Ecogeographical rules and the macroecology of food webs

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Abstract

Aim: How do factors such as space, time, climate and other ecological drivers influence food web structure and dynamics? Collections of well-studied food webs and replicate food webs from the same system that span biogeographical and ecological gradients now enable detailed, quantitative investigation of such questions and help integrate food web ecology and macroecology. Here, we integrate macroecology and food web ecology by focusing on how ecogeographical rules [the latitudinal diversity gradient (LDG), Bergmann's rule, the island rule and Rapoport's rule] are associated with the architecture of food webs.

Location: Global.

Time period: Current.

Major taxa studied: All taxa.

Methods: We discuss the implications of each ecogeographical rule for food webs, present predictions for how food web structure will vary with each rule, assess

empirical support where available, and discuss how food webs may influence ecogeographical rules. Finally, we recommend systems and approaches for further advancing this research agenda.

Results: We derived testable predictions for some ecogeographical rules (e.g. LDG, Rapoport's rule), while for others (e.g., Bergmann's and island rules) it is less clear how we would expect food webs to change over macroecological scales. Based on the LDG, we found weak support for both positive and negative relationships between food chain length and latitude and for increased generality and linkage density at higher latitudes. Based on Rapoport's rule, we found support for the prediction that species turnover in food webs is inversely related to latitude.

Main conclusions: The macroecology of food webs goes beyond traditional approaches to biodiversity at macroecological scales by focusing on trophic interactions among species. The collection of food web data for different types of ecosystems across biogeographical gradients is key to advance this research agenda. Further, considering food web interactions as a selection pressure that drives or disrupts ecogeographical rules has the potential to address both mechanisms of and deviations from these macroecological relationships. For these reasons, further integration of macroecology and food webs will help ecologists better understand the assembly, maintenance and change of ecosystems across space and time.

1 | INTRODUCTION

Most food web research has emphasized individual datasets compiled for a particular location as a means of investigating the organization and dynamics of various taxa interacting within communities. This long-standing approach has led to detailed understanding of the structure and dynamics of specific systems (e.g., Boit, Martinez, Williams, & Gaedke, 2012; Hall & Raffaelli, 1991; Martinez, 1991; Polis, 1991). In addition, comparisons across well-studied food webs revealed generalities in their structure (e.g., Cohen, Briand, & Newman, 1990; Dunne, Labandeira, & Williams, 2014; Pimm, 1982; Riede et al., 2010; Stouffer, Camacho, Guimera, Ng, & Nunes Amaral, 2005; Williams & Martinez, 2000) and prompted investigations of different aspects of food web dynamics such as robustness (Dunne, Williams, & Martinez, 2002; Staniczenko, Lewis, Jones, & Reed-Tsochas, 2010), persistence (Otto, Rall, & Brose, 2007; Sahasrabudhe & Motter, 2011) and stability (Allesina et al., 2015). As more well-resolved empirical food webs become available, expanding food web ecology to include macroecologically inspired spatial or temporal gradients is emerging as a key research agenda (Gilarranz, Mora, & Bascompte, 2016; Tylianakis & Morris, 2017).

Collections of well-studied food webs and replicate food webs of the same system allow detailed investigation of how factors such as space, time, climate and other ecological drivers influence and interact with food web structure, dynamics and stability. For example,

dozens of small mangrove islet food webs, compiled from a classic island biogeography experiment on recolonization following defaunation (Simberloff & Wilson, 1969), were used to show that the proportion of specialists increased through time while the proportion of generalists and connectance decreased (Piechnik, Lawler, & Martinez, 2008). Similarly, hundreds of intertidal food webs from a small North Pacific archipelago sampled at different spatial scales revealed that connectance decreases with spatial scale of sampling while species richness increases (Wood, Russell, Hanson, Williams, & Dunne, 2015). A third example showed that across hundreds of pitcher plant food webs, at sites stretching from Florida to Canada, network structure is more variable at lower latitudes (Baiser, Gotelli, Buckley, Miller, & Ellison, 2012).

In addition to revealing novel patterns and processes, network data across broad spatial scales and gradients lend themselves to re-examining more classical lines of ecological research (Kissling & Schleuning, 2015). One potentially fertile area of research lies in integrating food web ecology and macroecology. While researchers have approached macroecology from many perspectives (Blackburn & Gaston, 2006), a stalwart approach is to develop and test ecogeographical "rules" that describe scaling relationships in species' diversity (e.g., Pianka, 1966), range sizes (e.g., Stevens, 1989,1992) or body masses (e.g., Bergmann, 1847) across abiotic or geospatial gradients. The study of ecogeographical rules has experienced a resurgence over the last decade due to the increase in available data and insights

from studying species invasion (Lomolino, Sax, Riddle, & Brown, 2006; Mathys & Lockwood, 2009) and global change (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Millien et al., 2006) at macroecological scales. We posit that ecogeographical rules also play a key role in understanding variation in food web structure at macroecological scales and vice versa. Changes in abundance, body size and range size described by ecogeographical rules may constrain trophic interactions and influence the structure and dynamics of food webs along biogeographical gradients. On the other hand, food web interactions may also influence the expression of ecogeographical rules either by amplifying them and making relationships stronger or by subverting them and making relationships weaker for certain taxa or regions. Knowledge of feedbacks between ecogeographical rules and the structure of food webs is a vital first step to studying ecological networks across large spatial scales.

Here, we integrate macroecology and food web ecology by exploring a subset of ecogeographical rules (Table 1) and their connections to food webs: (a) the latitudinal diversity gradient (LDG): the increase in species richness from the poles to the equator, (b) Bergmann's rule: the increase in body size with decreasing temperature, (c) the island rule: the increase in size of small species and decrease in size of large species on islands, and (d) Rapoport's rule: larger species ranges at high latitudes. We describe each rule, discuss their implications for food webs, present heuristic predictions for how food web structure will vary with each rule, and assess empirical support for these predictions where available (Table 2).

2 | THE LATITUDINAL DIVERSITY GRADIENT

The most well-known, oldest and perhaps most influential macroecological rule is the LDG of increasing species richness from the poles to the tropics (Brown, 2014; Darwin, 1859; Dobzhansky, 1950; Mittelbach et al., 2007; Pianka, 1966; Rohde, 1992; Wallace, 1878). Hypothesized mechanisms for the LDG are abundant, often non-exclusive, and difficult to test (Brown, 2014; Pianka, 1966; Rohde, 1992). Prominent explanations for the LDG build on purported differences between the tropics and other regions, suggesting that higher species richness in the tropics may be due to greater productivity (Currie, 1991; Hutchinson, 1959), higher rate of origination (e.g., "out of the tropics" concept; Jablonski, Roy, & Valentine, 2006), phylogenetic niche conservatism (Wiens & Graham, 2005), and rapid evolution and speciation due to either temperature (Brown, 2014; Rohde, 1992) or stronger biotic interactions (Dobzhansky, 1950; Schemske, 2002).

Gradients in species richness also play a central role in our understanding of food web structure (Dunne, 2005; Pimm, Lawton, & Cohen, 1991). For example, increased species richness often decreases the fraction of species at top and basal trophic levels while increasing the fractions of intermediate species and links per species (Martinez, 1991,1994) as well as affecting practically all other properties of food web architecture (Vermaat, Dunne, & Gilbert, 2009; Williams & Martinez, 2000). Such food web patterns should also apply to changes in species richness along the LDG specifically. While explanations for the LDG imply changes in food web structure with latitude, explicit exploration of such changes has begun only recently (Baiser et al., 2012; Cirtwill, Stouffer, & Romanuk, 2015).

2.1 | Predictions for food web structure based on LDG hypotheses

2.1.1 | LDG, productivity, and food chain length

One of the more prominent LDG hypotheses asserts that greater productivity at low latitudes is responsible for the LDG (Currie, 1991; Pianka, 1966; Storch, Bohdalková, & Okie, 2018). Relationships between productivity and food chain length (FCL) have also been documented in both natural and experimental systems (Kaunzinger & Morin, 1998; Post, 2002; Takimoto & Post, 2013; Ward & McCann, 2017). Different mechanisms underlying productivity–FCL relationships lead to different predictions about how FCL changes with latitude. One mechanism by which FCL can increase is simply through a sampling effect (Huston, 1997) where high species richness in productive regions increases the probability that a food web will contain a top predator or consumer that can elongate FCL. A mechanism based on energy flow posits that low productivity, coupled with inefficient energy transfer across trophic levels, sets limits on how much energy can reach top trophic levels and as a result, can limit

TABLE 1 Summary of ecogeographical rules used to explore food web structure

Rule	Description	Focal response	Hypothesized drivers	Focal taxa
Latitudinal diversity gradient (LDG)	Increase in species richness from the poles to the equator	Species richness	Temperature, energy, productivity, competition, predation	All taxa
Bergmann's rule	Increase in body size with decreasing temperature	Body size	Temperature, productivity, starvation tolerance	Mammals and birds, but tested across many taxa
Island rule	Increase in size of small species and decrease in size of large species on islands	Body size	Competition, predation, resource subsidies	Vertebrates
Rapoport's rule	Larger species ranges at high latitudes	Range size	Climatic variation/stability, competition, differential extinction	All taxa

TABLE 2 Predictions and empirical support for ecogeographical rules and food web structure. For rules that precluded predictions (Bergmann's and island rules), we put forth approaches to explore the relationship between these ecogeographical rules and food webs. If no citation is given for empirical support, the results are included in this paper

Rule	Prediction	Empirical support
LDG	Longer FCL at lower latitudes	- No evidence across five types of ecosystems - No evidence in stream, lake and marine systems (Vander Zanden & Fetzer, 2007) - Weak evidence in pitcher plant food webs
LDG	Shorter FCL at lower latitudes	- Evidence in lakes - Non-significant trends in streams and lakes (Vander Zanden & Fetzer, 2007)
LDG	Linkage density, generality and vulnerability should increase with latitude	- No evidence in pitcher plant food webs - Generality increased toward the poles in lake and stream food webs (Cirtwill et al., 2015) - Linkage density and vulnerability showed no relationship with latitude across five ecosystem types (Cirtwill et al., 2015) - Linkage density of host–parasitoid interactions peaks in colder climates (Gravel et al., 2019)
Rapoport's	[a]**At low latitudes, we expect high species turnover and little to no interaction turnover**	- Confirmed in pitcher plant food webs
Rapoport's	[a]**At high latitudes, food webs should show low species turnover and high interaction turnover**	- Confirmed in pitcher plant food webs
Rapoport's	High-latitude webs will have greater interaction turnover than low-latitude webs	None available
Rule	**Prediction**	**Potential approaches**
Bergmann's	None made	Compare predator–prey biomass ratios across latitude or temperature
Island	None made	Compare predator–prey biomass ratios between island and mainland systems

FCL = food chain length; LDG = latitudinal diversity gradient.
[a]We were only able to test the portion of the prediction that is bold for Rapoport's rule given our data.

FCL (Fretwell & Barach, 1977; Hutchinson, 1959; Lindeman, 1942). *Both the sampling effect and flow-based mechanisms predict longer FCL at lower latitudes*. However, consideration of the effects of omnivory on energy flow may reverse these predictions. High productivity food webs may increase the biomass of high-trophic-level predators that reduce consumer abundance forcing such predators to also feed on lower trophic levels effectively reducing FCL (Tunney, McCann, Lester, & Shuter, 2012; Ward & McCann, 2017). Such considerations predict *that FCL is shorter in highly productive (i.e., at lower latitudes) ecosystems because of increased omnivory*.

We explored how FCL (measured as mean FCL, averaged over all species) varied across latitudinal gradients in six ecosystems, based on 164 food webs from lake, estuary, stream, marine and terrestrial environments globally (compiled in Cirtwill et al., 2015) and 780 pitcher plant food webs from 39 sites across North America (Baiser et al., 2012). We found significantly longer FCL at higher latitudes for lake food webs (Figure 1) and a significant decrease in FCL with latitude for pitcher plant food webs (Figure 1). However, latitude describes a small proportion of variation in FCL in both cases (R^2 = 0.07 and

0.02, respectively). FCL for food webs in estuaries, marine systems, streams and in terrestrial systems showed no relationship with latitude (Figure 1). Our empirical results corroborate those of Vander Zanden and Fetzer (2007), who used stable isotopes to show that streams and lakes had a trend (non-significant) of increasing FCL with latitude, while marine ecosystems showed no relationship between latitude and FCL.

All but one of the empirical ecosystems explored here and in Vander Zanden and Fetzer (2007) are aquatic and latitude is a coarse indicator of productivity in freshwater ecosystems (Kalff, 2002). Further, recent theoretical and empirical work has shown that the influence of productivity on FCL in aquatic systems is contingent on ecosystem size (Post, 2002; Tunney et al., 2012; Ward & McCann, 2017), disturbance (Sabo, Finlay, Kennedy, & Post, 2010), and assembly history (Post, 2002). As a result, there may be large differences in FCL in aquatic ecosystems within a given latitude due to variation in ecosystem size, nutrient inputs, and disturbance (e.g., Tunney et al., 2012). One possibility is that regional species pools may show latitudinal gradients in FCL but, as species filter into local food webs, interactions between ecosystem size, productivity, and assembly

FIGURE 1 Mean food chain length (FCL; measured as mean food chain length, averaged over all species) for estuary, lake, marine, stream, terrestrial, and pitcher plant (*Sarracenia purpurea*). Pitcher plant food web data are from Baiser et al. (2012). All other data are from Cirtwill et al. (2015). Contrary to our prediction, mean FCL in lake food webs increases with latitude (slope = 0.02, R^2 = 0.07. *p*-value = 0.05) while FCL decreases with latitude in pitcher plant food webs (slope = −0.002, R^2 = 0.02. *p*-value = 0.01)
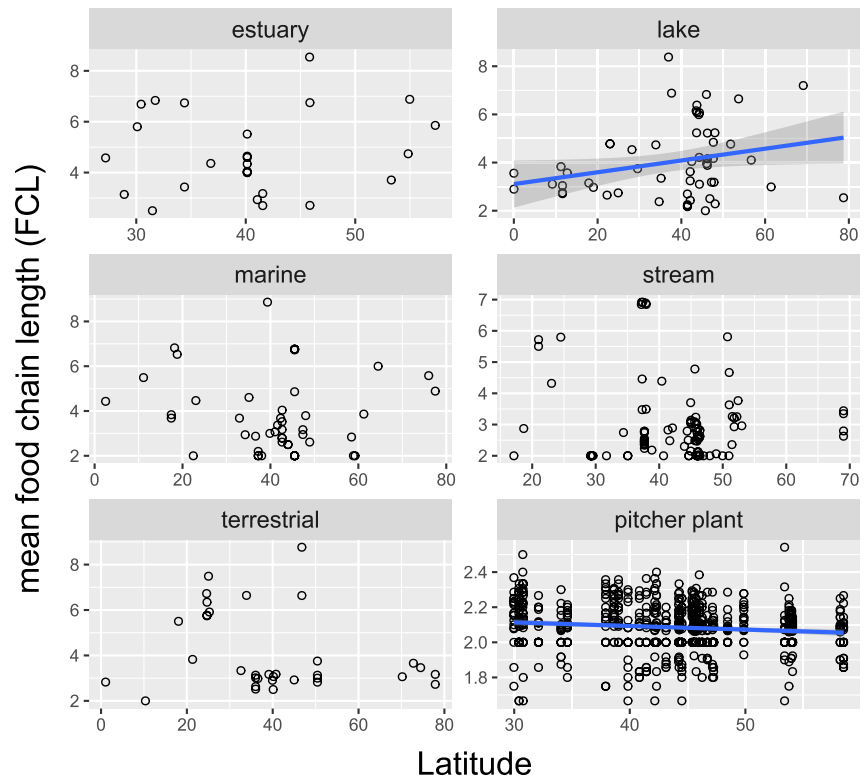
history govern FCL and ultimately obscure any local-scale latitudinal patterns.

2.1.2 | LDG, niche breadth, and connectance

One hypothesis for the LDG is that species in the tropics are more specialized relative to temperate species, allowing greater packing along niche axes (MacArthur, 1972). Narrow niches in the tropics may be due to a more stable climate (MacArthur, 1972), stronger biotic interactions (Dobzhansky, 1950; Schemske, 2002), and faster speciation coupled with niche conservatism (Brown, 2014). Several studies have found support for this hypothesis (e.g., Dyer et al., 2007; Krasnov, Shenbrot, Khokhlova, Mouillot, & Poulin, 2008; Salisbury, Seddon, Cooney, & Tobias, 2012; but see Vázquez & Stevens, 2004). If niches are narrower and species exhibit more specialism in the tropics, tropical species should on average have fewer prey and fewer predators than their temperate counterparts. At the network level, the consequence would be fewer total links (linkage density), prey (generality) and predators (vulnerability) per species. This leads to a prediction that *linkage density, generality, and vulnerability should increase with latitude*.

However, linkage density, generality, and vulnerability also increase with species richness (Martinez, 1994; Riede et al., 2010). Therefore, one needs to address effects of richness on food web metrics to make robust inferences about how network structure varies with latitude independently from species richness. One can control for species richness by analysing residuals of the relationship between species richness and food web properties (Bengtsson,

1994; Olesen & Jordano, 2002; Tylianakis, Tscharntke, & Lewis, 2007). Another approach is to explore the variation of interaction richness with species richness using a power-law, $L = bS^u$, where *b* is a scaling parameter, and *u* describes the dependence of the number of links (*L*) on the number of species (*S*) (Cirtwill et al., 2015). A positive relationship between the exponent (*u*) of this power-law relationship and latitude would indicate that species in the tropics gain fewer links per species (i.e., are more specialist) compared to their high-latitude counterparts (Cirtwill et al., 2015).

Contrary to our prediction of narrower niches in the tropics, Cirtwill et al. (2015) found that the scaling exponent for the relationship between measures of trophic niche breadth and species richness did not change with latitude in most ecosystem types. The major exception to this trend was an increasingly strong scaling relationships for generality towards the poles in lakes and streams. Additionally, we did not detect a relationship between latitude and the scaling of trophic niche breadth measures with species richness in pitcher plant food webs across North America (Supporting Information Figure S1).

2.2 | The influence of food webs on the LDG

Several hypotheses for the LDG invoke trophic interactions. Stronger predation pressure in the tropics has been asserted to increase diversity through keystone effects (Paine, 1966), create negative density-dependence (Connell, 1971; Janzen, 1970), accelerate diversification rates (Dobzhansky, 1950; Mittelbach et al., 2007) and promote greater regional diversity (Freestone, Osman, Ruiz, & Torchin,

2011) – each with consequences for food web properties. Predation pressure may also cause systematic latitudinal variation in the proportion of basal prey, intermediate taxa and top predators in food webs. Keystone predation may, for example, increase lower-trophic-level diversity, which in turn would raise the proportion of intermediate and basal species (i.e., species that are consumed) in food webs. Similarly, an increase in diversification rates due to predation pressure could provide the opportunity for both prey and predators to increase in richness in the tropics, thus we would expect proportions of each trophic level to increase concomitantly.

3 | BERGMANN'S RULE

Bergmann's rule (Bergmann, 1847) theorizes that species inhabiting regions with lower temperatures (i.e., high latitudes) have larger body sizes than species inhabiting regions with high temperatures (i.e., low latitudes). The lower surface-area-to-volume ratio in large animals was hypothesized to be an adaptation to colder climates. Other potential mechanisms for Bergmann's rule include latitudinal differences in primary productivity (Geist, 1987; Rosenzweig, 1968) and lower environmental predictability at higher latitudes (Meiri & Dayan, 2003). Debate is still on-going about the taxonomic level at which Bergmann's rule applies (interspecific versus intraspecific). The strongest evidence for Bergmann's rule comes from mammals (Ashton, Tracy, & Queiroz, 2000; Blackburn & Hawkins, 2004; Meiri & Dayan, 2003) and birds (Ashton, 2002; Blackburn & Gaston, 1996; Meiri & Dayan, 2003, but see Riemer, Guralnick, & White, 2018), but it has been observed in other taxonomic groups (e.g., fish – Rypel, 2014; amphibians – Olalla-Tárraga & Rodríguez, 2007; and insects – Zeuss, Brunzel, & Brandl, 2017).

3.1 | The influence of Bergmann's rule on food webs

Temperature-based variation in inter- and intraspecific body size described by Bergmann's rule has important implications for food webs. Body size plays a strong role in determining who eats whom within a food web (Beckerman, Petchey, & Warren, 2006; Gravel, Poisot, Albouy, Velez, & Mouillot, 2013; Williams & Martinez, 2000), interaction strengths (Berlow et al., 2009), food web structure (Petchey, Beckerman, Riede, & Warren, 2008), and the consequences of species losses (Brose et al., 2016).

The probability of a trophic interaction occurring between two species is dependent on the probability they encounter each other and that their traits enable a predator–prey relationship (Pawar, Dell, & Savage, 2012; Poisot, Stouffer, & Gravel, 2015). Encounter probability may be neutral in that high abundances of two species increases encounter probability and low abundances of one or both species leads to the opposite (Canard et al., 2012). Interactions also involve trait matching between the predators and the prey (e.g., predator–prey biomass ratio; Brose, Jonsson, et al., 2006; Brose, Williams, & Martinez, 2006; Yeakel et al., 2014) where traits determine the species' niches (Coux, Rader, Bartomeus, & Tylianakis, 2016). Based on

encounter probability and trait matching, Bergmann's rule may alter network structure by (a) temperature effects on body size altering the potential for interaction if body size or a trait highly correlated to it (e.g., gape size) primarily determines interaction potential (Brose, Jonsson, et al., 2006; Rohr, Scherer, Kehrli, Mazza, & Bersier, 2010) and (b) altering encounter probability via the negative relationship of body size and population size and the positive relationship of body size with range size (Brown, Gillooly, Allen, Savage, & West, 2004; Peters, 1983) and maximum migration distance (Hein & Gillooly, 2011).

The relevance of Bergmann's rule to food webs of course depends on which species follow the rule, what their trophic roles are, and the extent of size constraints on the occurrence of interactions. There are different implications if both predator and prey body sizes change with temperature as opposed to just one or the other (Figure 2). While some species may vary their size by 100% within their range (e.g., Huston & Wolverton, 2011), others will not vary at all. The variation among which and how many species within a food web will follow Bergmann's rule may obscure general predictions for how food web structure responds to the rule.

3.2 | The influence of food webs on Bergmann's rule

Trophic interactions may be an alternative to temperature-based energetic mechanisms responsible for Bergmann's rule. For example, food availability regulated by net primary production (NPP; Huston & Wolverton, 2011) and resource availability in general (McNab, 2010) have been put forth as mechanisms driving Bergmann's rule. Also, more intense predation at lower latitudes may cause prey body sizes to be smaller in ectotherms (Angilletta, Niewiarowski, Dunham, Leaché, & Porter, 2004; Manyak-Davis, Bell, & Sotka, 2013). Conversely, the expression of Bergmann's rule may be subverted if predation acts as a selective pressure that is inverse to energetic-based selective pressures – providing a plausible explanation for instances when Bergmann's rule is not observed (e.g., Riemer et al., 2018). Overall, when predation acts as a stronger filter on body size than temperature, we expect to find variation beyond that characterized by Bergmann's rule. The inclusion of trophic data (e.g., trophic level or guild) as a covariate with temperature should help elucidate such deviations.

4 | ISLAND RULE

Islands provide us with some of the most dramatic examples of ecological and evolutionary phenomena including adaptive radiations (Gavrilets & Losos, 2009), community assembly (Thornton, 1997), species invasions (Sax & Gaines, 2003) and catastrophic extinctions (Olson & James, 1982). The island rule emerged from the eco-geographical study of insular biotas (Foster, 1964; Van Valen, 1973). Specifically, the island rule codifies the observation that small vertebrates increase in body size over generations, while large vertebrates decrease, relative to mainland conspecifics or ancestors. The island rule was originally postulated for mammals (Foster, 1964; Heaney, 1978; Lomolino, 1985; Van Valen, 1973), but support for the island
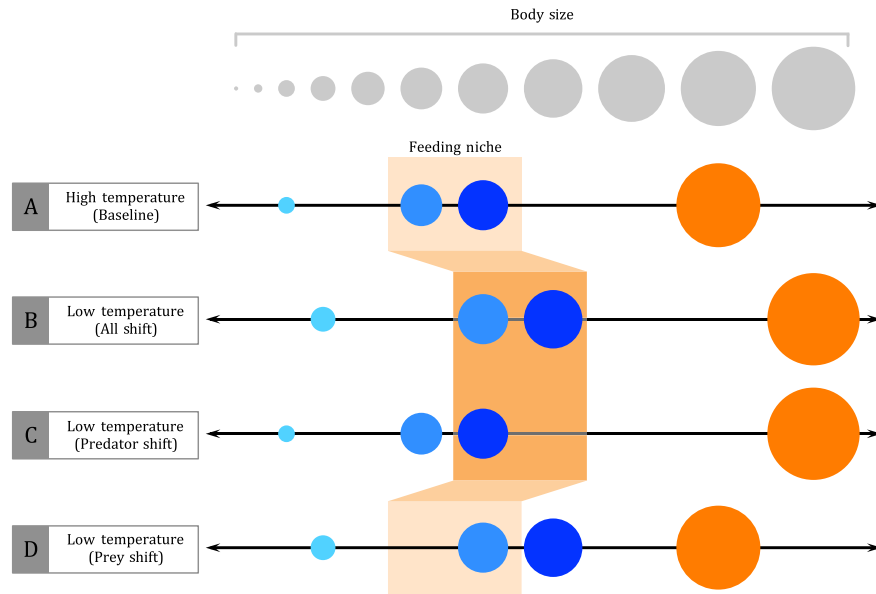
FIGURE 2 Schematic diagram of Bergmann's rule. The orange circle depicts the predator and the niche of the predator (i.e., size of prey it can eat, sensu the niche model; Williams & Martinez, 2000) is the tan box. Blue circles represent potential prey items. (A) The high temperature (low latitude) case where the predator (i.e., the orange circle) has two prey species that fall within its niche. Each of the following scenarios (B–D) are compared to the high temperature baseline (A). (B) A low temperature (high latitude) scenario where all species' body sizes increase according to Bergmann's rule. In this case, the prey species remain the same for the predator. (C) A scenario where only the predator's body size increases. As a result, one prey species is no longer in the predator's feeding niche. (D) The case where only the prey species increase in body size, which results in the loss of a prey species for the predator

rule has also been found for birds (Cassey & Blackburn, 2004; Clegg & Owens, 2002; Mathys & Lockwood, 2009) and snakes (Boback & Guyer, 2003), but support was not found for turtles (Itescu, Karraker, Raia, Pritchard, & Meiri, 2014).

4.1 | The influence of the island rule on food webs

Changes in body size associated with the island rule have similar implications for food web structure as Bergmann's rule (see Bergmann's rule section above). Under the island rule, however, variance in the distribution of body sizes is reduced as species converge toward the same body size for a given island. This contrasts with changes to the mean body mass under Bergmann's rule. A given predator might lose prey species when it gets smaller and its prey gets larger (Figure 3a). On the other hand, changes in body size due to the island rule may bring new species into the feeding niche of a given predator (Figure 3b). Which scenario occurs will depend on the distribution of body sizes on the mainland, the extent of body-size changes on islands, and the widths of predators' feeding niches.

The importance of body size to prey selection, food web structure, and dynamics suggests that the island rule likely has dramatic effects on island food webs. Island biogeography theory holds that island food webs have fewer species than mainland food webs due to the decrease in both the area and the distance that species must travel to colonize islands (MacArthur & Wilson, 1967). While the original theory does not include trophic interactions, including such interactions has improved the fit of island biogeography models

to empirical data and diversified predictions (Cirtwill & Stouffer, 2015; Gravel, Massol, Canard, Mouillot, & Mouquet, 2011; Jacquet, Mouillot, Kulbicki, & Gravel, 2017). Further incorporating changes in body size observed under the island rule may continue such improvements by more precisely predicting extinctions or the establishment of species in island ecosystems.

Predictions for the island rule are complicated (Figure 3) by the variation in size distribution of organisms initially colonizing an island. Empirical data on comparable mainland and island food webs are needed to further explore the influence of the island rule on food web structure. One possible system is the Bahamian island food webs of Schoener et al. (e.g., 2016), which could be paired with mainland food webs in Florida, USA.

4.2 | The influence of food webs on the island rule

The generality of the island rule may be limited (Lokatis & Jeschke, 2018). For example, Lomolino, Sax, Palombo, and Geer (2012) concluded that the change in body size following an ecological release from mammalian predators and competitors is context dependent. Food web structure may hold information on which types of webs are likely to experience changes in accordance with the island rule and which are not. Food webs with few trophically similar species (i.e., low maximum trophic similarity) can facilitate changes in body size on islands due to competitive release (Lomolino et al., 2012). Similarly, food webs with few consumers (i.e., low vulnerability) may promote change in body size due to predation release. Another important
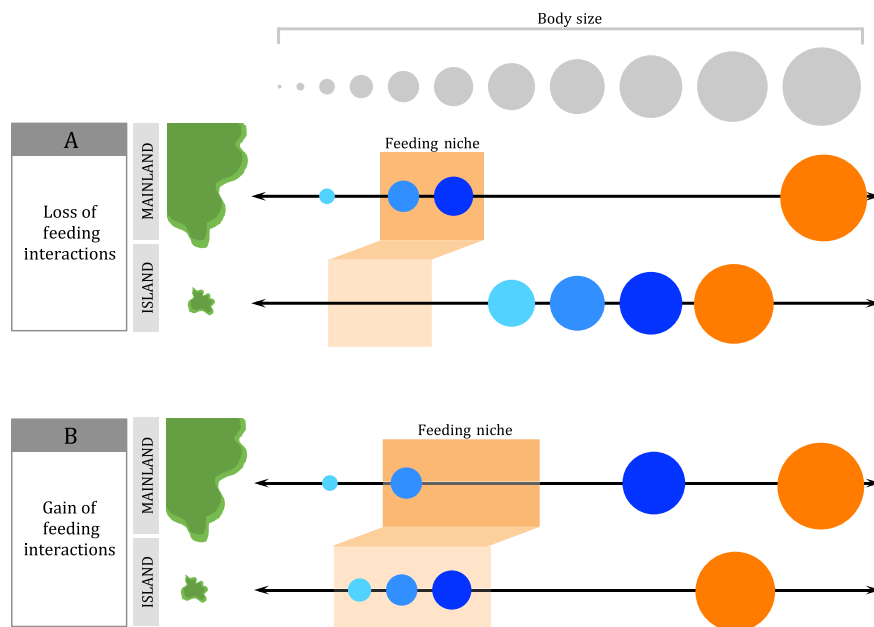
FIGURE 3 Schematic diagram of how the island rule can affect food webs. The predator is the orange circle and its body size foraging niche is indicated by the tan box. Blue circles represent potential prey items. (A) In this scenario, the predator loses all its feeding interactions as the increase in prey size coinciding with the decrease in predator size moves all prey species out of the predator's feeding niche. (B) A predator can also gain prey species as a result of body size changes due to the island rule. In this case, both the increase and decrease in body size of potential prey items and the decrease in size of the predator bring new species into the predator's foraging niche

factor identified in body size changes on islands are marine subsidies, which increase body size (Lomolino et al., 2012). Further incorporating marine subsidies through food web models that include biomass dynamics (e.g., Delmas, Brose, Gravel, Stouffer, & Poisot, 2017) may help to understand and predict the strength of the island rule.

5 | RAPOPORT'S RULE

Rapoport's rule describes the increase in range size with latitude (Stevens, 1989) and was later extended to include a positive relationship between altitude and range size (Stevens, 1992). Rapoport's rule has received mixed support for birds (Blackburn & Gaston, 1996; Gaston & Blackburn, 1996), fish (Rohde, Heap, & Heap, 1993), mammals (Pagel, May, & Collie, 1991; Smith, May, & Harvey, 1994) and invertebrates (France, 1992; Roy, Jablonski, & Valentine, 1994), which has led some to suggest that it should be designated as Rapoport's "effect" (Blackburn & Gaston, 1996). While the generality of this rule has been challenged, recent evidence suggest that Rapoport's rule at least holds at higher latitudes in the Northern Hemisphere (Gaston, Blackburn, & Spicer, 1998; Ruggiero & Werenkraut, 2007; Whitton, Purvis, Orme, & Olalla-Tárraga, 2012).

Stevens' (1989) initial hypothesis for Rapoport's rule suggests that more variable climate at high latitudes results in broader physiological tolerances allowing species to inhabit larger ranges. Another hypothesis is that species with narrow tolerance are more likely to go extinct at high latitude due to glaciation and climate change, thus leaving behind species with large ranges (Brown, 1995; Kolasa, Hewitt, & Drake, 1998). Lower levels of competition due to lower species richness in temperate regions has also been proposed as an explanation for Rapoport's rule (Stevens, 1996), thus linking Rapoport's rule with the LDG.

5.1 | The influence of Rapoport's rule on food webs

Rapoport's rule has implications for the turnover of food web structure over the latitudinal gradient (Baiser et al., 2012; Poisot, Canard, Mouillot, Mouquet, & Gravel, 2012). Turnover in food web structure – quantified in terms of β-diversity – arises from spatial variation in species composition and variation in pairwise interactions (Poisot et al., 2012). Species common between two webs can differ in their interactions (i.e., rewiring) or, alternatively, two webs can share few to no species and changes in network structure can be solely the result of species turnover.

At low latitudes, we expect *high species turnover and little to no interaction turnover* as species replacement predominantly drives network β-diversity due to the small ranges of species in the tropics as predicted by Rapoport's rule and others (Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Janzen, 1967). On the other hand, *high latitude food webs should show low species turnover and high interaction turnover* due to large ranges of species. We predict that *high latitude webs will have greater interaction turnover as compared to those at low latitudes* due to the fact that species with large ranges are more likely to experience habitat heterogeneity across their range (Rosenzweig, 1995). Habitat heterogeneity implies the potential for changes in abundance or influx of prey (e.g., Fahimipour & Anderson, 2015; Steenhof & Kochert, 1988), new prey species or competitors (Araújo et al., 2008; Werner & Hal, 1976), and varying environmental conditions (Griffen & Byers, 2006). All of these factors can lead to prey switching, making pairwise interaction turnover more likely across large, more heterogeneous ranges observed at high latitudes.

Our empirical pitcher plant data only allow network dissimilarity to arise from the spatial variation in species composition and not the variation in pairwise interactions among shared species due to the metaweb approach used to construct the web (i.e., if two species are known to interact, they are assumed to interact whenever they co-occur: see Baiser

et al., 2012). As a result, we only test the hypothesis that *dissimilarity in network structure due to species turnover is greater at lower latitudes*. We find a significant negative relationship between network turnover and latitude (Figure 4) revealing that the structure of food webs is more variable as a function of species turnover at lower latitudes. It is unclear if Rapoport's rule plays a part in this observation because ranges for the majority of the species in these food webs are unknown.

5.2 | The influence of food webs on Rapoport's rule

Rapoport's rule is conceptually tied to the LDG in that narrower niche breadths are expected to lead to both smaller range sizes and greater species niches in the tropics (Stevens, 1989). While climate niches leading to smaller distributions in the tropics is the focus of Rapoport's rule, trophic niches may also play a part. Simply put, if a consumer's prey have larger ranges, then that consumer may also have a larger range. Climatic niches may work in tandem with trophic niches. For example, if a species has a narrow climatic niche and subsequent range, it may specialize on prey items in that range. As a result, even if the species could disperse to a new area with a similar climatic niche, it may not be able to establish without its specialized prey (Holt, Lawton, Polis, & Martinez, 1999). Conversely, species with broader trophic niches are more likely to find suitable prey as their range expands. While this is clearly speculative, exploring how trophic interactions can extend (or constrain) climate-based fundamental niches using species distribution models (Wisz et al., 2013)
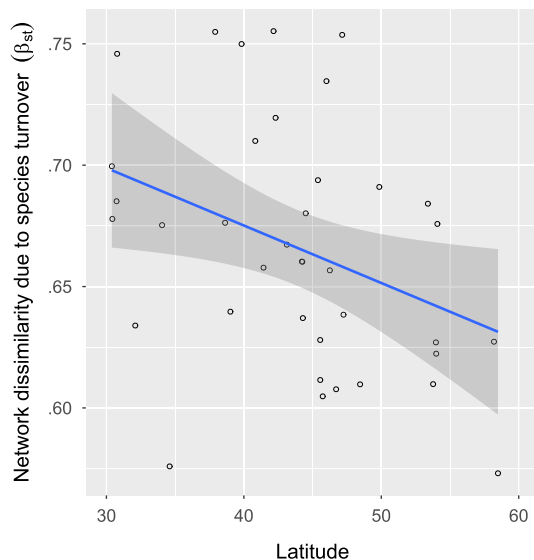

FIGURE 4 Network dissimilarity due to species turnover (β_{ST}; Poisot et al., 2012) across latitude for pitcher plant food webs. β_{ST} ranges from zero in which all species and interactions are shared between two food webs and one where no species (and no interactions) are shared. Each point on the graph represents the average β_{ST} from 20 pitchers at the given latitude. As we predicted, based on Rapoport's rule, β_{ST} shows an inverse relationship with latitude (slope = −0.002, R^2 = 0.12. *p*-value = 0.03). However, we cannot conclude that Rapoport's rule is driving this pattern because ranges for the majority of the species in these food webs are unknown

may lend insight into the role that food web interactions play in driving Rapoport's rule.

6 | DISCUSSION

In order to understand how entire food webs change over large-scale gradients, we need to know how the diversity, identity and traits of their constituent species change. Observations of macroecological patterns are a first step, as ecogeographical rules provide insight into how species' characteristics such as body size, range size, and community properties such as species richness change over large spatial scales. While we were able to derive testable predictions for some of the ecogeographical rules (LDG, Rapoport's rule), others (Bergmann's and island rules) have less clear implications for the variation in food web structure over macroecological scales (Table 2). Empirical tests of heuristic predictions are essential to advance this research agenda. Towards that end, we highlight the following ecosystems and approaches for studying the macroecology of food web networks.

6.1 | Potential systems for studying the macroecology of food webs

Due to their scale and extent, the sampling effort needed to gather enough data to validate and calibrate models of food webs across macroecological scales is substantial. Several types of ecosystems are predisposed to integrating macroecology and food web ecology due to their tractability, distributions and existing natural history knowledge. Natural microcosms or "container" habitats (such as pitcher plants, bromeliad tanks, tree holes) are examples of tractable systems (Baiser et al., 2012; Kitching, 2000; Srivastava et al., 2004). Lakes (Morlon, Kefi, & Martinez, 2014; Tunney et al., 2012) and islands (Rominger et al., 2016) including "sky islands" also provide bounded tractable systems albeit less tractable than container habitats. Intertidal communities are a relatively well-studied, broadly distributed system of taxa (Pielou, 1977) with extensive knowledge on trophic ecology where important factors such as body size and abundance can be readily measured and manipulated in the field over tractable time-scales (e.g., Novak & Wootton, 2008). One alternative approach to collecting field data is to use synthetic datasets (Poisot et al., 2016) that are assembled by merging data from varied sources (e.g., climatic data, species occurrences, taxonomy, traits, and interactions), through a reproducible pipeline, into a single cohesive dataset, with fixed taxonomic and spatial limits. Finally, well-known collections of food webs (Briand & Cohen, 1984; Dunne, Williams, & Martinez, 2004; Martinez, 1994; Riede et al., 2010; Vermaat et al., 2009) are also useful for studying the macroecology of food web networks.

6.2 | Potential approaches for studying the macroecology of food webs

Collecting food web data at large biogeographical scales necessitates more tractable, alternative approaches that answer specific

macroecological questions related to food webs. For example, to test the relationship between latitude and FCL, stable isotopes can be utilized (e.g., Vander Zanden & Fetzer, 2007) obviating the need to measure every trophic interaction across a set of food webs. In a similar vein, stable isotope analysis (Jackson, Inger, Parnell, & Bearhop, 2011) and DNA barcoding of gut contents or faeces (Kartzinel et al., 2015) can provide estimates of diet breadth testing the long-held hypothesis that niches are narrower at lower latitudes. For exploring the role of Bergmann's and the island rule on food webs, comparisons of predator–prey biomass ratios can provide a feasible approach. Further, such comparisons of predator–prey biomass ratios along temperature/latitudinal gradients or between islands and mainlands can lead to insights on the stability and structure of food webs (Brose, 2010; Brose, Jonsson, et al., 2006; Brose, Williams, & Martinez, 2006). This approach can be facilitated by global databases of predator–prey interactions and body sizes (e.g., Barnes et al., 2008, Brose et al., 2005; Poelen, Simons, & Mungall, 2014).

While detailing every trophic interaction in a food web is clearly challenging, sampling food webs across broad geographical scales at relevant time-scales is even more prohibitive. One possible approach is to test different mechanisms hypothesized to drive macroecological relationships independent of geography and then apply results to geographical extents. For example, if productivity is hypothesized to drive FCL, exploring food webs within the same region that vary in productivity can specifically test this hypothesis (e.g., Vander Zanden, Shuter, Lester, & Rasmussen, 1999; Ziegler, Solomon, Finney, & Gregory-Eaves, 2015) independent of geographical and historical contingencies (Kolasa et al., 1998). The next step in this approach is to extend results across biogeographical regions to see if productivity is the key driver to FCL or if other biogeographical factors exert control over macroecological scales.

6.3 | What can food webs tell us about ecogeographical rules?

Two recurring themes in the literature on ecogeographical rules are that (a) mechanisms remain elusive and (b) there are deviations (sometimes large) from predictions. Studies of ecogeographical rules often focus on specific taxonomic groups or guilds and do not consider the food webs in which they are embedded. Considering trophic interactions as a selection pressure that can drive or disrupt ecogeographical rules has the potential to address both mechanisms of and deviations from these long-studied patterns.

7 | CONCLUSION

Several areas of research are critical to advancing our understanding of the macroecology of food webs. First and foremost is the collection of food web data across biogeographical gradients. We have suggested several model systems and approaches for testing the generality of patterns and hypotheses.

Second, the macroecology of food webs goes beyond traditional approaches because it not only describes the state of the system, but also opens the door to exploring food web dynamics at macroecological scales. An integrated exploration of ecogeographical rules and dynamics through mathematical modelling, empirical data and statistical models (e.g., Boit et al., 2012), and novel network analyses (Allesina et al., 2015) will elucidate how macroecological processes influence food web dynamics. Third, considering the macroecology of food webs within the context of global change will provide insight into what future food webs will look like. As species go extinct or adapt to anthropogenic conditions in their environment, ecogeographical rules give us an idea of how they will respond to these changes (Millien et al., 2006) and could even be used to test against known changes to food webs in the recent or distant past (Dunne et al., 2014, 2016; Yeakel et al., 2014). Increasing temperature due to global change, for instance, should result in smaller body sizes as suggested by Bergmann's rule (Gardner et al., 2011). Furthermore, species within islands of fragmented habitats created by land use change have been observed to follow the island rule (Schmidt & Jensen, 2003; Fietz & Weis-Dootz, 2012; but see Lomolino & Perault, 2007). These anthropogenically induced changes in species can then be integrated with food web models to explore and predict changes in species interactions and entire food webs subjected to anthropogenic disturbance.

The relevance of ecogeographical rules to food webs does not end with the examples and rules we present here. As large-scale ecological and evolutionary phenomena found in macroecology have implications for species interactions – and hence network structure and dynamics – there is much insight to be gained in further studying these relationships in the context of ecological networks. Additionally, macroecological relationships do not exist in isolation, but interact in complex ways (Gaston, Chown, & Evans, 2008; Lomolino et al., 2006) that will likely influence food webs. Further testing the predictions and implementing the approaches we detailed here (Table 2) provide a pathway for integrating macroecology and food webs to better understand the assembly, maintenance and change of ecosystems in the near and distant future.

DATA ACCESSIBILITY

Food webs analysed in this paper are available from the University of Canberra's GlobalWeb database (www.globalwebdb.com).

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REFERENCES

Allesina, S., Grilli, J., Barabás, G., Tang, S., Aljadeff, J., & Maritan, A. (2015). Predicting the stability of large structured food webs. *Nature Communications*, 6(1), 7842. https://doi.org/10.1038/ncomms8842

Angilletta, M. J., Jr., Niewiarowski, P. H., Dunham, A. E., Leaché, A. D., & Porter, W. P. (2004). Bergmann's clines in ectotherms: Illustrating a life-history perspective with sceloporine lizards. *The American Naturalist*, 164(6), E168–E183. https://doi.org/10.1086/425222

Araújo, M. S., Guimaraes, P. R., Jr., Svanbäck, R., Pinheiro, A., Guimarães, P., Reis, S. F. D., & Bolnick, D. I. (2008). Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology*, 89, 1981–1993. https://doi.org/10.1890/07-0630.1

Ashton, K. G. (2002). Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, 11, 505–523.

Ashton, K. G., Tracy, M. C., & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *The American Naturalist*, 156, 390–415.

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. https://doi.org/10.1111/j.1466-8238.2011.00705.x

Barnes, C., Bethea, D. M., Brodeur, R. D., Spitz, J., Ridoux, V., Pusineri, C., … Jennings, S. (2008). Predator and prey body sizes in marine food webs: Ecological Archives E089051. *Ecology*, 89, 881–881. https://doi.org/10.1890/07-1551.1

Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences USA*, 103, 13745–13749. https://doi.org/10.1073/pnas.0603039103

Bengtsson, J. (1994). Confounding variables and independent observations in comparative analyses of food webs. *Ecology*, 1282–1288. https://doi.org/10.2307/1937453

Bergmann, K. G. L. C. (1847). Über die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, 3, 595–708.

Berlow, E. L., Dunne, J. A., Martinez, N. D., Stark, P. B., Williams, R. J., & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences*, 106(1), 187–191.

Blackburn, T. M., & Gaston, K. J. (1996). Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 897–912.

Blackburn, T. M., & Gaston, K. J. (2006). There's more to macroecology than meets the eye. *Global Ecology and Biogeography*, 15, 537–540. https://doi.org/10.1111/j.1466-8238.2006.00276.x

Blackburn, T. M., & Hawkins, B. A. (2004). Bergmann's rule and the mammal fauna of northern North America. *Ecography*, 27, 715–724.

Boback, S. M., & Guyer, C. (2003). Empirical evidence for an optimal body size in snakes. *Evolution*, 57, 345–451. https://doi.org/10.1111/j.0014-3820.2003.tb00268.x

Boit, A., Martinez, N. D., Williams, R. J., & Gaedke, U. (2012). Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. *Ecology Letters*, 15, 594–602. https://doi.org/10.1111/j.1461-0248.2012.01777.x

Briand, F., & Cohen, J. E. (1984). Community food webs have scale-invariant structure. *Nature*, 307(5948), 264.

Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, 24, 28–34. https://doi.org/10.1111/j.1365-2435.2009.01618.x

Brose, U., Blanchard, J. L., Eklöf, A., Galiana, N., Hartvig, M., Hirt, R. M., … Jacob, U. (2016). Predicting the consequences of species loss using size-structured biodiversity approaches. *Biological Reviews of the Cambridge Philosophical Society*, 92(2), 684–697.

Brose, U., Cushing, L., Berlow, E. L., Jonsson, T., Banasek-Richter, C., Bersier, L.-F., … Martinez, N. D. (2005). Body sizes of consumers and their resources. *Ecology*, 86(9), 2545–2545. https://doi.org/10.1890/05-0379

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L. F., … Cohen J. E. (2006). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417.

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228–1236.

Brown, J. H. (1995). *Macroecology*. Chicago: University of Chicago Press.

Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, 41, 8–22. https://doi.org/10.1111/jbi.12228

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. https://doi.org/10.1890/03-9000

Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of structural patterns in neutral trophic networks. *PLoS ONE*, 7, e38295. https://doi.org/10.1371/journal.pone.0038295

Cassey, P., & Blackburn, T. (2004). Body size trends in a Holocene island bird assemblage. *Ecography*, 27, 59–67. https://doi.org/10.1111/j.0906-7590.2004.03585.x

Cirtwill, A. R., & Stouffer, D. B. (2015). Knowledge of predator–prey interactions improves predictions of immigration and extinction in island biogeography. *Global Ecology and Biogeography*, 25(7), 900–911.

Cirtwill, A. R., Stouffer, D. B., & Romanuk, T. N. (2015). Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151589.

Clegg, S. M., & Owens, P. F. (2002). The 'island rule' in birds: Medium body size and its ecological explanation. *Proceedings of the Royal Society B: Biological Sciences*, 269, 1359–1365. https://doi.org/10.1098/rspb.2002.2024

Cohen, J. E., Briand, F., & Newman, C. M. (1990). *Community food webs: Data and theory*. New York: Springer-Verlag.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer, & G. R. Gradwell (Eds.), *Dynamics of populations* (pp. 298–312). Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.

Coux, C., Rader, R., Bartomeus, I., & Tylianakis, J. M. (2016). Linking species functional roles to their network roles. *Ecology Letters*, 19(7), 762–770. https://doi.org/10.1111/ele.12612

Currie, D. J. (1991). Energy and large-scale patterns of animal and plant-species richness. *The American Naturalist*, 137, 27–49.

Darwin, C. (1859). *On the origin of species by means of natural selection*. London, UK: J. Murray.

Delmas, E., Brose, U., Gravel, D., Stouffer, D. B., & Poisot, T. (2017). Simulations of biomass dynamics in community food webs. *Methods in Ecology and Evolution*, 8(7), 881–886. https://doi.org/10.1111/2041-210X.12713

Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist*, 38, 208–221.

Dunne, J. A. (2005). The network structure of food webs. In M. Pascual & J. A. Dunne (Eds.), *Ecological networks: Linking structure to dynamics in food webs* (pp. 27–86). New York: Oxford University Press.

Dunne, J. A., Labandeira, C. C., & Williams, R. J. (2014). Highly resolved early Eocene food webs show development of modern trophic structure after the end-Cretaceous extinction. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20133280. https://doi.org/10.1098/rspb.2013.3280

Dunne, J. A., Maschner, H., Betts, M. W., Huntly, N., Russell, R., Williams, R. J., & Wood, S. A. (2016). The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Scientific Reports*, *6*, 21179. https://doi.org/10.1038/srep21179

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology letters*, *5*(4), 558–567.

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.

Dyer, L. A., Singer, M. S., Lill, J. T., Stireman, J. O., Gentry, G. L., Marquis, R. J., … Diniz, I. R. (2007). Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, *448*(7154), 696–699.

Fahimipour, A. K., & Anderson, K. E. (2015). Colonisation rate and adaptive foraging control the emergence of trophic cascades. *Ecology Letters*, *18*, 826–833. https://doi.org/10.1111/ele.12464

Fietz, J., & Weis-Dootz, T. (2012). Stranded on an island: Consequences of forest fragmentation for body size variations in an arboreal mammal, the edible dormouse (Glis glis). *Population Ecology*, *54*(2), 313–320. https://doi.org/10.1007/s10144-012-0310-0

Foster, J. B. (1964). The evolution of mammals on islands. *Nature*, *202*, 234–235. https://doi.org/10.1038/202234a0

France, R. (1992). The North American latitudinal gradient in species richness and geographical range of freshwater crayfish and amphipods. *The American Naturalist*, *139*, 342–354.

Freestone, A. L., Osman, R. W., Ruiz, G. M., & Torchin, M. E. (2011). Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology*, *92*(4), 983–993. https://doi.org/10.1890/09-2379.1

Fretwell, S. D., & Barach, A. L. (1977). The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine*, *20*(2), 169–185. https://doi.org/10.1353/pbm.1977.0087

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology and Evolution*, *26*, 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Gaston, K. J., & Blackburn, T. M. (1996). Global scale macroecology: Interactions between population size, geographic range size and body size in the Anseriformes. *Journal of Animal Ecology*, *65*, 701–714. https://doi.org/10.2307/5669

Gaston, K. J., Blackburn, T. M., & Spicer, J. I. (1998). Rapoport's rule: Time for an epitaph? *Trends in Ecology and Evolution*, *13*, 70–74. https://doi.org/10.1016/S0169-5347(97)01236-6

Gaston, K. J., Chown, S. L., & Evans, K. L. (2008). Ecogeographical rules: Elements of a synthesis. *Journal of Biogeography*, *35*, 483–500. https://doi.org/10.1111/j.1365-2699.2007.01772.x

Gavrilets, S., & Losos, J. B. (2009). Adaptive radiation: Contrasting theory with data. *Science*, *323*, 732–737. https://doi.org/10.1126/science.1157966

Geist, V. (1987). Bergmann's rule is invalid. *Canadian Journal of Zoology*, *65*, 1035–1038.

Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J., & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, *46*(1), 5–17. https://doi.org/10.1093/icb/icj003

Gilarranz, L. J., Mora, C., & Bascompte, J. (2016). Anthropogenic effects are associated with a lower persistence of marine food webs. *Nature Communications*, *7*(1), 10737. https://doi.org/10.1038/ncomms10737

Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J. P., Martinez, N. D., Nyman, T., … Roslin, T. (2019). Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, *42*(3), 401–415.

Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology Letters*, *14*, 1010–1016. https://doi.org/10.1111/j.1461-0248.2011.01667.x

Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator–prey body size relationships. *Methods in Ecology and Evolution*, *4*, 1083–1090. https://doi.org/10.1111/2041-210X.12103

Griffen, B. D., & Byers, J. E. (2006). Partitioning mechanisms of predator interference in different habitats. *Oecologia*, *146*, 608–614. https://doi.org/10.1007/s00442-005-0211-4

Hall, S. J., & Raffaelli, D. (1991). Food-web patterns: Lessons from a species-rich web. *Journal of Animal Ecology*, 823–841. https://doi.org/10.2307/5416

Heaney, L. R. (1978). Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, *32*(1), 29–44.

Hein, A. M., & Gillooly, J. F. (2011). Predators, prey, and transient states in the assembly of spatially structured communities. *Ecology*, *92*, 549–555. https://doi.org/10.1890/10-1922.1

Holt, R. D., Lawton, J. H., Polis, G. A., & Martinez, N. D. (1999). Trophic rank and the species–area relationship. *Ecology*, *80*(5), 1495–1504.

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, *110*(4), 449–460. https://doi.org/10.1007/s004420050180

Huston, M. A., & Wolverton, S. (2011). Regulation of animal size by eNPP, Bergmann's rule and related phenomena. *Ecological Monographs*, *81*, 349–405.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, *93*, 145–159.

Itescu, Y., Karraker, N. E., Raia, P., Pritchard, P. C., & Meiri, S. (2014). Is the island rule general? Turtles disagree. *Global Ecology and Biogeography*, *23*, 689–700. https://doi.org/10.1111/geb.12149

Jablonski, D., Roy, K., & Valentine, J. W. (2006). Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science*, *314*, 102–106. https://doi.org/10.1126/science.1130880

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jacquet, C., Mouillot, D., Kulbicki, M., & Gravel, D. (2017). Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. *Ecology Letters*, *20*(2), 135–146. https://doi.org/10.1111/ele.12716

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, *101*, 233–249. https://doi.org/10.1086/282487

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*(940), 501–528. https://doi.org/10.1086/282687

Kalff, J. (2002). *Limnology: Inland water ecosystems*. Prentice Hall, NJ.

Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., … Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences USA*, *112*(26), 8019–8024. https://doi.org/10.1073/pnas.1503283112

Kaunzinger, C. M., & Morin, P. J. (1998). Productivity controls food-chain properties in microbial communities. *Nature*, *395*, 495–497. https://doi.org/10.1038/26741

Kissling, W. D., & Schleuning, M. (2015). Multispecies interactions across trophic levels at macroscales: Retrospective and future directions. *Ecography*, *38*, 346–357. https://doi.org/10.1111/ecog.00819

Kitching, R. L. (2000). *Food webs and container habitats: The natural history and ecology of phytotelmata*. New York: Cambridge University Press.

Kolasa, J., Hewitt, C. L., & Drake, J. A. (1998). Rapoport's rule: An explanation or a byproduct of the latitudinal gradient in species richness? *Biodiversity and Conservation*, 7(11), 1447–1455.

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(4), 592–601. https://doi.org/10.1111/j.1365-2699.2007.01800.x

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–417.

Lokatis, S., & Jeschke, J. M. (2018). The island rule: An assessment of biases and research trends. *Journal of Biogeography*, 45(2), 289–303. https://doi.org/10.1111/jbi.13160

Lomolino, M. V. (1985). Body size of mammals on islands: The island rule reexamined. *The American Naturalist*, 125, 310–316. https://doi.org/10.1086/284343

Lomolino, M. V., & Perault, D. R. (2007). Body size variation of mammals in a fragmented, temperate rainforest. *Conservation Biology*, 21, 1059–1069. https://doi.org/10.1111/j.1523-1739.2007.00727.x

Lomolino, M. V., Sax, D. F., Palombo, M. R., & Van Der Geer, A. A. (2012). Of mice and mammoths: Evaluations of causal explanations for body size evolution in insular mammals. *Journal of Biogeography*, 39, 842–854. https://doi.org/10.1111/j.1365-2699.2011.02656.x

Lomolino, M. V., Sax, D. F., Riddle, B. R., & Brown, J. H. (2006). The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography*, 33, 1503–1510. https://doi.org/10.1111/j.1365-2699.2006.01593.x

MacArthur, R. H. (1972). *Geographical ecology: Patterns in the distribution of species*. New York, NY: Harper & Row.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography* (Vol. 1). Princeton, NJ: Princeton University Press.

Manyak-Davis, A., Bell, T. M., & Sotka, E. E. (2013). The relative importance of predation risk and water temperature in maintaining Bergmann's rule in a marine ectotherm. *The American Naturalist*, 182(3), 347–358. https://doi.org/10.1086/671170

Martinez, N. D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs*, 367–392. https://doi.org/10.2307/2937047

Martinez, N. D. (1994). Scale-dependent constraints on food-web structure. *The American Naturalist*, 935–953. https://doi.org/10.1086/285719

Mathys, B. A., & Lockwood, J. L. (2009). Rapid evolution of great kiskadees on Bermuda: An assessment of the ability of the island rule to predict the direction of contemporary evolution in exotic vertebrates. *Journal of Biogeography*, 36, 2204–2211. https://doi.org/10.1111/j.1365-2699.2009.02169.x

McNab, B. K. (2010). Geographic and temporal correlations of mammalian size reconsidered: A resource rule. *Oecologia*, 164(1), 13–23. https://doi.org/10.1007/s00442-010-1621-5

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, 30, 331–351.

Millien, V., Kathleen Lyons, S., Olson, L., Smith, F. A., Wilson, A. B., & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: Revisiting the rules. *Ecology Letters*, 9, 853–869. https://doi.org/10.1111/j.1461-0248.2006.00928.x

Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., ... Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, 10, 315–331.

Morlon, H., Kefi, S., & Martinez, N. D. (2014). Effects of trophic similarity on community composition. *Ecology Letters*, 17(12), 1495–1506. https://doi.org/10.1111/ele.12356

Novak, M., & Wootton, J. T. (2008). Estimating nonlinear interaction strengths: An observation-based method for species-rich food webs. *Ecology*, 89(8), 2083. https://doi.org/10.1890/08-0033.1

Olalla-Tárraga, M. Á., & Rodríguez, M. Á. (2007). Energy and interspecific body size patterns of amphibian faunas in Europe and North America: Anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography*, 16, 606–617.

Olesen, J. M., & Jordano, P. (2002). Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83, 2416–2424.

Olson, S. L., & James, H. F. (1982). Fossil birds from the Hawaiian Islands: Evidence for wholesale extinction by man before western contact. *Science*, 217, 633–635. https://doi.org/10.1126/science.217.4560.633

Otto, S. B., Rall, B. C., & Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, 450(7173), 1226.

Pagel, M. D., May, R. M., & Collie, A. R. (1991). Ecological aspects of the geographical distribution and diversity of mammalian species. *The American Naturalist*, 137, 791–815.

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100, 65–75.

Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, 486(7404), 485. https://doi.org/10.1038/nature11131

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 USA*, 105, 4191–4196. https://doi.org/10.1073/pnas.0710672105

Peters, R. H. (1983). *The ecological implications of body size*. UK: Cambridge University Press.

Pianka, E. R. (1966). Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist*, 33–46. https://doi.org/10.1086/282398

Piechnik, D. A., Lawler, S. P., & Martinez, N. D. (2008). Food-web assembly during a classic biogeographic study: Species' "trophic breadth" corresponds to colonization order. *Oikos*, 117, 665–674. https://doi.org/10.1111/j.0030-1299.2008.15915.x

Pielou, E. C. (1977). The latitudinal spans of seaweed species and their patterns of overlap. *Journal of Biogeography*, 4, 299–311.

Pimm, S. L. (1982). *Food webs*. Dordrecht, The Netherlands: Springer.

Pimm, S. L., Lawton, J. H., & Cohen, J. E. (1991). Food web patterns and their consequences. *Nature*, 350(6320), 669. https://doi.org/10.1038/350669a0

Poelen, J. H., Simons, J. D., Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to share and analyze species-interaction datasets. *Ecological Informatics*, 24, 148–159.

Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology Letters*, 15, 1353–1361. https://doi.org/10.1111/ele.12002

Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M. J., Baiser, B., ... Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological hypotheses. *Ecography*, 39(4), 402–408.

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251.

Polis, G. A. (1991). Complex trophic interactions in deserts: An empirical critique of food-web theory. *The American Naturalist*, 123–155. https://doi.org/10.1086/285208

Post, D. M. (2002). The long and short of food-chain length. *Trends in Ecology and Evolution*, 17, 269–277. https://doi.org/10.1016/S0169-5347(02)02455-2

Riede, J. O., Rall, B. C., Banasek-Richter, C., Navarrete, S. A., Wieters, E. A., Emmerson, M. C., ... Brose, U. (2010). Scaling of food-web properties with diversity and complexity across ecosystems. *Advances in Ecological Research*, 42, 139–170.

Riemer, K., Guralnick, R. P., & White, E. P. (2018). No general relationship between mass and temperature in endothermic species. *eLife*, 7. https://doi.org/10.7554/eLife.27166

Rohde, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Oikos*, 65, 514–527. https://doi.org/10.2307/3545569

Rohde, K., Heap, M., & Heap, D. (1993). Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *The American Naturalist*, 142(1), 1–16. https://doi.org/10.1086/285526

Rohr, R. P., Scherer, H., Kehrli, P., Mazza, C., & Bersier, L.-F. (2010). Modeling food webs: Exploring unexplained structure using latent traits. *The American Naturalist*, 176, 170–177. https://doi.org/10.1086/653667

Rominger, A. J., Goodman, K. R., Lim, J. Y., Armstrong, E. E., Becking, L. E., Bennett, G. M., ... Martinez, N. D. (2016). Community assembly on isolated islands: Macroecology meets evolution. *Global Ecology and Biogeography*, 25(7), 769–780.

Rosenzweig, M. L. (1968). Net primary productivity of terrestrial communities: Prediction from climatological data. *The American Naturalist*, 102, 67–74. https://doi.org/10.1086/282523

Rosenzweig, M. L. (1995). *Species diversity in space and time*. UK: Cambridge University Press.

Roy, K., Jablonski, D., & Valentine, J. W. (1994). Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for "Rapoport's rule". *Proceedings of the National Academy of Sciences USA*, 91, 8871–8874.

Ruggiero, A., & Werenkraut, V. (2007). One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Global Ecology and Biogeography*, 16, 401–414. https://doi.org/10.1111/j.1466-8238.2006.00303.x

Rypel, A. L. (2014). The cold-water connection: Bergmann's rule in North American freshwater fishes. *The American Naturalist*, 183, 147–156.

Sabo, J. L., Finlay, J. C., Kennedy, T., & Post, D. M. (2010). The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science*, 330(6006), 965–967. https://doi.org/10.1126/science.1196005

Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal gradient in dispersal constraints: Ecological specialisation drives diversification in tropical birds. *Ecology Letters*, 15(8), 847–855. https://doi.org/10.1111/j.1461-0248.2012.01806.x

Sax, D. F., & Gaines, S. D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution*, 18(11), 561–566.

Sahasrabudhe, S., & Motter, A. E. (2011). Rescuing ecosystems from extinction cascades through compensatory perturbations. *Nature Communications*, 2, 170.

Schemske, D. (2002). Tropical diversity: Patterns and processes. In R. Chazdon, & T. Whitmore (Eds.), *Ecological and evolutionary perspectives on the origins of tropical diversity: Key papers and commentaries* (pp. 163–173). IL: University of Chicago Press.

Schmidt, N. M., & Jensen, P. M. (2003). Changes in mammalian body length over 175 years - adaptations to a fragmented landscape? *Conservation Ecology*, 7, 6.

Schoener, T. W., Spiller, D. A., & Piovia-Scott, J. (2016). Variation in ecological interaction strength with island area: Theory and data from the Bahamian archipelago. *Global Ecology and Biogeography*, 25(7), 891–899.

Simberloff, D. S., & Wilson, E. O. (1969). Experimental zoogeography of islands: The colonization of empty islands. *Ecology*, 50(2), 278–296. https://doi.org/10.2307/1934856

Smith, F. D. M., May, R. M., & Harvey, P. H. (1994). Geographical ranges of Australian mammals. *Journal of Animal Ecology*, 63, 441–450.

Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., ... Trzcinski, M. K. (2004). Are natural microcosms useful model systems for ecology? *Trends in Ecology and Evolution*, 19, 379–384. https://doi.org/10.1016/j.tree.2004.04.010

Staniczenko, P. P., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology letters*, 13(7), 891–899.

Steenhof, K., & Kochert, M. N. (1988). Dietary responses of three raptor species to changing prey densities in a natural environment. *Journal of Animal Ecology*, 57, 37–48. https://doi.org/10.2307/4761

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, 133, 240–256. https://doi.org/10.1086/284913

Stevens, G. C. (1992). The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, 140, 893–911. https://doi.org/10.1086/285447

Stevens, G. C. (1996). Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography*, 23, 149–154. https://doi.org/10.1046/j.1365-2699.1996.00977.x

Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, 21(6), 920–937. https://doi.org/10.1111/ele.12941

Stouffer, D. B., Camacho, J., Guimera, R., Ng, C. A., & Nunes Amaral, L. A. (2005). Quantitative patterns in the structure of model and empirical food webs. *Ecology*, 86(5), 1301–1311.

Takimoto, G., & Post, D. M. (2013). Environmental determinants of food-chain length: A meta-analysis. *Ecological Research*, 28, 675–681. https://doi.org/10.1007/s11284-012-0943-7

Thornton, I. W. (1997). *Krakatau: The destruction and reassembly of an island ecosystem*. Cambridge, MA: Harvard University Press.

Tunney, T. D., McCann, K. S., Lester, N. P., & Shuter, B. J. (2012). Food web expansion and contraction in response to changing environmental conditions. *Nature Communications*, 3, 1105. https://doi.org/10.1038/ncomms2098

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48, 25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, 445, 202–205. https://doi.org/10.1038/nature05429

Van Valen, L. (1973). Pattern and the balance of nature. *Evolutionary Theory*, 1, 31–49.

Vander Zanden, J. M., & Fetzer, W. W. (2007). Global patterns of aquatic food chain length. *Oikos*, 116(8), 1378–1388. https://doi.org/10.1111/j.0030-1299.2007.16036.x

Vander Zanden, M. J., Shuter, B. J., Lester, N., & Rasmussen, J. B. (1999). Patterns of food chain length in lakes: A stable isotope study. *The American Naturalist*, 154(4), 406–416.

Vázquez, D. P., & Stevens, R. D. (2004). The latitudinal gradient in niche breadth: Concepts and evidence. *The American Naturalist*, 164, E1–E19. https://doi.org/10.1086/421445

Vermaat, J. E., Dunne, J. A., & Gilbert, A. J. (2009). Major dimensions in food-web structure properties. *Ecology*, 90(1), 278–282.

Wallace, A. R. (1878). *Tropical nature and other essays*. London, UK: Macmillan.

Ward, C. L., & McCann, K. S. (2017). A mechanistic theory for aquatic food chain length. *Nature Communications*, 8(1), 2028. https://doi.org/10.1038/s41467-017-02157-0

Werner, E. E., & Hal, D. J. (1976). Niche shifts in sunfishes: Experimental evidence and significance. *Science*, 191, 404–406. https://doi.org/10.1126/science.1246626

Whitton, F. J., Purvis, A., Orme, C. D. L., & Olalla-Tárraga, M. Á. (2012). Understanding global patterns in amphibian geographic range size: Does Rapoport rule? *Global Ecology and Biogeography*, 21, 179–190. https://doi.org/10.1111/j.1466-8238.2011.00660.x

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, 36, 519–539.

Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774), 180–183.

Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., … Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88(1), 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

Wood, S. A., Russell, R., Hanson, D., Williams, R. J., & Dunne, J. A. (2015). Effects of spatial scale of sampling on food web structure. *Ecology and Evolution*, 5, 3769–3782. https://doi.org/10.1002/ece3.1640

Yeakel, J. D., Pires, M. M., Rudolf, L., Dominy, N. J., Koch, P. L., Guimarães, P. R., … Gross, T. (2014). Collapse of an ecological network in Ancient Egypt. *Proceedings of the National Academy of Sciences USA*, 111(40), 14472–14477. https://doi.org/10.1073/pnas.1408471111

Zeuss, D., Brunzel, S., & Brandl, R. (2017). Environmental drivers of voltinism and body size in insect assemblages across Europe. *Global Ecology and Biogeography*, 26(2), 154–165. https://doi.org/10.1111/geb.12525

Ziegler, J. P., Solomon, C. T., Finney, B. P., & Gregory-Eaves, I. (2015). Macrophyte biomass predicts food chain length in shallow lakes. *Ecosphere*, 6(1), 1–16. https://doi.org/10.1890/ES14-00158.1

BIOSKETCH

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SUPPORTING INFORMATION

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