Article title: Biodiversity shows unique responses to land-use change across regional biomes

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Data availability:
All data used in this manuscript is downloaded from open source locations. The PREDICTS database can be downloaded from the Natural History Museum Data portal (https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database).

Geographical data used to delineate regional biome boundaries in this manuscript can be downloaded from The Nature Conservancy's Geospatial Conservation Atlas (https://geospatial.tnc.org/datasets/b1636d640ede4d6ca8f5e369f2dc368b/about).

All R code used to run analysis presented in this manuscript can be found at https://github.com/PeggyBevan/RegionalBiomes

Abstract

Aim: Biogeography has a critical influence on how ecological communities respond to threats and how effective conservation interventions are designed. For example, the resilience of ecological communities is linked to environmental and climatic features, and the nature of threats impacting ecosystems also varies geographically. Understanding community-level threat responses may be most accurate at fine spatial scales, however

collecting detailed ecological data at such a high resolution would be prohibitively resource intensive. In this study, we aim to find the spatial scale that could best capture variation in community-level threat responses whilst keeping data collection requirements feasible.

Location: Global Terrestrial

Time period: 1980 – Present

Major Taxa studied: Terrestrial Plants & Animals

Methods: Using a database of biodiversity records with extensive global coverage, we modelled species richness and total abundance (the responses) across land-use types (reflecting threats), considering three different spatial scales: biomes, biogeographical realms, and *regional biomes* (the interaction between realm and biome). We then modelled data from three highly sampled biomes separately to ask how responses to threat differ between regional biomes.

Results: We found strong support for regional biomes in explaining variation in species richness and total abundance compared to biomes or realms alone. Responses to disturbed land-use types compared to primary vegetation were more pronounced and more distinct between regional biomes in the tropics compared to the temperate zone.

Main conclusions: Our results suggest that regional biomes have potential as a reasonable spatial scale for understanding how ecological communities respond to threats and designing effective conservation interventions, but the lack of variation in response to land-use change between temperate regional biomes could mean that this framework would be more beneficial for refining the monitoring of tropical habitats.

Introduction

Despite multiple internationally agreed science-based conservation targets, biodiversity continues to decline across the globe, with the consequent loss of essential ecosystem services (Tittensor *et al.*, 2014; Brooks *et al.*, 2015; Ceballos, Ehrlich and Dirzo, 2017; Isbell *et al.*, 2017; Mace *et al.*, 2018; IPBES, 2019; Ingram *et al.*, 2021). As new targets are developed, such as the up-coming post-2020 Convention on Biological Diversity goals and

the proposed Global Deal for Nature (Dinerstein *et al.*, 2019; CBD, 2020), it is vital to develop biodiversity monitoring systems that are able to quantify the relationship between anthropogenic threat and biodiversity response metrics (*e.g.,* abundance, species richness). Such threat-response relationships will be influenced by specific life-history traits, biogeography and the ecological scale being measured (*e.g.*, a community, population or individual) (Isaac and Cowlishaw, 2004; Murphy, 2021; Suraci *et al.*, 2021). Habitat disturbance caused by land-use change is a major factor contributing to biodiversity loss (Newbold *et al.*, 2015), but the impact of disturbance on biodiversity varies with the intensity of change (Felipe-Lucia *et al.*, 2020) and the original habitat (Monsarrat, Jarvie and Svenning, 2019). This variation of impact of habitat loss also means that protection interventions should be proportionate to the threat. To create realistic predictions of biodiversity trends, the underlying biogeographic processes contributing to variation in threat-response relationships should be considered when modelling global biodiversity trends.

The biogeography of a species or ecological community can impact its sensitivity to an anthropogenic threat. Tropical biomes, particularly tropical forest, have higher species richness, smaller species' ranges, and higher number of specialist species compared to temperate biomes (Stevens, 1989; Gaston, 2000; Brown, 2014). Habitat specialisation and small range size have been associated with stronger negative response to land-use change (Newbold *et al.*, 2013), suggesting communities in tropical biomes have lower resilience to environmental disturbance compared to communities in similar temperate biomes. Furthermore, the history of land use and environmental disturbance is not uniform across the globe and will further contribute to modern day responses to anthropogenic threats. Historic anthropogenic disturbance has been more intense in temperate biomes and these areas have already lost a large number of species (Goldewijk *et al.*, 2011). Areas with a history of disturbance have been found to contain fewer threatened species than less disturbed counterparts, reflecting the significance of historic disturbance on threat-sensitive species

(Yang *et al.*, 2021). Incorporating an understanding of biogeography and historical knowledge of an environment could play an important role in global biodiversity monitoring.

Given the implications of biogeography for threat-response relationships, monitoring biodiversity at the smallest possible scale would be appropriate. However, there are currently 37,000 threatened species on the red list (IUCN, 2021), all of which cannot have unique conservation plans created for them. There is a necessity to find an appropriate scale to monitor biodiversity that finds a balance between presenting global trends and efficiently implementing local-scale interventions (Ingram *et al.*, 2021). One way to account for biogeographic variation in threat responses is to split the world into spatial units, however the method for this is contended. For example, creating national statistics for biodiversity is helpful for feeding into policy, but creates accuracy issues as biodiversity is not nationally constrained (Murphy, 2021). Secondly, a global framework has been suggested for monitoring biodiversity at an ecoregional level (Dinerstein *et al.*, 2017, 2019; Smith *et al.*, 2018). Ecoregions (n = 814) are described as unique spatial areas that are determined by ecological features (Olson and Dinerstein, 2002) but are more ecologically distinct in some regions than others (McDonald *et al.*, 2005; Smith *et al.*, 2020). The ecoregion framework is powerful when measuring variables that can be obtained using remote sensing or global species lists (*e.g.*, Dinerstein *et al.*, 2017; Smith *et al.*, 2020), but many ecoregions are lacking the required field data to practically study population responses to human pressure at this resolution (Stephenson *et al.*, 2015). There is a need to test whether coarser spatial scales can capture variation in threat-response relationships so that data collection resources can be prioritised, whilst still providing meaningful evidence on biodiversity trends.

The broadest spatial unit of terrestrial habitats is the climatically-defined biome, of which there are 14 (Olson *et al.*, 2001). Responses of animal and plant populations to threats do differ between biomes (Greenville *et al.*, 2018; Green *et al.*, 2020) and species richness is particularly sensitive to land use change in tropical forest, tropical grassland and

Mediterranean biomes compared to temperate and desert biomes (Newbold *et al.*, 2020). In addition to biomes, there are 8 biogeographic realms (Olson *et al.*, 2001; UNEP-WCMC 2004). Data from the Living Planet Database (Collen *et al.*, 2009; WWF, 2022) has shown that decreases in vertebrate populations are more pronounced in southern hemisphere realms, particularly the Neotropics (Green *et al.*, 2020; WWF, 2022). Although there is evidence for variation in threat-response relationships between biomes and between realms, the interaction between these two intersecting spatial units is rarely considered, which may mean a large amount of variation is unaccounted for when monitoring biodiversity in biomes or realms alone.

A potential, intermediate spatial framework for monitoring biodiversity are regional biomes (the interaction of realms and biomes) (n = 64) (Ingram *et al.*, 2021). Regional biomes contain 11 ecoregions on average, ranging from 1-81 ecoregions (Olson and Dinerstein, 2002). Separating biomes by biogeographic realms can account for differences in vegetative structure, threats and socioeconomic status that occur between realms (Moncrieff, Bond and Higgins, 2016; Allan *et al.*, 2019). Furthermore, threats are not spread evenly across the world and can be region-specific (Bowler *et al.*, 2020); for example tropical forest in southeast Asia is a threat ‘hotspot’, whereas large parts of the Amazon rainforest act as threat ‘refugia’ (Allan *et al.*, 2019). Some areas of forest biomes are being afforested, mainly in the northern hemisphere, whilst others experience mass deforestation (Song *et al.*, 2018). Regional variation in sensitivity to anthropogenic pressure within biomes has been mainly explored in tropical biomes. In Asian tropical forests, species richness was found to be significantly more sensitive to disturbance than other regions (South America and Africa) (Gibson *et al.*, 2011; Phillips, Newbold and Purvis, 2017). On the other hand, vertebrate abundance is declining more in the Neotropics and Afrotropics than in the Indo-Pacific region (Green *et al.*, 2020). Regional biomes may present a middle-ground between the finer scale monitoring of ecoregions and the coarser biome scale, and where adequate sampling of biodiversity responses is more achievable.

Here, we use the PREDICTS database (Hudson *et al.*, 2017) to analyse data from over 400 field studies to explore the efficacy of regional biomes as a spatial monitoring unit for terrestrial species. We ask if regional biomes have more explanatory power than realms or biomes alone when modelling the effect of land-use change on species richness and total abundance. Due to the known explanatory power of biomes and realms (Phillips, Newbold and Purvis, 2017; Newbold *et al.*, 2020), we expect the interaction between realm and biome to have increased power in explaining variation in biodiversity metrics between different land-use types. Secondly, as case studies we model the three most data-rich biomes (Tropical Forest, Temperate Forest, Tropical Grasslands) in the PREDICTS database separately to explore how responses to land-use change and use-intensity vary between regional biomes. Our expectation is that there will be negative responses to human-dominated land-use types compared to primary vegetation, but the magnitude of response will differ between regional biomes. We expect the highest variation but also uncertainty in predicted responses between tropical regional biomes due to ecoregions being more distinct in these biomes (Smith *et al.*, 2020) and less variation in response between temperate regional biomes due to biotic homogenization (Newbold *et al.*, 2018).

Methods

The PREDICTS database

We used species abundance and occupancy data from the PREDICTS database (Hudson et al 2017; 22678 sites, 480 sources, 666 studies, 47,000 species). We chose to use the PREDICTS database due to high global coverage compared to other databases (Hudson *et al.*, 2017), making it suitable for a study comparing many regional biomes. The PREDICTS project (Predicting Responses of Ecological Diversity In Changing Terrestrial Systems; www.predicts.co.uk) is a database that collates biodiversity studies with comparable measures of terrestrial biodiversity from sites of different land uses and land-use intensity (Hudson *et al.*, 2017). All sampled sites are classified by stage of disturbance or recovery

which can be used as a substitute for actual temporal change at a single site (Walker *et al.*, 2010; Srivathsa *et al.*, 2018). This space-for-time substitution methods allows for specific measurements of biodiversity over distinct land-use types, acting as a proxy for anthropogenic pressure. PREDICTS does not include marine or freshwater data but does have extensive global coverage and has made attempts to reduce taxonomic and geographic bias (Hudson *et al.*, 2017).

We summarised occurrence and abundance records by site using the *predictsFunctions* R package (Newbold, 2018). The PREDICTS database covers 47 out of 64 regional biomes (70%), with some regional biomes more comprehensively sampled than others (Table S1). For analysis, we excluded data from three biomes with fewer than 50 sites in total from the dataset (Flooded Grasslands and Savannahs, Tundra, Deserts & Xeric Shrublands and Mangroves). Additionally, regional biomes were considered data deficient and excluded from analysis if they had no sites in primary vegetation land-use types (our reference level), or no sites in any kind of managed land use (cropland, pasture and plantation forest). This ensured that regional biomes included in analysis had data points (sites) across a gradient of increasingly anthropogenic land-use types. After removing data deficient regional biomes, a total of 30 regional biomes were available for analysis (Fig. 1; 20555 sites, 561 studies).

Using the predominant land use and use-intensity classifications from the PREDICTS database (land use: primary vegetation, mature secondary vegetation, intermediate secondary vegetation, young secondary vegetation, plantation forest, pasture, cropland and urban; use intensity: minimal, light, intense) (Hudson *et al.*, 2017), we created two land-use variables – *LandUse* and *UseIntensity*. We combined the three secondary vegetation classes (mature, intermediate and young) into one and removed all data from urban land-use types. Because some combinations of regional biome and *LandUse* class have low sample sizes, we tested 5 variations of this variable where categories were aggregated to find the most parsimonious grouping that still explained variation in the model well. For

202 example, to make the *LandUse2* variable we grouped primary vegetation and secondary
203 vegetation as 'natural vegetation'. Full descriptions of each land-use type and the 5
204 variations of *LandUse* can be found in Table S2. *UseIntensity* is a combination of
205 predominant land-use type and use-intensity. To create this variable, we grouped 'minimal'
206 and 'light' use-intensities into 'minimal' and combined with groups from *LandUse3* (defined
207 as primary vegetation, secondary vegetation and agriculture) to give categories primary
208 vegetation, minimal secondary vegetation, intense secondary vegetation, minimal
209 agriculture, intense agriculture. Primary vegetation sites were not split by use intensity as
210 there is no difference in biodiversity metrics between primary vegetation sites with differing
211 use-intensities (Newbold *et al.*, 2015).
212
213 Statistical Analysis
214 We used generalised mixed-effects models (Bolker *et al.*, 2009) to test for differences in
215 species richness and total abundance in response to land use, biome, realm and regional
216 biome (an interaction of biome and realm). Both response variables (species richness and
217 total abundance) were log transformed (natural logarithm) and modelled with a gaussian
218 distribution. We included study as a random intercept to account for site-level differences
219 and data collection methods. We ran a series of models with species richness and total
220 abundance against each *LandUse* variable (i.e. *LandUse1, LandUse2, or LandUse3* – see
221 the previous section) and selected the best fitting variable using Akaike Information Criterion
222 (AIC) (Burnham, Anderson and Huyvaert, 2011). We found that *LandUse1* (Primary
223 vegetation, Secondary vegetation, Agriculture, Plantation Forest, Cropland) had the most
224 support and was used for remaining analyses (Table S3).
225
226 Global analysis of regional biomes
227 To see if including regional biome helps to explain more variation in biodiversity than realm
228 or biome, we ran a model selection process using ΔAIC values to assess the support for
229 each variable. The fixed effect structures tested were *LandUse, LandUse:Realm,*

230 *LandUse:Biome,* and *LandUse:RegionalBiome* and species richness and total abundance
231 were used as response variables. We tested model robustness in two ways. First, we
232 increased the sample size threshold that would allow a regional biome to be included in the
233 model (minimum 1, 5, 25 or 50 sites in each regional biome-land use combination) and
234 checked if the model selection process gave the same results in each case. Second, we ran
235 a series of 100 hold-out models where each iteration randomly removed 10% of studies to
236 see if this would change the results of model selection.
237
238 Biome-specific case studies
239 As case studies, we investigated the differences in biodiversity response to land-use change
240 between regional biomes by selecting the three biomes which had three or more regional
241 biomes with at least 100 sites in the PREDICTS database (Fig. 2). The biomes selected
242 were tropical and subtropical moist broadleaf forest (Tropical Forest) (3 realms; Indo-Malay:
243 1781 sites; Neotropics: 2274 sites; Afrotropics: 2081 sites), temperate broadleaf and mixed
244 forests (Temperate Forest) (4 realms; Palearctic: 3986 sites; Neotropics: 577 sites; Nearctic:
245 856 sites; Australasia: 336 sites) and tropical and subtropical savannahs, grasslands and
246 shrublands (Tropical Grassland) (3 realms; Afrotropic: 1663 sites; Neotropics: 190 sites;
247 Australasia: 502 sites). For each biome and biodiversity metric (species richness and total
248 abundance), we ran four models that used the *LandUse* or *UseIntensity* variables and tested
249 if including *Realm*, which in this case represents regional biomes. We then predicted the
250 average change in species richness and total abundance in each land-use type in each
251 realm using the *StatisticalModels* R package (Newbold, 2015).
252
253 Results
254 Global analysis of regional biomes
255 Including regional biome as a variable improved model fit and better explained the effect of
256 land-use change on species richness and total abundance (Fig. 3). Models with realm or
257 biome alone had lower support and this was consistent across 100 iterations of hold-out

models (Fig. 3). Increasing the sample size threshold for regional biomes did not change the overall outcome (Table S4). Furthermore, marginal R^2 values showed that regional biome explained more variation in both species richness and total abundance than biome or realm interacting with land use (Table S4).

Biome-specific case studies

We found that species richness and total abundance in each regional biome of tropical forest showed a distinct response to land-use change. Species richness reduced in human-dominated land-use types compared to primary vegetation in all realms but to different degrees at each land-use type (Fig 4a). The largest loss of species richness was seen in Afrotropical cropland (-53% reduction compared to primary vegetation), followed by Indo-Malayan cropland (-50%) and plantation forest (-43%). Conversely, the Neotropics did not show a significant species richness reduction in cropland and a barely significant reduction in plantation forest (-20%), with species richness for this regional biome being worst affected in pasture land-use types (-30%). When predicting responses of total abundance to land-use change in the tropical forest biome there was much higher uncertainty. The negative responses to land-use type seen in the species richness models did not always carry over to the abundance models, for example there was no sign of a negative response in Neotropical pasture. However, total abundance was significantly lower in Indo-Malay plantation forest compared to other regional biomes, mirroring the pattern in species richness (Fig 4c). For the models including *UseIntensity*, a negative response to increased disturbance can be observed in Indo-Malayan and Afrotropical regional biomes, with declines >50% compared to primary vegetation in both species richness and total abundance (Fig 4b, d). This extreme response is not seen in the Neotropical regional biome.

In temperate forest regional biomes, species richness and total abundance both showed low to no response in human-dominated land-use types compared to primary vegetation (Fig 5a, c). The exception is the Palearctic regional biome, where total abundance reduced by 55%

in cropland land-use types. There were also reductions in species richness in plantation forest and cropland in this regional biome, but the upper confidence limits just surpassing 0 (Fig 5a). This was the only response from any temperate forest regional biome that showed a significant change from primary vegetation (95% confidence intervals do not include 0). Furthermore, predictions for change in species richness and total abundance have high levels of uncertainty for all realms except palearctic.

Similar to temperate forest, biodiversity metrics in most tropical grassland regional biomes showed little or no response to any land-use type when compared to primary vegetation (Fig. 6). Predictions of total abundance change showed a high degree of uncertainty across all regional biomes, except for the Afrotropics where there was a strong response to intense agriculture (-67%), although this was the only regional biome with enough datapoints to predict in this category so cannot be compared. Species richness in Australasia showed negative responses to pasture and minimally used agricultural land, but with the upper confidence interval just passing zero in both cases (Fig. 6a, b).

Discussion

Global analysis of regional biomes

Our results show that including regional biome when modelling the effects of land use on biodiversity can increase explanatory power. There is a need for a biodiversity monitoring spatial framework that finds the balance between having feasible data collection requirements and adequate global coverage, at a realistic scale that captures true variation in ecological resilience to disturbance (Ingram *et al.*, 2021). It has been previously shown that biodiversity shows different responses to disturbance across biomes (Greenville *et al.*, 2018; Blowes *et al.*, 2019; Newbold *et al.*, 2020) and across realms (Gibson *et al.*, 2011; Phillips, Newbold and Purvis, 2017; WWF, 2020), but for the first time, we have shown the important interaction between biome and realm. The combination of these two spatial delineations gives us more information about ecological processes. This result is important for biodiversity monitoring and conservation interventions as not only are the magnitude of biodiversity responses to anthropogenic pressure different between regions but that threatening processes (i.e., land-use types) are affecting regional biomes differently.

Biome-specific case studies

Whilst our models suggest that regional biome can modulate the effect of land-use change on species richness and abundance on a global scale, a more focused analysis found that the influence of regional biome is stronger in some biomes than others. Generally, species richness and total abundance in tropical biomes showed negative responses to disturbed land-use types, the degree of which changed with realm. In temperate forest, however, there was no significant response to land-use change overall, excluding the palearctic realm. The observed difference between tropical and temperate regional biomes is expected as responses to land-use change are stronger in tropical biomes compared to temperate biomes, especially tropical forest (Newbold *et al.*, 2020). However, ecoregions in tropical biomes are considered more ecologically distinct than neighbouring ecoregions compared to those in temperate biomes (Smith *et al.*, 2018). As each regional biome is a group of many

ecoregions, it would follow that predicted responses to disturbance in tropical regional biomes would contain more uncertainty than temperate, but the opposite is true for our case studies. The high uncertainty in predicted responses produced by the temperate forest models may be due to low sample sizes or variation in sampled taxa, considering that predictions for palearctic temperate forest have very low uncertainty compared to all other regional biomes, and is also the most extensively sampled regional biome in the PREDICTS database (Table S1).

For tropical forest regional biomes, our model predictions suggest Indo-Malayan species richness and total abundance respond most strongly to disturbance, followed by the Afrotropics. There was no significant change in species richness in the Neotropics tropical forest in any land-use type except for pasture. Biodiversity in Asian tropical forest is repeatedly found to be extremely sensitive to land-use change and disturbance (Sodhi *et al.*, 2009; Gibson *et al.*, 2011; Phillips, Newbold and Purvis, 2017). The islands of south east Asia have a rich biogeographical history which has led to this region having the highest number of endemic species and biodiversity hotspots (Myers *et al.*, 2000; Sodhi *et al.*, 2004) compared to other tropical regions. This area also has the highest proportion of species under threat in the world (Allan *et al.*, 2019). This high baseline for species richness combined with high levels of specialisation may partly explain why the response to land-use change is so pronounced in this regional biome. Response metrics in Neotropical tropical forest have the smallest response to disturbed land-use types compared to similar regional biomes. However, temporal trends from the Living Planet Index suggest that populations of vertebrates in south America have decreased by 94% since 1970 (WWF, 2020). Our results are not directly comparable to this, but the difference is a demonstration of the importance of testing multiple data types and of assessing the regional biome framework using time-series biodiversity data in the future. Further research is needed to understand how biological and taxonomic differences between these tropical forest realms might be impacting sensitivity to land-use change.

The intensity and history of habitat disturbance in each regional biome will also impact the observed response of biodiversity and may even cause biases in our data set. There is a strong focus on palm oil as a driver of biodiversity loss in Asian tropics, which may lead to a publication bias in this area. Temperate forest biomes have a long history of human habitation and extinction events, meaning the baseline in primary vegetation is much lower in these regional biomes compared to less historically disturbed biomes (Monsarrat and Svenning, 2022). The lack of variation in responses observed in temperate forest regional biomes may well be because of this lower baseline in primary vegetation. Indeed, trends of vertebrate abundance have been increasing in the northern hemisphere since 1970 (Leung, Greenberg and Green, 2017) as well as forest cover (Song *et al.*, 2018). The drivers that cause differences in sensitivity to habitat disturbance are related to both biogeographic and human history; splitting the world into regional biomes can further account for these differences.

Although regional biomes may be a valuable spatial monitoring unit, our models were limited by sample size for some regional biomes. The PREDICTS database is the most extensive collection of terrestrial biodiversity records available, but there are still gaps. Under-sampling was pronounced in non-forested temperate biomes like Montane Grasslands and Shrublands, and realms were unevenly sampled, for example studies from Palearctic temperate forest dominate the database but there are no studies at all on Palearctic temperate grasslands (Table S1). Prioritising data collecting in under-represented regional biomes highlighted here would enhance progress towards an effective monitoring framework (Ingram *et al.*, 2021). Furthermore, taxon is an important factor to consider and would add even more information. We could not include taxon as a predictor due to the already high number of parameters combined with low sample sizes. This study focuses only on terrestrial regional biomes, as these are more extensively sampled, and we were specifically testing the effect of land-use change on species richness and abundance. We acknowledge

that marine biodiversity is showing stronger responses to disturbance than terrestrial (Blowes *et al.*, 2019), and suggest a similar monitoring framework could be adapted for marine ecosystems.

Conclusion

Our results show that regional biomes have the potential to be a powerful unit for monitoring biodiversity and implementing conservation action. Resources for data collection and biodiversity monitoring on the ground is sparse, and the regional biome framework implies that monitoring studies could be more evenly spread across regional biomes, optimising resource allocation for data collection. Here we have highlighted that there is within-biome variation in how biodiversity is responding to disturbance. We show that the difference between realms may be more important in tropical biomes than temperate, and that spatial resolution should be carefully considered in any attempts at monitoring global biodiversity trends. Although more data are needed, regional biomes have the potential to be a meaningful scale at which to prioritise monitoring. These results will be beneficial for informing upcoming policy discussions such as the CBD's COP16 on the best way to monitor progress towards biodiversity targets and effect change on the ground.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Allan, J.R. *et al.* (2019) 'Hotspots of human impact on threatened terrestrial vertebrates', *PLOS Biology*. Edited by P. Jordano, 17(3), p. e3000158. Available at: https://doi.org/10.1371/journal.pbio.3000158.

Blowes, S.A. *et al.* (2019) 'The geography of biodiversity change in marine and terrestrial assemblages', *Science*, 366(6463), pp. 339–345. Available at: https://doi.org/10.1126/science.aaw1620.

Bolker, B.M. *et al.* (2009) 'Generalized linear mixed models: a practical guide for ecology and evolution', *Trends in Ecology & Evolution*, 24(3), pp. 127–135. Available at: https://doi.org/10.1016/j.tree.2008.10.008.

Bowler, D.E. *et al.* (2020) 'Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes', *People and Nature*, 2(2), pp. 380–394. Available at: https://doi.org/10.1002/pan3.10071.

Brooks, T.M. *et al.* (2015) 'Harnessing biodiversity and conservation knowledge products to track the Aichi Targets and Sustainable Development Goals', *Biodiversity*, 16(2–3), pp. 157–174. Available at: https://doi.org/10.1080/14888386.2015.1075903.

Brown, J.H. (2014) 'Why are there so many species in the tropics?', *Journal of Biogeography*, 41(1), pp. 8–22. Available at: https://doi.org/10.1111/jbi.12228.

Burnham, K.P., Anderson, D.R. and Huyvaert, K.P. (2011) 'AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons', *Behavioral Ecology and Sociobiology*, 65(1), pp. 23–35. Available at: https://doi.org/10.1007/s00265-010-1029-6.

CBD, (Convention on Biological Diversity) (2020) *Update of the zero draft of the post-2020 global biodiversity framework*. CBD/POST2020/PREP/2/1., p. 9.

Ceballos, G., Ehrlich, P.R. and Dirzo, R. (2017) 'Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines', *Proceedings of the National Academy of Sciences*, 114(30), pp. E6089–E6096. Available at: https://doi.org/10.1073/pnas.1704949114.

Collen, B. *et al.* (2009) 'Monitoring Change in Vertebrate Abundance: the Living Planet Index', *Conservation Biology*, 23(2), pp. 317–327. Available at: https://doi.org/10.1111/j.1523-1739.2008.01117.x.

Dinerstein, E. *et al.* (2017) 'An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm', *BioScience*, 67(6), pp. 534–545. Available at: https://doi.org/10.1093/biosci/bix014.

Dinerstein, E. *et al.* (2019) 'A Global Deal For Nature: Guiding principles, milestones, and targets', *Science Advances*, 5(4), p. eaaw2869. Available at: https://doi.org/10.1126/sciadv.aaw2869.

Felipe-Lucia, M.R. *et al.* (2020) 'Land-use intensity alters networks between biodiversity, ecosystem functions, and services', *Proceedings of the National Academy of Sciences*, p. 11. Available at: https://doi.org/www.pnas.org/cgi/doi/10.1073/pnas.2016210117.

Gaston, K.J. (2000) 'Global patterns in biodiversity', *Nature*, 405(6783), pp. 220–227. Available at: https://doi.org/10.1038/35012228.

Gibson, L. *et al.* (2011) 'Primary forests are irreplaceable for sustaining tropical biodiversity', *Nature*, 478(7369), pp. 378–381. Available at: https://doi.org/10.1038/nature10425.

Goldewijk, K.K. *et al.* (2011) 'The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years', *Global Ecology and Biogeography*, 20(1), pp. 73–86. Available at: https://doi.org/10.1111/j.1466-8238.2010.00587.x.

Green, E.J. *et al.* (2020) 'Below the canopy: global trends in forest vertebrate populations and their drivers', *Proceedings of the Royal Society B: Biological Sciences*, 287(20200533). Available at: http://dx.doi.org/10.1098/rspb.2020.0533.

Greenville, A.C. *et al.* (2018) 'Biodiversity responds to increasing climatic extremes in a biome-specific manner', *Science of The Total Environment*, 634, pp. 382–393. Available at: https://doi.org/10.1016/j.scitotenv.2018.03.285.

Hudson, L.N. *et al.* (2017) 'The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project', *Ecology and Evolution*, 7(1), pp. 145–188. Available at: https://doi.org/10.1002/ece3.2579.

Ingram, D.J. *et al.* (2021) 'Targeting Conservation Actions at Species Threat Response Thresholds', *Trends in Ecology & Evolution*, 36(3), pp. 216–226. Available at: https://doi.org/10.1016/j.tree.2020.11.004.

IPBES (2019) *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J. Settele, S. Díaz, and H. T. Ngo (editors)*. Bonn, Germany: IPBES secretariat.

Isaac, N.J.B. and Cowlishaw, G. (2004) 'How species respond to multiple extinction threats', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1544), pp. 1135–1141. Available at: https://doi.org/10.1098/rspb.2004.2724.

Isbell, F. *et al.* (2017) 'Linking the influence and dependence of people on biodiversity across scales', *Nature*, 546(7656), pp. 65–72. Available at: https://doi.org/10.1038/nature22899.

IUCN (2021) *The IUCN Red List of Threatened Species. Version 2021-1*. Available at: https://www.iucnredlist.org (Accessed: 17 May 2021).

Leung, B., Greenberg, D.A. and Green, D.M. (2017) 'Trends in mean growth and stability in temperate vertebrate populations', *Diversity and Distributions*, 23(12), pp. 1372–1380. Available at: https://doi.org/10.1111/ddi.12636.

Mace, G.M. *et al.* (2018) 'Aiming higher to bend the curve of biodiversity loss', *Nature Sustainability*, 1(9), pp. 448–451. Available at: https://doi.org/10.1038/s41893-018-0130-0.

McDonald, R. *et al.* (2005) 'Species compositional similarity and ecoregions: Do ecoregion boundaries represent zones of high species turnover?', *Biological Conservation*, 126(1), pp. 24–40. Available at: https://doi.org/10.1016/j.biocon.2005.05.008.

Moncrieff, G.R., Bond, W.J. and Higgins, S.I. (2016) 'Revising the biome concept for understanding and predicting global change impacts', *Journal of Biogeography*, 43(5), pp. 863–873. Available at: https://doi.org/10.1111/jbi.12701.

Monsarrat, S., Jarvie, S. and Svenning, J.-C. (2019) 'Anthropocene refugia: integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(20190219). Available at: https://doi.org/10.1098/rstb.2019.0219.

Monsarrat, S. and Svenning, J.-C. (2022) 'Using recent baselines as benchmarks for megafauna restoration places an unfair burden on the Global South', *Ecography*, 2022(4). Available at: https://doi.org/10.1111/ecog.05795.

Murphy, S.J. (2021) 'Sampling units derived from geopolitical boundaries bias biodiversity analyses', *Global Ecology and Biogeography*, 30(9), pp. 1876–1888. Available at: https://doi.org/10.1111/geb.13352.

Myers, N. *et al.* (2000) 'Biodiversity hotspots for conservation priorities', *Nature*, 403(6772), pp. 853–858. Available at: https://doi.org/10.1038/35002501.

Newbold, T. *et al.* (2013) 'Ecological traits affect the response of tropical forest bird species to land-use intensity', *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), p. 20122131. Available at: https://doi.org/10.1098/rspb.2012.2131.

Newbold, T. *et al.* (2015) 'Global effects of land use on local terrestrial biodiversity', *Nature*, 520(7545), pp. 45–50. Available at: https://doi.org/10.1038/nature14324.

Newbold, T. (2015) 'StatisticalModels'. Available at: https://github.com/timnewbold/StatisticalModels.

Newbold, T. (2018) 'predictsFunctions: Functions for reading and processing the PREDICTS data'.

Newbold, T. *et al.* (2018) 'Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide', *PLOS Biology*. Edited by H. Morlon, 16(12), p. e2006841. Available at: https://doi.org/10.1371/journal.pbio.2006841.

Newbold, T. *et al.* (2020) 'Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change', *Nature Ecology & Evolution* [Preprint]. Available at: https://doi.org/10.1038/s41559-020-01303-0.

Olson, D.M. *et al.* (2001) 'Terrestrial Ecoregions of the World: A New Map of Life on Earth', *BioScience*, 51(11), p. 933. Available at: https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

Olson, D.M. and Dinerstein, E. (2002) 'The Global 200: Priority Ecoregions for Global Conservation', *Annals of the Missouri Botanical Garden*, 89(2), pp. 199–224. Available at: https://doi.org/10.2307/3298564.

Phillips, H.R.P., Newbold, T. and Purvis, A. (2017) 'Land-use effects on local biodiversity in tropical forests vary between continents', *Biodiversity and Conservation*, 26(9), pp. 2251–2270. Available at: https://doi.org/10.1007/s10531-017-1356-2.

Smith, J.R. *et al.* (2018) 'A global test of ecoregions', *Nature Ecology & Evolution*, 2(12), pp. 1889–1896. Available at: https://doi.org/10.1038/s41559-018-0709-x.

Smith, J.R. *et al.* (2020) 'The biogeography of ecoregions: Descriptive power across regions and taxa', *Journal of Biogeography*, 47(7), pp. 1413–1426. Available at: https://doi.org/10.1111/jbi.13871.

Sodhi, N.S. *et al.* (2004) 'Southeast Asian biodiversity: an impending disaster', *Trends in Ecology & Evolution*, 19(12). Available at: https://doi.org/doi:10.1016/j.tree.2004.09.006.

Sodhi, N.S. *et al.* (2009) 'A Meta-Analysis of the Impact of Anthropogenic Forest Disturbance on Southeast Asia's Biotas', *Biotropica*, 41(1), pp. 103–109. Available at: https://doi.org/10.1111/j.1744-7429.2008.00460.x.

Song, X.-P. *et al.* (2018) 'Global land change from 1982 to 2016', *Nature*, 560(7720), pp. 639–643. Available at: https://doi.org/10.1038/s41586-018-0411-9.

Srivathsa, A. *et al.* (2018) 'Substituting space for time: Empirical evaluation of spatial replication as a surrogate for temporal replication in occupancy modelling', *Journal of Applied Ecology*, 55(2), pp. 754–765. Available at: https://doi.org/10.1111/1365-2664.13005.

Stephenson, P.J. *et al.* (2015) 'Overcoming the challenges to conservation monitoring: integrating data from *in-situ* reporting and global data sets to measure impact and performance', *Biodiversity*, 16(2–3), pp. 68–85. Available at: https://doi.org/10.1080/14888386.2015.1070373.

Stevens, G.C. (1989) 'The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in the Tropics', *The American Naturalist*, 133(2), pp. 240–256. Available at: https://doi.org/10.1086/284913.

Suraci, J.P. *et al.* (2021) 'Disturbance type and species life history predict mammal responses to humans', *Global Change Biology*, 00, pp. 1–14. Available at: https://doi.org/10.1111/gcb.15650.

Tittensor, D.P. *et al.* (2014) 'A mid-term analysis of progress toward international biodiversity targets', *Science*, 346(6206), pp. 241–244. Available at: https://doi.org/10.1126/science.1257484.

Walker, L.R. *et al.* (2010) 'The use of chronosequences in studies of ecological succession and soil development', *Journal of Ecology*, 98(4), pp. 725–736. Available at: https://doi.org/10.1111/j.1365-2745.2010.01664.x.

WWF (2020) *Living Planet Report 2020: bending the curve of biodiversity loss*. Available at: https://edepot.wur.nl/531235 (Accessed: 20 October 2020).

WWF (2022) *Living Planet Report 2022 - Building a nature positive society*. Gland, Switzerland: WWF. Available at: https://wwflpr.awsassets.panda.org/downloads/lpr_2022_full_report_1.pdf (Accessed: 17 October 2022).

Yang, X. *et al.* (2021) 'Threatened bird species are concentrated in regions with less historical human impacts', *Biological Conservation*, 255, p. 108978. Available at: https://doi.org/10.1016/j.biocon.2021.108978.

Data Accessibility Statement

All data used in this manuscript is downloaded from open-source locations. The PREDICTS database can be downloaded from the Natural History Museum Data portal (https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database).

Geographical data used to delineate regional biome boundaries in this manuscript can be downloaded from The Nature Conservancy's Geospatial Conservation Atlas (https://geospatial.tnc.org/datasets/b1636d640ede4d6ca8f5e369f2dc368b/about).

All R code used to run analysis presented in this manuscript is accessible in a github repository (not included here to maintain anonymity)

Figures

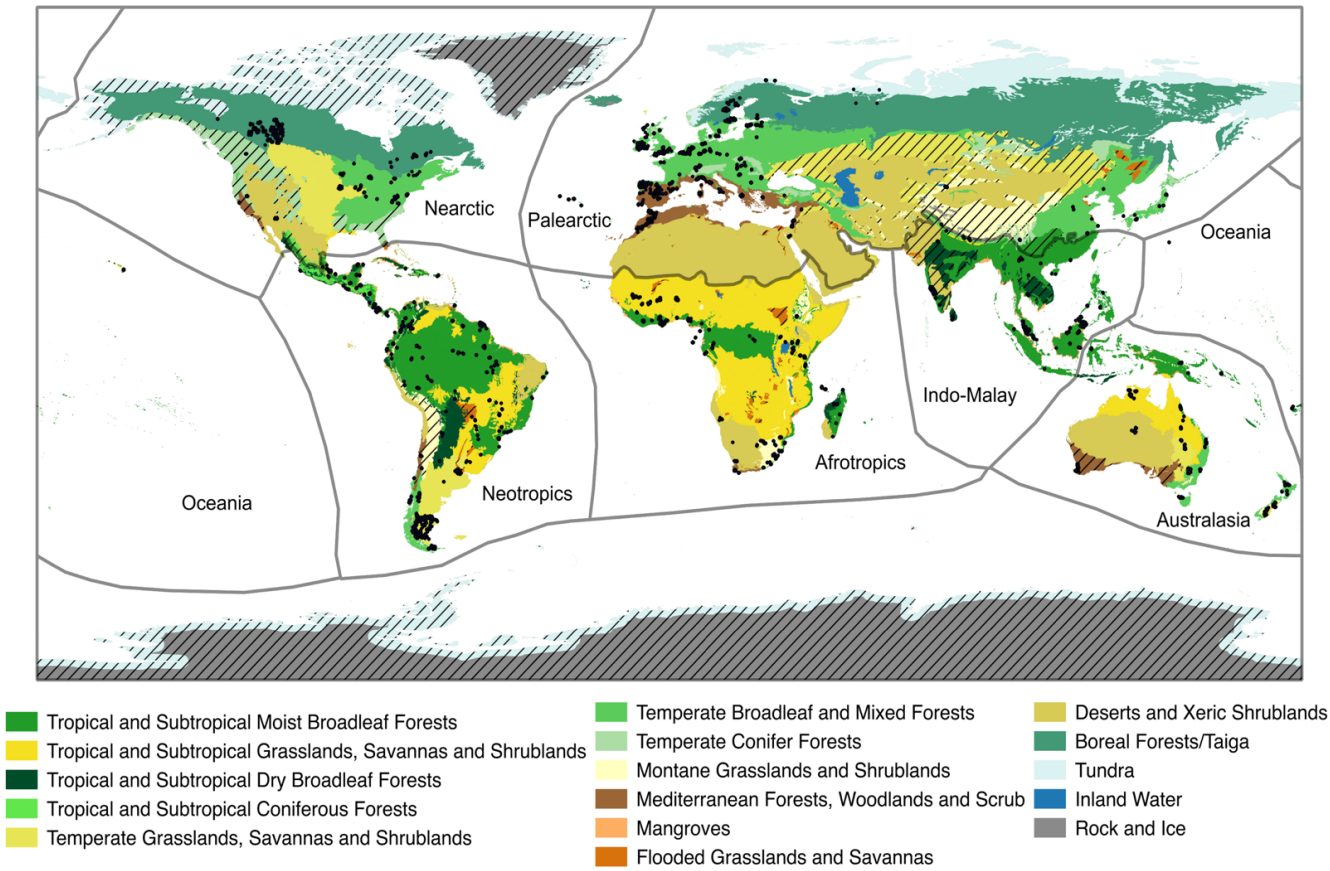

Fig 1. A map of regional biomes. Solid coloured areas represent biomes (see legend). Black lines separate out biogeographic realms. Black dots represent sites in the PREDICTS database used in our global model (Hudson et al 2014). Hashed coloured areas represent regional biomes that were not included in analysis due to data deficiency (see methods). Biome and biogeographic realm spatial data from (Olson *et al.*, 2001).

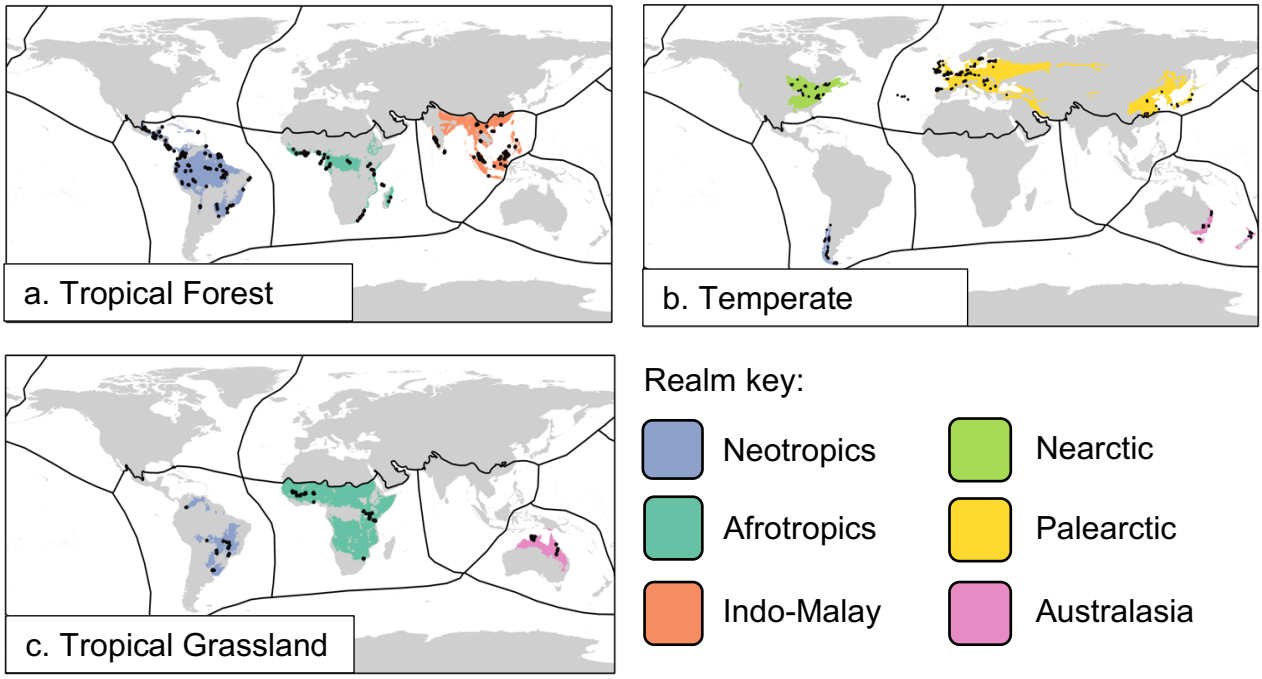

Fig. 2. Three case-studies of regional biomes: distribution of data. The PREDICTS database was subset into studies from three biomes that included at least 25 data points in each land use category from a minimum of three biogeographic realms. The figures show ranges of regional biomes, coloured by realm, for (a) Tropical Forest, (b) Temperate Forest and (c) Tropical grassland. Black dots represent a data point (record of species richness or total abundance) from the PREDICTS dataset. Regional biome distribution data from (Olson *et al.*, 2001).

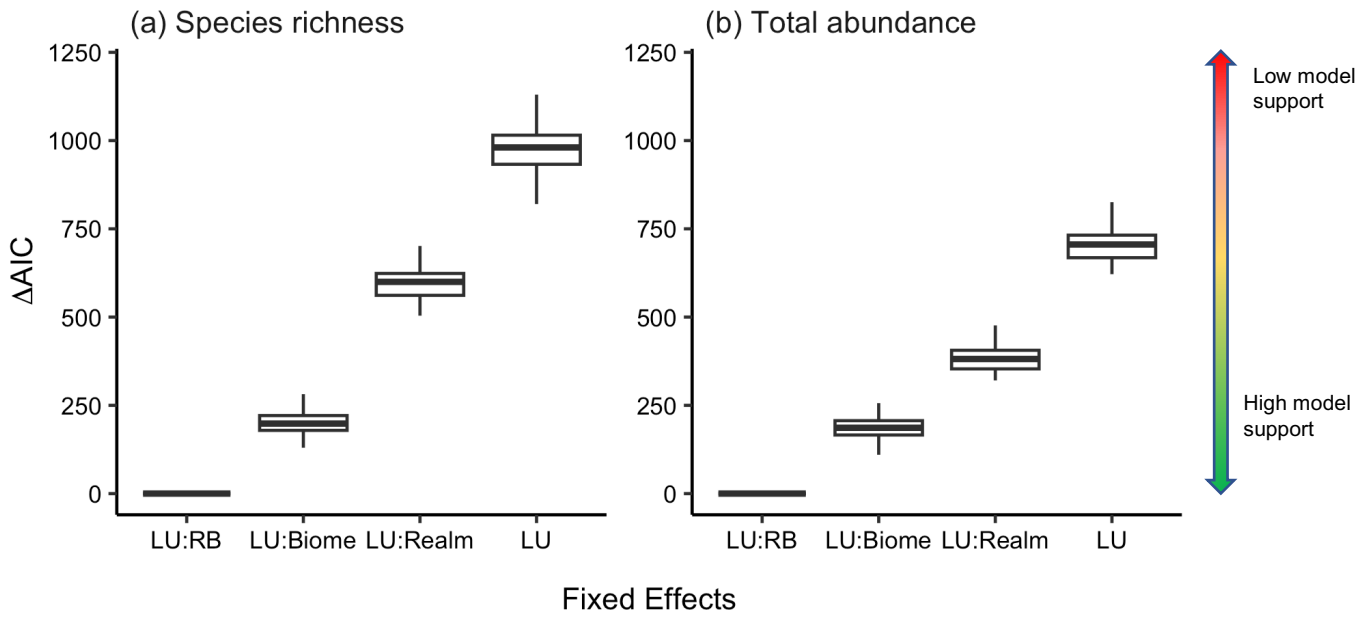

Fig 3. Change in Akaike's Information Criterion (ΔAIC) for Generalised Linear Mixed Models (GLMMs) predicting change in a global dataset of (a) species richness and (b) total abundance consistently suggests models including regional biome have highest support when modelling response to land-use change. Four GLMMs with differing fixed-effect structures containing Land Use (LU) interacting with Regional Biome (RB), Biome or Realm were compared using AIC values. A model with low AIC is considered to have higher support. ΔAIC is calculated as the difference in AIC from the lowest scoring model. The box and whisker plots represent a summary of ΔAIC values of 100 hold-out models, where each iteration removed 10% of studies at random as a test of model robustness. Importantly, for a given dataset in this hold-out analysis, LU:RB model had the lowest AIC in 100% of iterations. The PREDICTS dataset was subset to only include data from regional biomes with 25 data points per combination of regional biome and land-use type. Land Use is a discrete variable with Primary Vegetation, Secondary Vegetation, Plantation Forest, Pasture and Cropland as its categories (see Table S2 for descriptions).

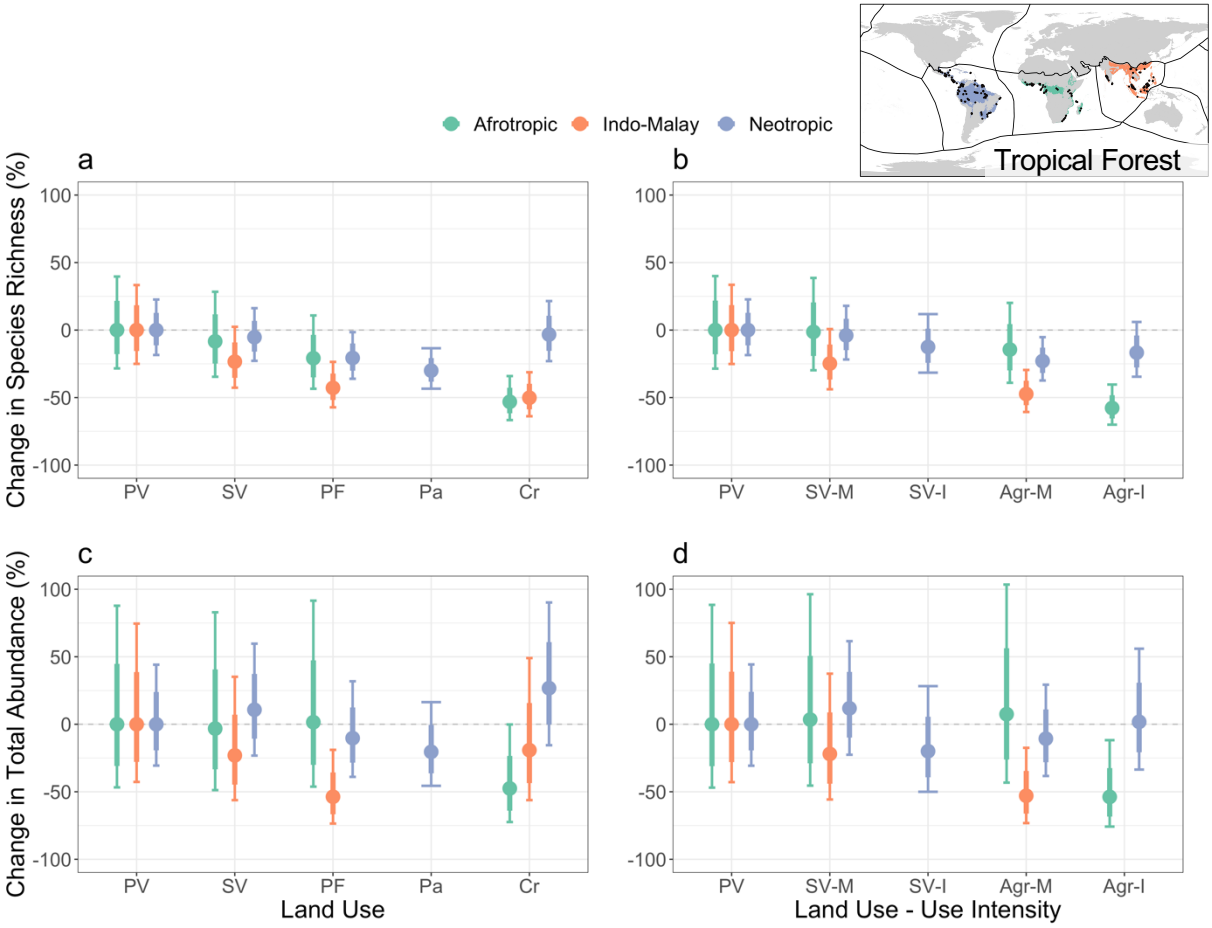

Fig 4. Responses of biodiversity to land-use change are unique across tropical forest regional biomes. The results of GLMMs predicting the response of two biodiversity metrics across land-use types and land-use intensity, when compared to primary vegetation (PV) across tropical forest regional biomes. Responses of species richness (top row) and total abundance (bottom row) of plants and animals were predicted across land-use types (a, c) including secondary vegetation (SV), plantation forest (PF), pasture (Pa) and cropland (Cr). Responses were also predicted for two levels of land-use intensity: minimal (M) or intense (I) in secondary vegetation (SV) and agriculture (Agr) land use types. Each point represents mean prediction, with 75% confidence intervals (thick whiskers) and 95% confidence intervals (thin whiskers). Responses are considered significantly different from primary vegetation if the 95% confidence intervals do not pass 0 (dotted line).

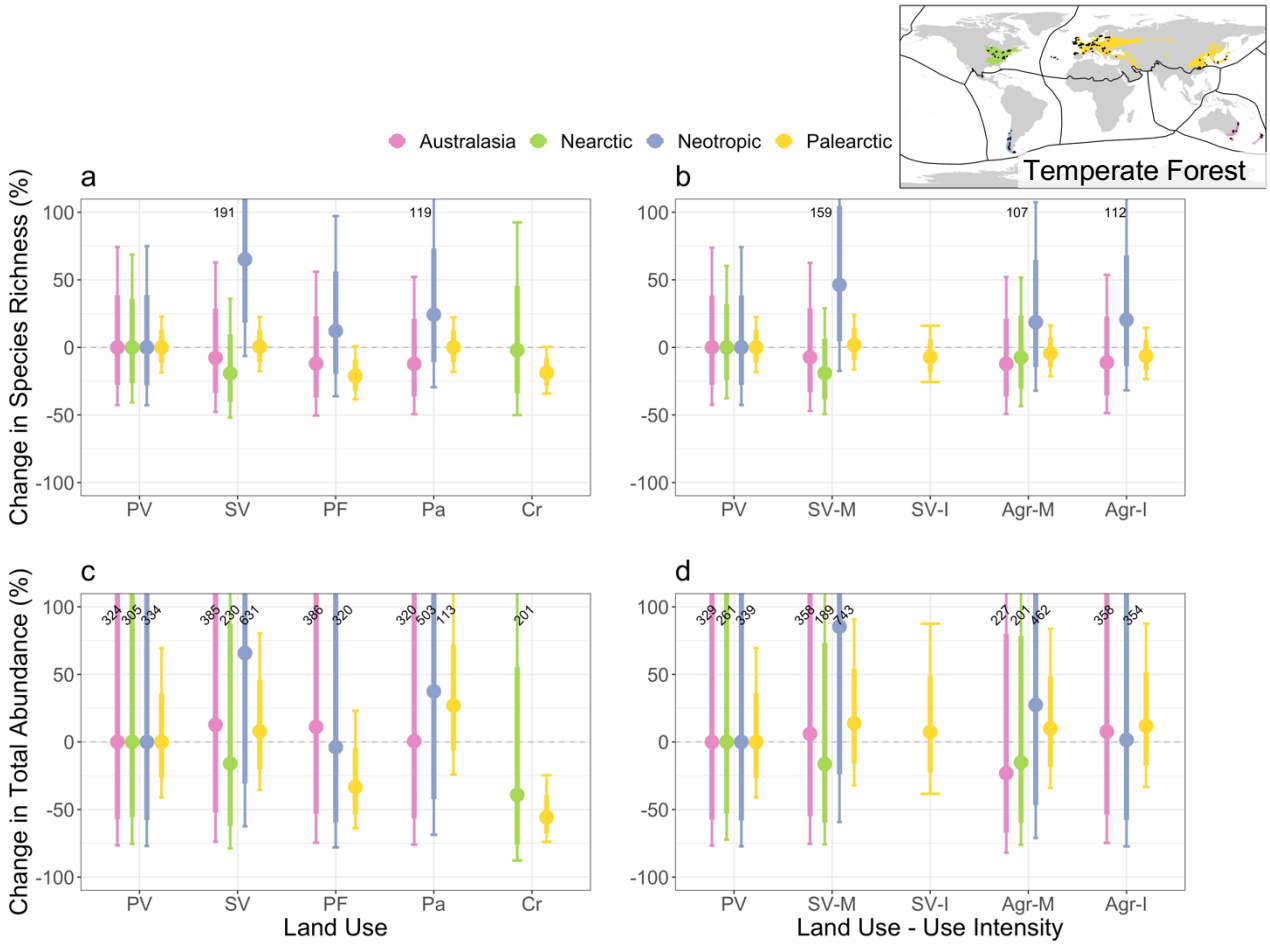

Fig 5. Responses of biodiversity to land-use change are hard to predict across temperate forest regional biomes. The results of GLMMs predicting the response of two biodiversity metrics across land-use types and land-use intensity, when compared to primary vegetation (PV) across temperate forest regional biomes. Responses of species richness (top row) and total abundance (bottom row) of plants and animals were predicted across land-use types (a, c) including secondary vegetation (SV), plantation forest (PF), pasture (Pa) and cropland (Cr). Responses were also predicted for two levels of land-use intensity: minimal (M) or intense (I) in secondary vegetation (SV) and agriculture (Agr) land-use types. Each point represents mean prediction, with 75% confidence intervals (thick whiskers) and 95% confidence intervals (thin whiskers). To keep scales consistent, upper 95% CIs greater than 100 have been included as text instead. Responses are considered significantly different from primary vegetation if 95% confidence intervals do not pass 0 (dotted line).

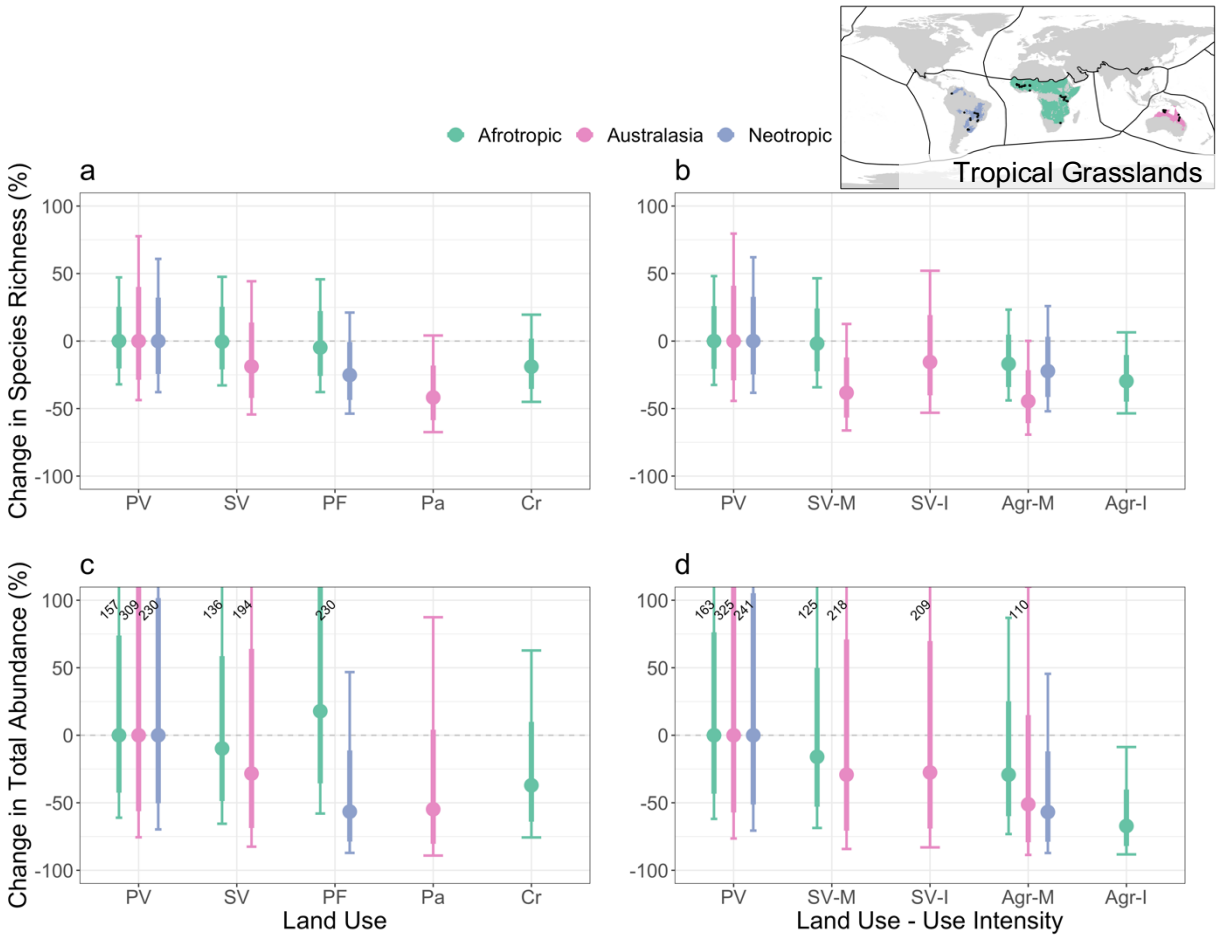

Fig 6. Responses of biodiversity to land-use change are hard to predict across tropical grassland regional biomes. The results of GLMMs predicting the response of two biodiversity metrics across land-use types and land-use intensity, when compared to primary vegetation (PV) across tropical grassland regional biomes. Responses of species richness (top row) and total abundance (bottom row) of plants and animals were predicted across land-use types (a, c) including secondary vegetation (SV), plantation forest (PF), pasture (Pa) and cropland (Cr). Responses were also predicted for two levels of land-use intensity: minimal (M) or intense (I) in secondary vegetation (SV) and agriculture (Agr) land use types. Each point represents mean prediction, with 75% confidence intervals (thick whiskers) and 95% confidence intervals (thin whiskers). To keep scales consistent, upper 95% CIs greater than 100 have been included as text instead. Responses are considered significantly different from primary vegetation if 95% confidence intervals do not pass 0 (dotted line).