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Received: 20 February 2023 | Revised: 31 August 2023 | Accepted: 11 October 2023

DOI: 10.1111/cobi.14208

Conservation Biology

CONTRIBUTED PAPERS

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

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

Funding information
Royal Society

Abstract

Land-use and climate change are major pressures on terrestrial biodiversity. Species' extinction risk and responses to human pressures relate to ecological traits and other characteristics in some clades. However, large-scale comparative assessments of the associations between traits and responses to multiple human pressures across multiple clades are needed. We investigated whether a set of ecological characteristics that are commonly measured across terrestrial vertebrates (ecological traits and geographic range area) are associated with species' responses to different land-use types and species' likely sensitivity to climate change. We aimed to test whether generalizable patterns in response to these pressures arise across both pressures and across vertebrate clades, which could inform assessments of the global signature of human pressures on vertebrate biodiversity and guide conservation efforts. At the species level, we investigated associations between land-use responses and ecological characteristics with a space-for-time substitution approach, making use of the PREDICTS database. We investigated associations between ecological characteristics and expected climate-change sensitivity, estimated from properties of species realized climatic niches. Among the characteristics we considered, 3 were consistently associated with strong land-use responses and high climate-change sensitivity across terrestrial vertebrate classes: narrow geographic range, narrow habitat breadth, and specialization on natural habitats (which described whether a species occurs in artificial habitats or not). The associations of other traits with species' land-use responses and climate-change sensitivity often depended on species' class and land-use type, highlighting an important degree of context dependency. In all classes, invertebrate eaters and fruit and nectar eaters tended to be negatively affected in disturbed land-use types, whereas invertebrate-eating and plant- and 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 results highlight a consistently higher sensitivity of narrowly distributed species and habitat specialists to land-use and climate change, which provides support for capturing such characteristics in large-scale vulnerability assessments.

KEYWORDS
CENFA, climate change, diet, geographic range area, habitat specialization, land use, land-use intensity, life-history traits, sensitivity, terrestrial vertebrates

Correlaciones a nivel de especie de las respuestas al uso de suelo y la susceptibilidad al cambio climático en los vertebrados terrestres

Resumen: El uso de suelo y el cambio climático tienen una presión importante sobre la biodiversidad terrestre. En algunos clados, el riesgo de extinción de las especies y las respuestas a las presiones humanas se relacionan con los rasgos ecológicos y otras características. Sin embargo, varios clados necesitan evaluaciones comparativas a gran escala de las asociaciones entre los rasgos y las respuestas a las presiones humanas. Investigamos si un conjunto de rasgos ecológicos medidos comúnmente en los vertebrados terrestres (rasgos ecológicos y extensión del área geográfica) está asociado con la respuesta de las especies a los diferentes tipos de uso de suelo y la posible susceptibilidad de la especie al cambio climático. Buscamos comprobar si los patrones generalizables de las respuestas a estas presiones surgen en ambas presiones y en todos los clados de vertebrados, lo que podría guiar las evaluaciones de la huella mundial de presiones humanas sobre la diversidad de vertebrados y los esfuerzos de conservación. Investigamos las asociaciones entre la respuesta al uso de suelo y los rasgos ecológicos a nivel de especie con una estrategia de reemplazo de espacio por tiempo y con información de la base de datos PREDICTS. También investigamos las asociaciones entre los rasgos ecológicos y la susceptibilidad al cambio climático esperada, la cual estimamos a partir de las propiedades de los nichos climáticos de las especies. Entre las características que consideramos, tres estuvieron asociadas de manera regular con respuestas fuertes al uso de suelo y alta susceptibilidad al cambio climático en las diferentes clases de vertebrados: la extensión geográfica limitada, la amplitud reducida de hábitat y la especialización en los hábitats naturales (la cual describe si una especie está presente en un hábitat artificial o no). Las asociaciones de otros rasgos con la respuesta de la especie al uso de suelo y su susceptibilidad al cambio climático con frecuencia dependieron de la clase de la especie y el tipo de uso de suelo, lo que resalta un grado importante de dependencia del contexto. En todas las clases, los frugívoros, nectarívoros y los que comen invertebrados eran propensos a sufrir efectos negativos en los usos de suelo de tipo perturbado, mientras que se estimó que las aves herbívoras, las que se alimentan de semillas y las que se alimentan de invertebrados eran más susceptibles al cambio climático, lo que incrementa la preocupación por la continuación de los procesos ecológicos que viven estas especies bajo los cambios globales. Nuestros resultados resaltan una susceptibilidad al uso de suelo y al cambio climático cada vez mayor en las especies con distribución limitada y las especialistas de hábitat, lo que proporciona un respaldo para la captura de dichas características en las evaluaciones a gran escala de la vulnerabilidad.

PALABRAS CLAVE
cambio climático, CENFA, dieta, especialización de hábitat, extensión del área geográfica, intensidad de uso de suelo, rasgos de historia de vida, uso de suelo, vertebrados terrestres

INTRODUCTION

Land-use change is currently an important driver of biodiversity loss (Maxwell et al., 2016), and is likely to cause further losses in the 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, and demography, traits can provide information on species use of resources and space, as well as on community and population-level processes (Capdevila et al., 2022). 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 geographic 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), whereas 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 general patterns and idiosyncrasies in the associations between extinction risk and traits. Chichorro et al. (2022) propose 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 of extinction risk (warranting further research); and other traits, such as body size, as useful only to predict extinction risk within specific taxonomic groups.

Thus, while geographic range area and habitat specialism emerge as consistent correlates of extinction risk, no consensus has been reached for other traits, which tend to show context-dependent associations with responses to human disturbance. However, focusing on extinction risk precludes an explicit consideration of the pressures to which species are exposed (Chichorro et al., 2019). Some traits can be associated with negative or positive 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). Previous studies were often restricted in their taxonomic coverage, and few consider several vertebrate classes together. Thus, comparative investigations among vertebrate classes remain rare and it remains unclear whether the effects of traits on vertebrate responses to environmental change can be generalized across vertebrate taxa, regions, and types of pressure. Past work shows, for instance, 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).

We investigated whether general patterns emerge in the associations between terrestrial vertebrates' ecological characteristics (Table 1, ecological traits plus geographic range area) and species' responses to land use and to expected climate-change sensitivity. We compared responses across vertebrate classes and across the 2 pressures. We included species geographic range area in our analyses because it is an important correlate of species' responses to land use (Newbold et al., 2018) and climate change (Thuiller et al., 2005) and 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 because of limited data availability, such as dispersal ability (Capurucho et al., 2020). Because geographic 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 asked the following questions: 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 considered (Table 1), some may directly influence species survival by mediating resource acquisition and use: body mass, diet, and diet breadth. Other characteristics (e.g., life span and litter or 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 depend on the degree of specialization, which we captured with characteristics reflecting specialization in time (i.e., diel activity) and use of space (e.g., habitat breadth and geographic range area). We hypothesized that narrower geographic range area, narrower habitat breadth, and specialism on natural habitats are consistently associated with more negative land-use responses and higher climate-change sensitivity (Chichorro et al., 2019, 2022). We also expected longer life spans, smaller litter or clutch sizes, and more specialized 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 looked for commonalities in the associations with human pressures across terrestrial vertebrate taxa (see Table 1).

Given the differences in the threats we considered and the differing data and methods available to quantify sensitivity to these threats, we used 2 independent approaches to estimate sensitivity to land use and climate change. Therefore, we were not able to consider interactive effects between the pressures. To infer species' land-use responses, we used a space-for-time substitution approach, modeling occurrence probability across different land-use types. We estimated species' expected sensitivity to future climate change from properties of species realized climatic niches. Niche properties are strong indicators of species' climate-change sensitivity (Thuiller et al., 2005) and are straightforward to use at large scales given the availability of species distribution data. We then brought together the results of both approaches to identify consistent associations between species ecological characteristics and their land-use responses or climate-change sensitivity.

METHODS

Ecological characteristics

We obtained the following traits from Etard et al. (2020): body size; a proxy for species life span; litter or clutch size; diel activity; habitat breadth; and use of or preference for artificial habitats, as defined in the IUCN Habitats Classification Scheme (e.g., arable land, urban areas [IUCN, 2020] (Table 1). We chose these traits because they were available across vertebrate classes, at least for a subset of species, and thus allowed for a comparative assessment (Appendix S1). We also chose these traits 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) Q3 and can notably buffer against extinction under threatening processes (González-Suárez & Revilla, 2012). Q4 However, because multiple measurements do not exist for many vertebrate species, we could not 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

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	Definition	Expectations and previous evidence examples
Continuous			
life span 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 life span and lower reproductive output should be more sensitive to land-use and climate change (Albaladejo-Robles et al., 2023; Purvis et al., 2000).
litter or 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 et al. (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 et al. (2020) from IUCN (2020)	number of habitats known to be used by a species	We expect narrower geographic range area and narrower habitat breadth to correlate with higher sensitivity to land-use and climate change (Chichorro et al., 2019).
geographic range area	distribution maps: birds, BirdLife International (http://datazone.birdlife.org/species/requestdis); mammals and 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) and additional sources (see appendices); mammals and 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 and seed eaters, fruit and nectar eaters, omnivores (see text and appendices for details)	In all classes and diet categories, we expect declines in occurrence probability in disturbed land-use types, because we expect resources of all types to be less abundant in disturbed land-use types. From past evidence, we also expect insectivorous birds to be particularly sensitive to 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).
diel activity	compiled in Etard et al. (2020) from a range of sources	Whether a species is strictly nocturnal, or non-nocturnal.	Some past evidence suggests nocturnal species may be favored in disturbed landscapes, although many studies have focused on behavioral responses at the intraspecific level (Shamoon et al., 2018).
Artificial habitat use	compiled in Etard et al. (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). Q1

mammals, we collected estimates of species primary diet (i.e., the diet category representing the combination of food items totaling 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 because 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 (in terms of presence and 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; over 75% of the species were missing information (Appendix S1). For reptiles, there was no readily available database describing diet. For reptiles and amphibians, we supplemented the existing data sets by collecting data on species consumption from published sources (recording the presence or 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). More information on diet compilation and data sources is in Appendix S2.

We standardized diet information across the vertebrate classes by grouping species into 5 different categories: vertebrate eaters; invertebrate eaters; plant and seed eaters; fruit and 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 nonbreeding seasons and areas falling outside species known elevational limits (following Etard et al., 2020). We estimated species geographic range areas with 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 program 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 (Appendix S1). We imputed missing trait values with random forests, implemented with the missforest function of the missForest package in R 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 (Appendix S3), so we included 10 phylogenetic eigenvectors in the imputations (Penone et al., 2014) and taxonomic order as a categorical variable (included to account for the taxonomic positions of species that were not represented in the phylogenies). Appendix S3 contains details and estimations of out-of-bag imputation errors. After imputation, continuous traits were transformed to $\log_{10}$ to improve normality (except for habitat and diet breadth, which we transformed to the square root). We considered all traits in the imputations, even those with the lowest coverage. We checked the robustness of our results by running our models with traits that were imputed and nonimputed traits (i.e., running complete-case analyses by excluding missing values). We highlighted which traits had low coverage ($< 40\%$) when displaying the results.

Vertebrate assemblage composition in different land-use types

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 of 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 occurrence only (~7%). For the purposes of our analyses, we converted all abundance measurements into occurrence. The vertebrate subset represented 4107 species sampled across 7689 sites (Figure 1) (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 1 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 Appendix S4 and Hudson et al., 2014, 2017 for detailed definitions). Each site is also characterized in terms of land-use intensity (minimal, light, or intense) based on land-use-specific criteria reflecting the degree of human transformation and impacts (e.g., mechanization degree, crop diversity, and agricultural inputs for agricultural areas [Hudson et al., 2014]) (Appendix S4). We considered minimally used primary vegetation to be the least-disturbed reference land-use type against which we compared other more disturbed land-use types. We grouped pasture and cropland together into a category termed *agricultural* (keeping plantation forests separate because they tend to have arboreal vegetation structures that are largely lost in cropland and pastures). Because the design of the PREDICTS database is not balanced, sample sizes varied among classes and land-use types (Appendix S4).

Land-use models

We investigated whether the ecological characteristics, land use, and land-use intensity explained species occurrence probability. We fitted 4 binomial generalized linear mixed-effects

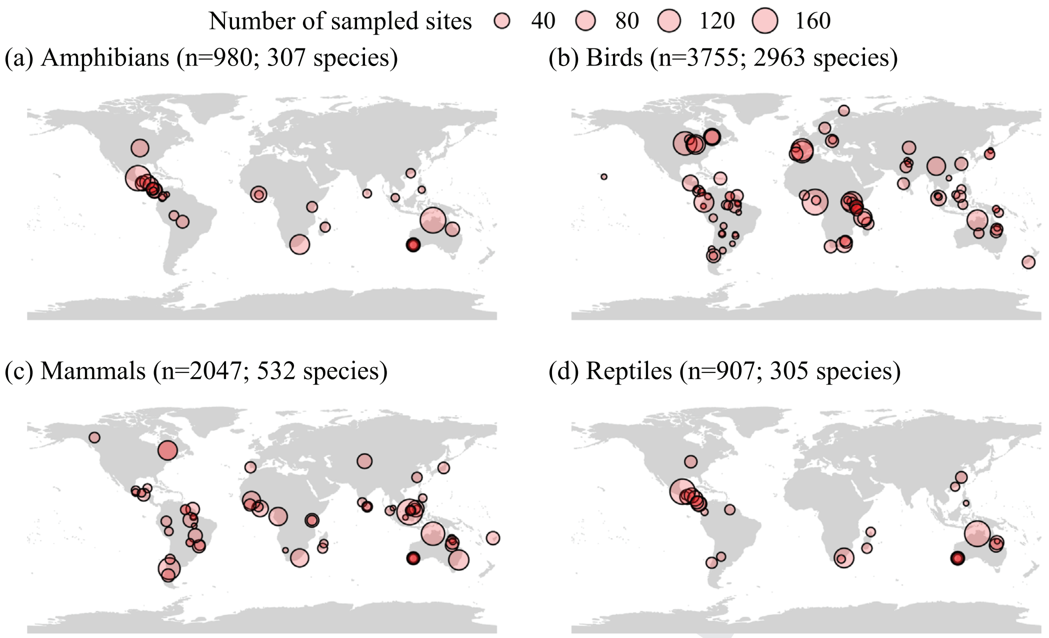


FIGURE 1 Spatial distribution, number of sampling sites (*n*), and number of species from the PREDICTS database for (a) amphibians, (b) birds, (c) mammals, and (d) reptiles.

models (1 for each class because we were interested in the effects of ecological characteristics within classes rather than in the effects of taxonomic class in itself) with the lme4 package 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 nonindependence, 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 generalized 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 were more than 2 levels for this trait; thus, models investigating the effects of diet were built separately (see next paragraph). 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 with Pagel's λ (Pagel, 1999). To verify that the models' estimates were robust to violations of distributional assumptions, we fitted the models again with a Bayesian framework (MCMCglmm package 2.32 [Hadfield, 2010]).

For the partial models, we included a single species-level characteristic at a time. These models were fitted to visualize 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 visualization purposes only.

Associations between categorical and continuous ecological characteristics and occurrence probability

The influence of categorical traits on species responses to land use and land-use intensity can be assessed in 2 ways: 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 2). To assess within-land-use-type effects, we focused on the interactive effects between land-use and ecological characteristics (and between land-use intensity and ecological characteristics) for all ecological characteristics except diet. For diet, assessing within-land-use-type effects is complicated by the fact that there are more than 2 levels for this trait; thus, we examined among land-use type effects (Figure 2) by comparing the occurrence probability for species with different diet categories between disturbed land-use types and primary vegetation.

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 2). When an ecological characteristic negatively affects occurrence probability in a disturbed land-use type, we expected the slope of the relationship to be more negative than the slope for the reference land use (minimally used primary vegetation). Focusing on slopes

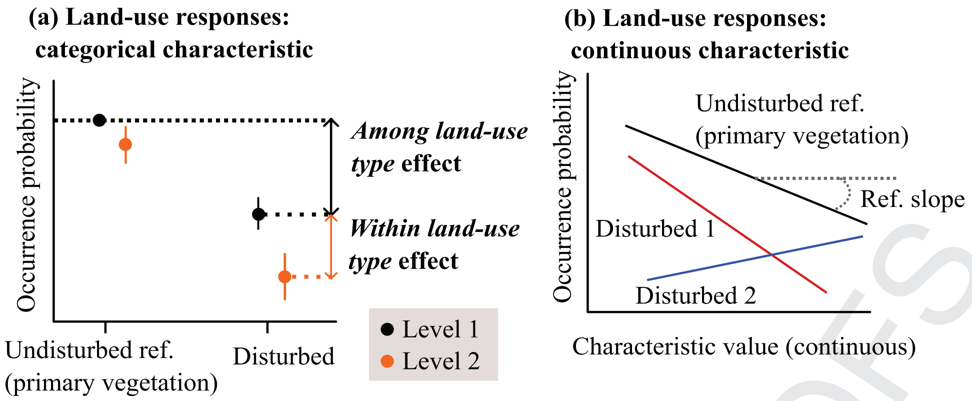


FIGURE 2 Assessment of the effects of ecological characteristics on occurrence probability within land-use types (within-land-use-type effects) (a) for all categorical characteristics except diet and (b) for continuous characteristics (level 1, level of reference to a categorical trait; level 2, another level of reference to the same categorical trait disturbed 1, a disturbed land-use type, e.g., agricultural; disturbed 2, another disturbed land-use type, e.g., urban). The focus is on significant differences in occurrence probability among species with different levels of the same trait within a particular land-use type. A more positive slope in a disturbed land-use type 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, and vice-versa.

does not allow an inference of absolute changes in occurrence probability across land-use types; thus, we captured only 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 nonimputed 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 life span for amphibians because there were too many missing values (85%) (Appendix 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 and Lawler (2019), implemented with the CENFA R package 1.1.1 (Rinnan, 2021). The CNFA is a spatial approach for estimating species climate-change sensitivity, exposure, and vulnerability. It combines distribution data with climatic variables to estimate sensitivity from properties of species realized climatic niches. The CNFA quantifies 2 main factors that reflect the position and the size of the species' climatic niche within a reference climatic space (here, the global climatic space): marginality and sensitivity. 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 was calculated as the mean of the sensitivity factor (transformed to the square root) and thus reflects the average specialization in each climatic variable. The 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 and Lawler (2019).

We used global climate data from WorldClim 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 (with a conservative threshold of 0.65 for Spearman correlation coefficients [Dormann et al., 2013). We obtained 6 groups of intercorrelated variables (with the removeCollinearity function from the virtualspecies R package 1.5.1 [Leroy et al., 2016]) and randomly selected 1 climatic variable from each group. The final set comprised 6 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 (Appendix S5).

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 (Appendix S5), 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 (Appendix S5). Thus, we excluded species with a range area ≤ 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

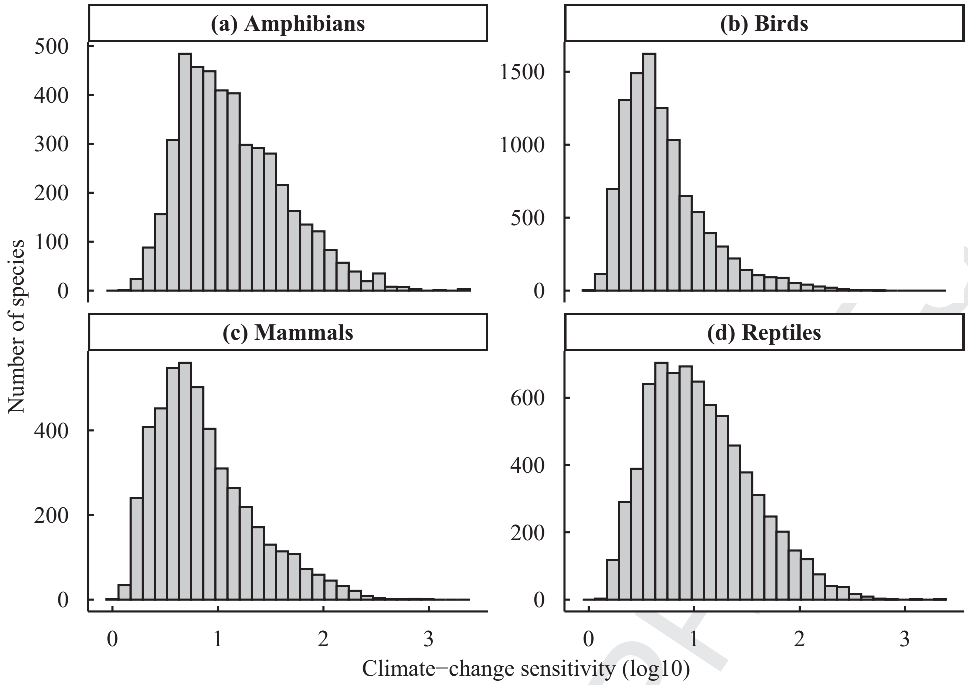


FIGURE 3 Distribution of climate-change sensitivity in amphibians, birds, mammals, and reptiles estimated with the climate-niche factor analysis (CNFA) approach.

computationally prohibitive for all vertebrate species. The final sample sizes were thus 4537 amphibians, 10,198 birds, 4721 mammals, and 7330 reptiles (Figure 3).

Because we considered only breeding ranges, we may have misrepresented the realized climatic niches of migratory species. However, considering nonbreeding 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 because CNFA requires the use of a 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 (congruent results are not shown). Finally, because coarser spatial resolutions are often used 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

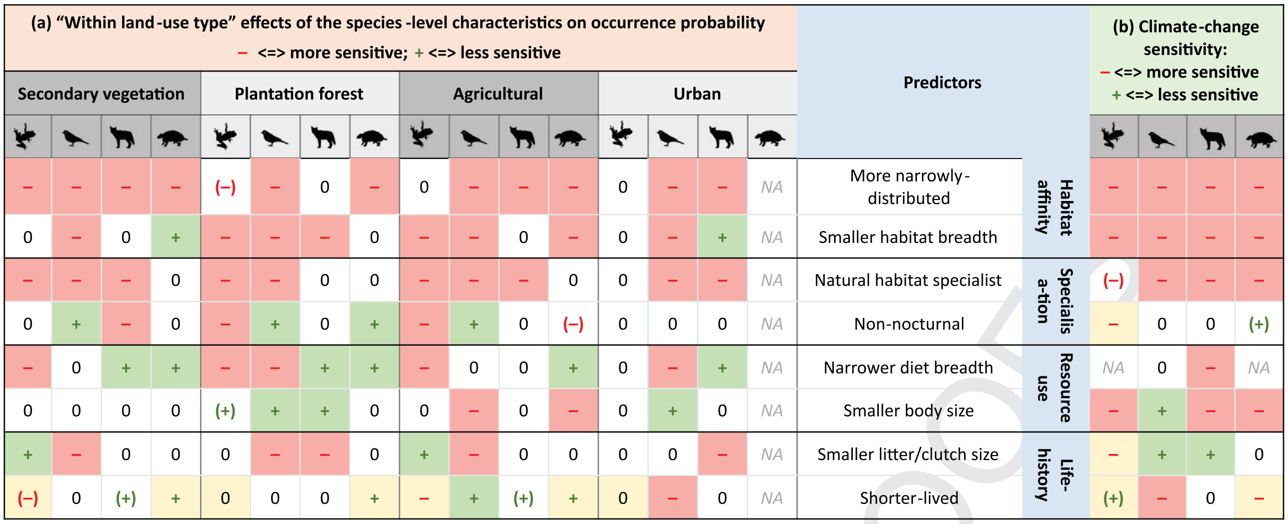
We used phylogenetic least-squares (PGLS) regressions, implemented in the caper R package 1.0.1 (Orme, 2012), to assess the effects of ecological characteristics on species estimated climate-change sensitivity while controlling for phylogenetic relationships among species. We combined the ecological characteristics and the phylogenies with 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 with 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 because there were many missing values). For the continuous predictors, we considered third-order polynomials to allow for nonlinear 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 and 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., nonimputed) trait estimates. We fitted first-order polynomials here because of the substantially reduced sample sizes.

RESULTS

Effects within land uses

Land-use, land-use intensity, and species ecological characteristics and their interactions had significant effects on species occurrence probability (Figure 4a & Appendix S6). Significant interactive effects between land-use and ecological



(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 4 Summary of the effects of the ecological characteristics (except for diet) on (a) species' responses to disturbed land-use types and (b) species' estimated climate-change sensitivity for each class of terrestrial vertebrates (**–**, characteristic has a significant negative effect on occurrence probability within a disturbed land-use type for any of the land-use intensities or the characteristic is significantly associated with a higher sensitivity to climate change; **+**, characteristic has a significantly positive effect on occurrence probability within a disturbed land-use type for any of the land-use intensities or is significantly associated with lower sensitivity to climate change; yellow shading, traits for which coverage was low before trait imputation [<40%]). Within-land-use-type effects are reported, which for a given disturbed land-use type denote whether there were significant differences in occurrence probability among species with different trait values (Figure 2).

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 4a). Across all classes, species with narrower geographic range areas, smaller habitat breadth, and an inability to exploit artificial habitats (i.e., natural habitat specialists) tended to show greater decreases in occurrence probability in disturbed land-use types than species with larger range areas, broader habitat breadth, and an ability to exploit artificial habitats. The exception was reptiles in secondary vegetation and mammals in urban areas, where smaller habitat breadth was associated with increased occurrence probability. The effects of the other ecological characteristics differed in direction depending on class and land use, impeding any generalization (Figure 4a). For instance, longer life spans were associated with decreases in occurrence probability in several classes and land-use types (e.g., birds in agricultural areas), yet we detected opposite effects in other land-use types (e.g., birds in urban areas).

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

Effects among land uses

In all classes, occurrence probability declined substantially for natural habitat specialists (i.e., species unable to exploit artificial habitats) in disturbed land-use types compared with primary vegetation (Appendix S6.2), whereas 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-use types (e.g., in intensely used agricultural areas [Appendix S6.2]). The occurrence probability of nocturnal and non-nocturnal species was negatively affected in disturbed land-use types compared with primary vegetation (Appendix S6.2), 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-use types (Figure 5). Overall, invertebrate eaters tended to be negatively affected in disturbed land-use types (e.g., −66% average decline in occurrence probability for amphibians in intensely used agricultural areas compared with minimally used primary vegetation). Omnivores were negatively and positively affected, depending on class and land-use type and intensity. Occurrence probability showed large decreases (e.g., −81% for reptiles in intensely used plantation forest) and increases (e.g., +43% for lightly used urban areas in birds). Overall, fruit and nectar eaters showed large declines in occurrence probability for mammals and birds, as opposed to plant and seed eaters, whose occurrence probability tended to be strongly and 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. There were some declines for mammals in agricultural areas (−75% on average in intense uses), but there were 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 in Appendix S6.3). However, when estimated from a Bayesian framework, the models' estimates were mostly

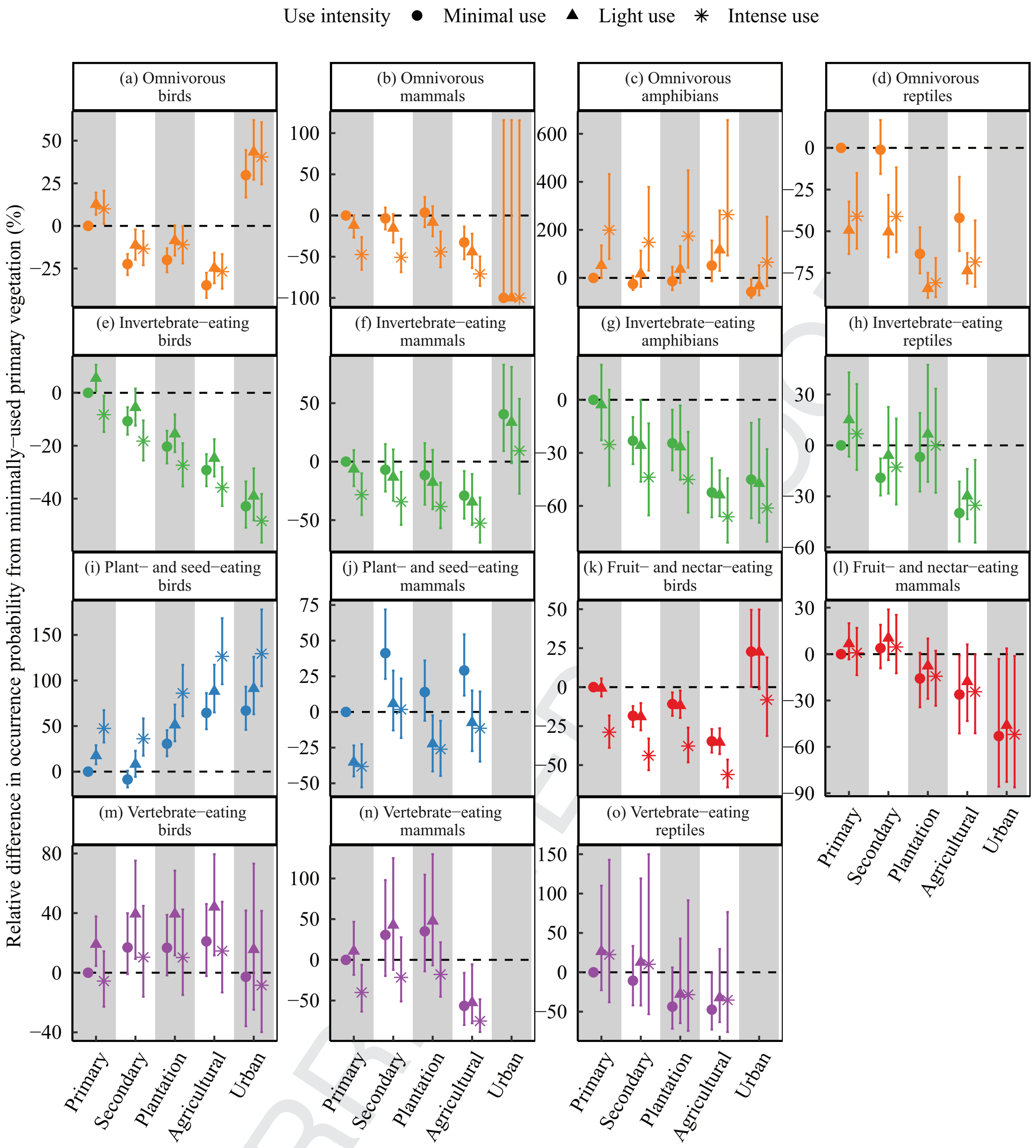


FIGURE 5 Predicted difference in occurrence probability relative to minimally used primary vegetation (%) as a function of land use, land-use intensity, diet, and their interactions for each class of terrestrial vertebrate (symbols, medians; bars, 95% confidence intervals; primary, primary vegetation; secondary, secondary vegetation; plantation, plantation forest; agricultural, cropland and pasture). Effects could not be estimated for urban reptiles or for urban vertebrate eaters, fruit and nectar eaters or plant and seed eaters for mammals because there were no sampled species. For some classes, there were no species in some of the diet categories (amphibians and reptiles, no fruit- and nectar-eating or plant- and seed-eating species; amphibians, no vertebrate-eating species).

congruent (Appendix S6.4), 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 4b & Appendix S7). Overall, climate-change sensitivity was highest for amphibians, followed by reptiles, mammals, and birds. In all classes, narrower geographic range area, smaller habitat breadth, and being specialized on natural habitats (i.e., not found to occur in artificial 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, associations varied in significance and direction. For instance, although we found negative associations between body mass and climate-change sensitivity for mammals, amphibians, and reptiles, there was a positive association for birds (Figure 4b). We additionally found invertebrate-eating, plant- and seed-eating, and omnivorous birds to be more climate-change sensitive than birds with other diet types, but we did not detect significant differences among dietary groups for mammals (Appendix S8). The PGLS models were robust to distributional assumptions (Appendix S9).

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, and 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, and 0.57 for reptiles). The effects that explained the most variation differed among classes; interactions between land use and habitat breadth explained the most variation for amphibians and birds, interactions between land-use intensity and body mass explained the most variation for mammals, and interactions between land use and life span explained the most variation for reptiles (Figure 6a).

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 geographic range area (about 60% in all classes [Figure 6b]), 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 6c). Body mass explained the most variation for mammals and reptiles, and litter and clutch size explained the most variation for amphibians and birds.

ROBUSTNESS TO REMOVAL OF IMPUTED VALUES

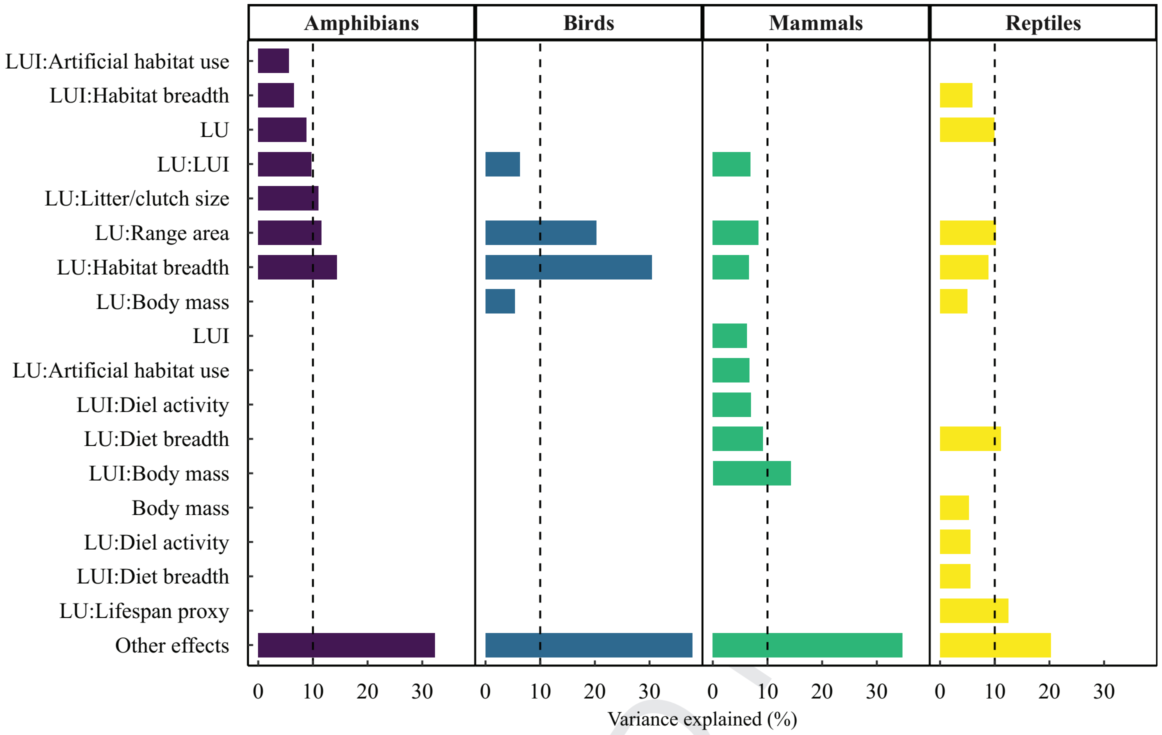
Running the models again with data subsets for which we had empirical, nonimputed values only for the ecological characteristics showed that our conclusions were likely robust to imputation uncertainty: across classes, the associations of geographic range area, habitat breadth, and use of artificial habitats with climate-change sensitivity and land-use responses were consistent with the main models (Appendix S10).

DISCUSSION

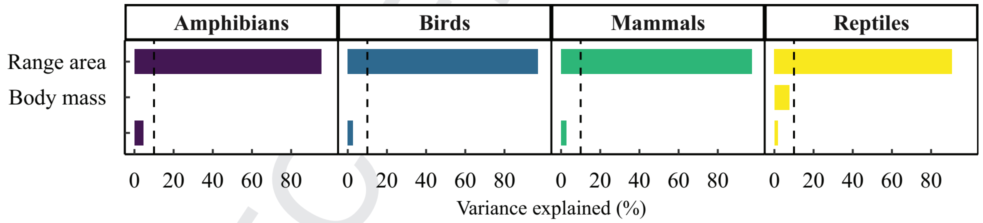
We investigated whether species ecological characteristics were associated with sensitivity to 2 major human pressures on biodiversity (land-use and climate change) across terrestrial vertebrate classes. Geographic range area, habitat breadth, and specialization on natural habitats were the only characteristics 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 show extinction risk is associated with habitat breadth and range area (Chichorro et al., 2019) and range shifts under contemporary climate change are associated with species' historical range limits and habitat breadth (MacLean & Beissinger, 2017). They also align 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, we are the first to compare associations among vertebrate classes and explicitly between 2 major human pressures. Our results have important implications for conservation because they mean that land-use and climate change are not randomly affecting terrestrial vertebrates. Species with narrower geographic ranges and natural habitat specialists (here, species unable to exploit artificial habitats) typically experienced significant declines in occurrence probability in disturbed land-use types and had consistently higher sensitivity to climate change, maybe because stricter niche requirements hinder adaptation to disturbed environments (Slatyer et al., 2013). The higher sensitivity of such species is concerning because they can support unique ecosystem functions complementing those supported by generalists (Dehling et al., 2021; Leitão et al., 2016; Loiseau et al., 2020). Further, geographic 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 specialization as being highly relevant for large-scale vulnerability assessments, such as in Foden et al. (2013).

Our results highlight context dependency in the associations between most other traits and responses to anthropogenic pressures. In the case of land use, we found that the directionality of the responses often depended not only on taxonomic class, but also on land-use type, further complicating the patterns. Contrary to Chichorro et al.'s (2022) findings on extinction risk, we did not find consistent associations between life-history traits (i.e., life span 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, whereas our approach relied on occurrence data captured at a single moment in time and thus was based on the assumption that populations were 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 contains taxonomic and geographic 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). Q5 For instance, because our results highlight the usefulness of traits for understanding species' sensitivity to human pressures, further work could investigate geographic variation in the associations across vertebrate classes, which was not possible here

(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)

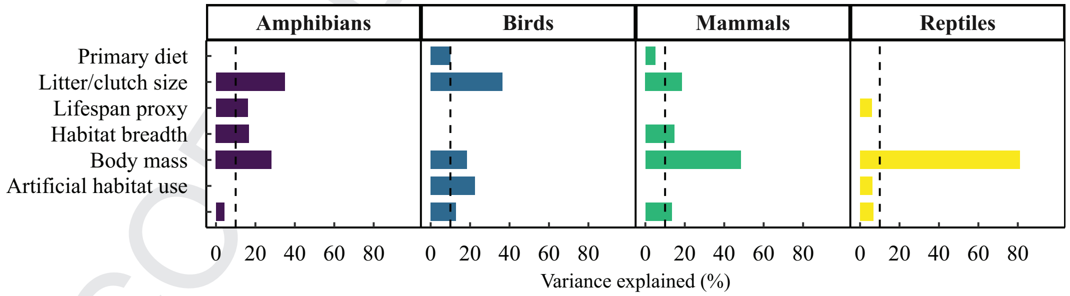


FIGURE 6 Percentage of explained variance attributable to each of the main effects for (a) the mixed-effects models that fitted the effects of land use, land-use intensity, and ecological characteristics on species occurrence probability (after factoring out residual variation); (b) the phylogenetic least-squares regressions used to investigate whether the ecological characteristics explained climate-change sensitivity (after factoring out residual variation); and (c) the phylogenetic least-squares regressions used to investigate whether the ecological characteristics explained climate-change sensitivity (after factoring out variance explained by geographic range area and residual variation) (dashed vertical lines, 10% explained variance; LU, land use; LUI, land-use intensity; other effects, effects that explain <5% of overall variation; PGLS, phylogenetic least-squares regressions).

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 [preprint]; 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 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 trait-based approaches yielded 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 the 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.

Characteristics we did not investigate 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 we did not consider. 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 are 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.

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). Although 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 researchers 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).

Our results indicated that land-use and climate change do not randomly affect terrestrial vertebrates 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 and nectar eaters. We also found higher climate-change sensitivity for invertebrate eaters and for plant- and 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, and pollination (Civantos et al., 2012; Fricke et al., 2022; González-Varo et al., 2013), which emphasizes the need for mitigation and conservation measures. By showing consistent effects of geographic range size and habitat specialization 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.

ACKNOWLEDGMENTS

This work was supported by a Royal Society University Research Fellowship to T.N. and a Royal Society Research Grant to T.N., which supported the PhD studentship of A.E. The authors thank Rhiannon Osborne-Tonner for her contribution to the diet data collection for amphibians and reptiles.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Etard, A., & Newbold, T. (2024). Species-level correlates of land-use responses and climate-change sensitivity in terrestrial vertebrates. *Conservation Biology*, e14208. https://doi.org/10.1111/cobi.14208