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Research Article

Species traits mediate terrestrial mammal density responses to human impacts

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Human activities are reshaping ecosystems, but their effects on species population density remain poorly understood. Most studies focus on species presence–absence, thus limiting insight into how anthropogenic pressures affect population density. Emerging evidence suggests that responses of natural populations to human disturbance are highly variable, often contingent on species-specific traits. Here, we test how species traits mediate the density responses of terrestrial mammal populations to different forms of human impact. We quantified the correlations between mammalian population densities and urban cover, cropland cover, and human population abundance, using 7785 population density estimates across 263 species belonging to 18 taxonomic orders. Using Bayesian inference, we then conducted three phylogenetically corrected correlation meta-analyses, and subsequently tested the effects of body mass, diet, and life history traits on the correlations using meta-regression models. We found no overall directional effect on mammal population density with any of the three human impact variables, however, responses to impact gradients deviated from these overall effects depending on species' traits. Omnivores and large-bodied species density was positively correlated with agricultural cover, herbivores and frugivores density declined with urbanization and human population density. We also found weaker evidence that large carnivores declined with human population abundance and urbanization, while reproductive strategy and velocity mediated responses to urbanization and cropland. Anthropogenic landscapes, where natural habitat is interspersed with anthropogenic land use and human settlements, do not support lower population density on average, but alter species relative abundance by favouring some species over others. Higher

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densities can result from multiple factors, including resource supplementation, ecological release effects due to the decrease or disappearance of competitor or predator species, or density compensation associated with shifts toward smaller-bodied assemblages. This study underscores the complexity of human–nature interactions and the importance of species traits in mediating ecological outcomes.

Keywords: agricultural landscapes, ecological filtering, human impact, population abundance, species vulnerability, trait-based ecology, urbanization

Introduction

Humans have long impacted the environment (Ellis et al. 2021), directly and indirectly, driving habitat destruction, pollution, climate change, and species invasions. These impacts, together with an increased rate of human exploitation of biodiversity, have contributed to a surge in extinctions (Ceballos et al. 2015), and rapid biodiversity changes, including measurable taxonomic (Dornelas et al. 2014, Blowes et al. 2019), functional (Barnagaud et al. 2017, Martins et al. 2023), and phylogenetic changes (Li et al. 2020). While much research has focused on species declines, recent studies highlight that the Anthropocene has produced both ‘winners’ and ‘losers’ (Dornelas et al. 2019, Leung et al. 2020), where some species thrive while others suffer due to human activities. Such contrasting responses can be largely explained by species traits that are linked with increases or decreases in fitness as selection pressures change (Pacifi et al. 2017, Suraci et al. 2021). Traits, such as body size, play a crucial role in determining species’ vulnerability to human activities and specific threats (Chichorro et al. 2019). In mammals, large-bodied species are often more sensitive to habitat fragmentation (Keinath et al. 2017) and more prone to human–wildlife conflicts or hunting, while smaller species may be more sensitive to habitat degradation (González-Suárez et al. 2013, Ripple et al. 2017). Diet and life history traits also shape species’ responses, with diet determining species’ adaptability to different resources and possible conflicts with humans (Barnagaud et al. 2018, Losada et al. 2024), and life history traits determining demographic responses to disturbance (Capdevila et al. 2022) and exploitation (Hutchings et al. 2012).

Previous studies investigating mammal responses to human impact gradients have mainly focused on changes in occurrence using occupancy models, and remained mostly biased towards medium- and large-sized mammals such as ungulates and carnivores. Such studies often depict a generalized negative impact of humans and associated activities on species occupancy at landscape or regional scale (i.e. proportion of occupied area; Cavada et al. 2019, Torre et al. 2022, Haight 2023, Milda et al. 2023), although some highlight diverse responses across species (Schuette et al. 2013, Goad et al. 2014, Suraci et al. 2021, Li et al. 2022). Yet, more rarely, such responses are associated with species traits (Suraci et al. 2021, Haight 2023). Surprisingly, few efforts have been made to explore human impacts on population density (number of individuals per unit area). This is

particularly key since, while occupancy is sometimes used as a proxy for density (Clare et al. 2015, Parsons et al. 2017), the relationship between occupancy and density trends is complex and scale-dependent, with species sometimes showing opposite patterns in occurrence and density (Parsons et al. 2017, Weber et al. 2017, Dallas and Hastings 2018, Santini et al. 2019a). Urbanization, for instance, may reduce occupancy due to habitat loss but increase local population densities in the remaining habitat due to resource concentration (Hubert et al. 2011, Kuhn 2014, Šálek et al. 2015). Thus, density can increase or decrease depending on the spatial scale of analyses. For example, Lewis et al. (2015) found that occupancy was insensitive to human impact gradients in large felids, whereas density decreased with increasing human impact, therefore suggesting that population density is a more sensitive and nuanced indicator of species responses to human impact gradients.

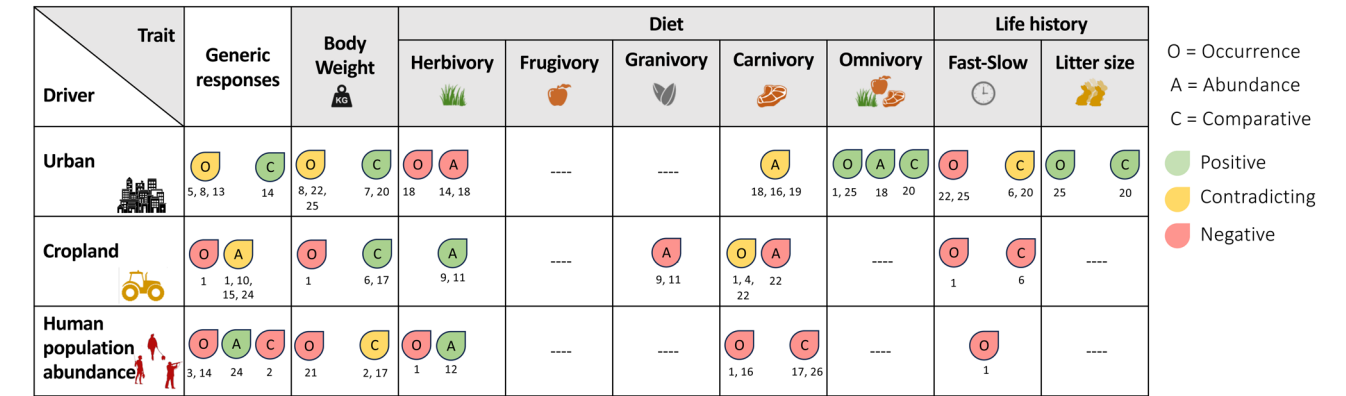
Comparative studies on actual species abundance remain limited due to data constraints (Callaghan et al. 2024). Meta-analyses focusing on changes in relative density in impacted areas have typically shown negative effects of human impact on mammal density (Benítez-López et al. 2010, 2017, 2019, de Jonge et al. 2022). Animal movement and home range comparative studies reported reduced movements in anthropogenic areas (Tucker et al. 2018, O’Donnell and DelBarco-Trillo 2020, Hirt et al. 2021, Broekman et al. 2024), possibly explained by higher resource availability for some species (Newsome et al. 2015), such as domestic animals for predators in peri-urban and rural areas (e.g. leopards *Panthera pardus*; Athreya et al. 2016) or crops for ‘crop raider’ species (e.g. baboons *Papio anubis*; Mamo et al. 2021), as well as crucial resources during seasonal shortages (e.g. jackal *Lupulella mesomelas*; Reasoner et al. 2024). Other studies found that species population densities increased along human impact gradients (Šálek et al. 2015, Tucker et al. 2021).

This paradox – where local densities increase along a human impact gradient – may be explained by factors such as ecological release, whereby the decline of some species allows others to increase, and the human shield effect, where prey species benefit from the absence of predators (Crooks and Soulé 1999, Terborgh et al. 1999, Berger 2007, Hoeks et al. 2020) and, in a minority of cases, by synanthropic species that thrive in highly disturbed habitat (e.g. rats, *Rattus rattus* and *R. norvegicus*; Cavia et al. 2009). Changes in landscape composition and diversity can further shape species responses mediated by their phenotypic traits or strategies. For instance, landscape simplification can negatively impact diversity but

increase the abundance of the species that persist, as shown in local studies (Pelosi et al. 2025). Additionally, multiple local studies have shown that marginal habitats can alter resource distributions or disturbance levels, favouring some species (Bayne and Hobson 1998, Passamani and Fernandez 2011, Lenz et al. 2014, da Rosa et al. 2018, Campera et al. 2022).

However, synthesizing responses to human impact across multiple species presents a methodological challenge. Species differ in their population densities and their exposure to the human impact gradient. The only study assessing average mammal response to human impact on a large set of species globally is the one by Tucker et al. (2021), which addressed the challenge using a mixed-effect modeling approach treating species as random effects. While this approach identifies general trends, it assumes a constant relationship across species and fails to disentangle intra- from inter-species variation. Furthermore, the uneven range of impact variables experienced by specialists versus generalists may bias results toward the latter. A more robust option involves using simple rank correlations for each species to inspect general monotonic trends. Although this method does not define the specific shape of relationships, it provides the flexibility to examine how traits influence correlations across many small samples while accounting for variations in sample size, and ensures that inference is focused on intra-specific variation in species response.

Here we assess the role of three human impact variables on the population densities of terrestrial mammals, and the role of traits in mediating these relationships. We first ran a meta-analysis aimed at estimating the average effect size of urban cover, cropland cover, and human population abundance. Contrary to studies at a more local scale (Panzacchi et al. 2010), we do not compare density in different habitat types (e.g. natural, cropland, urban), but rather examine changes in density along increasing proportions of these habitat types. As such, the responses we report can arise from the presence in, as well as occasional use of such habitats, the use of marginal habitats, and/or spillover effects. Subsequently, we ran meta-regression models to test the mediating effect of species body mass, diet, and reproductive traits on such correlations. Here we deliberately focused on traits that are not directly linked to habitat preferences (e.g. habitat generalism, forest specialism, synanthropic species) to avoid circularity. Based on previous research, body mass, diet, and reproductive traits are expected to influence species population density responses to urban, cropland, and human population abundance (Fig. 1). However, this empirical body of evidence is based on a limited number of studies, often relying on a small set of species and focused on different response variables (Fig. 1). Furthermore, existing theory and observations are at odds regarding the directional effect on species response due to the number of competitive mechanisms. For instance, if human impacts influence



(1) Bernard, et al. (2024). *Journal of Applied Ecology*, 61, 2470–2482; (2) Cardillo, et al. (2005). *Science* (1979), 309, 1239–1241; (3) Cavada, et al. (2019). *PLoS One*, 14, e0215682; (4) Ferreira, et al. (2018). *Mamm Rev*, 48, 312–327; (5) Goad, et al. (2014). *Biol Conserv*, 176, 172–182; (6) González-Suárez, et al. (2013). *Ecosphere*, 4, 1–16; (7) Hahs, et al. (2023). *Nat Commun*, 14, 4751; (8) Haight, J.D. (2023). *Nat Ecol Evol*, 7, 1654–1666; (9) Heroldová, et al. (2007). *Agric Ecosyst Environ*, 120, 206–210; (10) Kuipers, et al. (2023). *Glob Chang Biol*, 29, 6234–6247; (11) de la Peña, et al. (2003). *Landsc Ecol*, 18, 265–278; (12) Leite de Oliveira, et al. (2025). *Journal of Applied Ecology*, 62, 470–479; (13) Lewis, et al. (2015). *Ecological Applications*, 25, 1880–1895; (14) Li, et al. (2023). *Ecol Evol*, 13, e10634; (15) Panzacchi, et al. (2010). *For Ecol Manage*, 259, 1536–1545; (16) Pereira, et al. (2024). *Perspect Ecol Conserv*, 22, 55–62; (17) Ripple, et al. (2017). *Proceedings of the National Academy of Sciences*, 201702078; (18) Saito, et al. (2015). *Acta Oecologica*, 67, 34–39; (19) Šálek, et al. (2015). *Mamm Rev*, 45, 1–14; (20) Santini, et al. (2019). *Ecol Lett*, 22, 365–376; (21) Schuette, et al. (2013). *Biol Conserv*, 158, 301–312; (22) Suraci, et al. (2021). *Glob Chang Biol*, 27, 3718–3731; (23) Torre, et al. (2022). *Diversity*, 14, 133; (24) Tucker, et al. (2021). *Ecography*, 44, 1–13; (25) Weiss, et al. (2023). *Ecology*, 104, e4055; (26) Woodroffe, R. (2000). *Anim Conserv*, 3, 165–173

Figure 1. Evidence of natural population responses along gradients of three human impact variables, presented both as overall trends (i.e. trait-independent) and stratified by species trait. ‘Occurrence’ denotes studies investigating presence or occupancy, while ‘Abundance’ refers to studies evaluating responses on species abundance. ‘Comparative’ refers to comparative studies in conservation or macroecology investigating how traits influence species extinction risk or use of certain habitat types. This synthesis is not exhaustive but offers a representative overview of current multi-species studies, aiming to highlight emerging patterns and knowledge gaps in trait-mediated responses to human pressures.

resource availability, we expect the effect of urban and cropland cover, and human population, to be mediated by species diet, with omnivorous and granivorous species being favoured and herbivory and frugivory being disadvantaged (de la Peña et al. 2003, Heroldová et al. 2007, Saito and Koike 2015, Santini et al. 2019b). We also expect that increasing resource stability may differently affect species with diverse life history strategies, potentially favouring those adapted to more stable environments (Stearns 1976). In contrast, if human impacts occur via landscape modification, we expect urban and cropland effects being mediated by body mass and diet, with larger and carnivorous (more space-demanding) species responding more negatively (Keinath et al. 2017, Hirt et al. 2021). Finally, if human impacts occur through direct mortality, we expect human population abundance to show more negative responses in large-bodied, reproductively slow, and carnivore species (Ripple et al. 2017). In the face of these potentially conflicting mechanisms, a quantitative framework offers a powerful tool to disentangle specific trait-based responses from apparent idiosyncrasies.

Material and methods

To assess how mammal population density responds to human impact, we first extracted and filtered data from the TetraDENSITY 2.0 database, and intersected the density records with the three human impact layers (Fig. 2). We then calculated correlation coefficients between population density and human impact variables for each species using sets of comparable estimates, and standardized them into Fisher's z-scores while also estimating their variance based on sample size. Finally, we performed three meta-analyses to determine the average correlation and variability for each human impact variable, followed by meta-regression models to investigate how species traits influenced these responses across impact gradients (Fig. 2).

Data collection

Population density data

To test our hypotheses, we extracted population density estimates of terrestrial mammals from TetraDENSITY 2.0 (Santini et al. 2024). We only retained population density estimates with documented time, location, and estimation method. The method to estimate density can influence the estimate (Palencia et al. 2021), and should be accounted for in comparative analyses of density (Santini et al. 2018). Methods were broadly classified as Census, Counts, Distance sampling, Encounter models, Home range, Mark recapture, Minimum number alive, Mixture models, and Spatial capture–recapture (Santini et al. 2022). To align with our environmental variables, we excluded estimates collected before 1990. Estimates of non-native species are a minority in the dataset and comprise a small set of species in a limited number of locations (mostly islands). Hence, considering the different mechanisms explaining non-native species abundance (e.g. competition and predator release) and the imbalance of estimates, we removed all records referring to non-native populations. This

first selection resulted in 17 730 density estimates spanning 710 mammal species from 20 orders. We then excluded all species lacking trait data (see Biological trait data), resulting in 17 270 estimates for 659 species from 20 orders.

Finally, we aggregated the density estimates per species, location, and sampling method by averaging, resulting in 10 056 density estimates (Fig. 3). Here, location refers to the exact coordinates reported in the database, hence reflecting what was reported in the original studies. This dataset was then used to generate one dataset of correlation coefficients per human impact variable (see Data processing).

Overall, the dataset shows a wide global coverage, but is mostly limited to a few well-sampled taxa, namely ungulates, carnivores, primates, rodents, rabbits, and hares (Fig. 3). The species present a wide trait distribution, but small and insectivorous species are underrepresented (Supporting information). Because available population density estimates might be biased toward common or threatened species, potentially affecting the representativity of the sample and interpretation of the results, we compared the distribution of Red List categories for the species included in the dataset with the global distribution of Red List categories for terrestrial mammals (IUCN 2025). Species in the dataset show a similar distribution of Red List categories to the global distribution across mammals, with a slightly higher proportion of threatened species (Supporting information).

Biological trait data

To assess how species traits mediate responses to human impact, we extracted adult body mass and diet composition from the EltonTraits database for the retained species (Wilman et al. 2014). Diet in EltonTraits is coded as the percentage of consumption of different diet elements (e.g. carnivory, herbivory). As such, we followed Losada et al. (2024) to derive four dietary axes representing the variability in mammal diets. We derived these axes by converting all diet variables into fuzzy variables (0–1 scale), computing a Gower distance matrix (Pavoine et al. 2009), and performing a principal coordinates analysis (PCoA). The first four axes explained 88% of dietary variance (Supporting information). As in Losada et al. (2024), the first axis correlated positively with insectivory and negatively with herbivory, the second correlated negatively with frugivory, the third positively with granivory, and the fourth negatively with carnivory (Supporting information). To facilitate the interpretation, we multiplied by -1 the first, second, and the fourth axes, which we refer to as herbivory, frugivory, and carnivory, respectively. To these, we added an omnivory variable measuring deviation from an intermediate proportion of meat in the diet. We first computed the overall percentage of meat in the diet (%meat) and then defined omnivory as:

$$\text{Omn} = 50 - |\% \text{meat} - 50|$$

such that omnivory decreases linearly and symmetrically with increasing distance from 50% meat in the diet, reaching 0 when the diet consists of either 0 or 100% meat.

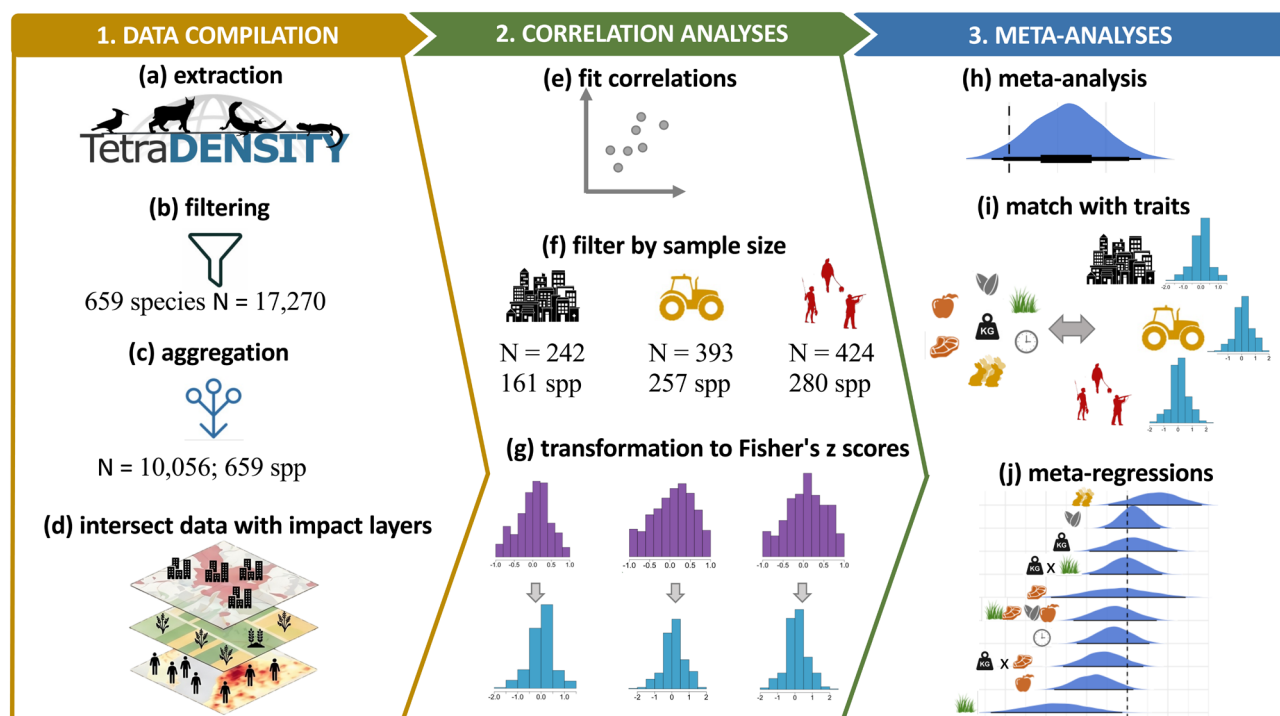


Figure 2. Schematic workflow of the analytical steps, from data compilation to the analyses. We (a) extracted data from the TetraDENSITY 2.0 database, (b) filtered them based on data completeness and nativeness, (c) and aggregated by species, location and sampling method. We then (d) intersected density records with the three human impact layers with a yearly temporal resolution. Subsequently, (e) we calculated Spearman's rank correlation coefficients between population density and human impact variables for each species, using sets of comparable estimates. From these, (f) we excluded all correlation coefficients based on fewer than four independent pairs of data, and (g) transformed them into Fisher's z-scores while also estimating their variance based on sample size. Finally, we (h) performed three meta-analyses to determine the average correlation and variability for each human impact variable, (i) matched the correlation coefficients with trait data, and (j) fitted meta-regression models to investigate how species traits influenced these responses across impact gradients.

In addition to diet, we characterized species life history traits, key parameters of a species' life cycle that reflect important aspects of their reproductive strategies (Paniw et al. 2018, Capdevila and Salguero-Gómez 2019, Healy et al. 2019). Using well-established approaches in comparative demography (Gaillard et al. 1989, Salguero-Gómez et al. 2016), we characterized life history traits using two axes: a fast-slow continuum variable represented by age at sexual

maturity, ranging from fast-living species to slow-living species, and reproductive strategy variable represented by litter size ranging from risk-averse species investing in small (high quality) litter size, to risk-taking species investing in large (low quality) litter size (Bielby et al. 2007). Sexual maturity age and litter size were extracted from the imputed version of the COMBINE database (Soria et al. 2021). To remove the effect of body mass from sexual maturity age and litter

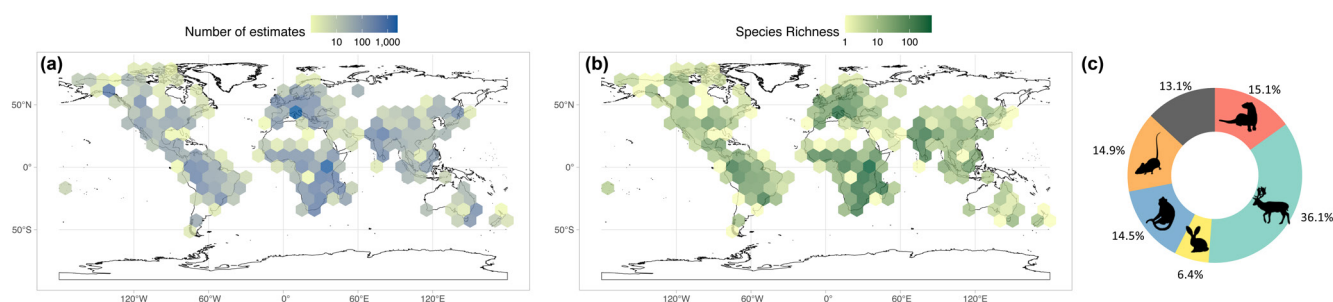


Figure 3. Mammal population density estimates retained for the final model ($n = 17\,270$; $n\text{ species} = 659$, large map) obtained from the TetraDENSITY 2.0 database (Santini et al. 2024). Hexagon maps report (a) the number of density estimates and (b) the number of distinct species per hexagon of 10 degree diameter. (c) The donut plot illustrates the taxonomic distribution of density estimates across the major taxonomic orders in the dataset (Carnivora, Cetartiodactyla, Lagomorpha, Primates, Rodentia). All remaining orders are represented in dark grey. Animal silhouettes obtained from www.phylopic.com.

size (Healy et al. 2019), we $\log_{10}$ -transformed both variables, regressed them by the $\log_{10}$ -transformed body mass, and retained the respective residuals for the next steps in our analytical pipeline. Fast–slow and reproductive strategy variables were then interpreted as their deviation from that predicted by adult body mass. We fitted the relationships using phylogenetic generalized least squares (PGLS) including the phylogenetic correlation structure based on the phylogeny in Upham et al. (2019) using the ‘nlme’ package (Pinheiro et al. 2024).

Environmental and human impact data

Our primary focus was on species population density responses to specific human pressures, namely cropland and urban land cover and human population abundance. Each population density estimate was linked to human impact variables at the corresponding geographic location. If the coordinates represented a single location, we calculated the average environmental values within a window of 0.1 degree around that location; if coordinates were reported as longitudinal and latitudinal ranges covering regions larger than a 0.1×0.1 degree, we calculated the average environmental value across the polygon covering the study area extent. To capture land-use effects, we extracted land use data from ESA CCI Land Cover (ESA 2017). The dataset provides annual land cover data at a 300 m resolution for the period 1990–2022. The land cover yearly layers were first reclassified into cropland (classes 10–40) and urban (class 190) separately, and then used to extract the percentage coverage of these land use categories. To assess the effect of human disturbance and potential exploitation, we used the GlobPOP gridded population dataset (Liu et al. 2024) that harmonizes human population gridded data from 1990 to 2020 at 0.0083 degrees-resolution. Land use, and human population density data were extracted for the years corresponding to the study period of the density estimates. If estimates covered a period spanning across the extremes of the time series (1990 and 2020 or 2022), we only considered the available years.

To assess the representativity of the sample in terms of gradients of impact covered, we compared the global distribution of impact values with the distribution of values across the species in our sample. Despite the high heterogeneity in the available data across species, the three datasets cover well the variation in human impact variable (Supporting information). We conducted GIS analyses using the ‘terra’ (Hijmans et al. 2021), ‘sf’ (Pebesma and Bivand 2023), and ‘sp’ (Pebesma and Bivand 2005) packages in R ver. 4.3.1 (www.r-project.org).

Data processing

To conduct the meta-analysis, we first calculated Spearman’s rank correlations between each human impact variable and population density. This was done separately for each species and sampling method category to capture monotonic relationships without assuming linearity (but see the Supporting information). We then excluded all correlation coefficients based on fewer than four independent pairs of density and

human impact variable values, as the sampling variance of such correlations cannot be reliably estimated (Viechtbauer 2010). Overall, we obtained impact–population density correlations for 282 species using a total sample of 8984 density estimates. Based on the correlation coefficients, we derived one dataset for each human impact variable: urban, cropland, and human population abundance. The ‘urban’ dataset included 242 correlation coefficients for 161 species across 15 orders, based on a total sample of 7330 density estimates. The ‘cropland’ dataset comprised 393 correlation coefficients for 257 species in 17 orders, based on a total of 8681 density estimates. Finally, the dataset assessing human population abundance contained 424 correlation coefficients for 280 species across 18 orders, based on a total sample of 8938 density estimates.

Meta-analysis

We estimated the effect of urban, cropland, and human population abundance on species population density using a Bayesian correlation meta-analytical mixed-effect model (Borenstein et al. 2009). We transformed the correlation coefficients to Fisher’s z scores using the `escalc()` function in the ‘metafor’ package (Viechtbauer 2010) in R ver. 4.4.2. We then fitted an intercept-only model to estimate the overall pooled effect size, weighting observations by their inverse sampling variance, using the ‘brms’ package (Bürkner 2017). The model included sampling methods as random intercept, while to account for phylogenetic non-independence we included a phylogenetic variance–covariance matrix based on the phylogeny in Upham et al. (2019). Priors for the intercept were set to normal distribution centered on 0 and with SD of 1. For the SD of the random effect we used a Student- t prior with 3 degrees of freedom, location 0 and scale 1. We used 4 Monte Carlo Markov chains (MCMC) implemented via Hamiltonian Monte Carlo (HMC), each comprising 4000 iterations, with the first 2000 used as warmups. The ‘adapt_delta’ parameter was set to 0.99 to avoid divergent transitions.

In a second step, we ran meta-regression models to test for the effect of moderators on the species response to the impact gradient. These models extended the previous meta-analytical models by including biological traits as fixed effects (moderators) to explain the observed heterogeneity in effect sizes. We included body mass, the four diet axes (herbivory, frugivory, granivory, carnivory), omnivory, and the fast–slow and reproductive strategy axes. As we expected carnivores and herbivores to respond differently to human impact depending on their body size, we also included the interaction between body mass and these two diet axes. Priors for the moderators were set to normal distribution centered on 0 and with SD of 1. We tested all predictor variables for collinearity; no pairs had Pearson’s $r > |0.7|$, ensuring their independent contributions to the model.

We summarized the posterior distributions of the effect sizes using the median and 95% credible intervals (CrI). For each coefficient, we also reported the probability of direction

(pd) using the ‘bayestestR’ package, an index of confidence in the effect that strongly correlates to the frequentist p-value (Makowski et al. 2019). Its value varies between 50 and 100% and describes the probability of the parameter being different from zero. We evaluated model convergence by inspecting the R-hat statistic, ensuring that all values were below 1.01 (Supporting information).

To evaluate model variance structure and decompose heterogeneity, we calculated variance components and generalized heterogeneity metrics following Nakagawa and Santos (2012). For all models, total variance was partitioned into phylogenetic variance, sampling method variance, and typical sampling variance (within-study sampling variance) calculated following Higgins and Thompson (2002). From these components we quantified total heterogeneity as the proportion of total variance not arising from sampling error, and partitioned this into phylogenetic structure and sampling method. For meta-regressions incorporating ecological traits, we reported the Bayesian marginal R^2 to measure total variance explained by fixed-effect moderators, alongside the relative reduction in variance compared to the intercept-only models.

Results

Species exhibited variable correlation coefficients across land-use and human impact gradients, with the majority showing positive associations with the proportion of urban area (55.3%), cropland (58.8%), and human population abundance (56.9%) (Fig. 4; Supporting information). Across all intercept-only models, total heterogeneity was high ($I^2 > 92\%$; Supporting information), driven almost entirely by phylogenetic structure ($I^2 = 91.4\text{--}93.1\%$).

However, we found no clear overall effect of urban area on species population densities (pd=52.7 %; median $\pm$ SD = -0.028 ± 0.375 ; 95% CrI: $-0.772\text{--}0.715$; Fig. 5a; Supporting information). Nonetheless, among moderators, herbivory (pd=98.2%; -0.173 ± 0.082 ; 95% CrI: -0.205 to -0.003) and frugivory (pd=95%; -0.082 ± 0.050 ; 95% CrI: $-0.180\text{--}0.015$) exhibited high probability of negative effects, indicating that the population density of herbivore and frugivore species decreases with urban coverage.

Reproductive strategy (pd=88.5%; 0.071 ± 0.059 ; 95% CrI: $-0.046\text{--}0.183$) and the interaction between body mass and carnivory (pd=87.9%; -0.058 ± 0.050 ; 95% CrI: $-0.158\text{--}0.039$) also exhibited moderately high probabilities of direction, respectively suggesting that mammals with large litters exhibit higher densities in urbanized landscapes, whereas large carnivores reach lower densities. Overall, ecological traits in the meta-regression explained 20.6% of the variance (marginal R^2) in species responses to urban area (95% CrI: $14.4\text{--}27.5\%$; Supporting information).

Similarly, cropland also showed no overall effect on species population densities (pd=58.8%; 0.108 ± 0.501 ; 95% CrI: $-0.883\text{--}1.119$; Fig. 4b; Supporting information). Despite the lack of overall signals, we observed several deviations (Fig. 5b). Omnivory (pd=98%; 0.103 ± 0.050 ; 95% CrI: $0.004\text{--}0.202$) and body mass (pd=97%; 0.102 ± 0.054 ; 95% CrI: $-0.004\text{--}0.208$) were associated with more positive responses to cropland, suggesting that omnivorous and large species are more likely to benefit in agricultural landscapes. We also found weak evidence of negative effect for frugivores (pd=86.3%; -0.054 ± 0.050 ; 95% CrI: $-0.150\text{--}0.045$), whereas slow-reproducing species (pd=87.2%; 0.058 ± 0.050 ; 95% CrI: $-0.041\text{--}0.155$) and granivore species exhibited positive effects (pd=84.2%; 0.036 ± 0.036 , 95% CrI: $-0.034\text{--}0.105$). The inclusion of ecological moderators accounted for 19.8% of the total variance (marginal R^2) across agricultural landscapes (95% CrI: $15.3\text{--}24.9\%$; Supporting information).

Finally, human population abundance showed no overall mean effect on population densities (pd=53.1%; 0.038 ± 0.424 ; 95% CrI: $-0.783\text{--}0.872$; Fig. 4c; Supporting information), but several traits displayed evidence of deviation from this overall effect (Fig. 5c). Herbivory (pd=97.8%; -0.148 ± 0.074 ; 95% CrI: -0.296 to -0.005) and frugivory (pd=99.1%; -0.104 ± 0.043 ; 95% CrI: -0.188 to -0.020) yielded evidence of negative effect. The interaction between body mass and carnivory had also a moderately high probability of directional effect (pd=89.6%; -0.061 ± 0.048 ; 95% CrI: $-0.158\text{--}0.033$), indicating lower densities of large carnivores in highly populated areas. In contrast, omnivory (pd=82.2%; 0.040 ± 0.043 ; 95% CrI: $-0.045\text{--}0.126$) showed relatively weak evidence of a positive association. Ecological traits explained 16.3% of the variance (marginal

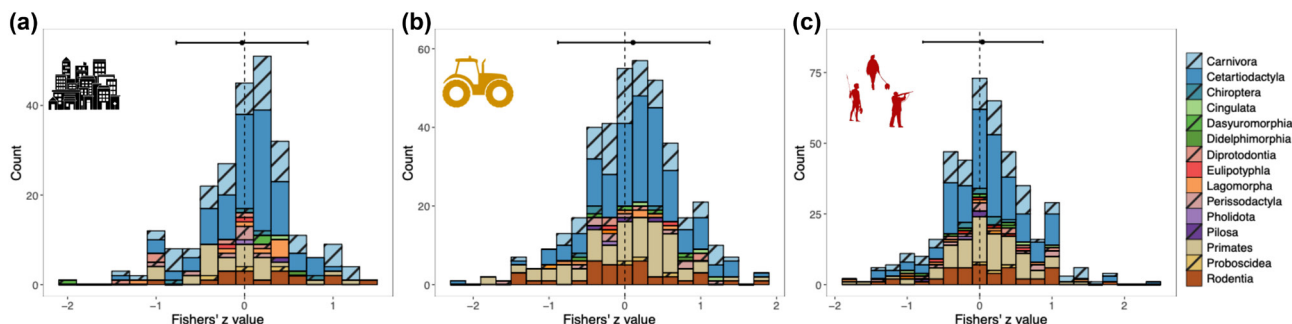


Figure 4. Distribution of Fishers' z values by taxonomic order across the three human impact variables: (a) urban, (b) cropland, and (c) human population abundance. The error bars indicate the overall pool effect size estimates ($\pm$ 95% CrI) from the three meta-analyses.

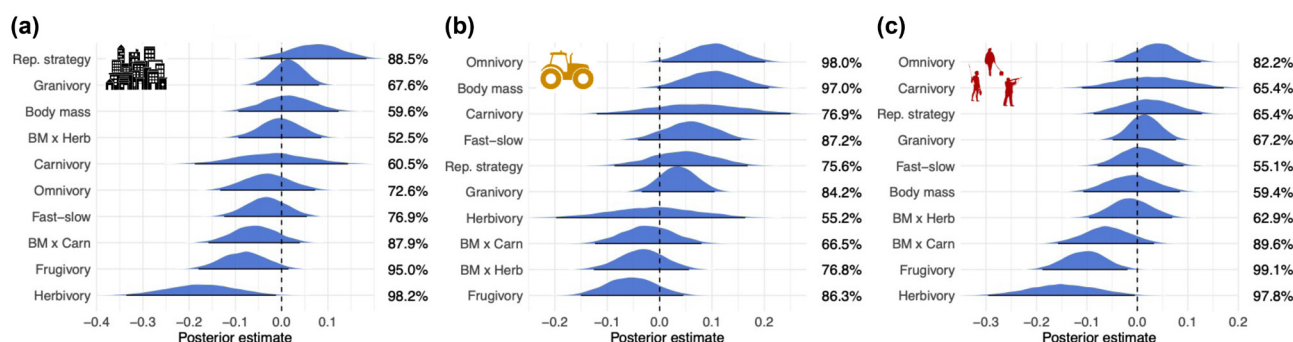


Figure 5. Posterior distributions of the species traits as moderators of the effect of the three human impact variables: (a) urban, (b) cropland, and (c) human population abundance. The effects represent the deviation from the intercept-only model. BM $\times$ Carn/Herb indicates the interaction term between body mass and carnivory or herbivory. The percentages are the probabilities of direction (pd), indicating the confidence that the effects differ from zero. Reproductive strategy ranges from small (low values) to large litter sizes (high values), whereas the fast-slow axis ranges from fast-living (low values) to slow-living (high values).

R^2) in response to human population abundance (95% CrI: 12.3–20.7%; Supporting information).

Discussion

As humans increasingly encroach on natural habitats, understanding how wildlife respond to human activities is essential for assessing their vulnerability to global change. Our results highlight substantial variation in population density responses depending on species size, diet, and life history traits, as well as the type of human impact.

Mammal population density in peri-urban areas

While a relatively small proportion of mammals are adapted to urban environments, either by entirely living in urban areas (urban dwellers) or benefitting from visiting them (urban visitors; Santini et al. 2019), here we focused on the effect of urban spillover; that is, the effect of increasing urban cover on neighbouring populations not occurring in cities. Although urban areas are sparse and occupy a small fraction of land surface, they exert important spillover effects in neighbouring areas. Urban areas can alter microclimate, increase the presence of humans and disturbance, are associated with the presence of infrastructure that might provide habitat cover structures, and influence mobility. Furthermore, waste production in these areas can provide additional trophic resources (Santini et al. 2019b). While we did not find an overall effect, in line with previous research (Saito and Koike 2015, Li et al. 2023) we observed a negative effect of herbivory indicating that highly herbivorous species tend to show lower densities in peri-urban areas. A decrease in herbivorous species density likely reflects changes in primary productivity (Pettorelli et al. 2009), which is reduced in urbanized landscapes, as well as hunting pressure, which is typically intensified near inhabited centers (Benitez-Lopez et al. 2019). The negative relationship with herbivores may also be interpreted as a positive effect for insectivores (at the other end of the axis), which are common urban-dwelling mammals (Santini et al. 2019b). Although some large carnivores, such as leopards *Panthera pardus*, may

adapt to urban landscapes (Bateman and Fleming 2012), and others like wolves can occupy highly anthropogenic areas, exhibiting high densities at intermediate distances from urban centers (Zanni et al. 2023), more sensitive species show lower densities in peri-urban landscapes (Lewis et al. 2015, Benson et al. 2019).

Unexpectedly, and contrary to previous research (Saito and Koike 2015, Santini et al. 2019b, Weiss et al. 2023, Bernard et al. 2024), omnivory did not show any effect, which may reflect the fact that our definition of omnivory related to the average percentage of meat in diet at the species level, does not directly account for flexibility (i.e. intra-specific variability). Conversely, we found species producing large litters to exhibit higher densities in peri-urban areas. This aligns with previous studies showing that such species are more likely to be typical urban visitors or exploiters (Santini et al. 2019b), and show higher occupancies in urban landscapes (Weiss et al. 2023). Although we did not detect a signal on the fast-slow axis, whose effect has been shown to vary across mammalian taxa (Santini et al. 2019b), our result is in agreement with comparative demographic work showing how faster-living species and more prolific species are more capable of taking advantage of disturbances (Capdevila et al. 2022), particularly in proximity of human settlements (Merrien et al. 2022).

Mammal population density in agricultural landscapes

Cropland expansion is one of the most important drivers of biodiversity change (Newbold et al. 2015, Rigal et al. 2023), replacing natural habitat while altering ecosystem structure and resource availability. While agricultural intensification generally reduces species richness, moderate levels of cropland can lead to increases in species abundance (Outhwaite et al. 2022). Our results show no consistent effect of cropland cover on the average mammal population densities, but also highlight that such effect varies substantially across functionally different species. In our analyses, large and omnivorous mammals showed positive

relationships with cropland cover. Although with weaker evidence, a positive effect was also observed in slow-reproductive and granivorous species. Larger species, thanks to their greater mobility, might exploit cropland areas without permanently residing in them by making foraging incursions from nearby natural areas. Furthermore, studies have shown small species to be more threatened by habitat conversion than large species (González-Suárez et al. 2013, Ripple et al. 2017). Omnivorous mammals have plastic diets allowing them to also benefit from agricultural landscapes (e.g. wild boar *Sus scrofa*). Similarly, granivorous mammals typically benefit from cropland due to increased seed availability; for instance, studies of rodents in Europe have shown that species such as mice (Muridae) can increase in abundance in seed-rich crops, while species such as voles (Cricetidae) can increase in abundance in crops with green biomass (de la Peña et al. 2003, Heroldová et al. 2007). The positive response of slow-reproducing species may stem from the more constant and predictable resource availability provided by agricultural landscapes (Stearns 1976). In contrast, frugivorous mammals showed negative relationships with cropland. Frugivory is typically associated with forest habitat, both in terms of mode of locomotion and trophic resources, so a negative effect is expected. Our analysis does not differentiate between agricultural types and intensity, which has been shown to produce diverse effects on species (Costa et al. 2021), but it supports the finding that the effect of cropland on mammal density is trait-dependent.

Mammal population density in highly populated areas

We did not find a consistent effect of human population density on wild mammal density. However, we observed a negative effect on herbivores, large carnivores, and frugivores, as well as an apparently positive effect – though less certain – on omnivores. Our findings align with previous studies supporting a strong association between human population density and the decline of large carnivores (Woodroffe 2000), which explains the extensive global range contractions observed in this group (Wolf and Ripple 2017).

The effect on herbivores is more complex to interpret, as several factors that may influence their densities in densely populated landscapes in opposing directions. Herbivores may suffer from direct exploitation or from competition with livestock, both of which contribute to explain the large-scale collapse of large herbivores (Ripple et al. 2015). Conversely, large herbivores may benefit from the absence of large carnivores (Wardle and Bardgett 2004), and in some regions like Europe from supplemental feeding and hunting regulation (Carpio et al. 2021). In contrast, smaller herbivores can be exploited, as well as penalized by the meso-predator release effect (Prugh et al. 2009). Our results support a generalized negative effect on herbivores but not on its interaction with body mass, suggesting no clear difference between small and large herbivores. Understanding the underlying mechanisms would require moving beyond purely correlative approaches that rely on indirect proxies of impact.

A note of caution

Here, we modeled the response to three human impact gradients across a large set of mammal species globally, resulting in no clear directional effect. By using rank correlations we focused on monotonic increases or decreases, while not making a priori assumptions on the shape of the relationship. This is because, while considerable data are available overall, the amount of data per species based on similar methods is typically small, or at least insufficient to investigate non-linearities (Supporting information). However, local studies have indicated non-linear hump-shaped relationships, with peaks in density at moderate impact levels (Li et al. 2023, Hansen et al. 2024, Allen et al. 2025). Symmetric hump-shaped relationships would yield no correlation, but asymmetric or truncated relationships might lead to positive or negative relationships. Assuming no systematic bias in the distribution of data along the impact gradients, or systematically asymmetric hump-shaped relationships, this would not be a problem. However, it is plausible that the majority of data comes from natural and semi-natural areas, while a minority of estimates are available in highly anthropogenic areas or areas where species are rare. As such, while we highlight heterogeneous responses to impact gradients, our results must conservatively be interpreted as the heterogeneous effect of moderate levels of human influence on the environment. However, this does not diminish the relevance of the results, because while human influence is now pervasive and can reach high values locally (Venter et al. 2016), global coverage of cropland is around ~ 20%, urban areas ~ 1%, and human population distribution is highly skewed and concentrated in a minority of areas (Supporting information). As a consequence, our results depict a trend from more natural to more anthropogenic landscapes, which is representative of the global context (Supporting information).

Our results are correlative in nature, and largely based on the space-for-time substitution assumption, which implicitly assumes that the realized densities are in equilibrium with the level of impact (Damgaard 2019). For instance, temporary crowding due to displacement may contribute to the correlations; however, these are short-term responses that can introduce noise but are unlikely to bias a global analysis.

Finally, uncertainty remains high around many results (e.g. life history traits), although some show evidence in the expected direction. This suggests that, considering the many sources of uncertainty around population density estimates, available data may still be insufficient to test some hypotheses.

Conclusions

The ecological and conservation literature has often highlighted a general impact on human presence and land use transformation on biodiversity, e.g. focusing on patterns of occupancy with increasing human impact that can be explained by habitat loss and species avoidance ('landscape of fear') (Cavada et al. 2019, Torre et al. 2022, Haight 2023,

Milda et al. 2023). This body of literature has also highlighted diverse responses across species (Schuette et al. 2013, Goad et al. 2014, Suraci et al. 2021). Yet, rarely have such differences been explained while explicitly incorporating species traits (Suraci et al. 2021, Haight 2023). Population density is expected to be a more sensitive metric of species response to human impact (Lewis et al. 2015, Callaghan et al. 2024). Our findings highlight that moderate levels of human modification and presence both positively and negatively affect mammal population density, while also highlighting a clear role of traits on species response, which in some cases differ from previous research focusing on occupancy (Suraci et al. 2021, Haight 2023). These findings challenge the notion that human influence is universally negative on wildlife population abundances, suggesting instead that while some species decrease or disappear, many other species adapt and thrive in anthropogenic landscapes.

Overall, human impact probably generates two contrasting effects: a decrease in species richness due to increased absence of some species, and a concomitant increase and decrease in the abundance of remaining species (Cazalis 2022). Such an increase likely stems from competitor and predator release effects (Crooks and Soulé 1999, Terborgh et al. 1999, Hoeks et al. 2020). Furthermore, while we excluded non-native species from the analyses, these can provide abundant resources for native predators (Pintor and Byers 2015). Pristine areas are therefore likely characterized by richer communities living at low density, while anthropogenic areas are characterized by depleted communities where some species live at higher density. This is analogous to what is observed in insular ecosystems, which are poorer in species but exhibit higher average abundances (the so-called 'island syndrome'; MacArthur et al. 1972, Adler and Levins 1994). Hence, a general increase in abundance can reflect a gradual impoverishment of communities. This would explain the apparent discrepancy between the absence of an overall signal in the intra-specific patterns found in this study, and the positive cross-species pattern observed by Tucker et al. (2021): while an approximately equal number of species show positive or negative relationships, anthropogenic areas are mostly occupied by species living at high densities. Yet, increasing evidence suggests that species richness is not universally decreasing, due to the expansion of generalist and non-native species (Dornelas et al. 2014). An alternative, non-mutually exclusive explanation is based on the community-level downsizing driven by anthropogenic pressures (Ripple et al. 2015, Wolf and Ripple 2017, Benítez-López et al. 2019, Martins et al. 2023). As communities become increasingly depleted of large species, energy is redistributed among smaller organisms, which can attain higher population densities. However, the data we used do not allow us to directly test the concomitant trend in richness, abundance, community composition, body size distribution, and energy flux or biomass. Further research integrating different types of data (Dennis et al. 2019, Callaghan et al. 2024, Loft et al. 2025) will be essential to understand how biodiversity is restructuring under human influence.

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Author contributions

Luca Santini: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (lead). **Diana E. Bowler:** Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Roberto Salguero-Gómez:** Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Inês S. Martins:** Visualization (equal); Writing – review and editing (equal). **Franziska Shrodt:** Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Romain Frelat:** Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Mickael Hedde:** Writing – review and editing (equal). **Naia Morueta-Holme:** Writing – review and editing (equal). **Pierre Gaüzère:** Writing – review and editing (equal). **Cyrille Violle:** Writing – review and editing (equal). **Romain Goury:** Writing – review and editing (equal). **Joaquim Estopinan:** Writing – review and editing (equal). **Miriam Beck:** Writing – review and editing (equal). **Wilfried Thuiller:** Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

The dataset and code used in this work are available from the Figshare digital repository: <https://figshare.com/s/8f0991578bdadea3ca4e> (Santini et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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