

Generality in food webs scales with species richness, not latitude

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Introduction

[[Add something about ecosystem type since it's in the methods]]

Food webs –networks of feeding links between species– have been used for over a century to summarize the structure of ecological communities (Williams & Martinez, 2000; ?) and to understand how that structure relates to environmental variables such as land use [[lets really consider the three env variables used here. there really is not a lot of work on land use....i get why prim prod and climate are included....maybe focus on habitat types since you focus on habitats in the analysis]] (Townsend *et al.*, 1998; ?; ?), primary productivity (), and climate(). 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 (). [[maybe climatic regimes? the issue is that there really are not a lot of studies that look at these things.....]] These variables affect both the resources available and species' metabolisms (?), and have been proposed as

determinants of the strength of interspecific interactions (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; ?; ?).

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, higher productivity of the tropics (?) may result in a broader niche space (?) which could also allow greater diversification even if niche sizes are globally similar. Although the assumptions of the latitude-niche breadth hypothesis are only equivocably 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 decreased seasonality or higher productivity is the cause of higher species-richness in the tropics, then there should be other effects of latitudinal gradients on food-web structure. Attempts to unravel these effects, however, are complicated by known relationships between species richness and many other network properties (Riede *et al.*, 2010)[[Check that I don’t say that richness causes structural effects elsewhere]]. In particular, narrower niches imply fewer links per species (i.e., greater specialization in the tropics ()). 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 (?). 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 in the main text.

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 S , Z , G , V , B , I , and T . 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 (Z , G , and V) and S . The scaling relationship between Z and 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 S and G or S and V 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 S and Z . This is because the links taken into account in calculating G and V are subsets of the total links included when calculating Z . As with Z , we explicitly compared the error distributions of models for G and V 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. [[If the species-rich tropics truly have narrower niches (?), then we would expect to see less increase in mean numbers of links, predators, and prey with increasing species richness in the tropics.]] 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 B , proportion of intermediate consumers I , or proportion of top predators T . 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). In the best-fit versions of equation (1) for link density and vulnerability, there were once again significant relationships with latitude in stream food webs, but after the removal of three outliers these trends were no longer significant. Link density and vulnerability did not vary with latitude in any other ecosystem type. Similarly, the best-fit version of equation (1) for generality did not include any effect of latitude in any ecosystem type.

The relationships between the proportions of species at each trophic level with latitude were broadly similar to the relationship between species richness and latitude. 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 and proportions of basal resources, intermediate consumers, and 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; $\beta_0=0.745$, $p<0.001$; $\beta_0=0.675$, $p<0.001$; and $\beta_0=0.745$, $p<0.001$ respectively). For estuarine, marine, and terrestrial food webs this increase did not vary with latitude ($\beta_{Latitude}=-0.001$, $p=0.334$ for link density; $\beta_{Latitude}=-0.001$, $p=0.354$ for generality; and $\beta_{Latitude}=-0.001$, $p=0.334$ for vulnerability). In lake food webs, link density, generality, and vulnerability all increased more quickly towards the poles ($\beta_{Latitude:Lake}=0.004$, $p=0.008$; $\beta_{Latitude:Lake}=0.005$, $p=0.002$; 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; $\beta_{Latitude}=-0.001$, $p=0.526$ 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 (), 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 latitudinal gradients in food-web properties in this dataset contrasts strongly with other studies which have found consistent variation in species richness, [[other properties]] (). 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 (). 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 (?). In lake food webs, in contrast, scaling of each property was much stronger in high-latitude food webs. In stream food webs, scaling of links per species and vulnerability varied little over latitude while scaling of generality was stronger in high-latitude food webs. This means that species in tropical freshwater communities gain fewer additional feeding links per additional species in the web and is consistent with the hypothesis that greater stability in the tropics leads to narrower niches (?) and a higher proportion of specialists ().

In lake food webs, species in tropical food webs also gained fewer predators, and therefore fewer links overall. Conversely, for species in high-latitude food webs numbers of predators, prey, and links per species all increased rapidly with increasing species richness. As there were proportionally fewer top predators in high-latitude lakes yet generality, vulnerability, and links per species all increased more rapidly than near the equator, it appears that high-latitude predators are more likely to be generalists. This may reflect prey switching as different food sources become available in different seasons ().

Surprisingly species in high-latitude stream food webs, while gaining many additional prey species per additional species in the food web, did not receive any more predators

or links than species in low-latitude streams. This may be partly due to the increasing proportion of the food web made up of basal resources at higher latitudes. If any additional species is more likely to be a basal resource at high latitudes, it will have predators but no prey. Combined with the potential for prey-switching between seasonal resources, this could account for the sharper increase in generality with increasing species richness in high-latitude streams. Vulnerability and mean links per species, on the other hand, increased at the same rate across latitude. [[Still working on why]]

Conclusion

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Figures

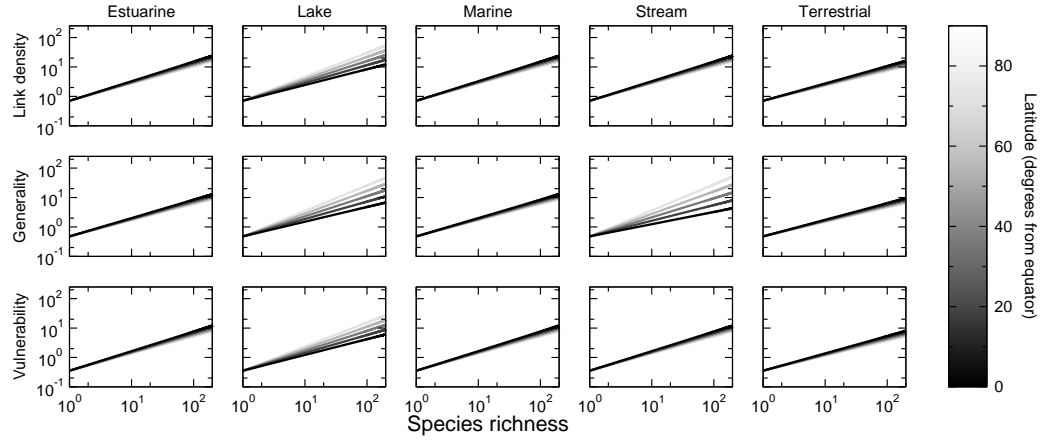


Figure 1: Scaling of link density, generality, and vulnerability with species richness varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) from the equator. We did not include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

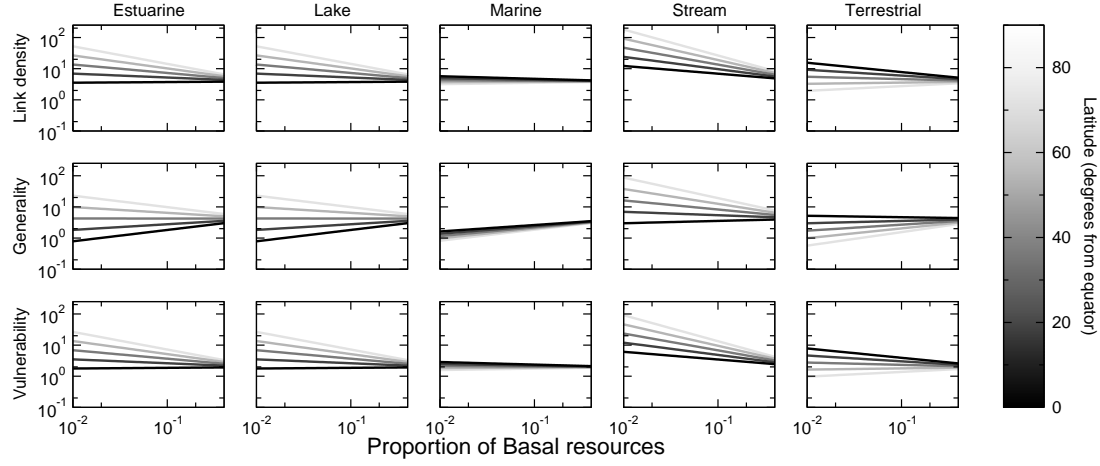


Figure 2: Scaling of link density, generality, and vulnerability with the proportion of basal resources in a food web varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) 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.

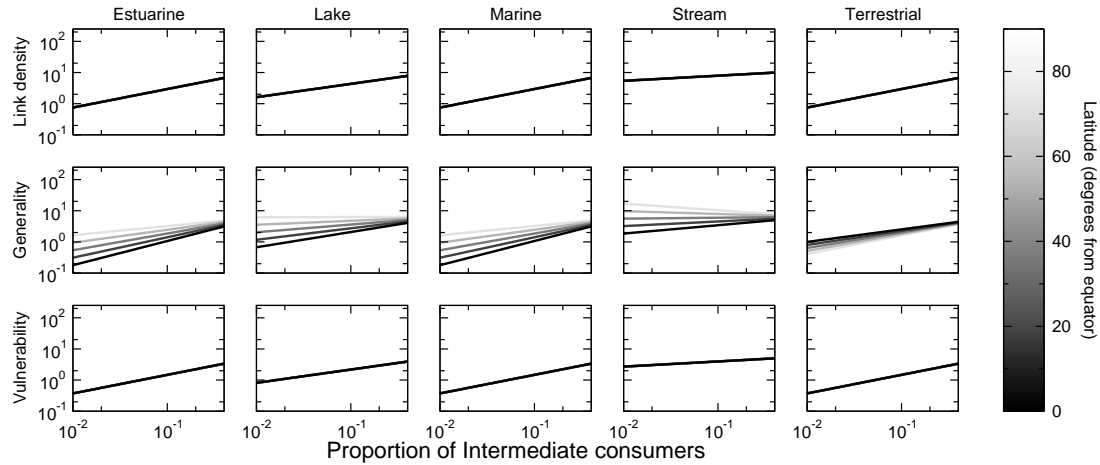


Figure 3: Scaling of link density, generality, and vulnerability with the proportion of intermediate consumers in a food web varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest 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.

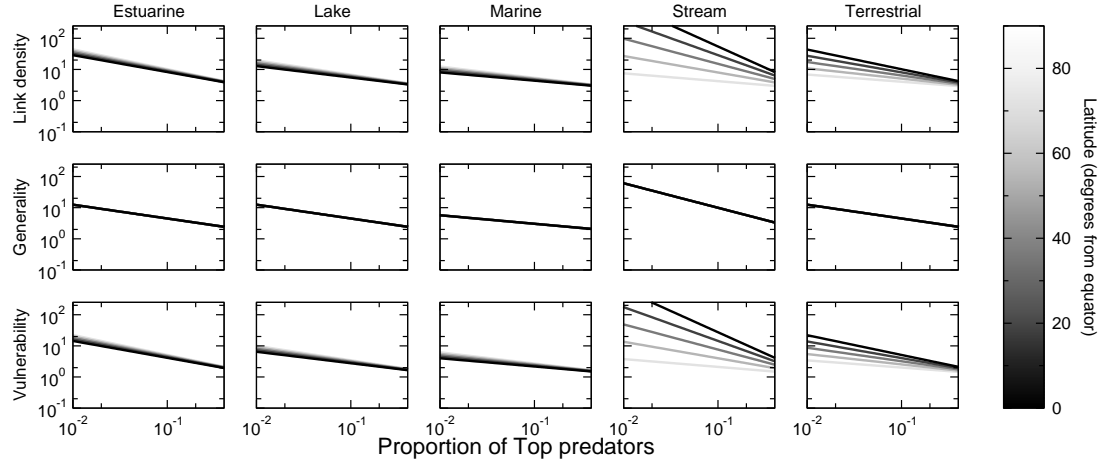


Figure 4: Scaling of link density, generality, and vulnerability with the proportion of top predators in a food web varies across ecosystem types and over latitude. For each property we show prediction curves for food webs at the equator (darkest line) and at 20°, 40°, 60°, and 80° (lightest line) from 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.

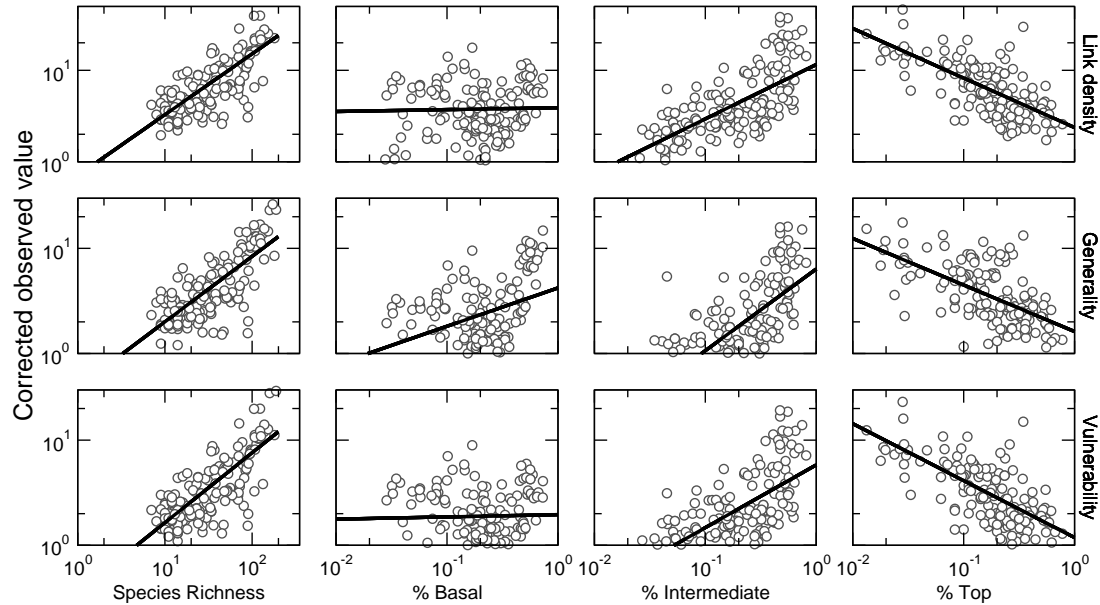


Figure 5: Scaling relationships for link density, generality (number of prey), and vulnerability (number of predators) against the proportions of basal resources (% Basal), intermediate consumers (% Intermediate), top predators (% Top), and species richness of a food web. For each relationship we show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