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# ECOGRAPHY

## Research article

### Regional Biomes outperform broader spatial units in capturing biodiversity responses to land-use change

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Biogeographic context, such as biome type, has a critical influence on ecological resilience, as climatic and environmental conditions impact how communities respond to anthropogenic threats. For example, land-use change causes a greater loss of biodiversity in tropical biomes compared to temperate biomes. Furthermore, the nature of threats impacting ecosystems varies geographically. Therefore, monitoring the state of biodiversity at a high spatial resolution is crucial to capture variation in threat–responses caused by biogeographical context. However such fine-scale ecological data collection could 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. 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 to ask how responses to threat differ between regional biomes and taxonomic group. We found strong support for regional biomes in explaining variation in species richness and total abundance compared to biomes or realms alone. Our biome case studies demonstrate that there is variation in magnitude and direction of threat responses across both regional biomes and taxonomic group, although the interpretation is limited by sampling bias in the literature. All groups in tropical forest showed a consistently negative response, whilst many taxon–regional biome groups showed no clear response to threat in temperate forest and tropical grassland. Our results provide the first empirical evidence that the taxon–regional biome unit has potential as a reasonable spatial unit for monitoring how ecological communities respond to threats and designing effective conservation interventions to bend the curve on biodiversity loss.



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Keywords: Biodiversity monitoring, biogeography, biome, land-use change, regional biomes

## 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, Isbell et al. 2017, Ceballos et al. 2017, Mace et al. 2018, IPBES 2019, Ingram et al. 2021). Habitat disturbance caused by land-use change is a major factor contributing to biodiversity loss (Newbold et al. 2015). However, the impact of disturbance on biodiversity (its response) varies spatially and is contingent on factors such as the intensity of environmental change (Felipe-Lucia et al. 2020), the original habitat (Monsarrat et al. 2019) and taxon studied. Such threat–response relationships will further be influenced by specific life-history traits, biogeographic context, and the ecological scale being measured (e.g. a community, population or individual) (Isaac and Cowlshaw 2004, Murphy 2021, Suraci et al. 2021). Understanding the variability in how biodiversity responds to threats such as habitat disturbance can help to improve conservation decisions. With the adoption of new targets such as the Kunming-Montreal Global Biodiversity Framework (CBD 2022) and the Global Deal for Nature (Dinerstein et al. 2019), it is vital to develop spatial frameworks for biodiversity monitoring that can accurately measure indicators at an appropriate spatial scale that optimises available resources with the resolution necessary to inform successful conservation actions.

The specific location of a species or ecological community on the planet, or biogeographic context, plays a crucial role in determining its sensitivity to an anthropogenic threat. This could be due to the climate, historical natural disturbances, or the history of human activity in the area. For example, studies on biodiversity in tropical areas have been shown to have higher levels of fragmentation-sensitive species, stronger negative responses to land-use change and faster declining abundance than comparable temperate areas (Betts et al. 2019, Newbold et al. 2020, WWF 2022). This could be explained by the extinction filter hypothesis, which suggests that ecosystems with a history of disturbance will be more resilient in the present day due to the previous filtering of sensitive species (Balmford 1996). Tropical biomes are considered to have a history of low natural disturbance and a stable climate, whereas temperate biomes have been subject to elevated levels of glaciation, widespread fires, and human-caused forest loss in the last 10 000 years (Betts et al. 2019). In addition, traits typically associated with tropical species (Stevens 1989, Gaston 2000, Brown 2014), including habitat specialisation and small range size, have also been associated with stronger negative responses to land-use change (Newbold et al. 2013). 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 (Klein Goldewijk et al. 2011, Yang et al. 2021). Incorporating an

understanding of biogeography and historical knowledge of an environment could play a key role in global biodiversity monitoring.

Considering the influence of biogeography on threat–response relationships, monitoring biodiversity at the smallest possible scale would be appropriate. However, there are currently more than 42 000 threatened species on the IUCN red list (IUCN 2022), all of which cannot have unique conservation plans created for them. Therefore, indicators must be used at a higher ecological and spatial scale that strikes a balance between presenting global trends and understanding local scale responses to human pressure (Ingram et al. 2021). One way to account for biogeographic variation in threat responses is to use a monitoring framework based on spatial units, but choosing the correct unit is challenging. For example, creating national statistics for biodiversity is helpful for feeding into policy, but biodiversity is not nationally constrained (Murphy 2021). A global framework has been suggested for monitoring biodiversity at an ecoregional level ( $n=867$ ) (Dinerstein et al. 2017, 2019, Smith et al. 2018). This framework is powerful when measuring variables that can be obtained using remote sensing or global species lists (Dinerstein et al. 2017, Smith et al. 2020), but many ecoregions are lacking the required field data or access to study population responses to human pressure at this resolution (Stephenson et al. 2015). It is therefore critical to evaluate whether broader spatial units, already used in many global monitoring studies (Newbold et al. 2016, Blowes et al. 2019, WWF 2022), can effectively capture the diversity in threat–response relationships across different biogeographic contexts.

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, which broadly follow the continents (Olson et al. 2001). 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 intersection of these two spatial units is rarely investigated, 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 each cover 11 ecoregions on average, ranging from 1 to –81 ecoregions (Olson and Dinerstein 2002). Separating biomes

by biogeographic realms can account for differences in evolutionary history, vegetative structure, threats and socio-economic status that occur between realms (Moncrieff et al. 2016, Allan et al. 2019). Furthermore, threats are not spread evenly across the world and can be region-specific (Lewis et al. 2015, 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, particularly in the Northern Hemisphere, are being afforested, whilst others experience mass deforestation (Song et al. 2018). In Asian tropical forests, species richness was found to be significantly more sensitive to disturbance compared to similar regions in South America and Africa (Gibson et al. 2011, Phillips et al. 2017). Conversely, vertebrate abundance is declining more in the Neotropics and Afrotropics than in the Indo-Pacific region (Green et al. 2020, WWF 2022). These conflicting trends highlight the necessity of understanding and clearly reporting how biogeographical variation contributes to threat responses. Regional biomes may present a middle-ground between the finer scale monitoring of ecoregions and the coarser biome scale, facilitating robust reporting of biodiversity responses, but there is a lack of empirical evidence comparing this unit to biomes or realms.

Here, we use the PREDICTS database to analyse data from over 400 field studies to explore the efficacy of regional biomes as a spatial monitoring unit for terrestrial species. 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 therefore hypothesise that regional biomes present a more parsimonious explanation of responses of biodiversity to land-use change than realms or biomes alone. We then model the three most data-rich biomes (tropical forest, temperate forest, tropical grasslands) in the PREDICTS database to explore how responses to land-use change vary between regional biomes. Here, we also consider the impact of taxonomic group (vertebrate, invertebrate, plant) on the threat–response relationship within 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 smaller and less variable responses between temperate regional biomes due to the history of natural and anthropogenic disturbance leading 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; 22 678 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](http://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 (Srivathsa et al. 2017, Walker et al. 2010). 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 and taxon using the 'predictsFunctions' R package ([www.r-project.org](http://www.r-project.org), Newbold 2018). 'Taxa' were categorised as vertebrate ( $n=7488$  sites), invertebrates ( $n=7946$  sites), plants ( $n=5306$  sites) or fungi ( $n=467$  sites). The PREDICTS database contains biodiversity data from 47 of 64 regional biomes (70%), with some regional biomes more comprehensively sampled than others. Only 14 regional biomes had data available for  $\geq 50\%$  of their ecoregions (Supporting information). For analysis, we excluded data from three biomes with fewer than 50 sites in total from the dataset (flooded grasslands and savannahs, tundra, deserts and 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; 20011 sites, 545 studies).

Using the predominant land use classification from the PREDICTS database (primary vegetation, mature secondary vegetation, intermediate secondary vegetation, young secondary vegetation, plantation forest, pasture, cropland and urban) (Hudson et al. 2017), we created the *LandUse* variable. We combined the three secondary vegetation classes (mature, intermediate, and young) into one and removed data from urban land-use types due to the low quantity of samples compared to other land-types (917 sites from 53 studies). Because some combinations of regional biome and *LandUse* class have low sample sizes, we tested five variations of this variable where categories were aggregated to find the most parsimonious grouping that still explained variation in the model well. For example, to make the *LandUse2* variable we grouped primary vegetation and secondary vegetation as 'natural vegetation'. Full descriptions of each land-use type and the five variations of *LandUse* can be found in Supporting information.

### Statistical analysis

We used generalised mixed-effects models (Bolker et al. 2009) to test for differences in species richness and total abundance in response to land use, biome, realm and regional

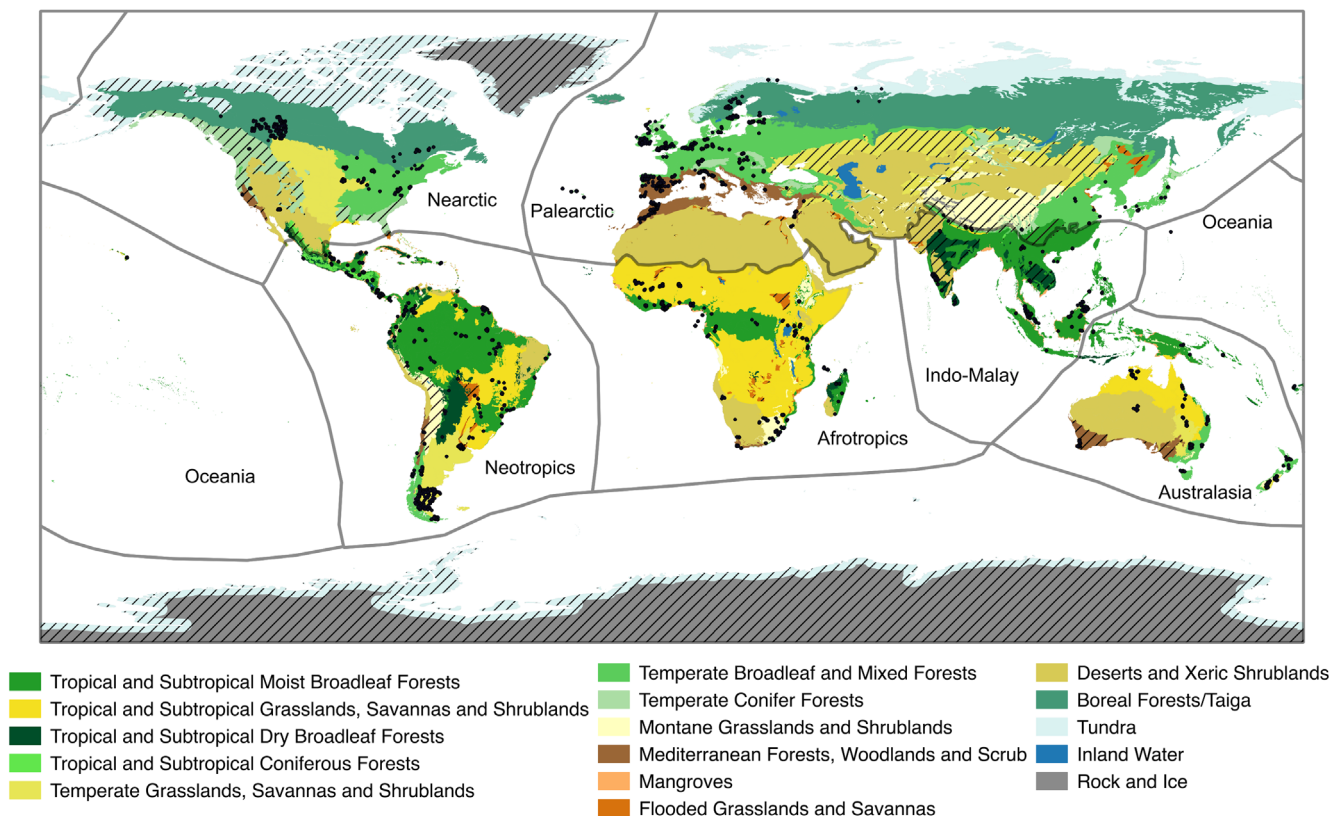


Figure 1. Map of regional biomes. Solid coloured areas represent biomes. Black lines separate out biogeographic realms. Black dots represent sites in the PREDICTS database used in our global model (Hudson et al. 2017). Hashed coloured areas represent regional biomes that were not included in analysis due to data deficiency (see methods). Biome and biogeographic realm spatial data from (Olson et al. 2001).

biome (an interaction of biome and realm). Species richness was modelled using a Poisson distribution and total abundance was log transformed (natural logarithm) and modelled with a Gaussian distribution. In all models, we included study and taxa as random intercepts to account for site-level differences, data collection methods and scale differences between response metrics of vertebrates, invertebrates, plants and fungi. We ran a series of models with species richness and total abundance against each *LandUse* variable (i.e. *LandUse1*, *LandUse2*, *LandUse3* etc.) and selected the best fitting variable using Akaike information criterion (AIC) (Burnham et al. 2011). We found that *LandUse1* (primary vegetation, secondary vegetation, agriculture, plantation forest, cropland) had the most support and was used for remaining analyses (Supporting information).

### Global analysis of regional biomes

To see if including regional biome is a more parsimonious explanation for changes in biodiversity than realm or biome, we ran a model selection process using  $\Delta$ AIC values to assess the support for each variable. The fixed effect structures tested were *LandUse*, *LandUse:Realm*, *LandUse:Biome* and *LandUse:RegionalBiome* and species richness and total abundance were used as response variables. We tested model robustness in two ways. First, we increased the sample size

threshold that would allow a regional biome to be included in the model (minimum 1, 5, 25 or 50 sites in each regional biome-land use combination) and checked if the model selection process gave the same results in each case. Second, we ran a series of 100 hold-out models using the 25-site threshold dataset where each iteration randomly removed 10% of studies to see if this would change the results of model selection.

### Biome-specific case study

As case studies, we investigated the differences in biodiversity response to land-use change between regional biomes by selecting the three biomes which had three or more regional biomes with at least 100 sites in the PREDICTS database (Supporting information). The biomes selected were tropical and subtropical moist broadleaf forest (tropical forest) (4 realms; Indo-Malay: 1702 sites; Neotropics: 2314 sites; Afrotropics: 2174 sites; Australasia: 178 sites), temperate broadleaf and mixed forests (temperate forest) (4 realms; Palearctic: 3965 sites; Neotropics: 653 sites; Nearctic: 856 sites; Australasia: 336 sites) and tropical and subtropical savannas, grasslands and shrublands (tropical grassland) (3 realms; Afrotropic: 2174 sites; Neotropics: 190 sites; Australasia: 502 sites). To allow fair comparison between regional biomes, a down-sampling process was implemented to remove extremely high sample sizes. The range of studies in each regional biome was

13–127 (mean = 42, median = 24), and the range of sites was 178–3941 (mean = 1293, median = 856). The large difference between mean and median demonstrates the presence of extremely high sample numbers in two regional biomes: Neotropical tropical forest ( $n = 116$  studies) and Palearctic temperate forest ( $n = 127$  studies). We chose to down-sample these two regional biomes only because their values were more than double the mean number of studies. We randomly selected 50% of studies from each of these regional biomes to bring their sample size within range of the other regional biomes. This reduced the range of study numbers per regional biome to 13–63 (mean = 32, median = 24) and the range of sites to 178–2100 (mean = 1019, median = 856) (Supporting information). We chose total studies, rather than total sites, as the down-sampling factor as this would keep entire studies intact in the final dataset.

For each biodiversity metric (species richness and total abundance), we modelled the interaction between *LandUse* and regional biome and predicted the average change in species richness and total abundance, relative to primary vegetation, for each land-use type in each regional biome using the ‘StatisticalModels’ R package (www.r-project.org, Newbold 2015).

In addition to the biome case study, we did a further analysis to investigate how taxonomic group further influences the responses of species richness to land-use change across regional biomes. We ran one model using species richness as the response variable and *LandUse*, *Realm* and *Taxa* (vertebrate, invertebrate and plant) as fixed interaction terms. As above, we predicted the average change in species richness relative to primary vegetation.

## Results

### Global analysis of regional biomes

Including regional biome as a variable improved model fit and better explained the effect of land-use change on species richness and total abundance (Fig. 2). Models with realm or biome alone had lower support and this was consistent across 100 iterations of hold-out models (Fig. 2). Increasing the sample size threshold for regional biomes did not change the overall outcome (Supporting information). 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 (Supporting information).

### Biome-specific case studies

We found that species richness and total abundance in each regional biome of tropical forest (except Australasia) showed a strong response to land-use change. Species richness reduced in human-dominated land-use types compared to primary vegetation in all realms except Australasia but to different degrees at each land-use type (Fig. 3a). The largest loss of species richness was predicted in Indo-Malayan cropland (–55% reduction compared to primary vegetation,

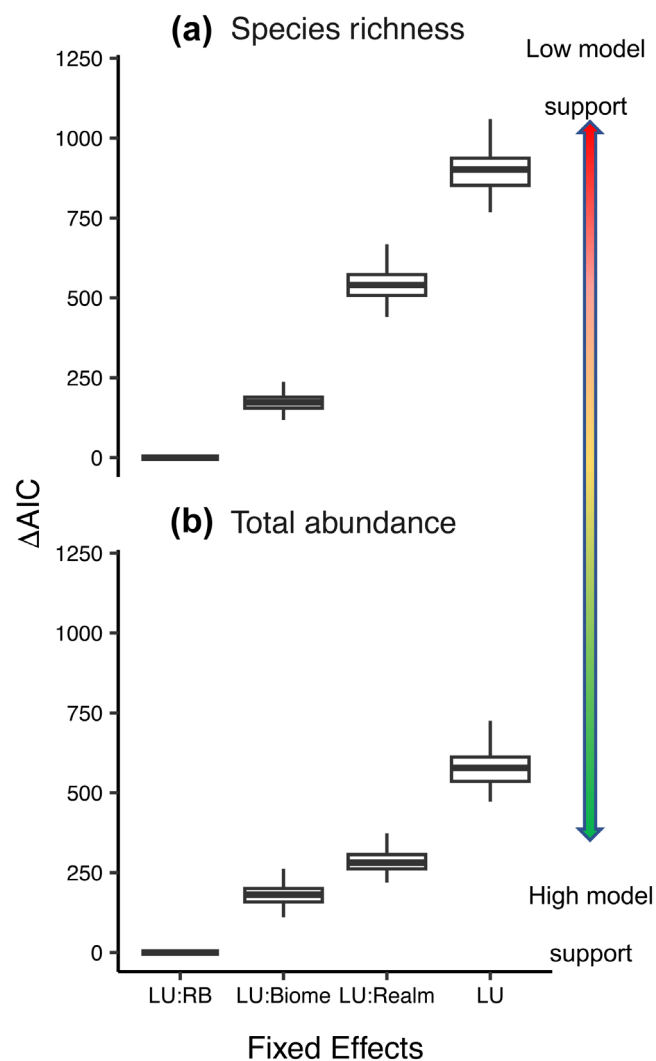


Figure 2. Change in Akaike's information criterion ( $\Delta AIC$ ) for generalised linear mixed models (GLMMs) predicting change in a global dataset of (a) species richness and (b) total abundance consistently suggests models including regional biome have highest support when modelling response to land-use 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.  $\Delta AIC$  is calculated as the difference in AIC from the lowest scoring model. The box and whisker plots represent a summary of  $\Delta AIC$  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 the Supporting information for descriptions of land-use types).

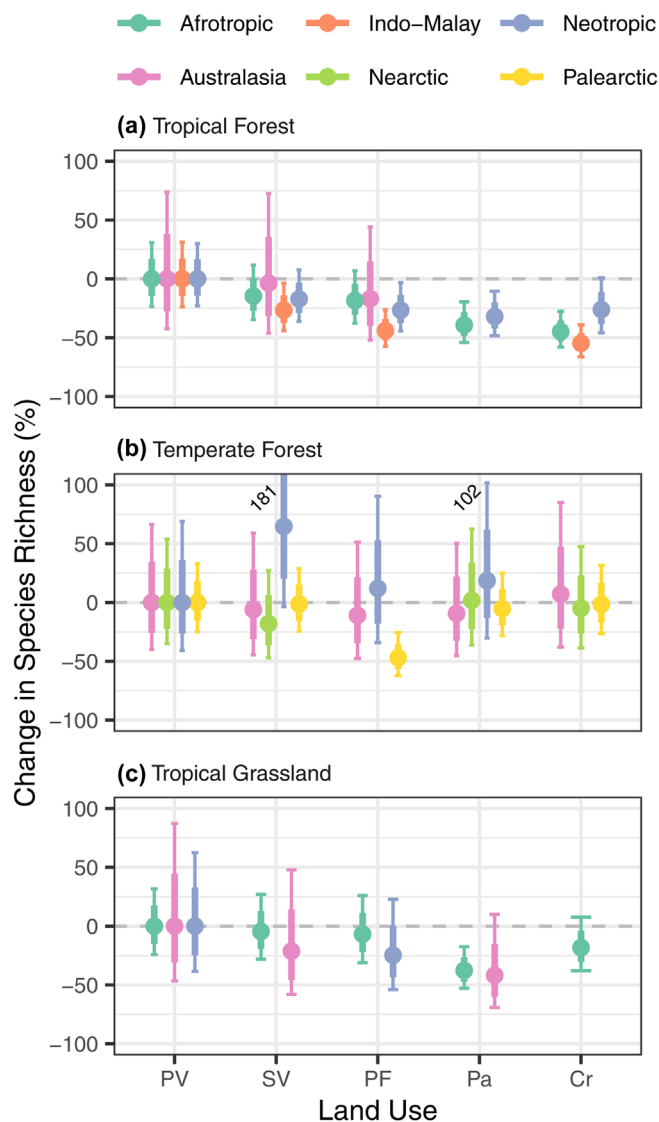


Figure 3. Responses of species richness to land-use change across regional biomes. The results of a GLMM predicting the response of species richness to land-use within regional biomes from tropical forest (a), temperate forest (b) and tropical grasslands and savannahs (c) across land-use types when compared to primary vegetation (PV). Responses of species richness of plants and animals were predicted across land-use types including secondary vegetation (SV), plantation forest (PF), pasture (Pa) and cropland (Cr). Each point represents mean prediction, with 75% confidence intervals (thick whiskers) and 95% confidence intervals (thin whiskers). Responses are considered significantly different from PV if the 95% confidence intervals do not overlap 0. To keep scales consistent, upper 95% CIs greater than 100 have been included as text instead.

95% CI:  $[-66\%, -39\%]$ ), followed by Afrotropical cropland ( $-44\%$ , 95% CI  $[-57\%, -27\%]$ ). Conversely, the Neotropics did not show a significant species richness reduction in cropland and had a small, but significant reduction in plantation forest ( $-26\%$ , 95% CI  $[-44\%, -3\%]$ ), with species richness for this regional biome being worst affected in pasture land-use types ( $-31\%$ , 95% CI  $[-48\%, -10\%]$ ).

When predicting responses of total abundance to land-use change in the tropical forest biome there were high levels of 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 longer a sign of a negative response in Neotropical pasture. The only negative responses that were significantly different from primary vegetation was seen in Indo-Malayan plantation forest ( $-52\%$ , 95% CI  $[-72\%, -18\%]$ ) and Afrotropical pasture ( $-45\%$ , 95% CI  $[-68\%, -6\%]$ ) (Fig 4a).

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. 3b, 4b). The exception is the Palearctic regional biome, where species richness reduced by 47% (95% CI  $[-62\%, -25\%]$ ) in plantation forest land-use types. 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. 3c, 4c). Predictions of species richness and total abundance change showed a high degree of uncertainty across all regional biomes, except for the Afrotropics, where there was a strong negative response to pasture (species richness:  $-38\%$ , 95% CI  $[-53\%, -17\%]$ ; total abundance:  $-59\%$ , 95% CI  $[-76\%, -31\%]$ ).

Including taxon as an interaction term reveals distinct responses to land-use change across different taxonomic groups within regional biomes, although prediction uncertainty for some groups is increased (Fig. 5). In tropical forest, there is still a general trend of negative responses to human-dominated land-use types, but for some regional biomes there is high variation in responses. For example, Afrotropical vertebrates have no observable response to cropland and plantation forest, but plants in the same regional biome display negative responses of species richness at these land-use types. Conversely, in Neotropical tropical forest, invertebrates show a negative response to pasture land, whilst plants and vertebrates do not, although note high levels of uncertainty in these predictions. In temperate forest, the addition of taxon groups creates a high level of uncertainty in predicting species richness responses, highlighting the level of incomplete sampling in the dataset. In tropical grassland, strong responses of invertebrates to plantation forest and cropland are observed in the Neotropics and Afrotropics, respectively. This reveals responses that were not seen when taxa was not accounted for (Fig. 3c).

## Discussion

### Global analysis of regional biomes

Our results show that including regional biome when modelling the global effects of land use on biodiversity can increase

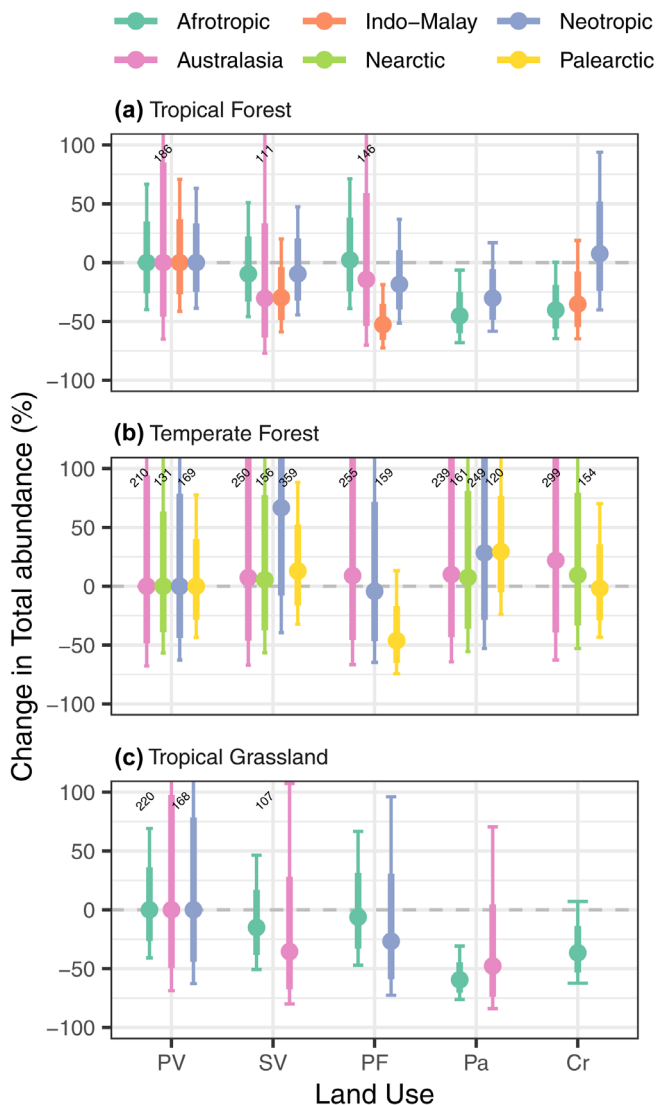


Figure 4. Responses of total abundance to land-use change across regional biomes. The results of a GLMM predicting the response of total abundance to land-use within regional biomes from tropical forest (a), temperate forest (b) and tropical grasslands and savannahs (c) across land-use types when compared to primary vegetation (PV). Responses of total abundance of plants and animals were predicted across land-use types including secondary vegetation (SV), plantation forest (PF), pasture (Pa) and cropland (Cr). Each point represents mean prediction, with 75% confidence intervals (thick whiskers) and 95% confidence intervals (thin whiskers). Responses are considered significantly different from PV if the 95% confidence intervals do not overlap 0. To keep scales consistent, upper 95% CIs greater than 100 have been included as text instead.

explanatory power, providing the first empirical test of regionally-separated biomes as a potential spatial monitoring framework. Although a small spatial unit would be optimal for monitoring biodiversity trends, our analysis excluded spatial units smaller than a regional biome, such as ecoregions, due to data deficiency. The PREDICTS database contains data from only 36% of ecoregions (237 of 867), highlighting the

practical difficulty in achieving high global coverage with this spatial unit. In this study, we sought to explore 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 et al. 2017, WWF 2022), but for the first time, we have shown the important interaction between biome and realm. The combination of these two spatial delineations gives more information about ecological processes.

One reason for the increase in model support after adding regional biome is that the comparison of land-use types will change as spatial unit becomes more localised. For example, a comparison of any primary vegetation with cropland is quite general and will be hard to characterise, but the relationship between biodiversity in Indo-Malayan tropical forest and cropland has a high specificity and contains less variation in response. In all our models, we attempted to control for this localised specificity by including study as a random effect, which may control for differing methodologies, site conditions or sampling bias. Future models using the PREDICTS database or other global databases could also consider using regional biome as a random effect to control for more regional variation that reflects environmental and ecological differences between these spatial units.

### Biome-specific case study

Whilst our global 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 (tropical forest and tropical grassland) showed negative responses to disturbed land-use types, the degree of which changed with realm and taxonomic group. 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; 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 and tropical grassland models are most likely explained by low sample sizes and the high variation in responses of taxonomic groups. Predictions in palearctic temperate forest have very



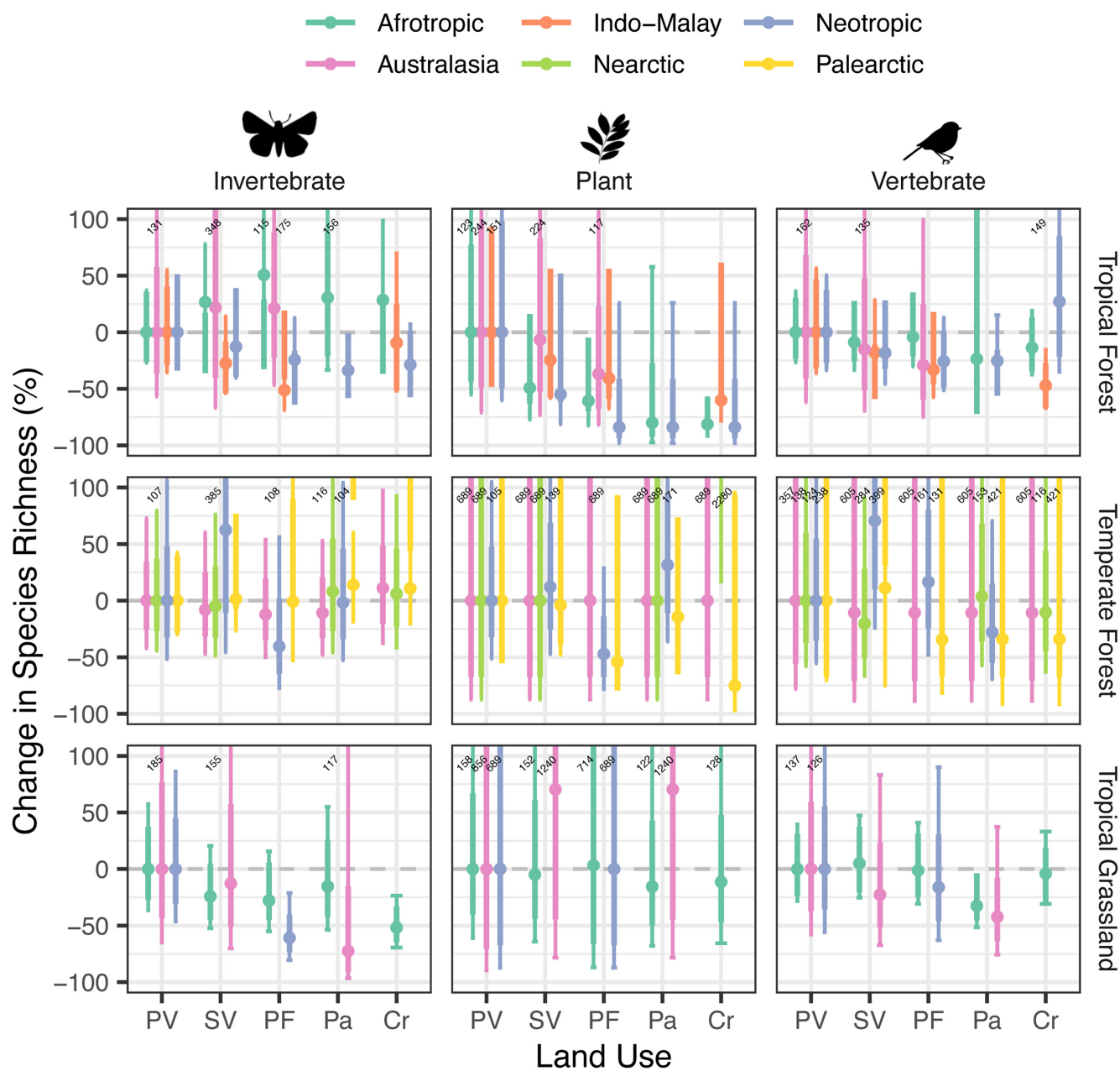


Figure 5. Responses of species richness in individual taxa groups to land-use change across regional biomes. The results of a GLMM predicting the response of species richness across land-use types, regional biomes in three biomes (tropical forest, temperate forest and tropical grassland) and three taxon groups (vertebrate, invertebrate and plants) when compared to primary vegetation (PV). Responses of species richness were predicted across disturbed land-use types including secondary vegetation (SV), plantation forest (PF), pasture (Pa) and cropland (Cr). 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 if the 95% confidence intervals do not overlap 0.

low uncertainty compared to all other regional biomes and is also the most extensively sampled regional biome in the PREDICTS database (Supporting information).

For tropical forest regional biomes, our model predictions suggest Indo-Malayan biodiversity responds most strongly to land-use change (plantation forest and cropland), followed by the Afrotropics (pasture and cropland). Species richness in Neotropic tropical forest responded to plantation forest and

pasture, but to a lesser degree than other regional biomes. Adding taxon to the model showed that these responses are nuanced and driven by different taxonomic groups, but the patterns between regional biomes remain largely the same. 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 et al. 2017). The islands of south east Asia have a rich geographical 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 2022). In addition, other studies in this region have shown a decline in biodiversity due to land-use change (Bogoni et al. 2020, Gaona et al. 2021, Quintero et al. 2023). It is possible that the responses observed in our results are due to data collection methods and sampling bias, rather than an ecological distinction, demonstrating the importance of testing multiple data types and of assessing the regional biome framework using time-series biodiversity data and across multiple threat gradients 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. A limitation of our comparison across regional biomes is that we could not control for publication bias in threat-types e.g. there is a high focus in the literature on palm oil in the Asian tropics. Such publication biases will impact the interpretation of community threat-responses both within and between regional biomes as some crop types are more damaging to biodiversity than others, for example cacao crops, common in the Neotropics, are less damaging than oil palm, more common in Asia (Oakley and Bicknell 2022). 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 et al. 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 Paelearctic temperate forest dominate the database but there are no studies at all on Paelearctic temperate grasslands

(Supporting information). Furthermore, taxonomic under sampling was highlighted in our model that included taxonomic group. For example, Fig. 3 suggests that Afrotropical tropical forests have a greater response to cropland compared to the Neotropical regional biome. However, this response is driven by plants in the Afrotropics and Invertebrates and vertebrates in the Neotropics, making the impact of cropland hard to compare. Prioritising data collection in under-represented regional biomes and taxonomic groups highlighted here would enhance progress towards an effective monitoring framework (Ingram et al. 2021). In this study, we used a crude classification of all animals and plants into only three groups. A further investigation that would benefit from increased sampling would be to split taxonomic group further, for example flying and non-flying vertebrates, who may respond differently to land-use pressures. Furthermore, 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 the taxa-regional biome unit has the potential to be a powerful spatial framework for monitoring biodiversity and implementing conservation action, although further work is needed to disentangle the statistical artefacts of the sparse dataset verses real ecological signal. Resources for data collection and biodiversity monitoring on the ground are limited, and the regional biome framework implies that monitoring studies could be more evenly spread across regional biomes and taxonomic groups instead of the national or ecoregional scale, optimising resource allocation for data collection. Here we have highlighted that there is within-biome variation in how biodiversity is responding to disturbance, but the difference between realms may be more prevalent 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 ongoing policy discussions, such as the monitoring framework for the CBD's Kunming-Montreal Global Biodiversity Framework, on the best way to monitor progress towards biodiversity targets and effect change on the ground.

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## Author contributions

**Peggy A. Bevan:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Methodology (lead); Project administration (equal); Visualization (lead); Writing - original draft (lead); Writing - review and editing (lead). **Guilherme Braga Ferreira:** Conceptualization (supporting); Supervision (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). **Daniel J. Ingram:** Conceptualization (supporting); Supervision (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). **Marcus Rowcliffe:** Supervision (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). **Lucy Young:** Conceptualization (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). **Robin Freeman:** Conceptualization (supporting); Formal analysis (supporting); Supervision (supporting); Visualization (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). **Kate E. Jones:** Conceptualization (equal); Supervision (lead); Visualization (supporting); Writing - original draft (supporting); Writing - review and editing (supporting)

## Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/ecog.07318>.

## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dr7sqvb5m> (Bevan et al. 2024), and all R code to run the analyses from Github, <https://github.com/PeggyBevan/RegionalBiomes>.

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-v1-1>).

Geographical data used to delineate regional biome boundaries in this manuscript can be downloaded from Resource Watch (<https://resourcewatch.org/data/explore/bio021a-Terrestrial-Ecoregions?section=Discover&selectedCollection=&zoom=3&lat=0&lng=0&pitch=0&bearing=0&basemap=dark&labels=light&layers=%255B%257B%2522dataset%2522%253A%2522d0968f74-f5c1-40a1-b2b5-5bac5de5cb15%2522%252C%2522opacity%2522%253A1%252C%2>

[522layer%2522%253A%252201152647-80b6-41fb-9ebc-48a5f2411327%2522%257D%255D&aoi=&page=1&sort=most-viewed&sortDirection=-1](https://doi.org/10.1111/ecog.07318)).

## Supporting information

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

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