

- 1 **Trait-matching models predict pairwise interactions across regions, not food web**
- 2 **properties**
- 3
- 4 **Running title:** Interaction models transferability
- 5
- 6 **Abstract**
- 7 **Aim:** Trophic interactions are central to our understanding of essential ecosystem functions as
- 8 well as their stability. Predicting these interactions has become increasingly common due to the
- 9 lack of empirical data on trophic interactions for most taxa in most ecosystems. We aim to
- 10 determine whether and how accurately we can extrapolate to new communities both in terms of
- 11 pairwise predator-prey interactions and higher-level food web attributes (i.e., species position,
- 12 food web-level properties).
- 13 **Location:** Canada, Europe, Tanzania.
- 14 **Time period:** Current.
- 15 **Major taxa studied:** Terrestrial vertebrates
- 16 **Methods:** We use a trait-based model of pairwise trophic interactions, trained independently on
- 17 four different terrestrial vertebrate food webs (Canadian tundra, Serengeti, alpine south-eastern
- 18 Pyrenees, and entire Europe) and assess the ability of each instance of the model to predict
- 19 alternative food webs. We test how well predictions recover individual predator-prey interactions
- 20 as well as higher level food web properties across geographical locations.
- 21 **Results:** We find that, given enough phylogenetic and environmental similarities between food
- 22 webs, trait-based models predict most interactions and their absence correctly ($AUC > 0.82$),
- 23 even across highly contrasting environments. However, network metrics were less well-predicted

24 than single interactions by our models. Predicted food webs were more connected, less modular,
25 and had higher mean trophic levels than observed.

26 **Main conclusions:** Theory predicts that the variability observed in food webs can be explained
27 by differences in trait distributions and trait-matching relationships. Trait-matching relationships
28 are conserved across regions and ecosystems. This suggests that food webs vary spatially
29 primarily through changes in trait distributions. These models, however, are less good at
30 predicting system level food web properties. Predicting ecological networks will require a
31 modelling approach that simultaneously address trophic interactions and the structure of food
32 webs across time and space.

33

34 **Key Words:** ecological predictions; food web; model transferability; terrestrial vertebrates; trait
35 matching; trophic interactions

36 **Introduction**

37 Ecosystem functions (e.g., energy flows and material cycling) and community stability depend
38 on the trophic relationships that link species within a community (Harvey et al., 2017). Despite
39 the importance of food webs for understanding ecosystem structure and dynamics, recognized
40 over the last 80 years (Lindeman, 1942), we still face major challenges to develop accurate
41 descriptions of natural food webs. The lack of trophic interactions data across most locations and
42 taxa (Poisot et al., 2021) lies at the core of the fundamental technical and practical challenges in
43 food web ecology. Observing interactions is more challenging than observing species because
44 two individuals need to be simultaneously detected while interacting (Jordano, 2016). This
45 challenge is exacerbated by the fact that the number of possible interactions in food webs
46 increases quadratically with the number of species, making the potential set of observations to be
47 made extremely large. Determining all possible interactions among species within a food web is
48 thus difficult even in species-poor ecosystems, which calls for a systematic approach to predict
49 links.

50

51 Food web theory predicts that the matching between the functional traits of predators and those
52 of their prey (e.g., smaller predators eat smaller prey) should identify interactions that are
53 feasible (Morales-Castilla et al. 2015). Trait-based models have been used to predict food webs
54 in freshwater streams (Pomeranz et al., 2019), marine fishes (Albouy et al., 2014), terrestrial
55 systems comprising vertebrate (Caron et al., 2022; Fricke et al., 2022) and invertebrate species
56 (Laigle et al., 2018), among others. Phylogenetic relationships are also informative since they
57 can serve as proxy for trait relationships, and because interactions and species role (i.e., species

58 positions in the food web) tend to be evolutionary conserved (Gómez et al., 2010; Stouffer et al.,
59 2012).

60

61 It is, however, still unclear how well predictive models of pairwise trophic interactions can
62 transfer knowledge across different regions. If trait-matching rules determining interactions are
63 general, then i) we should observe the same traits-interaction relationships across regions and ii)
64 a model trained in a location should be transferable to another one. Strydom et al. (2022)
65 provided illustration of model transferability, but it needs to be tested more rigorously. The
66 authors use a mammal phylogeny to map latent traits extracted from the European mammalian
67 food web to predict its Canadian counterpart, and were able to recover 90% of known trophic
68 interactions among Canadian mammals without any prior information on the food web. Europe
69 and Canada share similar bioclimatic conditions and, despite the few species common to both
70 regions, more than half of Canadian mammals have congeneric species in Europe. Thus, this
71 demonstration of model transferability results raise the question of how trait-based inferences of
72 trophic interactions would transfer to more contrasting environments?

73

74 It is also unclear how well trophic interaction models can predict the underlying structure of
75 entire food webs emerging from pairwise trophic interactions. Food web structure encompasses
76 system-level properties such as connectivity or number of trophic levels, as well as species traits
77 such as number of prey or their position within the food web. Most studies are aimed at
78 predicting either the properties of food webs (e.g., Williams and Martinez 2008) or their pairwise
79 interactions (e.g., Laigle et al. 2018; Pomeranz et al. 2019). They rarely assess how well

80 predicted interactions can recover food web structure. Despite being able to recover most trophic
81 interactions among European tetrapods, Caron et al. (2022) found that food web connectance
82 was systematically overpredicted across Europe by 2-4 times. However, to our knowledge, how
83 well trophic interaction models predict other food web properties (e.g., maximum trophic level,
84 modularity) or species positions (e.g., trophic level, centrality) has never been tested.

85

86 Here, we test whether predictive trait-matching models trained using a network of predator-prey
87 interactions (i.e. a food web) from one geographical region of the world can reliably predict
88 pairwise interactions, species role, and food web structure in other regions. We use terrestrial
89 vertebrate food webs from Europe, the Pyrenees, Northern Québec and Labrador, and the
90 Serengeti, to fit trait-based Bayesian hierarchical models to study transferability across regions.
91 We aim to (1) identify the factors (i.e., geographic, environmental, functional, or phylogenetic
92 distances) influencing the generality of trait-matching models of pairwise interactions across
93 geographical regions, (2) predict trophic roles across species and (3) quantify the predicted food
94 web properties. First, we expect more similar food webs will yield better transferability since the
95 similarity of the functional relationships driving interactions should depend on the similarity of
96 the environment and species composition of the respective food webs (Gravel et al., 2016).
97 Second, , we expect the prediction of pairwise interactions to be better to that of food web
98 properties. Some processes constraining food web properties (e.g., the number of feasible
99 interactions) act at scales different than the processes driving pairwise, which is commonly the
100 focus of trophic interaction models (Strydom et al., 2021). This scale mismatch between the
101 processes modelled and the processes influencing food web properties are likely to create
102 discrepancies between the predicted and observed food webs.

103

104 **Methods**

105 *Food web data*

106 We extracted predator-prey interactions among terrestrial vertebrates (mammals, birds,
107 amphibians and reptiles) from four well-resolved food webs (Table 1, Figure 1): the European
108 food web of tetrapods (Maiorano et al., 2020), the Pyrenees vertebrate food web (Lurgi et al.,
109 2012), the Northern Québec and Labrador food web (Berteaux et al., 2018), and the Serengeti
110 food web (de Visser et al., 2011). All four food webs were compiled from literature review and
111 completed by expert knowledge. The four food webs document the predator-prey interactions
112 between all known terrestrial vertebrates in their respective geographical region. Trophic
113 interaction is defined as a binary variable where 0 represents the absence and 1 the presence of a
114 predator-prey interaction between two species. Since all food webs document *potential*
115 interactions (i.e., the predator could feed on the prey species), and use expert knowledge to
116 define these trophic relations, we assume that they are less sensitive to incomplete sampling than
117 observation-based food webs (i.e., interactions and non-interactions are similarly uncertain).
118 Nodes in the original Serengeti food web represent trophic groups including one or more
119 vertebrate species. In this study, we assumed that species within a trophic group share the same
120 predator and prey species. Thus, we can expect more false positives (i.e., non-interactions
121 documented as interactions) in the Serengeti than in the other three food webs. Food webs are
122 fully described in Appendix S1.

123

124 The species composition of the four food webs are different (Table 1). There are no amphibians
125 or reptiles in Northern Québec and Labrador; the Pyrenees food web is dominated by birds

126 (67%) and mammals (23%), with very few reptiles (8%); the European food web has a
127 comparable number of reptiles (21%) and mammals (25%), and almost half (46%) of the
128 Serengeti food web are mammals. The Europe, Pyrenees, and Northern Québec and Labrador
129 food webs all have comparable mean trophic levels (between 1.24 and 1.3) and connectance
130 (between 0.02 and 0.05) compared to the Serengeti food web (mean trophic level: 1.61;
131 connectance: 0.12). Here, the first trophic level (i.e., basal species) are defined as species not
132 feeding on any other terrestrial vertebrates. In Europe, the Pyrenees and Northern Québec and
133 Labrador most species are basal species (e.g., insectivores, herbivores, piscivores), whereas
134 many more species feed on terrestrial vertebrates (non-basal species) in the Serengeti.

135

136 *Trait data*

137 We extracted functional traits from the database compiled by Etard et al. (2020). This dataset
138 combines species-level information from large freely available secondary trait databases (e.g.,
139 EltonTraits: Wilman et al. (2014), AmphiBIO: Oliveira et al. (2017)). Overall, the database
140 includes traits for 6 990 amphibian, 11 634 bird, 5 380 mammal, and 10 612 reptile species. We
141 extracted the available body mass (mean: 11 kg; range: 0.001–4 220 kg), longevity (mean: 5 885
142 days; range: 91–46 386 days), litter or clutch size (mean: 131 offspring; range: 1–20 000
143 offspring), habitat breadth (number of habitats a species uses, using level 2 of the IUCN Habitat
144 Classification Scheme; mean: 10 habitats, range: 1–90 habitats), trophic level (3 levels:
145 herbivore, omnivore, carnivore), activity time (2 categories: nocturnal, non-nocturnal) and
146 habitat use (12 categories: forest, savanna, shrubland, grassland, wetland, rocky
147 areas/cave/subterranean, desert, marine, marine/intertidal or coastal/supratidal, artificial,
148 introduced vegetation) for every species considered in our study.

149

150 We standardized species names following the taxonomic backbone of the Global Biodiversity
151 Information Facility (GBIF) using the function *name_backbone* from the package *rgbif*
152 (Chamberlain et al., 2022) in the R statistical language (R Core Team, 2022). We excluded
153 species for which no taxonomic information or none of the traits were available. Species traits
154 were available for more than 80% of species across all food webs (Table 1; Appendix S2). For
155 remaining species, we imputed missing traits using the MissForest algorithm implemented in the
156 *missForest* R package (Stekhoven & Buehlmann, 2012) for amphibians, birds, mammals and
157 reptiles separately. MissForest uses random forests to iteratively predict missing data from the
158 known data. Each random forest uses a different trait as response variable and the remaining
159 traits as predictors.

160

161 *Phylogeny data*

162 We used phylogenetic data to measure how model transferability was influenced by phylogenetic
163 relatedness. We used published global phylogenies for birds (Jetz et al. 2012), amphibians (Jetz
164 and Pyron 2018), squamates (Tonini et al., 2016), turtles (Thomson et al., 2021), and mammals
165 (Upham et al., 2019). All five phylogenies were built from molecular data and delivered as a
166 posterior distribution of trees. We sampled 100 trees from the posterior of each phylogeny and
167 calculated the mean cophenetic distance from these samples between all species of the four food
168 webs. Following Letten & Cornwell (2015), we square root transformed cophenetic distances to
169 better relate to ecological processes such as trophic interactions.

170

171 *Predictive models*

172 We trained a Bayesian hierarchical generalized linear model on each of the four food webs
173 (Figure 1a) with trophic interactions following a Bernoulli distribution. Because Caron et al.
174 (2022) found that trait-interaction relationships vary between predator groups, we added varying
175 slope and intercept terms for the taxonomic order of predators. For each model, we randomly
176 drew 30% of the data for validation to keep the prevalence of trophic interaction in the validation
177 subset equal to the prevalence of the entire food web. We used all predator-prey interactions of
178 the remaining 70% of the data and an equal number of absence of interactions for calibration.

179

$$L_{ij} \sim \text{Bernoulli}(p_{ij}),$$

180

$$\text{logit}(p_{ij}) = \alpha + \alpha_{\text{predator}[j]} + \sum_{k=1}^{13} (\beta_k \times T_k + \beta_{k,\text{predator}[j]} \times T_k),$$

181 where L_{ij} is the occurrence of interaction between predator j and prey i , p_{ij} is the associated
182 probability of interaction, α is the fixed intercept and β_k the slope corresponding to the trait-
183 based predictor T_k in the linear model. Similarly, $\alpha_{\text{predator}[j]}$ is the random intercept and
184 $\beta_{k,\text{predator}[j]}$ the random slope corresponding to the trait-based predictor T_k for the order of
185 predator j .

186

187 We used 13 trait-based predictors in the models: five predator traits (trophic level, body mass,
188 habitat breadth, longevity, and clutch size), five prey traits (trophic level, body mass, habitat
189 breadth, longevity, and clutch size), and three trait-match predictors (match in activity time,
190 habitat use and body mass). Since the activity time trait is binary (nocturnal and non-nocturnal),
191 activity time match is also a binary variable where a 1 means the predator and the prey share the
192 same activity time trait. Habitat match is the Jaccard similarity index between the habitat used by
193 the prey and the predator across the 12 habitat categories, which takes into account overlap in

194 habitat and specialization to shared habitats. Body mass match is the squared difference between
195 the log-transformed body mass of the prey and the predator, because we expect predators to eat
196 prey within a given body mass interval (small enough to be handled, but large enough to be
197 profitable. We log-transformed body mass, longevity and clutch size, and scaled each continuous
198 predictor (after transformation) by subtracting out the mean and dividing by two times the
199 standard deviation so coefficients of continuous predictors are comparable to unscaled binary
200 predictors (Gelman, 2008).

201

202 Fixed effects were drawn from a normal distribution with a mean of 0 and a standard deviation of
203 1. Random effects were drawn from normal distributions. We used a normal distribution with a
204 mean of 0 and a standard deviation of 1 as prior for the mean and a Half-Cauchy distribution
205 with a scale parameter of 5 as prior for the standard deviation of the random effects:

206 $\alpha, \beta \sim Normal(0, 1)$

207 $\alpha_{predator[j]}, \beta_{k,predator[j]} \sim Normal(\mu, \sigma)$

208 $\mu \sim Normal(0, 1)$

209 $\sigma \sim HalfCauchy(0, 5)$

210 Model parameters were estimated with Hamiltonian Monte Carlo (Neal, 2011). We ran four
211 chains, each with 2000 warm-up iterations, followed by 2000 iterations for inference. We
212 diagnosed convergence and adequacy with trace rank plots, posterior predictive checks, and we
213 calculated the rank-normalized potential scale reduction factor on split chains for all runs
214 (Vehtari et al. 2021; Appendix S6). We conducted the analyses using Stan (Carpenter et al., 2017)
215 through the package *brms* in R (Bürkner 2017).

216

217 *Predicting species interactions*

218 We used each model to predict the food web on which it was trained and that of the other regions
219 considered (Figure 1a). For each possible predator-prey pair, we extracted the mean of the
220 posterior as the probability of interaction, and the standard deviation of the posterior as the
221 uncertainty around the predicted probability of interaction. We compared the predicted
222 interaction probabilities to the validation subset of the same food web (i.e., within food web
223 predictions) and compared the predicted interaction probabilities to entire empirical food webs
224 (i.e., between food web predictions). We measured performance with the area under the receiver
225 operating characteristic curve (AUC; Hanley and McNeil 1982). AUC varies from 0 to 1 where
226 0.5 indicates that the model failed to rank interactions higher than absences of interactions (i.e.,
227 random predictions), and 1 indicates that the model systematically ranked interactions higher
228 than non-interactions (i.e., perfect predictions). We also measured the area under the precision-
229 recall-gain curve (AUPRG; Flach & Kull, 2015). AUPRG is independent of the true negative
230 rate, making it useful for highly imbalanced datasets, like food webs where there are many more
231 non-interactions than interactions to predict (Saito & Rehmsmeier, 2015). AUPRG takes a value
232 of 0 for random predictions, and a value of 1 for perfect predictions.

233

234 We assessed the performance of models to predict each food web using three distance measures:
235 geographic distance, environmental dissimilarity, and phylogenetic relatedness. We measured
236 geographic distance as the [great-circle distance](#) between the polygon centroid delimiting the
237 spatial domain of each food web. Environmental dissimilarity was quantified using all 19
238 bioclimatic variables in WorldClim (Hijmans, 2021). We extracted the bioclimatic data for all

239 pixels (10' resolution) falling within the spatial domain of the food webs, and used the mean of
240 each bioclimatic variable to calculate the bioclimatic centroid of each food web. We calculated
241 environmental distance as the Euclidean distance between the food web bioclimatic centroids.
242 We used the mean cophenetic distance to the nearest taxon of every species in the predicted food
243 web to measure phylogenetic relatedness. We averaged over all species in the predicted food web
244 the cophenetic distance to the phylogenetically closest species in the food web used for
245 calibration. This approach measures the amount of evolutionary history in the predicted food
246 web undocumented by the food web on which the model was trained.

247

248 We also analyzed predictive performance at the species level. For each combination of predicted
249 food web models (i.e., curves in Figure 1b), we measured how accurately the set of prey and
250 predators of each species were predicted also using the AUC. We modelled species-specific
251 performance against how connected the focal species is and how distinct the focal species is to
252 the species pool used to train the predictive model. To do this, we used species normalized
253 degree (number of interactions divided by the maximum possible number of interactions), the
254 functional mean pairwise distance (Mouchet et al., 2010) and distance to nearest taxon (Tucker et
255 al., 2017). Functional mean pairwise distance is the average Gower distance (Gower, 1971)
256 between the focal species and all species in the food web used for calibration. To calculate
257 Gower distances, we used all traits available in Etard (2020) through the function *funct.dist* from
258 the R package mFD (Magneville et al., 2022). Distance to nearest taxon was quantified as the
259 cophenetic distance between the focal species and the closest relative in the species in the food
260 web used for model calibration.

261

262 *Predicting species' functional roles*

263 Next, we were interested in how well species functional roles were predicted. The functional role
264 of a species is determined by its position in the food web (Cirtwill et al., 2018), which we
265 quantified using five metrics related to the species centrality within the food webs (number of
266 prey, number of predators, betweenness, closeness, eigenvector centrality), two metrics related to
267 their trophic position (trophic levels and omnivory), two module-based metrics (within-module
268 degree and participation coefficient; Guimerà & Amaral, 2005), and the motif profile of each
269 species (Stouffer et al., 2012). We detail each metric, their relation to functional role, and how
270 they were calculated in Appendix S4.

271

272 We compared each species position metric in empirical food webs to the species position in
273 predicted food webs. We measured each role metric on 100 samples of the posterior distribution
274 of predicted food webs with the mean as the best point estimate for the metric and the standard
275 deviation as measure of uncertainty. For each combination of model, predicted food web, and
276 species role metric, we fitted a linear regression between the predicted position and the empirical
277 position and used the coefficient of determination (R^2). We also explored prediction biases (e.g.,
278 systematic overestimation/underestimation) using the simple linear models' coefficients. We
279 expect an intercept of zero for unbiased predictions of species role. An intercept greater than zero
280 would suggest an overall overestimation of the role metric, whereas an intercept less than zero
281 would suggest a systematic underestimation of the role metric. We expect a slope of one for
282 perfect predictions. A slope less than one would suggest that the role values at the lower range
283 are overpredicted, whereas the role values at the upper range are underpredicted (i.e., more
284 homogeneous values across species than in the empirical food web). A slope greater than one

285 would suggest the opposite (i.e., more heterogeneous values across species than in the empirical
286 food web).

287

288 *Predicting food web properties*

289 Finally, we investigated how well the global properties of food webs were predicted. We selected
290 a range of metrics commonly used to quantify food web structure and which have been shown to
291 influence food web functioning and stability: connectance, mean trophic level, maximum trophic
292 level, motifs distribution, food web diameter, number of clusters, and modularity (Borrelli, 2015;
293 Vermaat et al., 2009). As for species position, we evaluated these properties on the empirical
294 food webs and compared them to the properties predicted using the mean of 100 samples of the
295 posterior food web prediction. We detail each metric, their relation to food web function, and
296 how they were calculated in Appendix S4.

297

298 *Boosted regression trees*

299 To make sure results are general and not dependent on the model framework chosen (i.e.,
300 Bayesian hierarchical generalized linear models), we fitted boosted regression trees (BRTs) on
301 each food web and ran the same analyses (Appendix S5). BRTs are a machine learning algorithm
302 that allows non-linear relationships between predictors and the response variable (Friedman,
303 2001). To make results comparable, we used the exact same training/validation splits and same
304 predictor variables to train and measure performance of BRTs and Bayesian hierarchical
305 generalized linear models.

306

307 **Results**

308 *Predicting pairwise interactions*

309 For all food webs, pairwise interactions were better predicted by the model trained on the same
310 food web (within food web predictions) than by models trained on other food webs (between
311 food web predictions; Table 2). For within food web predictions, AUC varied between 0.92 and
312 0.96 and AUPRG varied between 0.93 and 0.96. Model performance was also good (AUC >
313 0.82; AUPRG > 0.84) for transfer between the Europe, Pyrenees, and Northern Québec and
314 Labrador food webs, except for the model trained on the Pyrenees web when predicting the
315 Europe web. For this case, AUC was high (0.89) whereas AUPRG (0.63) was comparatively
316 small, suggesting that the model was much better at discriminating the absence of interactions
317 rather than their presence. Models did not transfer as well from and to the Serengeti food web,
318 but performance was still good (AUC > 0.75; AUPRG > 0.73). The transferability of the
319 Serengeti food web was expected to be more challenging because nodes do not represent species
320 (as is the case for the other food webs), but trophic groups, as mentioned in the *Food web data*
321 subsection. The area under the precision-recall-gain curve, true positive rate, true negative rate,
322 positive predictive value, and negative predictive value were all positively correlated with AUC
323 and showed the same overall pattern (Appendix S6).

324

325 We explored the factors influencing transferability with comparison of performance relative to
326 the geographic, environmental, and phylogenetic distances between the predicted food web and
327 the food web used for training (Figure 2). Overall, performance tended to decrease with
328 environmental (direct effect estimate: -0.29, 95%CrI = [-0.91, 0.33]) and phylogenetic distance
329 (direct effect estimate: -0.31, 95%CrI = [-0.68, 0.05]). Performance also tended to decrease with
330 geographic distance (total effect estimate: -0.57, 95%CrI = [-0.78, -0.35]), but this effect largely

331 disappeared after controlling for phylogenetic and environmental distances (direct effect
332 estimate: -0.24, 95%CrI = [-0.84, 0.36]). Overall, these results suggest that model transferability
333 decreases with geographic distance mainly because the environment and phylogeny diverged
334 between the predicted food webs and the ones used to train the model.

335

336 We also analyzed transferability at the species level with comparison of species-specific
337 performance as a function of phylogenetic and functional distance between the focal species and
338 the species pool used to train the models (Figure 3). As expected, species with phylogenetically
339 close relatives in the species pool used for calibration were, on average, better predicted than
340 distant relatives (Figure 3a). Species-specific performance slightly decreased at low and
341 intermediate phylogenetic distances, and then dropped significantly at large distances. Models
342 trained and predicted across classes (e.g., mammals to amphibians) had the lowest performance,
343 as expected. This situation only occurs with the Northern Québec and Labrador model predicting
344 the other three food webs as there are no amphibians or reptiles in Northern Québec and
345 Labrador. Surprisingly, predictive performance remained qualitatively unchanged by functional
346 distance (Figure 3b). We also found that interactions of specialist (i.e., species with few
347 interactions) and generalist species (i.e., species with many interactions) were, on average, better
348 predicted than interactions of species of intermediate specialization (Figure 3c).

349

350 *Predicting species functional role*

351 We found significant variation in how well species trophic positions were predicted across
352 models (Figure 4). Species roles were slightly better predicted by within food web predictions
353 than by between food web predictions. Interestingly, some measures of centrality (betweenness

354 and closeness) were not well predicted, whereas others (number of prey and predators,
355 eigenvector centrality) were relatively well predicted.

356

357 We also found important biases in the predictions of species roles when we fitted linear
358 regressions between species roles in predicted food webs to their roles in the empirical food
359 webs. The number of prey, predators, trophic level, omnivory, and the frequency of motif
360 positions tended to be similarly overestimated across species (intercept greater than 0). For other
361 measures such as eigenvector centrality, betweenness, closeness, and module-based roles, species
362 had more similar values between predicted and empirical food webs (Appendix S7, slopes less
363 than 1).

364

365 *Predicting food web properties*

366 The majority of food web properties were not well predicted by our interaction models (Figure
367 5). Connectance, mean and max trophic levels, and the frequency of most motifs were
368 overpredicted, whereas modularity was slightly underpredicted. Mean and variance of relative
369 errors were greater for between- compared to within-food web predictions. In general, predicted
370 food webs were more connected, displayed a higher frequency of most motifs, and were less
371 modular and with less basal species, which increased the trophic level of most species.

372

373 *Boosted regression trees*

374 We found the same general results with BRT (Appendix S5). Overall, BRT performed similarly
375 to our linear model to predict interactions within and across food webs (AUC between 0.69 and
376 0.98; AUCPR between 0.73 and 0.96). Species functional role and food web properties were

377 slightly better predicted by the BRT, but we still found similar biases in predictions (Appendix
378 S5).

379

380 **Discussion**

381 Predictive models of trophic interactions have recently become central in filling knowledge gaps
382 about how predator-prey interactions vary across space and time. Here, we first showed that our
383 trait-based trophic interaction models can predict pairwise interactions across biogeographical
384 regions. We found that, given enough phylogenetic and environmental similarities between the
385 system on which the model is trained and the system for which the predictions are made, models
386 predicted most interactions reasonably well ($AUC > 0.82$). Our results suggest that, for terrestrial
387 vertebrate food webs, trait-matching relationships appear to be relatively general even in highly
388 contrasting environments. Second, although models correctly predicted most interactions, they
389 failed to predict higher-level food web properties. We found systematic biases in the species
390 position and food web properties predictions. Biases varied across metrics, but overall, the
391 predicted food webs were more highly connected, less modular, had more trophic levels, with
392 species within them being more homogeneously connected than their observed counterparts.
393 These higher-level properties of food webs were especially poorly predicted when making
394 between food web predictions (i.e., knowledge transfer). Both these findings do not seem to be
395 specific to Bayesian hierarchical generalized linear models since we found the same overall
396 patterns using boosted regression trees (Appendix S5)

397

398 Food web theory proposes that variation across food webs arises through differences in the trait-
399 matching rules driving interactions (e.g., body mass relationships between predators and their

400 prey) and the distribution of traits in different systems (Gravel et al., 2016). Spatial
401 transferability of trait-based models depend on the generality of the trait-matching rules driving
402 interactions. Therefore, our ability to predict food web interactions across contrasting
403 environments suggests that spatial food web variation is mainly driven by changes in the
404 distribution of functional traits, and less so by the variation of trait-matching relationships. These
405 results are in line with previous research finding generalities made on trait-interactions
406 relationships across European bioregions (Caron et al., 2022), predator-prey body-size ratios
407 within habitat, predator, and prey types (Brose et al., 2006), and the trait-interactions
408 relationships in soil invertebrates across three forest areas in Germany (Laigle et al. 2018). Given
409 that trait-matching rules driving species interactions seem general in reasonably similar
410 environments, it should be possible to use data from well-studied areas to predict interactions in
411 areas we know very little about or forecast (and hindcast) food webs given new trait
412 distributions.

413

414 We also highlighted a major limitation of trophic interaction models: trophic interaction models
415 predict interactions, not food webs. Even if most interactions and absences of interactions are
416 well predicted (high true positive and negative rates), there are many more absences of
417 interactions to predict than presences in real food webs (low connectance). This might explain
418 why our models systematically overpredicted the number of interactions (number of prey and
419 predators) across species (Appendix S7). Most food webs, even expert-based, are missing some
420 interactions (e.g., cryptic and opportunistic interactions), so the additional interactions predicted
421 by our models could be candidate for further investigation. However, our models overestimated
422 the number of interactions by two fold even for the Serengeti food web which is already

423 probably overestimating interactions since species are grouped into trophic groups. This overall
424 overestimation of the number of prey and predators probably propagated through the food webs,
425 explaining why the centrality of species was more evenly distributed, and why the predicted food
426 webs were more connected, less modular, and with higher trophic levels.

427

428

429

430 Food webs are more than a collection of independent pairwise interactions (Strydom et al.,
431 2021). Some factors constrains their global properties (e.g., degree distribution, connectance),
432 whereas others influence the position species occupy within the food web (e.g., trophic level).
433 The inability of our models to predict higher-level network properties from pairwise interactions
434 suggests that trophic interactions models cannot capture the constraints acting on the structure of
435 food web. A consequence of such constraints is the spatial and temporal variations of ecological
436 network, which have gained a lot of interest recently (Baiser et al., 2019; Gravel et al., 2019).

437 Area also influences the structural properties of food webs (Galiana et al., 2018). Here, we
438 compared food webs with very different areas (ranging from 36 thousand km² for Serengeti to 11
439 million km² for Europe), which could hinder predictions across systems. Within-food webs
440 predictions, however, produced similarly biased higher-level properties. Area, thus, does not
441 seem to be the major constraint explaining model failure to predict realistic networks.

442

443 Correcting biases in higher-level property predictions presents an opportunity to improve species
444 interaction predictions. Stacked species distribution models have similar challenges, where
445 models can predict well the distribution of individual species but less higher-level properties of

446 the community (e.g., species richness). Methods have been developed to harness biases in
447 higher-level properties to correct distribution predictions. For example, Leung et al. (2019)
448 combined predicted species distributions and expected species richness to quantify species and
449 spatial biases. They correlated those biases to species traits and environmental co-variates to
450 improve predicted species distribution. Similar methods combining predictions of interactions
451 and networks have the potential to provide better food web predictions. For Bayesian interaction
452 models, we could penalize posterior food web predictions resulting into improbable food web
453 structure based on predictions of structural food web models (Williams & Martinez, 2008) to
454 update pairwise interaction probabilities.

455

456 Our study suffers from a few limitations that, if overcome, could move us closer to a
457 comprehensive framework for ecological interactions and networks prediction. First, our study
458 relied on terrestrial vertebrates. Although there is no clear *a priori* reason not to be applicable in
459 other systems, our results are unlikely to be general across all taxa and types of interactions. We
460 are not aware of another test of interaction model transferability, but it would be interesting
461 to investigate if our results hold for systems where trait-matching relationships are stronger or
462 weaker. The exclusion of non-vertebrates (e.g., plants, invertebrates, parasites) also influence the
463 empirical and predicted species role and food web properties. For example, the first trophic
464 levels in our food webs were not primary producers, but species not feeding on terrestrial
465 vertebrates (e.g., herbivores, invertivores). However, extension of trait-matching models to also
466 include invertebrates can be achieved with a coarser resolution (Li et al., 2023) or with additional
467 traits (Laigle et al., 2018). Second, the food webs we used were potential and binary food webs.
468 Trait-matching models predict the probabilities that a species could eat another species given

469 they are encountering each other. Additional data, such as co-occurrence and abundance data, are
470 needed to make predictions of realized and quantitative interactions. Finally, due to the scarcity
471 of food web data, we only had four food webs to work with. This means we only had four sets of
472 within food web predictions, and 12 sets of between food web predictions. This explains the
473 large uncertainty for some of our results (e.g., Figure 2).

474

475 Overall, we found that our trait-based interaction models can transfer knowledge relatively well
476 given enough phylogenetic and environmental similarities between systems. They are useful for
477 producing initial expectations even in contrasting ecosystems. This, and other recent research
478 (Brose et al., 2006; Caron et al., 2022; Laigle et al., 2018), suggests there are fundamental trait-
479 based constraints on trophic interactions that are generalizable to some extent. The nature of this
480 constraint also appears to result from species traits rather than the ‘match’ between a predator
481 and its prey, which has interesting ties to the broader question of how traits vary between regions
482 and along gradients (Gravel et al., 2016). Future research could better link subfields within trait-
483 based ecology for a comprehensive understanding of how species relate to their environment and
484 to other species, and to enable better predictions of the responses of species and ecosystems to
485 threats and global change.

486

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488 **Data Accessibility Statement**

489 All data sources have been previously published. All data used in the analyses and relevant code
490 will be archived on a Open Science Framework repository.

Table 1: Summary statistics of the food webs used in this study after excluding species for which no match was found in the GBIF Backbone Taxonomy or was not documented in the trait database. Trait coverage is the percentage of traits documented in Etard et al. (2020) before imputing missing traits.

	Europe	Pyrenees	North Québec and Labrador	Serengeti
No. of species	1135	196	200	298
Prop of amphibians	0.09	0.02	0	0.06
Prop of birds	0.45	0.67	0.78	0.35
Prop of mammals	0.25	0.23	0.22	0.46
Prop of reptiles	0.21	0.08	0	0.13
No. of interactions	57 746	831	1 098	11 038
Connectance	0.05	0.02	0.03	0.12
Mean trophic level	1.24	1.25	1.3	1.61
Trait coverage (%)	83.9	92.1	96.3	81.9

493 *Table 2: Area under the receiver operating curve (AUC) and area under the*
 494 *precision-recall-gain curve (AUPRC) where each food web model is used to*
 495 *predict food web data.*

		Food web				
		Model	Europe	Pyrenees	North Québec and Labrador	Serengeti
		AUC				
497	Europe		0.96	0.89	0.9	0.8
498	Pyrenees		0.86	0.95	0.85	0.79
499	North Québec And Labrador		0.82	0.9	0.95	0.75
500	Serengeti		0.85	0.78	0.77	0.92
AUPRG						
501	Europe		0.96	0.63	0.91	0.84
	Pyrenees		0.9	0.95	0.94	0.84
	North Québec And Labrador		0.88	0.9	0.93	0.8
	Serengeti		0.84	0.73	0.77	0.93

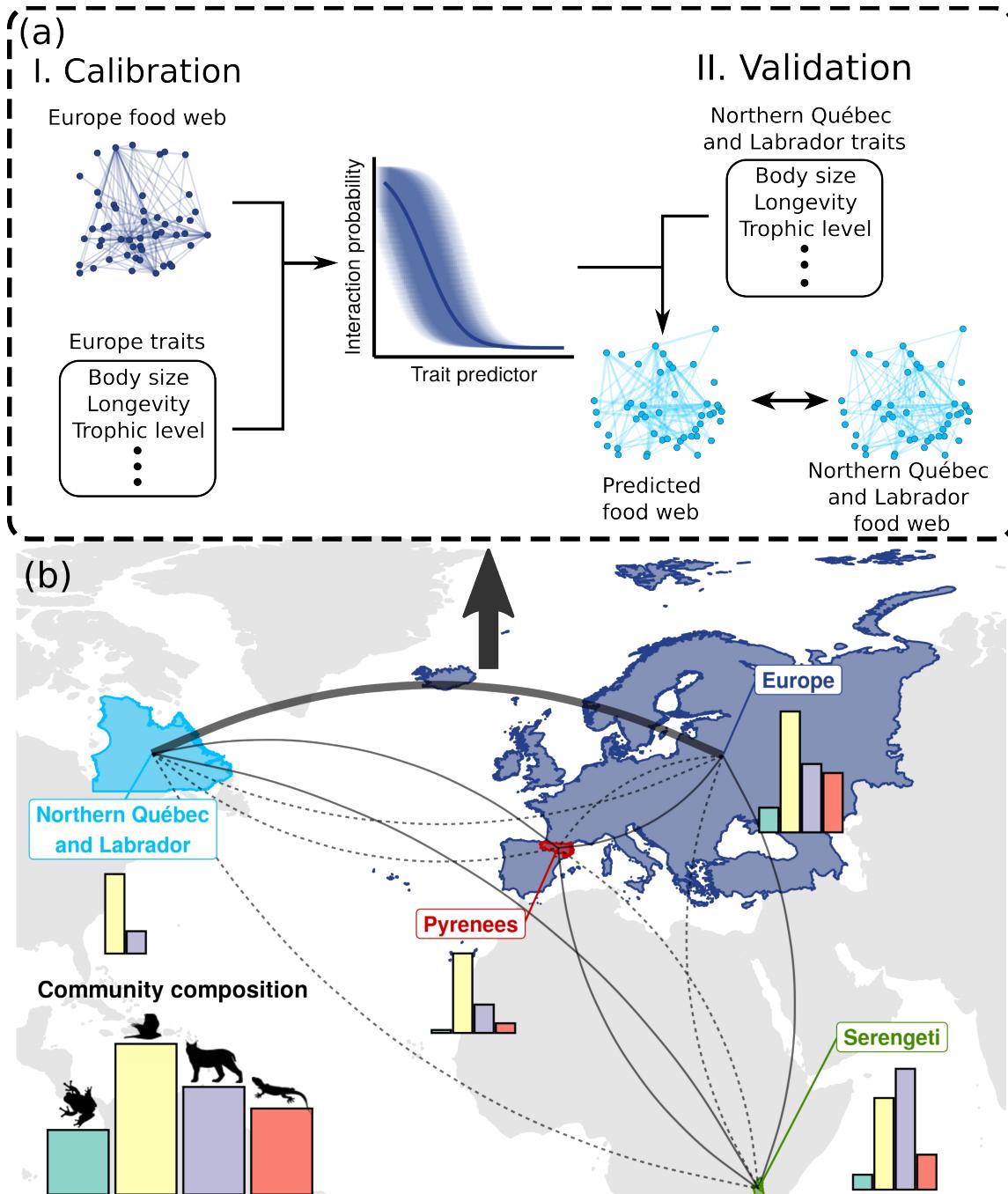


Figure 1: Trophic interactions model transferability analysis workflow. Panel (a) shows an example workflow for between food web predictions. We trained a trophic interaction model using each food web considered in this study (panel a.I). We measured the performance of the four models on a validation subset for within food web predictions, and the entire food webs for between food web predictions (panel a.II). Panel (b) maps the spatial domain of each food web. The curves present the pairs of food web model used to make between food web predictions. Within food web predictions are not shown in the figure. Bar plots illustrate the proportion of amphibians (green), birds (yellow), mammals (purple), and reptiles (red) in each food web.

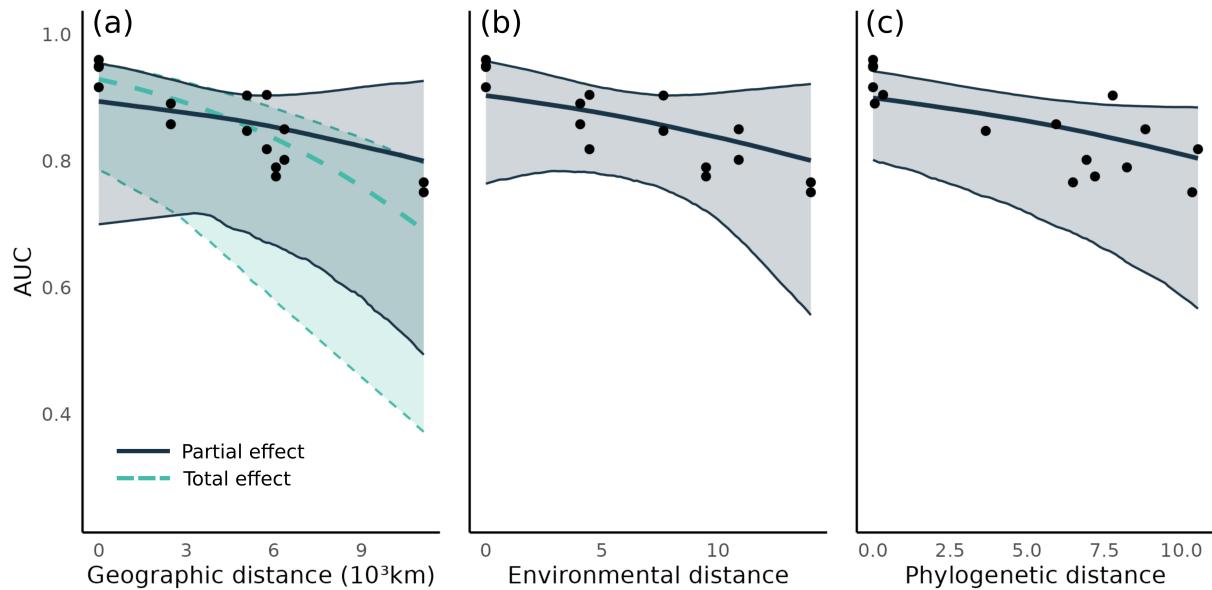


Figure 2: Transferability of predictive models across geographic, environmental and phylogenetic distance. Independently of each panel, the points present the predictive performance (as area under the receiver operating curve, AUC) of a model food web prediction combination (16 combination; Table 2). For each panel, the thick line is the median effects while the envelop is the 95% credible interval on predictive performance built using the posterior predictive distribution of geographic, environmental, and phylogenetic distances. Panel (a) illustrate the total (includes the indirect effects of environmental and phylogenetic distances; turquoise) and partial (controlling for environmental and phylogenetic distances; dark blue) effects of geographic. Panel (b) shows the effect of environmental distance after controlling for geographic distance Panel (c) present the effect of phylogenetic distance after controlling for geographic distance.

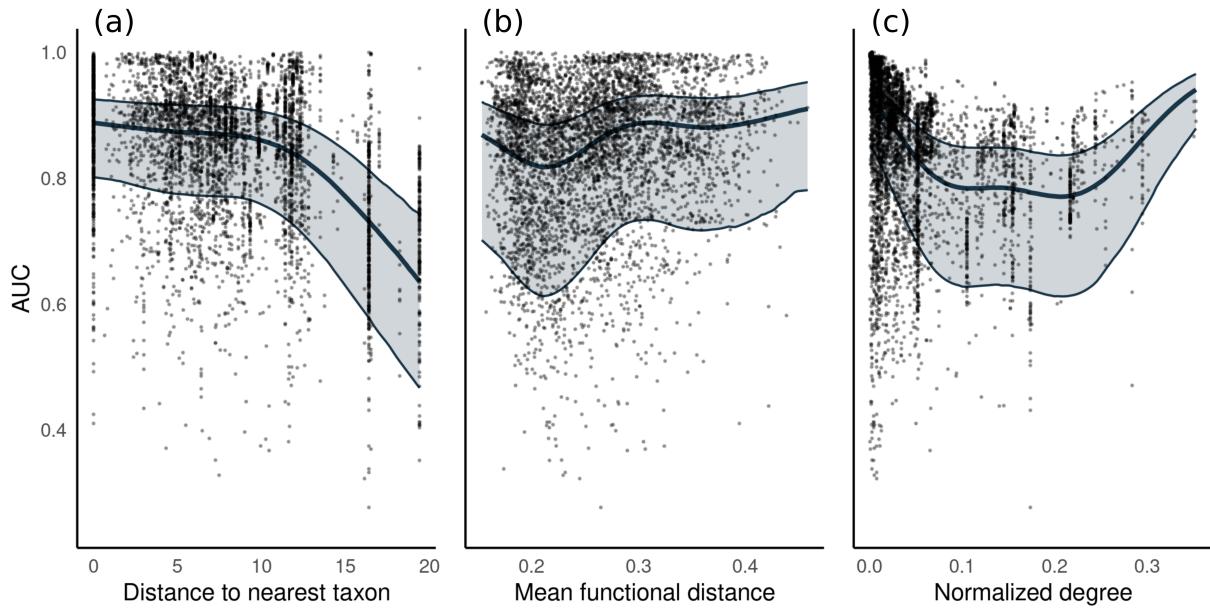


Figure 3: Predicting species interactions. Model predictive performance for the species interactions in alternative food webs. Each point shows the model performance in predicting the prey and predators of a single species using area under the receiver operating curve (AUC) as a metric. For each panel, the thick line is the median effects while the shaded area is the 95% credible interval on predictive performance built using the posterior predictive distribution of (a) distance to the nearest taxon, (b) mean functional pairwise distance, and (c) normalized degree on predictive performance.

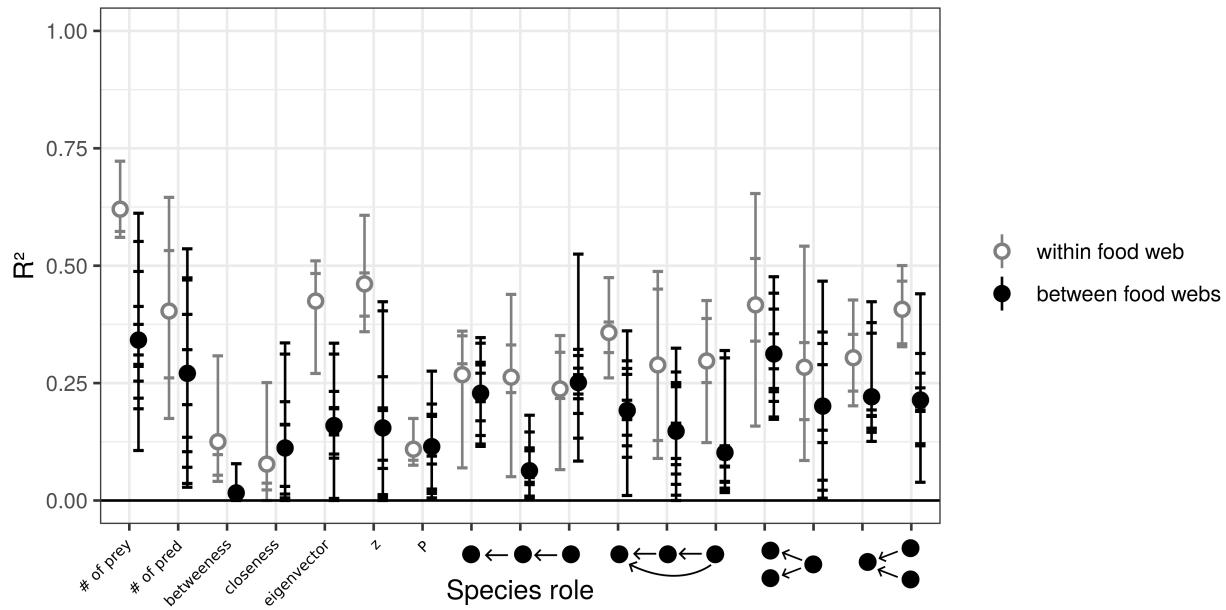


Figure 4: Predicting species functional role. Performance of models to predict species functional role measured as the proportion of the variance in trophic positions explained by the models (R^2). From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, eigenvector centrality, within-module degree (z), participation coefficient (P), times the species is at a specific position in the linear chain (predator – consumer – resource), intraguild predation (omnivore – consumer – resource), direct competition (2 consumers – 1 resource), and apparent competition motifs (1 consumer – 2 resources). The short horizontal lines highlight the R^2 for each role, model, and food web predicted combination. Grey open dots are the mean R^2 for within food web predictions. Full black dots are the mean R^2 for between food web predictions.

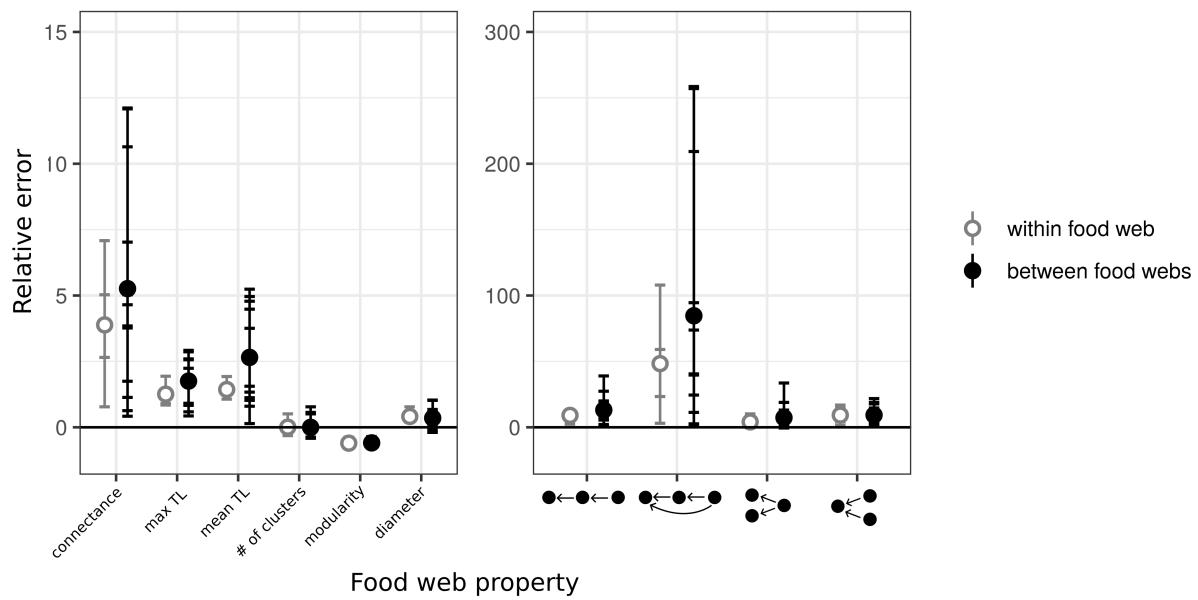


Figure 5: Prediction error of global food web properties. Relative error is the difference between the predicted and the empirical estimates divided by the empirical estimate. From left to right, the figure shows the relative error for connectance, maximum trophic level, mean trophic level, number of clusters, modularity, diameter, number of linear chain (predator – consumer - resource), intraguild predation (omnivore – consumer - resource), direct competition (2 consumers – 1 resource), and apparent competition (1 consumer – 2 resources) motifs. Short horizontal lines are the relative errors for each property, model, and food web predicted combination. Grey open dots are the mean relative errors for within - food web predictions and full black dots are the mean relative errors for between - food web predictions. We divided the figure in two panels because the food web properties in panels (a) and (b) had widely different relative errors.