a large geographic range, for example, whilst still predicting how the response of species depends on the interaction between its properties (e.g. range size) and its environment. In this sense, geographic range size is a promising species property for estimating land-use sensitivity, particularly when individual traits are impossible to compare between taxonomic groups (e.g. morphology, behaviour, Verberk et al. 2013, Wong et al. 2018). However, why geographic range size predicts species' land-use response is often unclear because not all the many traits that relate to large range size also lead to resistance to land-use change (Bartomeus et al. 2013, Laube et al. 2013, Newbold et al. 2013, Rader et al. 2014), and species' niches may be a common driver of responses to environmental change and geographic range size (Staude et al. 2020).

In contrast to geographic range size, species' realized niches should map more clearly onto organismal traits that determine land-use responses (i.e. physiological limits) because land-use change causes dramatic environmental shifts in temperature and moisture – thus providing a mechanistic link between species properties and environmental change. Specifically, land-use change that removes forest cover causes a shift to microclimates that are on average warmer, drier and more diurnally and seasonally variable in temperature (Chen et al. 1999, Hardwick et al. 2015, Latimer and Zuckerberg 2017, Senior et al. 2017, De Frenne et al. 2019).

These microclimatic shifts can cause 5–10°C difference in maximum temperatures between land-use types (Suggitt et al. 2011, Senior et al. 2017, De Frenne et al. 2019), and thus set up several predictions for how species properties interact with their local environment to influence local community structure (Woods et al. 2015, Pincebourde et al. 2016). For example, we expect an increase in the occurrence and abundance of species that can tolerate warm and dry environments when mature forest transitions to agroecosystems. Species whose performance optima and critical limits are at higher temperatures persist more frequently in agroecosystems (Frishkoff et al. 2015, Nowakowski et al. 2018a), leading to assemblages containing, on average, more species with ranges centred in warmer regions (Barnagaud et al. 2013, Williams and Newbold 2019, Williams et al. 2019).

The realized niche of species – whilst on average strongly related to geographic range size – provides a more direct mechanism to understand species land-use responses. Species with wider geographic ranges often have wider niche breadths (though not always: Serrano-Rodríguez et al. 2018), and range limits are expected to be driven by environmental limits to physiological processes (Slatyer et al. 2013, Lee-Yaw et al. 2016, Kambach et al. 2019). We therefore hypothesise that, if local climatic shifts caused by land-use change in turn drives environmental filtering of species assemblages, niche limits may explain species' responses to land-use change better than do species' geographic range sizes. As yet this hypothesis remains untested, and a major challenge remains in determining whether poorly sampled 'realized' niches can be predictive of biodiversity change expected with land-use change. In addition, a key aim of this paper is to compare between different species properties that are easily – if imperfectly – estimated for all species with occurrence records, i.e. estimates of realized niches and geographic range sizes.

Here, we estimate realized niches from occurrence records for over 700 insect species from multiple taxonomic groups worldwide. We test whether realized niches predict differences between species' presence in mature forest (cool-wet-stable) and nearby agroecosystems (warm-dry-variable). Insects are an excellent model for three reasons: 1) ectothermy means that occurrence is likely to depend strongly on temperature; 2) the sheer diversity of insects makes finding comparable land-use response traits amongst taxonomic groups challenging; 3) there is an urgent need to identify mechanisms that could underpin recent insect declines (Hallmann et al. 2017, Seibold et al. 2019, Harvey et al. 2020, Klink et al. 2020). Previous work on specific insect groups has identified that urban environments filter for species with warmer affinities (ants, Menke et al. 2011; carabid beetles, Piano et al. 2017), but whether such results generalise across multiple insect taxa and agroecosystems is unknown.

Our analysis asks, does the occupancy of mature forest and nearby agroecosystems depend on properties of species' geographic range and realized niche? Does any relationship match expected microclimatic gradients in temperature and

moisture between mature forest and agroecosystems? If so, are species' occurrences in different land-use types better predicted by their realized niches or their geographic range sizes? In doing so, we help establish if range and realized niche metrics obtained from relatively low-cost and unstructured sources of species distribution data can be useful in predicting biodiversity change in under-sampled groups such as insects (Cardoso et al. 2011, Ballesteros-Mejia et al. 2013, Amano et al. 2016).

## Methods and material

### Species' occurrences in land-use types

For this analysis comparing assemblages between mature forests and agroecosystems, we used the 'Projecting Responses of Ecological Diversity in Changing Terrestrial Systems' (PREDICTS) database, accessed in July 2017 (Hudson et al. 2017), which provides space-for-time comparisons of species assemblage response to land-use change (Purvis et al. 2018). The PREDICTS database is a compilation of 480 data sources investigating the species composition and diversity of over 26 000 sites aligned to a common scheme of land-use classes (see Hudson et al. 2017 for full details). Sites are the unit of replication in the PREDICTS dataset and represent a location in which an ecological assemblage is sampled within a given land-use in a particular study. Within each site several samples may have been taken and, if so, were pooled together. We filtered the PREDICTS dataset to include only insect species where binomial names are recorded in full to match with sources of species distribution data, and to include only sites within forested biomes (based on The Nature Conservancy (2009) definitions, extracted from biome maps in Hudson et al. 2017). We included only estimates of species' abundance, density or occurrence for studies where two or more species were recorded, to ensure studies are focussed on communities, and converted all data to presence-absences. We included only five of PREDICTS' land-use classes, combining primary forest and mature secondary forest into a 'mature forest' class, and combining plantation forest, pasture and cropland into an 'agroecosystem' class (for full definitions see Hudson et al. 2017), thereby focusing on land-use contrasts for which the direction of thermal and moisture gradient was most distinct (Senior et al. 2017). We retained studies with at least one mature forest site for comparison and at least two sites in total. In total, our final dataset contained 25 studies with a total of 563 sites and 764 species for analysis, with a total of 23 693 site by species presence-absence observations. Most data were from Coleoptera and Lepidoptera, and the Palearctic and Neotropics were the most commonly studied biogeographic realms (Fig. 1, Supplementary material Appendix 1 Fig. A1). Because a few studies provided a high proportion of observations (Supplementary material Appendix 1 Fig. A2), we also performed sensitivity tests to examine the influence of data-rich studies (see below).

### Metrics of geographic range and realized niche properties

We described species' distributions from occurrence records in GBIF (<www.gbif.org>), accessed on the 25 July 2017 (provided by Dr. Tim Newbold). We excluded 1729 species with occurrences in fewer than 20 unique  $0.1 \times 0.1^\circ$  grid cells, giving a median of 718 occurrence records per species (5th percentile = 29; 95th percentile = 6452; Supplementary material Appendix 1 Fig. A3). In addition, we checked for and removed potentially erroneous records in the range data provided using 'CoordinateCleaner' package (Zizka et al. 2019; by excluding records within 1000 m of capital cities and country centroids; with equal absolute latitudes and longitudes; were located in the gbif headquarters; were within 100 m of research institutions; or contained absolute zeros). The median number of species occurrence records per PREDICTS study was 126, suggesting that most species in a given study have a high number of occurrence records and a relatively well sampled geographic range and realized niche (Wiszniewski et al. 2008, Feeley and Silman 2011). We used a lower cut-off (i.e. 20 presence records) than required for species distribution modelling because we simply want to describe the realized niche of species in an often under-sampled taxonomic group, rather than project the potential geographic range of species from a realized niche. To estimate the realized niche of the 764 species that remained in the dataset, we matched their GBIF occurrence records with rasterised environmental variables in WorldClim v2.0 at a 1 km scale at the equator ( $\sim 0.01^\circ$ ; Fick and Hijmans 2017). For each occurrence we extracted annual mean, monthly minimum and monthly maximum temperatures; and annual total precipitation and total precipitation in the wettest and driest months.

We characterised 28 metrics of species' geographic ranges and realized niches (based on species geographic and the environmental values of species distribution records), as defined fully in Supplementary material Appendix 1 Table A1 and Fig. 1. We attempted to provide a set of conceptually distinct metrics (Gaston and Fuller 2009). For example, the 'extent of occurrence' (EOO) is defined as 'overall geographic spread of the localities at which a species occurs' and provided a simple metric to represent a species' ability to occupy broad areas. Area of occupancy (AOO) represents the area of observed occupied habitat which is, by definition, never larger than EOO. The metrics have different assumptions; for example, the value of AOO is strongly influenced by the size of grid cells used, whereas EOO ignores range discontinuities and thereby includes areas species may never occupy (Gaston and Fuller 2009). The expected direction of effect for each distribution metrics is outlined in Table 1 and Supplementary material Appendix 1 Table A1.

We next grouped our set of 28 metrics into four groups representing conceptually different measures of species' realized niches and geographic ranges: niche location, niche breadth, geographic range location, geographic range breadth. 'Location' metrics measure the mean or 5th and

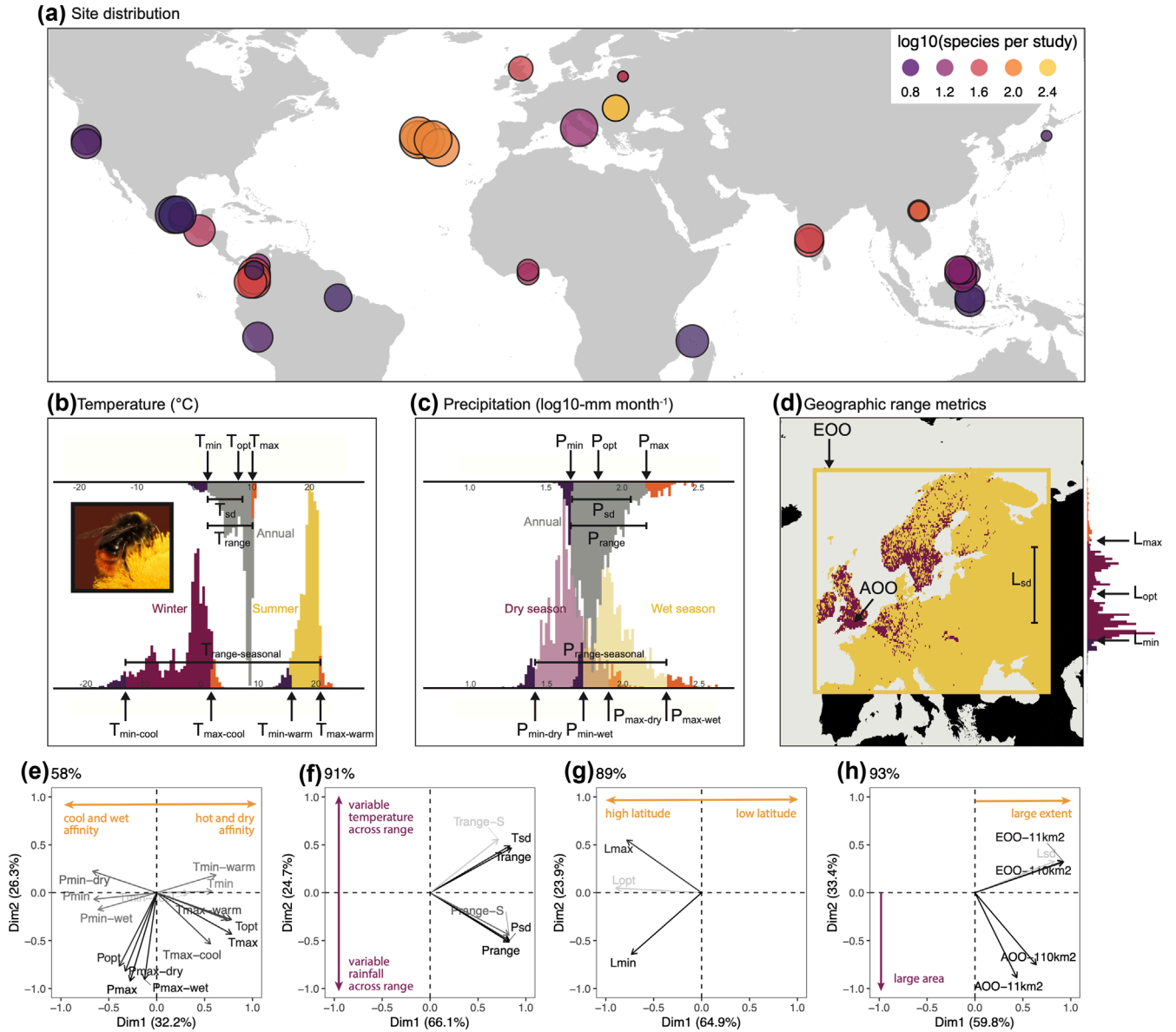


Figure 1. Methodological overview showing (a) worldwide distribution of study sites, (b–d) range metrics illustrated for *Bombus pratorum* and (e–h) principal components of range metrics. Study sites are shown in (a) are coloured by the number of species in a given study, and point sizes represent the number of sites per study. Occurrences were obtained from GBIF and matched with environmental rasters to show annual and seasonal variation limits for (b) temperature, (c) precipitation and (d) range metrics. Principal components of the 28 metrics for (e) niche location, (f) niche breadth, (g) range location and (h) range size, percentage variation in range properties for first and second components shown on axis and total variation on top of panel. Acronyms are described in Supplementary material Appendix 1 Table A1. Photo credit: Donald Hobern from Copenhagen, Denmark via Wikimedia Commons.

95th percentiles of species' geographic ranges or realized niches. 'Breadth' metrics quantify variation in species' geographic range or realized niches (standard deviations and range between 5th and 95th percentile). For example,  $T_{opt}$  is a measure of thermal realized niche location, whereas  $T_{sd}$  measures thermal realized niche breadth. Species' realized niche and geographic range metrics were standardised at a study scale (transformed to have a mean of zero and standard deviation of one). That is, each metric was transformed within a given PREDICTS study so that we compare the

available range property variation across the species within a study regardless of the absolute differences in range properties between studies. By considering only variation between species within the study-level species pool, this step removed some of the correlation that occurs across broad geographic gradients when the species pool is considered globally, and thereby reduced model multicollinearity (Supplementary material Appendix 1 Fig. A4).

Finally, we reduced the dimensions of our geographic range and realized niche properties using principal component



Table 1. Summary of principal components (PC) of species niche and geographic range properties. Qualitative interpretation of PC values are provided with expected direction of effects in agroecosystems relative to human-dominated land use.

Metric	Axis	Proportion var. explained	No. PCs for 95% explained var.	Low PC values	High PC values	Expected effect in agroecosystems (i.e. interaction between niche/range properties and land use type)
Niche location	PC1	0.32	8	Cool and high minimum rainfall	Warm and low minimum rainfall	<b>Positive</b> Higher occupancy of warm and dry affinity species expected in agroecosystems compared to mature forests
Niche location	PC2	0.26		High maximum and mean rainfall	Low maximum and mean rainfall	<b>Positive</b> Higher occupancy of species with tolerance to lower rainfalls across range expected in agroecosystems compared to mature forests
Niche breadth	PC1	0.66	3	Low variation in rainfall and temperature	High variation in rainfall and temperature	<b>Positive</b> Species with broader niches in general are expected to have higher occupancy in agroecosystems
Niche breadth	PC2	0.25		Variable precipitation but stable temperature	Variable temperature but stable rainfall	<b>Positive or negative</b> Depends on whether rainfall variation or temperature variation determines occupancy of agroecosystems
Geographic location	PC1	0.65	3	Lower latitude geographic range	Higher latitude geographic range	<b>Positive</b> Species of more temperate climates are expected to have lower sensitivity to land-use change
Geographic location	PC2	0.24		Low maximum latitude but high minimum latitude	High maximum latitude but low minimum latitude	<b>Positive</b> Proxy for range size, larger range sizes expected to have greater occupancy in agroecosystems
Geographic breadth	PC1	0.60	3	Small range extent of occurrence	Large range extent of occurrence	<b>Positive</b> Large area of occurrence expected to relate to higher occupancy in agroecosystems
Geographic breadth	PC2	0.33		Large range area of occurrence	Small range area of occurrence	<b>Negative</b> Small area of occurrence expected to relate to lower occupancy in agroecosystems

analysis. We extracted the first two dimensions for niche breadth, niche location, geographic range breadth and geographic range location, giving a total of eight metrics describing the properties of species geographic ranges and realized niches (Table 1, Fig. 1). Reducing the realized niche and geographic range properties to key dimensions of variation allowed easier interpretation of shared effects of the 28 niche metrics which were sometimes correlated (Supplementary material Appendix 1 Fig. A4, A5); for example, the first component of realized niche location explained a continuum from cool-wet affinity to warm-dry affinity species (see Fig. 1, Table 1 for PC-axis descriptions). Large proportions of variation in metrics of realized niche breadth, geographic range area and geographic range location could be explained by two principal components whereas realized niche location required 8 principal components to explain > 95% variation (Table 1, Fig. 1; Supplementary material Appendix 1 Fig. A6).

## Statistical modelling

Estimating how realized niche and geographic ranges affect species' response to land use change is traditionally termed a 'trait–environment interaction': here we replace species traits with species range properties. A major statistical challenge exists in establishing how species properties interact with the local environment to determine community dynamics (Jamil et al. 2013, Peres-Neto et al. 2017), because environmental gradients are measured at the site level but traits are measured at the species level causing pseudo-replication (Miller et al. 2019). Frequently, community-weighted mean trait values are estimated for each site and regressed against environmental gradients (Funk et al. 2017), but this approach does not account for pseudo-replication of species amongst sites (Miller et al. 2019) and can be sensitive to outliers (Bowler and Böhning-Gaese 2017). We used generalised

linear mixed-effects models (GLMMs), which produce better type-1 error control and higher statistical power than do approaches with similar aims such as community-weighted mean correlations or matrix-correlation (i.e. fourth-corner; Miller et al. 2019). Specifically, we followed the GLMM approach of Jamil et al. (2013) and focused on how presence-absence of species depends on the interaction between land-use class and properties of species' geographic range and realized niche.

We modelled species' presence-absence as a function of land use interacting with species' geographic range and realized niche properties. The full GLMM structure was:

$$\text{logit}(p_{ij}) = a_0 + (a_1 z_j) + (b_0 + \varepsilon_{\beta_j})x_{hi} + (b_1 z_j x_{hi}) + \varepsilon_{\alpha j} + \gamma_{hi} \quad (1)$$

which modelled probability of occurrence ( $p$ ) of species  $j$  in site  $i$ , as a linear function of geographic range or realized niche metric ( $z$ ), the land-use type ( $x$ ) and the interaction between land use and range metric ( $xz$  – a trait–environment interaction). We modelled  $p$  with a binomial error distribution and a logit–link function. We included random intercepts for species ( $\varepsilon_{\alpha j}$ ) and sites nested within studies ( $\gamma_{hi}$ ). This nested site- and study-level random effect was included to account for environmental and methodological differences amongst studies. We also included a random slope to capture variation among species' responses to land-use type ( $\varepsilon_{\beta_j} x_{hi}$ ). We tested whether fitting a site- and block-level random effect (i.e. rather than site- and study-level) influenced our results; however, the average coefficient difference was in the order of  $10^{-4}$  because only 5 studies have  $> 1$  block. Species-specific random slopes were supported by likelihood-ratio tests using restricted estimates of maximum likelihood (REML; Zuur et al. 2009).

We aimed to identify the most important metrics amongst the set of eight geographic range and realized niche properties, using a model selection approach similar to Jamil et al. (2013) (Supplementary material Appendix 1 Fig. A7). We first fitted one model for each geographic range and realized niche property and tested the significance of the 'range property–environment interaction' terms (i.e. land use  $\times$  range/niche metric) by likelihood-ratio tests (Zuur et al. 2009, Jamil et al. 2013). We also estimated the influence of multiple comparisons by applying conservative (i.e. non-sequential) Bonferroni corrections to p-values ( $n=8$ ). Next, for significant geographic range and realized niche properties in individual models we fitted models with multiple range property–environment interactions. Doing so should remove the influence of correlations amongst covariates that could drive range property–environment interactions in individual models. We fitted models using maximum likelihood and performed likelihood-ratio tests by dropping each range property–environment interaction term. We did not perform further model selection because each metric had an expected direction of effect and model selection can lead to greater certainty in model coefficients than is warranted in the presence of even the relatively weak collinearity

often present amongst our metrics (Morrissey and Ruxton 2018). If variance inflation factors were  $> 3$  or Pearson's correlation coefficient ( $r$ ) amongst metrics were  $> 0.7$  we removed the least explanatory variable (indicated by  $\chi^2$  values; Imdadullah et al. 2016). We present the final models refitted after removing two studies identified as influential based on Cook's distance (final analyses included 23 studies containing 553 sites and 483 species, giving a total of 21 237 site by species observations remaining, all supporting statistical analyses are presented in Supplementary material Appendix 1 Table A2–A6).

## Case studies

Fitting the above global models allowed the estimation of overall effects of geographic range and realized niche metrics, controlling for heterogeneity of effects among studies. The relatively small number of studies in the final dataset may result in poorly estimated effects in a global-model framework, unless there is strong agreement in the direction of range property–environment interactions amongst studies. Agreement of effects amongst studies may be unlikely given the comparison of heterogeneous studies in PREDICTS, so context-dependencies may influence model parameters. Whilst it may be preferable to address model heterogeneity as random slopes for trait–environment interactions, such models had convergence issues (i.e. a Hessian of fixed effects that was not positive definite). However, seven studies (Vanbergen et al. 2005, Vu pers. comm. 2005, Baur et al. 2006, Dolia et al. 2008, Vu 2009, Meijer et al. 2011, Cabra-García et al. 2012) were well-replicated and amenable to independent analyses (having more than 30 species in addition to more than 100 observations). We separated Baur et al. (2006) into day-flying and night-flying Lepidoptera, giving a total of eight case-studies. We analysed these studies following the above protocol to examine support for the global model's range property–environment interactions. We modified the study-level random effects to block-level random effects where studies had multiple blocks.

All analysis were performed in R (ver. 3.4.0). We used the package 'glmmTMB' to fit statistical models (Brooks et al. 2017); however, 'glmmTMB' did not provide software for influence analysis, for which we used the function 'influence' in the package 'lme4' (Bates et al. 2015).

## Results

The effect of land-use change depended on properties of species' niches and, to a lesser extent, on their geographic range properties (Table 2, Fig. 2). PC1 of realized niche location was by far the best predictor of occupancy differences amongst land-use types (Fig. 2a). This PC describes an axis from relatively 'cool-wet' to 'warm-dry' affinity species within a particular study's total community pool. Warm- and dry-affinity species had occupancy rates that were significantly higher in agroecosystems relative to

Table 2. Model summaries for the first two principal components of species realized niches and geographic range properties. Univariate models represent realized niche and range properties fitted individually and multivariate models represent terms fitted together after selecting the supported terms ( $p < 0.05$ ) from the univariate model.  $\beta$  values indicate the effect of realized niche or range properties on species occupancy rates within mature forest and agroecosystems, with associated standard error (SE). A significant interaction is tested using likelihood-ratio tests to derive  $\chi^2$  and p-values with 1-degree of freedom, significant terms are in bold.

Terms	Mature forest		Agriculture		LRT		
	$\beta$	SE	$\beta$	SE	$\chi^2$	p-value	p-adjust
Univariate models							
Niche location PC1	−0.26	0.05	0.06	0.07	25.02	< 0.001	< 0.001
Niche location PC2	−0.21	0.05	−0.03	0.07	7.77	< 0.01	< 0.05
Niche breadth PC1	0.09	0.05	0.11	0.07	0.13	0.72	0.82
Niche breadth PC2	−0.36	0.08	−0.05	0.10	10.28	< 0.01	< 0.01
Range location PC1	0.07	0.07	−0.11	0.09	3.95	< 0.05	0.07
Range location PC2	0.08	0.12	0.11	0.16	0.04	0.84	0.84
Range breadth PC1	0.02	0.06	0.10	0.07	1.27	0.26	0.35
Range breadth PC2	−0.13	0.09	−0.38	0.11	4.58	< 0.05	0.06
Multivariate models							
Niche location PC1	−0.31	0.06	0.15	0.07	38.69	< 0.001	
Niche location PC2	−0.06	0.07	−0.10	0.09	0.16	0.69	
Niche breadth PC2	−0.27	0.09	0.04	0.12	6.36	< 0.05	
Range location PC1	0.14	0.09	−0.16	0.11	7.20	< 0.01	
Range breadth PC2	−0.06	0.09	−0.37	0.12	6.60	< 0.05	

mature forest, whereas cool- and wet-affinity species had higher occupancy in mature forests. Niche breadth also influenced species occupancy of different land-uses. Species with wider precipitation niches but narrower thermal niches had higher occupancy in mature forest compared to agroecosystems (Fig. 2b). Agroecosystems did not strongly filter for niche breadth; instead species with wide thermal niches and narrow precipitation niches had a declining occupancy in mature forests. Species living at relatively higher latitudes were favoured in agroecosystems compared to their lower latitude counterparts (Fig. 2c). Interestingly, the effect of range location increased after the potentially confounding influence of realized niches (i.e. low latitude is correlated with warmer affinity) was accounted for (i.e. multivariate models in Table 2). Geographic range breadth also influenced occurrence in land-use types, whereby species with larger area of occupancy (but not larger total extent) were disproportionally found in agroecosystems (Fig. 2d). Species' geographic range properties were not significantly related to occupancy differences across land-use when influential studies were present in final models, but the identified realized niche effects remain qualitatively identical (Supplementary material Appendix 1 Table A2). Furthermore, our main results were not very sensitive to the exclusion of 34% of species with fewer than 100 range locations used to quantify realized niche and geographic range properties (Supplementary material Appendix 1 Table A3, Fig. A8).

Investigating potential context-dependency effects within studies revealed that 4 out of 8 case studies supported significant range property–environment interactions (Supplementary material Appendix 1 Table A4). However, the particular range property–environment interaction that was most important often varied amongst studies. Two case studies supported realized niche–environment interactions

and two supported geographic range–environment interactions. Niche–environment interactions were frequently in the directions expected from the microclimatic changes across land-use gradients: agroecosystems benefit species with warmer–warm limits, cooler–cool limits, drier affinities and broader realized niches; in addition, species with larger ranges were favoured in agroecosystems (Supplementary material Appendix 1 Table A4). Any terms that appeared contradictory to our initial hypothesis were highly correlated with better fitting terms that did match our hypothesis, so were probably picking up the signal of strong correlations rather than being true contradictions (Supplementary material Appendix 1 Table A4).

Analysing species' range properties independently revealed that summer thermal maximum ( $T_{\max\text{-warm}}$ ) and precipitation minima in the dry season ( $P_{\min\text{-dry}}$ ) are the most likely single realized niche axes to drive our analysis of principal components (Supplementary material Appendix 1 Fig. A9, Table A5, A6). Species with warmer summer limits (high  $T_{\max\text{-warm}}$ ) relative to other species in the community, and species living in environments with low minimum precipitation (low  $P_{\min\text{-dry}}$ ), had higher occupancy in agroecosystems compared to mature forests. Analysed in this way, geographic range metrics were never significant in predicting occurrence across land-uses. Sensitivity analysis revealed that three studies were strongly influential and, in excluding these studies, only minimum precipitation ( $P_{\min}$ ) significantly affected species' occupancy, with higher occurrence of dry-affinity species in agroecosystems compared to mature forests – largely concurrent with our main results (Supplementary material Appendix 1 Table A5, A6). Investigating case-studies independently for each metric showed qualitatively similar results to investigating the case studies of principal components of realized niche and geographic range properties (Supplementary material Appendix 1 Table A7).

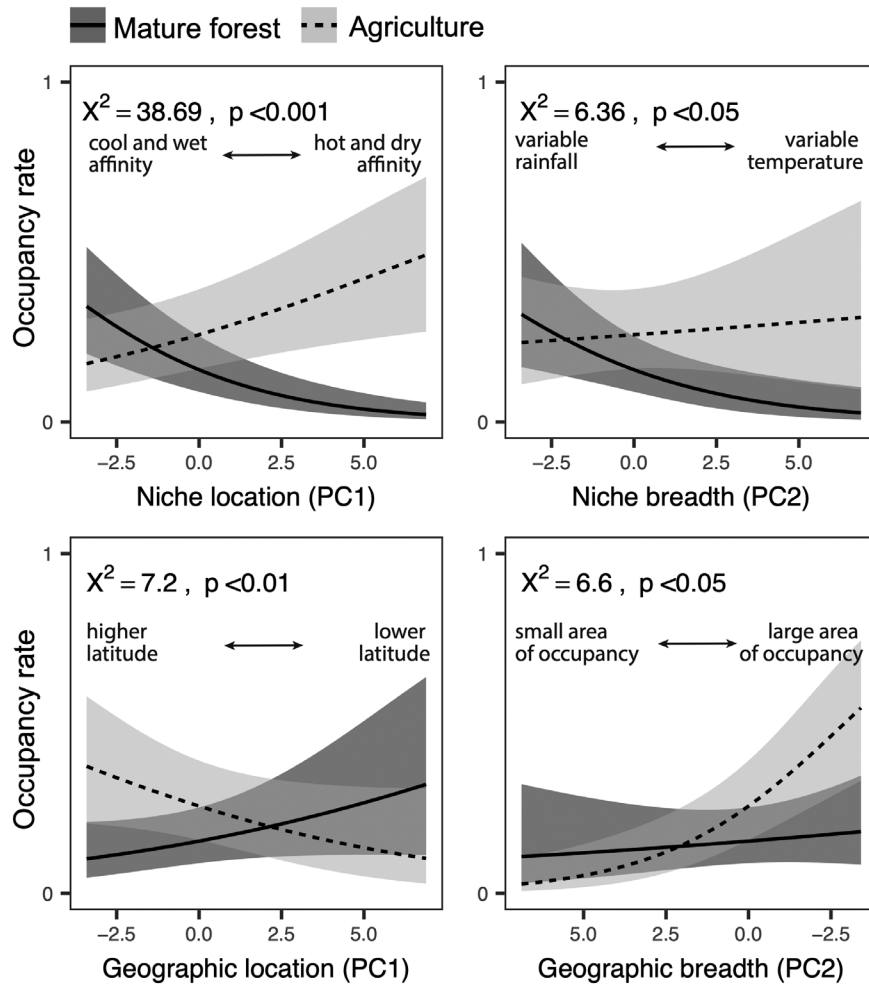


Figure 2. Fitted relationship showing how species' occurrence in different land-uses depends on species' realized niche and geographic range properties. The presented interactions between realized niche and range properties with land-use showed a significant reduction in log-likelihood when removed from the full model (Table 2), p-values indicate significance of terms describing realized niche and geographic range properties interactions with land-use,  $\chi^2$  statistics presented with 1-degree of freedom. Effects shown are marginal effects, holding all other variables in the models at their mean values. Shaded regions are 95% confidence intervals.

## Discussion

A wide-ranged 'winners' versus narrow-ranged 'losers' pattern is emerging as a consistent response of local assemblages to habitat change (Cleary and Mooers 2006, Scott et al. 2006, Cofre et al. 2007, Nowakowski et al. 2017, Newbold et al. 2018), but does not explain the mechanism whereby the winners win and losers lose (Stauder et al. 2020). Our results suggest that species' realized niches are at least part of the answer: realized niches more strongly predict species' presence-absences across land-use classes than do their geographic ranges. This suggests that the explanatory power of geographic ranges in other studies may arise from the correlation between larger geographic range size and the wider environmental limits and wider physiological tolerances that influence range formation (Slatyer et al. 2013, Kambach et al. 2019) – a pattern supported in insects (Calosi et al. 2010, Diamond and Chick

2018). We expect physiological limits to constrain species' performance within the different microclimatic environments of agricultural and forested locations; therefore, the realized niches quantified here crudely approximate this physiological signal but in doing so provide a quantifiable mechanistic link to land-use sensitivity (Nowakowski et al. 2018b, Williams and Newbold 2019). Our detectable fingerprint of realized niches is also supported in vertebrate taxa, where researchers have a much clearer idea of geographic ranges size of charismatic species (Frishkoff et al. 2015, Williams et al. 2019). Our study suggests understanding the factors contributing to geographic range sizes is key to unlock why species with smaller ranges are more sensitive to land use (Stauder et al. 2020). Although for many groups behavioural flexibility or diet breadth may also be important, realized niches should always be considered as a potential factor given the strong microclimate shifts with land-use change.



We interpret the significant realized niche–environment interactions as a signal of environmental filtering: overall, the microclimatic filtering of warm, dry affinity species may be a general principle in assemblage responses to change from forested to non-forested land-uses (Andersen 2018, Nowakowski et al. 2018b, Williams and Newbold 2019). Here we establish this environmental filtering only indirectly and site microclimates are assumed to change but remain unmeasured. Supporting this micro-environmental filtering hypothesis, however, is the finding that amongst populations of insects, particular life-history traits are fitter in warmer and drier agricultural landscapes (Rigal et al. 2018) suggesting strong selective pressure from microclimatic land-use change (Karlsson and Wiklund 2005).

The local niche filtering inferred here has consequences for how land use affects local richness and community composition in agroecosystems (Staude et al. 2020). For example, the overall biodiversity differences between local assemblages (in different land uses) depend on environmental responses available within the source pool of species (i.e. response diversity; Elmquist et al. 2003). Whilst the role of regional niche diversity in facilitating or moderating shifts of biodiversity and ecosystem function may be generally underappreciated (Dee et al. 2016, Garcia et al. 2018), the traits and niches of regional native species pools help determine the ‘winners’ and ‘losers’ of biodiversity change (Tabarelli et al. 2012, McCune and Vellend 2013, Staude et al. 2020). For example, if the regional species pool is a mix of warm- and cool-tolerant species, then local richness will be maintained by the local turnover of species identity with land-use change. Alternatively, if there is little thermal diversity in the regional pool then cool-affinity species cannot be replaced by warm-affinity species and richness is lost with land-use change (i.e. ecological or biogeographic constraints limit community re-assembly, Bertrand et al. 2016). Regional thermal response diversity may facilitate assemblage change; for example, high topographic heterogeneity (linked to thermal heterogeneity that harbours response diversity) correlated with stronger assemblage re-organisation after an extreme drought event in UK butterfly assemblages (De Palma et al. 2017). Spatial management of topographically complex regions is recognised as a tool in mitigating the ecological impacts of climate warming (Heller and Zavaleta 2009); assemblage reorganisation to land-use changes that modify microclimates may therefore depend on topographic complexity (Borges et al. 2006, Oliver et al. 2010, Lenoir et al. 2013, Katayama et al. 2014) and open space management (Smith et al. 2007).

Morphological and life-history traits mediate individuals’ interactions with abiotic environments, however, the important traits in determining sensitivity to land use change often varies among taxonomic groups. This variation greatly reduces the prospect of finding general traits that predict species-level responses to environmental change. However, similarities in the biochemistry of life – demand for water, thermodynamics of protein functioning, thermal constraints to metabolic rates – mean that environmental tolerances, often mediated

by physiology, are likely to strongly influence the limits of species’ realized niches (Corkrey et al. 2012, Sunday et al. 2012, Lee-Yaw et al. 2016). The properties of realized niche limits may therefore provide a predictive factor – one that is generalisable amongst a wide variety of taxa – explaining species-level response to environmental change. Realized niches simplify the complex issue of cross-taxon trait comparisons (Verberk et al. 2013, Wong et al. 2018), but some of the niche context-dependencies identified here amongst case-studies suggests that a major challenge remains in understanding which of many axes of species’ multi-dimensional niche are most relevant (Rozen-Rechels et al. 2019).

We demonstrate that the effects of realized niche limits on species responses to land-use change can be context-dependent. Among our case studies, effects of thermal and precipitation realized niches and geographic ranges are all supported. However, in our ‘global’ model of realized niche and range principal components, context-dependency may have been relegated to the model’s random effect terms by forcing a globally consistent response to land-use change (i.e. no random slopes amongst studies or taxonomic groups). Multiple unidentified factors may underlie these context-dependencies even though we study a well-established directional microclimatic change. First, even if species respond only to their abiotic environment, local temperature, water availability and humidity change simultaneously, leading to complex environmental changes during a land-use transition. Second, responses can interact amongst abiotic stressors; for example, the thermal tolerance of individual organisms can depend on the variability in precipitation and temperature experienced by the source population (Clusella-Trullas et al. 2011, Kellermann et al. 2012). Finally, species abiotic responses may affect other species through interactions such as competition or predation. Niche context-dependency is also apparent in field studies of different insect groups; for example, temperature is important for ants (Menke et al. 2011, Kaspari et al. 2015) but humidity and desiccation tolerance may be more important for other groups (Borges et al. 2006; e.g. termites Woon et al. 2019). In general, whilst taxonomic groups and study regions here varied in the important range factors underpinning responses to land-use change, when effects were present, we found support consistent with our hypothesised direction of effect. Therefore, future work should attempt to identify the nature of context-dependent effects to better ascertain when and why certain niche dimensions are important.

Two strong caveats must be acknowledged in interpreting our results. First, we quantify realized niches without considering their mechanistic basis and simply correlate occurrence to environmental variables. Second, there is a substantial difference in spatial scale between niche limits defined from large-scale climate gradients with the small-scale microenvironments that insects experience. A single leaf can have a larger thermal gradient than average climates spanning hundreds of kilometres of latitude (Pincebourde and Woods 2012, Pincebourde et al. 2016). Sources of microclimate

variation are an important driver of ecological processes, facilitating behavioural thermoregulation, space-use and thermal niche partitioning (Kaspari et al. 2015). Given that we find correlative power in our simple niche metrics, the potential for microclimate variation, and the extremes of this variation, appears to be constrained by the broader climate within which a habitat is nested (Graae et al. 2012) – individuals and populations often move within and experience this larger scale climate variability as a whole (Sears et al. 2011, 2016). As such, the use of climate gradients to estimate species' realized niches can still be predictive – but incorporating finer-scale variation defining realized niche limits may improve predictions.

In addition, the decision to bundle multiple agricultural practices into a single agroecosystem class may add to the heterogeneous picture presented here, but was necessary to simplify models. Niche effects may be less important to explain assemblage differences between mature and secondary forest as these involve less extreme microclimatic differences (Senior et al. 2017, 2018). By necessity our results are biased towards relatively common species that have available occurrence data. Distribution metrics may be less predictive in rare species for which range limits may be strongly limited by processes such as dispersal limitation, interspecific interactions and fundamental–niche availability.

Simple predictive metrics of species' sensitivity to environmental change are needed, given the data paucity researchers face for the vast majority of biodiversity (Ballesteros-Mejia et al. 2013, Faith et al. 2013, Amano et al. 2016). Realized niches have the benefit of estimating niche properties for assemblages of species, which remains a considerable challenge for direct thermal tolerances measures (but see Bates et al. 2010). Large-scale distribution data are undoubtedly far from perfect (Meyer et al. 2015), but this analysis demonstrates their utility in helping predict the response of biodiversity to land-use change. This work suggests niche and range properties derived from species' distributions appear to be a simple but relatively predictive tool that could be estimated for many thousands of species from open-access biodiversity repositories (e.g. GBIF).

## Data availability statement

Data and corresponding scripts for analyses available from the Zenodo Digital Repository: <<http://dx.doi.org/10.5281/zenodo.3605507>> (Waldock et al. 2020).

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Supplementary material (available online as Appendix ecog-05162 at <[www.ecography.org/appendix/ecog-05162](http://www.ecography.org/appendix/ecog-05162)>). Appendix 1.