

Generality in food webs scales with species richness, not latitude

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Abstract

Several properties of food webs—the networks of feeding links between species—vary systematically with the species richness of the underlying community. Under the “latitude-niche breadth hypothesis”, which predicts that species in the tropics will tend to evolve narrower niches, one might expect that these scaling relationships could also be affected by latitude. To test this hypothesis, we analysed the scaling relationships between species richness and average generality, vulnerability, and links per species across a set of 163 empirical food webs. We also investigated scaling relationships between the three food-web properties and the proportions of the web made up by basal resources, intermediate consumers, and top predators. While we observed no effect of latitude on scaling relationships in the estuarine, marine, and terrestrial food webs, there were strong effects of latitude on scaling relationships in the freshwater food webs. In these communities, the latitude-niche breadth hypothesis appears to hold true while in other habitat types

niches appear to be broader in the tropics. These contrasting findings indicate that it is important to account for habitat type when exploring gradients in food-web structure.

Introduction

Food webs –networks of feeding links between species– have been used for several decades to summarize the structure of ecological communities (Petchey *et al.*, 2008; Williams & Martinez, 2000; Paine, 1966) and to understand how that structure relates to environmental variables such as habitat type (Shurin, Gruner & Hillebrand, 2006; Briand, 1983), primary productivity (Vermaat, Dunne & Gilbert, 2009; Thompson & Townsend, 2005; Townsend *et al.*, 1998), and climate (Baiser *et al.*, 2012; Petchey, Brose & Rall, 2010). The latter variables in turn have strong gradients over latitude, with productivity and temperature both being higher in the tropics while climate is more variable at high latitudes (Field *et al.*, 1998). These variables affect both the resources available and species’ metabolisms (Hechinger *et al.*, 2011; White *et al.*, 2011; O’Connor *et al.*, 2009; White *et al.*, 2007), and have been proposed as determinants of the strength of interspecific interactions (Lang, Rall & Brose, 2012; Schleuning *et al.*, 2012; Schemske *et al.*, 2009a). By modulating interactions between species, latitudinal gradients may also shape food-web structure. Indeed, these latitudinal environmental gradients have been put forward as potential drivers for the latitudinal gradient in species richness, one of the most general and robust patterns in ecology (Schemske *et al.*, 2009b; Macpherson, 2002; Kaufman, 1995).

One proposed link between species richness and latitude is the “latitude-niche breadth hypothesis” (Vázquez & Stevens, 2004). This hypothesis predicts that decreased seasonality in the tropics should lead to more stable populations, which in turn should evolve smaller niches (Vázquez & Stevens, 2004). These narrow niches should therefore allow more species to coexist in the tropics than at higher latitudes. Alternatively, the higher

productivity of the tropics (Brown, 2004) may result in a broader niche space (Davies *et al.*, 2007) which could also sustain greater biodiversity even if niche sizes are globally similar. Although the assumptions of the latitude-niche breadth hypothesis are only equivocally supported (Vázquez & Stevens, 2004), it remains a compelling potential mechanism for the latitudinal gradient in species richness (Lappalainen & Soininen, 2006; Krasnov *et al.*, 2008; Slove & Janz, 2010).

If the latitude-niche breadth hypothesis is correct, there should also be direct relationships between latitude and the degree of specialization (i.e., niche breadth) of species within food webs. Attempts to unravel these effects, however, are complicated by known relationships between species richness and many other network properties (Riede *et al.*, 2010). For example, narrower niches imply fewer links per species (i.e., greater specialization in the tropics (Dyer *et al.*, 2007; Marra & Remsen, 1997) but see (Schleuning *et al.*, 2012)). However, average numbers of links per species tend to increase in larger food webs (Dunne, 2006; Riede *et al.*, 2010). This means that a latitudinal effect on specialization may be obscured by a latitudinal gradient in species richness. If this is the case, it may still be possible to uncover effects of latitude on specialization by examining the shape of the scaling relationship between specialization and species richness over changing latitude. Here, we use three measures of specialization: mean links per species, mean generality (number of prey), and mean vulnerability (number of predators). By testing whether latitude affects the scaling of each property with species richness, we test effects of latitude on specialization implied by the “latitude-niche breadth hypothesis”.

Methods

Data Set

We compiled a list of 163 empirical food webs from multiple sources (see Supplemental Information for web origins and selection criteria). We recorded study site latitude from the original source where possible or, where study sites were described but exact coordinates were not given, obtained estimated coordinates using Google Earth (Google Inc., 2015). We then divided the species in each web into basal resources (those species with consumers but no prey), top predators (those species with prey but no predators), and intermediate consumers (species with both predators and prey, including cannibalistic species).

As the food webs in this dataset are derived from a variety of sources and were compiled over many decades, it is likely that they vary in their resolution and in the amount of sampling effort invested in their assembly. Many analyses of food-web structure attempt to reduce this variation by aggregating species with identical predator and prey sets to form “trophic species” webs (e.g. (Martinez, 1991; Vermaat, Dunne & Gilbert, 2009; Dunne, Williams & Martinez, 2004; Dunne *et al.*, 2013)). As this study is concerned directly with the number of species at a particular latitude, however, we did not wish to ignore species with redundant sets of interactions. We therefore analysed both original and trophic-species versions of the dataset; in each case using the number of species (S) and links (L) in each web to calculate the mean number of links per species (Z), mean generality (G), and mean vulnerability (V) of the web. The version of the dataset used did not qualitatively change the results, suggesting that the scaling relationships between species richness, other food-web properties, and latitude are very similar whether or not redundant species are included. For simplicity, we present only the results for the original

webs.

Relationships with Latitude

To determine whether there were latitudinal gradients in food-web structure, we first examined simple linear relationships between latitude and each of species richness, links per species, generality, vulnerability, and proportions of basal resources, intermediate consumers, and top predators. We fit models of the form

$$S_i = \alpha_0 + \alpha_1 L_i + \alpha_2 E_i + \alpha_3 L_i E_i + \epsilon_i, \quad (1)$$

where S_i is the species richness of web i , L_i its absolute latitude (degrees north or south regardless of direction), E_i is a categorical variable indicating the ecosystem type of network i (comprising terms for stream, marine, lake, and terrestrial networks with estuarine networks providing the intercept) and ϵ_i a residual error term. We next calculated the AIC of the maximal model as well as the AIC's of a suite of candidate simplified models identified using the R (R Development Core Team, 2014) function dredge from package MuMIn (Barto, 2014). Simplified models were obtained by systematically removing all possible combinations of terms from the full model. The best-fitting model was then determined to be the model with the fewest terms where $\Delta\text{AIC} < 2$. If several models shared the fewest number of terms and had $\Delta\text{AIC} < 2$, the model with the lowest AIC in that set was chosen as the best-fit model.

Scaling Relationships with S

Next, we examined the form of the scaling relationship between each property (links per species, generality, and vulnerability) and species richness. The scaling relationship between links per species (Z) and species richness (S) has been shown to be a power

law (Riede *et al.*, 2010) of the form

$$Z_i \sim \alpha S_i^\beta, \quad (2)$$

which is often re-expressed in logarithmic form

$$\log Z_i \sim \log \alpha + \beta \log S_i. \quad (3)$$

Although these relationships are very similar, they imply different error distributions (Xiao *et al.*, 2011). Specifically, equation (2) implies a normally-distributed, additive error and equation (3) a lognormal, multiplicative error. As we have no *a priori* reason to believe that our dataset has one error distribution over another, we follow the recommendations in Xiao *et al.* (2011) and compared the two model formulations explicitly. The model with the error distribution most resembling that observed in the empirical data was then used to test for potential effects of latitude.

Although scaling relationships between species richness and generality or species richness and vulnerability have not been explicitly examined (but see scaling relationships for the standard deviations of each property in Riede *et al.* (2010)), we expect that they will follow power laws similar to that of the relationship between species richness and links per species. This is because the links taken into account in calculating generality and vulnerability are subsets of the total links included when calculating links per species. As with links per species, we explicitly compared the error distributions of models for generality and vulnerability using both the power-law and logarithmic formulations. In each case, we used the best-fitting equation as a template when assessing the effect of latitude on scaling with species richness.

Effect of Latitude on Scaling

We then assessed the impact of latitude on the scaling relationships between species richness and link density, generality, vulnerability. In the context of the scaling relationships above, note that this implies that we aim to determine the effect of latitude on the scaling exponent β . As when examining the relationships between latitude and each food web property directly, we included a categorical variable for ecosystem type (stream, lake, terrestrial, marine, or estuary), as well as interactions between food web type and latitude.

We therefore began by considering models of the form

$$Z_i = \alpha S_i^{\beta_0 + \beta_1 L_i + \beta_2 E_i + \beta_3 LE_i} + \epsilon_i, \quad (4)$$

where S_i , L_i , and E_i are as defined previously. The logarithmic formulation of this model is

$$\log Z_i = \log \alpha + \beta_0 \log S_i + \beta_1 L \log S_i + \beta_2 E \log S_i + \beta_3 LE \log S_i + \epsilon_i. \quad (5)$$

For each property in link density, generality, and vulnerability, we used the form of the equation that was best supported when describing the scaling of the property with species richness alone (Xiao *et al.*, 2011). We then simplified each model following the same procedure as for the relationships between latitude and food-web properties, except that species richness was retained in all reduced models.

Scaling by Trophic Levels

We were also interested in the ways that scaling relationships with species richness might be affected by changes to the distribution of species among trophic levels. To that end, we repeated all of the above analyses replacing species richness by proportion of basal

resources, proportion of intermediate consumers, or proportion of top predators. All model fitting and model simplification procedures were identical to those described for species richness.

Results

Relationships with Latitude

Contrary to the expected latitudinal gradient, the best-fit version of equation (1) for species richness did not include a significant effect of latitude for any ecosystem type except streams ($\beta_{Latitude}=0.095$, $p=0.626$; $\beta_{Latitude:Stream}=-1.69$, $p=0.007$). This relationship was robust to the removal of three outliers (based on Cook's Distance). There were also relationships between latitude and link density and latitude and vulnerability in stream food webs, but these trends were non-significant after the removal of three outliers. Link density and vulnerability did not vary with latitude in any other ecosystem type. The best-fit version of equation (1) for generality did not include any effect of latitude in any ecosystem type.

The relationships between latitude and the proportions of species at each trophic level were broadly similar to the relationship between latitude and species richness. The proportion of basal resources increased towards the poles in stream webs ($\beta_{Latitude:Stream}=0.012$, $p<0.001$) but did not vary with latitude in estuarine, marine, lake, or terrestrial food webs ($\beta_{Latitude}=0.001$, $p=0.139$). The proportion of intermediate consumers did not vary with latitude in any ecosystem type. The proportion of top predators did not vary with latitude in estuarine, marine, or terrestrial food webs ($\beta_{Latitude}=0.001$, $p=0.136$) but decreased towards the poles in stream and lake food webs ($\beta_{Latitude:Stream}=-0.006$, $p=0.030$; $\beta_{Latitude:Lake}=-0.006$, $p=0.001$). All of these trends were robust to the removal of outliers.

Form of scaling relationships

When considering the relationships between species richness or the proportions of basal resources, intermediate consumers, or top predators and all response variables (link density, generality, vulnerability), equation (3) had a lower AIC than did equation (2). This indicates that the data support an assumption of multiplicative lognormal error better than an assumption of additive normal error. That is, models where ϵ is modelled as an additive term on the logarithmic scale provide a better description of the data than models where ϵ is modelled as an additive term on the arithmetic scale. We therefore used logarithmic-form models when assessing the effect of latitude on scaling relationships with species richness.

Effect of Latitude on Scaling with S, B, I, and T

Link density, generality, and vulnerability each increased with increasing species richness (Fig. 1; $\beta_0=0.666$, $p<0.001$; $\beta_0=0.623$, $p<0.001$; and $\beta_0=0.666$, $p<0.001$ respectively). For estuarine, marine, and terrestrial food webs this increase did not vary with latitude ($\beta_{Latitude}=-0.001$, $p=0.267$ for link density; $\beta_{Latitude}=-0.001$, $p=0.363$ for generality; and $\beta_{Latitude}=-0.001$, $p=0.267$ for vulnerability). In lake food webs, link density, generality, and vulnerability all increased more quickly towards the poles ($\beta_{Latitude:Lake}=0.005$, $p=0.008$; $\beta_{Latitude:Lake}=0.005$, $p=0.002$; and $\beta_{Latitude:Lake}=0.005$, $p=0.008$, respectively). In stream food webs generality increased more rapidly towards the poles ($\beta_{Latitude}=0.007$, $p=0.002$) while link density and vulnerability did not vary with latitude.

In general, link density, generality, and vulnerability decreased as the proportion of basal resources in a web increased (Fig. 2). For estuarine, lake, and stream food webs these decreases were more gradual towards the poles ($\beta_{Latitude}=-0.007$, $p=0.006$ for link density; $\beta_{Latitude}=-0.009$, $p=0.002$ for generality; and $\beta_{Latitude}=-0.007$, $p=0.006$

for vulnerability). In marine food webs there was very little effect of latitude on the strength of scaling ($\beta_{Latitude:Marine}=0.009$, $p=0.047$; $\beta_{Latitude:Marine}=0.011$, $p=0.028$; and $\beta_{Latitude:Marine}=0.009$, $p=0.047$ respectively), while in terrestrial food webs link density, generality, and vulnerability decreased more gradually towards the equator ($\beta_{Latitude:Terrestrial}=0.013$, $p=0.002$; $\beta_{Latitude:Terrestrial}=0.015$, $p=0.001$; and $\beta_{Latitude:Terrestrial}=0.013$, $p=0.002$).

In contrast to the proportion of basal resources, link density, generality, and vulnerability tended to increase with increasing proportions of intermediate consumers (Fig. 3;). The best-fit models for scaling of link density and vulnerability with the proportion of intermediate consumers did not include any effect of latitude on scaling in any ecosystem type. Generality increased more rapidly towards the equator in estuarine, lake, marine, and stream food webs ($\beta_{Latitude}=-0.006$, $p=0.009$) and varied little with latitude in terrestrial food webs ($\beta_{Latitude:Terrestrial}=0.008$, $p=0.053$). In lake and stream food webs, generality increased more slowly with the proportion of intermediate consumers such that, at low proportions, the effect of latitude could negate or reverse the increase.

As with the proportion of basal resources; link density, generality, and vulnerability decreased as the proportion of top predators increased. For estuarine, lake, and marine food webs scaling of link density, generality, and vulnerability did not vary significantly with latitude ($\beta_{Latitude}=-0.001$, $p=0.527$ for link density; $\beta_{Latitude}=-0.001$, $p=0.521$ for vulnerability; the best-fit model for generality did not include any terms for latitude in any ecosystem type). In stream and terrestrial food webs, the decrease in link density and vulnerability was less sharp towards the poles, although this trend was significant only in streams ($\beta_{Latitude:Stream}=0.015$, $p<0.001$ and $\beta_{Latitude:Terrestrial}=0.006$, $p=0.069$ for link density; $\beta_{Latitude:Stream}=0.015$, $p<0.001$ and $\beta_{Latitude:Terrestrial}=0.006$, $p=0.067$ for vulnerability).

Discussion

The tendency of food-web structure to exhibit scaling relationships with species richness has been well-established (Dunne, Williams & Martinez, 2004; Riede *et al.*, 2010). As species richness in particular is also known to vary systematically over latitude (Schemske *et al.*, 2009b; Macpherson, 2002; Kaufman, 1995), intuitively one might suspect that any relationship between food-web properties such as generality might be due to the latitudinal gradient in species richness. In this dataset, however, we did not find overall latitudinal gradients in species richness, links per species, generality, vulnerability, or the proportions of food webs accounted for by basal resources, intermediate consumers, and top predators.

The lack of a latitudinal gradient in species richness in this dataset contrasts strongly with other studies (Schemske *et al.*, 2009b; Macpherson, 2002; Kaufman, 1995). As numbers of species and links included in a food web vary strongly with sampling effort as well as with the underlying diversity of the study area, it is possible that the lack of latitudinal trends here is a result of researchers tending to expend similar amounts of sampling effort across studies. This could result in food webs describing species-rich tropical communities omitting more species and links than species-poor arctic communities. In addition, it is worth noting that gradients in species richness are generally measured for a single taxonomic group at a time (e.g. (Kaufman, 1995)). It is possible that these taxa are not well-represented in our food webs and that the dominant taxa in them do not have an underlying latitudinal gradient in richness. In either case, the lack of association between species richness and latitude in any ecosystem type nevertheless means that any effect of latitude on scaling relationships between species richness and other properties is not being driven by underlying variation in species richness, allowing us to more clearly assess effects of latitude on scaling with species richness and proportions of species in different

trophic levels.

Scaling of links per species, generality, and vulnerability with species richness varied strongly across ecosystem types. In estuarine, marine, and terrestrial food webs scaling of each property varied little with latitude. This is consistent with the idea that species' niche breadths do not vary systematically with temperature and productivity but that the niche space might be larger in species-rich communities (Davies *et al.*, 2007). Rather than niche space depending on temperature and productivity, it may be that species diversity itself affects the niche space available to species (although climate may affect speciation rates and therefore the diversity in a region (Currie *et al.*, 2004)).

Unlike other ecosystem types, in lake and stream food webs the scaling of generality was stronger in higher-latitude food webs. In lake food webs, this trend was echoed in the scaling relationships between species richness and links per species and vulnerability. This means that species in tropical freshwater communities gain fewer additional feeding links per additional species in the web and that species in tropical lakes also gain fewer predators, and fewer links in general, per additional species. These trends are consistent with the hypothesis that greater stability in the tropics leads to narrower niches (Brown, 2004) and a higher proportion of specialists. This may be partly due to high-latitude species tending to switch between different seasonally-available prey (Isaac *et al.*, 2012; Wilhelm *et al.*, 1999) while tropical freshwater ecosystems may have more stable composition.

Conclusion

Our results were consistent with the latitude-niche breadth hypothesis in estuarine, marine, and terrestrial communities but instead consistent with the hypothesis of greater specialization in the tropics in stream and lake food webs. This suggests that different mechanisms may structure food webs in different habitat types and that freshwater food

webs in particular may be strongly affected by seasonal variation. In addition, different relationships between latitude and niche breadth in different habitat types goes some way towards explaining the equivocal support for the opposing hypotheses of Brown (2004) and Davies *et al.* (2007); both have merit but appear to apply to different systems.

References

- Baiser, B., Gotelli, N.J., Buckley, H.L., Miller, T.E. & Ellison, A.M. (2012) Geographic variation in network structure of a nearctic aquatic food web. *Global Ecology and Biogeography*, **21**, 579–591.
- Barto, K. (2014) *MuMIn: Multi-model inference*. R package version 1.10.5.
- Briand, F. (1983) Environmental control of food web structure. *Ecology*, **64**, 253–263.
- Brown, J.H. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O’Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.
- Davies, K.F., Harrison, S., Safford, H.D. & Viers, J.H. (2007) Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology*, **88**, 1940–1947.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2004) Network structure and robustness of marine food webs. *Marine Ecology Progress Series*, **273**, 291–302.
- Dunne, J. (2006) The Network Structure of Food Webs. *Ecological networks: linking structure to dynamics in food webs* (eds. M. Pascual & J.A. Dunne), chap. 2, pp. 27–86. Oxford University Press, New York.
- Dunne, J.A., Lafferty, K.D., Dobson, A.P., Hechinger, R.F., Kuris, A.M., Martinez, N.D., McLaughlin, J.P., Mouritsen, K.N., Poulin, R., Reise, K., Stouffer, D.B., Thieltges, D.W., Williams, R.J. & Zander, C.D. (2013) Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biology*, **11**, e1001579.

- Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morais, H.C., Diniz, I.R., Kursar, T.A. & Coley, P.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696–699.
- Field, C., Behrenfeld, M., Randerson, J. & Falkowski, P. (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**, 237–40.
- Google Inc. (2015) Google Earth (Version 7.1.2.2041) [software]. Available from <https://earth.google.com>.
- Hechinger, R.F., Lafferty, K.D., Dobson, A.P., Brown, J.H. & Kuris, A.M. (2011) A common scaling rule for abundance, energetics, and production of parasitic and free-living species. *Science*, **333**, 445–448.
- Isaac, E.J., Hrabik, T.R., Stockwell, J.D. & Gamble, A.E. (2012) Prey selection by the Lake Superior fish community. *Journal of Great Lakes Research*, **38**, 326–335.
- Kaufman, D. (1995) Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy*, **76**, 322–334.
- Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Mouillot, D. & Poulin, R. (2008) Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. *Journal of Biogeography*, **35**, 592–601.
- Lang, B., Rall, B.C. & Brose, U. (2012) Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, **81**, 516–23.

- Lappalainen, J. & Soininen, J. (2006) Latitudinal gradients in niche breadth and position-regional patterns in freshwater fish. *Die Naturwissenschaften*, **93**, 246–50.
- Macpherson, E. (2002) Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society of London B*, **269**, 1715–20.
- Marra, P.P. & Remsen, J.V. (1997) Into the Maintenance of High Species Diversity in the Neotropics : Habitat Tropical Selection and in Understory and Temperate Foraging Birds of Forests. *Ornithological Monographs*, **48**, 445–483.
- Martinez, N.D. (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs*, **61**, 367–392.
- O’Connor, M.I., Piehler, M.F., Leech, D.M., Anton, A. & Bruno, J.F. (2009) Warming and resource availability shift food web structure and metabolism. *PLoS Biology*, **7**, 3–8.
- Paine, R.T. (1966) Food Web Complexity and Species Diversity. *The American Naturalist*, **100**, 65–75.
- Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4191–4196.
- Petchey, O.L., Brose, U. & Rall, B.C. (2010) Predicting the effects of temperature on food web connectance. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2081–91.
- R Development Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Riede, J.O., Rall, B.C., Banasek-Richter, C., Navarrete, S.A., Wieters, E.A., Emmerson, M.C., Jacob, U. & Brose, U. (2010) Scaling of food-web properties with diversity and complexity across ecosystems. *Advances in Ecological Research* (ed. G. Woodward), vol. 42, pp. 139–170. Elsevier Ltd., Burlington.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009a) Is There a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245–269.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009b) Is There a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245–269.
- Schleuning, M., Fründ, J., Klein, A.M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K.S., Bazzazian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.C., Tscharrntke, T., Watts, S., Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F. & Blüthgen, N. (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, **22**, 1925–1931.
- Shurin, J.B., Gruner, D.S. & Hillebrand, H. (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society of London B*, **273**, 1–9.
- Slove, J. & Janz, N. (2010) Phylogenetic analysis of the latitude-niche breadth hypothesis in the butterfly subfamily Nymphalinae. *Ecological Entomology*, **35**, 768–774.

- Thompson, R.M. & Townsend, C.R. (2005) Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos*, **108**, 137–148.
- Townsend, C.R., Thompson, R.M., McIntosh, A.R., Kilroy, C., Edwards, E. & Scarsbrook, M.R. (1998) Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, **1**, 200–209.
- Vázquez, D.P. & Stevens, R.D. (2004) The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist*, **164**, E1–19.
- Vermaat, J.E., Dunne, J.A. & Gilbert, A.J. (2009) Major dimensions in food-web structure properties. *Ecology*, **90**, 278–282.
- White, C.R., Blackburn, T.M., Martin, G.R. & Butler, P.J. (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. *Proceedings of the Royal Society of London B*, **274**, 287–293.
- White, C.R., Grémillet, D., Green, J.a., Martin, G.R. & Butler, P.J. (2011) Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in great cormorants. *Ecology*, **92**, 475–86.
- Wilhelm, F.M., Parker, B.R., Schindler, D.W. & Donald, D.B. (1999) Seasonal Food Habits of Bull Trout from a Small Alpine Lake in the Canadian Rocky Mountains. *Transactions of the American Fisheries Society*, **128**, 1176–1192.
- Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180–183.
- Xiao, X., White, E.P., Hooten, M.B. & Durham, S.L. (2011) On the use of log-

transformation vs. nonlinear regression for analyzing biological power laws. *Ecology*, **92**, 1887–94.

Figures

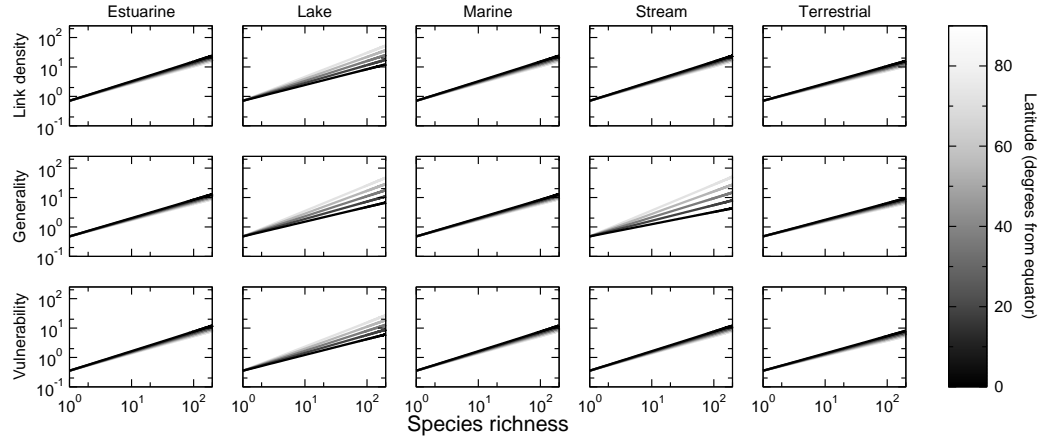


Figure 1: Scaling of link density, generality, and vulnerability with species richness varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) from the equator. We did not include direction (i.e., North or South) in our analyses. All curves are based on N=163 empirical food webs.

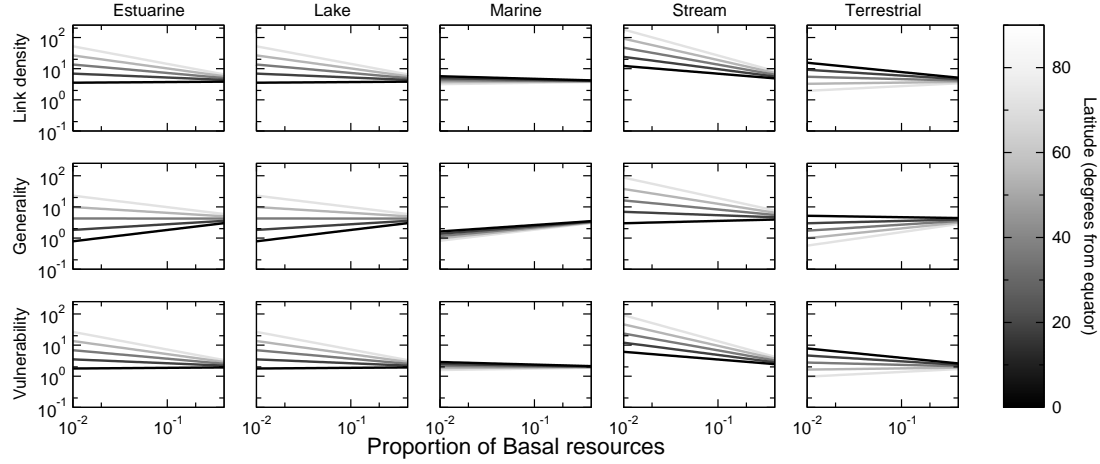


Figure 2: Scaling of link density, generality, and vulnerability with the proportion of basal resources in a food web varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) from the equator. We did not include direction (i.e., North or South) in our analyses. All curves are based on N=163 empirical food webs.

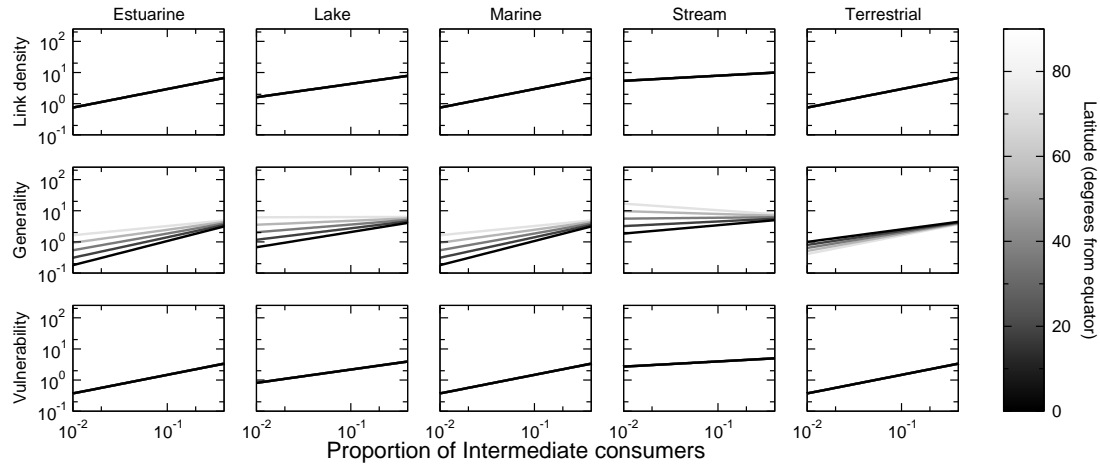


Figure 3: Scaling of link density, generality, and vulnerability with the proportion of intermediate consumers in a food web varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) from the equator. We did not include direction (i.e., North or South) in our analyses. All curves are based on N=163 empirical food webs.

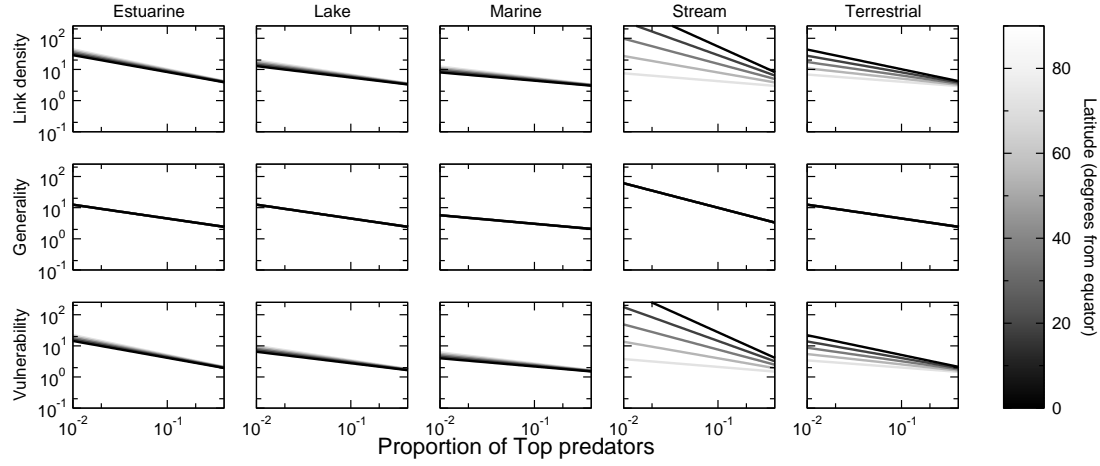


Figure 4: Scaling of link density, generality, and vulnerability with the proportion of top predators in a food web varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) from the equator. We did not include direction (i.e., North or South) in our analyses. All curves are based on N=163 empirical food webs.

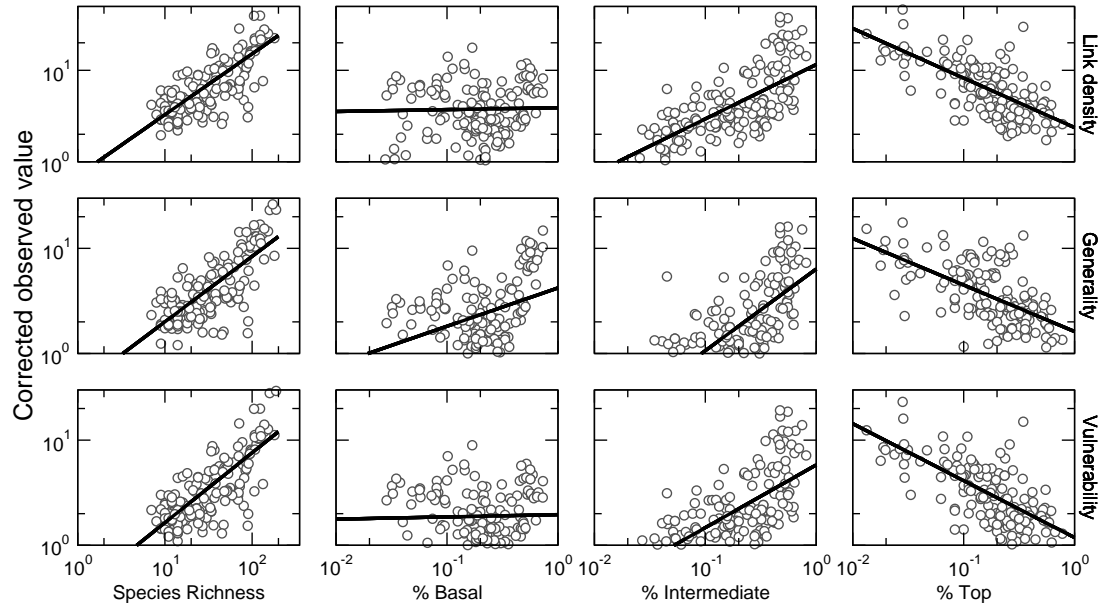


Figure 5: Scaling relationships for link density, generality (number of prey), and vulnerability (number of predators) against the proportions of basal resources (% Basal), intermediate consumers (% Intermediate), top predators (% Top), and species richness of a food web. For each relationship we show observed values corrected for ecosystem type and latitude (grey circles), as well as the overall scaling relationship (N=163 food webs).