

1 Predation risk influences food-web structure by constraining species
2 diet choice

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13 HH and SP conceived the idea. HH developed it with input from JT and SP. HH conducted the simulation and analysis.

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17 Empirical food-web data are from published literature, as listed in the SI. The R scripts that can reproduce simulation
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38 **Abstract**

39 The foraging behaviour of species determines their diet and, therefore, also emergent food-web structure.
40 Optimal foraging theory (OFT) has previously been applied to understand the emergence of food-web
41 structure through a consumer-centric consideration of diet choice. However, the resource-centric
42 viewpoint, where species adjust their behaviour to reduce the risk of predation, has not been considered.
43 We develop a mathematical model that merges metabolic theory with OFT to incorporate the effect of
44 predation risk on diet choice to assemble food webs. This “predation-risk-compromise” (PR) model
45 better captures the nestedness and modularity of empirical food webs relative to the classical optimal
46 foraging model. Specifically, compared with optimal foraging alone, risk-mitigated foraging leads to
47 more-nested but less-modular webs by broadening the diet of consumers at intermediate trophic levels.
48 Thus, predation risk significantly affects food-web structure by constraining species’ ability to forage
49 optimally, and needs to be considered in future work.

50 Introduction

51 Understanding food-web structure—the arrangement of who-eats-whom interactions—is necessary for
52 understanding biomass (ergo, energy) flows and the stability of ecosystems (May 1972; Allesina &
53 Tang 2012; Rossberg 2013; Gravel *et al.* 2016). The trophic interactions in a food web are, in fact,
54 accumulations of foraging events between individual organisms; all structural properties of food webs
55 therefore emerge from individual foraging behaviours driven by metabolic demands (Brose *et al.* 2008;
56 Petchey *et al.* 2008; Pawar *et al.* 2012; Portalier *et al.* 2019). Although this idea is intuitive, food-web
57 structure, foraging behaviour, and metabolic constraints have historically been studied independently
58 until recently (Abrams 2010; Beckerman *et al.* 2010; Loeuille 2010; Stouffer 2010; Valdovinos *et al.*
59 2010). To mechanistically understand the emergence of food-web structure, it is therefore important
60 to explore the underpinning, metabolically-driven diet choice of species. To this end, previous work
61 has used optimal foraging theory (OFT; Charnov & Orians 1973; Stephens & Krebs 1986; Krebs *et al.*
62 1977) combined with metabolic theory (Brown *et al.* 2004) to model the diet choice of consumers in
63 food webs (Beckerman *et al.* 2006; Petchey *et al.* 2008). Optimal foraging theory stochastically models
64 a series of decisions for each consumer, between whether to pursue or ignore each encountered resource
65 item, such that their final diet composition maximises its net energy intake rate.

66 By using metabolically-constrained search and handling parameters in the classical OFT diet-choice
67 model as the mechanism for trophic link formation, Petchey *et al.* (2008), building on previous work
68 by Beckerman *et al.* (2006), showed that the resulting “Allometric Diet Breadth Model” (ADBM)
69 could help predict links in real food webs. This result highlighted the importance of metabolic
70 constraints (through size-scaling) in determining diet choice, and supported the idea that OFT can
71 help explain food-web structure. The ADBM and its variants has since then been used to predict the
72 effects of temperature (Petchey *et al.* 2010) and behavioural size-dependence (Thierry *et al.* 2011)
73 on food-web structure. Nevertheless, the predictive abilities of ADBM type models remain limited,
74 raising doubts about the utility of body size and OFT alone for predicting food-web structure (Allesina
75 2011). Additional factors may thus be needed to explain how food-web structure emerges from foraging
76 decisions (Berlow *et al.* 2008; Eklöf *et al.* 2013; van Leeuwen *et al.* 2013; Jonsson *et al.* 2018).

77 Here, we argue that the ability of OFT to predict empirical food-web structure is limited partly
78 because the classical model is consumer-centric, i.e., a consumer chooses without constraints from a
79 set of potential resources. In reality, all species in food webs excluding top predators and basal taxa
80 are both a consumer and a resource, and must experience risk of predation while foraging. Indeed,
81 anti-predator behaviour is common—consumers from practically all taxonomic lineages modify their
82 foraging behaviour to mitigate predation risk (Laurila *et al.* 1997; Schmitz *et al.* 1997; DeWitt *et al.*
83 1999; Altwegg *et al.* 2004; Jousset 2012), with these strategies playing a significant role in determining
84 the forager’s fitness (Lima 1998). Studies have also found that predation-risk-driven behavioural
85 responses of prey can strongly reduce their own consumption rates as predators and influence their diet
86 choice (Lima & Valone 1986; Metcalfe *et al.* 1987; Beckerman *et al.* 1997; Pangle *et al.* 2012; McMahon
87 *et al.* 2018). Thus, most consumers cannot possibly forage optimally (in a strict OFT sense) all the
88 time, but still need to meet their metabolic demands while living in an “ecology of fear” (Brown *et al.*
89 1999). We therefore propose that predation risk, by modulating optimal foraging (Berlow *et al.* 2008),
90 should be an additional key factor structuring food webs (Beckerman *et al.* 1997; Schmitz *et al.* 1997;
91 Kondoh 2007; Bucher *et al.* 2015). Yet, to our knowledge, no study has investigated how predation risk
92 and metabolic constraints together influence the foraging decisions that generate food-web structure.

93 In this study, we include predation risk and metabolic constraints into the classical OFT diet choice

94 model to study the emergence of food-web structure. Using this “predation-risk-compromise” (PR)
 95 model, we assemble food webs *in silico*, and test whether the new model better captures empirically
 96 observed food-web structure than the ADBM type approach based on classical OFT. We focus our
 97 discussion on nestedness and modularity as measures of food-web structure (Table S3). Empirical
 98 food webs are known to be nested and modular (Kondoh *et al.* 2010; Krause *et al.* 2003; Teng &
 99 McCann 2004; Montoya *et al.* 2006; Guimerà *et al.* 2010), and both properties have been proposed to
 100 promote the dynamical stability of food webs (Krause *et al.* 2003; Thébault & Fontaine 2010; Stouffer
 101 & Bascompte 2011; Grilli *et al.* 2016; Gilarranz *et al.* 2017). We show that the PR model outperforms
 102 the OF model in capturing empirical food-web structure across multiple communities, and quantify
 103 the the relative importance of optimal foraging vs. predation risk in determining food-web structure.

104 Materials and Methods

105 Foraging models

106 The OF model derives the optimal diet of an individual consumer that maximises its net energy
 107 intake rate according to classical OFT (Charnov & Orians 1973; Krebs *et al.* 1977). We use biomass
 108 consumption rate as a proxy for energy intake rate, under the assumption that the energy content per
 109 unit biomass of resource and conversion efficiency (i.e., from biomass to energy) of consumer are both
 110 approximately constant irrespective of consumer or resource identity (Kondoh 2007; Petchey *et al.*
 111 2008), and independent of body size (Peters 1986; DeLong *et al.* 2010; Lang *et al.* 2017). The total
 112 biomass consumption rate of the j^{th} consumer species in a food web can be written as

$$113 \quad C(D_j) = \sum_{i \in D_j} \left(\frac{\epsilon a_{ij} A_{ij} X_i}{1 + \sum_{k \in D_j} a_{kj} A_{kj} h_{kj} X_k} \right) \quad (1)$$

114 where D_j is the set of species in its diet, ϵ its conversion efficiency (here assumed constant), and, for
 115 its i^{th} resource species, a_{ij} is mass-specific search rate ($\text{m}^2 \cdot \text{kg}^{-1} \cdot \text{s}^{-1}$), A_{ij} its attack success probability,
 116 h_{ij} its mass-specific handling time (s) (the time from pursuing to subjugating the resource), and X_i
 117 the resource’s biomass abundance (density) ($\text{kg} \cdot \text{m}^{-2}$). Equation (1) is a multi-resource extension of the
 118 classical (single-resource) type-II functional response (Holling 1959)(SI section 1.1), and is the expected
 119 energy intake over a large sample of iterated, stochastically-spaced foraging bouts (Charnov & Orians
 120 1973). The consumer’s biomass consumption rate depends on its diet set, as well as the abundances
 121 of those resource species. Using eqn (1), we use OFT to assign trophic links in a community with
 122 given and fixed species abundances (SI section 1.4) as follows. For a consumer, the profitability of
 123 each resource species is calculated as its attack success probability divided by mass-specific handling
 124 time (SI section 1.2; eqn (S12)). According to OFT, given the profitability ranking of resource species,
 125 lower-rank resource would not be eaten without higher-rank ones being included in the consumer’s
 126 diet (SI section 1.1). We therefore calculate, for each consumer species in the given community, the
 127 biomass consumption rate across the whole range of diet breadth, i.e., from eating only the most
 128 profitable species to sequentially including others ordered by profitability until it eats all species (SI
 129 section 1.2). The resource set that produces the highest consumption rate, C_{opt} , constitutes the OF
 130 diet (Fig. 1A–B).

131 OF can be seen as a predation-risk-free state of a consumer, where it has the luxury of being “picky”
 132 by ignoring not-so-profitable resources to achieve optimality. The PR model is an extension of the OF

133 model to include metabolic expenditure and predation risk as additional constraints on (objectives
 134 for) consumer foraging decisions as follows. First, we include a minimum mass-specific consumption
 135 rate, C_{\min} (s^{-1}) that the consumer needs to balance its energy loss to somatic maintenance (Fig. 1C)
 136 (Rizzuto *et al.* 2018). Second, we introduce the effect of predation risk on every species as follows.
 137 First, we quantify realised predation risk (P_{risk}) for every species as

$$138 \quad P_{\text{risk}} = \left(\frac{\sum X_{\text{real}}}{\sum X_{\text{all}}} \right)^{e_P} \quad (2)$$

139 where $\sum X_{\text{real}}$ is the total biomass of all its realised consumers, $\sum X_{\text{all}}$ is the total biomass of all
 140 (including the realised) consumer species, and the exponent e_P determines how P_{risk} increases with
 141 $\sum X_{\text{real}}$ (Fig. S1). Thus, P_{risk} is bounded between 0 and 1 (Fig. 1D). Then, for a given species' P_{risk}
 142 value, its corresponding risk-compromised consumption rate, C_{risk} , necessarily lies between the optimal
 143 (OF) consumption rate C_{opt} and C_{\min} (Fig. 1C–D), such that:

$$144 \quad C_{\text{risk}} = C_{\min} + (1 - P_{\text{risk}})(C_{\text{opt}} - C_{\min})$$

145 Then, the resource set that yields the closest-but-higher consumption rate than this risk-compromised
 146 value is the predicted predation-risk-compromise (PR) diet (the diet set above the dashed line in Fig. 1D
 147 that is closest to it). That is, the P_{risk} value determines where a species lies between two extremes,
 148 depending upon its trophic position in the food web. When there is no risk ($X_{\text{real}} = P_{\text{risk}} = 0$), predator
 149 avoidance is unnecessary, and the population can forage optimally (well exceeding its C_{\min}). This is
 150 essentially equivalent to the classical OFT condition (i.e., the OF model). At the other extreme, where
 151 the consumer bears maximum predation risk because all possible species forage on it ($X_{\text{real}} = X_{\text{all}}$, so
 152 $P_{\text{risk}} = 1$), the need for predator avoidance outweighs the optimal consumption objective, such that the
 153 consumer forages in a way that minimises predation risk, while still meeting the C_{\min} threshold. This
 154 can be accomplished by taking a suboptimal diet that requires the least time spent doing risky foraging
 155 actions (searching/waiting vs. handling), yielding a consumption rate closest to, or exactly at, the
 156 threshold C_{\min} . Thus, in the PR model, consumers are simultaneously trying to meet three objectives:
 157 foraging optimally, mitigating predation risk, and meeting an energetically-minimum consumption rate.
 158 This approach is in the spirit of foraging models that use multiple-objective dynamic programming by
 159 Rothley *et al.* (1997).

160 There are two possible ways that consumers can mitigate risk, depending on which of searching
 161 (waiting, if the consumer adopts sit-and-wait foraging) and handling is the riskier action. If handling is
 162 less risky than searching, the consumer can accept more resource types (i.e., becomes more generalised),
 163 effectively lowering the time allocated to searching/waiting within a foraging bout relative to what
 164 OFT would predict (resulting in a “diet-broadening” strategy). Conversely, if searching is less risky
 165 than handling, it can pursue only the more profitable resources which require less time to handle for
 166 gaining the same amount of energy (i.e., it becomes more specialised), effectively lowering the total
 167 time allocated to handling within a foraging bout (resulting in a “diet-narrowing” strategy) (SI section
 168 1.3). In the following sections, we focus on the diet-broadening strategy because assuming handling
 169 being the less risky action is empirically supported (see “Discussion”), and the diet-narrowing strategy
 170 also effectively converges to the OF model in our simulation. Simultaneously allowing both strategies
 171 converges to the broadening case. For full results of all strategies, see SI section 7. Finally, note
 172 that we define P_{risk} (eqn (2)) to be monotonic under the assumption that other mechanisms affecting
 173 predation risk of a species, such as interference between its consumers, are less important than the

174 effect of increasing the abundance of those consumers *per se*.

175 **Building food webs using the foraging models**

176 We use metabolic scaling theory to parameterise the foraging models (SI section 1.4–1.5). In short, X ,
177 a , A , and h of eqn (1) and the C_{\min} of the PR model are specified using body mass-based scaling rules.
178 These update the ADBM model parameterisations (Petchey *et al.* 2008) with new, empirically-validated
179 relationships (Table S1). We recognise that there is uncertainty in both the mathematical structure and
180 exact parameterisation of the quantities. Therefore, we test the robustness of our results to variation
181 in these formulations as described in the “Synthetic food webs” section.

182 Given the values of parameters, we generated predicted food webs by applying each of the above
183 two foraging models to every consumer species in a given community. The set of species could either
184 be from an empirical community or a synthetic one, as explained further below. All simulations and
185 analyses were performed using R (ver. 3.4.4) (R Core Team 2013).

186 To assemble OF webs, we simply apply the OFT diet criteria simultaneously to each consumer
187 species in the communities (eqn (1); Fig. 1A–B). In contrast, PR webs were assembled using the the
188 following iterative algorithm (pseudocode in SI section 2):

- 189 1. Generate an initial web following the OF diet choice rules using eqn (1). Notably, this is not the
190 OF web against which the PR web will be compared.
- 191 2. Calculate the predation-risk index (P_{risk}) of each species using eqn (2).
- 192 3. Re-assign resource links for each species according to the diet-broadening strategy (Fig. 1C–E).
- 193 4. Repeat steps 2–3 until both P_{risk} and the web’s topology do not change anymore.

194 In step 3 we choose the diet-broadening strategy because using a diet-narrowing strategy effectively
195 reproduces the food-web structure predicted by the OF model (SI section 7). Thus, in each iteration of
196 steps 2–3, predation risk of certain consumers increases, which broadens the diet of those consumers
197 in order to find the best risk-compromised diet, which, in turn, imposes additional predation risk to
198 those newly-consumed species. This results in a sequential broadening of diets across trophic levels in
199 each iteration until a steady state where no more diet broadening (and therefore no more change in
200 predation risk) occurs.

201 Most food-web topological features, and nestedness and modularity in particular, are connectance-
202 dependent (Thébault & Fontaine 2010). Therefore, to generate PR and OF webs with comparable
203 connectance to the empirical web, we manipulated the magnitude of handling time (h_0 ; SI section
204 1.4) while generating the model webs, keeping species’ abundances fixed (SI section 3). We choose to
205 manipulate handling time instead of abundance to control food-web connectance because the aim of
206 our foraging models is to generate a predicted food web based on given information, and abundance
207 across a wide range of species is arguably better-quantified empirically (i.e., measured or estimated)
208 than handling time.

209 We note that the aim of this study is not to make the best model to reproduce food webs, but to
210 quantify the effect of predation risk and maintenance metabolic rate constraining optimal foraging
211 in food webs. We therefore focus on the difference between the foraging models *per se*, and do not
212 compare these with existing web-generating models such as the cascade (Cohen & Newman 1985)
213 and niche (Williams & Martinez 2000) models and their variants. This is also the reason why our

214 OF food-web assembly method differs fundamentally from the ADBM in that we do not search for
215 parameters that optimise the fit of the OF or PR models, as this would prevent us from effectively
216 comparing performance (predictive ability) of the OF and PR models for each set of parameterisations.

217 **Comparing ability of the foraging models to capture empirical food-web structure**

218 To compare the ability of the OF and PR models to capture real-world food-web structural properties,
219 we used twelve terrestrial and aquatic empirical food webs with nodes well resolved to the species
220 level (SI section 5). Because of the size-ratio biased (i.e., large-eats-small) nature of the allometric
221 constraints we use (also see Petchey *et al.* 2008), we confined our study to carnivorous, herbivorous,
222 and detritivorous interactions, excluding pathogenic, parasitic, and symbiotic interactions from each
223 empirical food web.

224 Based on four attributes of each empirical food web—species richness, identities of basal species,
225 species’ body masses, and connectance—we generated fifty OF- and PR-predicted food-web counterparts
226 each. The parameters X , a , A , h , and C_{\min} used for web-generation were specified as above-mentioned
227 but with the constant and exponent(s) re-sampled from a normal distribution with means equal to
228 the specified values and standard deviation as one tenth of the respective mean. This allowed us to
229 account for parameter uncertainty. The preferred body-size ratio, R_p , was set to be the observed
230 median resource-consumer body-mass ratio of each empirical web.

231 The connectance for the OF and PR model webs was matched to the empirical value by manipulating
232 h_0 value as mentioned above. The consumption rate threshold, C_{\min} , of the PR model automatically
233 set an upper bound for h_0 , preventing it from being biologically unfeasible. When h_0 becomes too
234 large, even the optimal consumption rate for certain species falls below C_{\min} , which is unfeasible and a
235 PR food web cannot be generated. This also imposes a lower-bound on the connectance that PR food
236 webs can achieve. During the simulation of PR food webs, we began by assuming a linear relationship
237 between predation risk of the focal consumer and the total biomass of its predators (i.e., e_P in eqn (2),
238 equals one). Whenever the combination of empirical community attributes and the parameter values
239 failed to produce a PR counterpart with acceptably close-to-empirical connectance (i.e., within 10%),
240 we lowered the extent of the diet-broadening effect by increasing e_P by 0.25 and re-assembled the PR
241 food web (SI section 1.5). This process was repeated until an acceptable PR food web was produced.
242 The summary of connectance and e_P values of the fifty replicates of each empirical community can be
243 found in Table S4 and shows that the mean value of e_P was typically not much larger than one.

244 Nestedness and modularity of empirical and model food webs were measured using the NODF and
245 modularity indices, respectively (Table S3). We quantified how well the two foraging models captured
246 these features of empirical food webs by calculating their absolute deviations from the empirical value.
247 The comparison of performance was made by collapsing the fifty replicates of the twelve communities
248 to 600 paired observations (paired by identity of replicates, as for each replicate the OF and PR web
249 are generated with the same set of re-sampled parameters), then checking whether the deviations
250 are smaller in PR than in OF. These paired observations were then compared using a linear mixed
251 model (LMM, using the `lmer` function of the R package `lme4` (Bates *et al.* 2014)), where the type of
252 model (OF vs. PR) was set as the fixed effect, and community and iteration as nested random effects.
253 To test if the performance results were consistent across different communities, we also conducted a
254 community-specific comparison of the above-mentioned deviations using a paired-Wilcoxon test. Along
255 with nestedness and modularity, we also analysed how well the two models captured several additional
256 metrics that are commonly used in the literature to quantify food-web structure (results in SI section

257 7).

258 **Synthetic food webs**

259 We also generated synthetic food webs to gain further insights into the differences in food-web structures
260 generated by the OF and PR models, the mechanisms generating these differences, and to test their
261 structural sensitivity. For this, we assembled and compared synthetic food webs based on the OF
262 model, PR model, and a null model where the links are randomly assigned. Structural differences
263 between OF and null food webs allow us to identify structural signatures of optimal foraging *per se*,
264 while differences between OF and PR webs allow us to understand the additional structural effects of
265 predation risk.

266 To test the sensitivity of our results to the structures of the metabolic models used for the foraging
267 parameters and in food-web attributes, we repeated the above simulations and comparisons across
268 fourteen schemes (Table S2). Each of these schemes is a unique combination of food-web attributes
269 (species richness, proportion of basal species, mean and variation of species body masses) and parameters
270 of foraging models (X , a , A , h , and e_P ; eqns (1) & (2)). Note that scheme 1 served as a baseline, with
271 all others varying one attribute or parameter at a time. For further details about schemes, see SI
272 section 1.4.

273 Thus, we independently simulated fifty synthetic communities for each scheme based on scheme-
274 dependent attributes and parameters. For each simulation, a given number of species were generated,
275 and a designated number of these were randomly picked to be basal species. Species body masses were
276 randomly drawn from a log-normal distribution (Preston 1948; Engen & Lande 1996; Pawar 2015)
277 with scheme-dependent mean and standard deviation, which were considered to cover a range that is
278 representative of empirical values (Table S4). Biomass densities of species were then derived based
279 on a scheme-dependent scaling exponent. Across the three derived food webs (OF, PR, and null) for
280 each synthetic community, the total number of links and the identities of basal species were kept the
281 same. Also, cases where extra basal species (i.e., additional species with no resource other than the
282 pre-picked basal species) or isolated basal species (i.e., basal species with no species consuming them)
283 were by chance produced were discarded and replaced with new simulations. As the parameters were
284 kept constant under each scheme, the variation among replicates here is due to the difference in species
285 composition among synthetic communities. Structure quantification was done in the same way as
286 described in the previous section. For each scheme, we compared the model-generated nestedness and
287 modularity by LMM with the type of model (i.e., OF vs. PR vs. null) as the fixed and iteration as the
288 random effect.

289 **Results**

290 In general, the PR model predicts the two key empirical food-web features better than the OF model.
291 For nestedness, the PR model deviates significantly less from empirical networks than does the OF
292 model (Fig. 2), though empirical food webs tend to be more nested than the counterparts predicted by
293 either foraging model (Fig. 3A). The PR model produces closer-to-empirical nestedness in nine out of
294 twelve empirical communities (Fig. 3A). In terms of modularity, the deviations of the PR model are
295 again significantly smaller than those of the OF model (Fig. 2). How model-predicted webs differed
296 from the empirical webs was community-dependent (Fig. 3B). Here again, the PR model performs
297 better in nine out of twelve empirical communities (Fig. 3B).

298 Our analysis of synthetic food webs demonstrates that the structural features generated by the
299 foraging models are largely insensitive to variation in food-web attributes or specification of the
300 mathematical structure of the foraging parameters (Fig. 4). The OF model tends to produce more-
301 nested synthetic food webs than the null model in practically all schemes, and the PR model consistently
302 generates more-nested food webs than the OF model (Fig. 4A). In contrast, the modularity of model-
303 generated synthetic webs, in comparison to null webs assembled at random, did depend on the scheme.
304 Nevertheless, the differences between the OF and PR model predictions *per se* remain robust across
305 schemes, with OF food webs nearly always being more modular (Fig. 4B).

306 Besides the focal structural measures of nestedness and modularity, we also measured several other
307 food-web structural metrics. The PR model also better captured empirical values than the OF model
308 in the level of clustering, and variation in resource-consumer body-size ratios. Synthetic webs also
309 showed a systematic and robust difference between the two models for all metrics. For further details,
310 see SI section 7.

311 Discussion

312 Understanding the mechanisms and constraints that lead to the typically non-random structures of food
313 webs remains a central challenge in ecology (May 1973; McCann 2000; Allesina & Tang 2012; Rossberg
314 2013). We have shown that predation risk constrains optimal foraging in ways that have significant
315 consequences for food-web structure. Specifically, an assembly model that incorporates predation risk
316 (PR) generates more nested but less modular food webs than by optimal foraging (OF) alone, providing
317 a better fit to the empirical data for both of these measures (Fig. 2–3). In addition, PR also causes
318 other food-web features to deviate systematically from those produced by the consumer-centric OF
319 model (SI section 7).

320 Under both OF and PR assembly, the trophic level of consumers increases with their body mass,
321 and in-degree (diet breadth) has a dome-like relationship with body mass (Fig. S4 & S5) because the
322 preferred body-size ratio (R_p) is fixed. However, predation risk results in a broader diet at intermediate
323 trophic levels than OF alone (Fig. 5B–C), which is also more empirically realistic (Fig. 5A). Furthermore,
324 nestedness quantifies how much the diet of some consumers are subsets of the others, so it increases
325 with the average diet overlap among species. The risk-driven increase in diet breadth of intermediate
326 trophic-level (also intermediate-sized) consumers, effectively increases diet overlap, and therefore also
327 nestedness. Thus, the predation-risk constraint helps to explain why empirical food webs are more
328 nested than randomly-connected ones. Modularity, on the other hand, is essentially a measure of
329 compartmentalisation—the degree to which species’ can be rearranged as highly connected groups with
330 few inter-group connections. A food web has high modularity if the diet matrix can be arranged in
331 distinct blocks. Thus, the diet-broadening effect of predation risk at intermediate trophic levels may
332 increase the diet overlap within groups, making them more strongly connected, effectively increasing
333 modularity. However, it may also blur the distinction among groups, effectively decreasing modularity.
334 Therefore, the change in modularity produced by PR is less predictable than nestedness, and largely
335 depends on the body-size structure of the community (Fig. 4B).

336 Overall, incorporating predation risk improves the predictive ability of OFT-based assembly models.
337 This improvement is not tremendous but significant. Although we compared empirical and model-
338 generated food-web structures using a particular model structure, our study of synthetic food webs
339 shows that our results are robust to variation in model structures and parameterisations. Thus, in

340 nature, predation risk likely affects consumers' diet choice in a similar manner to the mechanisms we
341 modelled. Specifically, consumers essentially have to meet multiple objectives or constraints while
342 choosing their diet composition: maximizing consumption rate and (classical consumer-centric optimal
343 foraging), meanwhile mitigating predation risk and maintaining a minimal consumption rate necessary
344 for somatic maintenance. Nevertheless, the PR-predicted food-web structures still show considerable
345 discrepancies from empirical webs. In particular, empirical food webs are consistently much more
346 nested than model-predicted webs. There may be a number of reasons for these discrepancies, and our
347 general framework can be extended in multiple ways to arrive at more precise models for predicting
348 trophic links in real food webs.

349 First, the conversion coefficient (ϵ ; eqn (1)), the dimensionality of search rate (a ; SI section 1.4),
350 and preferred body-size ratio (R_p ; SI section 1.4) are each assumed to be constant across species.
351 However, all of these likely vary in the real world. R_p , in particular, determines the shape of attack
352 success probability (A ; SI section 1.4) and handling time (h ; SI section 1.4) across the spectrum of
353 resource-consumer body-size ratios. This, in turn, influences the degree of diet overlap among species
354 and therefore the web's nestedness. Comparing scheme 12 to scheme 1 (Table S2) of the synthetic food
355 webs as an example, we showed that the way null webs differ from the OF and PR webs in nestedness
356 is mainly affected by the shape of the chosen handling time function (eqn (S21) vs. eqn (S23); Fig. 4A).
357 Therefore, improved data on species-wise R_p 's will likely improve the the ability of both OF and
358 PR models to predict the nestedness of empirical webs. Similarly, literature has shown that ϵ differs
359 between consumer types (e.g., carnivores vs herbivores) (Lang *et al.* 2017), and the exponent as well as
360 intercept of the body-size scaling of search rate varies between 2D and 3D interactions (Pawar *et al.*
361 2012). Incorporating better-resolved information on these parameters, if available, would be expected
362 to generally improve the predictive ability as well.

363 Second, when assembling food webs, we allowed all species in the community to be a potential
364 resource of each consumer. However, in reality, species may have foraging or anti-predator traits,
365 or spatio-temporal differences in phenology (Holomuzki 1986; Tollrian 1995; Relyea 2001; Turner &
366 Montgomery 2003; Mikolajewski *et al.* 2010; Eklöf *et al.* 2013) that essentially forbid certain links.
367 These body-size irrelevant constraints could possibly be better captured by food-web models based on
368 phylogenetic relatedness (Cattin *et al.* 2004; Naisbit *et al.* 2012), which encodes such information. In
369 this study, we adopt a size-driven mechanistic modelling approach to focus on our aim, which is to
370 explore how our understanding of food-web structure can be improved by including metabolic and
371 predation-risk constraints into OFT, but necessarily ignore these other constraints.

372 Third, the form of the predation-risk index (P_{risk}) function (eqn (2)) could also be refined. We
373 have assumed that the risk to a focal species increases monotonically with the number of its realised
374 consumer species and their abundances, with the rationale that other mechanisms affecting predation
375 risk are less important than consumer abundance itself. More work on the mechanistic basis of the
376 predation risk function may lead to more accurate PR assembly models. For example, at high consumer
377 densities, interference among consumers is expected to increase (Skalski & Gilliam 2001), possibly
378 leading to a non-monotonic predation-risk index.

379 Lastly, animals may respond to predation risk by decreasing total foraging time (Lima & Dill 1990;
380 Beckerman *et al.* 1997) and pay the cost of predator evasion through an increased metabolic rate (e.g.,
381 Hawlena & Schmitz 2010). These can practically be incorporated into the PR model by switching
382 C_{min} from a fixed value to a risk-dependent variable, such that if the increasing predation risk results
383 in the total foraging time of a consumer being cut by half (or its metabolic rate being doubled), its

384 C_{\min} should also become twice as large according to the energy balance concept. Moreover, it is also
385 possible that a risk-driven response of animals leads to a re-ranking of their profitabilities (e.g., forming
386 a defensive group, thereby lowering the consumer’s attack success) which would, in turn, influence the
387 OFT-based diet predictions. Such nuanced behaviours highlight the potential of extending the PR
388 model.

389 Although the empirical webs we used are all relatively well-sampled (SI section 5), food webs
390 are known to be under-sampled generally (i.e., existent links are not detected), which leads to poor
391 estimates of food-web metrics (Goldwasser & Roughgarden 1997; Martinez *et al.* 1999; Banašek-Richter
392 *et al.* 2004; Tylianakis *et al.* 2010; Wood *et al.* 2015). However, the two features we focus on—nestedness
393 and modularity—have been shown to be robust to such artefacts (Nielsen & Bascompte 2007; Tylianakis
394 *et al.* 2010; Rivera-Hutinel *et al.* 2012; Vizentin-Bugoni *et al.* 2016). More importantly, there is no
395 reason to expect that sampling artefacts are likely to bias construction of PR counterparts more
396 than OF ones, and our results should hold qualitatively even as higher quality food-web data become
397 available. A related food-web sampling issue is the common practise of using the average adult state as
398 being representative of a species’ role in the ecosystem. In reality, individuals of a species vary in body
399 size, and often forage differently across life stages. Omitting such intraspecific variation or ontogenetic
400 shifts in diet could fundamentally bias our understanding of empirical food-web structure (Clegg *et al.*
401 2018). In this study, we have also ignored such diet variation in both our modelling and empirical
402 validation due to limits on the resolution of empirical data. Nonetheless, our models could also be
403 applied to webs resolved to the ontogenetic level if data are available—the same assembly algorithm
404 can be used.

405 Predation risk is also likely to have consequences for food-web dynamics and stability (Kondoh
406 2007), which we have not explored here. That is, we fixed species biomass abundances to generate
407 food-web structures. Our model can be extended to tackle species dynamics within a food web by
408 setting biomass abundance as a variable, and letting species adjust their diet in an abundance-dependent
409 manner (adaptive foraging, Kondoh 2003). Note that predation risk in such cases can also be an
410 abundance-dependent dynamical feature of species. Future work can build on our metabolic framework
411 for incorporating predation risk effects, and investigate both the dynamics of species abundance and
412 predation risk, and their joint effects on food webs.

413 Our results also provide novel insights for foraging ecology. Firstly, the diet-broadening (instead of
414 diet-narrowing) strategy implicit in our PR model is consistent with empirical evidence that consumers
415 tend to broaden their diet by taking less-profitable resources (Lima & Valone 1986; Metcalfe *et al.* 1987;
416 Rothley *et al.* 1997). That the PR model, through this diet-broadening strategy, results in food-web
417 structures closer to reality than the OF model (same as diet-narrowing; SI section 7), suggests that
418 searching/waiting may be indeed riskier than handling across food webs—likely because animals can
419 hide or be camouflaged while handling food (Charnov & Orians 1973). Secondly, most empirical tests
420 of OFT indeed show that the classical model frequently under-predicts diet breadths (Krebs *et al.* 1977;
421 Elner & Hughes 1978; Mittelbach 1981; Sih & Christensen 2001). This discrepancy has been proposed
422 to be due to consumers’ imperfect foraging information. Our study suggests that predation risk could
423 also give rise to such broader-than-optimal diets. We encourage future work to validate this risk-driven
424 diet-broadening effect via empirical experiments. Thus, our results suggest that not just OFT-based
425 food-web assembly rules, but also OFT itself needs to be revisited by incorporating predation risk.
426 This may re-vitalise OFT, which has gradually faded from the research focus of ecologists (SI section
427 9).

428 In conclusion, our study answers the call to add further dimensions beyond body size (Allesina
429 2011; Eklöf *et al.* 2013; Jonsson *et al.* 2018), including non-trophic effects (Terry *et al.* 2017), into
430 food-web models. It shows that predation risk could be a significant factor affecting food-web assembly
431 and the emergent structure. Many models have been proposed to predict empirical food-web structure
432 over the last three decades (Cohen & Newman 1985; Williams & Martinez 2000; Beckerman *et al.*
433 2006; Petchey *et al.* 2008), but few have formally incorporated predation risk (Kondoh 2007). The
434 field has also not yet reached an effective synthesis of metabolic and foraging theories. Our study is
435 the first major advance in that direction since the ADBM study (Petchey *et al.* 2008). Food webs
436 represent the roles of species as both consumers and resources, and considering the joint constraints on
437 foraging behaviour of these dual roles (Naisbit *et al.* 2012) is a necessary step towards truly capturing
438 the complexity of real ecosystems.

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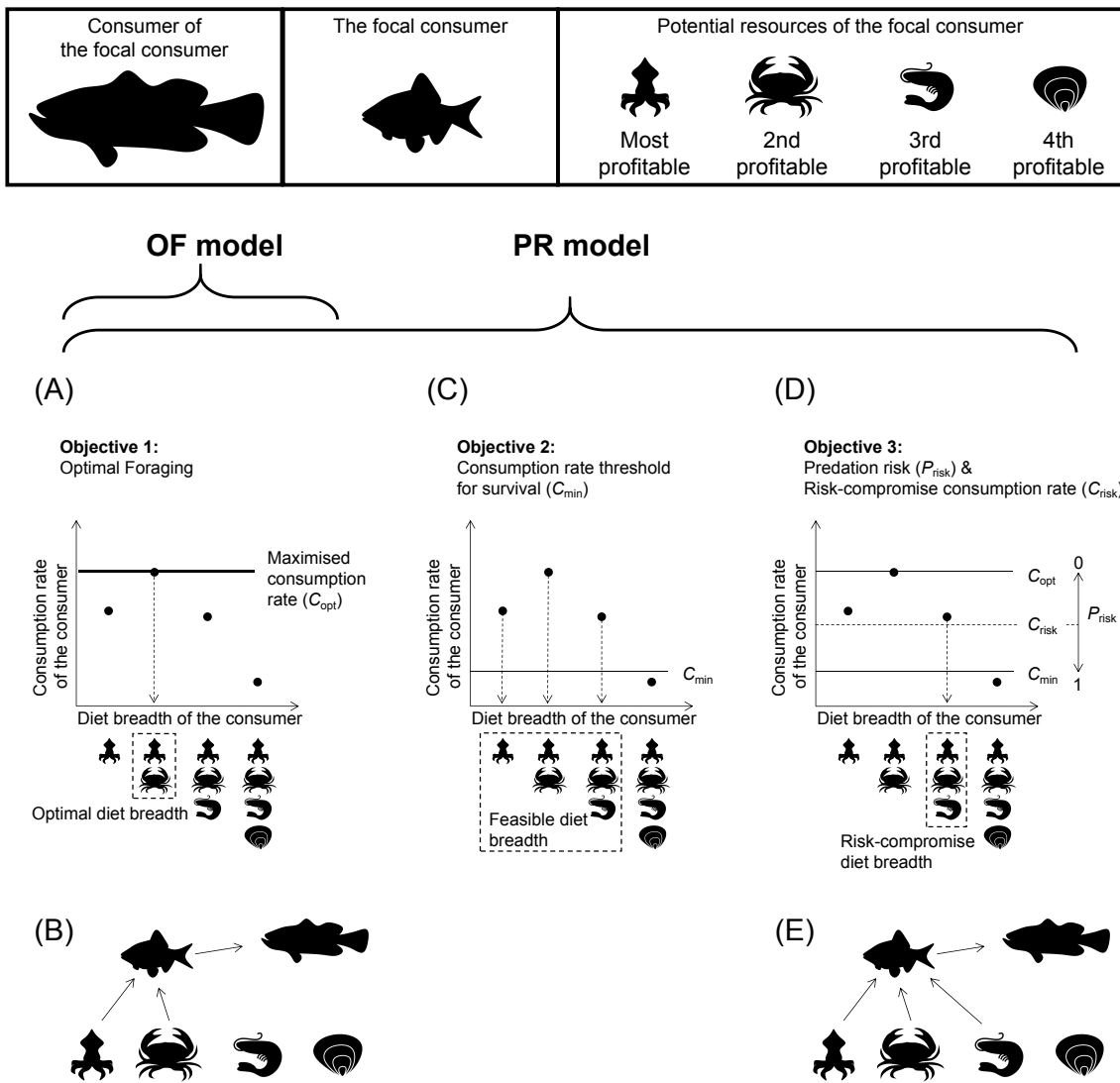


Figure 1: Illustration of the **Optimal Foraging (OF)** and **Predation Risk-Compromise (PR)** models for predicting the diet breadth of a focal consumer. Under the OF model (A–B), the predicted diet for a consumer is the one that yields maximum net consumption. Under the PR model (A, C–E) predation risk, P_{risk} , is incorporated as a constraint on optimal foraging, resulting in a suboptimal diet with a risk-compromise consumption rate (C_{risk} , the point closest to, while still being above, the horizontal dashed line in D) lying somewhere between the OF maximum, C_{opt} , and a minimum metabolically-feasible consumption rate threshold, C_{min} . Both models are applied to all consumer species in a community to assemble model food webs. Note that we focus on the diet-broadening strategy in the PR model, which “propagates” iteratively during food-web assembly, as described in the main text.

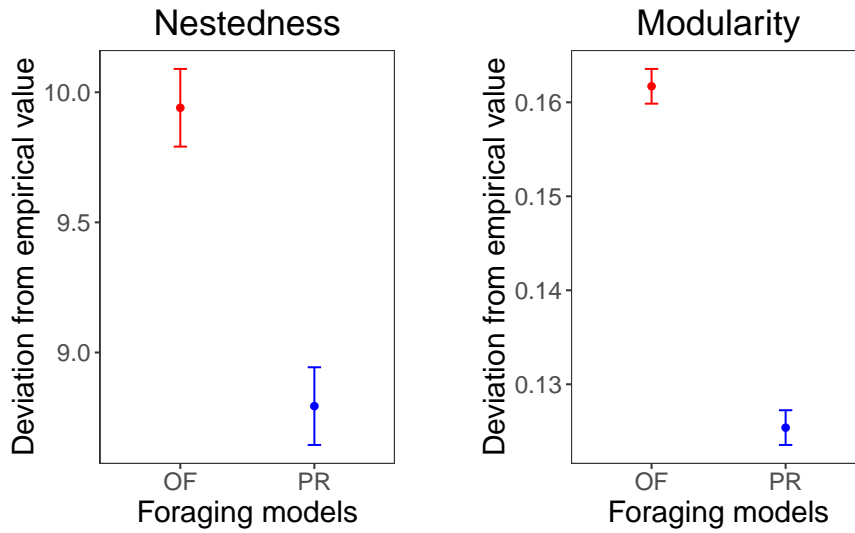


Figure 2: **Performance of the Optimal Foraging (OF) and Predation Risk-Compromise (PR) models in capturing nestedness and modularity of empirical food webs.** The absolute deviations from the empirical value of both foraging models are shown as mean \pm 95% CI (LMM fixed-effect uncertainty only). The PR model has deviations significantly smaller than those of the OF model in both nestedness and modularity measurements ($p < 0.001$ in both cases). Note that empirical nestedness reads 21.29 ± 14.30 and modularity 0.18 ± 0.15 (mean \pm SD). The absolute deviations of nestedness are not directly comparable with those of modularity. For results using standardised values, see Fig. S3.

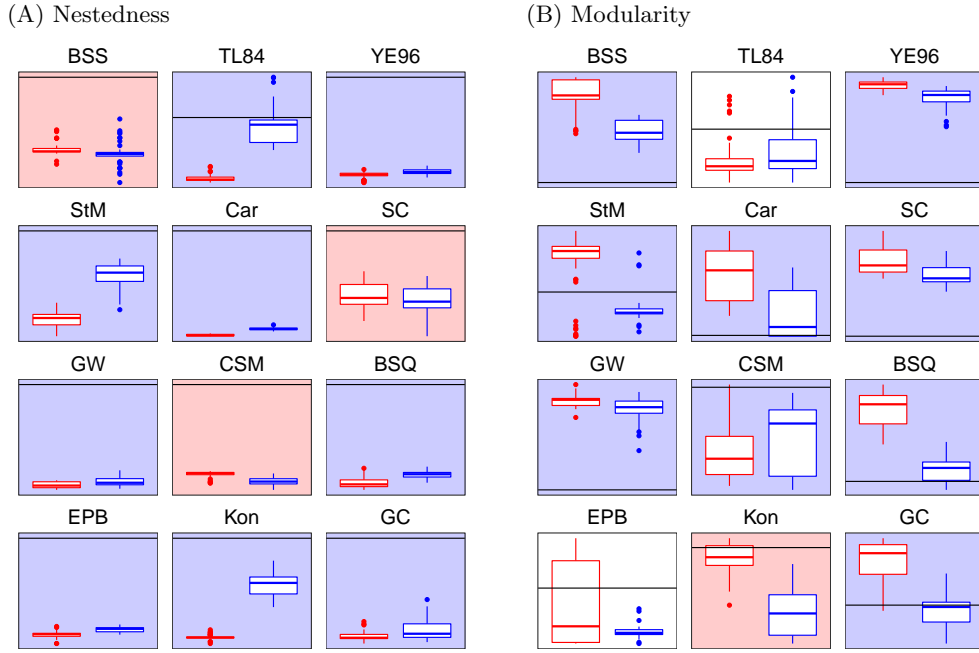
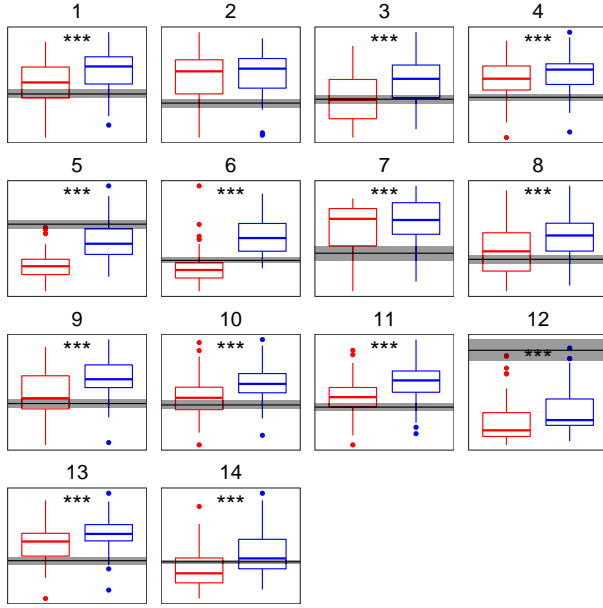


Figure 3: **Comparison of nestedness and modularity of empirical food webs and their model (OF and PR) counterparts.** Community name abbreviations are in Table S4. The red and blue colours refer to OF and PR food webs, respectively. The black horizontal line presents the empirical value, whereas the box plots present the model-generated values. The background of the plots are also coloured in red or blue shade to indicate which of the OF and PR value is significantly closer ($p < 0.05$, no shading if not significant) to the empirical one, according to a paired-Wilcoxon test on the deviations from the empirical values. Out of twelve empirical communities, the PR model produces closer-to-empirical nestedness (A) and modularity (B) values in nine communities for each metric, indicating its superior performance. As the relative, rather than absolute, values matter here, we have omitted the y-axes scales for simplicity (as in Fig. 4 and Fig. S4-S7.)

(A) Nestedness



(B) Modularity

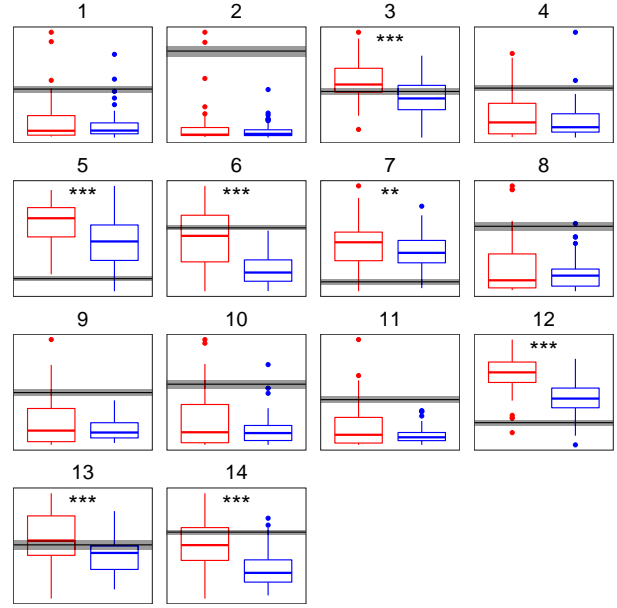
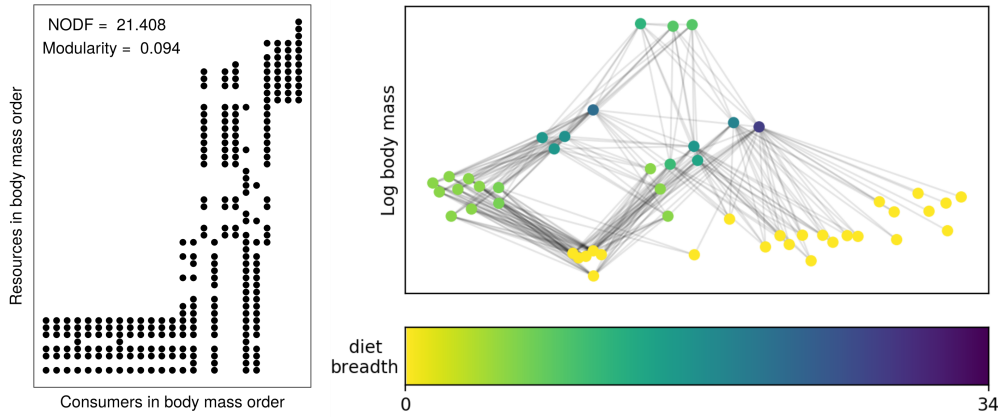
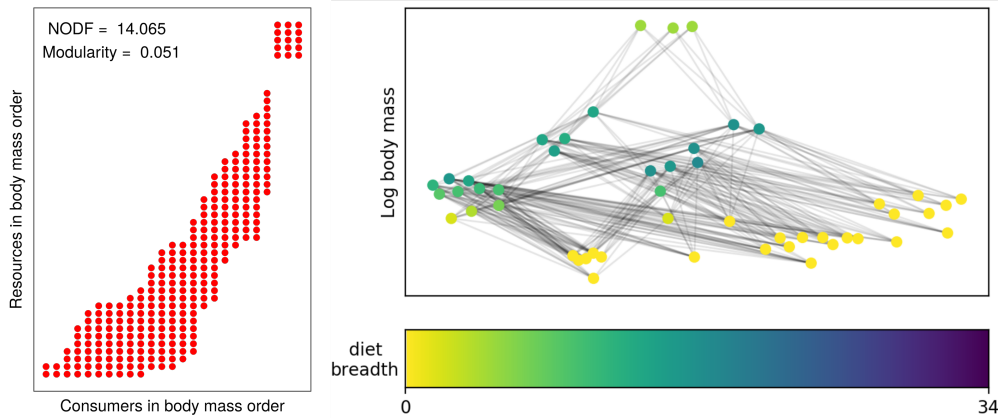


Figure 4: **Summary of nestedness and modularity of OF, PR, and null food webs.** Scheme IDs are indicated on the top of each plot (key in Table S2). Red and blue colours refer to OF and PR food webs, respectively. The black horizontal line with shade presents the mean \pm 95% CI of null food webs observations, whereas the box plots present the model-generated observations. The asterisks indicate whenever the OF/PR values are significantly larger than the other (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. LMM results may be based on transformed data to meet model assumptions, see SI section 6). There is a tendency for PR webs to be more nested than the OF webs (A), whereas the reverse is true for modularity (B).

(A) Empirical food web (TL84)



(B) Optimal foraging food web



(C) Optimal foraging with predation risk food web

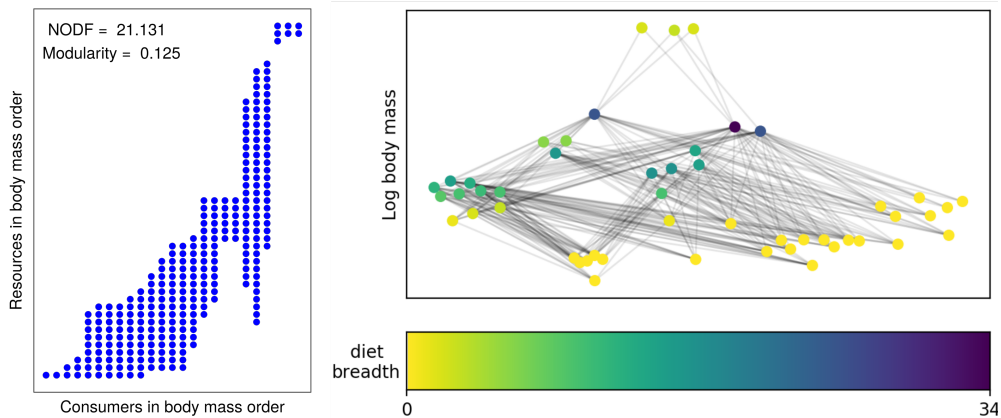


Figure 5: **Illustration of how predation risk affects nestedness and modularity of food webs by diet broadening at intermediate trophic levels.** The size-ordered diet matrix and corresponding network of empirical web TL84 (A) is shown, along with its OF (B) and PR (C) counterparts generated from a single model simulation. Each dot in the diet matrix indicate a trophic interaction between a consumer (column) and a resource (row) species. Each network representation was produced by a visualisation algorithm (Zheng *et al.* 2018, SI section 8); species' nodes are colored by diet breadth (darker nodes have broader diet).