Global effects of land use on biodiversity differ among functional groups

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Authors' Contributions

TN and AP conceived the study; TN, LFB, SLLH, EEB, BC and AP designed the analyses; TN, MJE, MH, GS and CHS collated the functional trait data; TN and LFB carried out the analyses; TN wrote the manuscript with contributions from all authors.

Data accessibility statement

The biodiversity data are already publicly available (DOI: 10.5519/0066354). The size-class and trophic-level data will be made publicly available on FigShare upon acceptance of the manuscript.

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Abstract

1. Human land use has caused substantial declines in global species richness. Evidence from different taxonomic groups and geographic regions suggests that land use does not equally impact all organisms within terrestrial ecological communities, and that different functional groups of species may respond differently.
2. We present the first global synthesis of land-use responses across functional groups using data from a wide set of animal species, including herbivores, omnivores, carnivores, fungivores and detritivores; and ranging in body mass from 2×10^{-6} g (an oribatid mite) to 3,825 kg (the African elephant).
3. We show that the abundance of large endotherms, small ectotherms, carnivores and fungivores (although in the last case, not significantly) are reduced disproportionately in human land uses compared with the abundance of other functional groups.
4. The results, suggesting that certain functional groups are consistently favoured over others in land used by humans, imply a substantial restructuring of ecological communities. Given that different functional groups make unique contributions to ecological processes, it is likely that there will be substantial impacts on the functioning of ecosystems.

Keywords

Land use, functional groups, biodiversity, ecosystem structure, ecosystem function, global

Introduction

Despite increased conservation effort, biodiversity continues to decline globally (Tittensor et al., 2014), but our understanding of the nature and drivers of biodiversity decline remains incomplete. Among the pressures on biodiversity, land use (including both expansion and intensification) is predominant (Maxwell, Fuller, Brooks, & Watson, 2016), but broad-scale studies of its effects on biodiversity have lagged behind those on the effects of climate change (Titeux et al., 2016). Recent years have seen the development of global models of land-use impacts on biodiversity (e.g. Newbold et al., 2015). However, these models have ignored potentially important variation in responses among groups of species (e.g. Newbold et al., 2015, but see Gibson et al., 2011).

One approach that could yield improved insights into biodiversity responses to land use is to divide species into functional groups that share similar ecological traits. Organisms within functional groups interact with each other and with their environment in a similar fashion (Blondel, 2003), and thus it is likely that responses to environmental changes will be relatively similar within but different between functional groups. Traits often used to define functional groups include body mass, diet (often simply trophic level) and thermal strategy (i.e. endothermy vs. ectothermy) (Harfoot et al., 2014). Body mass is likely to be particularly important in determining species' sensitivity, because it correlates with the rates of many important ecological processes such as feeding and metabolic rates (Brose et al., 2005; Brown, Gillooly, Allen, Savage, & West, 2004). The traits used to divide animal species into functional groups have often been shown to correlate with species' sensitivity to environmental changes. In small-scale studies, species in the highest trophic levels (i.e. predators) are often the most sensitive to habitat loss and fragmentation (Barnes et al., 2014; Gilbert, Gonzalez, & Evans-Freke, 1998; Smith & Schmitz, 2016; but see e.g. Simons, Weisser, & Gossner, 2016). Similarly, larger species are often more sensitive to land-use changes than smaller species (Newbold et al., 2013; Rytwinski & Fahrig, 2011). Understanding how different functional groups respond to environmental changes such as land-use change may also increase our understanding of the consequences of biodiversity change for ecosystem functioning. Studies have suggested that the diversity of functional groups within ecological communities is important for sustaining key ecosystem functions (Larsen, Williams, & Kremen, 2005; Soliveres et al., 2016).

There are several mechanisms that may lead to differences in responses to land use among functional groups. First, plant biomass is known to be reduced in land used by humans compared with natural habitat, first by land conversion and subsequently by crop harvesting (Haberl et al., 2007). On the other hand, changes in the nature of the vegetation may mean that the amount edible biomass is unchanged or even increased. Given the inefficiencies in the movement of energy up food chains, a reduction in plant biomass would mean disproportionate impacts of human land use on species in the highest trophic levels and – by association – of the largest size (Fretwell, 1977). Indeed, bottom-up effects of land-use change on higher trophic levels have been shown to be important in small-scale studies (Barnes et al., 2017). Second, key resources such as fruit, nectar, detritus or fungus (e.g. Baude et al., 2016; Oehl et al., 2004), which are needed by particular groups of animal species, might be lacking in land used by humans, whether or not plant biomass is reduced overall. However, this may not be the case in all human-used areas. For example, fungal diversity has been shown to be retained in organic farming systems (Oehl et al., 2004). A lack of key resources would be likely to cause declines in the dietary guilds that eat them (i.e., frugivores, nectarivores, detritivores and fungivores, respectively). Third, conversion of land to human use is almost always associated with fragmentation of the remaining natural habitat (Ewers & Didham, 2006). Among species that depend on natural habitat, strong dispersers are more likely than poor dispersers to move around remaining natural habitat patches and into non-natural land uses. Although many factors determine species' dispersal ability, across all animals there is a general tendency for larger organisms to be better dispersers, although this correlation is weak (Jenkins et al., 2007) and not linear for all trophic levels (Stevens et al., 2014). Overall though, we would expect the fragmentation associated with land use to lead to disproportionate declines of small organisms in human land uses. Alternatively, fragmentation is also associated with reductions in plant biomass (Haddad et al., 2015; Laurance et al., 2007), which could lead to disproportionate impacts on large-sized organisms via bottom-up effects (see above). Indeed, previous studies of the effects of fragmentation on bird body mass obtained rather mixed results (Bregman, Sekercioglu, & Tobias, 2014). Fourth, land-use change might indirectly affect biodiversity via changes in local climatic conditions. Land used by humans has substantially higher surface temperatures than nearby natural vegetation (Senior, Hill, González del Pliego, Goode, & Edwards, 2017). Higher temperatures may influence organisms through changes in thermoregulation ability. Specifically, larger endotherms conserve more heat (Blackburn, Gaston, & Loder, 1999) and thus might be more adversely affected by increased temperature than smaller endotherms. By contrast, large ectotherms, which gain heat from the environment more slowly than small ectotherms, might benefit from increased temperatures (Blackburn et al., 1999). Finally, land conversion might impact biodiversity through an associated increase in hunting of wild animals, facilitated by increased access as a result of the development of new roads (e.g. Benítez-López et al., 2017). Hunting will directly affect only the larger-sized organisms in an ecological community, and probably herbivores more than carnivores (Fa, Ryan, & Bell, 2005). Other mechanisms, such as indirect effects via top-down regulation, may also contribute to observed patterns, but our spatial database and correlative models were not sufficient to detect such patterns.

In this study, we investigate how land use affects the total abundance of organisms in different functional groups, as defined by species' size classes, trophic levels and thermal regulation strategies (i.e. endotherms vs. ectotherms). We analyse over 1 million records from 460 published studies, for over 20,000 species of invertebrates and vertebrates, at 13,676 sites, in all of the world's terrestrial biomes. We predict that carnivores and the largest organisms will be disproportionately negatively impacted by human land use, given the large reduction in available plant biomass associated with land conversion and crop harvesting. If other mechanisms play an important role, we may expect exceptions to this general pattern. First, large ectotherms, which may benefit from the warmer conditions in human land uses, are expected to experience less negative effects. Second, if fragmentation is important, we may expect smaller organisms, which generally have lower dispersal ability, to have the largest reductions in human land use. Third, hunting may lead to disproportionately large effects of human land use on large herbivores rather than large carnivores. Separately, we also predict that guilds that depend on key resources found most commonly in natural habitats (specifically detritivores and fungivores) will be less abundant in human land uses than in natural habitats.

Methods

Community composition data

Community composition data were taken from the database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) Project (Hudson et al., 2017). These data, extracted from the database on 1st July 2015, consisted of 1,184,542 records of the abundance of animal species, including all major terrestrial vertebrate and many invertebrate taxa (Hudson et al., 2017). The data represented 13,676 sites, from 424 studies, in 324 publications (listed in the Supporting Information). Sampled sites were located within 80 countries, and all of the world's 14 terrestrial biomes (Dinerstein et al., 2017). Most of the community composition data were originally collected in the field between the years 2000 and 2015 (Hudson et al., 2017). Sampling at most sites in the PREDICTS database spanned a distance of tens to hundreds of metres (inter-quartile range: 22 to 160 m). For the 16% of studies where sampling effort varied among sites, we corrected reported abundance measures by assuming that recorded abundance increases linearly with sampling effort (Hudson et al., 2017). To do so, we rescaled sampling effort within each study to have a value of one for the most-sampled site(s). We then divided all abundance values that are sensitive to sampling effort by this rescaled effort value. More sophisticated corrections of the abundance estimates were not possible because in most cases the authors of the original studies did not repeat biodiversity surveys at each site.

Each site's land use was classified, based on the description of the habitat given in the source publications, into 6 broad classes: primary vegetation (natural habitat with no recorded history of complete destruction), secondary vegetation (natural habitat known to have been destroyed in the past, but now recovering toward its natural state, divided according to stage of recovery into young, intermediate or mature), plantation forest (areas planted with tree or shrub crops), cropland (areas planted with herbaceous crops), pasture (areas regularly or permanently grazed by livestock), and urban (areas of human settlement, or areas managed for amenity). Three levels of human use-intensity were distinguished – minimal, light and intense – using criteria that depended on the land use in question (e.g. selective logging and bushmeat harvesting for natural habitats; and crop diversity, pesticide inputs and livestock densities for agricultural areas). For full details, see Hudson et al., (2017).

Functional group classification

We obtained estimates of the thermal strategy (endothermy or ectothermy), adult body mass and adult trophic level for as many of the animal species in the PREDICTS database as possible. For thermal strategy, mammals and birds were classified as endotherms, and all other species as ectotherms.

We classed species into one of four broad body-size classes (< 2 g, 2 - 20 g, 20 - 200 g, and > 200 g). For many of the best-sampled taxonomic groups (beetles, ants, arachnids, reptiles, amphibians, mammals and birds), species-level estimates of adult body mass were obtained from a combination of scientific and grey literature (see Table S1 for sources), interpolating missing values as the average of the value for congeners. For the remaining invertebrate groups, we used family-level estimates (sources in Table S1) calculated as the geometric mean of the minimum and maximum values reported for each family. Although such estimates are coarse, and ignore the often substantial variation in body mass within invertebrate families, any errors should have a very minor effect across the very broad ranges of body mass that we considered. We used such coarse body-size classes, rather than finer clade-specific divisions or even continuous species-level measures of body mass, because our intention in this study was to model total abundance changes in broad functional groups, and thus to infer changes to the overall structure of ecological communities.

Species' trophic level was classified as herbivore (feeding only on plants), omnivore (feeding on both plants and animals), carnivore (feeding only on animals), fungivore (feeding on fungi) and detritivore (feeding on detrital matter). The last category encompasses species feeding on carrion (necrophages), decaying organic matter (saprophages), and faecal matter (coprophages). Species with non-feeding adult stages were excluded. Species-level estimates of adult trophic level were available for beetles, ants, mammals and birds from a variety of sources (Table S1). Where trophic-level estimates were not available for a species, but where at least 95% of congeners belonged to one trophic level, we used this majority estimate. For the remaining invertebrate groups, and for reptiles and amphibians, we used family-level estimates (sources in Table S1). Where the available information indicated that at least 95% of species within a family belonged to one trophic level, then all species within the family were assumed to belong to that trophic level. Families that did not meet this criterion were excluded.

The data set used here represents a total of 25,166 animal species (1.8% of the number estimated to have been described: Chapman, 2009). All species could be assigned a thermal strategy; 22,244 could be assigned an estimate of either adult body mass or adult trophic level; 18,317 species had estimates of mass; 18,752 had estimates of trophic level; and 14,825 (1.0% of the estimated number of described animal species) had both (Table 1). There was a reasonable geographical spread of sites sampled for all functional groups, although large parts of Asia were under-sampled for several functional groups (Fig. 1). The spread of data across different taxa for each functional group was approximately as expected, with biases toward vertebrates (especially birds) and, within the invertebrates, toward insects (Table S2).

Statistical analysis

To test the overall effects of land use on different functional groups, we modelled the site-level total abundance of organisms in each functional group in response to land use. We were unable to model community functional composition itself as a response variable, because not all of the original published studies sampled all functional groups. For the initial models, we classified land use very coarsely, into primary vegetation, secondary vegetation, and human-used habitat (all agricultural and urban land uses). As functional groups, we considered combinations of body-size class and thermal strategy or combinations of body-size class and trophic level. It was not possible to consider combinations of all three traits simultaneously owing to the relatively small number of data available. For each functional group, log-transformed total abundance was related to land use using a linear mixed-effects model. A value of 1 was added to all total abundance estimates prior to transformation because the dataset contained zero values. Random intercepts were study identity (to account for the variation in sampled total abundance caused by differences in sampling methodology among the original studies) and spatial block within study (to account for the spatial structure of the sites sampled). Because our models were constructed at the site level, it was not necessary to include a random intercept to account for species identity. We also included a random slope of land use nested within study, to account for among-study variation in the effect of each land use. The AIC values of the land-use models were compared to AIC values of equivalent null models (i.e. random effects only).

To further investigate the effects of different intensities of land use on functional groups, we compared models fitting more refined classifications of land use. Specifically, we considered six different classifications of land use: 1) the same coarse classification as above, but excluding urban sites (there were too few urban sites to consider separately); 2) contrasting plantation forests with other agriculture (cropland and pasture), since the vertical structure and cooler local climate of plantation forests might benefit certain functional groups relative to more open agricultural habitats; 3) as in 2, but subdividing plantation forests and agriculture by land-use intensity (the three levels of intensity were collapsed into two – minimal vs light/intense – owing to the relatively small numbers of sites for some functional groups); 4) considering all human land uses as a single class, but subdividing secondary vegetation by stage of recovery toward natural habitat architecture (young, intermediate and mature), since secondary vegetation in an earlier stage of recovery is likely to have lower vegetation biomass; 5) dividing secondary vegetation by stage of recovery, and human land uses into plantation forest and agriculture; and 6) dividing secondary vegetation and human land use, and further subdividing the human land use by use intensity (two classes). These models were compared based on AIC values. For these models, we did not divide trophic levels by body-size class because some of the resulting data subsets would have been too small for modelling.

Results

Response to land use

Considering all human land uses together, the effects on different functional groups varied markedly. For ectotherms, species in the smallest size class (i.e. < 2 g) had a clear negative response to human land use (compared with null model, ΔAIC = -12), the second smallest size class (2 – 20 g) responded less negatively and with more uncertainty (ΔAIC = -1.2), whereas for the larger two size classes (20 - 200 g and > 200 g) there was little evidence of a response to land use (ΔAIC = 2.9 and -0.1, respectively; Fig. 2a). The opposite pattern was observed in endotherms, with weak evidence of a negative response to land use only for species in the largest size class (> 200 g) (ΔAIC = -2; for all other size classes, ΔAIC > 0).

For all but the largest size class, carnivores responded more negatively to human land use than herbivores (Fig. 2b), showing clear reductions (ΔAIC < -5) while herbivores did not (ΔAIC > 0). For the largest size class (> 200 g), herbivores (ΔAIC = -13) responded more negatively than carnivores (ΔAIC = +1; Fig. 2b). For no size class did omnivores respond negatively to land use, and in fact omnivores between 2 and 20 g showed a weak positive response (ΔAIC = -1.4; for all other size classes, ΔAIC > 0; Fig. 2b). Fungivores responded more negatively to human land use than all other trophic levels, although with high uncertainty (ΔAIC = -1.4; Fig. 2b). Larger detritivores also showed a relatively strong (but uncertain) negative response to land use (ΔAIC = -5.5), but smaller detritivores did not (ΔAIC = +3.1; Fig. 2b).

Response to land use and land-use intensity

The response of several functional groups (all individual trophic levels and ectotherms in all size classes except 20 – 200 g) showed clear differences depending on the intensity of human land use and/or stage of recovery of secondary vegetation (Figs. 3 – 5; Tables S3 & S4). Carnivores, small ectotherms and (to a lesser extent) herbivores tended to have lower abundance in more intensively used than in minimally used land (Figs. 4 & 5). This pattern was reversed for fungivores, with slightly higher abundance in intensively used land. Carnivores and fungivores were also less abundant in secondary vegetation at an earlier stage of recovery than in more mature secondary vegetation (Fig. 5). For large ectotherms the opposite pattern was observed, with the highest abundance in secondary vegetation at an earlier stage of recovery (Fig. 4).

Discussion

Overall, our results show that effects of land use are non-random across functional groups, implying that human land use causes a restructuring of ecological communities. Although previous geographically or taxonomically restricted analyses have shown that functional groups respond differently to land-use change (Barnes et al., 2014; Gilbert et al., 1998;

Newbold et al., 2013; Rytwinski & Fahrig, 2011; Simons et al., 2016; Smith & Schmitz, 2016), by conducting a global analysis using data from multiple taxonomic groups, we were able to find some general patterns. Small ectotherms, large endotherms, carnivores and fungivores (although in the last case not significantly) typically declined more in human-used land than other functional groups, with reductions of 25-50% compared to natural habitat. Our results support previous suggestions that the world's ecosystems are being functionally restructured, with disproportionate losses of the highest trophic levels (Estes et al., 2011). On the other hand, the largest carnivores were affected surprisingly little by human land use (Fig. 2). This is likely because most large carnivores, and probably the most sensitive species in particular, have been filtered by human activities historically and so no longer remain even in natural habitats (Balmford, 1996).

Given that different functional groups make a unique contribution to ecological processes, the patterns that we see will likely have important effects on ecosystem functioning (Brose et al., 2005; Brown et al., 2004; Estes et al., 2011; Larsen et al., 2005; Soliveres et al., 2016). In particular, carnivores play an important role in managing the sizes of populations at lower trophic levels, and so their generally large losses in response to human land use is likely to have substantial effects on the structure of whole ecosystems (Estes et al., 2011). An exception to the general trend of carnivores responding more negatively to human land use than herbivores and omnivores was seen for the largest size-class. For this largest size-class, herbivores showed a strong negative response. This result could be a signal of hunting by humans, which is a major pressure particularly on vertebrate biodiversity (Maxwell et al., 2016), and which may be facilitated by the increased accessibility to human-used areas. The loss of large herbivores will also likely have important effects on ecosystem functioning, for example increasing the risk of rodent-borne human disease (Young et al., 2014).

The results generally conformed to theoretical expectations. The conversion of land to human use is associated with removal of a large proportion of the natural plant biomass, and in many cases much of the biomass is removed for consumption by humans or livestock (Haberl et al., 2007). Through bottom-up resource limitation, which has been shown to be an important mechanism behind land-use impacts at small scales (Barnes et al., 2017), we expect a disproportionate effect on organisms at the highest trophic levels (Fretwell, 1977), which also tend to have the largest body masses. At least for endotherms, negative impacts on large-sized organisms via bottom-up effects may be compounded by the local climatic conditions that result from land-use change, because their thermoregulation ability will be most impacted by the hotter temperatures typically prevailing in human land use compared with natural habitats (Blackburn et al., 1999; Senior et al., 2017). For ectotherms by contrast, effects mediated through thermoregulation are expected to affect most negatively organisms of the smallest size (Blackburn et al., 1999). Consistent with these predictions, we found that carnivores tended to decline more than herbivores and omnivores, that there was a tendency toward stronger declines of larger than smaller endotherms (although none of the individual responses were significant), and that the smallest ectotherms responded most negatively to land use (Fig. 2). Furthermore, carnivores and small ectotherms showed the greatest decreases in land used most intensively by humans, where vegetation changes are likely more profound (Haberl et al., 2007) (Figures 4 & 5). In general, effects of trophic level were clearer than effects of body mass, which could point toward other factors distorting differences among size classes. For example, human land use is almost always associated with habitat fragmentation (Ewers & Didham, 2006), which would likely have the greatest effect on smaller organisms that tend to have lower dispersal abilities (Jenkins et al., 2007). A general caveat of correlative models, such as we present here, is that we cannot rule out alternative mechanisms. In addition to the predictions for herbivores, omnivores and carnivores, we also predicted that land use may have strong negative effects on detritivores and fungivores, because land used by humans tends to be depauperate in the decaying matter and fungi on which these groups feed (e.g. Oehl et al., 2004). Although uncertainty on the responses of these groups was high, probably owing to the relatively small sample sizes, our results generally matched this expectation. The relatively high abundances of fungivores in agricultural land (Figure 5) may reflect the fact that fungal diversity can be maintained in some farming systems (e.g. in organic farms; Oehl et al., 2004).

Understanding differences in responses across functional groups can help to guide the development of more refined models of human impacts on ecological communities. Most previous broad-scale biodiversity models have assumed that all species respond equally to land use (Newbold et al., 2015), or have divided species into broad clades (Gibson et al., 2011). Considering how the abundance of different functional groups is changing in response to environmental disturbances allows insights into the restructuring of ecological communities. In addition to statistical biodiversity models, recent years have seen the development of mechanistic models of ecosystem structure, although these models still have an inadequate representation of human impacts such as land-use change (Harfoot et al., 2014). Results such as ours can help to ensure that ecosystem models make more realistic predictions of changes in ecosystem structure.

All broad-scale models have limitations, with a few caveats that are particular to this study. Although the PREDICTS database is the largest and most representative of its kind (Hudson et al., 2017), sampling of animal species is biased toward vertebrates (especially birds) and certain invertebrate groups (insects). Whether this might lead to some systematic bias in the patterns reported here remains unclear. Furthermore, fitting models that group all organisms within coarse functional groups, based on coarse size and diet data, is likely to mask considerable variation among species, both among (Birkhofer et al., 2017; Birkhofer, Smith, Weisser, Wolters, & Gossner, 2015) and within (De Palma et al., 2015) different taxonomic groups. To explore fully the differences in the responses of functional groups to land use, we would ideally sample all organisms within multiple different land-use types in a consistent manner, or at least would sample organisms across multiple functional groups. Even the latter approach is rare (but see e.g. Barnes et al., 2014; Simons et al., 2016). In order to generalize patterns globally, it is necessary therefore to collate data from multiple data sources, and to account for differences in sampling methodology and the environment using hierarchical models. In so doing, we must assume that any observed differences driven by differences in sampling protocols or environment are random with respect to functional group. Another caveat is that our models relied on spatial comparisons of biodiversity in different land uses. This precludes a consideration of time-lagged responses. Furthermore, the responses that we modelled here may lead to indirect effects on other functional groups (e.g. through trophic cascades, Schmitz, Hambäck, & Beckerman, 2000), which we were not able to capture in our spatial models.

Conclusions

We show, globally and across many taxonomic groups, that the impacts of human land use do not fall equally on functional groups. Large endotherms, small ectotherms, carnivores and fungivores are disproportionately impacted by human land use. This result suggests that ongoing land-use changes are profoundly altering the functional structure of ecological communities. Further alterations to community structure are likely, given that more conversion to human land uses will almost certainly be needed to feed the human population. Ideally, we need mechanistic models that embody our understanding of ecological processes and how human actions affect them. However, current mechanistic terrestrial ecosystem models are limited in their treatment of human impacts (e.g. Harfoot et al., 2014). Large global syntheses can help to guide the development of ecosystem models toward producing realistic predictions of the effects of environmental changes. Although much work remains to understand better how human land use influences ecological communities, our results show that changes to the structure communities are probably more profound than suggested by simple models of overall biodiversity.

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Figures

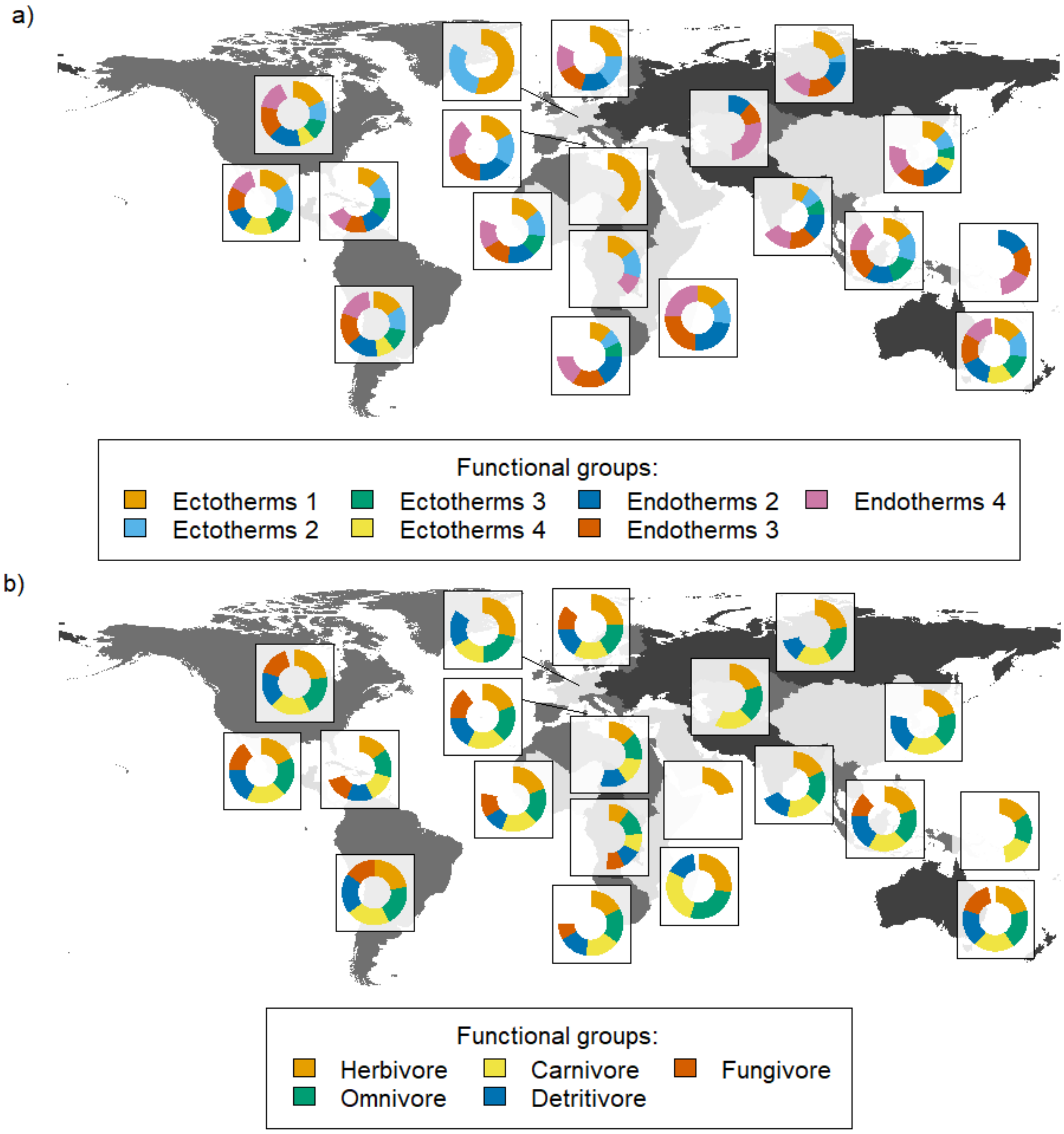

Figure 1. Global distribution of data for the functional groups included in the analysis: a) combinations of body-size class (1: < 2 g; 2: 2 – 20 g; 3: 20 – 200 g; 4: > 200 g) and thermal strategy (endotherms and ectotherms); b) trophic levels. Doughnut plots are shown for each United Nations sub-region, which are indicated on the map by different shades of grey. Lines connect the doughnut plots to their respective sub-regions, when it was not possible to achieve a complete overlap. The proportion of each doughnut's total circumference that is coloured is proportional to the total (log-transformed) number of sites sampled in a sub-

region. Individual colours are shown in proportion to the (log-transformed) number of sites sampled for each individual functional group.

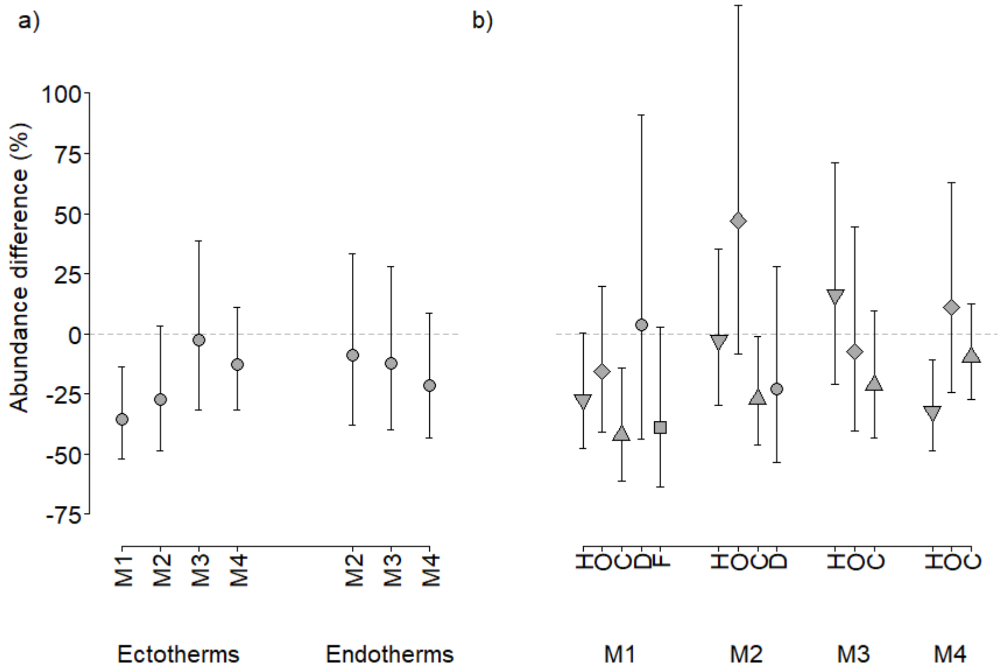

Figure 2. Relative total abundance of different functional groups of species in human-dominated land uses (cropland, pasture, plantation forest and urban) compared with primary vegetation. Negative values indicate lower, and positive values higher, overall abundance in human-dominated land uses compared with primary vegetation. Error bars show 95% confidence intervals. Each panel divides species by body-size class: M1: < 2 g; M2: 2 – 20 g; M3: 20 – 200 g; M4: > 200 g. Panel a further splits each size class by thermal strategy (ectotherms and endotherms); while panel b splits each size class by trophic level (H = herbivores, O = omnivores, C = carnivores, D = detritivores, and F = fungivores).

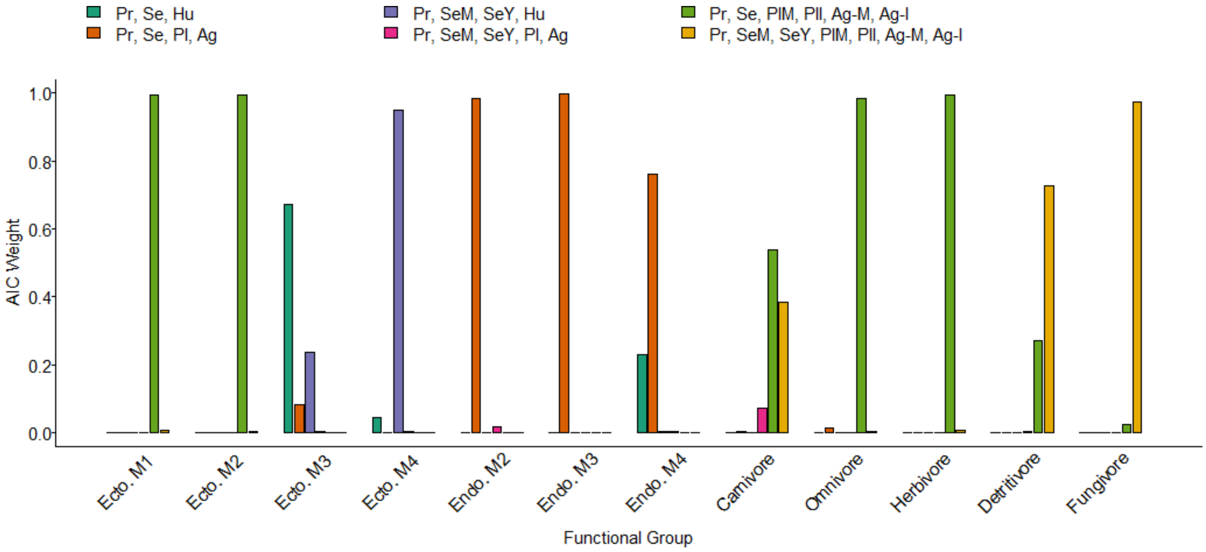

Figure 3. Comparison of model fit for land-use classifications of different degrees of complexity. The main models used a coarse land-use classification (simply dividing land use into primary vegetation, Pr, secondary vegetation, Se, or human-disturbed, Hu). Alternatively, we tested models that divided human-disturbed land use into plantation forests (Pl) and non-plantation agriculture (Ag), that further subdivided these human land uses into minimal (-M) and intensive (-I) use-intensity, that divided secondary vegetation into an early (SeY) and late (SeM) stage of recovery, and combinations of these. Relative model fit is shown as the AIC weight (across all six models, AIC weights sum to one).

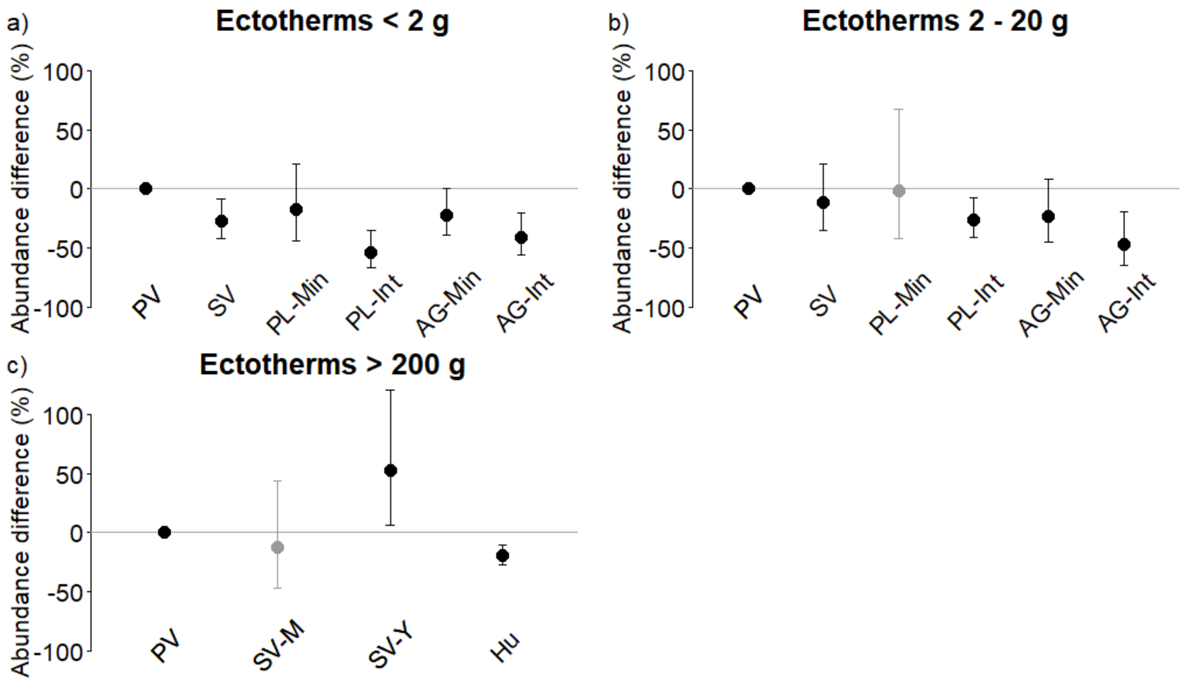

Figure 4. For combinations of body-size class (M1: < 2 g; M2: 2 – 20 g; M3 20 – 200 g; and M4: > 200 g) and thermal strategy (endotherms or ectotherms), relative total abundance in different land uses and land-use intensities, compared with primary vegetation (PV). Land use and intensity classes considered were: secondary vegetation (SV), at a later stage of recovery (SV-M), or at an earlier stage of recovery (SV-Y), plantation forest (PL), less intensively (PL-Min), or more intensively (PL-Int) used by humans; agriculture (arable cropland and pasture; AG), less intensively (AG-Min), or more intensively (AG-Int) used by humans. Functional-group combinations are only shown if a model that divided human land use in different intensities and/or secondary vegetation into different stages of recovery was better (ΔAIC < 0) than the models that grouped all secondary vegetation or human land use together. For each functional group, the division of land use shown here is the one that led to the best-fitting model. Error bars show 95% confidence intervals. Bars coloured grey indicate functional-group-land-use combinations for which there were fewer than 100 sampled sites.

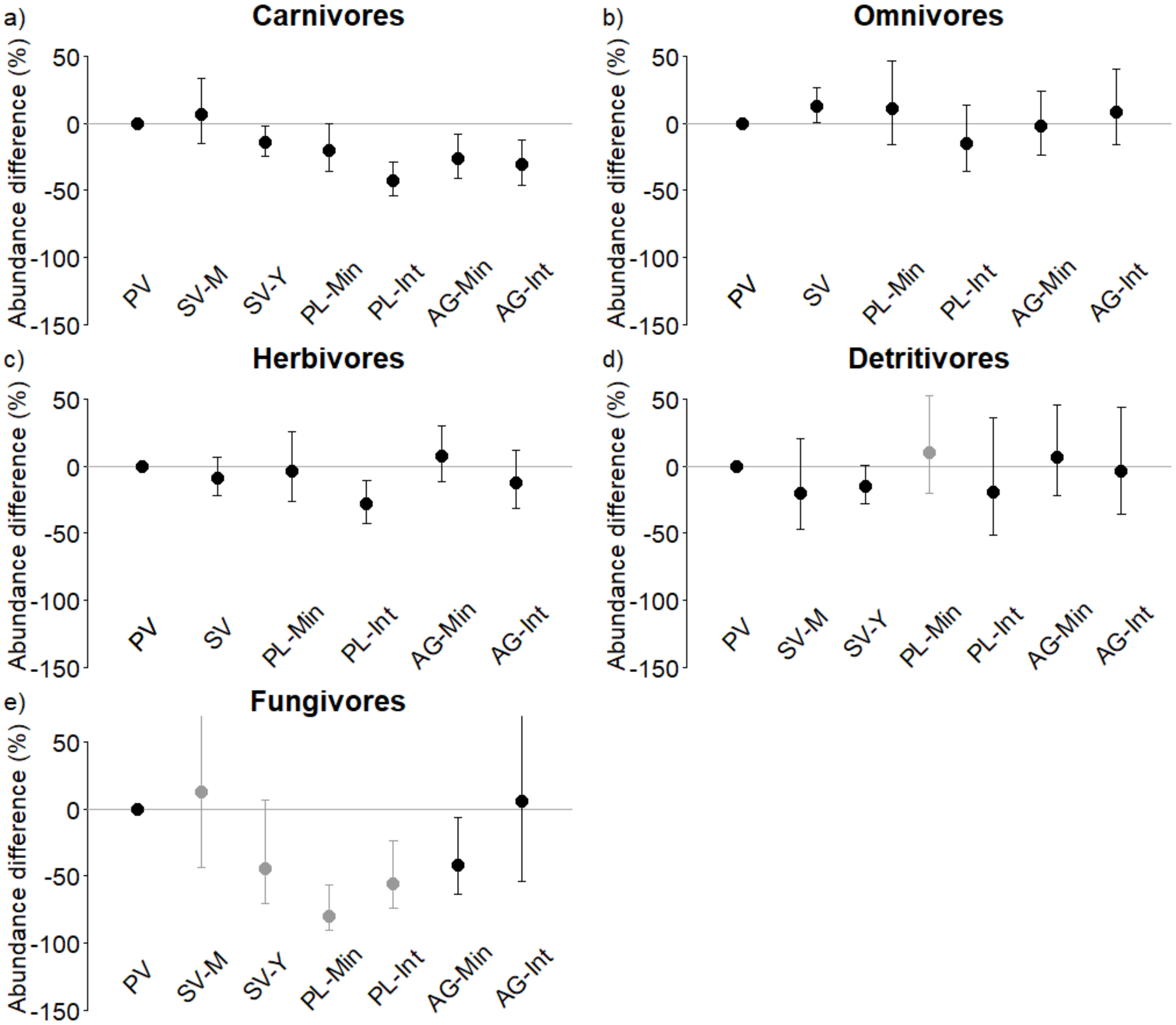

Figure 5. For each trophic level, relative total abundance in different land uses and land-use intensities, compared with primary vegetation (PV). Land use and intensity classes considered were: secondary vegetation (SV), at a later stage of recovery (SV-M), or at an earlier stage of recovery (SV-Y), plantation forest (PL), less intensively (PL-Min), or more intensively (PL-Int) used by humans; agriculture (arable cropland and pasture; AG), less intensively (AG-Min), or more intensively (AG-Int) used by humans. Trophic levels are only shown if a model that divided human land use in different intensities and/or secondary vegetation into different stages of recovery was better (ΔAIC < 0) than the models that grouped all secondary vegetation or human land use together. For each trophic level, the division of land use shown here is the one that led to the best-fitting model. Error bars show

95% confidence intervals. Bars coloured grey indicate trophic-level-land-use combinations for which there were fewer than 100 sampled sites.

Tables

Table 1. Numbers of species (spp.), sites or data-source studies for which we had data on either body mass or trophic level, or for body mass and trophic level individually. Numbers are shown for all species (in the first row), and for different taxonomic subsets of the data (subsequent rows). We divided species into Phyla (vertebrates, arthropods, molluscs and annelids), and then further sub-divided into individual Classes (shown in italics).

Group	**Body mass or trophic level**			**Body mass**			**Trophic level**		
	Spp.	**Sites**	**Studies**	**Spp.**	**Sites**	**Studies**	**Spp.**	**Sites**	**Studies**
All	22,244	14,789	460	18,317	13,486	418	18,752	14,344	446
Vertebrates	5,899	7,084	174	5,790	7,084	174	5,498	7,005	170
Amphibians	417	959	34	367	959	34	359	956	33
Reptiles	356	1,010	30	322	1,010	30	162	898	22
Mammals	581	1,660	55	581	1,660	55	559	1,660	55
Birds	4,545	4,724	94	4,520	4,724	94	4,418	4,724	94
Arthropods	16,293	7,452	277	12,527	6,469	246	13,202	6,964	265
Insects	14,297	6,894	257	10,746	5,911	226	11,284	6,402	244
Arachnids	1,848	958	38	1,707	954	37	1,770	958	38
Chilopods	25	342	8	22	342	8	25	342	8
Diplopods	13	216	3	13	216	3	13	216	3
Entognaths	110	204	7	39	188	5	110	204	7
Molluscs	35	351	9	0	0	0	35	351	9

Annelids	17	165	7	0	0	0	17	165	7