Species-level correlates of land-use responses and climate-change sensitivity in terrestrial vertebrates

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Terrestrial vertebrates with narrow ranges and high habitat specialization are most sensitive to human land use and climate change.

Abstract

Land-use and climate change are two major pressures on terrestrial biodiversity. Species' extinction risk and responses to human pressures have been shown to relate to ecological traits and other characteristics in some clades. However, we lack large-scale comparative assessments of the associations between traits and responses to multiple human pressures, across multiple clades. Here, we investigated whether a set of ecological characteristics that are commonly measured across terrestrial vertebrates (ecological traits and geographical range area) are associated with: (1) species' responses to different land-use types; and (2) species' likely sensitivity to climate change

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(based on properties of their realized climatic niche). Our aim was to test whether generalisable patterns in response to these pressures arise across both pressures and across vertebrate clades, which could help to assess the global signature of human pressures on vertebrate biodiversity, and to guide conservation efforts. Among the characteristics we considered, only three were consistently associated with strong land-use responses and high climate-change sensitivity across terrestrial vertebrate classes: narrow geographical range area, narrow habitat breadth and specialisation on natural habitats. The associations of other traits with species' land-use responses and with climate-change sensitivity often depended on class and land-use type, highlighting an important degree of context dependency. In all classes, invertebrate eaters and fruit/nectar eaters tended to be negatively affected in disturbed land uses, while invertebrate- and plant/seed-eating birds were estimated to be more sensitive to climate change, raising concerns about the continuation of ecological processes sustained by these species under global changes. Our work highlights a consistently higher sensitivity for narrowly distributed species and habitat specialists under land-use and climate change, which provides support for capturing such characteristics in large-scale vulnerability assessments.

Introduction

Land-use change is currently an important driver of biodiversity loss (Maxwell, et al., 2016), and is likely to cause further losses in coming decades (Li et al., 2022; Newbold et al., 2015; Powers & Jetz, 2019; Stehfest et al., 2019). However, biodiversity faces multiple pressures acting in combination. The impacts of climate change on biodiversity are projected to equate or surpass those of land-use change in their magnitude by 2070 (Newbold, 2018). Thus, understanding how different species respond to both these pressures is important to inform conservation in the face of global change.

It is well established that species differ in their ability to cope with environmental changes (Chichorro et al., 2022; Ferreira et al., 2022; Matich & Schalk, 2019; Newbold et al., 2013). Global average declines in biodiversity indices mask substantial interspecific variation in responses to environmental changes (Leung et al., 2020), which has important consequences for the prioritization of conservation efforts (Morelli et al., 2021). Mitigating land-use and climate change impacts on the world's biota requires an understanding of which species are at most risk from these pressures.

By capturing key aspects of species morphology, life-history, ecological strategies or demography, traits can inform on species use of resources and space, as well as on community and population-level processes (Capdevila et al., 2022). Previous studies have shown that species traits and properties of species range area are associated with extinction risk (Chichorro et al., 2019; Lucas et al., 2019), and with responses to human pressures, in particular land use (Newbold et al., 2013; Nowakowski et al., 2017; Tinoco et al., 2018) and climate change (Angert et al., 2011; Di Marco et al., 2021; Estrada et al. 2018; MacLean & Beissinger, 2017; Mccain & King, 2014; Pacifici et al., 2017; Pearson et al., 2014; Schloss et al., 2012).

In a meta-analytic study, Chichorro et al. (2019) highlighted significant associations between species geographical range size (not a trait in the strict sense, but an important characteristic to account for), habitat breadth, and extinction risk across a range of taxa (including terrestrial vertebrates), while other traits had inconsistent effects. Chichorro et al. (2022) further tested the universality of traits as predictors of extinction risk across a range of terrestrial taxa, highlighting both general patterns and idiosyncrasies in the associations between extinction risk and traits. Chichorro et al. (2022) proposed habitat breadth as a universal predictor of extinction risk across taxa, life-history traits (e.g., generation length, fecundity, and offspring size) as candidate universal predictors (warranting further research), while other traits, such as body size, as only useful to predict extinction risks within specific taxonomic groups. Thus, while geographical range area and habitat specialism emerge as consistent correlates of extinction risk, no consensus has been reached for other traits, tending to show context-dependent associations with responses to human disturbance. However, as underlined by Chichorro et al. (2019), focusing on extinction risk precludes an explicit consideration of the pressures to which the species were exposed. Some traits are associated with opposite responses depending on the pressure considered (Gonzalez-Suarez et al., 2013). Further, past work on specific pressures has mostly been conducted at local to regional scales (Davison et al., 2021; Hevia et al., 2017). In addition, previous studies have often been restricted in their taxonomic coverage, with few studies considering several vertebrate classes together, so that comparative investigations among vertebrate classes remain rare. Thus, it remains unclear whether the effects of traits on vertebrate responses to environmental change can be generalised across vertebrate taxa, regions, and types of pressure. Past work has for instance shown that longer-lived, larger tropical forest specialist birds are more sensitive to land-use change than shorter-lived, smaller, habitat generalists (Newbold et al., 2013); and that larger range sizes and larger diet breadth are associated with larger shifts in ranges in North-American Passeriformes under recent climate change (Angert et al., 2011).

Here, we investigate whether general patterns emerge in the associations between terrestrial vertebrates' ecological characteristics (Table 1: ecological traits plus geographical range area) and: (1) species' responses to land use; and (2) expected climate-change sensitivity. We compare responses across vertebrate classes and across the two pressures. We include species geographical range area in our analysis, as it is an important correlate of species' responses to land use (Newbold et al., 2018) and climate change (Thuiller et al., 2005), and also because it has emerged as a predictor of species' extinction risk (Chichorro et al., 2022). Range area may further correlate with other aspects of species' ecology that we could not consider here because of limited data availability, such as dispersal ability (Capurucho et al., 2020). Since geographical range area does not meet the strict definition of a trait (a property measurable at the level of individual organisms), we henceforth refer to all traits and range area as "ecological characteristics". We ask the following questions: (1) Are ecological characteristics associated with interspecific variation in responses to land use and with expected climate-change sensitivity? And are these associations similar across classes and pressure types?

Among the characteristics we consider (Table 1), some may directly influence species survival by mediating resource acquisition and use. These characteristics are body mass, diet, and diet breadth. Other characteristics (e.g., lifespan and litter/clutch size) may indirectly affect species persistence over time by influencing species reproductive output and demographic processes (Capdevila et al., 2022). Finally, responses to human pressures are known to depend on degree of specialisation, which we capture with characteristics reflecting specialisation in time (i.e., diel activity) and use of space (e.g., habitat breadth and geographical range area). From past research (Chichorro et al., 2019, 2022), we hypothesize that narrow geographical range area, narrow habitat breadth and specialism on natural habitats are consistently associated with more negative land-use responses and higher climate-change sensitivity. We also expect longer lifespans, smaller litter/clutch sizes, and more specialised diets (e.g., smaller diet breadth) to be associated with more negative land-use responses and higher climate-change sensitivity. For the remaining ecological characteristics (body mass and diel activity patterns), making predictions is complicated by the fact that past research has been inconclusive or has highlighted important context specificity. For these characteristics, we investigate whether we can identify commonalities in the associations with human pressures across terrestrial vertebrate taxa (see Table 1).

Given the different nature of the threats we consider and the differing data and methods available to quantify sensitivity to these threats, we use two independent approaches to estimate sensitivity to land use and to climate change. Therefore, we are not able to consider interactive effects between the pressures. To infer species' land-use responses, we use a space-for-time substitution approach, modelling occurrence probability across different land-use types. We estimate species' expected sensitivity to future climate change from properties of species realized climatic niches.

Niche properties have been shown to be strong indicators of species' climate-change sensitivity (Thuiller et al., 2005), and are also straightforward to use at large scales given the availability of species distribution data. We then bring together the results of both approaches to identify any consistent associations between species ecological characteristics and their land-use responses or climate-change sensitivity.

Methods

Ecological characteristics

Traits

We obtained the following traits from Etard et al. (2020): body size; a proxy for species lifespan; litter/ clutch size; diel activity; habitat breadth; and use of/preference for artificial habitats (Table 1). We chose these traits because they were available across vertebrate classes, at least for a subset of species, allowing for a comparative assessment (Figure S1); and because they relate to species life-history, ecology, and resource use, such that they might influence species land-use responses and climatic niche properties (and thus expected climate-change sensitivity). Intraspecific trait variation has important effects on ecological systems (Bolnick et al. 2011; Des Roches et al. 2018), and can notably buffer against extinction under threatening processes (González-Suárez and Revilla, 2012) However, as multiple measurements do not exist for many vertebrate species, we couldn't capture intraspecific variation in trait values, so we used species-level mean values for all traits (Etard et al., 2020).

We enhanced these data with species-level estimates of diet (lacking in Etard et al. (2020)). Diet is likely important for understanding species sensitivity to environmental change (Curtis et al., 2021; Newbold et al., 2013). For birds and mammals, we collected estimates of species primary diet (i.e., the diet category representing the combination of food items totalling more than 50% of species' consumption), from the EltonTraits database (Wilman et al., 2014). For amphibians and reptiles, obtaining species "primary" diet was not possible, as there were no data available on the relative consumption of different food items. For amphibians, the AmphiBIO database (Oliveira et al., 2017) provided information on species consumption of different food items (just in terms of presence/absence in the diet, but without estimation of their percent use), so we inferred diet on the basis of these reported food items (however the coverage was low, with more than 75% of the species missing information; Figure S1(a)). For reptiles, there was no available data collection describing diet. For both reptiles and amphibians, we supplemented the existing datasets by collecting data on species consumption from published sources (recording the presence/absence of different food items consumed by species), for an additional 108 amphibians (available at https://doi.org/10.6084/m9.figshare.12024312.v4) and for 239 reptiles (available at https://doi.org/10.6084/m9.figshare.12024309.v1). See S2, "Compiling diet information" for more information and for data sources.

We standardised diet information across the vertebrate classes, by grouping species into five different categories: vertebrate eaters; invertebrate eaters; plant/seed eaters; fruit/nectar eaters; and omnivores. We calculated species diet breadth – the total number of recorded food groups (invertebrate, vertebrate, plant, seed, nectar, or fruit) known to be consumed by a species.

Species distributions

We downloaded all available distribution maps from BirdLife International for birds, from the IUCN Red List for terrestrial mammals and amphibians (IUCN, 2020), and from Roll et al. (2017) for reptiles (downloaded April 2020). We excluded areas occupied during non-breeding seasons and areas falling outside species known elevational limits (following Etard et al. (2020)). We estimated species geographical range areas using a resolution of 1 × 1 km with a Behrmann equal-area projection.

Phylogenies

Class-specific phylogenetic trees were downloaded in April 2020 from https://zenodo.org/record/3690867#.Xyc5wyhKhPZ for mammals (Phylacine 1.2; Faurby *et al.* (2018, 2020)); and from https://data.vertlife.org/ for amphibians (Walter Jetz & Pyron, 2018), birds (W. Jetz et al., 2012) and squamates (Tonini et al., 2016). For each class, we used a consensus tree obtained with the TreeAnnotator programme of the BEAST software (Bouckaert et al., 2014), from an available distribution of 1000 trees.

Imputations of missing trait values

For some of the traits and classes, there was a substantial proportion of missing trait values (Figure S1). We imputed missing trait values using random forests, implemented with the 'missforest' function of the 'missForest' package in R (Version 1.4, Stekhoven & Bühlmann (2012); Stekhoven (2016). Missforest is one of the best methods for missing-value imputations when working with continuous and categorical variables, and when including species phylogenetic position as a predictor (Debastiani, et al., 2021; Penone et al., 2014). Several traits were strongly phylogenetically conserved (Table S1), so we included ten phylogenetic eigenvectors in the imputations (Penone *et al.* 2014), as well as taxonomic orders as a categorical variable (included to account for the taxonomic positions of species that were not represented in the phylogenies). See S3, "Imputing missing trait values", for more details and for estimations of out-of-bag imputation errors. After imputation, continuous traits were $\log_{10}$-transformed to improve normality (except for habitat and diet breadth, which we square-root transformed). We considered all traits in the imputations, even those with the lowest coverage. We checked the robustness of our results by running our models using both imputed traits and non-imputed traits (i.e., running complete-case analyses by excluding missing values). We further highlight which traits had low coverage (< 40%) when displaying the results (in Figure 2).

Land-use responses

Vertebrate assemblage composition

We used the PREDICTS database (Hudson et al., 2014, 2017), a collection of independent studies that sampled species assemblages in sites of varying land use and land-use intensity. It is one of the most comprehensive such databases to date, although inevitably taxonomic and geographic sampling biases exist. Samples are mostly of species abundance (~93% of the vertebrate records), but some report just occurrence (~7%). For the purposes of this analysis, we converted all abundance measurements into occurrence. The vertebrate subset represents 4,107 species sampled across 7,689 sites (Figure 1a-d; amphibians: 307 species, 980 sites; birds: 2963 species, 3755 sites; mammals: 532 species, 2047 sites; reptiles: 305 species, 907 sites). In PREDICTS, sites are assigned to one of the following land-use categories: primary vegetation (natural vegetation with no record of prior destruction); secondary vegetation (vegetation recovering after destruction of primary vegetation); plantation forest (harvested areas planted with crop trees or shrubs); pasture (areas grazed by livestock); cropland (harvested areas planted with herbaceous crops); urban (built-up areas) (see Table S2 and Hudson *et al.* (2014, 2017) for detailed definitions). Each site is also characterised in terms of land-use intensity (as minimal, light or intense) based on land-use-specific criteria reflecting the degree of human transformation and impacts (e.g. mechanisation degree, crop diversity and agricultural inputs for agricultural areas; Hudson *et al.* (2014); Table S2). We consider minimally used primary vegetation to be the least-disturbed reference land use against which we compare other more-disturbed land-use types. We grouped pasture and cropland together into a category termed "agricultural" (keeping plantation forests separate as they tend to have arboreal vegetation structures that are largely lost in cropland and pastures). As the design of the PREDICTS database is not balanced, sample sizes varied among classes and land-use types (Figure S3).

Land-use models

Full models. We investigated whether the ecological characteristics, land use and land-use intensity explained species occurrence probability. We fitted four binomial generalized linear mixed-effects models (one for each class, as we were interested in the effects of ecological characteristics within classes rather than in the effects of taxonomic class in itself), using the 'lme4' package (Version 1.1-23; Bates *et al.* 2015). Random effects accounted for study, site, and species identity, to control for the nested design of the database, taxonomic non-independence, and repeated observations among species. We did not consider interactions among the ecological characteristics, but we included interactions between land use and each ecological characteristic, and between land-use intensity and each ecological characteristic. Before fitting the models, we checked the degree of multicollinearity among explanatory variables using generalised variance inflation factors (GVIF; Fox & Monette 1992), with a threshold of 5 for the detection of collinearity. All ecological characteristics were included in these models, except diet (using the full models to assess the effect of diet on land-use responses was complicated by the fact that there are more than two levels for this trait, thus models investigating the effects of diet were built separately – see "Partial models"). We did not use phylogenetic random effects directly in the models because of the computational load required by such models when working with several hundred species. However, we checked the phylogenetic signal in the models' residuals using Pagel's λ (Pagel, 1999). To verify that the models' estimates were robust to any violation of distributional assumptions, we fitted the models again using a Bayesian framework (using the 'MCMCglmm' package Version 2.32, Hadfield (2010)).

Partial models. Here, we included a single species-level characteristic at a time. These models were fitted to visualise occurrence patterns for each characteristic independently of other characteristics. The partial models were used to investigate associations between diet and land-use responses. We also fitted partial models for other characteristics but for visualisation purposes only.

Associations between categorical ecological characteristics and occurrence probability

The influence of categorical traits on species responses to land use and land-use intensity can be assessed in two ways: either by comparing occurrence probability for species with the same traits among different land-use types (termed "among land-use type effects"); or by comparing occurrence probability in a given land-use type among groups of species with different traits (termed "within land-use type effects"; Figure 1e).

Associations between continuous ecological characteristics and occurrence probability

For a given continuous ecological characteristic, any effect of land use or land-use intensity can be assessed through changes in the slope of the relationship between the ecological characteristic and occurrence probability (Figure 1f). When an ecological characteristic negatively impacts occurrence probability in a disturbed land use, we expect the slope of the relationship to be more negative than the slope for the reference land use (minimally used primary vegetation). Focussing on slopes does not allow an inference of absolute changes in occurrence probability across land-use types, thus we only capture *within land-use type effects* for continuous predictors.

Validation on complete trait data subset (no imputed trait values)

To assess whether our results were robust to trait imputation uncertainty, we refitted the models for the subset of species for which we had non-imputed data for all ecological characteristics. The models' structure was unchanged for birds and mammals. Owing to multicollinearity issues, we excluded body mass for reptiles, and body length, clutch size, and habitat breadth for amphibians. We also excluded lifespan for amphibians because there were too many missing values (85%; Figure S1), which posed model-fitting issues.

Climate-change sensitivity

We estimated climate-change sensitivity across vertebrate species using the "Climate-niche Factor Analysis" (CNFA) approach developed by Rinnan & Lawler (2019), implemented with the 'CENFA' R package Version 1.1.1 (Rinnan, 2021). CNFA is a spatial approach for estimating species climate-change sensitivity, exposure, and vulnerability. CNFA combines distribution data with climatic variables to estimate sensitivity from properties of species realized climatic niches. CNFA quantifies two main factors, which reflect the position and the size of the species' climatic niche within a reference climatic space (here, the global climatic space): the marginality factor can be interpreted as the distance between the centroid of the climatic niche space occupied by the species and the centroid of the climatic space of reference, for each climatic variable; the sensitivity factor quantifies the amount of sensitivity in each climate dimension, reflecting the size of the niche relative to the climatic space of reference ('specialization'). A species' overall sensitivity is calculated as the mean of the sensitivity factor (square-rooted), and thus reflects the average specialization found in each climatic variable. CNFA is appropriate for interspecific comparisons given that the same reference climatic space is used. For a full mathematical description of the CNFA approach, see Rinnan & Lawler (2019).

Climate data

We used global climate data from WorldClim Version 2.1 (Fick & Hijmans, 2017). We downloaded 19 climatic variables at a resolution of 2.5 arcminutes (~4.6 km at the Equator). We removed variables that were strongly collinear with any other climatic variables (using a conservative threshold of 0.65 for Spearman correlation coefficients; Dormann *et al.* (2013)). We obtained six groups of intercorrelated variables (using the 'removeCollinearity' function from the 'virtualspecies' R package Version 1.5.1 (Leroy et al., 2016)), and randomly selected one climatic variable from each group. The final set comprised six climatic variables: annual mean temperature, mean diurnal temperature range, maximum temperature of the warmest month, annual precipitation, precipitation seasonality, and precipitation of the coldest quarter (Figure S4).

Estimating climate-change sensitivity from CNFA

All spatial data were reprojected to a resolution of 5 × 5 km in the Behrmann equal-area projection. We picked this resolution because climate-change sensitivity is underestimated for narrowly distributed species at progressively coarser resolutions (Figures S5-S6), but using finer resolutions has a very large computational memory requirement. At a 5 × 5-km resolution, there were still some narrowly distributed species for which sensitivity was likely underestimated (Figure S6). Thus, we excluded species with a range area $\leq$ 100 km^2 from further analyses (660 amphibian species, 142 bird species, 129 mammal species, and 615 reptile species), because climate-change sensitivity is likely not accurately estimated for these narrow-ranging species. Estimating climate-change sensitivity for such species would require distribution data resolved to finer resolutions, which is currently computationally prohibitive for all vertebrate species. The final sample sizes were thus: 4,537 amphibians; 10,198 birds; 4,721 mammals; and 7,330 reptiles. Because we considered only breeding ranges, we may misrepresent the realised climatic niches of migratory species. However, considering non-breeding ranges and breeding ranges together would pose further issues, such as using climatic data that match the time of the year when species are occurring in different parts of their ranges. In addition to not being directly implementable with the 'CENFA' package, this could be problematic for interspecific comparisons since CNFA requires the use of similar climatic space of reference for interspecific comparisons to be valid (Rinnan & Lawler 2019). Nevertheless, we checked that our results were robust to the exclusion of migratory species by removing species identified as migratory (155 mammals, identified from Gnanadesikan et al. (2017); and 2072 birds, identified from Avonet (Tobias et al., 2022)), and running the models again (the congruent results are not shown). Finally, since using coarser spatial resolutions is often employed to reduce the effect of commission errors (Di Marco et al., 2017), we verified that our results were robust to the use of coarser resolutions for wide-ranging species (congruent results not shown).

Climate-change sensitivity models

We used phylogenetic least-squares (PGLS) regressions, implemented in the 'caper' R package Version 1.0.1 (Orme, 2012), to assess the effects of ecological characteristics on species estimated climate-change sensitivity, while controlling for phylogenetic relationships among species. We combined the ecological characteristics and the phylogenies using the 'comparative.data' function from the 'caper' package, and then built class-specific models to explain climate-change sensitivity with the ecological characteristics. We checked for multicollinearity among the predictors using GVIF scores (see above). In all classes, the models included all ecological characteristics (except for amphibians and reptiles, for which we excluded diet and diet breadth as there were many missing values). For the continuous predictors, we considered third-order polynomials to allow for non-linear responses, but simplified these polynomials to second or first orders if more complex relationships were not significant. We included third order polynomials for the climate-change sensitivity models but not for the land-use models because the PGLS models had a simpler structure than the land-use models, were less computationally intensive, and because the number of estimated parameters was already high for the land-use models without allowing for third-order polynomials.

Finally, to assess the degree to which our results were robust to trait-imputation uncertainty, we fitted the models again for the subset of species for which we had empirical (i.e., non-imputed) trait estimates. We fitted first-order polynomials here because of the substantially reduced sample sizes.

Results

Land-use responses

Full models: effects within land uses

Land-use, land-use intensity, species ecological characteristics and their interactions had significant effects on species occurrence probability (Figure 2a; Figures S7-S11). Significant interactive effects between land use and ecological characteristics, and between land-use intensity and ecological characteristics, reflected differences in the ability of species with different ecological characteristics to cope *within* disturbed land-use types (Figure 2a). Across all classes, species with narrower geographical range areas, smaller habitat breadth, and an inability to exploit artificial habitats tended to show greater decreases in occurrence probability within disturbed land uses, than species with larger range areas, broader habitat breadth, and an ability to exploit artificial habitats (except for two opposite effects for mammals and reptiles for habitat breadth, in two land-use types). The effects of the other ecological characteristics differed in direction depending on class and land use, impeding any generalisation (Figure 2a). For instance, we found evidence that being longer-lived and having a smaller litter/clutch size was associated with decreases in occurrence probability in several classes and land-use types; yet we also found evidence of opposite effects.

The phylogenetic signals in the models' residuals were low and not significant (Pagel's $\lambda < 0.01$ for amphibians and reptiles, $p \approx 1$; $\lambda = 0.13$ for mammals, $p = 0.12$; $\lambda = 0.01$ for birds, $p = 0.46$).

Partial models: effects among land uses

In all classes, occurrence probability declined substantially for natural habitat specialists in disturbed land uses, compared with primary vegetation (Figure S12), while occurrence probability for artificial habitat users either increased or showed no difference. An exception to this general pattern was that, for reptiles, both natural habitat specialists and artificial habitat users declined in some disturbed land uses (e.g., intensely used agricultural areas, Figure S12d). The occurrence probability of both nocturnal and non-nocturnal species was negatively impacted in disturbed land uses compared with primary vegetation (Figure S13), such that land-use responses were not distinguishable between nocturnal and non-nocturnal species for all classes and land-use types.

In all classes, diet had significant effects on occurrence probability in disturbed land uses (Figure 3). Overall, invertebrate eaters tended to be negatively affected in disturbed land uses (e.g., -66% average declines in occurrence probability for amphibians in intensely used agricultural areas, compared with minimally used primary vegetation). Omnivores were both negatively and positively impacted, depending on class and land-use type/intensity, with occurrence probability showing both important decreases (e.g., -81% for reptiles in intensely used plantation forest) as well as increases (e.g., +43% for lightly used urban areas in birds). Overall, fruit/nectar eaters showed important declines in occurrence probability for mammals and birds, as opposed to plants/seeds eaters, whose occurrence probability tended to be strongly positively affected for birds, and dependent on land-use intensity for mammals (with increases in minimally used land-types, but not in more intensely used land types). Finally, we detected significant changes in occurrence probability for vertebrate eaters, with some declines for mammals in agricultural areas (-75% on average in intense uses), but also some increases (e.g., +43% on average for birds in lightly used agricultural areas).

Model diagnostics showed evidence of deviations from distributional assumptions (diagnostic plots for the full models are shown in Figures S14-S17). However, when estimated from a Bayesian framework, the models' estimates were mostly congruent (Figure S18-S23), showing that the frequentist approach we used with 'lme4' was robust.

Climate-change sensitivity

The ecological characteristics showed significant associations with estimated climate-change sensitivity in all classes (Figure 2b; Tables S3-S6). Overall, climate-change sensitivity was highest for amphibians, then reptiles, then mammals and birds. In all classes, narrower geographical range area, smaller habitat breadth, and being specialised on natural habitats were consistently associated with higher climate-change sensitivity. However, other characteristics did not have consistent associations with climate-change sensitivity across classes, in different cases varying in both significance and direction. For instance, while we found negative associations between body mass and climate-change sensitivity for mammals, amphibians and reptiles, there was a positive association for birds (Figure 2b). We additionally found invertebrate-, plant/seed-eating, and omnivorous birds to be more climate-change sensitive than birds with other diets, but we did not detect significant differences among dietary groups for mammals (Figure S24). The PGLS models were robust to distributional assumptions (Figures S25-S28).

Explanatory power of ecological characteristics

Land use, land-use intensity and the ecological characteristics (except diet) explained a relatively small amount of the variation in species' occurrence probability across land-use types (marginal R^2 for the full models: 0.15 for amphibians; 0.047 for birds; 0.087 for mammals; 0.13 for reptiles), in part because the random effects explained a substantial proportion of the variation (conditional R^2: 0.59 for amphibians; 0.60 for birds; 0.71 for mammals; 0.57 for reptiles). The effects that explained the most variation differed among classes, with interactions between land use and habitat breadth explaining the most variation for amphibians and birds, interactions between land-use intensity and body mass explaining the most variation for mammals, and interactions between land use and lifespan explaining the most variation for reptiles (Figure 4a).

The PGLS models explained an important proportion of the variation in estimated climate-change sensitivity (adjusted-R^2 = 0.64 for amphibians; 0.62 for birds; 0.63 for mammals and reptiles), although most variation was explained by geographical range area (about 60% in all classes; Figure 4b), which could reflect the design of the CNFA approach. When factoring out residual variation and variation explained by range area, the relative importance of traits as correlates of climate-change sensitivity varied among classes (Figure 4c), with body mass explaining the most variation for mammals and reptiles, and litter/clutch size explaining the most variation for amphibians and birds.

Robustness to removal of imputed values

Running the models again using data subsets for which we had empirical, non-imputed values only for the ecological characteristics showed that our conclusions are likely robust to imputation uncertainty: across classes, the associations of geographical range area, habitat breadth and use of artificial habitats with climate-change sensitivity and land-use responses were consistent with the main models (Figure S29-S30).

Discussion

We investigated whether species ecological characteristics were associated with sensitivity to two major human pressures on biodiversity (land-use and climate change), across terrestrial vertebrate classes. Geographical range area, habitat breadth, and specialisation on natural habitats were the only characteristics showing consistent associations across both pressures and vertebrate classes: narrower ranges, narrower habitat breadth, and inability to exploit artificial habitats were associated with more negative land-use responses and with higher climate-change sensitivity. Our results align with previous metanalyses that have found extinction risk to be associated with habitat breadth and range area (Chichorro et al., 2019), range shifts under contemporary climate change to be associated with species' historical range limits and habitat breadth (MacLean & Beissinger, 2017), and with many other studies on land-use responses or extinction risk (e.g., Nowakowski et al. 2017; Ripple *et al.* 2017; Newbold et al. 2018). To our knowledge, ours is the first study to compare associations among vertebrate classes and explicitly between two major human pressures. Our results have important implications for conservation, as they mean that land-use and climate change are non-randomly affecting terrestrial vertebrates, with a consistently higher risk for species with narrower geographical ranges and for habitat specialists, maybe underpinned by stricter niche requirements hindering adaptation to disturbed environments (Slatyer et al., 2013). The higher sensitivity of such species is concerning since they can support unique ecosystem functions complementing those supported by generalists (Dehling et al., 2021; Leitão et al., 2016; Loiseau et al., 2020). Further, geographical range area has been employed by the IUCN for many years in vulnerability assessments (Rodrigues et al., 2006), and our work provides additional support for its integration in large-scale assessments. Our results also highlight habitat specialisation as being highly relevant for large-scale vulnerability assessments, such as in Foden et al. (2013).

Our work highlights context-dependency in the associations between most other traits and responses to anthropogenic pressures. In the case of land use, we find that the directionality of the responses not only often depends on taxonomic class but also on land-use type, further complicating the patterns. Contrary to Chichorro et al. (2022)'s findings on extinction risk, we did not find consistent associations between life-history traits (i.e., lifespan and fecundity) and climate-change sensitivity or land-use responses. This could be because life-history traits likely affect extinction risk through long-term demographic processes, while our approach relies on occurrence data captured at a single moment in time, thus assuming populations are at equilibrium. This constitutes a fundamental limitation of space-for-time approaches, as emphasized in De Palma et al. (2018). Another limitation is that the PREDICTS database presents important taxonomic and geographical biases. Addressing these biases, notably by improving data coverage for the least-sampled classes (here, reptiles and amphibians), could help elucidate differences in responses among taxonomic groups or regions (e.g., Newbold et al. 2020). For instance, since our results highlight the usefulness of traits for understanding species' sensitivity to human pressures, further work could investigate geographical variation in the associations across vertebrate classes, which was not possible here given geographic variation in the intensity of sampling in the PREDICTS database.

In line with past work underlining the low explanatory power of traits when used to explain responses to human pressures (Angert et al., 2011; Cannistra & Buckley, 2021; Verberk et al., 2013), we found that traits explained a small proportion of the interspecific variation in land-use responses and in climate-change sensitivity. Despite their generally low explanatory power, traits have been used to assess species' vulnerability to human threats, in particular to climate change (Bohm et al., 2016; Foden et al., 2013). One of the conceptual appeals behind the use of traits is that if clear patterns in responses to environmental change can be identified across taxa, then it could be possible to generalize their effects in space and time, and to new species (Hamilton et al., 2020; Verberk et al., 2013; Williams et al., 2008), which is of interest for conservation – notably for data deficient species and/or those lacking estimates of abundance or population sizes. The class-specific influence of traits on climate-change sensitivity, coupled with their low explanatory power, could be one of the reasons why trait-based approaches were shown to give less consistent results than trend-based approaches (which rely on the use of long-term population data) for climate-change vulnerability assessments (Wheatley *et al.* 2017). Importantly, our results, which are based on a correlative assessment (i.e., the association between climate-change sensitivity – derived from properties of species realized climatic niche space – and traits), do not allow an inference of mechanistic links between traits and responses to global changes. Reinforcing our mechanistic understanding of how traits influence species' ability to cope with disturbances, for example by using long-term population data and demographic models (Hernández-Yáñez et al., 2022), may help elucidate some of the contrasting results we obtained.

In addition, characteristics that we did not investigate in our work have been shown to play an important role in shaping species' responses to environmental change (e.g., thermal tolerance limits; Williams et al. 2022; Williams & Newbold, 2021). Additional patterns might be uncovered by considering characteristics that we did not include here. Further, it is possible that some patterns are masked by interactions and trade-offs among traits. For instance, larger species tend to have larger dispersal distances and movement abilities (Jenkins et al., 2007), which could be beneficial to resource acquisition in disturbed areas (Hillaert et al., 2018), but also have higher energetic requirements (White, 2011) and lower reproductive output, which could be detrimental to their persistence in the face of environmental change. Interactions and trade-offs among traits have been shown to be important for understanding which species could persist in disturbed environments (Sayol et al., 2020), but little is known about interactive effects at large scales and for different pressures and across multiple different traits.

Moreover, we investigated climate-change sensitivity and land-use responses separately, not considering interactions between these pressures. However, human pressures act in combination (Capdevila et al., 2022; Harfoot et al., 2021; Segan et al., 2016), and a number of confounding factors could influence sensitivity. For example, larger species might be more sensitive to warming than smaller species (Hantak et al., 2021; Merckx et al., 2018), but they could also be better able to persist in fragmented landscapes, such that habitat fragmentation and climate warming may have opposite signatures. Thus, interactions among traits, among types of pressure, and among traits and pressures should ideally be considered together to understand species' responses to human disturbances more fully (Hantak et al., 2021). While considering all these effects simultaneously may be challenging because of data-limitation issues, model complexity, and difficulty in assessing and disentangling individual and interactive effects (Oliver & Morecroft, 2014), some studies have considered the combined effects of human pressures on vertebrates (Albaladejo-Robles et al., 2023; Newbold, 2018; Spooner et al., 2018; J. J. Williams et al., 2022).

To conclude, our results indicate that land-use and climate change impact terrestrial vertebrates non-randomly with respect to their ecological characteristics, which could have important consequences for ecosystem functioning (Duffy, 2003; Luck et al., 2012). We detected substantial declines in occurrence probability of certain dietary groups in disturbed land-use types, most notably invertebrate eaters and fruit/nectars eaters. We also found higher climate-change sensitivity for invertebrate- and plant/seed-eating birds. Our findings thus highlight the potential risks from global changes for ecosystem processes sustained by those species, such as pest control, seed dispersal or pollination (Civantos et al., 2012; Fricke et al., 2022; González-Varo et al., 2013), emphasizing the need for mitigation and conservation measures. By showing consistent effects of geographical range size and habitat specialisation on sensitivity to land use and climate change across terrestrial vertebrate classes, our findings provide support for the integration of these ecological characteristics into vulnerability assessments.

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References

Albaladejo-Robles, G., Böhm, M., & Newbold, T. (2023). Species life-history strategies affect population responses to temperature and land-cover changes. *Global Change Biology*, *29*(1), 97–109. https://doi.org/10.1111/gcb.16454

Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., & Chunco, A. J. (2011). Do species’ traits predict recent shifts at expanding range edges? In *Ecology Letters* (Vol. 14, Issue 7, pp. 677–689). https://doi.org/10.1111/j.1461-0248.2011.01620.x

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. https://doi.org/10.18637/jss.v067.i01

Bohm, M., Cook, D., Ma, H., Davidson, A. D., Garcï¿½a, A., Tapley, B., Pearce-Kelly, P., & Carr, J. (2016). Hot and bothered: Using trait-based approaches to assess climate change vulnerability in reptiles. *Biological Conservation*. https://doi.org/10.1016/j.biocon.2016.06.002

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., Suchard, M. A., Rambaut, A., & Drummond, A. J. (2014). BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Computational Biology*. https://doi.org/10.1371/journal.pcbi.1003537

Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M., & Böhning-Gaese, K. (2019). Long-term declines of European insectivorous bird populations and potential causes. *Conservation Biology*, *33*(5), 1120–1130. https://doi.org/10.1111/cobi.13307

Cannistra, A. F., & Buckley, L. B. (2021). Improving range shift predictions: enhancing the power of traits. *BioRxiv*, 2021.02.15.431292. https://doi.org/10.1101/2021.02.15.431292

Capdevila, P., Noviello, N., Mcrae, L., Freeman, R., Life, B., Building, S., & Circle, O. (2022). *Body mass and latitude as global predictors of vertebrate Running title : Global predictors of multiple threats*. 1–25.

Capdevila, P., Stott, I., Cant, J., Beger, M., Rowlands, G., Grace, M., & Salguero-Gómez, R. (2022). Life history mediates the trade-offs among different components of demographic resilience. *Ecology Letters*, *July 2021*, 1–14. https://doi.org/10.1111/ele.14004

Capurucho, J. M. G., Ashley, M. V., Tsuru, B. R., Cooper, J. C., & Bates, J. M. (2020). Dispersal ability correlates with range size in Amazonian habitat-restricted birds: Correlates of range size in birds. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1939). https://doi.org/10.1098/rspb.2020.1450rspb20201450

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*(June), 220–229. https://doi.org/10.1016/j.biocon.2019.07.001

Chichorro, F., Urbano, F., Teixeira, D., Väre, H., Pinto, T., Brummitt, N., He, X., Hochkirch, A., Hyvönen, J., Kaila, L., Juslén, A., & Cardoso, P. (2022). Trait-based prediction of extinction risk across terrestrial taxa. *Biological Conservation*, *274*(October). https://doi.org/10.1016/j.biocon.2022.109738

Civantos, E., Thuiller, W., Maiorano, L., Guisan, A., & Arajo, M. B. (2012). Potential impacts of climate change on ecosystem services in Europe: The case of pest control by vertebrates. *BioScience*, *62*(7), 658–666. https://doi.org/10.1525/bio.2012.62.7.8

Curtis, J. R., Robinson, W. D., Rompré, G., Moore, R. P., & McCune, B. (2021). Erosion of tropical bird diversity over a century is influenced by abundance, diet and subtle climatic tolerances. *Scientific Reports*, *11*(1), 1–13. https://doi.org/10.1038/s41598-021-89496-7

Davison, C. W., Rahbek, C., & Morueta-Holme, N. (2021). Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature. *Global Change Biology*, *27*(21), 5414–5429. https://doi.org/10.1111/gcb.15846

De Palma, A., Sanchez-Ortiz, K., Martin, P. A., Chadwick, A., Gilbert, G., Bates, A. E., Börger, L., Contu, S., Hill, S. L. L., & Purvis, A. (2018). Challenges With Inferring How Land-Use Affects Terrestrial Biodiversity: Study Design, Time, Space and Synthesis. In *Advances in Ecological Research*. https://doi.org/10.1016/bs.aecr.2017.12.004

Debastiani, V. J., Bastazini, V. A. G., & Pillar, D. (2021). *Ecological Informatics Using phylogenetic information to impute missing functional trait values in ecological databases*. *63*(April). https://doi.org/10.1016/j.ecoinf.2021.101315

Dehling, D. M., Bender, I. M. A., Blendinger, P. G., Böhning-Gaese, K., Muñoz, M. C., Neuschulz, E. L., Quitián, M., Saavedra, F., Santillán, V., Schleuning, M., & Stouffer, D. B. (2021). Specialists and generalists fulfil important and complementary functional roles in ecological processes. *Functional Ecology*, *35*(8), 1810–1821. https://doi.org/10.1111/1365-2435.13815

Di Marco, M., Pacifici, M., Maiorano, L., & Rondinini, C. (2021). Drivers of change in the realised climatic niche of terrestrial mammals. *Ecography*, *44*(8), 1180–1190. https://doi.org/10.1111/ecog.05414

Di Marco, M., Watson, J. E. M., Possingham, H. P., & Venter, O. (2017). Limitations and trade-offs in the use of species distribution maps for protected area planning. *Journal of Applied Ecology*, *54*(2), 402–411. https://doi.org/10.1111/1365-2664.12771

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Duffy, J. E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, *6*(8), 680–687. https://doi.org/10.1046/j.1461-0248.2003.00494.x

Estrada, A., Morales-Castilla, I., Meireles, C., Caplat, P., & Early, R. (2018). Equipped to cope with climate change: traits associated with range filling across European taxa. *Ecography*. https://doi.org/10.1111/ecog.02968

Etard, A., Morrill, S., & Newbold, T. (2020). Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography*, *November 2019*, 1–16. https://doi.org/10.1111/geb.13184

Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli1, A., & Svenning, J.-C. (2018). PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology*, *99*(11), 2626. https://doi.org/10.1002/ecy.2443

Faurby, S., Pedersen, R. Ø., Davis, M., Schowanek, S. D., Jarvie, S., Antonelli, A., & Svenning, J.-C. (2020). *MegaPast2Future/PHYLACINE_1.2: PHYLACINE Version 1.2.1*. Zenodo. https://doi.org/10.5281/zenodo.3690867

Ferreira, D. F., Gibb, R., López-Baucells, A., Nunes, N. J., Jones, K. E., & Rocha, R. (2022). Species-specific responses to land-use change in island insectivorous bats. *Journal for Nature Conservation*, 126177. https://doi.org/10.1016/j.jnc.2022.126177

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vié, J. C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekercioğlu, Ç. H., & Mace, G. M. (2013). Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0065427

Fox, J., & Monette, G. (1992). Generalized collinearity diagnostics. *Journal of the American Statistical Association*. https://doi.org/10.1080/01621459.1992.10475190

Fricke, E. C., Ordonez, A., Rogers, H. S., Svenning, J., Schneeberger, K., Stolz, G., Thyssen, M., Boone, J., & Sharp, C. (2022). *Track Climate Change*. *214*(January), 210–214.

Gnanadesikan, G. E., Pearse, W. D., & Shaw, A. K. (2017). Evolution of mammalian migrations for refuge, breeding, and food. *Ecology and Evolution*, *7*(15), 5891–5900. https://doi.org/10.1002/ece3.3120

Gonzalez-Suarez, M., Gomez, A., & Revilla, E. (2013). Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. *Ecosphere*. https://doi.org/10.1890/ES12-00380.1

González-Varo, J. P., Biesmeijer, J. C., Bommarco, R., Potts, S. G., Schweiger, O., Smith, H. G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M., & Vilà, M. (2013). Combined effects of global change pressures on animal-mediated pollination. *Trends in Ecology and Evolution*, *28*(9), 524–530. https://doi.org/10.1016/j.tree.2013.05.008

Hadfield, J. D. (2010). MCMCglmm: MCMC Methods for Multi-Response GLMMs in R. *Journal of Statistical Software*, *33*(2), 1–22. http://www.jstatsoft.org/

Hamilton, A. T., Schäfer, R. B., Pyne, M. I., Chessman, B., Kakouei, K., Boersma, K. S., Verdonschot, P. F. M., Verdonschot, R. C. M., Mims, M., Khamis, K., Bierwagen, B., & Stamp, J. (2020). Limitations of trait-based approaches for stressor assessment: The case of freshwater invertebrates and climate drivers. *Global Change Biology*, *26*(2), 364–379. https://doi.org/10.1111/gcb.14846

Hantak, M. M., McLean, B. S., Li, D., & Guralnick, R. P. (2021). Mammalian body size is determined by interactions between climate, urbanization, and ecological traits. *Communications Biology*, *4*(1), 1–10. https://doi.org/10.1038/s42003-021-02505-3

Harfoot, M. B. J., Johnston, A., Balmford, A., Burgess, N. D., Butchart, S. H. M., Dias, M. P., Hazin, C., Hilton-Taylor, C., Hoffmann, M., Isaac, N. J. B., Iversen, L. L., Outhwaite, C. L., Visconti, P., & Geldmann, J. (2021). Using the IUCN Red List to map threats to terrestrial vertebrates at global scale. *Nature Ecology and Evolution*, *5*(11), 1510–1519. https://doi.org/10.1038/s41559-021-01542-9

Hernández-Yáñez, H., Kim, S. Y., & Che-Castaldo, J. P. (2022). Demographic and life history traits explain patterns in species vulnerability to extinction. *PLoS ONE*, *17*(2 February), 1–15. https://doi.org/10.1371/journal.pone.0263504

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., & González, J. A. (2017). Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. In *Ecology and Evolution*. https://doi.org/10.1002/ece3.2692

Hillaert, J., Hovestadt, T., Vandegehuchte, M. L., & Bonte, D. (2018). Size-dependent movement explains why bigger is better in fragmented landscapes. *Ecology and Evolution*, *8*(22), 10754–10767. https://doi.org/10.1002/ece3.4524

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Alhusseini, T. I., Bedford, F. E., Bennett, D. J., Booth, H., Burton, V. J., Chng, C. W. T., Choimes, A., Correia, D. L. P., Day, J., Echeverrï¿½a-Londoï¿½o, S., Emerson, S. R., Gao, D., … Purvis, A. (2017). The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. *Ecology and Evolution*. https://doi.org/10.1002/ece3.2579

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Senior, R. A., Bennett, D. J., Booth, H., Choimes, A., Correia, D. L. P., Day, J., Echeverría-Londoño, S., Garon, M., Harrison, M. L. K., Ingram, D. J., Jung, M., Kemp, V., … Purvis, A. (2014). The PREDICTS database: A global database of how local terrestrial biodiversity responds to human impacts. *Ecology and Evolution*. https://doi.org/10.1002/ece3.1303

IUCN. (2020). *The IUCN Red List of Threatened Species. Version 2020-2*. Https://Www.Iucnredlist.Org. Downloaded on 09 July.

Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., Hillegass, M., Lyon, B. N., Metzger, G. A., Olandese, M. L., Pepe, D., Silvers, G. A., Suresch, H. N., Thompson, T. N., Trexler, C. M., Williams, G. E., Williams, N. C., & Williams, S. E. (2007). Does size matter for dispersal distance? *Global Ecology and Biogeography*, *16*(4), 415–425. https://doi.org/10.1111/j.1466-8238.2007.00312.x

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*. https://doi.org/10.1038/nature11631

Jetz, Walter, & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology and Evolution*. https://doi.org/10.1038/s41559-018-0515-5

Leitão, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortune, C., Mendonça, F. P., & Mouillot, D. (2016). Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1828). https://doi.org/10.1098/rspb.2016.0084

Leroy, B., Meynard, C. N., Bellard, C., & Courchamp, F. (2016). virtualspecies, an R package to generate virtual species distributions. *Ecography*, *39*(6), 599–607. https://doi.org/10.1111/ecog.01388

Leung, B., Hargreaves, A. L., Greenberg, D. A., McGill, B., Dornelas, M., & Freeman, R. (2020). Clustered versus catastrophic global vertebrate declines. *Nature*, *588*(7837), 267–271. https://doi.org/10.1038/s41586-020-2920-6

Li, G., Fang, C., Li, Y., Wang, Z., Sun, S., He, S., Qi, W., Bao, C., Ma, H., Fan, Y., Feng, Y., & Liu, X. (2022). Global impacts of future urban expansion on terrestrial vertebrate diversity. *Nature Communications*, *13*(1), 1–12. https://doi.org/10.1038/s41467-022-29324-2

Loiseau, N., Mouquet, N., Casajus, N., Grenié, M., Guéguen, M., Maitner, B., Mouillot, D., Ostling, A., Renaud, J., Tucker, C., Velez, L., Thuiller, W., & Violle, C. (2020). Global distribution and conservation status of ecologically rare mammal and bird species. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-18779-w

Lucas, P. M., González-Suárez, M., & Revilla, E. (2019). Range area matters, and so does spatial configuration: predicting conservation status in vertebrates. *Ecography*, *42*(6), 1103–1114. https://doi.org/10.1111/ecog.03865

Luck, G. W., Lavorel, S., Mcintyre, S., & Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology*. https://doi.org/10.1111/j.1365-2656.2012.01974.x

MacLean, S. A., & Beissinger, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, *23*(10), 4094–4105. https://doi.org/10.1111/gcb.13736

Matich, P., & Schalk, C. M. (2019). Move it or lose it: Interspecific variation in risk response of pond-breeding anurans. *PeerJ*, *7*, 1–16. https://doi.org/10.7717/PEERJ.6956

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*. https://doi.org/10.1038/536143a

Mccain, C. M., & King, S. R. B. (2014). Body size and activity times mediate mammalian responses to climate change. *Global Change Biology*. https://doi.org/10.1111/gcb.12499

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hendrickx, F., Higuti, J., Lens, L., Martens, K., … Van Dyck, H. (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature*. https://doi.org/10.1038/s41586-018-0140-0

Morelli, F., Benedetti, Y., Hanson, J. O., & Fuller, R. A. (2021). Global distribution and conservation of avian diet specialization. *Conservation Letters*, *14*(4), 1–12. https://doi.org/10.1111/conl.12795

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 20180792. https://doi.org/10.1098/rspb.2018.0792

Newbold, T., Hudson, L. N., Contu, S., Hill, S. L. L., Beck, J., Liu, Y., Meyer, C., Phillips, H. R. P., Scharlemann, J. P. W., & Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biology*. https://doi.org/10.1371/journal.pbio.2006841

Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. a, Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Dıáz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*. https://doi.org/10.1038/nature14324

Newbold, T., Scharlemann, J. P. W., Butchart, S. H. M., Sekercioğlu, C. H., Alkemade, R., Booth, H., & Purves, D. W. (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings. Biological Sciences / The Royal Society*. https://doi.org/10.1098/rspb.2012.2131

Nowakowski, A. J., Thompson, M. E., Donnelly, M. A., & Todd, B. D. (2017). Amphibian sensitivity to habitat modification is associated with population trends and species traits. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.12571

Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C., & Costa, G. C. (2017). AmphiBIO, a global database for amphibian ecological traits. *Scientific Data*. https://doi.org/10.1038/sdata.2017.123

Oliver, T. H., & Morecroft, M. D. (2014). Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. In *Wiley Interdisciplinary Reviews: Climate Change*. https://doi.org/10.1002/wcc.271

Orme, C. D. L. (2012). The caper package: comparative analyses in phylogenetics and evolution in R. See http://caper.r-forge.r-project.org/. *Http://Caper.R-Forge.R-Project.Org/.*, 1–36.

Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*. https://doi.org/10.1038/nclimate3223

Pagel, M. (1999). Inferring the historical patterns of biological evolution. In *Nature*. https://doi.org/10.1038/44766

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., Fordham, D. A., Raxworthy, C. J., Ryu, H. Y., Mcnees, J., & Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*. https://doi.org/10.1038/nclimate2113

Penone, C., Davidson, A. D., Shoemaker, K. T., Di Marco, M., Rondinini, C., Brooks, T. M., Young, B. E., Graham, C. H., & Costa, G. C. (2014). Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.12232

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change*, *9*(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2000.1234

Quesnelle, P. E., Lindsay, K. E., & Fahrig, L. (2014). Low reproductive rate predicts species sensitivity to habitat loss: A meta-analysis of wetland vertebrates. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0090926

Rinnan, S. (2021). *Package ' CENFA .'* https://doi.org/10.1111/ecog.03937>.Depends

Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1702078114

Rodrigues, A. S. L., Pilgrim, J. D., Lamoreux, J. F., Hoffmann, M., & Brooks, T. M. (2006). The value of the IUCN Red List for conservation. *Trends in Ecology and Evolution*, *21*(2), 71–76. https://doi.org/10.1016/j.tree.2005.10.010

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L., Hoogmoed, M., Itescu, Y., Kraus, F., Lebreton, M., … Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*. https://doi.org/10.1038/s41559-017-0332-2

Santini, L., Isaac, N. J. B., Maiorano, L., Ficetola, G. F., Huijbregts, M. A. J., Carbone, C., & Thuiller, W. (2018). Global drivers of population density in terrestrial vertebrates. *Global Ecology and Biogeography*, *27*(8), 968–979. https://doi.org/10.1111/geb.12758

Sayol, F., Sol, D., & Pigot, A. L. (2020). Brain Size and Life History Interact to Predict Urban Tolerance in Birds. *Frontiers in Ecology and Evolution*, *8*, 58. https://doi.org/10.3389/fevo.2020.00058

Schloss, C. A., Nunez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences*, *109*(22), 8606–8611. https://doi.org/10.1073/pnas.1116791109

Scott Rinnan; Joshua Lawler. (2019). Climate-niche factor analysis: a spatial approach to quantifying species vulnerability to climate change. *Ecography*, *42*, 1494–1503.

Segan, D. B., Murray, K. A., & Watson, J. E. M. (2016). A global assessment of current and future biodiversity vulnerability to habitat loss-climate change interactions. *Global Ecology and Conservation*, *5*, 12–21. https://doi.org/10.1016/j.gecco.2015.11.002

Shamoon, H., Maor, R., Saltz, D., & Dayan, T. (2018). Increased mammal nocturnality in agricultural landscapes results in fragmentation due to cascading effects. *Biological Conservation*, *226*(February), 32–41. https://doi.org/10.1016/j.biocon.2018.07.028

Sherry, T. W. (2021). Sensitivity of Tropical Insectivorous Birds to the Anthropocene: A Review of Multiple Mechanisms and Conservation Implications. *Frontiers in Ecology and Evolution*, *9*(May), 1–20. https://doi.org/10.3389/fevo.2021.662873

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, *16*(8), 1104–1114. https://doi.org/10.1111/ele.12140

Spooner, F. E. B., Pearson, R. G., & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*. https://doi.org/10.1111/gcb.14361

Staude, I. R., Overbeck, G. E., Fontana, C. S., Bencke, G. A., Silva, T. W. da, Mimet, A., & Pereira, H. M. (2021). Specialist Birds Replace Generalists in Grassland Remnants as Land Use Change Intensifies. *Frontiers in Ecology and Evolution*, *8*(January), 1–8. https://doi.org/10.3389/fevo.2020.597542

Stehfest, E., van Zeist, W. J., Valin, H., Havlik, P., Popp, A., Kyle, P., Tabeau, A., Mason-D'Croz, D., Hasegawa, T., Bodirsky, B. L., Calvin, K., Doelman, J. C., Fujimori, S., Humpenöder, F., Lotze-Campen, H., van Meijl, H., & Wiebe, K. (2019). Key determinants of global land-use projections. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-09945-w

Stekhoven, D. J. (2016). Nonparametric Missing Value Imputation using Random Forest. *R Package Version 1.4*. https://doi.org/10.1093/bioinformatics/btr597

Stekhoven, D. J., & Bühlmann, P. (2012). Missforest-Non-parametric missing value imputation for mixed-type data. *Bioinformatics*. https://doi.org/10.1093/bioinformatics/btr597

Thuiller, W., Lavorel, S., & Araújo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, *14*(4), 347–357. https://doi.org/10.1111/j.1466-822X.2005.00162.x

Tinoco, B. A., Santillán, V. E., & Graham, C. H. (2018). Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. *Ecology and Evolution*. https://doi.org/10.1002/ece3.3813

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581–597. https://doi.org/10.1111/ele.13898

Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, *204*, 23–31. https://doi.org/https://doi.org/10.1016/j.biocon.2016.03.039

Verberk, W. C. E. P., van Noordwijk, C. G. E., & Hildrew, A. G. (2013). Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science*. https://doi.org/10.1899/12-092.1

Wheatley, C. J., Beale, C. M., Bradbury, R. B., Pearce-Higgins, J. W., Critchlow, R., & Thomas, C. D. (2017). Climate change vulnerability for species—Assessing the assessments. *Global Change Biology*. https://doi.org/10.1111/gcb.13759

White, C. R. (2011). Allometric estimation of metabolic rates in animals. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *158*(3), 346–357. https://doi.org/10.1016/j.cbpa.2010.10.004

Williams, J. J., Freeman, R., Spooner, F., & Newbold, T. (2022). Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global Change Biology*, *28*(3), 797–815. https://doi.org/10.1111/gcb.15978

Williams, J. J., & Newbold, T. (2021). Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits. *Diversity and Distributions*, *27*(7), 1308–1323. https://doi.org/10.1111/ddi.13282

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, *6*(12). https://doi.org/10.1371/journal.pbio.0060325

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*. https://doi.org/10.1890/13-1917.1

Figures & Tables

Table 1. Ecological characteristics collected for terrestrial vertebrates, with data sources, definitions, and expectations for their associations with species land-use responses and climate-change sensitivity.

Ecological characteristic	*Source(s)*	*Definition*	*Expectations and examples of previous evidence*
Continuous			
Lifespan proxy	Compiled in Etard et al. (2020) from a range of sources.	Amphibians: age at sexual maturity; Birds & mammals: generation length; Reptiles: longevity.	Species with longer lifespan & lower reproductive output should be more sensitive to land-use and climate change (Albaladejo-Robles et al., 2023; Purvis et al., 2000).
Litter/clutch size	Compiled in Etard et al. (2020) from a range of sources.	Number of offspring (litter size) or eggs (clutch size).	
Body size	Compiled in Etard 2020 from a range of sources.	Adult body mass for all classes; also body length for amphibians (for use in validations on complete trait data subsets).	No consensus from past evidence (Chichorro et al., 2019): larger species could be more sensitive to land-use and climate change because of higher energetic requirements (White, 2011), lower reproductive outputs, and lower population densities (Santini et al., 2018), which could be detrimental to their persistence in disturbed environments. Conversely, smaller species could be more sensitive because of more limited dispersal abilities, hampering resource acquisition in disturbed landscapes (Hillaert et al., 2018).
Habitat breadth	Compiled in Etard 2020 from IUCN (2020).	Number of habitats known to be used by a species.	We expect narrower geographical range area & narrower habitat breadth to correlate with higher sensitivity to land-use and climate change (Chichorro et al., 2019).
Geographical range area	Distribution maps: birds: BirdLife International[1]; mammals, amphibians: IUCN (2020); reptiles: Roll et al. (2017).	Surface area occupied by species, calculated from distribution maps.	
Categorical			
(Primary) diet	Amphibians: Oliveira et al., 2017 & additional sources (see SI); Mammals, birds: Wilman et al., 2014. Reptiles: additional sources specified in: https://doi.org/10.6084/m9.figshare.12024309.v1	Classification of species into 5 diet categories: vertebrate eaters; invertebrate eaters; plant/seed eaters; fruit/nectar eaters; and omnivores; see main text and SI for details.	In all classes and diet categories, we expect declines in occurrence probability in disturbed land uses, because we expect resources of all types to be less abundant in disturbed land uses. From past evidence, we also expect insectivorous birds to be particularly sensitive to both land-use and climate change (Bowler et al., 2019; Newbold et al., 2013; Sherry, 2021).
Diet breadth	Calculated from (primary) diet.	Number of recorded food groups (invertebrate, vertebrate, plant, seed, nectar, or fruit) known to be consumed by a species.	We expect narrower diet breadth to correlate with higher sensitivity to land-use and climate change, because species that have less flexible diets should be less able to persist in the face of environmental change which affects the distribution of resources (Chichorro et al., 2022).

[1] http://datazone.birdlife.org/species/requestdis

Diel activity	Compiled in Etard 2020 from a range of sources.	Whether a species is strictly nocturnal, or non-nocturnal.	Some past evidence suggests that nocturnal species might be favoured in disturbed landscapes, although many studies have focused on behavioural responses at the intraspecific level (Shamoon et al., 2018).
Artificial habitat use	Compiled in Etard 2020 from IUCN (2020).	Whether any artificial habitat is suitable for a species (i.e., species are artificial habitat users or natural habitat specialists).	From past studies, we expect natural habitat specialism to correlate with higher sensitivity to land-use and climate change (Foden et al., 2013; Staude et al., 2021).

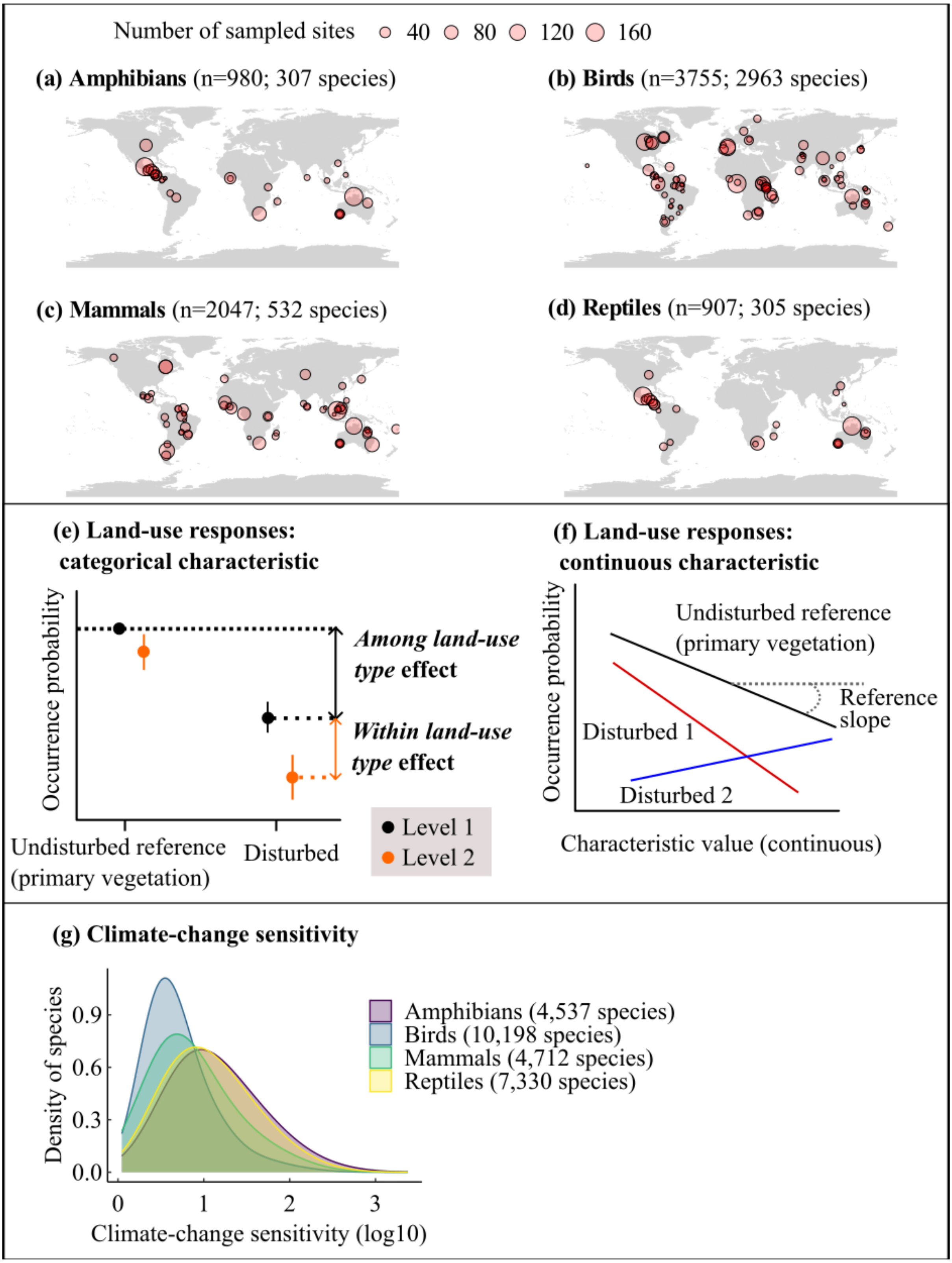
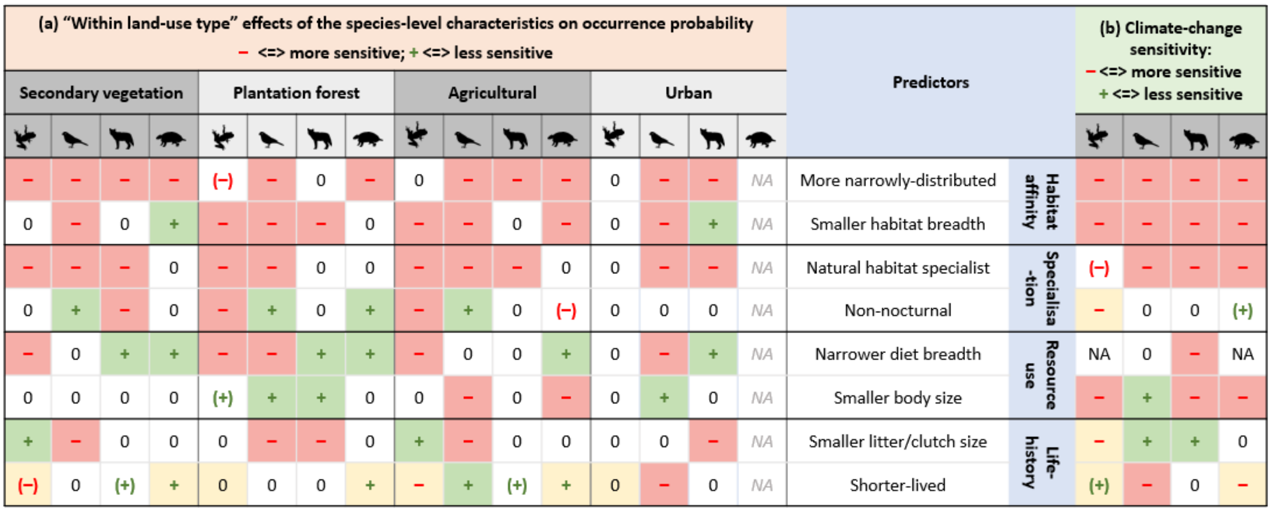


Figure 1. We used two independent approaches to assess the associations of ecological characteristics with species responses to land use and with species estimated climate-change sensitivity. To investigate associations with land use and land-use intensity, we combined the ecological characteristics with occurrence data from the PREDICTS database. **(a)-(d)** show the spatial distribution of the considered PREDICTS studies for each vertebrate class. **(e)** For all categorical characteristics, except diet, we look at "within land-use type effects", asking whether there are significant differences in occurrence probability among species with

different ecological characteristics within a particular land-use type. From the full models, we thus focus on the interactive effects between land use and ecological characteristics (and between land-use intensity and ecological characteristics). For diet, for which within land-use type effects are complicated by the fact that there are more than two levels for this trait, we look at “among land-use type effects”, comparing the occurrence probability for species with different diet categories between disturbed land uses and primary vegetation. **(f)** For continuous characteristics, we focus on the relationship with occurrence probability, and we investigate how the slope of this relationship is affected by land-use type. A more positive slope in a disturbed land use than in the reference land use indicates that higher values of the ecological characteristic are associated with relatively higher occurrence probability in the disturbed land-use type. Thus, we focus on “within land-use type effects” for continuous predictors. **(g)** shows the distribution of climate-change sensitivity across classes. To estimate sensitivity to climate change, we used the CNFA framework (Rinnan & Lawler (2019)), which combines species distributions with climatic variables to estimate sensitivity from properties of species realized climatic niches. We then built class-specific models to assess whether ecological characteristics are associated with species expected sensitivity to climate change.



(a) “Within land-use type” effects of the species-level characteristics on occurrence probability − <=> more sensitive; + <=> less sensitive																**Predictors**		**(b) Climate-change sensitivity:** − <=> more sensitive + <=> less sensitive			
Secondary vegetation				**Plantation forest**				**Agricultural**				**Urban**									
🐸	🐦	🦊	🐢	🐸	🐦	🦊	🐢	🐸	🐦	🦊	🐢	🐸	🐦	🦊	🐢			🐸	🐦	🦊	🐢
−	−	−	−	(−)	−	0	−	0	−	−	−	0	−	−	*NA*	More narrowly-distributed	**Habitat affinity**	−	−	−	−
0	−	0	+	−	−	−	0	−	−	0	−	0	−	+	*NA*	Smaller habitat breadth		−	−	−	−
−	−	−	0	−	−	0	0	−	−	−	0	0	−	−	*NA*	Natural habitat specialist	**Specialisa-tion**	(−)	−	−	−
0	+	−	0	−	+	0	+	−	+	0	(−)	0	0	0	*NA*	Non-nocturnal		−	0	0	(+)
−	0	+	+	−	−	+	+	−	0	0	+	0	−	+	*NA*	Narrower diet breadth	**Resource use**	NA	0	−	NA
0	0	0	0	(+)	+	+	0	0	−	0	−	0	+	0	*NA*	Smaller body size		−	+	−	−
+	−	0	0	0	−	−	0	+	−	0	0	0	0	−	*NA*	Smaller litter/clutch size	**Life-history**	−	+	+	0
(−)	0	(+)	+	0	0	0	+	−	+	(+)	+	0	−	0	*NA*	Shorter-lived		(+)	−	0	−

Figure 2. Summary of the effects of the ecological characteristics (except for diet) on (a) species responses' to disturbed land uses and on (b) species' estimated climate-change sensitivity, for each class of terrestrial vertebrates. The symbol – indicates where a characteristic has a significant negative effect on occurrence probability within a disturbed land-use type (within any of the land-use intensities), or where the characteristic is significantly associated with a greater sensitivity to climate change. A + indicates a significantly positive effect, or a significant association with lower sensitivity to climate change. For the land-use effects, we report *within* land-use type effects here, which for a given disturbed land-use type denote whether there were significant differences in occurrence probability among species with different trait values (see Figure 1). These effects were derived from the interactive terms of the full models. Yellow backgrounds indicate traits for which coverage was low before trait imputation (<40%).

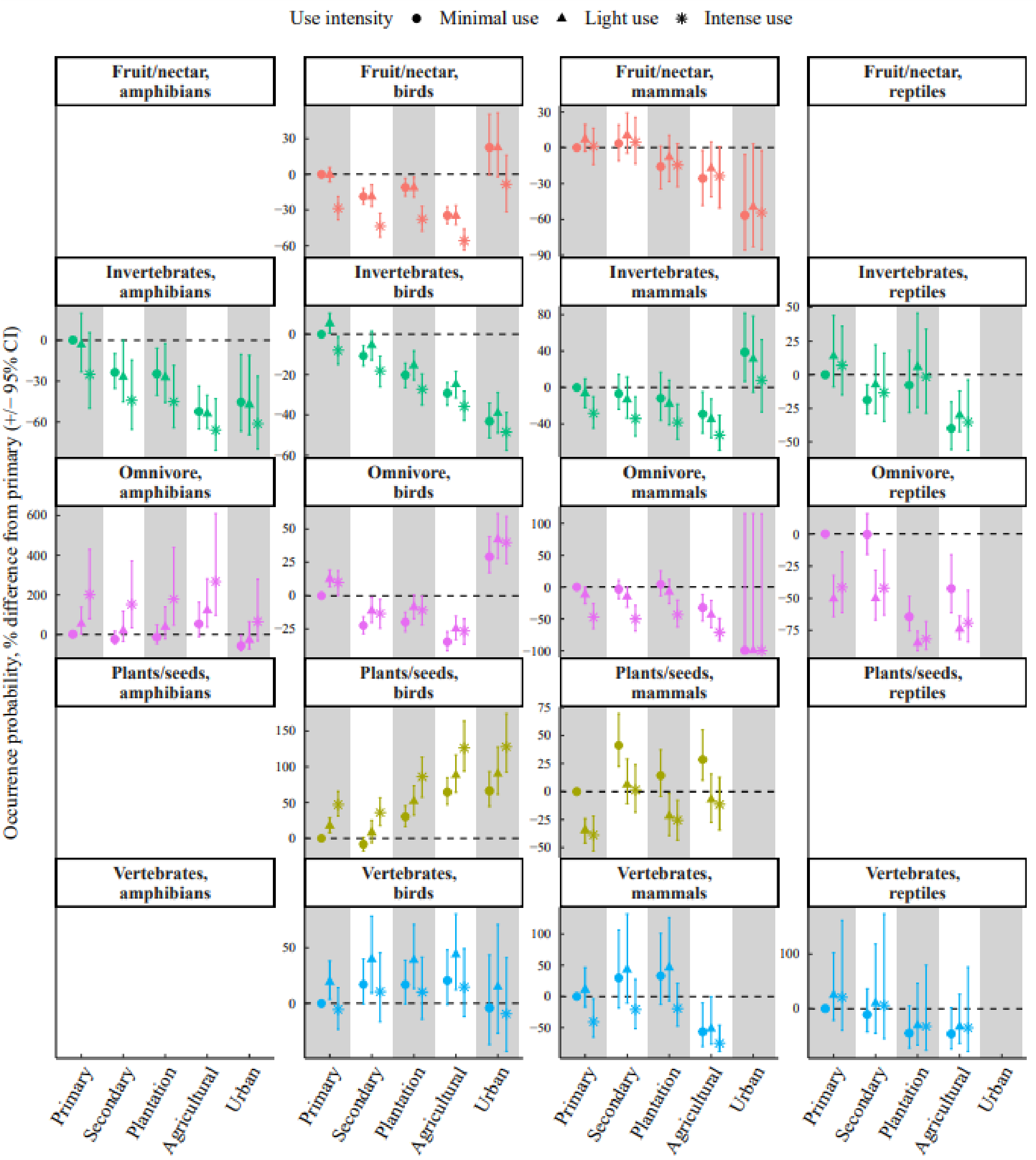
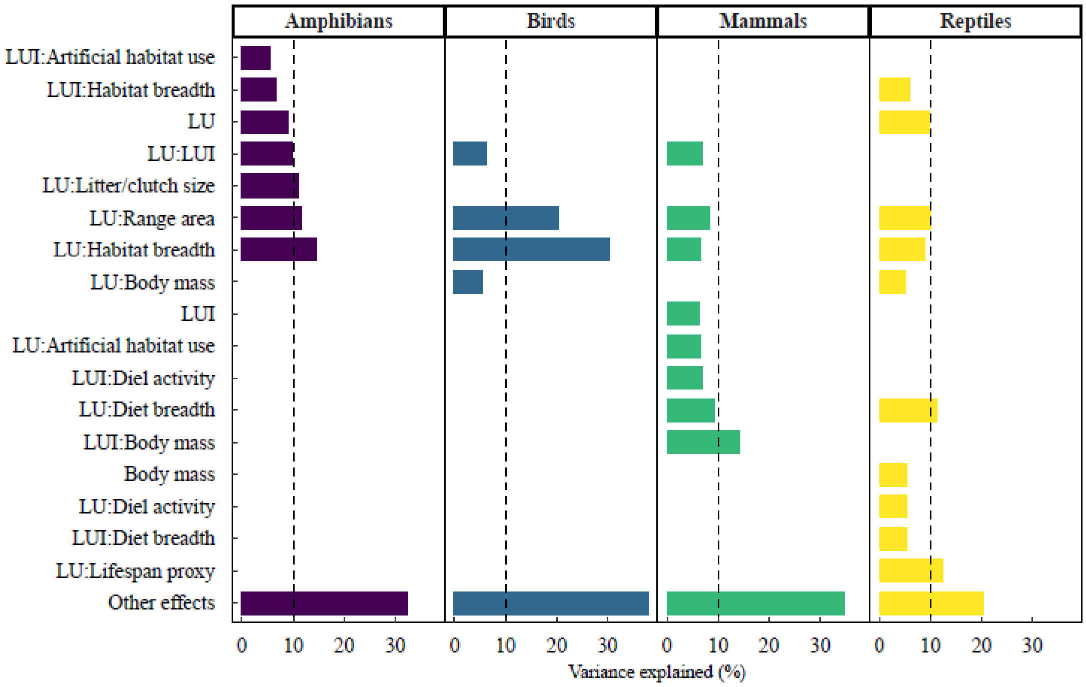
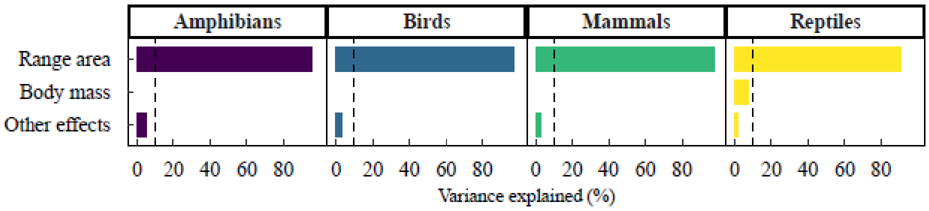


Figure 3. Predicted occurrence probability as a function of land use, land-use intensity, diet, and their interactions, for each class of terrestrial vertebrates (median +/- 95% confidence interval; predictions are expressed as a percentage difference compared to minimally used primary vegetation). The predictions were obtained from the partial models fitted for each class considering only diet from among the ecological characteristics. Panels are empty where there were no data for a diet category for a given class. Effects could not be estimated for urban reptiles, as well as for urban vertebrate, fruit/nectar and plant/seed eaters for mammals because there were no sampled species. Primary: primary vegetation; Secondary: secondary vegetation; plantation: plantation forest; agricultural: cropland and pasture.

(a) % variance explained by main effects (land−use models, factoring out residual variation)



(b) % variance explained by main effects (PGLS models, factoring out residual variation)



(c) % variance explained by main effects (PGLS models, factoring out residual variation and variation attributable to range area)

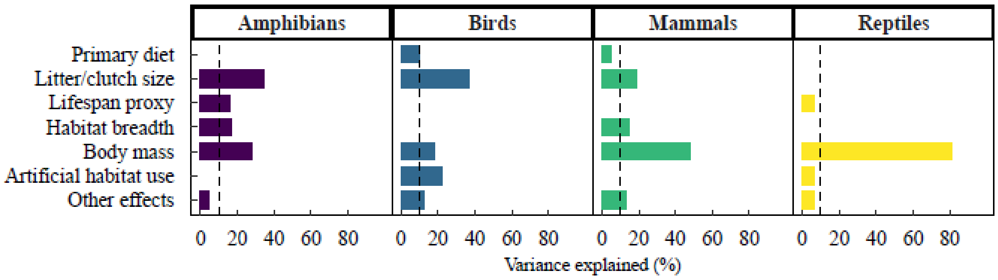


Figure 4. Proportion of the explained variance attributable to each of the main effects for (a) the mixed-effects models fitting the effects of land use, land-use intensity, and ecological characteristics on species occurrence probability (after factoring out residual variation); **(b)** for the phylogenetic least-squares regressions investigating whether the ecological characteristics explained climate-change sensitivity (after factoring out residual variation); and **(c)** for the phylogenetic least-squares regressions investigating whether the ecological characteristics explained climate-change sensitivity (after factoring out the variance explained by geographical range area and the residual variation). For visualisation purposes, the dashed vertical lines mark 10% explained variance. We individually show all the effects that explain more than 5% of the overall variation. Effects that individually explain less than 5% of the overall variation are grouped together as "Other effects".