

Title: 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 was 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 biogeographic gradients is key to advance this research

61 agenda. Further, considering food web interactions as a selection pressure that drives or disrupts
62 ecogeographical rules has the potential to address both mechanisms of and deviations from these
63 macroecological relationships. For these reasons, further integration of macroecology and food webs will
64 help ecologists better understand the assembly, maintenance, and change of ecosystems across space and
65 time.

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85 **Introduction**

86 Most food web research has emphasized individual datasets compiled for a particular location as a means
87 of investigating the organization and dynamics of various taxa interacting within communities. This
88 long-standing approach has led to detailed understanding of the structure and dynamics of specific
89 systems (e.g., Hall & Raffaelli 1991; Martinez 1991; Polis 1991; Boit et al. 2012). In addition,
90 comparisons across well-studied food webs revealed generalities in their structure (e.g., Pimm 1982;
91 Cohen et al. 1990; Williams & Martinez 2000; Stouffer et al. 2005; Riede et al. 2010; Dunne et al. 2014)
92 and prompted investigations of different aspects of food web dynamics such as robustness (Dunne et al.

93 2002; Staniczenko et al. 2010), persistence (Otto et al. 2007, Sahasrabudhe & Motter 2011) and stability
94 (Allesina et al. 2015). As more well-resolved empirical food webs become available, expanding food web
95 ecology to include macroecologically-inspired spatial or temporal gradients is emerging as a key research
96 agenda (Gilarranz et al. 2016; Tylianakis & Morris 2017).

97 Collections of well-studied food webs and replicate food webs of the same system allow detailed
98 investigation of how factors such as space, time, climate, and other ecological drivers influence and
99 interact with food web structure, dynamics, and stability. For example, dozens of small mangrove islet
100 food webs, compiled from a classic island biogeography experiment on recolonization following
101 defaunation (Simberloff & Wilson 1969), were used to show that the proportion of specialists increased
102 through time while the proportion of generalists and connectance decreased (Piechnik et al. 2008).
103 Similarly, hundreds of intertidal food webs from a small North Pacific archipelago sampled at different
104 spatial scales revealed that connectance decreases with spatial scale of sampling while species richness
105 increases (Wood et al. 2015). A third example showed that across hundreds of pitcher plant food webs, at
106 sites stretching from Florida to Canada, network structure is more variable at lower latitudes (Baiser et al.
107 2012).

108 In addition to revealing novel patterns and processes, network data across broad spatial scales and
109 gradients lend themselves to re-examining more classical lines of ecological research (Kissling &
110 Schleuning 2015). One potentially fertile area of research lies in integrating food web ecology and
111 macroecology. While researchers have approached macroecology from many perspectives (Blackburn &
112 Gaston 2006), a stalwart approach is to develop and test ecogeographical “rules” that describe scaling
113 relationships in species’ diversity (e.g., Pianka 1966), range sizes (e.g., Stevens 1989; 1992) or body
114 masses (e.g., Bergmann 1847) across abiotic or geospatial gradients. The study of ecogeographical rules
115 has experienced a resurgence over the last decade due to the increase in available data and insights from
116 studying species invasion (Lomolino et al. 2006; Mathys & Lockwood 2009) and global change (Millien
117 et al. 2006; Gardner et al. 2011) at macroecological scales. We posit that ecogeographical rules also play
118 a key role in understanding variation in food web structure at macroecological scales and vice versa.
119 Changes in abundance, body size, and range size described by ecogeographical rules may constrain
120 trophic interactions and influence the structure and dynamics of food webs along biogeographical
121 gradients. On the other hand, food web interactions may also influence the expression of ecogeographical
122 rules either by amplifying them and making relationships stronger or by subverting them and making
123 relationships weaker for certain taxa or regions. Knowledge of feedbacks between ecogeographical rules
124 and the structure of food webs is a vital first step to studying ecological networks across large spatial
125 scales.

126 Here, we integrate macroecology and food web ecology by exploring a subset of ecogeographical
127 rules (Table 1) and their connections to food webs: 1) the latitudinal diversity gradient (LDG): the
128 increase in species richness from the poles to the equator, 2) Bergmann's rule: the increase in body size
129 with decreasing temperature, 3) the island rule: the increase in size of small species and decrease in size
130 of large species on islands, and 4) Rapoport's rule: larger species ranges at high latitudes. We describe
131 each rule, discuss their implications for food webs, present heuristic predictions for how food web
132 structure will vary with each rule, and assess empirical support for these predictions where available
133 (Table 2).

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135 **The Latitudinal Diversity Gradient**

136 The most well-known, oldest, and perhaps most influential macroecological rule is the latitudinal
137 diversity gradient (LDG) of increasing species richness from the poles to the tropics (Darwin 1859;
138 Wallace 1878; Dobzhansky 1950; Pianka 1966; Rohde 1992; Mittelbach et al. 2007; Brown 2014).
139 Hypothesized mechanisms for the LDG are abundant, often non-exclusive, and difficult to test (Pianka
140 1966; Rohde 1992; Brown 2014). Prominent explanations for the LDG build on purported differences
141 between the tropics and other regions, suggesting that higher species richness in the tropics may be due to
142 greater productivity (Hutchinson 1959; Currie 1991), higher rate of origination (e.g., "out of the tropics"
143 concept; Jablonski et al. 2006), phylogenetic niche conservatism (Wiens & Graham 2005), and rapid
144 evolution and speciation due to either temperature (Rhode 1992; Brown 2014) or stronger biotic
145 interactions (Dobzhansky 1950; Schemske 2002).

146 Gradients in species richness also play a central role in our understanding of food web structure
147 (Pimm et al. 1991, Dunne 2006). For example, increased species richness often decreases the fraction of
148 species at top and basal trophic levels while increasing the fractions of intermediate species and links per
149 species (Martinez 1991, 1994) as well as affecting practically all other properties of food web architecture
150 (Williams and Martinez 2000, Vermatt et al. 2009). Such food web patterns should also apply to changes
151 in species richness along the LDG specifically. While explanations for the LDG imply changes in food
152 web structure with latitude, explicit exploration of such changes have begun only recently (Baiser et al.
153 2012; Cirtwill et al. 2015a).

154

155 **Predictions for food web structure based on LDG hypotheses**

156 LDG, productivity, and food chain length

157 One of the more prominent LDG hypotheses asserts that greater productivity at low latitudes is
158 responsible for the LDG (Pianka 1966; Currie 1991; Storch et al. 2018). Relationships between
159 productivity and food chain length (FCL) have also been documented in both natural and experimental

160 systems (Kaunzinger & Morin 1998; Post 2002; Takimoto & Post 2013, Ward and McCann 2018).
161 Different mechanisms underlying productivity-FCL relationships lead to different predictions about how
162 FCL changes with latitude. One mechanism by which FCL can increase is simply through a sampling
163 effect (Huston 1997) where high species richness in productive regions increases the probability that a
164 food web will contain a top predator or consumer that can elongate FCL. A mechanism based on energy
165 flow posits that low productivity, coupled with inefficient energy transfer across trophic levels, sets limits
166 on how much energy can reach top trophic levels and as a result, can limit FCL (Lindeman 1942;
167 Hutchinson 1959, Fretwell & Barach 1977). Both the sampling effect and flow-based mechanisms predict
168 longer FCL at lower latitudes. However, consideration of the effects of omnivory on energy flow may
169 reverse these predictions. High productivity food webs may increase the biomass of high-trophic-level
170 predators which reduce consumer abundance forcing such predators to also feed on lower trophic levels
171 effectively reducing FCL (Tunney et al. 2012, Ward and McCann 2018). Such considerations predict that
172 FCL is shorter in highly productive (i.e., at lower latitudes) ecosystems because of increased omnivory.

173 We explored how FCL (measured as mean FCL, averaged over all species) varied across
174 latitudinal gradients in six ecosystems, based on 164 food webs from lake, estuary, stream, marine, and
175 terrestrial environments globally (compiled in Cirtwill et al. 2015a) and 780 pitcher plant food webs from
176 39 sites across North America (Baiser et al. 2012). We found significantly longer FCL at higher latitudes
177 for lake food webs (Fig. 1) and a significant decrease in FCL with latitude for pitcher plant food webs
178 (Fig.1). However, latitude describes a small proportion of variation in FCL in both cases ($R^2 = 0.07$ and
179 0.02 , respectively). FCL for food webs in estuaries, marine systems, streams, and in terrestrial systems
180 showed no relationship with latitude (Fig. 1). Our empirical results corroborate those of Vander Zanden
181 and Fetzer (2007), who used stable isotopes to show that streams and lakes had a trend (non-significant)
182 of increasing FCL with latitude, while marine ecosystems showed no relationship between latitude and
183 FCL.

184 All but one of the empirical ecosystems explored here and in Vander Zanden and Fetzer (2007)
185 are aquatic and latitude is a coarse indicator of productivity in freshwater ecosystems (Kalf 2002).
186 Further, recent theoretical and empirical work has shown that the influence of productivity on FCL in
187 aquatic systems is contingent on ecosystem size (Post 2002, Tunney et al. 2012, Ward and McCann
188 2018), disturbance (Sabo et al. 2010), and assembly history (Post 2002). As a result, there may be large
189 differences in FCL in aquatic ecosystems within a given latitude due to variation in ecosystem size,
190 nutrient inputs, and disturbance (e.g., Tunney et al. 2012). One possibility is that regional species pools
191 may show latitudinal gradients in FCL but, as species filter into local food webs, interactions between

192 ecosystem size, productivity, and assembly history govern FCL and ultimately obscure any local-scale
193 latitudinal patterns.

194 LDG, niche breadth, and connectance

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

205 However, linkage density, generality, and vulnerability also increase with species richness
206 (Martinez 1994; Riede et al. 2010). Therefore, one needs to address effects of richness on food-web
207 metrics to make robust inferences about how network structure varies with latitude independently from
208 species richness. One can control for species richness by analyzing residuals of the relationship between
209 species richness and food web properties (Bengtsson 1994; Olesen & Jordano 2002; Tylianakis et al.
210 2007). Another approach is to explore the variation of interaction richness with species richness using a
211 power-law, $L = bS^u$, where b is a scaling parameter, and u describes the dependence of the number of
212 links (L) on the number of species (S) (Cirtwill et al. 2015a). A positive relationship between the
213 exponent (u) of this power-law relationship and latitude would indicate that species in the tropics gain
214 fewer links per species (i.e., are more specialist) compared to their high-latitude counterparts (Cirtwill et
215 al. 2015a).

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

222

223 **The influence of food webs on the LDG**

224 Several hypotheses for the LDG invoke trophic interactions. Stronger predation pressure in the tropics has
225 been asserted to increase diversity through keystone effects (Paine 1966), create negative density-
226 dependence (Janzen 1970; Connel 1971), accelerate diversification rates (Dobzhansky 1950; Mittlebach
227 et al. 2007), and promote greater regional diversity (Freestone et al. 2011) – each with consequences for
228 food web properties. Predation pressure may also cause systematic latitudinal variation in the proportion
229 of basal prey, intermediate taxa, and top predators in food webs. Keystone predation may, for example,
230 increase lower-trophic-level diversity, which in turn would raise the proportion of intermediate and basal
231 species (i.e., species that are consumed) in food webs. Similarly, an increase in diversification rates due
232 to predation pressure could provide the opportunity for both prey and predators to increase in richness in
233 the tropics, thus we would expect proportions of each trophic level to increase concomitantly.

234 **Bergmann's Rule**

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

246 ***The influence of Bergmann's rule on food webs***

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

252 The probability of a trophic interaction occurring between two species is dependent on the
253 probability they encounter each other and that their traits enable a predator-prey relationship (Pawar et al
254 2012, Poisot et al. 2015a). Encounter probability may be neutral in that high abundances of two species

255 increases encounter probability and low abundances of one or both species leads to the opposite (Canard
256 et al. 2012). Interactions also involve trait matching between the predators and the prey (e.g., predator-
257 prey biomass ratio; Brose et al. 2006a, b, Yeakel et al. 2014) where traits determine the species' niches
258 (Coux et al. 2016). Based on encounter probability and trait matching, Bergmann's rule may alter
259 network structure by 1) temperature effects on body size altering the potential for interaction if body size
260 or a trait highly correlated to it (e.g., gape size) primarily determines interaction potential (Brose et al.
261 2006 b; Rohr et al. 2010) and 2) altering encounter probability via the negative relationship of body size
262 and population size and the positive relationship of body size with range size (Peters 1983; Brown et al.
263 2004) and maximum migration distance (Hein & Gillooly 2011).

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

271

272 *The influence of food webs on Bergmann's rule*

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

283

284 **Island rule**

285 Islands provide us with some of the most dramatic examples of ecological and evolutionary phenomena
286 including adaptive radiations (Gavrilets & Losos, 2009), community assembly (Thornton 1997), species

287 invasions (Sax & Gaines 2003), and catastrophic extinctions (Olson & James 1982). The island rule
288 emerged from the ecogeographical study of insular biotas (Foster 1964; Van Valen 1973). Specifically,
289 the island rule codifies the observation that small vertebrates increase in body size over generations, while
290 large vertebrates decrease, relative to mainland conspecifics or ancestors. The island rule was originally
291 postulated for mammals (Foster 1964; Van Valen 1973, Heany 1978, Lomolino 1985), but support for the
292 island rule has also been found for birds (Clegg & Owen 2002; Cassey & Blackburn 2004; Mathys &
293 Lockwood 2009) and snakes (Boback & Guyer, 2003), but support was not found for turtles (Itescu et al.,
294 2014).

295 **The influence of the island rule on food webs**

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

304 The importance of body size to prey selection, food web structure, and dynamics suggests that the
305 island rule likely has dramatic effects on island food webs. Island Biogeography Theory holds that island
306 food webs have fewer species than mainland food webs due to the decrease in both the area and the
307 distance which species must travel to colonize islands (MacArthur & Wilson 1967). While the original
308 theory does not include trophic interactions, including such interactions has improved the fit of island
309 biogeography models to empirical data and diversified predictions (Gravel et al. 2011; Cirtwill & Stouffer
310 2015b; Jacquet et al. 2017). Further incorporating changes in body size observed under the island rule
311 may continue such improvements by more precisely predicting extinctions or the establishment of species
312 in island ecosystems.

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

318 **The influence of food webs on the island rule**

319 The generality of the island rule may be limited (Lokatis & Jeschke 2018). For example,
320 Lomolino et al. (2012) concluded that the change in body size following an ecological release from
321 mammalian predators and competitors is context dependent. Food web structure may hold information on
322 which types of webs are likely to experience changes in accordance with the island rule and which are
323 not. Food webs with few trophically similar species (i.e., low maximum trophic similarity) can facilitate
324 changes in body size on islands due to competitive release (Lomolino et al. 2012). Similarly, food webs
325 with few consumers (i.e., low vulnerability) may promote change in body size due to predation release.
326 Another important factor identified in body size changes on islands are marine subsidies, which increase
327 body size (Lomolino et al. 2012). Further incorporating marine subsidies through food web models that
328 include biomass dynamics (e.g., Delmas et al. 2017) may help to understand and predict the strength of
329 the island rule.

330

331 **Rapoport's Rule**

332 Rapoport's rule describes the increase in range size with latitude (Stevens 1989) and was later extended to
333 include a positive relationship between altitude and range size (Stevens 1992). Rapoport's rule has
334 received mixed support for birds (Blackburn & Gaston 1996; Gaston & Blackburn 1996), fish (Rohde et
335 al. 1993), mammals (Pagel et al. 1991; Smith et al. 1994), and invertebrates (France 1992; Roy et al.
336 1994), which has led some to suggest that it should be designated as Rapoport's "effect" (Blackburn &
337 Gaston 1996). While the generality of this rule has been challenged, recent evidence suggest that
338 Rapoport's rule at least holds at higher latitudes in the northern hemisphere (Gaston et al. 1998; Ruggiero
339 & Werenkraut 2007; Whitton et al. 2011).

340 Stevens' (1989) initial hypothesis for Rapoport's rule suggests that more variable climate at high
341 latitudes results in broader physiological tolerances allowing species to inhabit larger ranges. Another
342 hypothesis is that species with narrow tolerance are more likely to go extinct at high latitude due to
343 glaciation and climate change, thus leaving behind species with large ranges (Brown 1995, Kolasa et al.
344 1998). Lower levels of competition due to lower species richness in temperate regions has also been
345 proposed as an explanation for Rapoport's rule (Stevens 1996), thus linking Rapoport's rule with the
346 LDG.

347 ***The influence of Rapoport's rule on food webs***

348 Rapoport's rule has implications for the turnover of food web structure over the latitudinal gradient
349 (Poisot et al. 2012; Baiser et al. 2012). Turnover in food web structure—quantified in terms of β -

350 diversity—arises from spatial variation in species composition and variation in pairwise interactions
351 (Poisot et al. 2012). Species common between two webs can differ in their interactions (i.e., rewiring) or,
352 alternatively, two webs can share few to no species and changes in network structure can be solely the
353 result of species turnover.

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

365 Our empirical pitcher plant data only allow network dissimilarity to arise from the spatial
366 variation in species composition and not the variation in pairwise interactions among shared species due
367 to the metaweb approach used to construct the web (i.e., if two species are known to interact, they are
368 assumed to interact whenever they co-occur: see Baiser et al. 2012). As a result, we only test the
369 hypothesis that dissimilarity in network structure due to species turnover is greater at lower latitudes. We
370 find a significant negative relationship between network turnover and latitude (Fig. 4) revealing that the
371 structure of food webs is more variable as a function of species turnover at lower latitudes. It is unclear if
372 Rapoport's rule plays a part in this observation because ranges for the majority of the species in these
373 food webs are unknown.

374 ***The influence of food webs on Rapoport's rule***

375 Rapoport's rule is conceptually tied to the LDG in that narrower niche breadths are expected to lead to
376 both smaller range sizes and greater species niches in the tropics (Stevens 1989). While climate niches
377 leading to smaller distributions in the tropics is the focus of Rapoport's rule, trophic niches may also play
378 a part. Simply put, if a consumer's prey have larger ranges, then that consumer may also have a larger
379 range. Climatic niches may work in tandem with trophic niches. For example, if a species has a narrow
380 climatic niche and subsequent range, it may specialize on prey items in that range. As a result, even if the
381 species could disperse to a new area with a similar climatic niche, it may not be able to establish without

382 its specialized prey (Holt et al.1999). Conversely, species with broader trophic niches are more likely to
383 find suitable prey as their range expands. While this is clearly speculative, exploring how trophic
384 interactions can extend (or constrain) climate-based fundamental niches using species distribution models
385 (Wisz et al. 2013) may lend insight into the role that food web interactions play in driving Rapoport's
386 rule.

387 **DISCUSSION**

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

397 398 **Potential systems for studying the macroecology of food webs**

399 Due to their scale and extent, the sampling effort needed to gather enough data to validate and calibrate
400 models of food webs across macroecological scales is substantial. Several types of ecosystems are
401 predisposed to integrating macroecology and food web ecology due their tractability, distributions, and
402 existing natural history knowledge. Natural microcosms or "container" habitats (such as pitcher plants,
403 bromeliad tanks, tree holes) are examples of tractable systems (Kitching 2000, Srivastava et al. 2004;
404 Baiser et al. 2012). Lakes (Tunney et al. 2012, Morlon et al. 2014) and islands (Rominger et al. 2015)
405 including "sky islands" also provide bounded tractable systems albeit less tractable than container
406 habitats. Intertidal communities are a relatively well-studied, broadly distributed system of taxa (Pielou
407 1977) with extensive knowledge on trophic ecology where important factors such as body size and
408 abundance can be readily measured and manipulated in the field over tractable time scales (e.g., Novak &
409 Wootton 2008). One alternative approach to collecting field data is to use synthetic datasets (Poisot et al.
410 2016) that are assembled by merging data from varied sources (e.g., climatic data, species occurrences,
411 taxonomy, traits, and interactions), through a reproducible pipeline, into a single cohesive dataset, with
412 fixed taxonomic and spatial limits. Finally, well-known collections of food webs (Cohen & Briand 1984;

413 Martinez 1994; Dunne et al. 2004; Vermatt et al. 2009; Reide et al. 2010), are also useful for studying the
414 macroecology of food web networks.

415 **Potential approaches for studying the macroecology of food webs**

416 Collecting food web data at large biogeographic scales necessitates more tractable, alternative approaches
417 that answer specific macroecological questions related to food webs. For example, to test the relationship
418 between latitude and FCL, stable isotopes can be utilized (e.g., Vander Zanden and Fetzer 2007)
419 obviating the need to measure every trophic interaction across a set of food webs. In a similar vein, stable
420 isotope analysis (Jackson et al. 2011) and DNA barcoding of gut contents or feces (Kartzinel et al. 2015)
421 can provide estimates of diet breadth testing the long-held hypothesis that niches are narrower at lower
422 latitudes. For exploring the role of Bergmann's and the island rule on food webs, comparisons of
423 predator-prey biomass ratios can provide a feasible approach. Further, such comparisons of predator-prey
424 biomass ratios along temperature/latitudinal gradients or between islands and mainlands can lead to
425 insights on the stability and structure of food webs (Brose et al. 2006 a, b, Brose 2010). This approach can
426 be facilitated by global databases of predator-prey interactions and body sizes (e.g., Brose et al. 2005,
427 Barnes et al. 2008, Poelen et al. 2014).

428 While detailing every trophic interaction in a food web is clearly challenging, sampling food
429 webs across broad geographic scales at relevant time scales is even more prohibitive. One possible
430 approach is to test different mechanisms hypothesized to drive macroecological relationships independent
431 of geography and then apply results to geographic extents. For example, if productivity is hypothesized to
432 drive FCL, exploring food webs within the same region that vary in productivity can specifically test this
433 hypothesis (e.g., Vander Zanden et al. 2009, Ziegler et al. 2015) independent of geographical and
434 historical contingencies (Kolasa et al. 1998). The next step in this approach is to extend results across
435 biogeographic regions to see if productivity is the key driver to FCL or if other biogeographic factors
436 exert control over macroecological scales.

437 **What can food webs tell us about ecogeographical rules?**

438 Two recurring themes in the literature on ecogeographical rules are that 1) mechanisms remain elusive
439 and 2) there are deviations (sometimes large) from predictions. Studies of ecogeographical rules often
440 focus on specific taxonomic groups or guilds and do not consider the food webs in which they are
441 embedded. Considering trophic interactions as a selection pressure that can drive or disrupt
442 ecogeographical rules has the potential to address both mechanisms of and deviations from these long-
443 studied patterns.

444 **Conclusion**

445 Several areas of research are critical to advancing our understanding of the macroecology of food webs.
446 First and foremost is the collection of food web data across biogeographic gradients. We have suggested
447 several model systems and approaches for testing the generality of patterns and hypotheses.
448 Second, the macroecology of food webs goes beyond traditional approaches because it not only describes
449 the state of the system, but also opens the door to exploring food web dynamics at macroecological
450 scales. An integrated exploration of ecogeographical rules and dynamics through mathematical modeling,
451 empirical data, and statistical models (e.g., Boit et al. 2012), and novel network analyses (Allesina et al.
452 2015) will elucidate how macroecological processes influence food web dynamics. Third, considering the
453 macroecology of food webs within the context of global change will provide insight into what future food
454 webs will look like. As species go extinct or adapt to anthropogenic conditions in their environment,
455 ecogeographical rules give us an idea of how they will respond to these changes (Millien et al. 2006) and
456 could even be used to test against known changes to food webs in the recent or distant past (Dunne et al.
457 2014, 2016, Yeakel et al. 2014). Increasing temperature due to global change, for instance, should result
458 in smaller body sizes as suggested by Bergmann's rule (Gardner et al. 2011). Furthermore, species within
459 islands of fragmented habitats created by land use change have been observed to follow the island rule
460 (Schmidt & Jensen 2003; Fietz & Weis-Dootz 2012; but see Lomolino & Perault 2007). These
461 anthropogenically induced changes in species can then be integrated with food web models to explore and
462 predict changes in species interactions and entire food webs subjected to anthropogenic disturbance.

463 The relevance of ecogeographical rules to food webs does not end with the examples and rules we
464 present here. Since large-scale ecological and evolutionary phenomena found in macroecology have
465 implications for species interactions—and hence network structure and dynamics—there is much insight
466 to be gained in further studying these relationships in the context of ecological networks. Additionally,
467 macroecological relationships do not exist in isolation, but interact in complex ways (Lomolino et al.
468 2006; Gaston et al. 2008) that will likely influence food webs. Further testing the predictions and
469 implementing the approaches we detailed here (Table 2) provide a pathway for integrating macroecology
470 and food webs to better understand the assembly, maintenance, and change of ecosystems in the near and
471 distant future.

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828 **Data Accessibility**

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

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833 **Tables**

834 **Table 1.** Summary of ecogeographical rules used to explore food web structure.

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

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859 Table 1

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

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872 Table 2.

Rule	Prediction	Empirical support
LDG	Longer FCL at lower latitudes.	<ul style="list-style-type: none">- No evidence across 5 types of ecosystems- No evidence in stream, lake, and marine systems (Vander Zanden and Fetzer 2007)- Weak evidence in pitcher plant food webs
LDG	Shorter FCL at lower latitudes.	<ul style="list-style-type: none">- Evidence in lakes- Non-significant trends in streams and lakes (Vander Zanden and Fetzer 2007)
LDG	Linkage density, generality, and vulnerability should increase with latitude	<ul style="list-style-type: none">- No evidence in pitcher plant food webs- Generality increased toward the poles in lake and stream food webs (Cirtwill et al. 2015a)- Linkage density and vulnerability showed no relationship with latitude across 5 ecosystem types (Cirtwill et al. 2015a)- Linkage Density of host-parasitoid interactions peaks in colder climates (Gravel et al. 2018)

Rapoport's	*At low latitudes, we expect high species turnover and little to no interaction turnover	- Confirmed in pitcher plant food webs
Rapoport's	*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	na
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

873 *We were only able to test the portion of the prediction that is bold for Rapoport's rule given our data.

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888 **Figure Legends**

889 **Figure 1.** Mean FCL (measured as mean food chain length, averaged over all species) for estuary, lake,
890 marine, stream, terrestrial, and pitcher plant (*Sarracenia purpurea*). Pitcher plant food web data are from
891 Baiser et al. (2012). All other data is from Cirtwill et al. (2015a). Contrary to our prediction, mean FCL
892 in lake food webs increases with latitude (slope = 0.02, $R^2 = 0.07$. p-value = 0.05) while FCL decreased
893 with latitude in pitcher plant food webs (slope = -0.002, $R^2 = 0.02$. p-value = 0.01).

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895 **Figure 2.** Schematic diagram of Bergmann's rule. The orange circle depicts the predator and the niche of
896 the predator (i.e., size of prey it can eat, sensu the niche model; Williams & Martinez 2000) is the tan box.
897 Blue circles represent potential prey items. **A)** The high temperature (low latitude) case where the
898 predator (i.e., the orange circle) has two prey species that fall within its niche. Each of the following
899 scenarios (**B-D**) are compared to the high temperature baseline (**A**). **B)** A low temperature (high latitude)
900 scenario where all species' body sizes increase according to Bergmann's rule. In this case, the prey
901 species remain the same for the predator. **C)** A scenario where only the predator's body size increases. As
902 a result, one prey species is no longer in the predator's feeding niche. **D)** The case where only the prey
903 species increase in body size which results in the loss of a prey species for the predator.

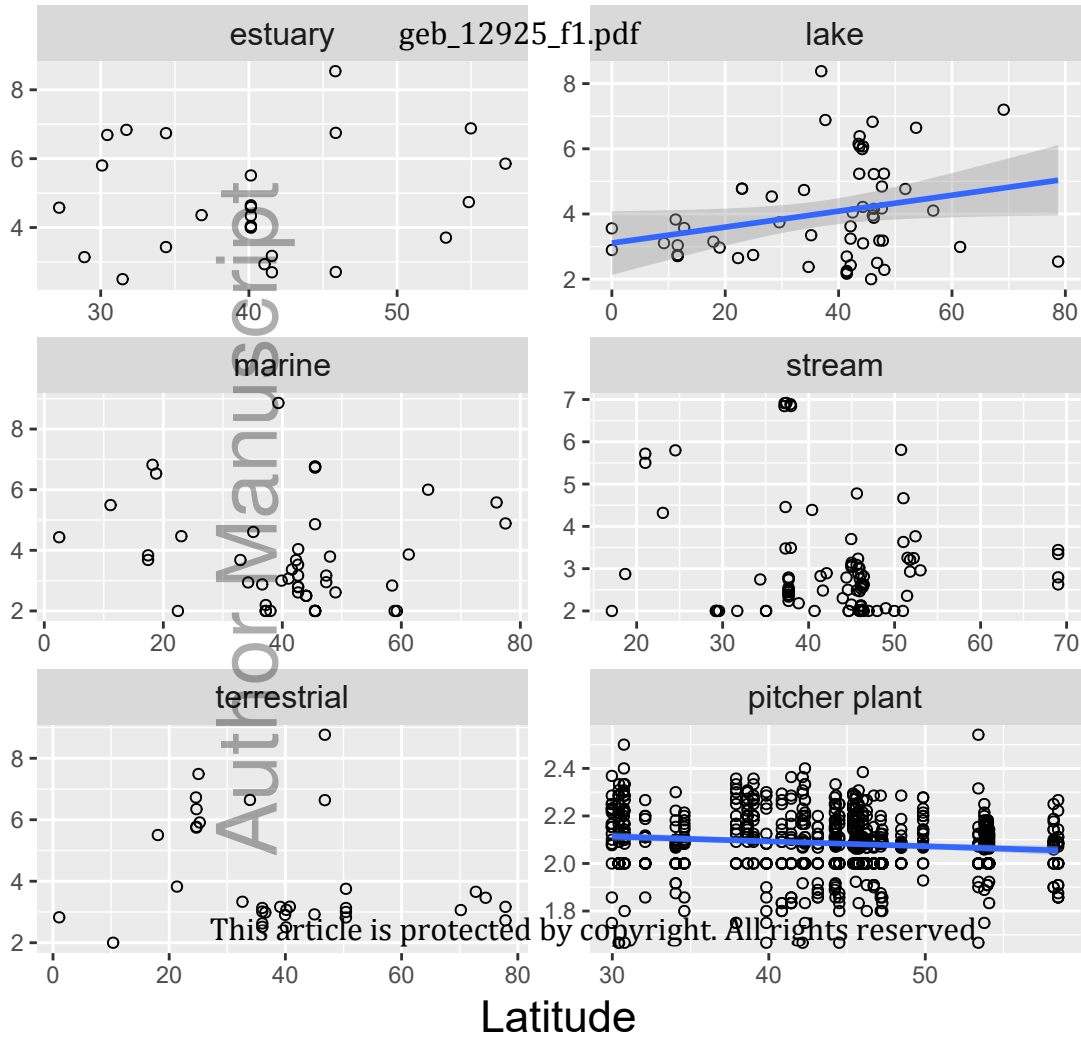
904 **Figure 3.** Schematic diagram of how the island rule can affect food webs. The predator is the orange
905 circle and its body size foraging niche is indicated by the tan box. Blue circles represent potential prey
906 items. **A)** In this scenario, the predator loses all its feeding interactions as the increase in prey size
907 coinciding with the decrease in predator size move all prey species out of the predator's feeding niche. **B)**
908 A predator can also gain prey species as a result of body size changes due to the island rule. In this case,
909 both the increase and decrease in body size of potential prey items and the decrease in size of the predator
910 bring new species into the predator's foraging niche.

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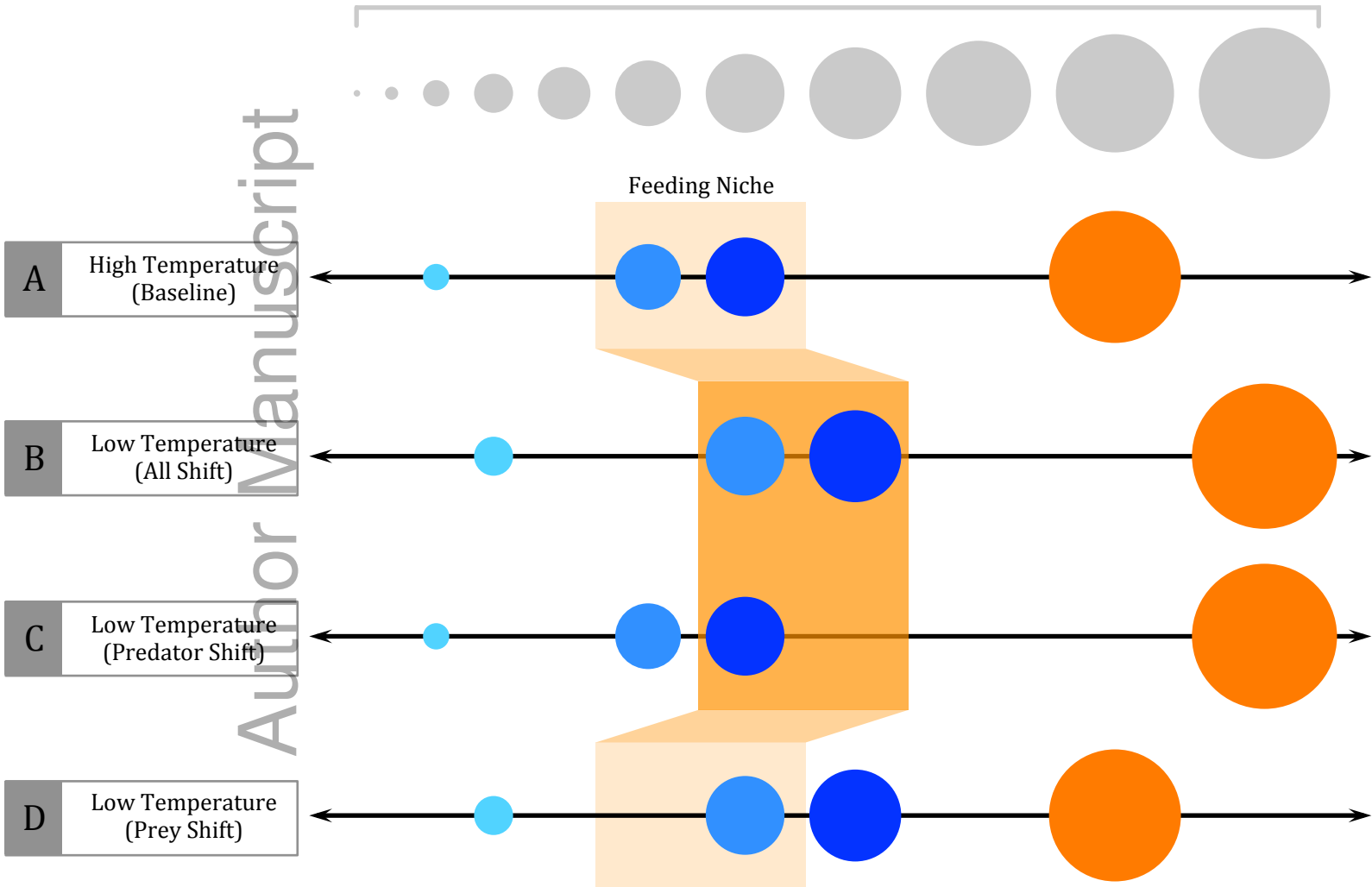
912 **Figure 4.** Network dissimilarity due to species turnover (β_{ST} ; Poisot et al 2012) across latitude for pitcher
913 plant food webs. β_{ST} ranges from zero in which all species and interactions are shared between two food
914 webs and one where no species (and no interactions) are shared. Each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

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mean food chain length (FCL)



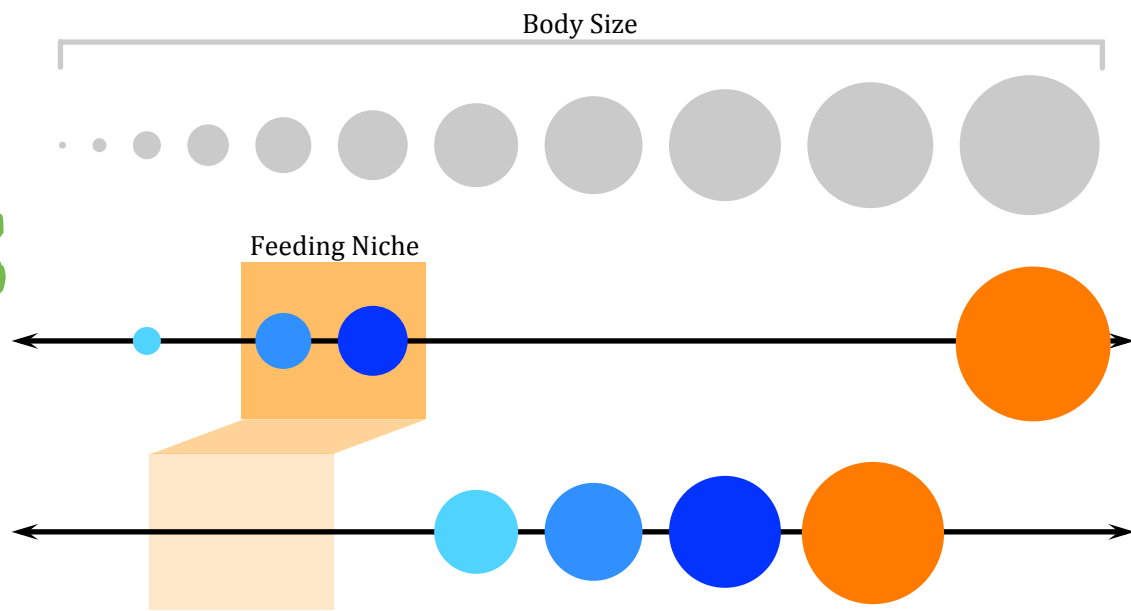
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A

Loss of Feeding Interactions

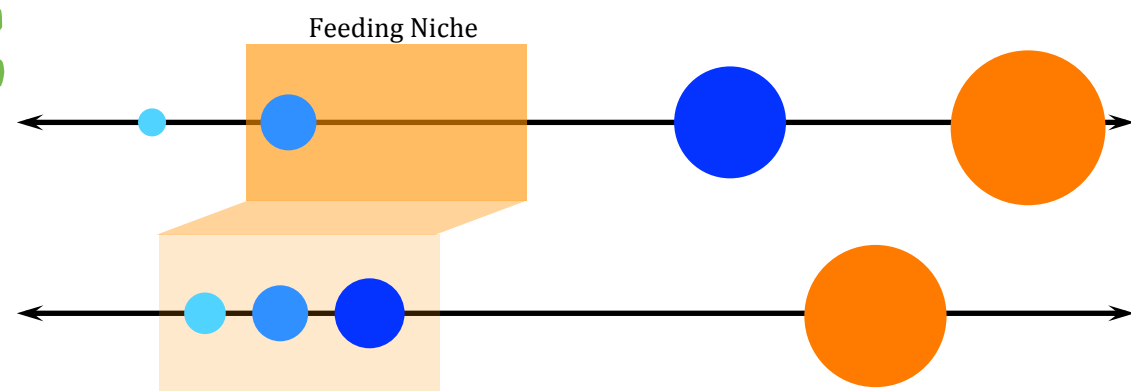
MAINLAND
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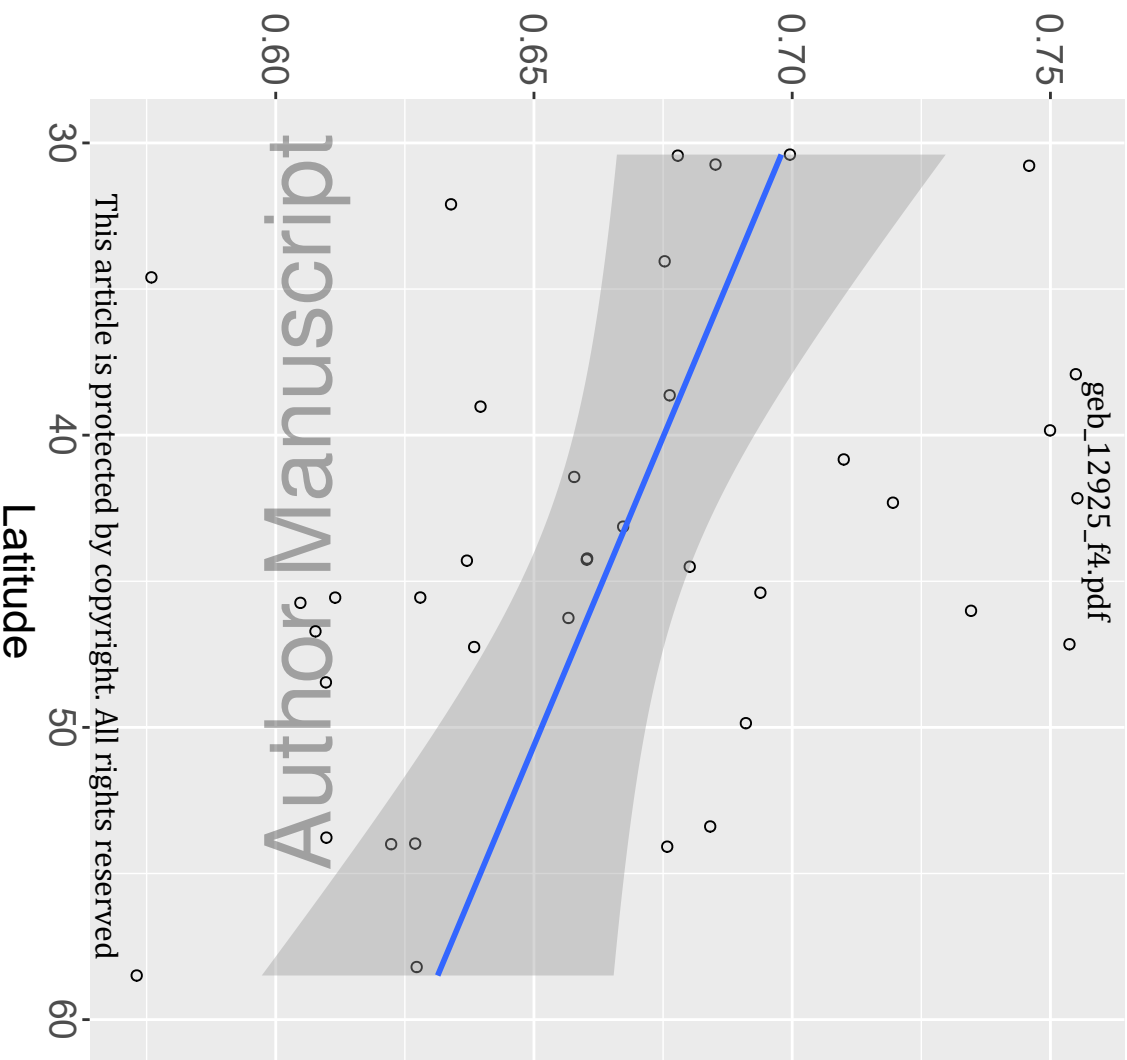
B

Gain of Feeding Interactions

MAINLAND
ISLAND



Network dissimilarity due to species turnover (β_{st})



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