Specialisation in food webs scales with species richness but not with latitude

Alyssa R. Cirtwill[1,2], Daniel B. Stouffer[1,3], Tamara N. Romanuk[2]

[1]School of Biological Sciences
University of Canterbury
Private Bag 4800
Christchurch 8140, New Zealand

[2]Department of Biology
Life Science Centre, Dalhousie University
1355 Oxford St., P0 BOX 15000
Halifax NS, B3H 4R2, Canada

[3]Centre for Integrative Ecology
School of Biological Sciences
University of Canterbury
Private Bag 4800
Christchurch 8140, New Zealand

Abstract

Several properties of food webs—the networks of feeding links between species—are known to 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 with species richness 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 niche breadth appears to vary little. These contrasting findings indicate that it may be more important to account for habitat than latitude when exploring gradients in food-web structure.

Introduction

Food webs –networks of feeding links between species– have been used for several decades to summarise the structure of ecological communities (Paine, 1966; Williams & Martinez, 2000; Petchey *et al.*, 2008) and to understand how that structure relates to environmental variables such as habitat type (Briand, 1983; Shurin, Gruner & Hillebrand, 2006), primary productivity (Townsend *et al.*, 1998; Thompson & Townsend, 2005; Vermaat, Dunne & Gilbert, 2009), and climate (Petchey, Brose & Rall, 2010; Baiser *et al.*, 2012). 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, 1998). These variables affect both the resources available and species' metabolisms (White *et al.*, 2007; O'Connor *et al.*, 2009; Hechinger *et al.*, 2011; White *et al.*, 2011), and have been proposed as determinants of the strength of interspecific interactions (Schemske *et al.*, 2009; Lang, Rall & Brose, 2012; Schleuning *et al.*, 2012). 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 (Kaufman, 1995; Macpherson, 2002; Schemske *et al.*, 2009).

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 specialisation (i.e., the breadth of the Eltonian niche; Elton, 1927) 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 specialisation) in the tropics (Marra & Remsen, 1997; Dyer *et al.*, 2007; 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 specialisation 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 specialisation by examining the shape of the scaling relationship between specialisation and species richness over changing latitude. Here, we use three measures of specialisation: 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 specialisation implied by the "latitude-niche breadth hypothesis".

Methods

Data Set

We compiled a list of 166 empirical food webs from multiple sources (see *Appendix S1* 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 (Martinez, 1991; Dunne, Williams & Martinez, 2004; Vermaat, Dunne & Gilbert, 2009; Dunne *et al.*, 2013). As our study is concerned directly with the number of species at a particular latitude, however, we did not wish to ignore species with identical sets of interactions. We therefore analysed both original and trophic-species versions of the dataset; in each case using the number of species and links in each web to calculate the mean link density (number of links per species), mean generality (number of prey per species), and mean vulnerability (number of predators per species) 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, here we present only the results for the original webs.

Scaling Relationships with S

The scaling relationship between link density (Z) and species richness (S) has been shown to be a power law (Riede *et al.*, 2010) of the form

$$Z_i \sim \alpha S_i^{\beta}, \tag{1}$$

which is often re-expressed in logarithmic form

$$\log Z_i \sim \log \alpha + \beta \log S_i. \tag{2}$$

As the two forms imply a statistical fit to the data to different error distributions, neither of which has strong *a priori* justification in our dataset, we followed the recommendations in Xiao *et al.* (2011) to compare the two model formulations explicitly (see *Appendix S2* for details). The logarithmic form (equation 2) provided the better fit to the data, as did the logarithmic forms of similar models for the scaling of generality and vulnerability. We therefore used and present logarithmic models throughout the rest of the study.

Effect of Latitude on Scaling

After determining the appropriate form of the scaling relationship, 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 wished to determine the effect of latitude on the scaling exponent β. 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

$$Z_i = \alpha S_i^{\beta_0 + \beta_1 L_i + \beta_2 E_i + \beta_3 L E_i} + \epsilon_i, \tag{3}$$

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 is a residual error term. The logarithmic formulation of this model is

$$\log Z_i = \log \alpha + \beta_0 \log S_i + \beta_1 L \log S_i + \beta_2 E \log S_i + \beta_3 LE \log S_i + \epsilon_i. \tag{4}$$

We then simplified each model. To do this, we 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 Core Team, 2014) function dredge from package MuMIn (Barton, 2014). Simplified models were obtained by systematically removing all possible combinations of terms from the full model with the restriction that species richness was retained in all reduced models. The best-fitting model was then determined to be the model with the fewest terms where ΔAIC<2. If several models shared the fewest number of terms and had ΔAIC<2, the model with the lowest AIC in that set was chosen as the best-fit model.

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

Link density, generality, and vulnerability each increased with increasing species richness (β_0=0.637, p<0.001; β_0=0.553, p<0.001; and β_0=0.637, p<0.001, respectively; Fig 1).For estuarine, marine, and terrestrial food webs the strength of this scaling did not vary with latitude ($\beta_{Latitude}$=-0.001, p=0.365 for link density; $\beta_{Latitude}$=-0.001, p=0.535 for generality; and $\beta_{Latitude}$=-0.001, p=0.366 for vulnerability; Fig. 2). In lake food webs, however, the scaling of each property was stronger towards the poles ($\beta_{Latitude:Lake}$=0.004, p=0.019; $\beta_{Latitude:Lake}$=0.005, p=0.004; and $\beta_{Latitude:Lake}$=0.004, p=0.018, respectively). In stream food webs, generality increased more rapidly towards the poles ($\beta_{Latitude:Stream}$=0.007, p=0.001) while link density and vulnerability did not vary with latitude.

Unlike species richness, only generality showed an overall increase with increasing proportions of basal resources in a web (β_0=0.019, p=0.859; β_0=0.383, p=0.001; and β_0=0.019, p=0.855 for link density, generality, and vulnerability, respectively; Fig. 1). In each case, however, there were substantial effects of latitude on the scaling relationships. Thus, the scaling exponents for link density and vulnerability were negative for estuarine, lake, and stream communities and became more negative towards the poles ($\beta_{Latitude}$=-0.008, $p<0.001$ and $\beta_{Latitude}$=-0.008, $p<0.001$, respectively; Fig. 3). For the scaling of link density and vulnerability in marine and terrestrial communities, the overall effect of latitude on scaling was positive ($\beta_{Latitude:Marine}$=0.011, p=0.020; $\beta_{Latitude:Terrestrial}$=0.016, $p<0.001$ and $\beta_{Latitude:Marine}$=0.011, p=0.020; $\beta_{Latitude:Terrestrial}$=0.016, $p<0.001$, respectively) such that there was weak scaling at most latitudes. In contrast, the scaling exponent of generality with the proportion of basal resources was positive near the equator and negative near the poles in estuarine, lake, and stream communities ($\beta_{Latitude}$=-0.010, $p<0.001$) while there was very little change in the scaling exponents for marine and terrestrial communities ($\beta_{Latitude:Marine}$=0.013, p=0.010; $\beta_{Latitude:Terrestrial}$=0.019, $p<0.001$).

As with species richness, link density, generality, and vulnerability generally increased with the proportion of intermediate consumers in a web (β_0=0.771, $p<0.001$; β_0=0.349, p=0.235; and β_0=0.771, $p<0.001$ respectively; Fig. 1). The best-fit models for link density and vulnerability did not include any effect of latitude. In contrast, the strength of the scaling relationship for generality increased weakly towards the poles in estuarine, marine, and terrestrial food webs ($\beta_{Latitude}$=0.008, p=0.204) but decreased towards the poles in lakes and streams ($\beta_{Latitude:Lake}$=-0.021, p=0.018 and $\beta_{Latitude:Stream}$=-0.035, p=0.001; Fig 3).

In contrast to the generally positive scaling relationships above, link density, generality, and vulnerability decreased as the proportion of top predators increased (β_0=-0.532, p<0.001; β_0=-0.454, p<0.001; and β_0=-0.532, p<0.001 respectively; Fig 1). For estuarine, lake, and marine food webs the strength of this scaling did not vary significantly with latitude ($\beta_{Latitude}$=-0.001, p=0.481 for link density; $\beta_{Latitude}$=-0.001, p=0.472 for vulnerability). In stream and terrestrial food webs, however, scaling was more strongly negative in the tropics and near zero near the poles ($\beta_{Latitude:Stream}$=0.012, p=0.001 and $\beta_{Latitude:Terrestrial}$=0.009, p=0.015 for link density; $\beta_{Latitude:Stream}$=0.012, p=0.001 and $\beta_{Latitude:Terrestrial}$=0.009, p=0.015 for vulnerability; Fig. 3. The best-fit model for generality did not include any terms for latitude in any ecosystem type.

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 (Kaufman, 1995; Macpherson, 2002; Hillebrand, 2000; Schemske *et al.*, 2009), 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, except in lake and stream food webs where the proportions of top predators tended to decrease towards the poles (see *Appendix S3* for details).

The lack of a latitudinal gradient in species richness in this dataset contrasts strongly with other studies (Kaufman, 1995; Macpherson, 2002; Hillebrand, 2000; Schemske *et al.*, 2009). 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 (Kaufman, 1995; Macpherson, 2002; Hillebrand, 2000; Schemske *et al.*, 2009). 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 a strong association between species richness and latitude in any ecosystem type means that any effect of latitude on other scaling relationships is not being driven by an underlying latitudinal gradient in species richness. The lack of confounding effects of latitude allows 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)). For example, as the plant diversity of a community increases both the variety of food available to herbivores and the structural variety of the habitat will also increase.

Unlike other ecosystem types, the scaling of generality in lake and stream food webs was stronger (i.e.,generality increased more steeply with increasing species richness) 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 than species in high-latitude lakes. These trends are consistent with the hypothesis that greater stability in the tropics leads to narrower niches (Vázquez & Stevens, 2004) and a higher proportion of specialists. This may be partly due to high-latitude species tending to switch between different seasonally-available prey (Magalhães, 1993; Wilhelm *et al.*, 1999; Isaac *et al.*, 2012) while tropical freshwater ecosystems may have more stable composition.

The scaling of link density, generality and vulnerability with proportions of species at different trophic levels, however, did not differ between lakes and most other food webs. Indeed, there was comparatively little variation in scaling with the trophic-level breakdown of a web across ecosystem types. Nevertheless, the negative relationships between the proportion of top predators in a web and link density and vulnerability were weaker (i.e., the scaling exponent was more strongly negative) in low-latitude stream ecosystems. This may imply that top predators in high-latitude streams tend to be more generalist than their low-latitude equivalents (Winemiller, Agostinho & Caramaschi, 2008), perhaps due to prey-switching during seasonal food shortages (Magalhães, 1993). More generally, the lack of correspondence between the scaling of food-web properties with species richness and with proportions of species at each trophic level suggests that the size and trophic breakdowns of a community can each provide different information (Downing & Leibold, 2002).

Conclusion

Overall, our results were inconsistent with the latitude-niche breadth hypothesis in estuarine, marine, and terrestrial communities but consistent with the hypothesis of greater specialisation 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 narrower niches in the tropics (Vázquez & Stevens, 2004) and broader niche space in the tropics (Davies *et al.*, 2007); both have merit but appear to apply to different systems.

Data Accessibility

Food webs used in this study were retrieved from the University of Canberra's GlobalWeb database (Caffrey & Thompson, 2015; *www.globalwebdb.com*) and from two papers (Riede *et al.*, 2011; *http://dx.doi.org/10.1111/j.1461-0248.2010.01568.x* and Dunne *et al.*, 2013; *http://dx.doi.org/10.1371/journal.pbio.1001579*). Original sources for the food webs are given in *Appendix S1*.

Acknowledgements

We thank members of the Romanuk, Stouffer, and Tylianakis labs for their comments on the manuscript. This research was supported by an NSERC USRA undergraduate scholarship and NSERC PGS-D graduate scholarship (to ARC).

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Figure Captions

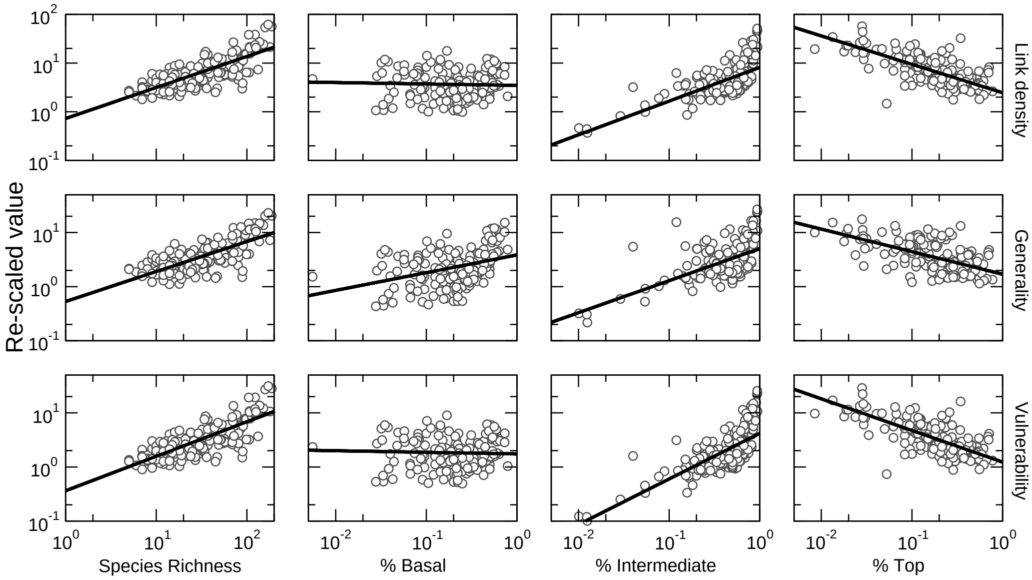

Figure 1: Scaling relationships for re-scaled link density, generality, and vulnerability relative to species richness and the proportions of basal resources (% Basal), intermediate consumers (% Intermediate), or top predators (% Top) in a food web. Link density, generality, and vulnerability were each re-scaled to remove the effects of latitude and ecosystem type. As these relationships take the form of power laws, we did this by dividing the food-web property (e.g. link density) by the predictor (e.g. % Basal) raised to an exponent including the effects of latitude and, where applicable, ecosystem type and the interaction between ecosystem type and latitude. Note that in all cases estuarine food webs were used as the baseline ecosystem type, but that at most two ecosystem types had interactions between ecosystem type and latitude retained in the best-fit model (see *results* for specifics). For each relationship, we show the re-scaled values (white circles) as well as the overall scaling relationship using estuarine ecosystems as a baseline (black line, N=166 food webs). For a figure with the uncorrected values, see Fig. *S1*, *Appendix S4*.

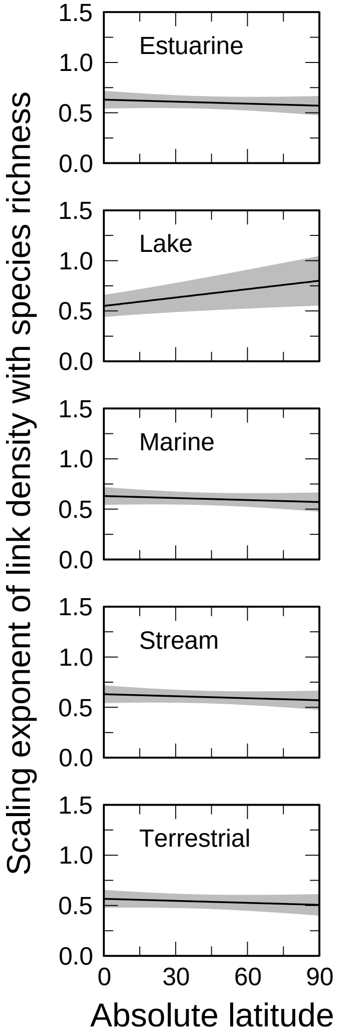

Figure 2: Changes to the scaling of link density with species richness across ecosystem types and over latitude. We show the estimated scaling exponent for species richness (black line) with its 95% confidence interval (in grey), based on N=166 empirical food webs. Latitude is given in degrees from the equator regardless of direction. The behaviour of exponents for the scaling of generality and vulnerability with species richness was very similar to those for link density, except for the scaling of generality in streams where the size of the exponent increased towards the poles. See Fig. *S2, Appendix 5* for all scaling relationships.

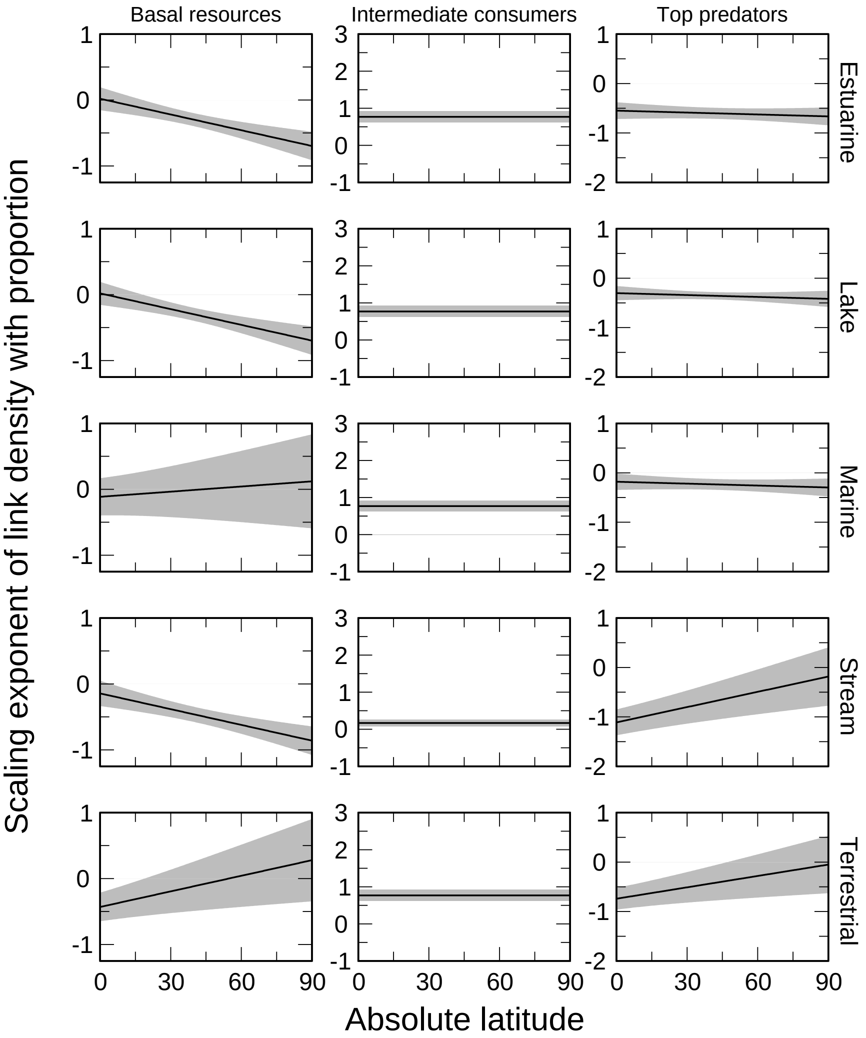

Figure 3: Changes to the scaling of link density with the proportions of basal resources, intermediate consumers, or top predators in a food web across ecosystem types and over latitude. For each proportion we show the estimated scaling exponent (black line) with its 95% confidence interval (in grey), based on N=166 empirical food webs. Latitude is given in degrees from the equator regardless of direction. The behaviour of exponents for the scaling relationships of generality and vulnerability with each proportion was very similar to those of the scaling relationships with link density, except for the scaling of generality with the proportion of top predators where there was no effect of latitude on the size of the exponent in any ecosystem type. See Figs. *S3-S5, Appendix 5* for all scaling relationships.