

Mammal predator and prey species richness are strongly linked at macroscales

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Abstract. Predator–prey interactions play an important role for species composition and community dynamics at local scales, but their importance in shaping large-scale gradients of species richness remains unexplored. Here, we use global range maps, structural equation models (SEM), and comprehensive databases of dietary preferences and body masses of all terrestrial, non-volant mammals worldwide, to test whether (1) prey bottom-up or predator top-down relationships are important drivers of broad-scale species richness gradients once the environment and human influence have been accounted for, (2) predator–prey richness associations vary among biogeographic regions, and (3) body size influences large-scale covariation between predators and prey. SEMs including only productivity, climate, and human factors explained a high proportion of variance in prey richness ($R^2 = 0.56$) but considerably less in predator richness ($R^2 = 0.13$). Adding predator-to-prey or prey-to-predator paths strongly increased the explained variance in both cases (prey $R^2 = 0.79$, predator $R^2 = 0.57$), suggesting that predator–prey interactions play an important role in driving global diversity gradients. Prey bottom-up effects prevailed over productivity, climate, and human influence to explain predator richness, whereas productivity and climate were more important than predator top-down effects for explaining prey richness, although predator top-down effects were still significant. Global predator–prey associations were not reproduced in all regions, indicating that distinct paleoclimate and evolutionary histories (Africa and Australia) may alter species interactions across trophic levels. Stronger cross-trophic-level associations were recorded within categories of similar body size (e.g., large prey to large predators) than between them (e.g., large prey to small predators), suggesting that mass-related energetic and physiological constraints influence broad-scale richness links, especially for large-bodied mammals. Overall, our results support the idea that trophic interactions can be important drivers of large-scale species richness gradients in combination with environmental effects.

Key words: biotic interactions; bottom-up effects; carnivores; mammal species richness; productivity hypothesis; structural equation models; top-down control; trophic interactions.

INTRODUCTION

Understanding the importance of predator–prey interactions for species diversity and community composition is a central theme in ecology. Trophic resource–consumer interactions are typically studied using experimental studies (e.g., Huffaker 1958), local observational (e.g., Sinclair et al. 2003, Vucetich and Peterson 2004)

and mathematical approaches (reviewed in Solé and Bascompte 2006), but may also be inferred from macroecological studies (Wisz et al. 2013). By analyzing patterns of species distribution and diversity at broad spatial and temporal scales, we may gain insights into the importance of biotic and abiotic drivers (MacArthur 1972, Brown and Maurer 1989). Emphasis in macroecological research has hitherto been on the effects of climate and other environmental factors on species richness (Field et al. 2009), as well as on human impacts on biodiversity (Balmford et al. 2001, Sanderson et al. 2002). Only a few recent studies have explored the role

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of trophic interactions as drivers of broad-scale species richness gradients (Hawkins and Porter 2003, Kissling et al. 2007, Jetz et al. 2009, Greve et al. 2012). No study has yet considered the importance of predator–prey associations as biotic drivers of continental and global species richness gradients.

To disentangle biotic and abiotic effects on species richness it is necessary to quantify both direct and indirect environmental effects on species richness because an apparent trophic richness correlation might simply arise from responses of both trophic levels to the same environmental factors (Kissling et al. 2008). For example, higher net primary productivity might sustain more individuals, enabling species to maintain larger populations and thereby increasing speciation and lowering extinction rates over evolutionary time (Waide et al. 1999). This may produce an apparent association between richness of prey and predators even in the absence of species interactions. For coarse trophic levels such as vascular plants and endothermic vertebrates, it has been suggested that primary productivity is a more important driver than trophic interactions at broad geographical scales (Jetz et al. 2009). However, specific tests for comparison of climate and productivity with predator–prey interactions have not yet been presented. Furthermore, productivity–richness relationships can differ among biogeographic regions (Qian 2010) so that global relationships might not reflect regional variation (Kissling et al. 2009). This regional variation in productivity–richness or cross-trophic richness relationships could indicate historical differences between realms, e.g., in Australia and Africa, which have distinct evolutionary and paleoclimatic histories (Morley 2000, Johnson 2006).

Richness at a given trophic level may be influenced by both bottom-up and top-down trophic interactions (Vucetich and Peterson 2004). From a bottom-up perspective, consumer richness might be driven by the diversity of resources (Armbrecht et al. 2004) because an increased resource diversity should provide more niches for the coexistence of consumer species (Hutchinson 1959, Chesson 2000, Sinclair et al. 2003, Kissling et al. 2007). In contrast, the top-down hypothesis (Hairston et al. 1960) suggests that species diversity is controlled from the top downward, i.e., that predator diversity promotes diversification or coexistence among prey species. A key component of both hypotheses is interspecific variability in prey and predator sizes because body size is a key constraint in food webs (Woodward et al. 2005) and determines which predators feed upon which prey species (Paine 1966, Sinclair et al. 2003, Hemmer 2004, Estes et al. 2011). A larger number of prey sizes (e.g., body mass categories) might therefore allow a larger number of predators to coexist, and a larger number of predators could facilitate higher prey species richness because a larger variety of predatory hunting strategies might provide opportunities for niche differentiation in defense and escape strategies of prey.

Whether such mechanisms structure trophic diversity gradients across broad spatial scales remains unclear.

Using global range maps, structural equation modeling, and comprehensive databases of dietary preferences and body masses of all terrestrial, non-volant mammals worldwide, we provide the first global-scale analysis of mammalian predator and prey species richness to test the relative roles of direct bottom-up and top-down mechanisms while simultaneously accounting for shared responses to environmental gradients and human influence. We further examine how these associations vary among biogeographic regions, and how body size constraints influence the co-variation between predator and prey richness. For the latter, we specifically test the links between predator–prey richness for small- and large-bodied species and expect trophic relationships within mass categories (e.g., large prey to large predator) to be stronger than between them (e.g., small prey to large predator). Our analyses provide new insights into large-scale determinants of species richness and the potential role of predator–prey interactions in shaping global and regional biodiversity gradients.

METHODS

Species distribution data

We used global species distribution maps for all 4091 terrestrial mammal species, excluding bats (IUCN 2010). Polygon range maps were converted to rasters on a Behrmann projection (a cylindrical equal area projection) with a resolution of 2° equivalents (~220 km). A species was counted as present in a cell if any part of the cell was covered by the species' range polygon. We then added up all species presences for each grid cell to quantify species richness. Grid cells with <50% land area were excluded, resulting in 3523 cells for our analysis. All data handling and plotting was performed in the R statistical program, version 2.15 (R Development Core Team 2012), using the raster, rgdal, and maptools packages (*available online*).⁸

Diet and mass data

Mammal diet descriptions were derived from a comprehensive new database (compiled by the authors, *unpublished data*) based on dietary information in Nowak (1999). This database describes dietary preferences of all mammal species using predefined food categories (e.g., mammals, birds, herptiles, fishes, invertebrates, seeds, fruits, leaves, etc.). For a given taxon, each food category in the database is ranked in importance according to whether it is a primary food item (rank 1), secondary food item (rank 2), or occasional food item (rank 3). For the purpose of our study, we defined predators ($n = 125$ species) as species that primarily feed on other mammals (see Plate 1), i.e., scoring rank 1 in the food category “mammals” and not

⁸ <http://CRAN.R-project.org/>

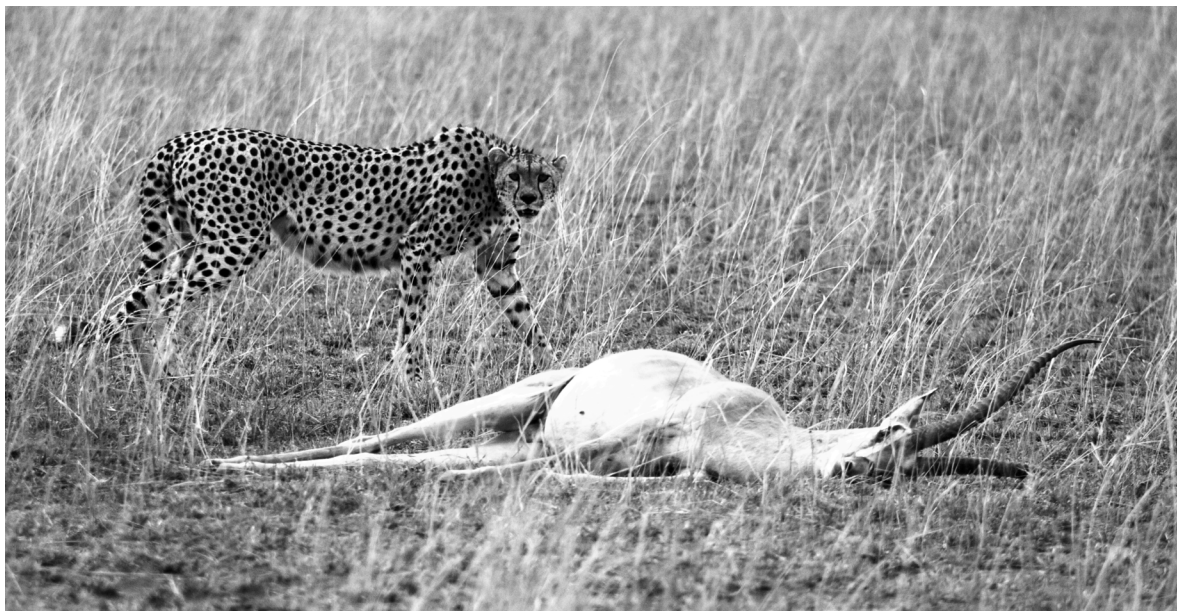


PLATE 1. Cheetah (*Acinonyx jubatus*) and prey impala (*Aepyceros melampus*). Photo credit: C. J. Sandom, Masai Mara, Kenya, 2007.

rank 1 in the food category “plants” (thus avoiding species that mainly feed on both mammals and plants). All other species that did not meet this criterion were classified as prey ($n = 3966$ species). Body mass data were gathered from Smith et al. (2003). Species-level mass data were available for 2845 species (70%). A further 1144 species (28%) were filled by taking the mean of species’ masses in the same genus, leaving 102 species (2%) without mass data that were excluded from the mass analysis. Species diet, body mass, and distribution data were matched using the International Union for Conservation of Nature (IUCN) taxonomy and recognized synonyms. Body size data were \log_{10} -transformed for further analysis to achieve normal distributions.

Climate, productivity, and human influence

We included five climatic variables that are commonly used as predictors of vertebrate species richness at broad spatial scales (Field et al. 2009). These variables are related to energy and water availability, seasonality, and microclimate (represented by topographic heterogeneity): mean annual temperature (MAT), mean annual precipitation (MAP), water balance (WB), temperature seasonality (SEAS), and topographical range (TOPO). Climate and topography data were obtained from Hijmans et al. (2005) and the CIGAR Consortium for Spatial Information at an original resolution of 1 km (data available online).⁹ Climate data were averaged for each grid cell and topographic range was calculated as the range in elevations per grid cell. These five variables were

combined using a principal component analysis (PCA). We included the first three PCA components as predictors of predator and prey richness, capturing 97.5% of the variation in our global dataset (PC1 = 44.5%, representing MAP and negative SEAS; PC2 = 33.7%, representing WB and negative MAT; PC3 = 19.3%, representing TOPO). To characterize net primary productivity, we used the normalized difference vegetation index (NDVI), downloaded from the European Distributed Institute of Taxonomy in the original resolution of 0.1° and calculated as mean per grid cell (data available online).¹⁰ In all analyses, we included direct effects of climate and productivity as well as indirect effects of climate via productivity on predator and prey species richness. Human influence was included via the human influence index (HII; Sanderson et al. 2002) with mean values calculated for each grid cell. All three categories of predictor variables (climate via PC1–3, productivity via NDVI, and human influence via HII) were included in all structural equation models. The following transformations were performed to approximate normal distributions: MAP, SEAS, HII, prey richness and predator richness were square-root transformed and TOPO was \log_{10} -transformed. All data layers were converted to a Behrman projection to create equal-area grid cells with the same resolution as the species richness grids.

Structural equation models at global and regional scales

Structural equation models (SEMs) were implemented with the R package lavaan (Rosseel 2012). SEMs are

⁹ <http://csi.cgiar.org/Aridity/>

¹⁰ <http://edit.csic.es/Soil-Vegetation-LandCover.html>

particularly well suited for evaluating multivariate hypotheses because direct and indirect effects of predictor variables can be tested (Grace 2006). We first built a priori theoretical SEMs reflecting hypothesized relationships among all variables, including direct effects of climate (PC1–PC3), productivity (NDVI), and human influence (HII) on species richness of predators and prey, and indirect effects of climate via productivity. Trophic interactions were tested with direct links from prey to predators (bottom up) and predators to prey (top down). For each of the theoretical SEMs, we then evaluated residual correlations, modification indices, and model fits to test whether important paths between variables were missing (Grace et al. 2012). We used the chi-square test, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit, and chose the best models according to the following criteria (Grace et al. 2012; J. B. Grace, *personal communication*): (1) *P* values of chi-square tests >0.05 ; (2) lower 90% confidence intervals of RMSEA close to 0; and (3) CFIs >0.90 . Missing paths were identified from large residuals and high modification indices and subsequently accounted for by adding error covariances between pairs of variables. We examined three different SEM structures: (1) an environment SEM, excluding any trophic links between prey and predators (i.e., the null expectation assuming no trophic interaction); (2) the prey bottom-up SEM, including a path from prey richness to predator richness to the environment model; and (3) the predator top-down SEM, including a path from predator richness to prey richness to the environment model. All SEMs were run at global and regional spatial scales. The global SEMs were calculated using all grid cells whereas the regional SEMs were implemented separately for each biogeographic region (Afrotropics, Australia, Indo-Malay, Nearctic, Neotropics, and Palearctic, following the realm classification of Udvardy [1975]). For the regional SEMs, climate PCA axes were calculated separately within each region.

Standardized path coefficients were used to evaluate and compare the relative importance of predictor variables. For the trophic interaction links between predators and prey, a positive relationship between both groups might be expected simply because predators and prey are a division of one taxonomic group into two subgroups. To account for this dependency and to provide a conservative comparison of the relative importance of predator–prey interactions, we additionally implemented null models for which we ran each SEM 1000 times with randomized dietary permutations (i.e., randomly assigning 125 species as predators and the remaining species as prey). In each permutation, we recorded the path coefficient of the predator–prey link (either bottom up or top down), resulting in 1000 null values for both predator–prey and prey–predator links. We finally corrected the standardized path coefficients of the predator–prey links in the SEMs by subtracting the

mean of the null simulations from the observed ones to test whether the strength of the trophic interaction remains even when accounting for an expected covariation between both mammal groups.

Testing large- vs. small-bodied species

To test for stronger links between predator and prey species richness within groups of matching body sizes, we repeated the global SEMs with predator and prey groups categorized by body mass. Large-bodied predators were defined as ≥ 21.5 kg and small-bodied predators <21.5 kg based on mass-related energetic requirements (Carbone et al. 1999). We defined prey species ≥ 10 kg (45% of 21.5 kg) as large-bodied prey and prey species <10 kg as small-bodied, following Carbone et al. (1999).

Spatial autocorrelation

To test for potential confounding effects of spatial autocorrelation (SAC), we first assessed the degree of SAC in model residuals by building our SEM models as a series of independent ordinary least squares (OLS) regressions. Standardized coefficients from OLS models are equivalent to path coefficients from SEMs and allow a direct comparison of residual spatial autocorrelation between spatial and nonspatial models (see Kissling et al. 2008). We computed correlograms of OLS model residuals using the *ncf* package in R, with distance classes of 1000 km (package *available online*).¹¹ All OLS models showed substantial SAC (see Appendix A: Fig. A1), so we reran these models using simultaneous autoregressive (SAR) models of the error type (Kissling and Carl 2008). These SAR models were implemented in the R package *spdep* (*available online*).¹² The spatial weights matrix was defined using the minimum geographic distance (652.5 km) that linked each occupied grid cell to at least one other occupied cell. These SAR models removed residual SAC (Appendix A: Fig. A1) and produced standardized coefficients that were similar to OLS methods (Appendix A: Fig. A2). Because the standardized coefficients from OLS models were similar to those of SAR models, we focus on the nonspatial path coefficients from the SEMs throughout the manuscript.

RESULTS

Global variation in predator and prey richness

Overall, species richness of both all mammals and prey showed a typical latitudinal gradient with peaks of richness around the equator (Fig. 1a, b). Predator species richness differed markedly (Fig. 1c), with high richness in parts of North America, Asia, and Africa and low richness in the tropical rainforests of South America, Africa, and most of Malaysia as well as in Australasia more broadly. Maximum prey species richness was 186 species per grid cell (in the Afrotropics)

¹¹ <http://CRAN.R-project.org/package=ncf>

¹² <http://CRAN.R-project.org/package=spdep>

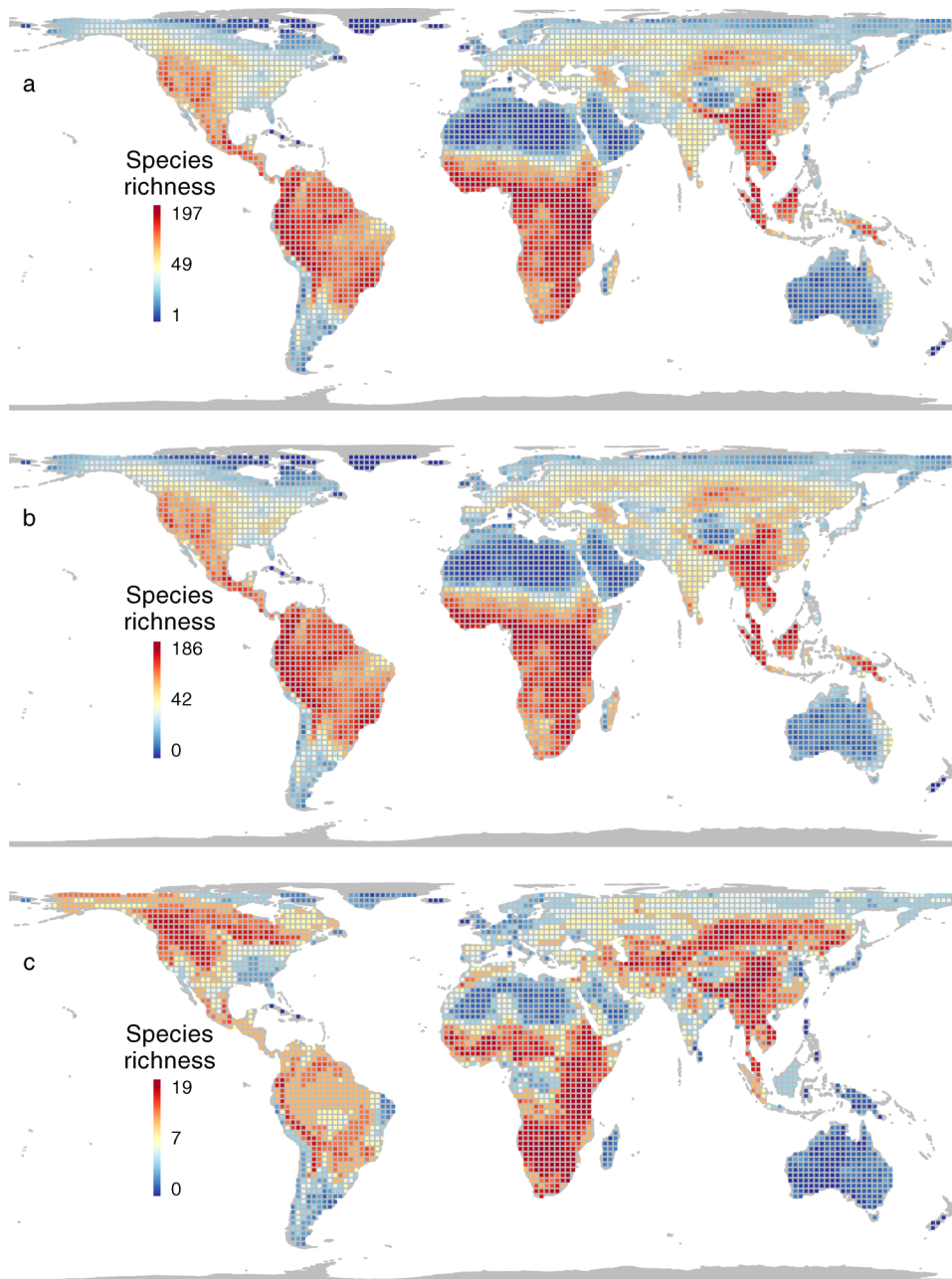


FIG. 1. Global patterns of species richness for (a) all mammals, (b) mammalian prey, and (c) mammalian predators. The grid is a Behrman projection (a cylindrical equal-area projection) with a resolution of 2° equivalents. Grid cells with less than 50% land cover or those covering Antarctica are not included.

and maximum predator richness was 19 (in the Palearctic).

Structural equation models at the global scale

The environment SEM without links between predators and prey (Fig. 2a) indicated that the combined influence of climate, productivity, and humans explains a large amount of variation in prey diversity ($R^2 = 0.56$), but much less in predator diversity ($R^2 = 0.13$). Overall,

productivity showed a stronger effect on prey than on predator richness. When the bottom-up prey-to-predator link was included (Fig. 2b), a strong positive direct effect was found (path coefficient = 1.01), resulting in a much higher explained variance of predator richness ($R^2 = 0.57$). Top-down trophic interactions (Fig. 2c) also revealed a strong positive effect (path coefficient = 0.51), with an increased explained variance of prey richness ($R^2 = 0.79$). However, the top-down effect was much

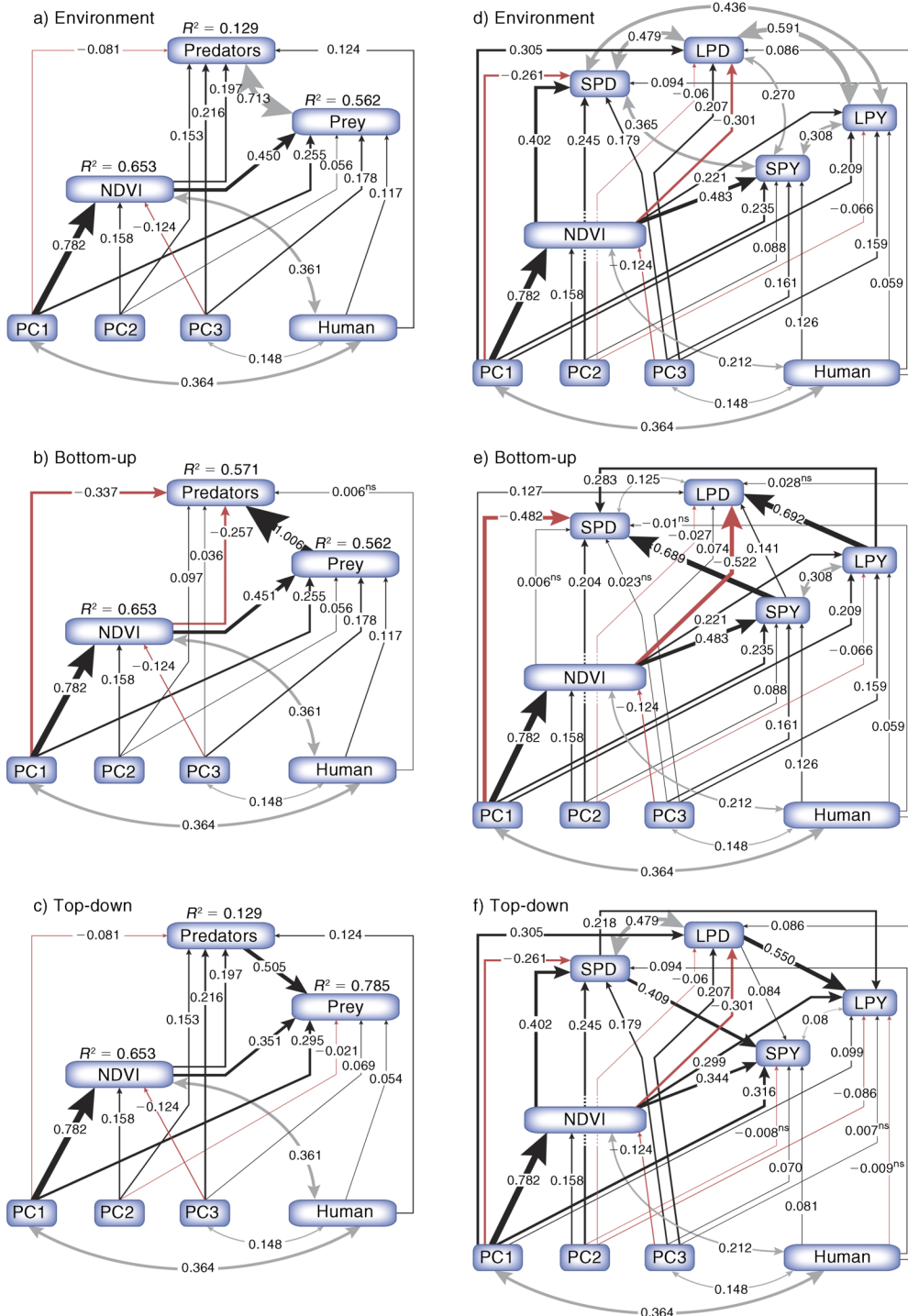


FIG. 2. Structural equation models (SEMs) representing direct and indirect effects of climate (PC1-PC3), productivity (normalized difference vegetation index [NDVI]), and human influence (Human) on predator and prey diversity and their associations. Three types of SEMs are represented: (a, d) environment (including productivity, climate, and human influence) SEMs without a direct link between predators and prey, (b, e) bottom-up SEMs including a direct link from prey to predator diversity, and (c, f) a top-down SEM including a direct link from predator to prey diversity. Panels on the left-hand side (a-c) represent global SEMs across all species whereas panels on the right-hand side (d-f) represent SEMs where mammals have been divided into large- and small-bodied species. Straight arrows (black, positive; red, negative) represent path coefficients (direct effects), with line thickness being proportional to coefficient strength for coefficients greater than 0.0625. The gray curved arrows are error covariances representing unanalyzed relationships between exogenous variables. Abbreviations are: SPD, small predators; LPD, large predators; SPY, small prey; LPY, large prey; "ns" stands for "not significant." See *Methods* for the definition of mass categories.

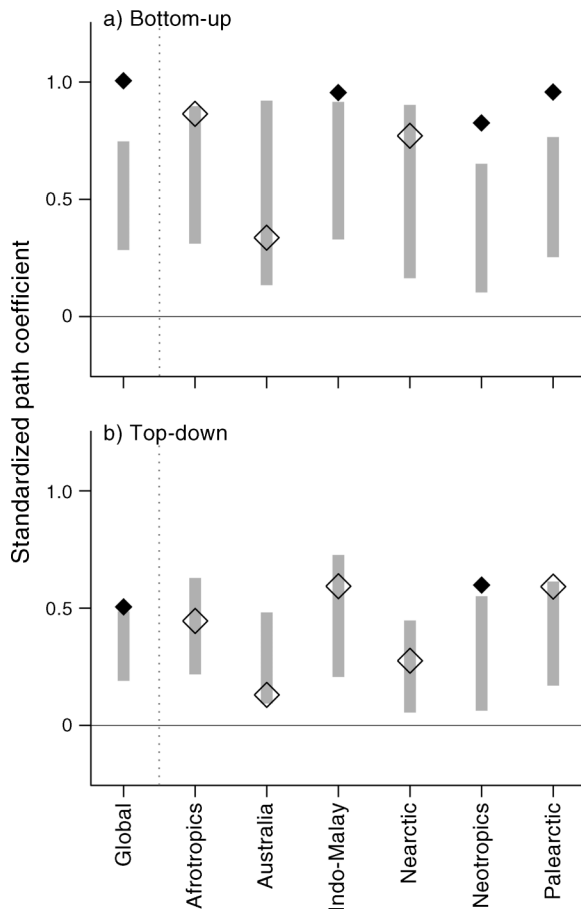


FIG. 3. Standardized path coefficients from structural equation models (SEMs, diamonds) vs. those from null models (gray bars) summarized for global and regional scales. (a) Bottom-up prey-to-predator interaction and (b) top-down predator-to-prey interaction. Gray vertical bars represent the 90% expectation from null models. Solid diamonds indicate significant deviations of path coefficients from the null expectation whereas open diamonds indicate path coefficients within the null expectation.

weaker than the bottom-up effect (Fig. 2b, c). Comparing the results from the SEMs with SAR models indicates a decrease in the strength of path coefficients (Fig. 2 and Appendix A, Fig. A2) when residual spatial autocorrelation is accounted for. However, both path coefficients describing trophic (prey-to-predator and predator-to-prey) interactions remained strong (>0.30) and significant (Appendix A, Fig. A2) in the SAR models. In global SEMs, trophic interaction links differed significantly from our null expectation, with path coefficients being stronger than expected from random associations (see Global in Fig. 3a, b). When correcting the path coefficients with the mean values from null models, a stronger coefficient was recorded for prey to predator (0.48) than for predator to prey (0.16; Table 1). Furthermore, the prey-to-predator link was stronger (0.48) than the NDVI-to-predator link (0.20), while the predator-to-prey link (0.16) was weaker than the one for NDVI-to-prey (0.45).

Predator–prey richness at regional scales

Consistent with the global analysis, path coefficients for the prey bottom-up links in regional SEMs were always larger than the predator top-down links (Table 1, Fig. 3; for full path coefficients see Appendix B). For prey–predator bottom-up interactions, the path coefficients for Indo-Malaya, the Neotropics, and the Palearctic all deviated significantly from the null expectation (Fig. 3a). The path coefficient for the Afrotropics was also close to the 95% confidence interval, but not significantly different from the random expectation. In contrast, Australia had a weak path coefficient that even fell below the mean of the null expectation (Fig. 3). After the prey-to-predator coefficients had been corrected with the mean from the null expectation, they showed intermediate to strong positive correlations in all biogeographic realms except Australia (Table 1). These corrected coefficients were stronger than NDVI-to-predator relationships in the Neotropics and Palearctic.

TABLE 1. A comparison of path coefficients for prey–predator, predator–prey, NDVI–predator, and NDVI–prey links from structural equation models (SEM), null models (i.e., mean values across 1000 randomizations), and differences between both for the trophic links.

Region	NDVI–predator	Bottom-up prey–predator			NDVI–prey	Top-down predator–prey		
		SEM	Null	Corrected		SEM	Null	Corrected
Global	0.197	1.006	0.524	0.482	0.451	0.505	0.346	0.159
Afrotropics	0.513	0.865	0.613	0.252	0.527	0.445	0.431	0.014
Australia	0.634	0.336	0.513	–0.176	0.294	0.130	0.283	–0.154
Indo-Malay	0.425	0.955	0.641	0.314	0.524	0.593	0.496	0.098
Nearctic	1.118	0.771	0.576	0.195	0.796	0.275	0.255	0.020
Neotropics	0.361	0.826	0.392	0.433	0.424	0.598	0.285	0.313
Palearctic	0.176	0.957	0.526	0.432	0.359	0.592	0.391	0.200

Notes: Values are provided for global and regional analyses. Corrected values (Corrected = SEM – Null) are shown in boldface type. NDVI stands for normalized difference vegetation index. See *Methods* for details of null model implementation.

For the top-down predator–prey links, all path coefficients from regional SEMs were large (>0.44), except for Australia and the Nearctic (Table 1). However, when the top-down prey-to-predator links were tested against null models, the Neotropics was the only biogeographic region where the SEM path coefficient deviated significantly from a random expectation (Fig. 3b). After correcting path coefficients, all remained positive except for Australia (Table 1). However, in most cases the strength of the corrected coefficients was relatively weak (<0.10), but they remained relatively strong (≥ 0.20) for the Neotropics and the Palearctic. There was no region where the coefficient for predator-to-prey was stronger than for NDVI-to-prey.

Patterns within and between body mass categories

Splitting the predator and prey categories into large-bodied and small-bodied species revealed a strong positive effect of productivity on species richness of both small predators and small prey (path coefficients >0.40), but a negative effect on large-bodied predators (Fig. 2d). For all mass categories, the direct effects of climate and human influence were generally weaker than the productivity effects. Adding bottom-up or top-down links (Fig. 2e, f) suggested that bottom-up effects were consistently stronger than top-down effects for both mass categories, confirming our analysis for all mammals (Fig. 2b, c). Much stronger correlations were recorded within size categories (e.g., correlation between large prey and large predators is 0.69) than between them (e.g., correlation between large prey and small predators is 0.28; Fig. 2e, f). The path coefficients linking large prey with large predators and small prey with small predators and vice-versa were similar (Fig. 2e, f). However, explaining the variation in large prey richness depended strongly on including a link from large predators (R^2 improved from 0.21 to 0.63), while small prey richness did not depend as strongly on the link from small predators (R^2 improved from 0.60 to 0.77).

DISCUSSION

Our results revealed strong associations between predator and prey richness at global and regional scales, even when covariation with climate, productivity, and human influence was accounted for. Predator species richness was strongly linked to prey richness, while the effects of productivity and climate were stronger than predator richness for prey richness. The effect of human influence on both predator and prey richness was generally weak at the studied scales. Interestingly, the top-down predator–prey link was stronger for large-bodied than small-bodied species, suggesting a strong functional dependence of large predators on relevantly sized prey at broad spatial scales. Our regional analyses revealed substantial spatial variation in predator–prey associations among realms, indicating that evolutionary and historical events might have left an imprint on

trophic relationships. Overall, our findings suggest that species interactions across trophic levels are important for creating and maintaining large-scale biodiversity gradients.

Global drivers of predator and prey richness

In accordance with previous findings that climate and productivity play a major role in shaping large-scale species richness gradients (Waide et al. 1999, Field et al. 2009, Jetz et al. 2009, Buckley et al. 2010, Davies et al. 2011), our SEMs revealed consistently strong effects of productivity on prey species diversity. However, the combined effects of climate and productivity were considerably lower for predator richness, indicating that these factors play a less important role at higher trophic levels. Adding bottom-up prey-to-predator interactions in our SEMs considerably increased the explained variance in predator richness at the global scale relative to the environment model. This effect might be mediated directly by the variety of prey resource types by reducing niche overlap and rates of competitive exclusion among predators (Evans et al. 2005), but may also involve a productivity effect (Wright 1983) via an increase in prey abundance. Our findings are in contrast with a previous analysis on global richness associations between plants and vertebrates where cross-trophic consumer links had been suggested to only weakly scale up to broad geographical scales (Jetz et al. 2009). However, Jetz et al. (2009) did not specifically test links between primary and secondary consumers, and the vertebrate species classified as primary consumers in their study might not necessarily feed directly on all the plant species (ferns, gymnosperms, and angiosperms) included in their investigation.

Our results offer less support for the predator top-down hypothesis as a key driver of prey diversity as path coefficients of the predator-to-prey link were weaker than the bottom-up links, and in most regional cases they did not differ from our null model. Including the predator-to-prey link in the global SEMs considerably improved the explained variance of prey species richness and the global predator-to-prey link also differed from the null expectation. These results at least partly support the idea that a larger number of predators facilitates higher prey species richness, maybe because a larger variety of predatory hunting strategies provides opportunities for niche differentiation in defense and escape strategies of prey (Apfelbach et al. 2005). Accounting for spatial autocorrelation decreased the strength of the top-down and bottom-up predator–prey interactions in the global models; however, the links remained statistically significant and much stronger than most other paths, supporting the validity of the SEM results. Including abundance data for predator and prey species could further deepen our understanding of the relative importance of productivity and predator–prey interactions as drivers of species diversity throughout food-webs (Herfindal et al. 2005, Pettorelli et al. 2009,

Carbone et al. 2011), but such data are currently scarce and completely lacking for a large number of species across broad spatial extents.

Regional patterns

The regional top-down effects were generally weaker than the bottom-up effects, and for the former the path coefficients did not significantly differ from the null expectation in most regions. These weak top-down effects might even be less pronounced when accounting for spatial autocorrelation and we suggest that our data offer little support for strong top-down effects at the regional scale.

Australia in particular differed from the other realms, having lower trophic interaction coefficients than the mean from the null models. Being the smallest continent with a low productivity due to poor soils and low rainfall, Australia can be expected to have fewer large-bodied predators given the limited scope for maintaining long-term viable population sizes of such species there given the particularly large home ranges that would be required (Burness et al. 2001). Perhaps as a result, many predatory niches have been filled by varanid lizards with lower metabolic rates (Burness et al. 2001). Furthermore, the diversification of Australia's marsupial carnivores might have been limited due to evolutionary constraints on jaw morphology (Werdelin 1987). These factors may explain why neither the bottom-up nor the top-down hypotheses were supported for this continent.

For Africa, the path coefficients for the prey-to-predator link were close to deviating from the null expectation. The major discrepancy between prey and predator richness was found in the tropical rainforests of the Congo basin where high prey-to-predator ratios were recorded (see Appendix C). Given the unique paleoclimatic history of Africa, especially the extreme drying and the loss of rainforests during the Cenozoic (Morley 2000), we additionally explored the effect of tropical rainforest vs. open habitats in Africa (results not shown). When removing tropical rainforest areas, the prey-to-predator coefficient in SEMs significantly deviated from the null model, suggesting that rainforest history plays an important role in explaining predator-prey diversity in Africa. Given their greater home range requirements (Stewart et al. 2010), large-bodied rainforest predators might have been extraordinarily affected by forest contraction in the late Tertiary and Quaternary, leading to high extinctions within this trophic level. There is some fossil evidence indicating that the contraction of closed forest habitats in Africa at this time led to the extinction of carnivores (Werdelin and Simpson 2009).

Body size and resource diversity and abundance data

We found trophic interactions to be stronger within equivalent mass categories than between them and the interactions were strongest for large-bodied mammals, suggesting that mass-related constraints could play a

role for large-scale mammalian richness gradients. Body size has been identified as an important factor in food webs (Woodward et al. 2005) and local studies of predator-prey communities also show that predator-prey systems are size structured (Carbone et al. 1999, 2011, Sinclair et al. 2003). Our results furthermore support the idea that energetic constraints related to body mass are especially important for large-bodied predators, as they show particularly strong dependencies on large-bodied prey to sustain their net energy expenditure (Carbone et al. 1999).

The lack of comprehensive resource abundance and diversity data for prey species (e.g., related to plant chemical defenses, fruit types or seeds, or body sizes of invertebrates and non-mammalian vertebrates) currently prevents analyses of biotic bottom-up effects on mammalian prey diversity at a global scale. Measuring primary productivity (as in our study) or alternatively the number of vascular plant species provide first approximations (Jetz et al. 2009). Other recent analyses across broad spatial scales have included the number of food or host plants, e.g., for butterflies (Hawkins and Porter 2003) and frugivorous birds (Kissling et al. 2007). Results might also depend on how resource diversity, e.g., prey richness, is defined or classified. Considering the link between primary productivity (included here as a proxy for vegetation abundance and quality) and prey one might expect a stronger path coefficient for herbivorous prey than for insectivores. We therefore reran the SEMs with prey defined as species that primarily consume plants (excluding the insectivores), but path coefficients (NDVI-to-prey and predator-to-prey) remained similar in magnitude, suggesting that herbivores and insectivores show similar diversity patterns. Finally, predator diversity may be partly driven by biotic interactions between predators themselves as predators can predate on other predators, which may account for some of the unexplained variance in the predator category.

Conclusions

While biotic interactions have long been suggested to be central for understanding the drivers of species diversity, most research has focused on local study sites, laboratory and field experiments, or the mathematical modeling of simplified system dynamics. However, there is increasing evidence from contemporary and paleoecological studies that biotic interactions have clearly left their mark on broad-scale species assemblages (Wisz et al. 2013). Our global analysis of predator-prey diversity of mammals supports this idea and suggests that climate and productivity become less important when ascending the trophic pyramid. To achieve a deeper understanding of broad-scale trophic interactions an increased availability of species functional trait and abundance data is desirable. We suggest that trophic interactions play a key role for structuring past, present and future ecosystems and that we need to better

understand the top-down and bottom-up drivers of broad-scale species richness gradients across trophic levels.

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SUPPLEMENTAL MATERIAL

Appendix A

Spatial autocorrelation analysis ([Ecological Archives E094-099-A1](#)).

Appendix B

Full SEM path coefficients for each biogeographic region ([Ecological Archives E094-099-A2](#)).

Appendix C

Prey-to-predator ratios ([Ecological Archives E094-099-A3](#)).