

Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits

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Abstract

Aim: Land-use change leads to local climatic changes, which can induce shifts in community composition. Indeed, human-altered land uses favour species able to tolerate greater temperature and precipitation extremes. However, environmental changes do not impact species uniformly across their distributions, and most research exploring the impacts of climatic changes driven by land use has not considered potential within-range variation. We explored whether a population's climatic position (the difference between species' thermal and precipitation tolerance limits and the environmental conditions a population experiences) influences their relative abundance across land-use types.

Location: Global.

Methods: Using a global dataset of terrestrial vertebrate species and estimating their realized climatic tolerance limits, we analysed how the abundance of species within human-altered habitats relative to that in natural habitats varied across different climatic positions (controlling for proximity to geographic range edge).

Results: A population's thermal position strongly influenced abundance within human-altered land uses (e.g. agriculture). Where temperature extremes were closer to species' thermal limits, population abundances were lower in human-altered land uses (relative to natural habitat) compared to areas further from these limits. These effects were generally stronger at tropical compared to temperate latitudes. In contrast, the influences of precipitation position were more complex and often differed between land uses and geographic zones. Mapping the outcome of models revealed strong spatial variation in the potential severity of decline for vertebrate populations following conversion from natural habitat to cropland or pasture, due to their climatic position.

Main conclusions: We highlight within-range variation in species' responses to land use, driven (at least partly), by differences in climatic position. Accounting for spatial variation in responses to environmental changes is critical when predicting population vulnerability, producing successful conservation plans, and exploring how biodiversity may be impacted by future land-use and climate change interactions.

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KEYWORDS

biodiversity, climate change, climatic position, cropland, global, land-use change, precipitation, temperature, thermal tolerances

1 | INTRODUCTION

Human impacts on the environment do not affect species uniformly across their distribution (Orme et al., 2019). Accordingly, spatially explicit predictions of risk of population decline are crucial for suitable and successful conservation plans (Wilson et al., 2005). Physiological tolerances to temperature and precipitation, and the proximity of individuals to these tolerance limits (i.e. how close environmental climatic conditions are to an individual's climatic tolerance limits), lead to important differences across species' ranges in responses to environmental change (Deutsch et al., 2008; Gerick et al., 2014; Kingsolver et al., 2013; Soroye et al., 2020). By predicting where populations will be pushed beyond their climatic tolerances (thus unlikely able to persist), species bioclimatic envelopes have frequently been used to project how species' ranges may shift under global climate change (Calosi et al., 2010; Pearson & Dawson, 2003). However, climatic changes are not only occurring at the global level. For example, land-use changes also lead to local-scale climatic changes (Williams & Newbold, 2020).

Human-altered land uses (e.g. agricultural areas) are often drier and experience greater extremes of temperature than natural, undisturbed habitats (De Frenne et al., 2019; Frishkoff et al., 2016). These local climatic changes occur partly due to vegetation changes; for example, evapotranspiration levels are linked to the leaf area and rooting depth of species present (Costa & Foley, 2000), and the canopy layer in naturally forested areas buffers temperature extremes, with these habitats found to have lower maximum and higher minimum (i.e. winter or night-time) temperatures compared to cleared land, such as pastures (Daily & Ehrlich, 1996; De Frenne et al., 2019; Ewers & Banks-Leite, 2013). Studies have recorded average maximum temperatures rising by up to 9°C in croplands, 7°C in pastures and 3°C in plantations compared to primary forests (Nowakowski et al., 2017; Senior et al., 2017).

These local climatic differences are associated, directly and indirectly, with shifts in community structure (Frishkoff et al., 2016; Piano et al., 2017; Williams et al., 2020; Williams & Newbold, 2020). Human-altered land uses have been found to favour species affiliated with, or able to tolerate, higher maximum and average temperatures, and lower minimum temperatures, compared to natural habitats (Angilletta et al., 2007; Frishkoff et al., 2015; Menke et al., 2011; Williams et al., 2020). Affiliations with drier climates have also been linked with a higher probability of occurrence within agricultural land uses (e.g. Neotropical birds; Frishkoff et al., 2016). In addition, human land uses have been found to be composed of proportionally more individuals of species from regions with wetter maximum precipitation levels (Williams et al., 2020). Together, this suggests human-altered land uses favour species able to tolerate

greater extremes of precipitation as well as temperature (Williams et al., 2020).

Most research, however, has not considered potential variation across species' ranges in responses to land use (Williams & Newbold, 2020; but see Srinivasan et al., 2019; Northrup et al., 2019 for regional examples). Consequently, populations at greater risk from land-use change may be overlooked. Here, we extend previous research by asking how populations' proximities to their species-level climatic tolerance limits affect their abundances in human-altered land uses compared to in natural habitat, across terrestrial habitats globally. Due to the local climatic differences, we hypothesize that, relative to abundances in natural habitat, human-altered land uses will filter out populations of species in environments where they experience temperature and precipitation extremes closer to their climatic tolerance limits. We hypothesize that this filtering will be greater at tropical compared to temperate latitudes. The effects of human land use, including community-level differences between natural and human-altered land uses, have previously been shown to be greater in the tropics (Newbold et al., 2020; Williams et al., 2020), potentially due to the past relative stability of the tropical climate, within which many of the taxa present have evolved (Corlett, 2011; Pacifici et al., 2017). This suggests that individuals within this region will be more sensitive to rapid climatic (particularly temperature) changes and extreme conditions (Corlett, 2011; Janzen, 1967; Pacifici et al., 2017).

The relationship between species' abundance and position within geographical or environmental space forms a lively debate (Santini et al., 2019; VanDerWal et al., 2009; Weber et al., 2017). Some studies, for example, report that environmental suitability or distance from the centre of a species' environmental space (environmentally-based centre) can be considered a reasonable proxy for abundance (or at least its upper limit; VanDerWal et al., 2009; Weber et al., 2017), while others find little support for a consistent relationship between species' abundance and environmental suitability or distance from geographically- or environmentally-based centres (Dallas et al., 2017; Dallas & Hastings, 2018; Santini et al., 2019). In this study, we compare species' abundances within human-altered land uses *relative* to that within primary vegetation in the same part of the species' climatic space, rather than absolute abundances across a species' environmental space. Thus, we do not expect our results to be unduly influenced by the presence or otherwise of abundance variation across environmental space. Nonetheless, a population's distance from its species' range edge can impact behaviour, such as responses to forest loss (Orme et al., 2019) or exploratory behaviour (Liebl & Martin, 2012), so we account for this in our analyses below.

Finally, we extend our results to produce spatially explicit maps of the potential severity of decline of vertebrate populations in human-altered land uses, depending on proximity to climatic tolerance limits.

We estimate expected average severity of decline by predicting the difference in abundance between natural and human-altered land uses depending on each population's climatic position and distance to range edge, all else being held equal (as such, actual abundance changes may differ due to other influential factors, which could be included in future work). Meeting the food demands of Earth's growing population is a major challenge and, alongside intensifying current agricultural land, this is leading to the conversion of natural habitat to agriculture (Foley et al., 2011; Millennium Ecosystem Assessment, 2005). It is important to understand how this land-use change will impact biodiversity and whether land-use impacts differ spatially (Molotoks et al., 2018); consequently, we focus on how the severity of decline following land conversion from natural habitats to agriculture (croplands and pastures) may differ across the globe. Being able to estimate how risk differs across species' ranges enhances our ability to produce suitable conservation and management strategies and plan for future land-use changes.

2 | METHODS

2.1 | Occurrence and abundance data

We acquired occurrence and abundance data for terrestrial vertebrate species from the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) Project database (Hudson et al., 2016, 2017). There are reasonably comprehensive distribution data available for terrestrial vertebrates; thus, we focused on this group so that we could estimate their realized climatic tolerance limits (see below). The PREDICTS database is a collection of data from studies around the globe that have made spatial comparisons of ecological assemblages across land uses (Hudson et al., 2014). We acquired occurrence data for 4,369 species (3,117 birds, 555 mammals, 377 amphibians and 320 reptiles; of these, 4,150 species also had abundance estimates), from 161 studies across 51 countries. The PREDICTS database is hierarchically structured, whereby data from a published *Source* are divided into *Studies* (split by sampling method), which are further divided into *Spatial blocks*, and then into

Sites (where the sampling of ecological assemblages takes place; Hudson et al., 2014). Within this manuscript, we use the term "population" to refer to groups of individuals of the same species at the same site.

2.2 | Land-use data

Each site within the PREDICTS database has an assigned land-use type (Table 1; see supporting information, Appendix S1, Table S1.1), allocated by the PREDICTS Project team using a set of criteria and based on the habitat description within the original source or provided by the original study authors (Hudson et al., 2014). Land uses were also split by the intensity with which humans used the land (minimal, light, or intense use), based on factors such as chemical use, crop diversity, and disturbance level (Hudson et al., 2014). We did not include data from minimally-used urban sites (which include extensive green spaces), as assemblages within these areas may not accurately reflect assemblages within more urbanized/human-dominated areas, which were of interest in this study.

2.3 | Distribution data

Expert-informed species' distribution maps (extent of occurrence maps; BirdLife International, 2012; IUCN, 2016) were used to estimate species-level realized climatic tolerance limits. We extracted species' native historical ranges (areas where species were resident, or used during breeding or non-breeding seasons, including areas where the species had been reintroduced or introduced). These distribution maps were transformed into equal-area raster files (Behrmann projection, 10 × 10 km pixels; ArcGIS 10.4). Distribution maps were cut by species' elevational limits, if known (2,410 species had known upper limits, 12 had lower limits and 730 had both; BirdLife International, 2018; IUCN, 2016). We also removed migratory bird species from our dataset (migratory statuses acquired from BirdLife International, 2018), since these species can move between

TABLE 1 Brief definitions of the land-use types considered in this study. For complete definitions, see Appendix S1, Table S1.1 and Hudson et al. (2014)

Land-use type	Definition
Primary vegetation	Natural vegetation with no evidence of previous destruction
Mature/ Intermediate/ Young secondary vegetation	Vegetation that is recovering after removal of the natural vegetation, split into three stages of recovery (mature sites being those that have been recovering for the longest, young sites being those that have started to recover most recently, and intermediate sites in between)
Plantation forest	Agricultural land used for cultivating woody crops, such as oil-palm, rubber, fruit, coffee, or timber
Cropland	Agricultural land used for cultivating herbaceous crops, including fodder for livestock
Pasture	Agricultural land used for livestock grazing
Urban	Areas of human habitation and buildings, from small green spaces, through to villages and cities

different parts of their ranges to avoid extreme climatic conditions (Robinson et al., 2009), which may lead to biases within our results.

2.4 | Climatic tolerance limits

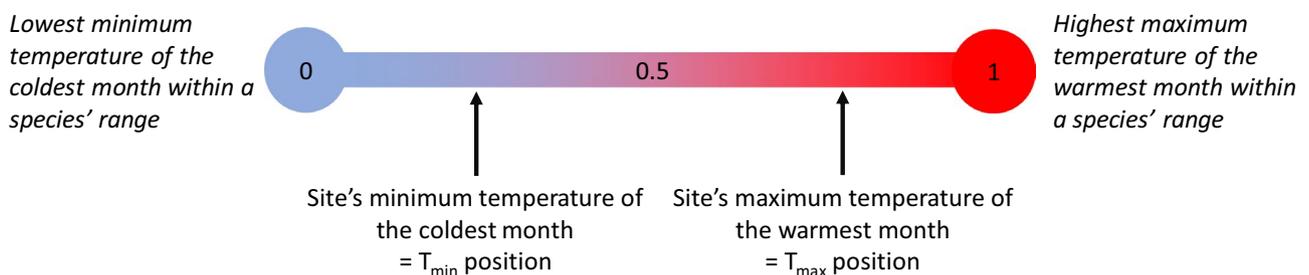
We estimated species' *realized* climatic tolerance limits, i.e., the highest and lowest temperature and precipitation a species' experiences within their geographic distribution. To calculate these, we overlaid the species distribution maps onto four climatic variables: precipitation of the wettest month (Pp_{max}), precipitation of the driest month (Pp_{min}), maximum temperature of the warmest month (T_{max}) and minimum temperature of the coldest month (T_{min} ; WorldClim Version 1.4; Hijmans et al., 2005). These climatic variable maps contained averaged annual values from 1960–1990, at a resolution of 30 arc-seconds, and were resampled (using bilinear interpolation) to 10 km equal-area projection (Behrmann projection) to match the species' distribution data. We extracted the highest Pp_{max} and T_{max} values and lowest Pp_{min} and T_{min} values within each species' distribution (ArcGIS 10.4). These maxima and minima provided our estimates of each species' temperature and precipitation tolerance limits (Figure 1).

Our analyses required data for a broad range of vertebrates from around the globe, for which the above extent of occurrence maps from the IUCN and BirdLife International are currently the best and most widely used (Allan et al., 2019; Herkt et al., 2017; Khaliq

et al., 2017; Shackelford et al., 2015). Species' extent of occurrence tends to be underestimated by expert-informed species distribution maps, whereas area of occupancy is overestimated (Herkt et al., 2017; Hurlbert & Jetz, 2007). Therefore, we tested the robustness of our results by (a) comparing population's climatic positions (see below) produced using the expert-informed distribution maps to those using occurrence records in the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>) and (b) running models using the same structure as our final models (see below) using the climatic positions derived from GBIF data (Appendix S2). GBIF provides data on species' area of occupancy, but has taxonomic and geographic biases (Meyer et al., 2015).

Biotic interactions and dispersal barriers also influence species' geographic ranges (HilleRisLambers et al., 2013; Peterson et al., 2011). Therefore, we compared our estimates of climatic position (see below) acquired from distribution maps to those using estimates of thermal tolerances derived from physiological experiments (acquired from GlobTherm; Bennett et al., 2017; Bennett et al., 2018). However, physiological thermal tolerance estimates also have issues (see Williams & Newbold, 2020). For example, the tolerance tests often lack real-world context due to being calculated in the absence of other factors and, for many vertebrate species, laboratory tests are not possible (see Mitchell et al., 2018; Rezende et al., 2014). Moreover, the metrics produced (such as critical thermal maxima and lethal maximums) are not comparable across studies

Thermal tolerance limits



Precipitation tolerance limits

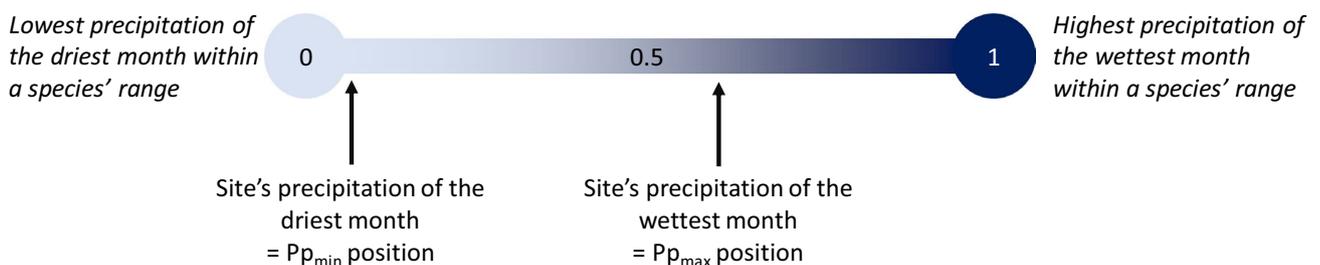


FIGURE 1 A visual example of how the four climatic positions (T_{max} , T_{min} , Pp_{max} and Pp_{min} position) were calculated for each population; 0 and 1 represent the species-level realized thermal or precipitation tolerance limits, extracted from species' distribution maps overlaid on climatic data; the climatic positions were calculated by standardizing the population's site-level climate data to range between 0 and 1 relative to the species-level climatic tolerance limits. For example, the closer the maximum temperature of the warmest month at a population's site is to the highest maximum temperature of the warmest month across a species' range, the closer a population's T_{max} position will be to 1. Similarly, the closer the precipitation of the driest month at a population's site is to the lowest precipitation of the driest month across a species' range, the closer a population's Pp_{min} position will be to 0

(Araújo et al., 2013), limiting the number of species that can be analysed.

2.5 | Climatic position

We calculated each population's "climatic position" with respect to their species-level climatic tolerance limits; this index describes the relative position of a site between the lower and upper realized tolerance limits of a species with respect to a given climatic variable. To estimate climatic position, for each study site we extracted climate data for the same four variables as described above (Pp_{max} , Pp_{min} , T_{max} , T_{min}), using climate variable maps resampled (using bilinear interpolation) to 500 m equal-area projection (Behrmann projection) to capture differences between climatic positions for very narrow-ranged species. Then, for each population, we standardized the site-specific climatic data to range between 0 and 1 relative to species' climatic tolerance limits: for thermal tolerance limits, 0 = minimum realized temperature tolerance limit and 1 = maximum realized temperature tolerance limit, and for precipitation tolerance limits, 0 and 1 are the minimum (dry) and maximum (wet) realized monthly precipitation tolerance limits, respectively (Figure 1).

A tiny subset of populations (<0.3%) had climatic position values below 0 or above 1, due to the climatic variable maps capturing slightly greater variation at the 500 m compared to the 10 km scale (Appendix S4, Table S4.6). We assumed that the very small scale of this discrepancy would mean there was very little influence on our results.

2.6 | Distance to range edge

To account for variation in population occurrence or abundance due to geographic position within their species' range (Orme et al., 2019), we produced a standardized distance to range edge measure for each population. We first found the shortest distance from each sampled population's location to their species' range edge (populations found outside of their stated distribution were removed from the analysis; BirdLife International, 2012; IUCN, 2016). We then found the largest shortest distance from any point in the species' distribution to their range edge (i.e. the furthest distance a population could be from their range edge), by transforming species' distributions maps into a grid of points. Finally, we used this to find the relative position of the sampled population to their range edge (i.e. to account for species' range size), where a measure of 0 refers to populations at their species' range edge and 1 refers to those nearest the range centre. This was completed in R 3.6.0 (R Core Team, 2019) using packages raster (Hijmans, 2019), rgdal (Bivand et al., 2019) and rgeos (Bivand & Rundel, 2019). As stated above, expert-informed species' distribution maps contain inaccuracies. To ensure that removing populations outside of their distributions did not impact our results, we reran our models (see below) without the distance to range edge measure and compared the results of models including and excluding populations

beyond their species' stated distributions (see Appendix S3 for more information).

Of the vertebrate species with occurrence data in the PREDICTS database, following the selection of species and land uses as described above, we were able to estimate tolerance limits, climatic positions, and distance from range edge for 88,007 populations, consisting of 2,103 species (384 mammals, 1,491 birds, 92 reptiles, 136 amphibians). Out of these, 81,913 populations (1,954 species) had abundance records (from studies that had sampled abundance, including those that recorded abundances of zero), and within this, 13,321 populations (1,594 species – 334 mammals, 1,087 birds, 87 reptiles, 86 amphibians) had non-zero abundance data. Ideally, we would have comparisons of species' abundance in different land uses across their geographical ranges, but samples do not exist for most species, particularly in the tropics; thus, we rely on collations of data such as the PREDICTS database, in which most of the species included have been recorded in multiple geographic locations and have several climatic position measures (Appendix S4, Table S4.4).

2.7 | Statistical analyses

We adopted a two-stage modelling approach (similar to a hurdle model) due to the high number (84%) of abundance records that were zero (Newbold et al., 2014; Potts & Elith, 2006). First, we used generalized linear mixed-effects models (with binomial error distributions) to model the probability of occurrence (assuming detection; $P(\text{Occ})$) of populations. Second, we used linear mixed-effects models to test for differences in log-transformed abundance (given presence; LogAbund). These models were used to assess whether a terrestrial vertebrate population's climatic position affected their abundance (a combination of a population's probability of occurrence and relative abundance given presence) across different land uses. Analyses were carried out in R 3.6.0 (R Core Team, 2019) using lme4 v.1.1.17 (Bates et al., 2015).

For both stages of modelling, we selected main effects and interactions using backwards stepwise variable selection, which uses maximum likelihood estimation to select terms and likelihood-ratio tests to compare the fit of different models (Zuur et al., 2009). Into this model selection, we added as potential explanatory variables: (1) land-use type (categorical variable); (2) geographic zone (categorical variable: tropical [between 23.44°S and 23.44°N] or temperate [between 23.44°N/S and 66.56°N/S, respectively]); (3) distance to range edge (continuous variable) and its interaction with land-use type; (4) climatic position with regard to each climatic variable (T_{max} , T_{min} , Pp_{max} and Pp_{min} position; continuous variables fitted as linear terms, we tested for correlations between these; Appendix S4, Table S4.5); and (5) the 2- and 3-way interactions between land-use type, geographic zone and each climatic position (e.g. land-use type \times geographic zone \times T_{max} position). We did not include interactions between climatic positions. A site's elevation was also considered as a continuous covariate due to its potential influence on population abundance (Williams

et al., 2010). For random effects, we included a nested random-intercept term for study (to account for study-dependent variation in methods or measures used) and for sampled site within studies. We also included a random-intercept term for species name, accounting for species-level differences unrelated to land-use type or climatic position. We then ran the final occurrence (assuming detection) and abundance (given presence) models, which included significant fixed effects and interaction terms, and any lower-order, non-significant interaction terms that were nested within significant higher-order interactions.

2.8 | Robustness checks

We also ran five separate sets of models (using the same structure as the final models above) that (1) only included species of mammals and birds (to ensure our results held for endothermic species, who may be less affected by local climatic changes), (2) excluded forest specialist species (to ensure our results held for species also found in naturally drier and/or open environments such as grasslands; forest specialist species were defined using species-level habitat preference data (IUCN, 2017); we acknowledge that forest specialism may differ across species' ranges, but unfortunately habitat preference data are currently not available at the population level; Appendix S8), (3) fitted climatic positions as quadratic terms (to test for hump-shaped relationships that might occur if populations are sensitive close to any climatic tolerance limit, rather than the specific limits we hypothesized), (4) combined mature and intermediate secondary vegetation land uses (to become an "advanced secondary" land-use type) and (5) again combined mature and intermediate secondary vegetation land uses but also removed populations within urban sites (to ensure the results were robust with and without the inclusion of land uses with a smaller number of sampled sites). Further, when working with complex datasets, results may potentially differ due to modeling method, so we ran our models using a range of optimizers (allFit function, lme4 package; Bates et al., 2015) to check the consistency of our results. We also ran a set of models (again with the same structure as the final models above) using a Bayesian modelling approach (MCMCglmm package; Hadfield, 2010); these models ran for 60,000 iterations and had a burn-in period of 3,000 iterations and a thinning interval of 10, and we used uninformative priors (the default priors in MCMCglmm), with convergence checked through visual inspection of the MCMC trace plots. Finally, responses to climatic position and land-use type may differ among species, so we ran a set of models including random slopes to account for interspecific differences (i.e. allowing the response of each species to climatic position or land-use type to vary).

2.9 | Severity of decline following land conversion

To highlight where vertebrate populations may experience more severe declines due to their climatic position and the local climatic

changes brought about by land-use change, we produced maps of estimated community-average abundance in cropland and pasture relative to that in primary vegetation, based on the climatic positions of populations within each community. We focused on agricultural land uses because the need to produce enough food to sustain Earth's growing population will likely result in agricultural expansion and intensification (Foley et al., 2011; Millennium Ecosystem Assessment, 2005). To do this, we used the available expert-informed terrestrial vertebrate species' distribution maps (BirdLife International, 2012; IUCN, 2016), processed them as described above and removed migratory bird species (BirdLife International, 2018). This left us with 22,267 species (5,074 mammals, 8,179 birds, 5,139 amphibians, 3,875 reptiles). For each species, we then produced maps of T_{\max} , T_{\min} , Pp_{\max} and Pp_{\min} (WorldClim Version 1.4; Hijmans et al., 2005) across their distribution and standardized them to between 0 and 1 in the same way as above. Then, using the main-effect and interaction estimates (Appendix S6, Table S6.7) from the final models (described above), we found the model-estimated probability of occurrence and abundance (given presence) of each species across their range, based on their climatic position, in primary vegetation (PV), cropland (Cr) and pasture (Pa). Following this, for each species, we multiplied the probability of occurrence ($P(\text{Occ})$) and the abundance (given presence; Ab) results together (separately for each land use) and then expressed this expected abundance in cropland and pasture relative to that in primary vegetation (i.e. relative abundance, RA; Equations (1) and (2), for relative abundance within cropland and pasture, respectively):

$$RA_{\text{Cr}} = \frac{P(\text{Occ})_{\text{Cr}} \times Ab_{\text{Cr}}}{P(\text{Occ})_{\text{PV}} \times Ab_{\text{PV}}} \quad (1)$$

$$RA_{\text{Pa}} = \frac{P(\text{Occ})_{\text{Pa}} \times Ab_{\text{Pa}}}{P(\text{Occ})_{\text{PV}} \times Ab_{\text{PV}}} \quad (2)$$

We then averaged and plotted the species-level results within each 10×10 km grid cell to display expected community-average severity of decline following conversion of primary vegetation to cropland or pasture, where the "community" included all the populations whose species' range covered that cell. This was completed in ArcGIS 10.4 (ESRI, 2015).

To ensure we did not extrapolate beyond the limits of our data, we found the predicted relative abundance within cropland and pasture for each population from the PREDICTS database included in our models (again using the main-effect and interaction estimates from our models). We then averaged these predicted values for populations in cropland or pasture within each PREDICTS site, producing site-level-average (i.e. community-average) relative abundances, and extracted the minimum and maximum site-level-average relative abundances for each land use. Finally, when producing the global maps described above showing the community-average severity of decline, we only plotted values that fell within these limits (only a very small proportion of the Earth's land surface was excluded in this way).

3 | RESULTS

3.1 | Summary

Overall, the relative abundance of a species across land uses differed depending on the populations' thermal position and Pp_{\min} position, with these effects differing between geographic zones (p -values from the backwards stepwise selection process for the interaction between land-use type, geographic zone and (a) T_{\max} position, $p_{P(\text{Occ})} = 0.012$, $p_{\text{LogAbund}} = 0.001$ (b) T_{\min} position, $p_{P(\text{Occ})} = 0.008$, $p_{\text{LogAbund}} = 0.186$ (the 3-way interaction was not significant, but the 2-way interaction between T_{\min} position and land use was, $p_{\text{LogAbund}} = 0.002$), (c) Pp_{\min} position, $p_{P(\text{Occ})} < 0.001$, $p_{\text{LogAbund}} < 0.001$; Figures 2 and 3, Table 2; for comprehensive plots for each climatic position, see Appendix S4, Figure S4.8–11; for coefficients and their 95% confidence intervals, see Appendix S9, Figure S9.20–21). The results supported our hypotheses with regard to thermal position, with populations in human-altered sites where temperature

extremes were closer to the species' maximum and minimum thermal limits generally having lower abundances relative to primary vegetation compared to populations that experience temperatures further from these tolerance limits (Figure 2). However, the precipitation position results were more mixed across land-use types (Figure 3), not always supporting our predictions. Large spatial differences in community-average severity of decline following agricultural conversion, when based on population's climatic positions, were also apparent in our global maps (Figure 4). Most of the observed results were driven by differences in populations' probability of occurrence, rather than by differences in the abundance of persisting species (Appendix S5, Figure S5.12–13). Due to the small number of urban sites in the dataset ($n_{\text{tropical}} = 41$, $n_{\text{temperate}} = 74$, from 2 and 3 studies, respectively), we exclude the results for this land-use type. We also advise caution when interpreting the results within temperate mature and intermediate secondary vegetation, as there were fewer than 50 sites sampled within these groupings (Appendix S4, Table S4.3).

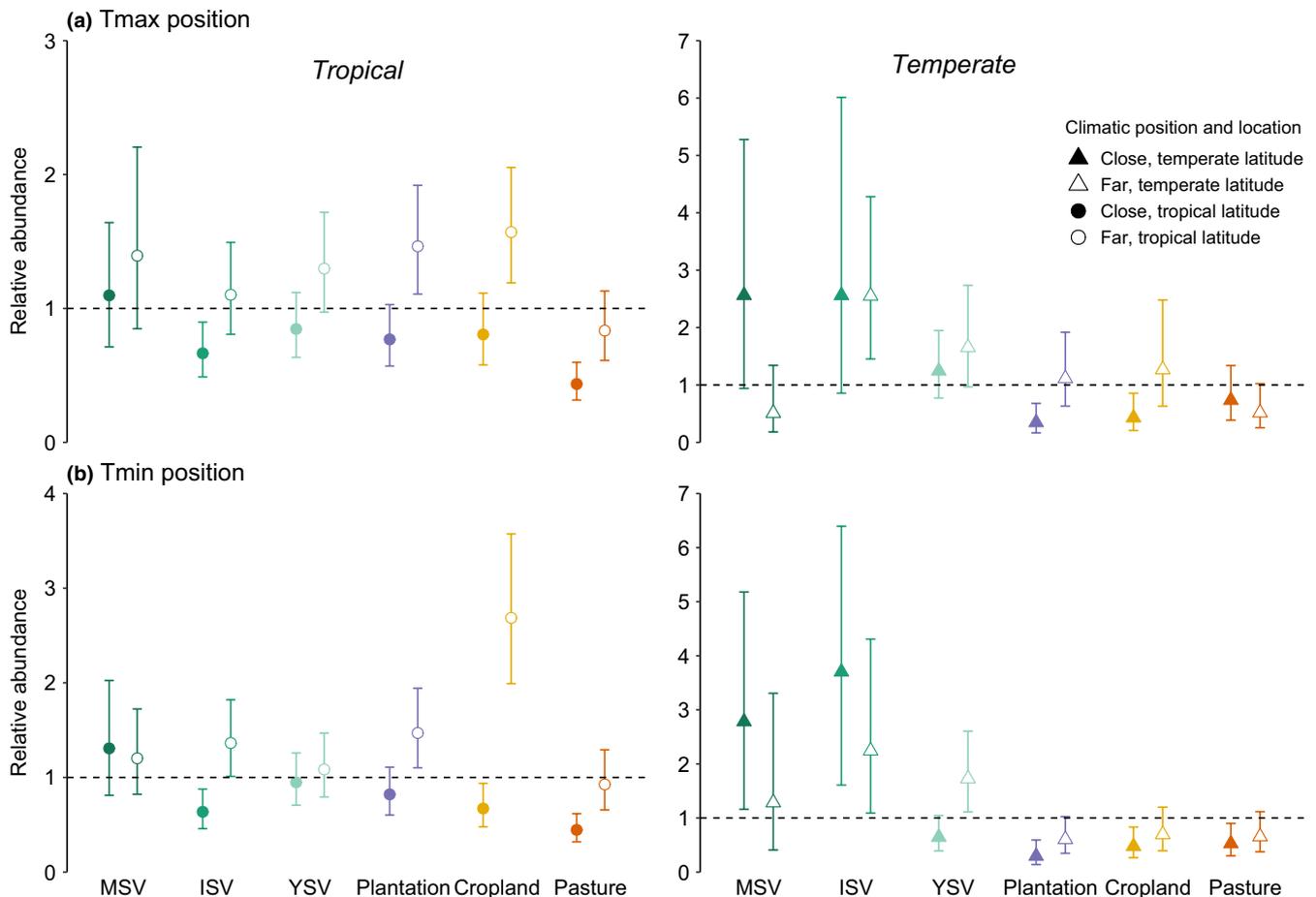


FIGURE 2 The abundance of species within each land-use type, relative to abundance in primary vegetation (indicated by the dotted line), for populations with T_{\max} or T_{\min} positions "close" or "far" from their thermal tolerance limits at tropical and temperate latitudes. For (a), a population's T_{\max} position, "close" and "far" refer to a position of 0.9 and 0.7, respectively, for both tropical and temperate latitudes. For (b), a population's T_{\min} position, "close" and "far" refer to a position of 0.2 and 0.6 at tropical latitudes, and 0.1 and 0.4 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of T_{\max} or T_{\min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ± 1 standard error. MSV, ISV and YSV stand for mature, intermediate and young secondary vegetation, respectively

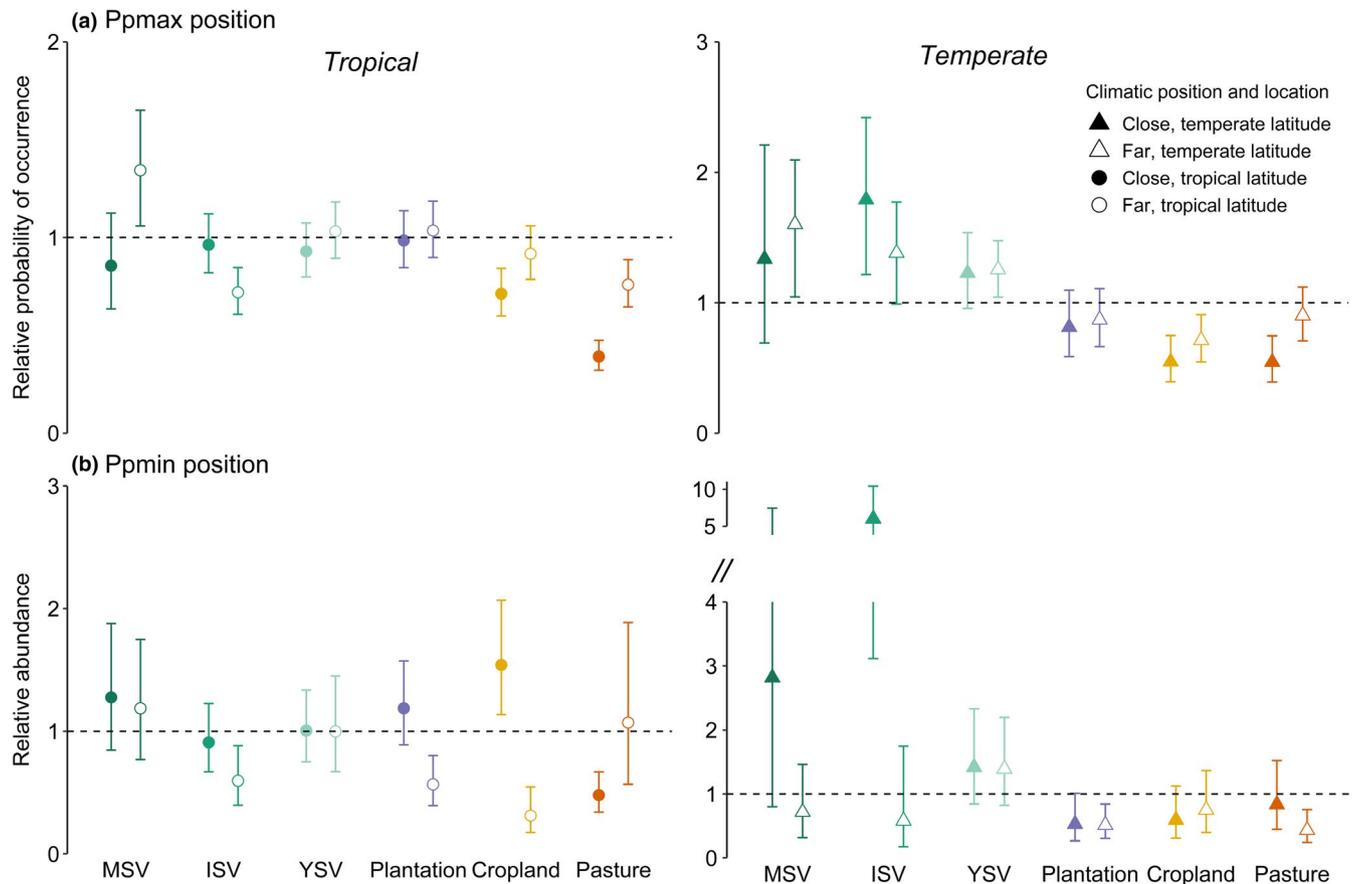


FIGURE 3 The (a) probability of occurrence or (b) abundance of species within each land-use type, relative to that in primary vegetation (indicated by the dotted line), for populations with (a) Pp_{\max} or (b) Pp_{\min} positions “close” or “far” from their precipitation tolerance limits at tropical and temperate latitudes. For (a), a population’s Pp_{\max} position, “close” and “far” refer to a position of 0.6 and 0.2 at tropical latitudes, and 0.4 and 0.1 at temperate latitudes, respectively. For (b), a population’s Pp_{\min} position, “close” and “far” refer to a position of 0 and 0.2 at tropical latitudes, and 0 and 0.1 at temperate latitudes, respectively. These positions reflect the 10th and 90th percentile of Pp_{\max} or Pp_{\min} positions (calculated separately within tropical and temperate latitudes). Error bars denote ± 1 standard error. MSV, ISV and YSV stand for mature, intermediate and young secondary vegetation, respectively. We plot relative probability of occurrence (rather than relative abundance) for Pp_{\max} positions because a population’s Pp_{\max} position was not found to have a significant effect on abundance, and so was not included in the final abundance (given presence) model. We use a broken y-axis (represented by //) on the plot for Pp_{\min} position at temperate latitudes so that the smaller effect sizes can be more easily interpreted

3.2 | Thermal position

At tropical latitudes, in most human-altered land uses, populations with high T_{\max} positions or low T_{\min} positions (thus in sites where they experience temperature extremes closer to their maximum or minimum thermal limits, respectively) had much lower abundances relative to those in primary vegetation (by 25%–50%), than populations in sites with temperatures further from their thermal limits (Figure 2). This filtering out of populations close to their thermal limits was not seen in mature secondary vegetation, where abundances showed little difference relative to primary vegetation. Interestingly, within tropical plantations and croplands, populations further from their thermal limits had higher abundances relative to populations with the same T_{\max} or T_{\min} position in primary vegetation.

At temperate latitudes, populations with high T_{\max} positions again had lower relative abundances in plantations and croplands, and those with low T_{\min} positions had lower relative abundances in

plantations, croplands and young secondary vegetation (Figure 2), compared to populations further from their thermal limits.

3.3 | Precipitation position

A population’s Pp_{\max} position was not found to influence abundance (given presence), but did effect their probability of occurrence at a site, which also differed across land uses (land-use type $\times Pp_{\max}$ position, $p_{\text{P(Occ)}} < 0.001$, Figure 3). Populations experiencing maximum monthly precipitation closer to their maximum precipitation limit (higher Pp_{\max} positions) had a lower relative probability of occurrence in croplands and pastures than populations with lower Pp_{\max} positions.

Contrary to expectations, in many human-altered land uses, and particularly at tropical latitudes, populations with lower Pp_{\min} positions (in sites with minimum monthly precipitation closer to their

TABLE 2 The final probability of occurrence ($P(\text{Occ})$) and abundance (given presence; LogAbund) model structures and the significance (p -values) of the climatic position \times land use type interaction terms included in the models (i.e. whether the slope of the relationship of probability of occurrence or abundance—given presence—with climatic position for a given land use was significantly different to the slope for primary vegetation). These final models were used to investigate the influence of climatic position with regard to maximum temperature of the warmest month (T_{max}), minimum temperature of the coldest month (T_{min}) and precipitation of the wettest (Pp_{max}) and driest (Pp_{min}) months, on a population's probability of occurrence, or abundance (given presence) across different land-use types (LU; these included primary vegetation, different stages of secondary vegetation (mature, intermediate and young; MSV, ISV and YSV respectively), plantations, croplands, pastures and urban areas) at tropical and temperate latitudes (geographic zone; GZ). Distance to range edge (Dist) was also added as a covariate. In terms of random effects, a nested random-intercept term for study (SS; to account for study-dependent variation in methods or measures used) and for sampled site within studies (SSBS) was included in all models, along with a random-intercept term for species name (Species). Statisticians advise caution when interpreting p -values from mixed-effects models (Bates et al., 2015; Luke, 2015)

Model structure	Probability of occurrence model							Abundance (given presence) model											
	$P(\text{Occ}) \sim \text{Intercept} + \text{LU} + \text{GZ} + T_{\text{max}} + T_{\text{min}} + Pp_{\text{min}} + Pp_{\text{max}} + \text{Dist} + \text{LU} \times \text{GZ} + \text{LU} \times \text{Dist} + \text{LU} \times T_{\text{max}} + \text{LU} \times T_{\text{min}} + \text{LU} \times Pp_{\text{max}} + \text{LU} \times Pp_{\text{min}} + T_{\text{max}} \times \text{GZ} + T_{\text{min}} \times \text{GZ} + Pp_{\text{max}} \times \text{GZ} + Pp_{\text{min}} \times \text{GZ} + \text{LU} \times T_{\text{max}} \times \text{GZ} + \text{LU} \times T_{\text{min}} \times \text{GZ} + \text{LU} \times Pp_{\text{min}} \times \text{GZ} + (1 \text{SS}) + (1 \text{SSBS}) + (1 \text{Species})$							$\text{LogAbund} \sim \text{Intercept} + \text{LU} + \text{GZ} + T_{\text{max}} + T_{\text{min}} + Pp_{\text{min}} + \text{Dist} + \text{LU} \times \text{GZ} + \text{LU} \times T_{\text{max}} + \text{LU} \times T_{\text{min}} + \text{LU} \times Pp_{\text{min}} + \text{GZ} \times T_{\text{max}} + \text{GZ} \times Pp_{\text{min}} + \text{LU} \times T_{\text{max}} \times \text{GZ} + \text{LU} \times Pp_{\text{min}} \times \text{GZ} + (1 \text{SS}) + (1 \text{SSBS}) + (1 \text{Species})$											
Significance of key terms [†]																			
Tropical latitudes	MSV	ISV	YSV	Plantation	Cropland	Pasture	MSV	ISV	YSV	Plantation	Cropland	Pasture	MSV	ISV	YSV	Plantation	Cropland	Pasture	
T_{max}		***	*	***	***	***													
T_{min}		***			***	**			*	*	*								
Pp_{max}		*			*	***													
Pp_{min}		*		**	***					*									
Temperate latitudes	MSV	ISV	YSV	Plantation	Cropland	Pasture	MSV	ISV	YSV	Plantation	Cropland	Pasture	MSV	ISV	YSV	Plantation	Cropland	Pasture	
T_{max}			*							*									
T_{min}			***																
Pp_{max}																			
Pp_{min}																			

[†]Hashed = interaction term was not included in this model, * = $p < .05$, ** = $p < .01$, *** = $p < .001$.

dry limit), had similar abundances to those in primary vegetation, whereas populations further from their dry limit had lower relative abundances. Different patterns were observed in tropical pastures, where populations with lower Pp_{min} positions were being filtered out (i.e. had lower relative abundances compared to populations with higher Pp_{min} positions). Within temperate plantations and croplands, there was little difference in relative abundances across Pp_{min} positions.

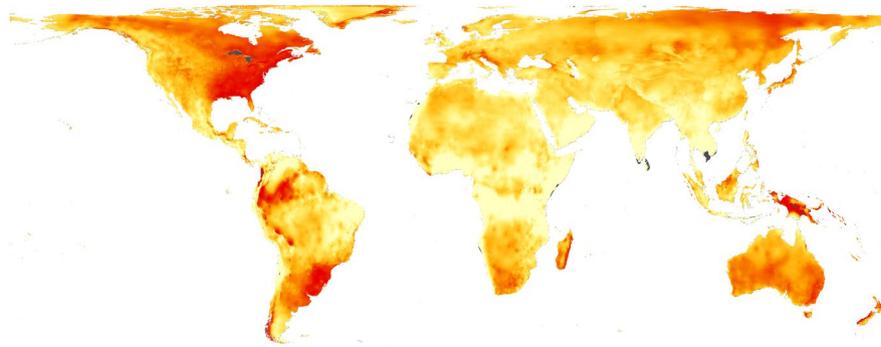
3.4 | Robustness checks

We used GBIF data to estimate realized climatic tolerance limits for 1,995 species (84,988 populations) included in our models. The climatic positions produced using these tolerance limits were moderately to strongly positively correlated to those using expert-informed species' distribution maps ($r > 0.67$; Appendix S2, Table S2.2). The results of the models run using these climatic positions (rather than those found using species' distribution maps) were qualitatively identical to the results presented above, but abundances within some land uses (such as mature secondary vegetation, croplands, and pastures) relative to primary vegetation differed slightly (Appendix S2, Figure S2.1–2).

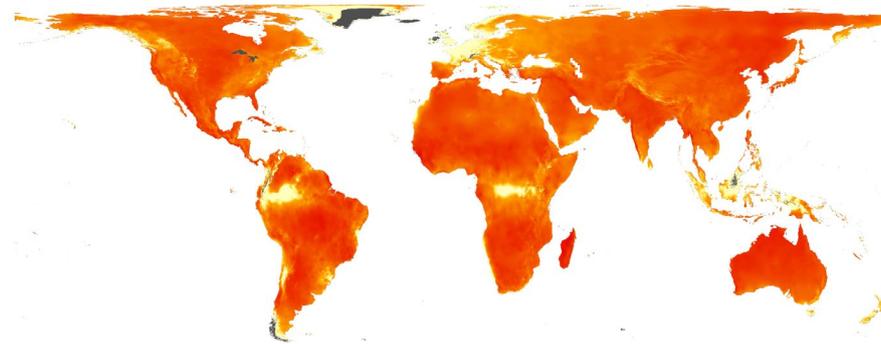
Only 76 species included in our models had estimates of physiological thermal tolerance limits within GlobTherm (Bennett et al., 2018). Four of these were estimates of critical thermal maxima and minima, 71 were estimates of thermal neutral zone boundaries, and one was an estimate of the lethal temperatures at which mortality of 50% or 100% of individuals occur. The measures of thermal position calculated using our estimates of realized thermal tolerance limits and using estimates of physiological thermal tolerance limits from GlobTherm were positively correlated (Pearson's correlation coefficient, T_{max} position, $r = 0.62$, T_{min} position, $r = 0.50$).

A population's relative abundance differed with their proximity to the species' range edge (Appendix S4, Figure S4.7), which further interacted with land use to impact a population's probability of occurrence ($p = 0.003$). When comparing models excluding this distance to range edge measure that included or excluded populations recorded outside of their species' distributions, as stated by the IUCN (2016) and BirdLife International (2012), the main qualitative results were very similar (Appendix S3, Figure S3.3–6). The only exception to the robustness of our results to including and excluding populations outside of their stated range maps was the relationship between Pp_{min} and relative abundance within tropical pastures. In this case, when populations outside of their stated ranges were included, the pattern now matched that seen within cropland and

(a) Cropland



(b) Pasture



Average severity of decline

Low High

FIGURE 4 The average severity of decline of terrestrial vertebrate communities following conversion of natural habitat to (a) cropland and (b) pasture, based on the climatic positions of populations within each community. We estimated severity of decline by calculating the abundance of populations in (a) croplands and (b) pastures, relative to that in primary vegetation (depending on each population's climatic position) and averaged this within each community (10×10 km pixel). We present global maps (Behrmann projection) to demonstrate how the potential severity of decline within communities may differ due to the local climatic changes following land-use change, while recognizing that land conversion from primary vegetation to agriculture is not possible, or has already happened, for large parts of the world (although these maps could also be useful in highlighting areas in which habitat restoration may be more beneficial, based on the climatic positions of the local populations). Dark grey areas represent locations that were not covered by any of the species' ranges in our dataset (some of the Great Lakes in North America, for example), or where community-average measures were beyond the limits of our dataset (see methods). The scale of severity is separate for each map, based on the limits of community-average abundances within each land-use type, relative to expected abundances within primary vegetation. For cropland and pasture, respectively, the deepest red (greatest average severity of decline) represents community-average relative abundances of 0.13 and 0.07 (to 2 decimal places), the lightest yellow (lowest average severity of decline) represents community-average relative abundances of above 2 and up to 1.61, and the middle colour of orange represents a community-average relative abundance of 1. Relative probability of occurrence patterns were similar, but for croplands patterns were generally more negative (Appendix S6, Figure S6.15). We also produced maps displaying the percentage of populations in each community with abundances in croplands and pastures predicted to be half or less than that in primary vegetation, based on populations' climatic positions (Appendix S6, Figure S6.14)

plantations (where populations with higher Pp_{\min} positions had lower relative abundances than those with lower Pp_{\min} positions). The majority of populations that were recorded outside of their species' distributions were relatively close to their range edges (with a median distance of 16.3 km, and with 75% of populations outside their ranges being within 71 km). Populations recorded furthest from their stated range edges, upon inspection, were found to be populations of species invasive to the recorded location.

The results of models only including endotherms or excluding forest specialists (Appendix S7-S8, Figure S7.16-17,

Figure S8.18-19) were very similar to those presented above. Fitting climatic positions as quadratic terms did not change the pattern of results. Further, including different combinations of land uses, using different optimizers (results not shown) or using Bayesian modelling (Appendix S9, Figure S9.20-21) all produced very similar results to those reported above. Finally, models including random-slope terms produced similar results to the models above (Appendix S10, Figure S10.22-24); we report the results from the random-intercept model here because of convergence issues with the random-slope models.

3.5 | Severity of decline following land conversion

Community-average severity of decline following conversion to agricultural land uses, based on populations' climatic positions, differed greatly across space (Figure 4). Communities expected to experience the most severe declines following conversion to cropland, due to the climatic positions of the populations present, appeared in north eastern North America, south eastern South America, Australia, and New Guinea. Conversely, the average severity of decline within communities across equatorial Africa and southeast mainland Asia appeared to be lower, which may be a result of local climatic changes following land-use change producing more favourable conditions (which could lead to population increases). Following conversion to pasture, communities in central North and South America, Australia, western Africa, and northeast Asia may experience the most severe declines, whereas equatorial Africa and parts of Europe were predicted not to experience such severe declines, based on the climatic positions of the populations present. As stated above, these maps are not displaying which areas *will* see abundance decreases or increases following land-use change, but instead present locations where the potential average severity of declines within communities *may* be higher or lower following conversion of natural habitat to agricultural land uses due to how close the local climatic conditions are to the realized climatic tolerance limits of the populations present. These maps can also be viewed as highlighting areas within which habitat restoration may be particularly effective, on the basis of the local populations' climatic positions.

4 | DISCUSSION

Populations' thermal positions strongly influenced abundance across land-use types, with stronger effects often observed at tropical latitudes. As predicted, human-altered land uses generally appeared to be filtering out populations experiencing temperature extremes close to their maximum or minimum thermal limit. Populations experiencing maximum monthly precipitation closer to their wet limit also had a lower probability of occurrence in human-altered land uses, in line with our predictions. However, the influences of climatic position regarding minimum monthly precipitation were more complex and did not consistently support our hypothesis. We also demonstrate how our results can be used to highlight communities that may experience more severe declines following habitat conversion due to the climatic positions of the populations present. Consequently, this study emphasizes how species' responses to human-altered land uses can differ significantly across their distributions, which is essential to account for when assessing risk, predicting future changes, and mitigating negative impacts from global drivers of change.

In general, agricultural land (plantations, croplands, and pastures) filtered out populations where maximum temperatures were close to species-level maximum thermal limits and populations at sites with minimum temperatures close to species-level minimum thermal limits. Conversion from a natural to human-altered land use

usually leads to hotter and colder local temperature extremes (De Frenne et al., 2019). For populations closer to their thermal limits, these climatic changes may push ambient temperatures beyond species' tolerance limits, directly impacting individuals (Frishkoff et al., 2016). Heat or cold stress can cause population decline because they can negatively impact processes such as reproduction (Manning & Bronson, 1990) and development (Russell et al., 2002), or lead to death (Welbergen et al., 2008). Temperature changes can also directly impact individual's metabolic rates (through effects on biochemical reaction rates; Gillooly et al., 2001), influencing energy use and, consequently, the demand for food and allocation of energy resources (Barneche et al., 2019; Dillon et al., 2010). For species relying on behavioural rather than physiological adaptations to cope with unfavourable temperatures, population declines could result from loss of thermal refugia following land-use change (Betts et al., 2018; Sunday et al., 2014). Populations closer to their thermal limits would be the most negatively impacted if individuals could no longer use refugia to escape thermal extremes. There were also geographical differences in the effect of thermal position on relative abundance within human-altered land uses. For instance, differences in relative abundance between populations with different climatic positions were greater at tropical compared to temperate latitudes; this is consistent with previous work suggesting species at lower latitudes are more sensitive to temperature changes due to the past stability of the tropical climate (Janzen, 1967). Interestingly, in tropical plantations and croplands, populations experiencing thermal extremes further from their thermal limits had higher abundances compared to populations at the same thermal position in primary vegetation. This could be due to the local climatic conditions within these human-altered land uses being more favourable for species found within the region than conditions within primary vegetation. Similar scenarios have been observed along elevational gradients, whereby localized warmer maximum temperatures following deforestation has facilitated the invasion of these areas by species from lower elevations (leading to these populations having higher abundances within human-modified land uses compared to nearby primary vegetation; Frishkoff et al., 2019).

Unexpectedly, populations at sites where minimum monthly precipitation was closer to species-level dry limits often had similar or higher relative abundances than populations further from this limit, particularly in tropical plantations and croplands. For 79% of populations with Pp_{\min} position values of 0 (i.e. in sites where they experience the lowest monthly precipitation of anywhere in the species' distribution), the absolute precipitation tolerance limit was zero (i.e. no rainfall in the driest month). Thus, we propose our results may be due to these populations already experiencing very low rainfall levels in their natural habitats, meaning they may have behavioural strategies to cope with droughts. Consequently, these populations that are already tolerant of very dry conditions (compared to those further from their dry limits) may be better at coping with, or less negatively impacted than expected by local climatic changes following conversion from natural to human-altered land uses. Additionally, the magnitude of change in minimum precipitation with land-use change may

be smaller in such dry areas, because although drought duration may increase, you cannot get less rainfall in the driest month if the minimum is already zero. However, we acknowledge that our minimum precipitation position measure cannot distinguish between populations that experience a single month versus multiple months of no rain. Therefore, complementary work using temporal data is needed to look at the impacts of land-use change on minimum precipitation in drier areas, and the variation in how local populations react to these changes.

Overall, the influence of a population's precipitation position was complex. As well as the unexpected results regarding Pp_{\min} position, a population's Pp_{\max} position was found to influence a population's probability of occurrence, but not their abundance if they were present. Previous work has highlighted the complexity of precipitation regime changes on biodiversity, partly due to its complex interactions with other abiotic (e.g. moisture) and biotic (e.g. plant growth) factors in the environment, making detecting the underlying mechanisms difficult (Brown et al., 2001; Fu et al., 2003; Williams & Newbold, 2020). For example, changes in the distribution of precipitation (timing and/or severity) impact soil water content, which can substantially affect plants and their processes (see Zeppel et al., 2014), but whether these effects are positive or negative depends (at least partly) on the initial climatic conditions, such as aridity and the season the changes occur in (Morecroft et al., 2004; Zeppel et al., 2014). These complicated impacts on vegetation likely have knock-on effects for local vertebrates and may act alongside or interact with the direct impacts of local water or moisture availability changes (Brown et al., 2001). Another complication of investigating the effects of local precipitation changes is that irrigation systems are often used within human-altered land uses, impacting water vapour concentration (Boucher et al., 2004). These artificial water systems may alter how populations are affected by local climatic changes. Consequently, although our results provide a start to exploring the impact of precipitation position on responses to human-altered land uses, due to the complexity of rainfall regimes, moisture availability, and human impact (through land-use change and irrigation), alternative methods using different precipitation measures are needed to explore the influence of precipitation changes and the mechanisms underlying its impact on vertebrate populations further. Ideally, biologically meaningful measures of moisture availability (at species-specific spatial scales) would be used with site-specific irrigation considered, but data on both are rare.

Secondary vegetation is suggested to be important in biodiversity conservation, potentially providing refugia from certain threats, such as global climatic changes (Dent & Wright, 2009; Senior et al., 2017). Generally, we find only mature secondary vegetation has the potential to provide thermal refugia, particularly at tropical latitudes. The inability of tropical earlier-stage secondary vegetation to provide refugia for populations close to their thermal tolerance limits is concerning, especially as thermal refugia are becoming increasingly important as land-use changes continue alongside global climate change, pushing temperatures

even higher (Collins et al., 2013; Frishkoff et al., 2016; Jarzyna et al., 2016).

Our results suggest the impacts of land use on vertebrate populations vary spatially, with the effect of temperature and precipitation changes differing with land use and latitude. For example, focusing on plantations, croplands, and pastures, it appears that while T_{\max} positions may have large impacts globally on how populations are impacted by these land uses, T_{\min} position has a greater impact on variation between populations at tropical compared to temperate latitudes. While we recognize land conversion from natural habitat to agriculture has already occurred or is not possible across large expanses of the Earth's terrestrial surface, we show that the potential severity of decline following land-use change likely differs greatly across space, depending on populations' climatic positions. We also observed that this spatial variation differed between conversion to cropland versus pasture, which may be due to the differences observed in the impact of a population's Pp_{\min} position within these two land uses (see Figure 3). This variation is critical to account for as we predict how vertebrate populations might react to future land-use changes. Further research is needed into the mechanisms underlying how local climatic changes impact populations with different climatic positions, which will help to refine these maps. Within our model, we had a larger number of sites at tropical compared to temperate latitudes (Appendix S4, Table S4.3), and gathering more data for sites within temperate latitudes may also help to refine results across this area. Our maps display estimates of mean potential severity of decline across the populations present in each cell, due to their climatic position, and do not make predictions of absolute abundance, which would require inclusion of other factors influencing species' responses to land-use change, such as biotic interactions and habitat preferences.

Overlaying climatic data on species' distribution maps to estimate species' realized climatic tolerance limits allowed us to include over 2,000 species within our models and study the impacts of temperature and precipitation positions across geographic zones. Using species' distribution or occurrence data with climatic data to calculate climatic affiliations has been widely used, especially when studying species' responses to land-use or global climate change (e.g. Barnagaud et al., 2012, 2013; Frishkoff et al., 2016; Oliver et al., 2017). Nevertheless, we acknowledge that by using global climate data, we do not account for the microclimates species experience or potential intraspecific variation in climatic tolerances. Furthermore, species' observed distributions are also influenced by biotic interactions and barriers to dispersal (HilleRisLambers et al., 2013; Peterson et al., 2011). Consequently, our approach, which estimates realized climatic tolerance limits, may not precisely reflect species' physiological tolerances. Unfortunately, estimates of physiological thermal limits are only available (or obtainable) for a very small number of vertebrate species (Araújo et al., 2013), and estimates of physiological precipitation or moisture tolerance limits are rare (Sunday et al., 2012). Even if they were available, physiological climatic tolerance limits estimated under laboratory settings also have limitations (see Williams & Newbold, 2020). Therefore,

we consider our approach to be the best with the data currently available. Lastly, we acknowledge that our approach is correlative, so there may be other factors underlying the differences in relative abundance across climatic positions between land uses, and, as previously mentioned, further work is needed to ascertain the underlying mechanisms.

In conclusion, our results suggest that the proximity of temperature extremes to species-level thermal limits affects the relative abundance of vertebrate populations across human-altered land uses, with populations in sites where temperature extremes are closer to their maximum or minimum thermal limit being filtered out of most human-altered land uses. Proximity to minimum and maximum monthly precipitation extremes was also found to influence species' relative abundance and probability of occurrence, respectively, in human-altered land uses. These results are likely due, at least in part, to the local climatic changes following land-use change directly and/or indirectly impacting vertebrate populations. Overall, we highlight variation in responses to human-altered land uses across a species' range, depending on population's climatic positions. This variation has important implications when assessing risk from land-use pressures, exploring interactions between environmental pressures, and producing conservation or management plans.

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13282>.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.sj3tx964n>) and code on a public GitHub repository (<https://github.com/JJWilliams24/Vertebrate-responses-to-human-land-use-are-influenced-by-their-proximity-to-climatic-tolerance-limit>). The original PREDICTS database can be downloaded from <https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database>. The WorldClim Version 1.4 climatic variable maps can be downloaded from <http://www.worldclim.com/version1>. Species distribution maps can be downloaded or requested from <https://www.iucnredlist.org/resources/spatial-data-download> and <http://datazone.birdlife.org/species/requestdis>, respectively.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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