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Author for correspondence:
Jian Zhang
e-mail: jzhang@des.ecnu.edu.cn

Trophic interactions among vertebrate guilds and plants shape global patterns in species diversity

Jian Zhang[1,2,3], Hong Qian[5], Marco Girardello[3], Vincent Pellissier[3], Scott E. Nielsen[6] and Jens-Christian Svenning[3,4]

[1]Tiantong National Station for Forest Ecosystem Research & Center for Global Change and Ecological Forecasting, School of Ecological and Environmental Science, East China Normal University, Shanghai 200241, People's Republic of China
[2]Shanghai Institute of Pollution Control and Ecological Security, Shanghai 200092, People's Republic of China
[3]Section for Ecoinformatics and Biodiversity, Department of Bioscience, and [4]Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, 8000 Aarhus C, Denmark
[5]Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, USA
[6]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1

JZ, 0000-0003-0589-6267; MG, 0000-0003-0699-8628; VP, 0000-0003-2809-0063; SEN, 0000-0002-9754-0630; J-CS, 0000-0002-3415-0862

Trophic interactions play critical roles in structuring biotic communities. Understanding variation in trophic interactions among systems provides important insights into biodiversity maintenance and conservation. However, the relative importance of bottom-up versus top-down trophic processes for broad-scale patterns in biodiversity is poorly understood. Here, we used global datasets on species richness of vascular plants, mammals and breeding birds to evaluate the role of trophic interactions in shaping large-scale diversity patterns. Specifically, we used non-recursive structural equation models to test for top-down and bottom-up forcing of global species diversity patterns among plants and trophic guilds of mammals and birds (carnivores, invertivores and herbivores), while accounting for extrinsic environmental drivers. The results show that trophic linkages emerged as being more important to explaining species richness than extrinsic environmental drivers. In particular, there were strong, positive top-down interactions between mammal herbivores and plants, and moderate to strong bottom-up and/or top-down interactions between herbivores/invertivores and carnivores. Estimated trophic interactions for separate biogeographical regions were consistent with global patterns. Our findings demonstrate that, after accounting for environmental drivers, large-scale species richness patterns in plant and vertebrate taxa consistently support trophic interactions playing a major role in shaping global patterns in biodiversity. Furthermore, these results suggest that top-down forces often play strong complementary roles relative to bottom-up drivers in structuring biodiversity patterns across trophic levels. These findings underscore the importance of integrating trophic forcing mechanisms into studies of biodiversity patterns.

1. Introduction

A long-standing question in ecology is whether resource availability limits biodiversity [1–3]. The 'bottom-up' hypothesis predicts that productivity and species composition of primary producers determine species diversity at all higher trophic levels, e.g. herbivores and their predators. The implications are that changes in species diversity and abundance at higher trophic levels should have no effect on diversity at lower trophic levels. However, for many terrestrial and aquatic ecosystems, the role of bottom-up forcing may be much weaker than typically considered [1–3]. In a recent review, Terborgh [4]

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argued that 'pervasive bottom-up thinking has blinded us to alternatives', suggesting that top-down forcing (herbivory and predation) should be incorporated into theories of species coexistence [4].

The question of whether top-down forcing regulates biodiversity more strongly than bottom-up forcing can be traced to the 'green world' hypothesis proposed by Hairston et al. [5]. Under this perspective, predators are the key to keeping the world 'green' because they limit herbivore abundance, thus releasing plants from herbivory and allowing them to flourish. Strong top-down forcing by high trophic levels also reduces competition from one or a few dominant species at lower trophic levels, promoting diversification or coexistence among lower trophic taxa [4]. There have been a number of tests of this hypothesis in recent decades, with evidence supporting both top-down and bottom-up controls of biodiversity [6–13]. This suggests that bottom-up and top-down forcing on biodiversity need not be mutually exclusive, and that resources and consumers interact to shape ecosystem composition [6–12]. The strength of these relationships may also vary among ecosystems depending on environmental conditions [14–19]. Generalizing from individual studies within single ecosystems, often at small spatial scales [15], may not therefore be warranted for inferring patterns at broad spatial scales. Large-scale assessments of these trophic relationships is thus important for testing the generality of the results found at regional scales, as well as understanding how these vary across spatial scales, both in terms of magnitude and direction [20]. More comparative examinations across ecosystems are needed, especially with respect to the strengths and interactions between bottom-up and top-down forces on diversity [4,16].

How bottom-up and top-down forces regulate biodiversity at regional and global scales is poorly understood [21,22]. The dynamics of trophic interactions over broad spatial scales can alter species composition and reshape biodiversity patterns by affecting immigration, extinction and speciation processes [23–25]. For example, immigrating consumers provide nutrients for primary producers [26], secondary extinction occurs when specialized consumers lose all of their prey [21,27] and strong trophic interaction favours coevolution and hence changes the optimum phenotype, resulting in faster speciation [25,28]. Understanding variation in trophic interactions across systems provides important insights into questions of biodiversity dynamics, species extinction risk and evolutionary dynamics [13,21,25]. For example, megafauna extinction during the Late Pleistocene and Early Holocene has had a major influence on contemporary ecosystems [29]. The influence of these losses is still evident today with lags in extinction [30] and long-term vegetation shifts [31]. Similar effects occur due to later trophic downgrading [32]. For example, the recent (past 150-year) decline of Australia's largest top predator, the dingo (Canis lupus dingo) has contributed to continent-wide declines of other mammals [33]. In addition, anthropogenic changes to key ecological processes, such as vegetation dynamics and fire, have further altered habitats and thus trophic interactions. Indeed, recent studies of predator–prey interactions have considered humans to be the ultimate superpredator [34–36], while fire is considered a major 'abiotic consumer' of plant biomass having major cascading effects on biodiversity [17,37]. Therefore, when assessing the role of trophic interactions on broad-scale

diversity patterns, potentially competing or interacting factors should also be considered.

In this study, we use a comprehensive global dataset on species richness of vascular plants, mammals and breeding birds (figure 1) to evaluate the role of trophic interactions in shaping large-scale diversity patterns. Specifically, we address the following questions. (i) Are relations in large-scale species richness patterns of plants and vertebrate dietary groups consistent with trophic interactions shaping biodiversity patterns? (ii) If so, which direction (top-down or bottom-up) is stronger, or are they complementary? (iii) Are trophic interactions similar among taxa and trophic levels? (iv) How important are trophic interactions relative to extrinsic factors?

2. Material and methods

(a) Plant and vertebrate data

We updated a global dataset on native vascular plant richness originally assembled by Qian and co-workers [38,39]. This dataset was built using a large number of literature sources, including floras, checklists, monographs, atlases and journal articles published during the past several decades, covering 381 geographical units worldwide. Most of these geographical units represent level 4 units referred as 'Basic Recording Units' in the International Working Group on Taxonomic Databases (TDWG; http://www.tdwg.org/). Most geographical units correspond to countries, but with the largest countries (e.g. USA, Canada, China, Brazil and Australia) divided into states or provinces. In a few locations, such as the Far East and Siberian regions of Russia, Mongolia and the Northwest Territories of Canada, data did not match the current political boundaries and thus phytogeographical regions were used for floristic surveys [39].

Species range maps for all terrestrial mammals, excluding bats (Order Chiroptera), were gathered from the IUCN Red List database [40]. For birds, we used breeding distributions of all bird species from the BirdLife International [41]. To match plant richness data, mammal and bird lists were summarized for each geographical unit by overlaying their distribution maps with defined geographical units. In total, we considered 364 geographical units, each of which had at least 10 species in each of the three taxa (i.e. plants, mammals and birds). These geographical units represent nearly 125×10^6 km^2 or approximately 95% of the total ice-free land of the world (figure 1). Only Antarctica was not represented. The average size of each geographical unit was 343 272 km^2, with 358 (98%) of 364 geographical units larger than 10 000 km^2.

(b) Trophic groups for mammals and birds

To assess bottom-up and top-down effects among trophic levels, we divided mammals and birds into three trophic groups: carnivores, predominantly feeding on vertebrates; invertivores, predominantly feeding on invertebrates; and herbivores, predominantly feeding on plant materials, such as fruits, nectar, plants and seeds. We used EltonTraits v.1.0 [42] as the primary literature and assigned each species of mammals and birds to one of these three trophic levels. Some mismatched species names in EltonTraits were corrected by checking their synonyms in the IUCN Red List website. When trait information from the EltonTraits database was not available for a species, we used dietary information from MammalDIET v.1.0 [43] to assign species to trophic groups. A small percentage (less than 10%) of species have little trait information in these databases or are difficult to assign to these trophic groups; accordingly, they were excluded from this study. For mammals, 3750 species were assigned to trophic levels, with 232 carnivores, 891
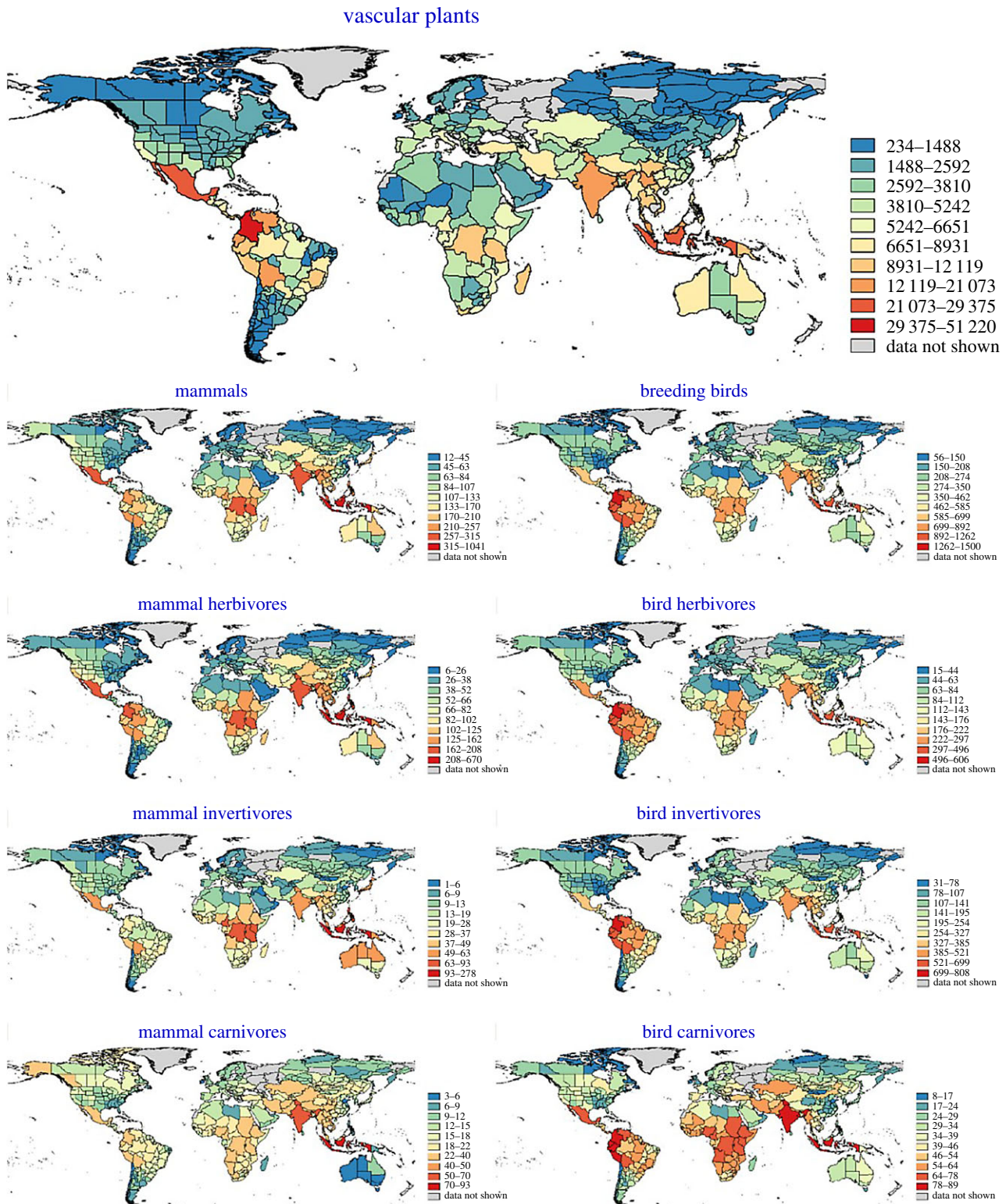
Figure 1. Global species richness patterns for vascular plants and for mammals and breeding birds overall and in separate dietary categories. (Online version in colour.)

invertivores and 2627 herbivores. For birds, 8278 species were assigned to trophic levels, with 520 carnivores, 4657 invertivores and 3101 herbivores.

(c) Geographical and environmental factors

In addition to accounting for interactions among trophic levels, we evaluated the importance of climate (current and historical) and environmental heterogeneity on patterns of species richness because these factors are widely known to affect broad-scale patterns in species richness. For current climate, we selected two commonly used variables: mean annual temperature (MAT, an indicator of ambient energy) and annual actual evapotranspiration (AET, a measure of water–energy balance). Data for MAT were obtained from the WorldClim Dataset of average climate data for the period 1960–1990 at the 30 arc-second resolution [44]. AET was obtained from the MODIS (Moderate Resolution Imaging Spectrometer) global terrestrial data for the period 2000–2013 at the 30 arc-second resolution [45]. In addition, we assessed the use of primary productivity, measured by the average of NDVI (Normalized Difference Vegetation Index) for the period 2000–2013 in each geographical unit (https://clarklabs.org/
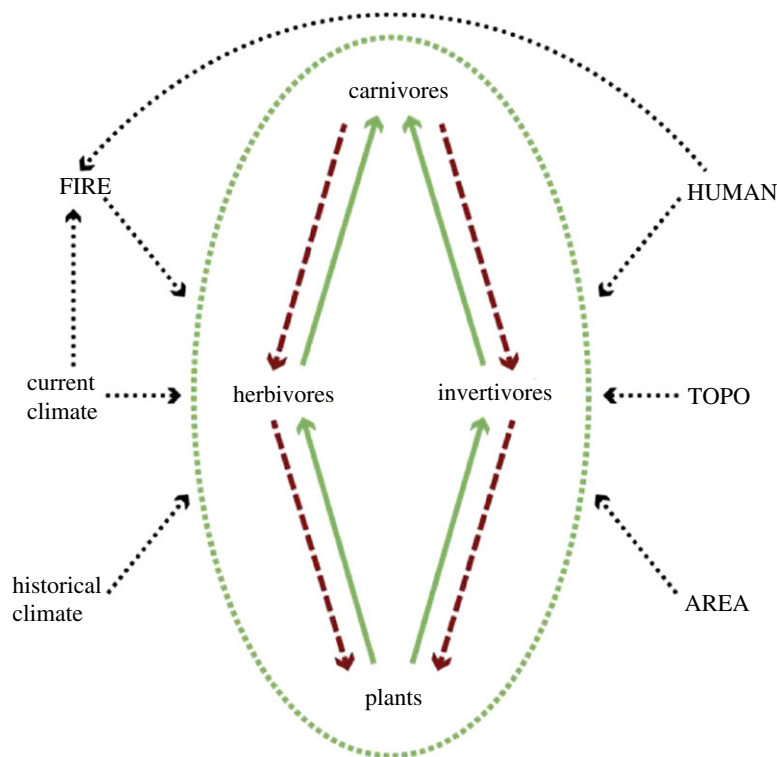
Figure 2. *A priori* SEM used to test bottom-up and top-down effects across trophic levels. Green solid arrows in the centre represent bottom-up effects, red-dashed arrows top-down effects and thin black-dashed arrows environmental effects, with direct paths to all four trophic levels within the green-dashed circle. The inter-action between plant and invertivore richness was treated as a direct path, because the data on invertebrate diversity were not available. FIRE: fire density; HUMAN: human influence index; TOPO: topographic relief; AREA: the areas of geographical units. (Online version in colour.)

additional-products/global-data-archives/) [46,47], but it showed very weak effects on species richness of trophic groups in prelimi-nary analyses and was therefore excluded from the final analysis.

For historical climate, we used velocity at 2.5 arc-minute resol-ution for mean annual temperature (tempVelo) and annual precipitation (precVelo) between Last Glacial Maximum (LGM; approx. 21 000 years ago) and the present (1950–2000) to represent climate stability [48]. Climate velocity was based on estimates of past mean annual temperature and annual precipitation from the Paleoclimate Modelling Intercomparison Project Phase II [49], using the averages of the CCSM3 and MIROC3.2 simulations.

For environmental heterogeneity, we used topographic relief (TOPO; maximum minus minimum elevation) within each geo-graphical unit [50]. TOPO was calculated from altitude data from WorldClim 30 arc-second data. All other variables were averaged within each geographical unit.

(d) Human and fire as top consumers

Recent studies of predator–prey interactions have considered humans as the ultimate superpredator [34,35,51] and fire as a widespread and key abiotic consumer of vegetation [17,37]. Accordingly, we used a 1 km resolution human influence index (HUMAN) as a surrogate for anthropogenic disturbance over the period 1995–2004 using the Global Human Influence Index Dataset v.2 [52], and fire density (FIRE) at a 0.1° resolution (avail-able at: http://preview.grid.unep.ch) to represent the fire regime. The HUMAN data were created from nine global data layers covering human population density, human land use and infra-structure, and human access. FIRE data were developed by UNEP/GRID-Europe using the World Fire atlas over the period 1997–2010 [53]. As for climate, HUMAN and FIRE variables were averaged for each geographical unit.

(e) Data analysis

We used structural equation models (SEMs) [54,55] to infer relative importance of bottom-up and top-down controls

among trophic levels. SEMs allow simultaneous testing of direct and indirect effects between predictor and response vari-ables [54], thus enabling the evaluation of hypothesized causal relationships among interacting trophic groups. We constructed SEMs based on the schematic diagrams (*a priori* model) in figure 2 using trophic richness and environmental data for each geographical unit. In this *a priori* SEM model, direct trophic interactions between plants and herbivores, herbivores and carnivores, and invertivores and carnivores were included. The forcing of plant species richness by invertivores was trea-ted as a direct path, because the data on invertebrate diversity were not available. Current climate (MAT and AET), historic climate (tempVelo and precVelo), environmental het-erogeneity (TOPO), human influence (HUMAN), fire disturbance (FIRE) and the area of geographical units (AREA) were considered as covariates of species richness for all four trophic groups.

Compared with traditional SEMs commonly used in ecology, our model (figure 2) was a non-recursive SEM model with reci-procal causal relationships that included pathways both for A towards B and for B towards A in the same model. We built non-recursive SEMs that can estimate two unidirectional relation-ships simultaneously [54] using the R package *systemfit* [56]. Compared with recursive models, non-recursive SEM can address the problem of endogeneity (i.e. the variable A is hypothesized to be both a cause and a consequence of the vari-able B) [57], and the system of equations is identified because all the pairs of variables linked by reciprocal effects have differ-ent sets of other predictors. The models in figure 2 were fitted using SEM by ordinary least squares, because all regressors are exogenous [55]. A standardized coefficient (β) for each path was calculated and used to compare the relative importance of trophic interactions and environmental effects for species rich-ness at each trophic level. Considering the potential influence of spatial autocorrelation in the modelled results, we adopted the function 'lavSpatialCorrect' by Jarrett Byrnes (https://github.com/jebyrnes/spatial_correction_lavaan). This function

(a) mammals

carnivores
0.569

0.412*** 0.296*** 0.284** 0.187***

herbivores
0.752

invertivores
0.648

0.328*** 0.360*** 0.298*** 0.007

McElroy's $R^2 = 0.828$

plants
0.790

(b) birds

carnivores
0.798

0.648*** 0.515*** 0.424*** 0.602***

herbivores
0.844

invertivores
0.857

0.006 0.127* 0.156** 0.299*

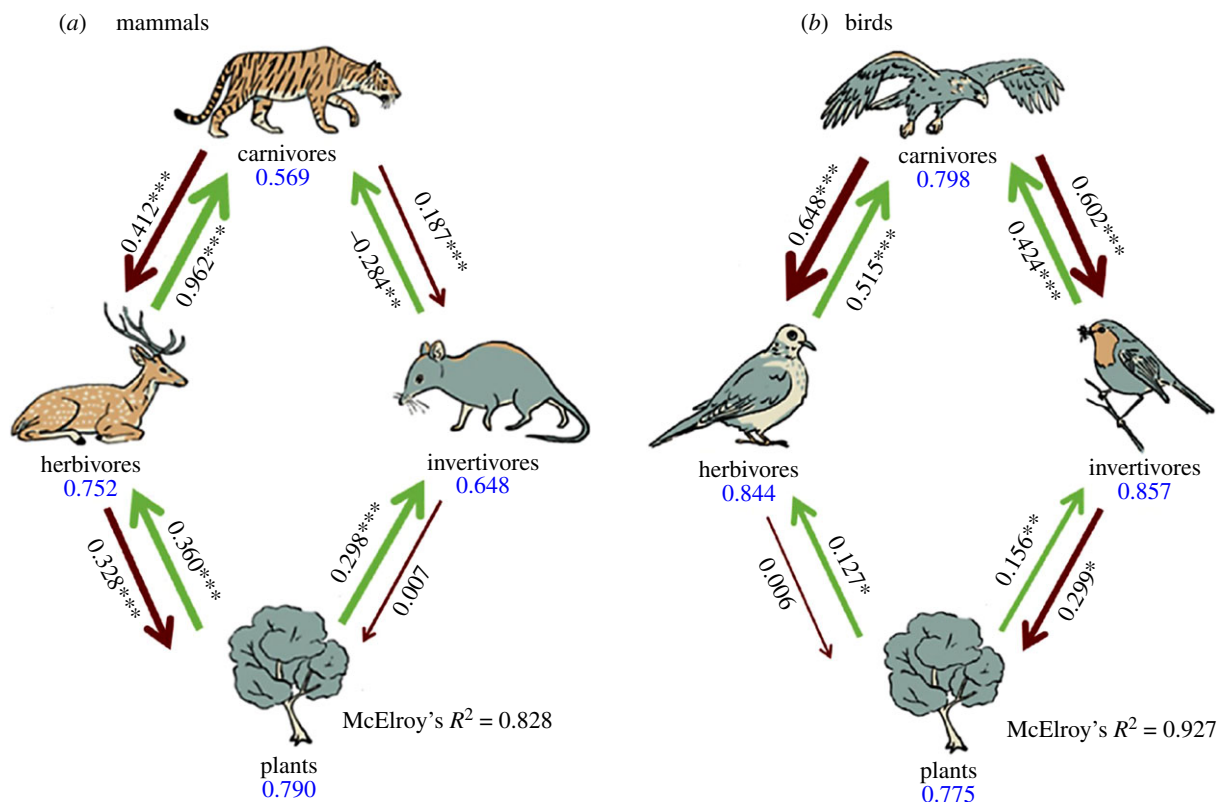McElroy's $R^2 = 0.927$

plants
0.775

Figure 3. Global-scale non-recursive SEM results for trophic interactions among plant, mammal and bird richness after accounting for environmental variables. Only the central parts of the *a priori* SEM model from figure 2 are shown here. Values next to arrow lines are standardized path coefficients (β). Green arrows represent bottom-up effects, and red-dashed arrows top-down effects. Arrow line thicknesses correspond to the strength of trophic interaction based on standardized coefficients. Significance levels after correcting sample sizes and standard errors in SEMs with spatial structure in the autocorrelation of endogenous variables are denoted by means of asterisks $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Adjusted R^2 of each path is shown (in blue). The goodness of fit of the whole model is shown as McElroy's R^2.

can address the problem of correcting sample sizes and standard errors in SEMs with spatial structure in the autocorrelation of endogenous variables. The goodness of fit of the whole model was measured by the McElroy's system R^2 value [58], which has been widely used in economics and sociology.

As a control, we also re-ran the analyses excluding 14 oceanic island units because trophic interactions on islands might be influenced by different processes from mainland regions [24,59]. Oceanic units were defined as regions smaller than Australia and surrounded by ocean [60]. To minimize regional and historical effects on trophic interactions, we also assigned the 364 units into six commonly used biogeographical realms [61], including Nearctic, Neotropical, Afrotropic (Ethiopian), Oriental, Palaearctic and Australasian. The Australasian region was excluded for this analysis because it had only eight geographical units and such a small sample size may invalidate SEM analyses. The Palearctic region was divided into eastern and western sections to make geographical extents more consistent among regions [62]. As a result, six biogeographical regions were used in this study. SEMs were performed for each region, and regional differences were assessed by comparing standardized coefficients among paths.

All statistical analyses were performed using the statistical software R v.3.2.2 [63]. All variables were log-transformed to improve normality. Pairwise correlations were conducted among trophic groups (electronic supplementary material, figure S1), while pairwise correlations among environmental variables were used to assess multicolinearity (electronic supplementary material, figure S2). The R script for non-recursive SEM and data used for the study are provided in the electronic supplementary material.

3. Results

The 364 geographical units include an average of 3487 (± 4335 s.d.) species of vascular plants, 86 (± 73) species of mammals and 298 (± 214) species of breeding birds. The three trophic levels within mammals and birds exhibited strong spatial variation in richness with moderate to high spatial congruence among taxa and trophic levels (figure 1).

At a global scale, plant richness showed positive relations to mammal herbivore richness, with stronger top-down than bottom-up relations (figure 3a). By contrast, plant richness and bird herbivore richness had strong bottom-up, but weak top-down interactions (figure 3b). Relationships between herbivore and carnivore richness were also all positive, with stronger bottom-up than top-down interactions in mammals (figure 3a), and stronger top-down than bottom-up interactions in birds (figure 3b). Relations between invertivore and carnivore richness were moderate and negative for bottom-up interactions and moderate and positive for top-down interactions in mammals (figure 3a), with stronger and positive interactions in both directions in birds (figure 3b). Links between plant and invertivore richness were moderate, with positive bottom-up interactions for both mammals and birds, but weak, top-down interactions for mammals and intermediate, top-down interactions for birds (figure 3). Analyses excluding 14 oceanic island regions yielded similar results (electronic supplementary material, figure S3).

Geographical and environmental factors had relatively consistent effects on species richness across taxa and trophic
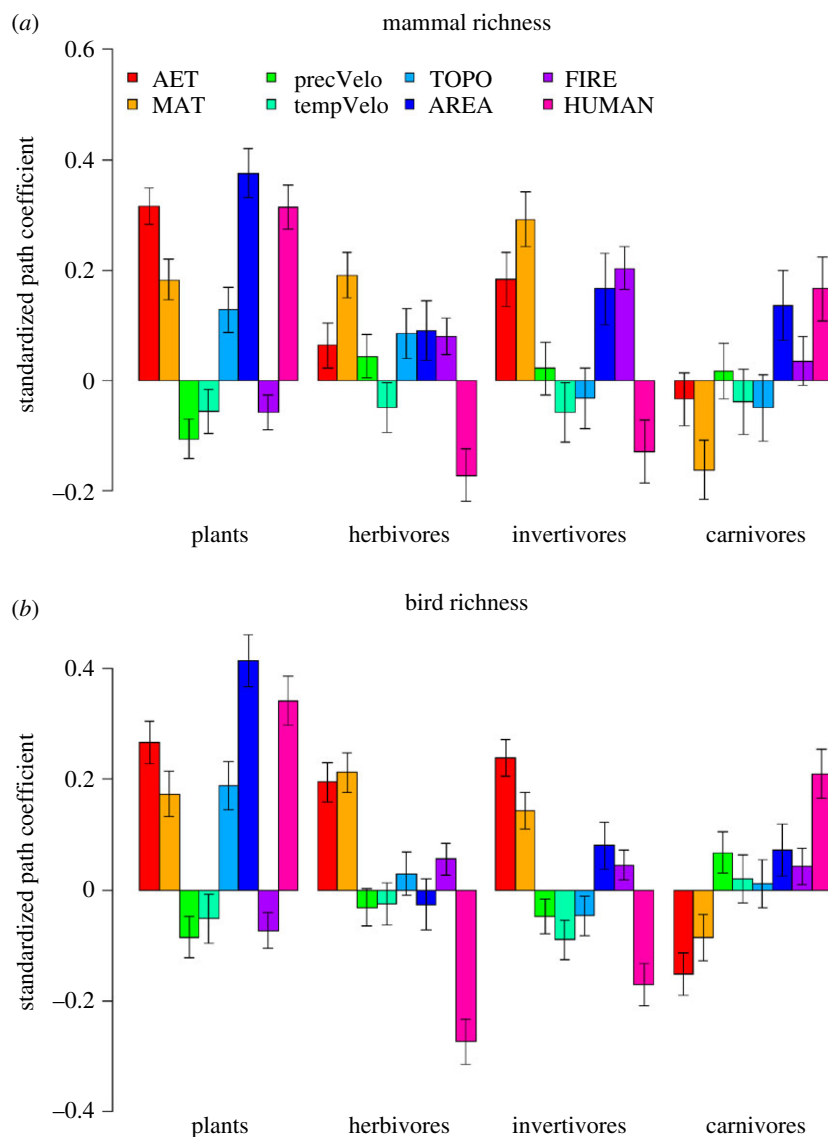
Figure 4. Standardized path coefficients of environmental variables for the four trophic levels in the non-recursive SEMs for global (*a*) mammal–plant and (*b*) bird–plant richness patterns. The direct path coefficients (±standard error after accounting for spatial autocorrelation in SEMs) for each environmental variable across the SEMs are shown. A positive value indicates a positive direct effect of one environmental variable on the richness of one trophic level. AET: annual actual evapotranspiration; MAT: mean annual temperature; precVelo: velocity of annual precipitation between the LGM and the present; tempVelo: velocity of mean annual temperature between LGM and the present. (Online version in colour.)

groups (figure 4). AET, MAT and AREA generally had the strongest effects, with the main difference being weak effects of AET on mammal carnivores and MAT on bird carnivores (figure 4). Topographic heterogeneity and glacial–interglacial velocity in temperature had weaker, but consistently positive or negative effects, respectively. By contrast, fire and human influence had highly variable effects across taxa and trophic groups. Notably, the relative importance of many geographical and environmental variables (figure 4) was much weaker than that of trophic interaction variables (figure 3).

Region-specific analyses demonstrated that trophic interactions were generally consistent among the six biogeographical realms and with that of trophic interactions at the global scale (electronic supplementary material, figure S4). The most inconsistent relationship was top-down interactions between bird invertivore richness and plant richness, which was strongly negative in the Neotropics and Oriental realms, but positive elsewhere. Other major differences included a strong negative top-down forcing between

bird herbivore and plant richness in the Afrotropics, and a strong negative bottom-up control between mammal invertivore and carnivore richness in the Oriental realm.

4. Discussion

(a) Bottom-up and top-down controls across trophic levels

Our global-scale analysis of species richness patterns in plant and vertebrate taxa documented patterns of statistical relationships between trophic groups that are consistent with trophic interactions playing a major role in shaping global patterns in biodiversity [4]. The region-specific trophic relations were generally consistent with the global-scale relations, although there were some regional differences in trophic links. After controlling for effects of current and historic climate, topography and disturbances from humans and fire, we detected a strong top-down effect of herbivores

7

on plant richness for mammals. A plausible mechanism would be that by directly reducing the abundance of preferred plant species and indirectly regulating nutrient cycling and soil fertility, mammal herbivores provide opportunities for growth and reproduction of other plant species and therefore increased plant diversity [4,11,64]. Positive top-down effects of invertivore richness on plant richness were identified for birds, consistent with a previous meta-analysis of plants, herbivorous insects and bird predators [65]. Weak top-down effects of bird herbivores and mammal invertivores on plant richness were detected, possibly due to confounding factors that have not been fully accounted for in the model structure.

We also found moderate to strong top-down interactions among trophic groups in mammals and birds. These findings are consistent with a number of prior experimental and field studies at local, regional and continental scales. The early work of Paine [6] on predator removal of the starfish *Pisaster* in a marine rocky intertidal community showed that predator removal led to sharp reductions in diversity (from 15 species to eight species) of both predator and prey species. In terrestrial systems, Schmitz *et al.* [11] examined 60 independent tests from 41 studies of top predator removal experiments, finding that top-down controls on plant-eater density were frequent (75%; 45 of 60 tests). At the regional scale, a well-known example of this is the top-down trophic cascade identified following the reintroduction of previously extirpated gray wolves (*C. lupus*) into Yellowstone National Park. With wolves (apex predator of ungulates) restored over the past two decades, the Yellowstone ecosystem has been restructured, including the recovery of woody plants and the riparian ecosystem [66,67]. At a continental scale, the decline of Australia's top mammal predator, the dingo, has resulted in the decrease in native mammals' diversity through release of invasive mesopredators [33]. In North and South America, Faurby & Svenning [24] used coarse-scale mammal distribution databases to reassess the influence of Great American Biotic Interchange for mammals and concluded that predation has played a critical role in the resulting long-term diversity dynamics. Overall, strong top-down forcing by high trophic levels may affect the processes of species immigration [26], extinction [27,33] and speciation [25,68], and thus reshape biodiversity patterns across space and time even across broad scales.

Bottom-up effects of plants on animals have been reported in a number of other studies [69–73]. However, top-down controls of animals on plants across large spatial scales have been less well explored, despite evidence from controlled experiments [12,18,74] and small-scale field observations [7,75]. Our findings also demonstrate that ascending prey–predator control is stronger than top-down forcing for mammal herbivores and bird invertivores. This is consistent with the findings by Sandom *et al.* [76] on global-scale mammal predator–prey interactions. By considering both bottom-up and top-down forces in regional and global analyses, our findings suggest that top-down and bottom-up trophic interactions among different trophic levels are not mutually exclusive [77,78]. Both forces should be incorporated in explanatory studies of biodiversity patterns [77,78].

It is worth mentioning that a large number of macroecological studies have documented correlations in species richness among taxa. Many studies have focused only on bottom-up effects of plants on animals [69–73], while

others have investigated cross-taxon congruence using pairwise correlations among major taxonomic groups [79–81]. However, the latter approach provides little insight into the magnitude or direction of trophic interactions and a correlation between two trophic levels does not necessarily mean that one drives the other. For example, we observed high pairwise correlations among global patterns in trophic groups (electronic supplementary material, figure S1), with plant and mammal herbivore richness being positively correlated (Pearson's correlation coefficient = 0.692, $p < 0.001$). This does not, however, provide evidence on the strength of top-down versus bottom-up effects. By disentangling the relative importance of top-down versus bottom-up effects, our analyses provide mechanistic insights into broad-scale trophic interactions.

(b) Importance of trophic versus extrinsic drivers on patterns of diversity

Climatic and topographic variables are often considered major drivers of broad-scale patterns in species richness [79–81]. However, our results suggest that interactions among taxa of different trophic levels may exert additional effects on species richness of particular taxa above and beyond environmental drivers. After considering the effects of trophic interactions, we found that the strength of the examined environmental variables was generally weaker than the influence from trophic levels. Previous studies that have tested plant–animal interactions after accounting for environmental conditions have shown mixed results. For instance, Hawkins & Pausas [70] found that mammal richness at a 100 km^2 resolution in northeast Spain was better described by climatic variables than by plant richness. Jetz *et al.* [71] found that environmental variables were better at predicting global patterns in vertebrate diversity than that of plant diversity. By contrast, Qian & Ricklefs [39] analysed cross-taxon correlations between plants and terrestrial vertebrates and found that richness of an animal group was best predicted by richness of other organism groups, rather than environmental variables. Likewise, Greve *et al.* [64] found that mammalian browsers in Africa were related more to patterns in acacias.

We do not suggest that the role of extrinsic drivers should be ignored when explaining biodiversity patterns for different trophic levels. Of the extrinsic variables examined in our study, AET and MAT were among the most important environmental determinants of richness for most trophic groups. The effects of humans and fire were also important for several trophic groups (e.g. mammal carnivores, and bird herbivores and invertivores), indicating their importance for studies of trophic interactions and biodiversity maintenance [17,51,82]. Additional studies are needed to assess how climate, topography, disturbance (fire and humans) and biotic factors interact to shape biodiversity patterns, and how their importance varies among trophic groups and across spatial and temporal scales.

(c) Limitations and caveats

Considering the ecological complexity of understanding and analysing trophic interactions [21,22], we point out a number of limitations of our work. The first is the broad extent used in sampling biodiversity (364 geographical units) and the

8

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large area of the sampling units [50,83]. Some sampling units we used could be larger than the range sizes of some plant and animal species. To reduce the potential influence of variation in geographical unit size, we included sampling area as a predictor in our analyses, which showed weak effects. Second, high-resolution diversity data on plants, vertebrates and invertebrates at a global, or even a regional, scale are scarce, thus limiting the potential for fine-grained, yet broad-scale analyses [50,83,84]. Data deficiency for species distribution, abundance and functional traits limits integrated analyses of trophic ecology and construction of complex food webs [85]. Use of more detailed data on species distribution and traits would further advance our understanding in this field. Third, lack of geographical independence could create spurious results. If some points are clustered in space (e.g. high richness of two trophic groups), it could bias estimates of relationships. However, we accounted for spatial autocorrelation in our analyses and furthermore found generally consistent global and regional patterns. We are therefore confident that our results are robust to spatial autocorrrelation. Finally, we divided mammals and birds into three mutually exclusive trophic levels based on their major dietary preferences [42,43], but interactions among trophic groups are more complex in the real world. While it might be relatively easy to construct complex food webs at small spatial scales, it is much more difficult to do so at broad spatial scales. When these data become available, future studies should evaluate how classification of trophic levels and length of food chains [42,43] affect estimates of trophic interactions at broad spatial scales and test the generality of top-down or bottom-up controls and the validity of these relationships across spatial scales [4].

(d) Conclusion

Our results demonstrate that there are consistent relationships between the large-scale species richness patterns of different trophic groups, consistent with a strong role of trophic interactions in shaping biodiversity patterns. Furthermore, our results suggest a particular importance of herbivores, notably mammalian, for structuring biodiversity patterns across trophic levels, via both top-down and bottom-up forcing [86,87]. These findings underscore the importance of integrating trophic forcing mechanisms into current theoretical studies of biodiversity maintenance [4,32].

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