

Energetic constraints and trophic group explain species persistence in disturbed land uses

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Keywords

Land use; land-use intensity; metabolic rates; energetic constraints; energetic requirements; terrestrial vertebrates; trophic group; occurrence.

Abstract

Land-use change is the primary driver of global biodiversity loss. In terrestrial vertebrates, previous work has shown that sensitivity to land-use change depends on species traits, but the extent to which energetic constraints explain species' responses to disturbed land uses remains largely unexplored. Here, I investigate relationships between the energetic requirements of terrestrial vertebrates (estimated from resting metabolic rates) and land use, at two levels of organisation. First, at the assemblage level I hypothesize that total energetic requirements in disturbed land uses are lower than in undisturbed land uses, assuming that there is less energy available in disturbed areas overall. Second, after controlling for the effects of body mass and taxonomy on metabolic rates, I predict that species with relatively lower energetic expenditure are favoured over species with relatively higher energetic expenditure in disturbed land uses, as resource efficiency will be beneficial in these resource-poor environments. Because trophic group influences species' ability to assimilate various types of food, I investigate whether my predictions are consistent among trophic groups (here, omnivores, carnivores or herbivores). The results challenged both hypotheses. I found that total assemblage-level energetic requirements did not systematically decrease in disturbed land uses. For instance, I detected significant increases for urban areas, highlighting that disturbed areas may not be as energy-poor

as I initially assumed. Second, I found a positive effect of metabolic rates (after controlling for body mass and taxonomy) on species probability of occurrence across all trophic groups for at least one of the most disturbed land uses I considered (pasture, cropland and urban). Some species for which there are exploitable resources in disturbed environments may benefit from having larger mass-independent energetic expenditure: they may display a set of characteristics rendering them more able to cope with disturbances and more able to acquire available resources, such as higher activity levels or bigger brain sizes. The findings of this Chapter highlight that land-use change has substantial impacts on vertebrate community metabolism.

1 Introduction

Land-use change is currently the strongest driver of global biodiversity declines (Maxwell et al., 2016; Newbold et al., 2015), with major and long-lasting impacts on the structure and functioning of ecological communities (Bregman et al., 2016; Fukasawa and Akasaka, 2019; Magioli et al., 2021; Marcacci et al., 2021). With land-use change likely to continue to intensify (Stehfest et al., 2019), it is vital to put into place conservation and mitigation measures to minimise future losses of biodiversity and negative impacts on ecosystem functioning. To this end, pressing questions remain as to what renders species able or unable to cope with human disturbance, and how losses of sensitive species might influence ecosystem functioning (Dirzo et al., 2014; Young et al., 2016).

Land-use change acts as an environmental filter affecting species persistence (Edwards et al., 2021; Evans et al., 2018). Past studies have shown that sensitivity to land-use change is distributed unevenly across the tree of life (Nowakowski et al., 2018), and across behavioural (Lowry et al., 2013; Samia et al., 2015) and ecological strategies (De Palma et al., 2015; Møller, 2009; Newbold et al., 2013). For instance, long-lived and large forest specialist birds respond more negatively to land-use change than generalist species (Newbold et al., 2013). In addition, human land uses impose energetic constraints on species, by modifying the amount and type of available resources (Inger et al., 2016; Zuñiga-Palacios et al., 2021). Consequently, land-use change brings about modifications in dietary and foraging strategies (Møller, 2009; Ramesh et al., 2017; Sévêque et al., 2020), which can have cascading effects on local trophic structure (e.g., mesopredator release; Crooks and Soulé (2010)). The impacts of land-use change on biodiversity also depend on land-use intensity (Davison et al., 2021; Newbold et al., 2015), that is, the magnitude of human disturbance in a given land-use type, which can vary importantly according to local practices and management (Dullinger et al., 2021). In particular, land-use intensity affects the types and availability of resources (by homogenising resources for example), which in turn may affect biodiversity patterns (Weiner et al., 2011).

Energetic requirements are likely to be important predictors of species' ability to cope with a disturbed environment where resource availability and resource types are strongly impacted (Auer et al., 2020). Past research has shown that metabolic rates (the amount of energy required for organismal maintenance and for other processes such as growth and reproduction) are heritable and subject to selection, for instance with species in energy-rich environments having evolved faster metabolic rates than species in less energy-rich environments (Mueller and Diamond, 2001). However, metabolic rates have received less attention than other life-history traits in studies aiming to understand different species' responses to land-use change. Body mass, known to explain much of the variation in metabolic rates (Bushuev et al., 2018; Hudson et al., 2013; White and Seymour, 2003), has been considered in past studies examining effects of land-use disturbance on assemblage composition (Hevia et al., 2017). Since metabolic rates correlate positively with body mass, the effects of land-use change on local energetic requirements have been indirectly assessed through investigations of changes in body-mass composition along land-use gradients (Newbold et al., 2020; Tinoco et al., 2018). However, to the best of my knowledge, no study has yet directly reported the effects of land-use change on assemblage-level energetic requirements.

Thus, the first objective of this Chapter is to investigate how land-use change impacts assemblage-level energetic requirements in terrestrial vertebrates. To this end, I use metabolic rates as a proxy for maintenance energetic requirements at the species level. I predict that, at the assemblage level, total energetic requirements in disturbed land uses are lower than in undisturbed land uses. This prediction relies on the assumption that there is less energy available overall in disturbed land uses than in undisturbed land uses (Figure 1c), with disturbed land uses being characterised by human appropriation of net primary productivity (Krausmann et al., 2013). Because species' ability to exploit particular resources and meet energetic demands also depends on food types and diet (McNab, 1986; Mendoza and Araújo, 2019), I test whether this prediction holds true within trophic groups (i.e., within herbivores, omnivores, and carnivores). Here, I consider energetic requirements at the assemblage level, not controlling for species' body mass, to obtain estimates of total energy expenditure in different land-use types (Figure 2a). Thus, any changes in assemblage-level energetic requirements could be ultimately driven by shifts in the size-spectrum of local assemblages.

Body mass explains much of the variation in metabolic rates, but species with similar body masses still display important variation in metabolic rates (Mueller and Diamond, 2001). Some of this variation can be explained by taxonomic position (which also accounts for differences in thermoregulatory strategy between endotherms and ectotherms). However, there remains substantial interspecific variation in metabolic rates even after accounting for body mass and taxonomic affiliation (Mueller and Diamond, 2001; White and Kearney, 2013). Food availability and food type might explain this residual variation in metabolic rates

among species (Mueller and Diamond, 2001). Species that evolved in areas with abundant resources assimilate and burn calories at high rates, regardless of their body mass – while species that evolved with limiting resources could process resources at lower rates, irrespectively of their body mass (Mueller and Diamond, 2001). Building upon this idea and the ‘allocation’ principle (i.e., the trade-offs in resource allocation; Auer et al. (2020)), species with lower energetic expenditure (than expected from body mass and taxonomy) may be able to cope with food scarcity better than those with larger energy expenditure (than expected from body mass and taxonomy). Indeed, regardless of their body mass, such species should need fewer resources to meet energetic demands (Clarke and Fraser, 2004). Thus, as land-use disturbance modifies the types and abundance of resources, I expect species energetic requirements –after removing the effects of body mass and taxonomic position– to influence responses to land-use change. Yet, whether energetic constraints explain species’ responses to land-use change in terrestrial vertebrates has not been investigated before (Hevia et al., 2017). Thus, the second objective of this Chapter is to characterise the influence of energetic constraints on species occurrence probability in disturbed land uses, compared to undisturbed land uses. I approximate energetic constraints at the species level from residual variation in metabolic rates, that is, the variation not explained by body mass or taxonomy. I predict that species with negative deviations (lower rates than expected from body mass and taxonomy) are more likely to persist in disturbed land uses than species with positive deviations (higher rates than expected from body mass and taxonomy; Figure 2b). Given that trophic group can influence resource acquisition and species’ ability to assimilate various types of food, I investigate whether this prediction is consistent among trophic groups.

To test both predictions, I use a space-for-time substitution approach, obtaining vertebrate assemblage composition data from the PREDICTS database (Hudson et al., 2014, 2017). I combine this database with trophic-group information (characterising species as either omnivores, herbivores, or carnivores), and with species-level estimates of resting metabolic rates and body mass.

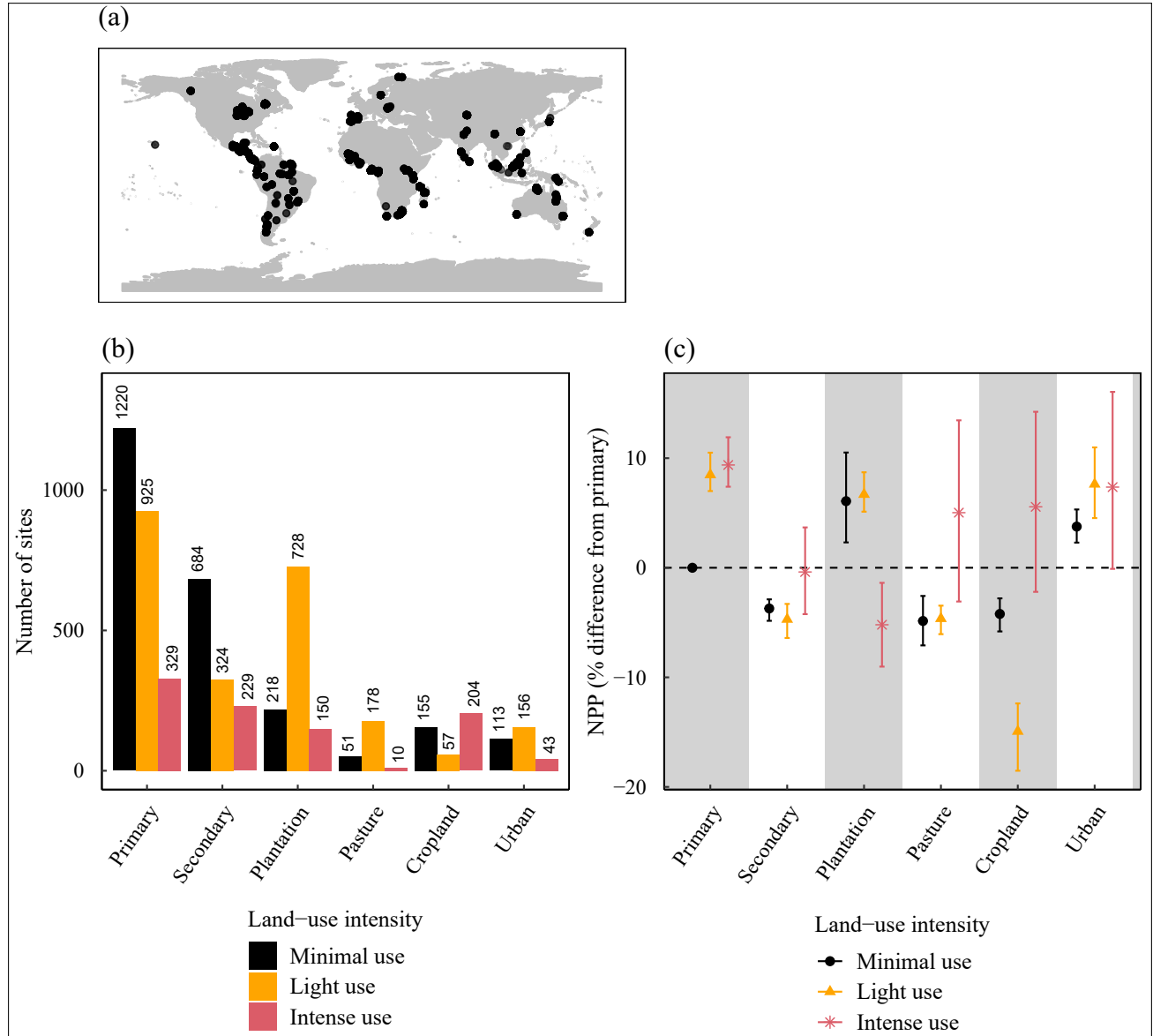
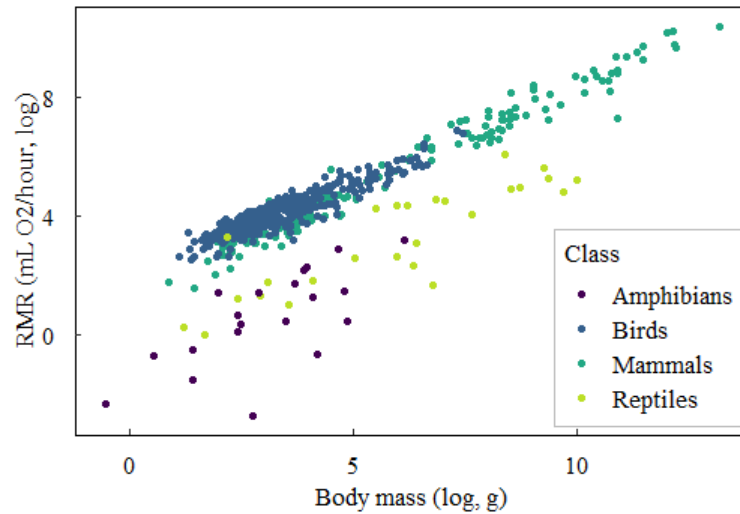


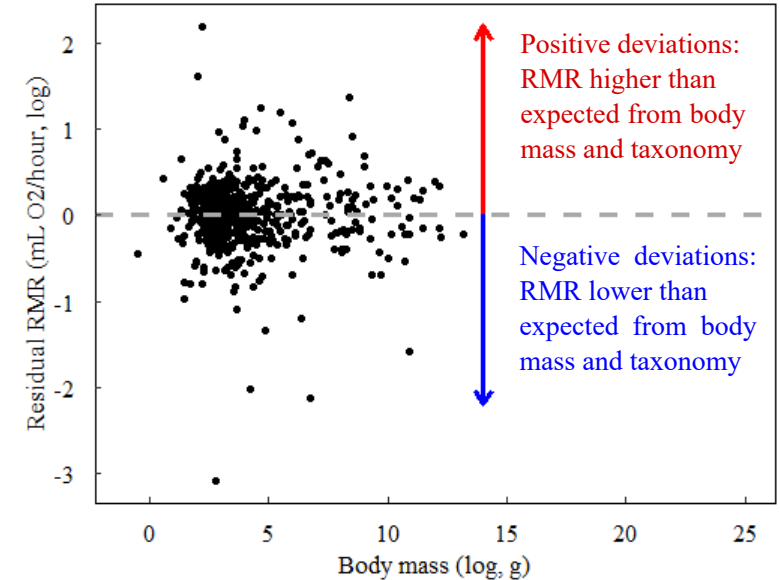
Figure 1: (a) Spatial distribution of the sampled sites from the PREDICTS database for terrestrial vertebrates (5,774 sites); (b) Number of sites in each land-use and land-use-intensity category; (c) Net primary productivity by land use and land-use intensity across PREDICTS sites (derived from MODIS satellite imagery), with model predictions plotted relative to minimally used primary vegetation (and rescaled with reference to that land-use type). Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

(a) Assemblage-level: there is less energy available to utilize by vertebrate assemblages in disturbed land uses than in undisturbed land uses.



residuals of
 $\log(\text{RMR}) - \log(\text{BM}) +$
 $(1 + \log(\text{BM}))|\text{Class/Order}$

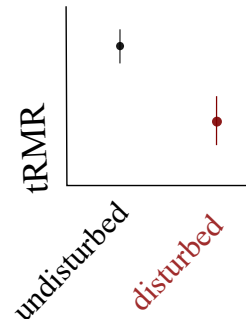
(b) Species-level: species with lower energetic expenditure than expected from body mass and taxonomy (negative deviations) do better in disturbed land uses than species with higher energetic expenditure than expected from body mass and taxonomy (positive deviations).



Prediction 1: within all trophic groups, total assemblage-level **mass-dependent** metabolic rates decrease in disturbed land uses compared to undisturbed land uses.

Assemblage level:
 $\text{tRMR} = \sum_i (\text{RMR}_i * a_i)$

Across assemblages - model 1:
 $\log(\text{tRMR}) \sim \text{LU} + \text{LUI} + \text{TG} +$
 $\text{LU:LUI} + \text{LU:TG} + \text{LUI:TG} +$
 $\text{LU:LUI:TG} + \text{RE}$



Prediction 2: within all trophic groups, species occurrence probability in disturbed land uses is negatively affected by **residual RMR**. The slope of the relationship between occurrence probability and residual RMR is significantly lower than the slope estimate for the undisturbed land uses.

Across species - model 2:

$P_{\text{occurrence}} \sim \text{LU} + \text{LUI} + \text{resRMR} + \text{TG} +$
 $\text{LU:LUI} + \text{LU:TG} + \text{LU:resRMR} +$
 $\text{LUI:TG} + \text{LUI:resRMR} + \text{TG:resRMR} +$
 $\text{LU:TG:resRMR} + \text{LUI:TG:resRMR} + \text{RE}$

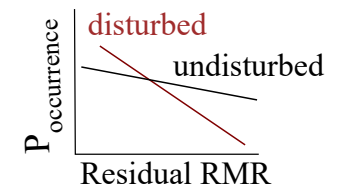


Figure 2: Framework for the predictions and models. I use resting metabolic rates (RMR) as a proxy for the amount of energy processed by vertebrate species. **(a)** I hypothesize that there is less energy overall that can be utilized by vertebrate species in disturbed land uses compared to undisturbed land uses. As such, I expect decreases in assemblage-level total metabolic rates (tRMR). tRMR is calculated as the sum, over all species occurring at a site, of species RMR (RMR_i) weighted by species abundance (a_i). **(b)** After removing the effects of body mass and taxonomy, I expect species with lower energy expenditure than expected to do better than species with higher energy expenditure than expected. I predict that the slope of the relationship between residual RMR and occurrence probability is more negative in disturbed land uses than in undisturbed land uses. For both (a) and (b), I test whether the predictions are consistent among trophic groups. LU: Land use; LUI: land-use intensity; TG: trophic group; RE: random effects. In *model 1*, random effects include the identity of the PREDICTS studies from which the assemblages are derived. In *model 2*, random effects include study, site, and species identity.

2 Methods

2.1 Vertebrate assemblage composition

I obtained vertebrate assemblage composition in different land uses from the PREDICTS database (Hudson et al., 2014, 2017). The PREDICTS database is a large collection of published studies that measure biodiversity across different land uses and is one of the most comprehensive global databases of its type. In each PREDICTS study, species occurrence and often abundance were recorded across different sites. Each site was assigned to one of the following land-use types: primary vegetation (natural, undisturbed vegetation), secondary vegetation (recovering after complete destruction of primary vegetation), plantation forest (woody crops), pasture (areas grazed by livestock), cropland (herbaceous crops) and urban (built-up areas). The land-use categories were assigned based on habitat descriptions from the original studies (Hudson et al., 2014), sometimes in consultation with the original study authors. Each site was also classified in terms of land-use intensity as either minimal, light or intense. The land-use-intensity assignment was also made on the basis of the habitat description in the original studies, and depended on criteria specific to each land use (such as degree of mechanisation, yield or chemical inputs for cropland; or the amount of green space in urban areas; Hudson et al. (2014)).

I subset the PREDICTS database for studies that sampled terrestrial vertebrates, and for which both land use and land-use intensity had been characterised. I further subset the database for species for which I could obtain an estimate of resting metabolic rates (see below). I thus obtained 154 studies for 529 species sampled across 5,774 sites (Figure 1a). Sample sizes varied across land uses and land-use intensities (Figure 1b).

2.2 Energy availability by land-use type and land-use intensity

The predictions of this Chapter rely on the assumption that resource types and abundance are modified in disturbed environments, with less energy available in disturbed compared to undisturbed land uses overall. To test this assumption, I used terrestrial net primary productivity (NPP) across land uses as a proxy for available energy. NPP quantifies the amount of atmospheric carbon fixed by plants and accumulated as biomass. NPP estimates were derived by Meghan Hayden, using imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS) on board NASA's Terra satellite. NPP estimates were based on a yearly composite of measures made at 8-day intervals, captured at 500-m spatial resolution (Running and Zhao, 2015). Meghan Hayden obtained NPP for 4,062 of the PREDICTS sites (matching the sites to the NPP data using the sampling year available in PREDICTS). I fit a linear mixed-effects model ('lme4' package,

version 1.1-23, Bates et al. (2015)) explaining site-level NPP by land use and land-use intensity, with a random intercept accounting for study identity, to control for differences in experimental design across studies. Model predictions showed that NPP decreased significantly in several land uses (e.g., pasture and cropland) compared with the primary vegetation reference level, although the strength and in some cases direction of the difference varied among land-use and land-use intensity combinations (e.g., increases in urban land uses; Figure 1c).

2.3 Resting Metabolic Rates (RMR)

As a proxy for species-level energetic expenditure, I used estimates of the minimum amount of energy required for organismal maintenance, i.e., basal metabolic rates (BMR) for endotherms, and resting metabolic rates (RMR) for ectotherms. From the literature, I obtained estimates of BMR for 719 species of birds and 685 mammals, and estimates of RMR for 126 amphibians and 173 reptiles (Appendix 4, Table S1). For endotherms, BMR are measured when species are in their thermoneutral zone, that is, when there is little to no energy expenditure allocated to thermoregulation. Thus, BMR estimates were derived from lab studies that mostly measured oxygen consumption of the organisms at rest under controlled conditions and in the thermoneutral zone of the species. For an ectotherm, there is no ‘basal’ metabolic rate, as body temperature mainly depends on environmental temperature. Their metabolic rates follow a hump-shaped relationship with environmental temperature, highest at an optimal temperature which corresponds to a performance peak. To be able to compare endotherms’ BMR with ectotherms’ RMR, Stark et al. (2020) used the metabolic rates that correspond to a performance peak for both groups (i.e., BMR in the thermoneutral zone for endotherms, and metabolic rates at optimal temperature for ectotherms). Thus, I used the data compiled in Stark et al. (2020) for ectotherms, and from the sources specified in Table S1 for endotherms. The units for BMR and RMR were standardized to mL of dioxygen consumed per hour (mLO₂/h). As in Stark et al. (2020), I henceforth refer to both basal and resting metabolic rates as RMR. I then matched the RMR data with the PREDICTS data, obtaining occurrence records for 529 species with known RMR values.

2.4 Trophic group and body mass information

I used body mass and trophic group information for terrestrial vertebrates compiled in Chapter 2. Body mass was compiled as a single measure at the species level, meaning I was unable to consider intraspecific variation. Trophic group described species as either carnivores, omnivores, or herbivores. Because there were gaps in the availability of the data, more so for trophic group than for body mass (Chapter 2), I imputed the missing trait values. To impute missing body mass and trophic groups, I used random forests algorithms (us-

ing the ‘missForest’ R package, (Stekhoven, 2016; Stekhoven and Bühlmann, 2012)), including as additional predictors phylogenetic information, added in the form of 10 phylogenetic eigenvectors (Diniz-Filho et al., 2012) following Penone et al. (2014), and also taxonomic order. I considered a wider set of life-history traits in the missing values imputations: lifespan, litter/clutch size, habitat breadth and use of artificial habitats (compiled in Chapter 2). Phylogenetic eigenvectors were extracted from the class-specific phylogenies using the ‘PVR’ package (Santos, 2018).

2.5 Effects of land use, land-use intensity and trophic group on assemblage-level total RMR (prediction 1; Figure 2a)

Here, I subset the PREDICTS database for species for which local abundance at the sites was recorded. In addition, since RMR correlate strongly with body mass (Figure 2), I imputed missing RMR values from body-mass information, phylogenetic relationships and taxonomic orders, also using the ‘missForest’ R package. The data subset contained 3,604 species sampled for abundance across 125 studies in 4,583 sites. Assemblage-level total RMR (tRMR) was then calculated by summing abundance-weighted RMR for the species occurring in each site.

I then fitted a linear mixed-effects model to explain \log_e -tRMR as a function of land use, land-use intensity and trophic group, with a random intercept accounting for study identity to control for differences in experimental design across studies. I started with a model allowing all two-way interactions among the predictors. I tested whether adding the three-way interaction among land use, land-use intensity and trophic group improved the fit of the model, using a likelihood-ratio test. The model that included the three-way interaction was retained ($P \ll 0.01$; *model 1*, Figure 2).

Model validation.

To ensure that imputation uncertainty did not affect the conclusions, I refitted *model 1* using the subset of species ($n = 426$) from PREDICTS for which there were empirical RMR information (i.e., excluding imputed RMR values).

Disentangling the effects of body mass and abundance on tRMR

Since RMR correlates strongly with body mass, changes in tRMR are likely to be driven in part by changes in the size-spectrum of ecological assemblages. I fitted an additional model to explain changes in species’ abundance (given presence) by land use, land-use intensity, trophic group, body mass and their interactions,

to understand the role of shifts in the body mass of species on observed changes in tRMR (Appendix 4, Figure S1).

2.6 Effects of land use, land-use intensity, trophic group and residual RMR on species occurrence probability (prediction 2; Figure 2b)

To control for the effects of body mass and taxonomy on RMR, I used the residual variation in RMR after accounting for these variables, from a linear mixed-effects model fitting \log_e -RMR as a function of \log_e -body mass with nested random taxonomic effects (random intercepts and slopes: $1 + \log_e(\text{body mass})|\text{Class/Order}$; Figure 2). Hence, I used a metric that describes how much more energy (positive deviations) or less energy (negative deviations) than expected from body mass and taxonomic position a species spends for organismal maintenance. Similar approaches have been used in previous papers (Furness and Speakman, 2008; Naya et al., 2013). Here, I only used the set of species for which I had an empirical estimate for RMR (to avoid circularity from extracting residuals after imputing RMR from body mass and phylogenetic position). As detailed earlier, I expect species with lower residual RMR to do better in disturbed land uses than species with higher residual RMR (prediction 2; Figure 2b) because, given any body mass, investing less energy in maintenance could contribute to persistence in a context of resource scarcity.

To test the second prediction, I fitted a binomial mixed-effects model explaining species occurrence with land use, land-use intensity, trophic group and residual RMR. I started with a complete model that included all two-way interactions among the main effects. Because I wanted to test whether the second prediction was valid for each trophic group, I needed to account for potential differences in the slope of the relationships between occurrence probability and residual RMR among trophic groups. Thus, I performed a forward stepwise selection procedure to test whether adding three-way interactions among (1) land use, trophic group and residual RMR and (2) among land-use intensity, trophic group and residual RMR improved model fit, using likelihood-ratio tests. The final model included both three-way interactions (Figure 2b; *model 2*). I fitted random effects that accounted for species identity, as well as for study and site identity within PREDICTS. I checked the phylogenetic signal in the model residuals using Pagel's λ (Pagel, 1999). Non-significant phylogenetic signal in the residuals would indicate that fitting species identity in the model's random effects was sufficient to account for residual phylogenetic variation in RMR. Because I used the subset of species for which I had empirical estimate of RMR, the sample size for this analysis was reduced (with 529 species sampled across 5,978 sites across 154 studies).

3 Results

3.1 Effects of land use, land-use intensity and trophic group on assemblage-level total RMR

Land use, land-use intensity, trophic group and their interactions had significant effects on assemblage-level total RMR (Figure 3). Overall, and contrary to my expectations, assemblage-level total RMR did not show systematic decreases in disturbed land uses. In fact, urban land uses were associated with strong significant increases in tRMR (e.g., a 163% average increase in tRMR in lightly-used urban areas for carnivores, compared with primary vegetation levels; +231% on average in lightly-used urban areas for herbivores). However, responses depended on trophic group and land-use intensity. Whilst for herbivores, disturbed land uses were typically associated with increases in tRMR, I detected decreases in tRMR for omnivores and carnivores in several land uses, most notably in intensely-used pasture for carnivores (-81%). Such effects could reflect changes in the size-spectrum of local assemblages (Appendix 4, Figure S2). For instance, in minimally-used urban areas, medium-sized and larger herbivores tended to occur at higher abundances compared to primary vegetation level; and in intensely-used pastures, carnivores tended to occur at lower abundances overall (Figure S2).

The model residuals were appropriately distributed (see diagnostic plots in Appendix 4, Figure S3). Investigating the sensitivity of the results to imputation uncertainty showed that the main conclusion was robust to the removal of all imputed estimates of RMR (i.e., tRMR not showing systematic declines in disturbed land uses, contrary to our expectations). The correlation coefficient was 0.72 between the two sets of model coefficients (Figure S4). Further, comparing model predictions showed that effects were mostly congruent, although there were some differences (Figure S5). In particular, for herbivores, effect sizes tended to be bigger for the model fitted on empirical data compared with the model that included imputed data. Thus, the main results appear to be conservative if anything. The model fitted on empirical data had larger standard errors, likely due to the reduction in sample size.

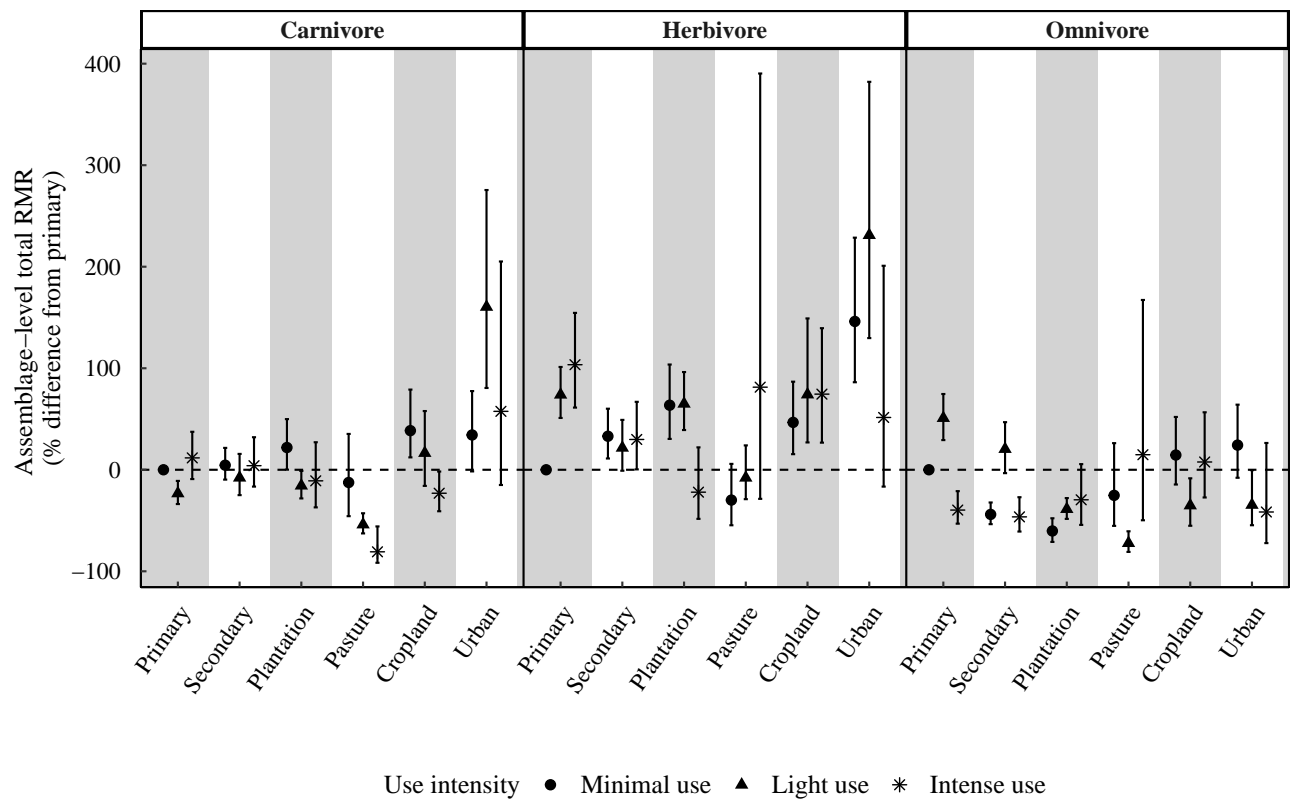


Figure 3: Effects of land use, land-use intensity and trophic group on assemblage-level total RMR (mean estimate $\pm 95\%$ confidence interval). Model predictions are rescaled with reference to minimally-used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

3.2 Effects of land use, land-use intensity, trophic group and residual RMR on species' occurrence probability

Species' occurrence probability was significantly affected by land use, land-use intensity, trophic group, residual RMR and their interactions (Figures 4 & 5). Contrary to my expectations, species with higher residual RMR (relative to their body mass and taxonomic position) tended to do better than species with lower residual RMR in a number of disturbed land uses. Overall, land-use type was more important for determining the relationship between occurrence probability and residual RMR than land-use intensity (Figure 4a).

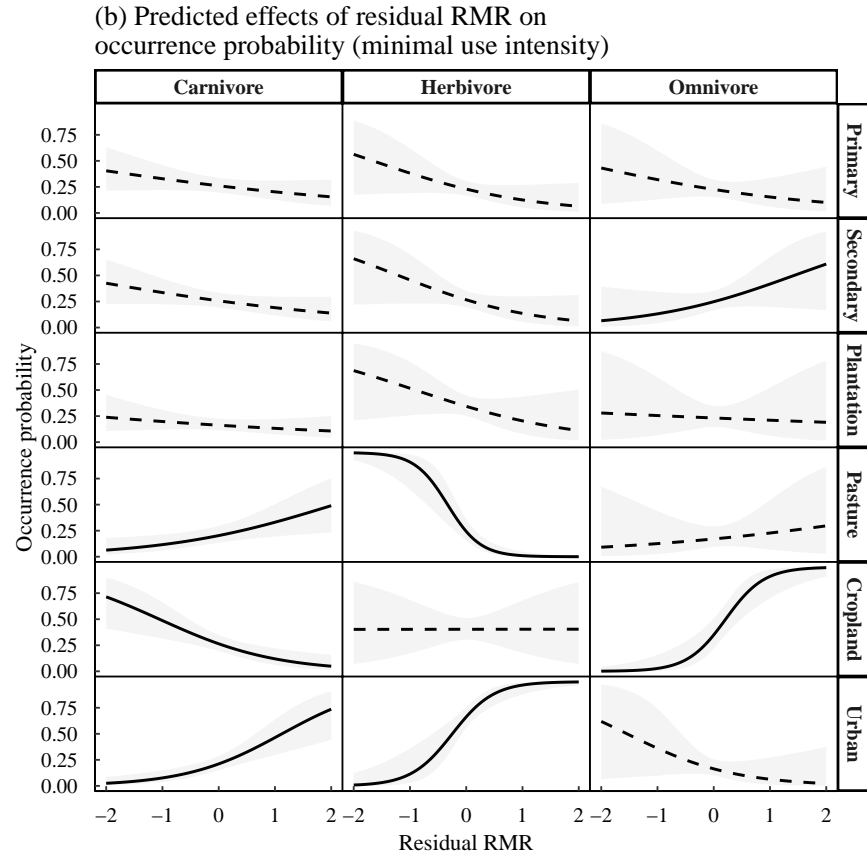
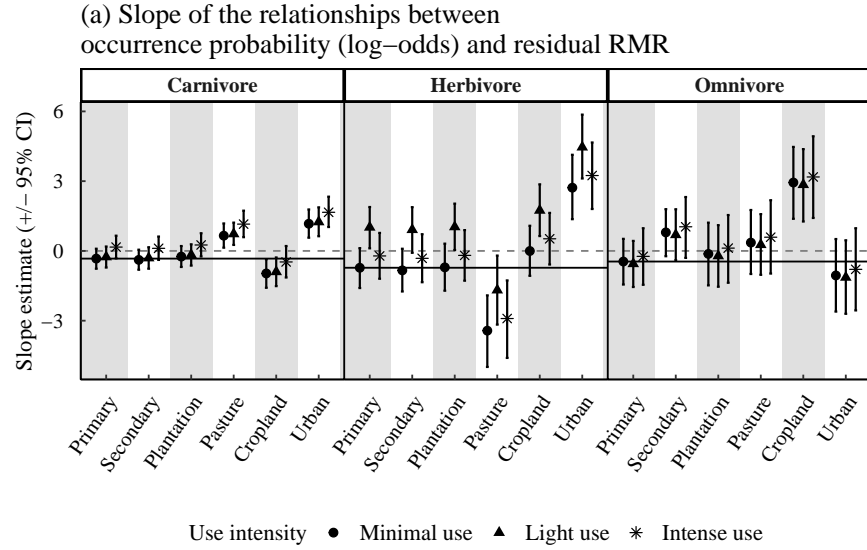


Figure 4: (a) Slope estimates for the relationship between residual RMR and occurrence probability in each land-use type and for the three levels of land-use intensity (mean estimate \pm 95% confidence interval). The black horizontal line indicates the slope for the reference level (primary vegetation) for minimal land-use intensity. The grey dashed line marks 0. **(b) Effect of residual RMR on species probability of occurrence within each trophic group and for each land-use type.** I plotted the predictions for minimal land-use intensity only. Solid lines represent significant relationships (with slopes significantly different from 0), and dashed lines are plotted where the slope was not significantly different from 0. Shaded areas represent 95% confidence intervals. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

For minimally-used primary vegetation (reference), residual RMR tended to be negatively associated with species occurrence probability in all trophic groups (although the relationship was not significant; Figure 4a). However, the directionality of this relationship was significantly reversed in some disturbed land uses in all trophic groups (in secondary vegetation and cropland for omnivores; in urban areas for herbivores; in pasture and urban areas for carnivores), with significant positive slopes, also significantly higher than those observed for primary vegetation (Figure 4a); in these land uses, residual RMR was thus positively associated with occurrence probability. However, the opposite pattern was also observed for herbivores in pastures and carnivores in cropland (Figure 4b), with residual RMR having a more negative effect on occurrence probability than in minimally-used primary vegetation.

I would like to emphasize that positive effects of residual RMR on occurrence probability in some of the most disturbed land uses (e.g., urban for carnivores) do not mean that there were absolute increases in species occurrence probability in disturbed land uses compared to primary vegetation (and vice-versa). I illustrate this point in Figure 5. For carnivores with a median value for residual RMR, occurrence probability was reduced by an average 21% in urban land uses compared to primary vegetation (but there was a significant positive association between residual RMR and occurrence probability for carnivores in urban areas; Figure 4).

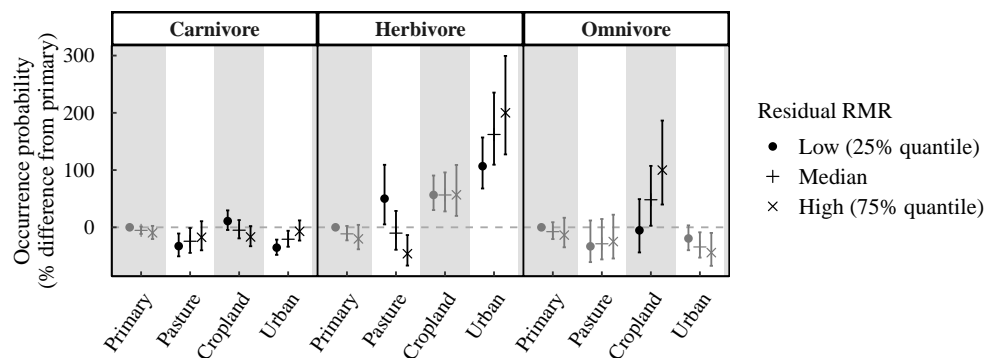


Figure 5: Predicted occurrence probabilities (mean effect \pm 95% confidence interval) in primary vegetation (primary) and for the most disturbed land uses where residual RMR was found to have a significant effect on occurrence probability. For visualisation purposes, I discretised residual RMR in three levels. The predicted probabilities of occurrence were rescaled with reference to primary vegetation for the lowest value of residual RMR (25% quantile). Here, the predictions are plotted for minimal land-use intensity (effects would be similar for light and intense land-use intensities). Black points and error bars are plotted where the relationship between occurrence probability and residual RMR was significant (and dark grey points and error bars represent non-significant trends).

Finally, the model showed some degree of deviation from distributional assumptions (diagnostic plots, Appendix 4, Figure S6). Nevertheless, the model's coefficients were similar when estimated with a Bayesian framework, suggesting that the estimates were robust (Figure S7). The phylogenetic signal in the model

residuals was weak and non-significant ($\lambda=0.001$, $P=0.92$).

4 Discussion

The results of this Chapter provide insights into the relationship between land-use change and energetic requirements at two levels of organisation (at the assemblage level and the species level), and contradict both my initial predictions. I found that total energetic requirements did not show systematic decreases in disturbed land uses. On the contrary, there were strong increases in all trophic groups, most notably in urban land uses. Further, in all trophic groups, species with higher energetic expenditure (than expected from body mass and taxonomy) tended to do better in some of the most disturbed land uses (that is, pasture, cropland and urban) than species with lower energetic expenditure (than expected from body mass and taxonomy).

At the assemblage level, the results first highlight the effects of land-use change on vertebrate community metabolism. Contrary to my expectations, I found differing effects of land use on total energetic requirements among trophic groups, reflecting changes in the size-spectrum of ecological assemblages (i.e., changes in the distribution of abundance along the body-mass gradient). On the one hand, decreases in total energetic requirements, such as observed for carnivores in intensely used pastures, are likely due to overall reductions in local abundance (with carnivorous species in pastures perceived as a threat to livestock (Eeden et al., 2018); or because of increased competition for fewer resources). On the other hand, increases in total energetic requirements could reflect higher levels of resource intake in some disturbed land-use types. On the basis of net primary productivity, I hypothesized that there would be fewer resources available in disturbed areas. However, it could be that the carrying capacity of some disturbed land-use types actually increases for some trophic groups compared to that of primary vegetation, because of the presence of novel or more abundant food sources. For instance, in urban areas, both wildlife feeding and the presence of anthropogenic food sources, such as human refuse or pet food, could lead to an increase in resource availability all year-round for species with a non-specialised diet that are able to exploit such food sources (Fischer et al., 2012). Past research on urban carnivores has shown that some species have adapted to urban environments by exploiting anthropogenic food sources, and also benefit from physical protection (with some human structures providing shelter) and from reduced occurrence of natural enemies (Bateman and Fleming, 2012). Herbivores and omnivores could also benefit from increased resources in urban areas, notably where the urban matrix includes semi-natural habitats, which is congruent with observed increases in occurrence probability in minimally used urban areas for these trophic groups. Further, anthropogenic ‘bottom-up food forcing’ has been shown to affect food-web dynamics, with decreases in predation rates, loss of anti-predator abilities

(Geffroy et al., 2020) and mesopredator release (Fischer et al., 2012). Thus, in urban areas, increases in anthropogenic food sources could provide support for a higher abundance of medium-sized species released from predation, increasing total energetic requirements.

I hypothesized that resource availability would be the main driver behind changes in energetic requirements. However, resource availability likely interacts with other factors to explain the patterns. In particular, past work has shown that brain size is an important determinant of species' ability to cope with disturbance, notably in urban settings (Sayol et al., 2020). Since brain size scales allometrically with body mass, it is possible that I observe increases in total energetic requirements where having larger brains is advantageous for resource acquisition, and in turn where resources are both exploitable and abundant enough to sustain the larger energetic expenditures associated with bigger brain sizes. In addition, body size, which explains an important proportion of the interspecific variation in mobility, likely interacts with characteristics of the landscape (such as fragmentation) with consequences for species persistence in disturbed land uses (Merckx et al., 2018). Hence, the patterns I observe in this Chapter could emerge from interactions and trade-offs among resource availability, diet, body size and human management of the landscape.

At the species level, the results underline the role of energetic constraints on species' responses to land-use change. After controlling for the effects of body mass and taxonomy, I found that residual energetic expenditure was significantly associated with species occurrence probability in some disturbed land uses. Contrary to my expectations, in several disturbed land uses and in all trophic groups, species with higher residual energetic expenditure tended to have a higher occurrence probability than species with lower residual energetic expenditure. In such cases, it could be that species with lower residual energetic requirements are less well equipped than species with higher residual energetic requirements at making use of the available food sources in disturbed land uses. Species in such disturbed land uses may need to display higher levels of feeding innovation (Coogan et al., 2018), have larger brains (Sayol et al., 2020), or be bolder and more active to make use of the available resources. In mammals, past research has shown that larger brains are associated with larger residual energetic expenditure (Isler and Van Schaik, 2006). At the individual level, past research suggests that metabolic rates are linked to differences in behaviour, with bolder and more active individuals exhibiting higher metabolic rates than less active individuals, with consequences for food acquisition (Biro and Stamps, 2010). Although I am not aware of similar evidence at the species level, I propose that residual metabolic rates interact with species' ecological traits, behavioural traits and foraging strategy in influencing species' responses to land use. Among species with an adaptable diet, able to make use of the resources available in a disturbed landscape, those with higher residual metabolic rates could present a set of behavioural characteristics that render them better at acquiring the available resources, hence

be more able to cope with land-use disturbance. This could be the case for urban carnivores and herbivores, as well as omnivores in cropland. Thus, it is possible that some disturbed land uses favour species with higher residual resting metabolic rates because such species are overall better competitors when faced with disturbance. In addition, release from predation in some disturbed land uses – most notably in urban areas – could favour bolder species, as they become less exposed to predation risks. Conversely, and in accordance with my initial hypothesis, the results also suggest that spending less energy than expected from body mass and taxonomy might be beneficial for persistence in some disturbed land uses (this could be the case for herbivores in pasture, and carnivores in cropland).

Finally, I would like to emphasize that energetic budget allocation is a fundamental aspect of organismal fitness (Burger et al., 2021). Past studies suggest that individuals exposed to food scarcity can lower their energetic expenditure to increase their chances of survival. For instance, Zhang et al. (2018) showed that, subjected to food restrictions, the Chinese bulbul (*Pycnonotus sinensis*) was able to lower its basal metabolic rate not only passively through body and organ mass reductions, but also by modifying enzymatic activity and metabolism in the muscles and liver. Other studies have also found that bird nestlings downregulate energetic costs allocated to maintenance when exposed to food shortage (Brzęk and Konarzewski, 2001; Moe et al., 2004), or to disturbances such as urban noise (Brischoux et al., 2017). Intraspecific variation in energetic expenditure could affect individual responses to land-use change, which in turn could affect species' ability to adapt to human pressures. However, the lack of spatially explicit estimates of metabolic rates precluded its consideration in this Chapter.

To conclude, the findings of this Chapter suggest important effects of land-use change on energetic fluxes, and thus potentially on ecosystem functioning. Further research is warranted as to the effects of these energetic patterns for ecosystem processes. Indeed, assemblage-level energy fluxes may serve as important indicators of change for ecosystem processes, such as decomposition (Barnes et al., 2014). Understanding these impacts is particularly important given increasing land-use change and biodiversity loss across the globe.

Supporting information

Table S1: Number of species for which RMR data was collected in each class & data sources, initial RMR coverage for PREDICTS species and phylogenetic signal in RMR.

Class	RMR data	Coverage for PREDICTS species	Phylogenetic signal (Pagel's λ , $\pm 95\%$ CI)
Amphibians	126 species from Stark et al. (2020)	16/379 species (4%)	0.89 (0.86-0.91)
Birds	719 species from McNab (2009) Fristoe et al. (2015) Londoño et al. (2015) Stark et al. (2020)	317/3129 species (10%)	0.97 (0.95-0.98)
Mammals	685 species from PanTHERIA (Jones et al., 2009) Fristoe et al. (2015) Stark et al. (2020)	148/556 species (27%)	0.99 (0.98-0.99)
Reptiles	173 species from Stark et al. (2020)	24/329 species (7.3%)	0.90 (0.86-0.92)

$$\begin{aligned} \log(\text{Abundance}) = & \text{LU} + \text{LUI} + \text{TG} + \log(\text{BM}) + \\ & \text{LU:LUI} + \text{LU:TG} + \text{LU:\log(BM)} + \text{LUI:TG} + \text{LUI:\log(BM)} + \text{TG:\log(BM)} + \\ & \text{LU:TG:\log(BM)} + \text{LUI:TG:\log(BM)} \end{aligned}$$

Figure S1: Formula for the abundance model, used to understand the role of shifts in the body mass of species on observed changes in tRMR (see Chapter 5, section 5.2.5, 'Disentangling the effects of body mass and abundance on tRMR'). I fitted a model to explain changes in species abundance (given presence) by land use, land-use intensity, trophic group, body mass and their interactions. The model included all two-way interactions among these predictors. To account for potential differences in the slope of the relationship between abundance and body mass among the different trophic groups, I also included two three-way interactions in the model (among land use, trophic group and body mass; and among land-use intensity, trophic group and body mass). Random effects included study, site and species identity. LU: land use; LUI: land-use intensity; TG: trophic group; BM: body mass.

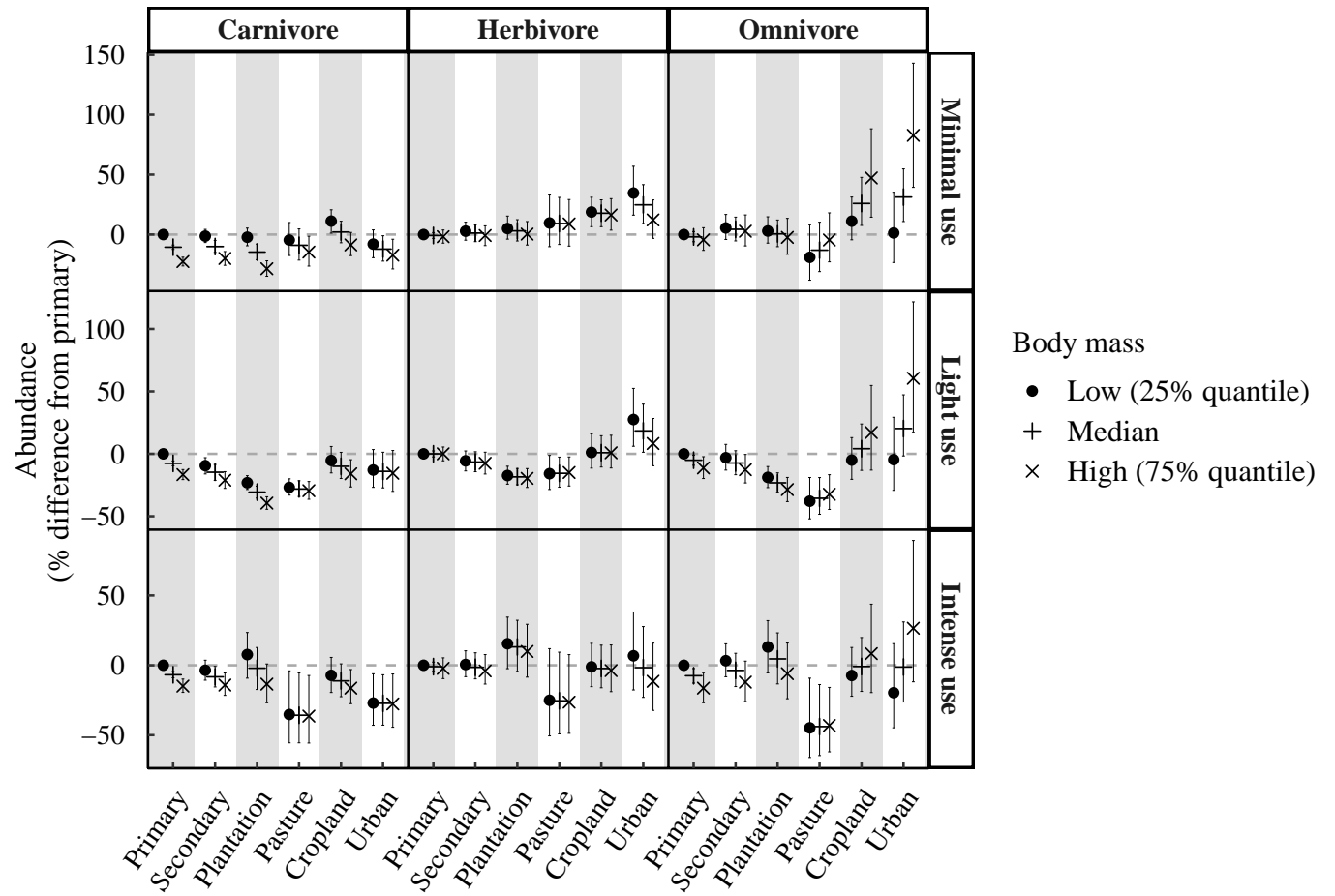
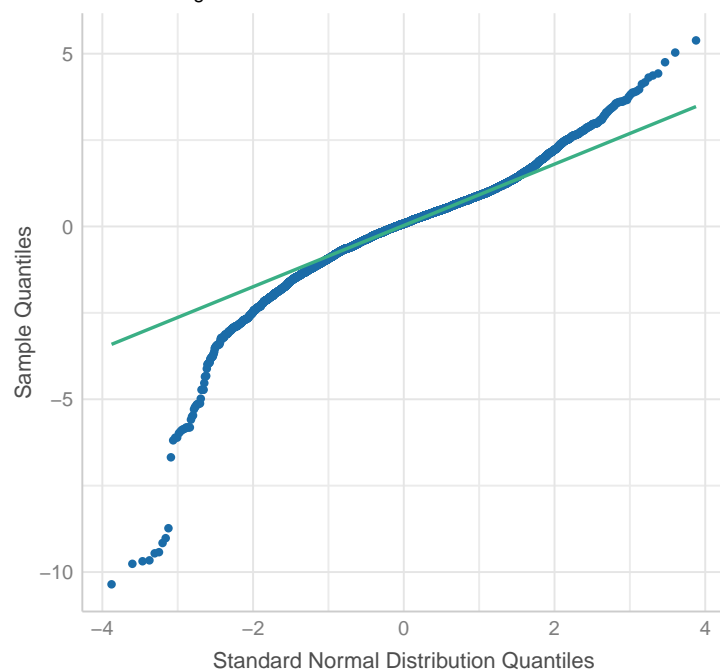


Figure S2: Effects of land use, land-use intensity, trophic group, body mass and their interactions on assemblage-level total abundance, estimated from the model specified in Figure S1. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest. For visualisation purposes, I plotted the predictions for three body mass levels (but body mass was considered as a continuous variable in the model).

Normality of Residuals
Dots should fall along the line



Normality of Residuals
Distribution should be close to the normal curve

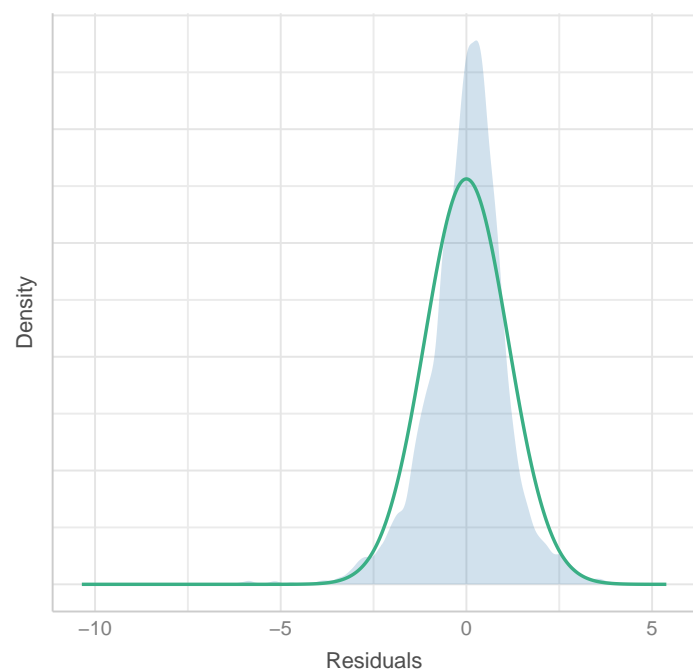


Figure S3: Diagnostic plots (qq-plot and residual distribution) for the linear mixed-effects model looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR (*model 1*). The diagnostic plots were obtained with the ‘performance’ R package (Lüdtke et al., 2021).

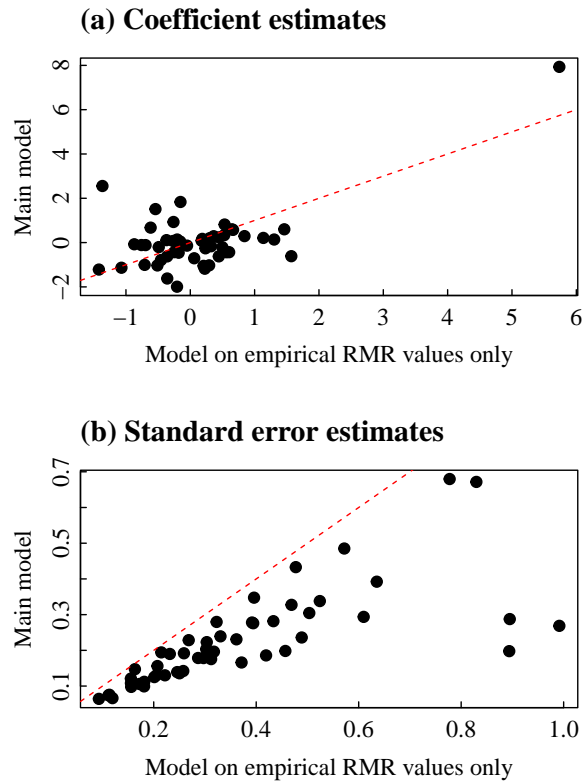


Figure S4: Estimates for the models looking at the effects of land use, land-use intensity, trophic group and their interactions on assemblage-level total RMR. I plotted the estimates from the model fitted on the empirical and imputed RMR values (*model 1*) on the y-axis, and the estimates from the model fitted on the empirical RMR values only on the x-axis.

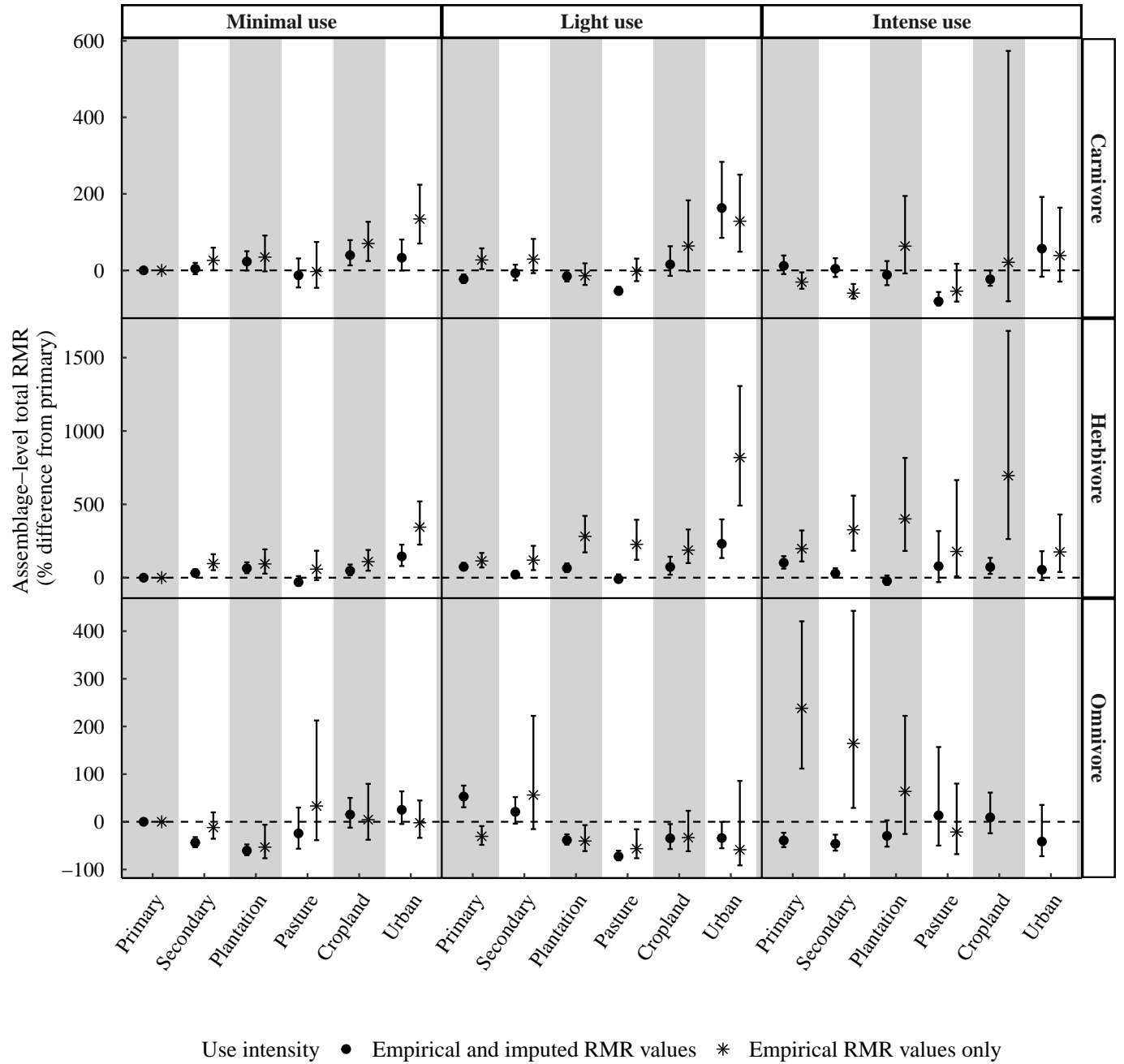


Figure S5: Effects of land use, land-use intensity, trophic level and their interactions on assemblage-level total RMR, estimated from the model fitted on the empirical and imputed RMR values (*model 1*) and from the model fitted on the empirical values only. The predictions are rescaled with reference to minimally used primary vegetation, considered to be the undisturbed baseline. Primary: primary vegetation; secondary: secondary vegetation; plantation: plantation forest.

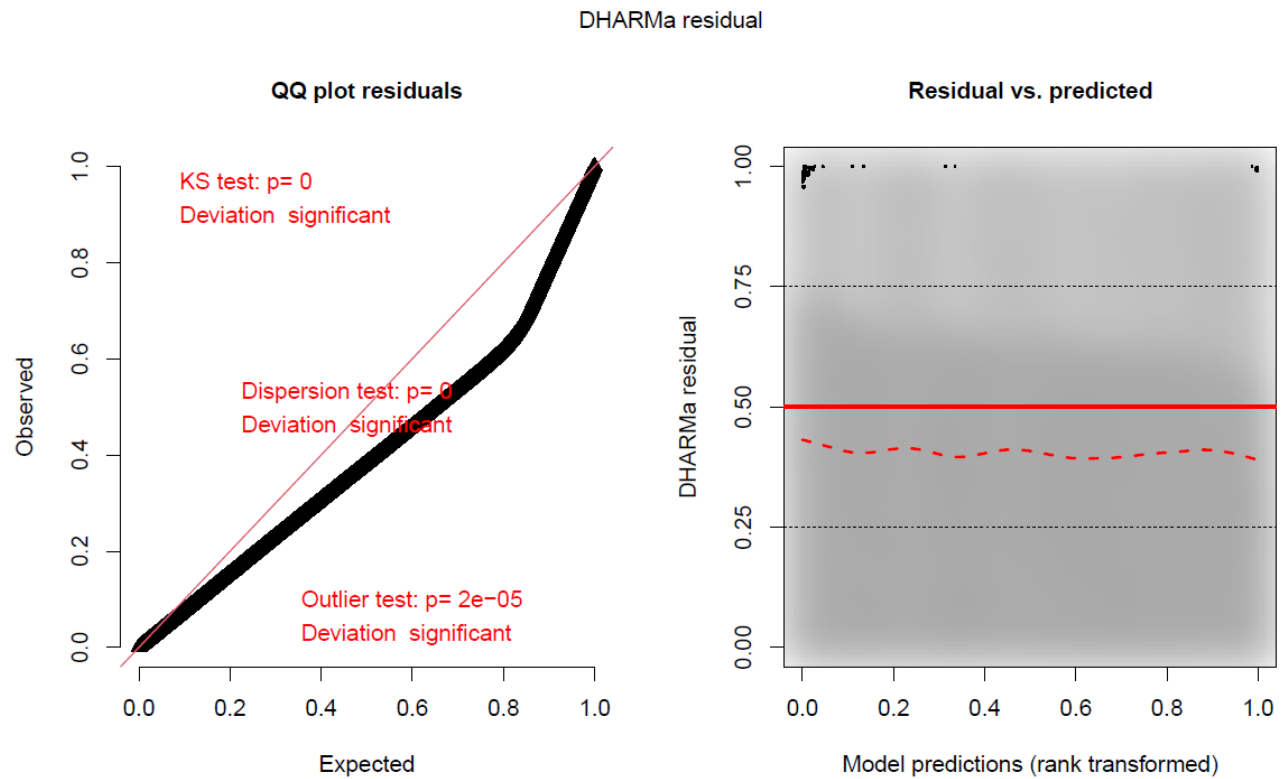


Figure S6: Diagnostic plots for the generalised mixed-effects model looking at the effects of land use, land-use intensity, trophic group, residual RMR and their interactions on species' probability of occurrence (*model 2*). The diagnostic plots were obtained with the 'DHARMA' R package (Hartig, 2021).

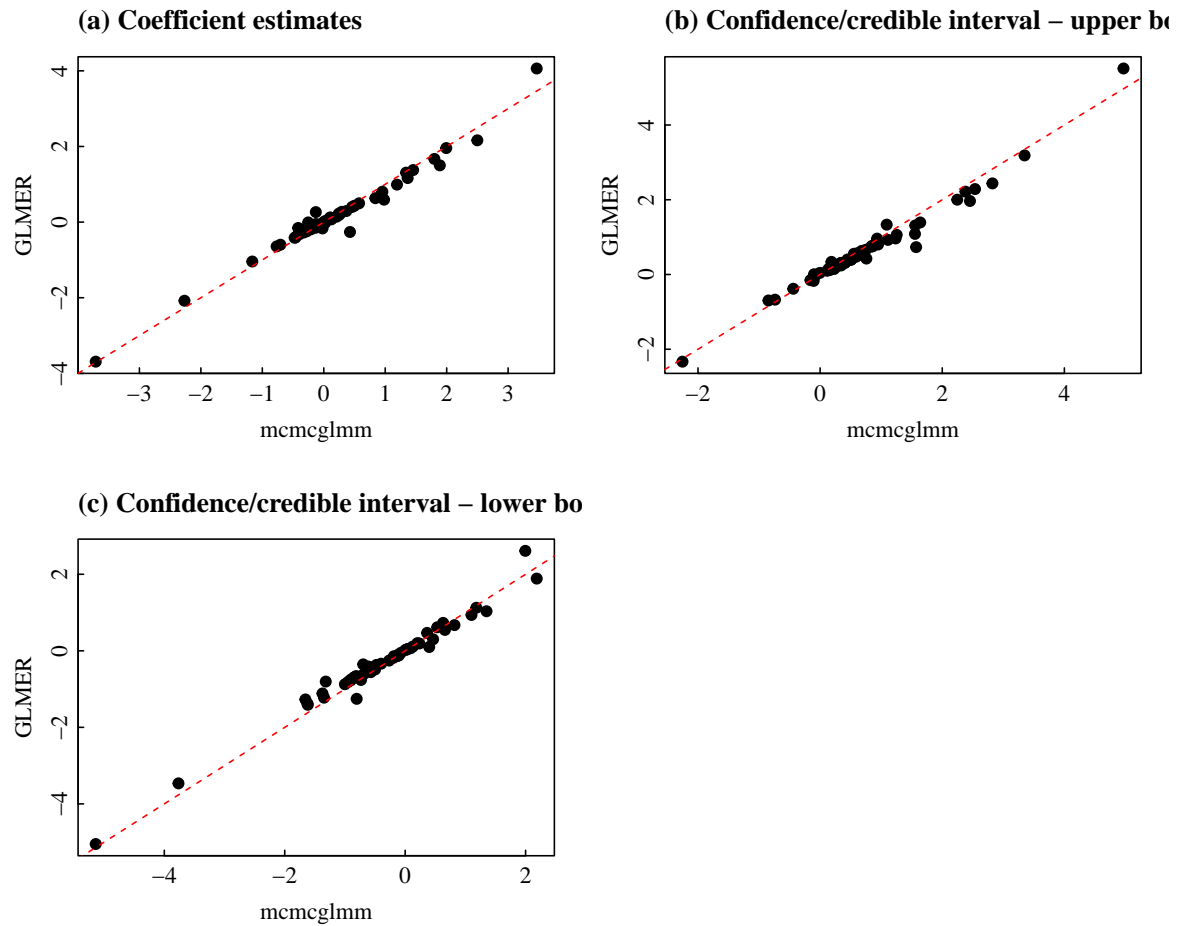


Figure S7: Model's coefficients from the occurrence model fitted using the 'lme4' package (Bates et al., 2015) against coefficients from the model fitted using a Bayesian framework with the 'MCMCglmm' package (Hadfield, 2010). The models were fitted to investigate the effects of land use, land-use intensity, trophic group and residual RMR on species occurrence probability (*model 2*).

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