

- 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. We show that trait-matching
28 relationships are conserved across regions and ecosystems. This suggests that food webs vary
29 spatially 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). Not only is
45 detection more difficult than for species, the number of possible interactions to detect in food
46 webs increases quadratically with the number of species resulting in extremely large sets of
47 potential interactions. Therefore, observing all possible interactions among species within a food
48 web is very difficult even in species-poor ecosystems, which calls for a systematic approach to
49 predict links for predicting interactions even when data from some regions are sparse or non-
50 existent.

51

52 One main approach is to identify feasible interactions by using food web theory to predict the
53 matching between the functional traits of predators and those of their prey (e.g., smaller
54 predators eat smaller prey; Bartomeus et al., 2016). Such trait-based models have been used to
55 predict food webs for freshwater streams (Pomeranz et al., 2019), marine fishes (Albouy et al.,
56 2014), terrestrial systems comprising vertebrate (Caron et al., 2022; Fricke et al., 2022) and
57 invertebrate species (Laigle et al., 2018), among others. Phylogenetic relationships are also
58 informative since they can serve as proxy for trait relationships, and because interactions and

59 species role (i.e., species positions in the food web) tend to be evolutionary conserved (Gómez et
60 al., 2010; Stouffer et al., 2012).

61

62 It is, however, still unclear how well predictive models of pairwise trophic interactions can
63 transfer knowledge across different regions. If trait-matching rules determining interactions are
64 general, then i) we should observe the same traits-interaction relationships across regions and ii)
65 a model trained in a location should be transferable to another one. Strydom et al. (2022)
66 provided an illustration of model transferability, which needs to be tested more rigorously. The
67 authors use a mammal phylogeny to map latent traits extracted from the European mammalian
68 food web to predict its Canadian counterpart, and were able to recover 90% of known trophic
69 interactions among Canadian mammals without any prior information on the food web. Europe
70 and Canada share similar bioclimatic conditions and, despite the few species common to both
71 regions, more than half of Canadian mammals have congeneric species in Europe. Thus, this
72 demonstration of model transferability results raise the question of how trait-based inferences of
73 trophic interactions would transfer to more contrasting environments? Transferability should
74 depend on the similarity of the environment and species composition of the respective food webs
75 (Gravel et al., 2016).

76

77 It is also unclear how well trophic interaction models can predict the underlying structure of
78 entire food webs emerging from pairwise trophic interactions. Food web structure encompasses
79 system-level properties such as connectivity or number of trophic levels, as well as species traits
80 such as number of prey or their position within the food web. These higher-level properties

81 emerge from the joint effect of trait-matching between interacting partners, the trait distribution
82 of species composing the food web (Gravel et al., 2016), and are influenced by the spatial scale
83 of the network (Galiana et al., 2018). Most studies are aimed at predicting either the properties of
84 food webs (e.g., Williams and Martinez 2008) or their pairwise interactions (e.g., Laigle et al.
85 2018; Pomeranz et al. 2019). They rarely assess how well predicted interactions can recover food
86 web structure. Despite being able to recover most trophic interactions among European
87 tetrapods, Caron et al. (2022) found that food web connectance was systematically overpredicted
88 across Europe by 2-4 times. This discrepancy could arise from fundamental differences in the
89 scale of ecological processes that constrain food web properties (e.g., the number of feasible
90 interactions) from those that drive pairwise interactions, which is commonly the focus of trophic
91 interaction models (Strydom et al., 2021). However, we are lacking sufficient knowledge on how
92 well trait-matching models predict other food web properties (e.g., maximum trophic level,
93 modularity) or species positions (e.g., trophic level, centrality) to make generalities.

94

95 Here, we ask whether predictive trait-matching models trained using a network of predator-prey
96 interactions (i.e. a food web) from one geographical region of the world can reliably predict
97 pairwise interactions, species role, and food web structure in other regions. We use terrestrial
98 vertebrate food webs from Europe, the Pyrenees, Northern Québec and Labrador, and the
99 Serengeti, to fit trait-based Bayesian hierarchical models to study transferability across regions.
100 We aim to (1) identify the factors (i.e., geographic, environmental, functional, or phylogenetic
101 distances) influencing the generality of trait-matching models of pairwise interactions across
102 geographical regions, (2) predict trophic roles (e.g., centrality) across species and (3) test how
103 well food web properties derived from models match empirical estimates. First, we expect more

104 functionally similar food webs will yield better transferability. Second, given the models focus
105 on pairwise interactions and based on previous results, we expect the prediction of pairwise
106 interactions to be better than that of food web properties.

107

108 **Methods**

109 *Food web data*

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

127

128 The species composition of the four food webs are different (Table 1). There are no amphibians
129 or reptiles in Northern Québec and Labrador; the Pyrenees food web is dominated by birds
130 (67%) and mammals (23%), with very few reptiles (8%); the European food web has a
131 comparable number of reptiles (21%) and mammals (25%), and almost half (46%) of the
132 Serengeti food web are mammals. The Europe, Pyrenees, and Northern Québec and Labrador
133 food webs all have comparable mean trophic levels (between 1.24 and 1.3) and connectance
134 (between 0.02 and 0.05) compared to the Serengeti food web (mean trophic level: 1.61;
135 connectance: 0.12). Here, the first trophic level (i.e., basal species) are defined as species not
136 feeding on any other terrestrial vertebrates. In Europe, the Pyrenees and Northern Québec and
137 Labrador most species are basal species (e.g., insectivores, herbivores, piscivores), whereas
138 many more species feed on terrestrial vertebrates (non-basal species) in the Serengeti.

139

140 *Trait data*

141 We extracted functional traits from the database compiled by Etard et al. (2020). This dataset
142 combines species-level information from large freely available secondary trait databases (e.g.,
143 EltonTraits: Wilman et al. (2014), AmphiBIO: Oliveira et al. (2017)). Overall, the database
144 includes traits for 6 990 amphibian, 11 634 bird, 5 380 mammal, and 10 612 reptile species. We
145 extracted the available body mass (mean: 11 kg; range: 0.001–4 220 kg), longevity (mean: 5 885
146 days; range: 91–46 386 days), litter or clutch size (mean: 131 offspring; range: 1–20 000
147 offspring), habitat breadth (number of habitats a species uses, using level 2 of the IUCN Habitat
148 Classification Scheme; mean: 10 habitats, range: 1–90 habitats), trophic level (3 levels:
149 herbivore, omnivore, carnivore), activity time (2 categories: nocturnal, non-nocturnal) and

150 habitat use (12 categories: forest, savanna, shrubland, grassland, wetland, rocky
151 areas/cave/subterranean, desert, marine, marine/intertidal or coastal/supratidal, artificial,
152 introduced vegetation) for every species considered in our study.

153

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

164

165 *Phylogeny data*

166 We used published global phylogenies for birds (Jetz et al. 2012), amphibians (Jetz and Pyron
167 2018), squamates (Tonini et al., 2016), turtles (Thomson et al., 2021), and mammals (Upham et
168 al., 2019). All five phylogenies were built from molecular data and delivered as a posterior
169 distribution of trees. We sampled 100 trees from the posterior of each phylogeny and calculated
170 the mean cophenetic distance from these samples between all species of the four food webs.

171 Following Letten & Cornwell (2015), we square root transformed cophenetic distances to better
172 relate to ecological processes such as trophic interactions.

173

174 *Predictive models*

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

182
$$L_{ij} \sim \text{Bernoulli}(p_{ij}),$$

183
$$\text{logit}(p_{ij}) = \alpha + \alpha_{\text{predator}[j]} + \sum_{k=1}^{13} (\beta_k \times T_k + \beta_{k,\text{predator}[j]} \times T_k),$$

184 where L_{ij} is the occurrence of interaction between predator j and prey i , p_{ij} is the associated
185 probability of interaction, α is the fixed intercept and β_k the slope corresponding to the trait-
186 based predictor T_k in the linear model. Similarly, $\alpha_{\text{predator}[j]}$ is the random intercept and
187 $\beta_{k,\text{predator}[j]}$ the random slope corresponding to the trait-based predictor T_k for the order of
188 predator j .

189

190 We used 13 trait-based predictors in the models: five predator traits (trophic level, body mass,
191 habitat breadth, longevity, and clutch size), five prey traits (trophic level, body mass, habitat
192 breadth, longevity, and clutch size), and three trait-match predictors (match in activity time,
193 habitat use and body mass). Since the activity time trait is binary (nocturnal and non-nocturnal),
194 activity time match is also a binary variable where a 1 means the predator and the prey share the

195 same activity time trait. Habitat match is the Jaccard similarity index between the habitat used by
196 the prey and the predator across the 12 habitat categories, which takes into account overlap in
197 habitat and specialization to shared habitats. Body mass match is the squared difference between
198 the log-transformed body mass of the prey and the predator, because we expect predators to eat
199 prey within a given body mass interval (small enough to be handled, but large enough to be
200 profitable. We log-transformed body mass, longevity and clutch size, and scaled each continuous
201 predictor (after transformation) by subtracting out the mean and dividing by two times the
202 standard deviation so coefficients of continuous predictors are comparable to unscaled binary
203 predictors (Gelman, 2008).

204

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

$$209 \quad \alpha, \beta \sim Normal(0, 1)$$

$$210 \quad \alpha_{predator[j]}, \beta_{k,predator[j]} \sim Normal(\mu, \sigma)$$

$$211 \quad \mu \sim Normal(0, 1)$$

$$212 \quad \sigma \sim HalfCauchy(0, 5)$$

213 Model parameters were estimated with Hamiltonian Monte Carlo (Neal, 2011). We ran four
214 chains, each with 2000 warm-up iterations, followed by 2000 iterations for inference. We
215 diagnosed convergence and adequacy with trace rank plots, posterior predictive checks, and we
216 calculated the rank-normalized potential scale reduction factor on split chains for all runs

217 (Vehtari et al. 2021; Appendix S6). We conducted the analyses using Stan (Carpenter et al., 2017)
218 through the package *brms* in R (Bürkner 2017).

219

220 *Predicting species interactions*

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

236

237 We assessed the performance of models to predict each food web using three distance measures:
238 geographic distance, environmental dissimilarity, and phylogenetic relatedness. We measured

239 geographic distance as the great-circle distance between the polygon centroid delimiting the
240 spatial domain of each food web. We quantified environmental dissimilarity using all 19
241 bioclimatic variables in WorldClim (Hijmans, 2021). We extracted the bioclimatic data for all
242 pixels (10' resolution) falling within the spatial domain of the food webs, and used the mean of
243 each bioclimatic variable to calculate the bioclimatic centroid of each food web. We calculated
244 environmental distance as the Euclidean distance between the food web bioclimatic centroids.
245 We used the mean cophenetic distance to the nearest taxon of every species in the predicted food
246 web to measure phylogenetic relatedness. We averaged over all species in the predicted food web
247 the cophenetic distance to the phylogenetically closest species in the food web used for
248 calibration. This approach measures the amount of evolutionary history in the predicted food
249 web undocumented by the food web on which the model was trained.

250

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

262 taxon as the cophenetic distance between the focal species and the closest relative in the species
263 in the food web used for model calibration.

264

265 *Predicting species' functional roles*

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

274

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

285 perfect predictions. A slope less than one would suggest that the role values at the lower range
286 are overpredicted, whereas the role values at the upper range are underpredicted (i.e., more
287 homogeneous values across species than in the empirical food web). A slope greater than one
288 would suggest the opposite (i.e., more heterogeneous values across species than in the empirical
289 food web).

290

291 *Predicting food web properties*

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

300

301 *Boosted regression trees*

302 To make sure results are general and not dependent on the model framework chosen (i.e.,
303 Bayesian hierarchical generalized linear models), we fitted boosted regression trees (BRTs) on
304 each food web and ran the same analyses (Appendix S5). BRTs are a machine learning algorithm
305 that allows non-linear relationships between predictors and the response variable (Friedman,
306 2001). To make results comparable, we used the exact same training/validation splits and same

307 predictor variables to train and measure performance of BRTs and Bayesian hierarchical
308 generalized linear models.

309

310 **Results**

311 *Predicting pairwise interactions*

312 For all food webs, pairwise interactions were better predicted by the model trained on the same
313 food web (within food web predictions) than by models trained on other food webs (between
314 food web predictions; Table 2). For within food web predictions, AUC varied between 0.92 and
315 0.96 and AUPRG varied between 0.93 and 0.96. Model performance was also good (AUC >
316 0.82; AUPRG > 0.84) for transfer between the Europe, Pyrenees, and Northern Québec and
317 Labrador food webs, except for the model trained on the Pyrenees web when predicting the
318 Europe web. For this case, AUC was high (0.89) whereas AUPRG (0.63) was comparatively
319 small, suggesting that the model was much better at discriminating the absences than presences
320 of interaction. Models did not transfer as well from and to the Serengeti food web, but
321 performance was still good (AUC > 0.75; AUPRG > 0.73). The transferability of the Serengeti
322 food web was expected to be more challenging because nodes do not represent species (as is the
323 case for the other food webs), but trophic groups, as mentioned in the *Food web data* subsection.
324 The area under the precision-recall-gain curve, true positive rate, true negative rate, positive
325 predictive value, and negative predictive value were all positively correlated with AUC and
326 showed the same overall pattern (Appendix S7).

327

328 We explored the factors influencing transferability with comparison of performance relative to
329 the geographic, environmental, and phylogenetic distances between the predicted food web and

330 the food web used for training (Figure 2). Overall, performance tended to decrease with
331 environmental (direct effect estimate: -0.30, 95%CrI = [-0.90, 0.32]) and phylogenetic distance
332 (direct effect estimate: -0.31, 95%CrI = [-0.69, 0.06]). Performance also tended to decrease with
333 geographic distance (total effect estimate: -0.57, 95%CrI = [-0.78, -0.36]), but this effect largely
334 disappeared after controlling for phylogenetic and environmental distances (direct effect
335 estimate: -0.26, 95%CrI = [-0.87, 0.35]). Overall, these results suggest that model transferability
336 decreases with geographic distance mainly because the environment and phylogeny diverged
337 between the predicted food webs and the ones used to train the model.

338

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

352

353 *Predicting species functional role*

354 We found significant variation in how well species trophic positions were predicted across
355 models (Figure 4). Species roles were slightly better predicted by within food web predictions
356 than by between food web predictions. Interestingly, some measures of centrality (betweenness
357 and closeness) were not well predicted, whereas others (number of prey and predators,
358 eigenvector centrality) were relatively well predicted.

359

360 We also found important biases in the predictions of species roles when we fitted linear
361 regressions between species roles in predicted food webs to their roles in the empirical food
362 webs. The number of prey, predators, trophic level, omnivory, and the frequency of motif
363 positions tended to be similarly overestimated across species (intercept greater than 0). For other
364 measures such as eigenvector centrality, betweenness, closeness, and module-based roles, species
365 had more similar values in the predicted than in the empirical food webs (Appendix S8, slopes
366 less than 1).

367

368 *Predicting food web properties*

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

375

376 *Boosted regression trees*

377 We found the same general results with BRTs (Appendix S5). Overall, BRTs performed similarly
378 to Bayesian linear model to predict interactions within and across food webs (AUC between 0.69
379 and 0.98; AUPRG between 0.73 and 0.96). Species functional role and food web properties were
380 also not well predicted by BRTs, and we found similar biases in predictions (Appendix S5).

381

382 **Discussion**

383 Predictive models of trophic interactions have recently become central in filling the substantial
384 knowledge gaps of how food webs vary across space and time. Overall, we found that: (1) our
385 models were able to predict pairwise interactions across ecosystems reasonably well (AUC >
386 0.82), (2) pairwise interactions were well predicted (AUC > 0.80) for most novel species unless
387 no species of the same class was present in the food web used for training, and (3) as expected,
388 models were not as good at predicting food web properties, over-estimating some metrics (e.g.
389 connectance, trophic level) and under-estimating others (e.g. modularity), especially when
390 extrapolating to new regions. Results suggest both optimism for the use of these models when
391 data for some regions are lacking or future communities with no current analog and the need for
392 novel approaches that combine pairwise interactions with higher-order food web metrics.

393

394 Theory describes how the variation in food webs arise from two key processes: trait-interaction
395 rules (e.g., body mass relationships between predators and their prey) and the distribution of
396 traits in different systems (Gravel et al., 2016). Our ability to predict food web interactions
397 across contrasting environments suggests that spatial food web variation is mainly driven by
398 changes in the distribution of functional traits, and less so by the variation of trait-interaction

399 relationships. These results are in line with previous research finding generalities made on trait-
400 matching relationships across European bioregions (Caron et al., 2022), predator-prey body-size
401 ratios within habitat, predator, and prey types (Brose et al., 2006), and the trait-interaction
402 relationships in soil invertebrates across three forest areas in Germany (Laigle et al. 2018). These
403 generalities in the trait-interaction relationships across space and within taxonomic groups
404 demonstrate the potential for using data from well-studied areas to predict interactions in areas
405 we know very little about or forecast (and hindcast) food webs given new trait distributions.

406

407 We also highlighted a major limitation of trophic interaction models: trophic interaction models
408 predict interactions, not food webs properties. Even if most interactions and absences of
409 interactions are well predicted (high true positive and negative rates), there are many more
410 absences of interactions to predict than presences in real food webs (low connectance). This
411 might explain why our models systematically overpredicted the number of interactions (number
412 of prey and predators) across species (Appendix S8). Most food webs, even expert-based, are
413 missing some interactions (e.g., cryptic and opportunistic interactions), so the additional
414 interactions predicted by our models could be candidates for further investigation. However, our
415 models overestimated the number of interactions by two fold even for the Serengeti food web
416 which probably already overestimates interactions since species are grouped into trophic groups.
417 This overall overestimation of the number of prey and predators probably propagated through the
418 food webs, explaining why the centrality of species was more evenly distributed, and why the
419 predicted food webs were more connected, less modular, and with higher trophic levels.

420

421 Food webs are more than a collection of independent pairwise interactions (Strydom et al.,
422 2021). Some factors, like area (Galiana et al., 2018), constrain their global properties (e.g.,
423 degree distribution, connectance) and influence the position species occupy within the food web
424 (e.g., trophic level). The inability of our models to predict higher-level network properties from
425 pairwise interactions suggests that trophic interactions models cannot capture the constraints
426 acting on the structure of food web. A consequence of such constraints is the spatial and
427 temporal variations of ecological network, which have gained a lot of interest recently (Baiser et
428 al., 2019; Gravel et al., 2019). Here, we compared food webs with very different areas (ranging
429 from 36 thousand km² for Serengeti to 11 million km² for Europe), which could hinder
430 predictions across systems. Within-food webs predictions, however, produced similarly biased
431 higher-level properties. Area, thus, does not seem to be the major constraint explaining model
432 failure to predict realistic networks.

433

434 Correcting biases in higher-level property predictions presents an opportunity to improve species
435 interaction predictions. Stacked species distribution models have similar challenges, where
436 models can predict well the distribution of individual species but less higher-level properties of
437 the community (Zurell et al., 2020). Methods have been developed to harness biases in higher-
438 level properties to correct distribution predictions. For example, Leung et al. (2019) combined
439 predicted species distributions and expected species richness to quantify species and spatial
440 biases. They correlated biases to species traits and environmental co-variates to improve
441 predicted species distribution. Similar methods combining predictions of interactions and
442 networks have the potential to provide better food web predictions. For example, we could

443 penalize posterior food web predictions resulting into improbable food web structure to update
444 pairwise interaction probabilities.

445

446 Our study suffers from a few limitations that, if overcome, could move us closer to a
447 comprehensive framework for ecological interactions and networks prediction. First, our study
448 relied on terrestrial vertebrates. Although there is no clear *a priori* reason not to be applicable in
449 other systems, our results are unlikely to be general across all taxa and types of interactions. We
450 are not aware of another other test of interaction model transferability, but it would be interesting
451 to investigate if our results hold for systems where trait-matching relationships are stronger or
452 weaker. The exclusion of non-vertebrates (e.g., plants, invertebrates, parasites) also influence the
453 empirical and predicted species role and food web properties. For example, the first trophic
454 levels in our food webs were not primary producers, but species not feeding on terrestrial
455 vertebrates (e.g., herbivores, invertivores). However, extension of trait-matching models to also
456 include invertebrates can be achieved with a coarser resolution (Li et al., 2023) or with additional
457 traits (Laigle et al., 2018). Second, the food webs we used were potential and binary food webs.
458 Trait-matching models predict the probabilities that a species could eat another species given
459 they are encountering each other. Additional data, such as co-occurrence and abundance data, are
460 needed to make predictions of realized and quantitative interactions. Finally, due to the scarcity
461 of food web data, we only had four food webs to work with. This means we only had four sets of
462 within food web predictions, and 12 sets of between food web predictions. This explains the
463 large uncertainty for some of our results (e.g., Figure 2).

464

465 Overall, we found that our trait-based interaction models can transfer knowledge relatively well
466 given enough phylogenetic and environmental similarities between systems. They are useful for
467 producing initial expectations even in contrasting ecosystems and for future communities. This,
468 and other recent research (Brose et al., 2006; Caron et al., 2022; Laigle et al., 2018), suggests
469 there are fundamental trait-based constraints on trophic interactions that are generalizable to
470 some extent. Food web variation thus result from species traits rather than the ‘match’ between a
471 predator and its prey, which has interesting ties to the broader question of how traits vary
472 between regions and along gradients (Gravel et al., 2016). Future research could better link
473 subfields within trait-based ecology for a comprehensive understanding of how species traits and
474 network structure relate to their environment , and to enable better predictions of the responses of
475 species and ecosystems to threats and global change.

476

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478 **Data Accessibility Statement**

479 All data sources have been previously published. All data used in the analyses and relevant code
480 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

483
 484 *Table 2: Area under the receiver operating curve (AUC) and area under the*
precision-recall-gain curve (AUPRG) where each food web model is used to
predict food web data.

		Food web				
		Model	Europe	Pyrenees	North Québec and Labrador	Serengeti
		AUC				
487	Europe		0.96	0.89	0.9	0.8
488	Pyrenees		0.86	0.95	0.85	0.79
489	North Québec And Labrador		0.82	0.9	0.95	0.75
490	Serengeti		0.85	0.78	0.77	0.92
AUPRG						
491	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

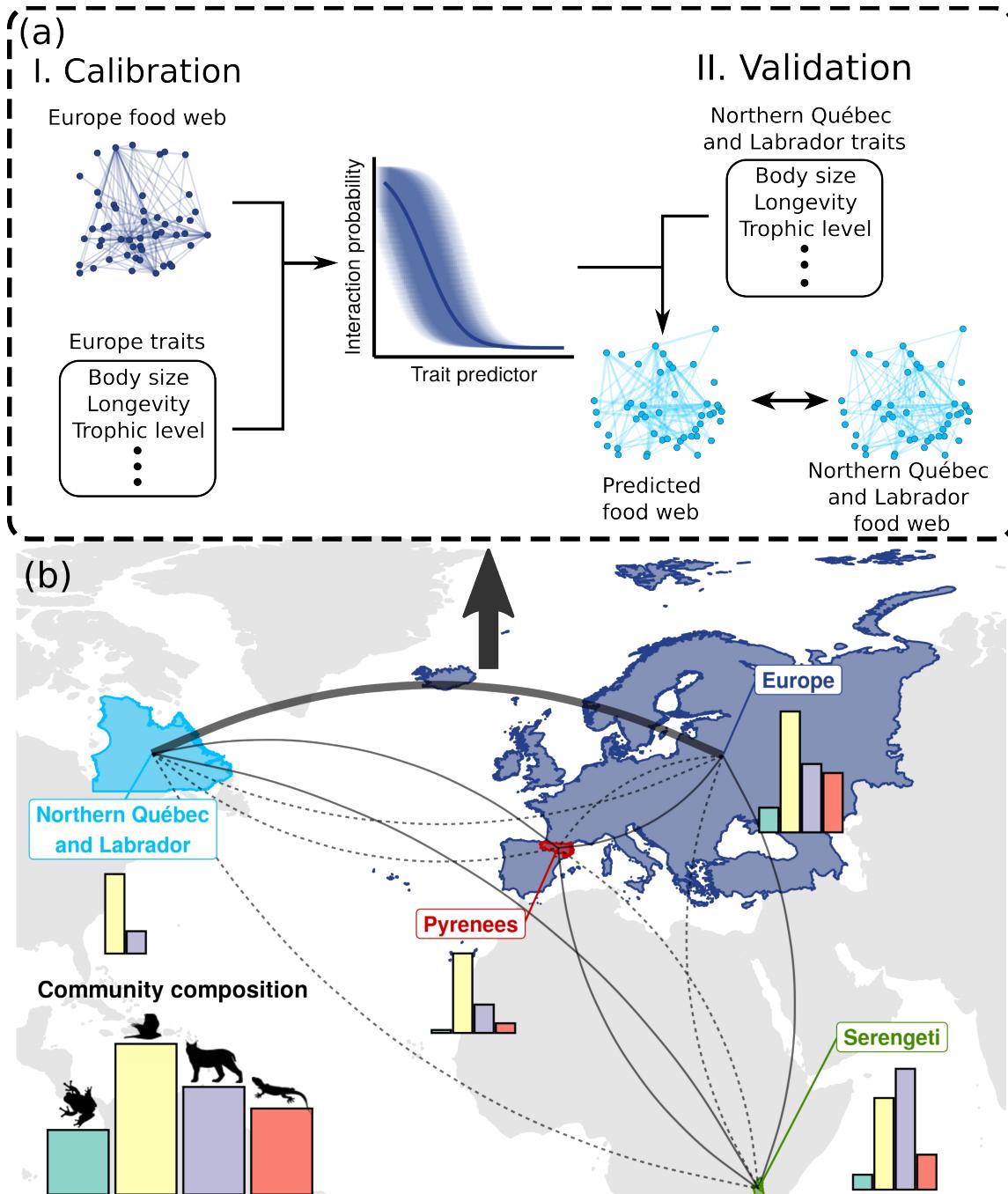


Figure 1: Trophic interactions model transferability analysis workflow. Panel (a) shows an example workflow for between food web predictions. We trained a trophic interaction model using each food web considered in this study (panel a.I). We measured the performance of the four models on a validation 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.

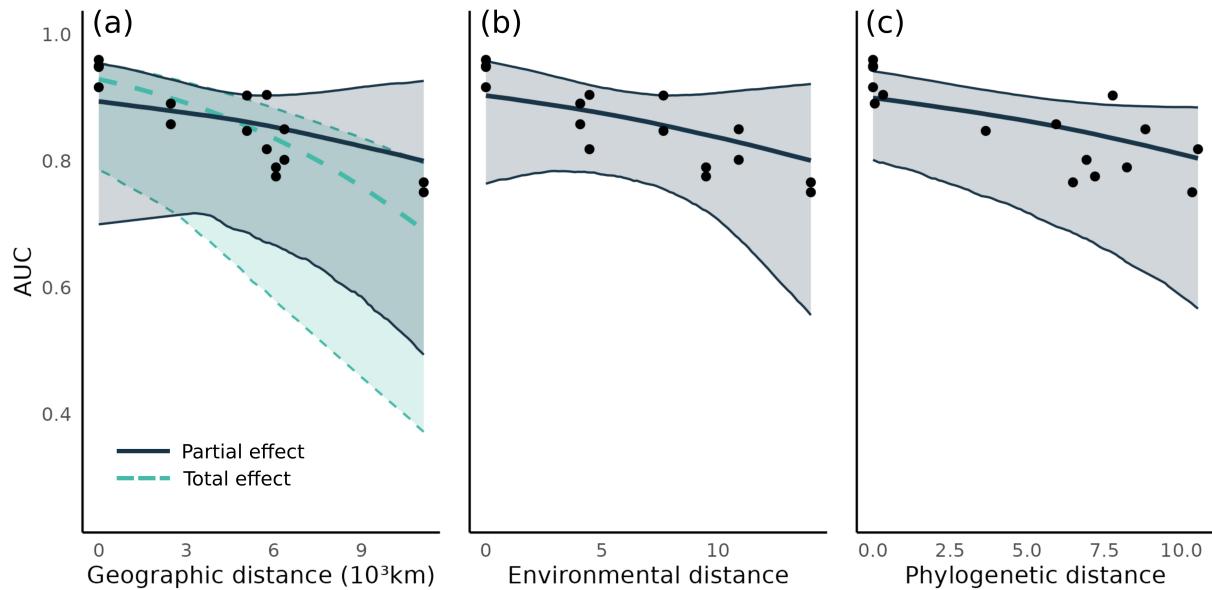


Figure 2: Transferability of predictive models across geographic, environmental and phylogenetic distance. Independently of each panel, the points present the predictive performance (as area under the receiver operating curve, AUC) of a model food web prediction combination (16 combination; Table 2). 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.

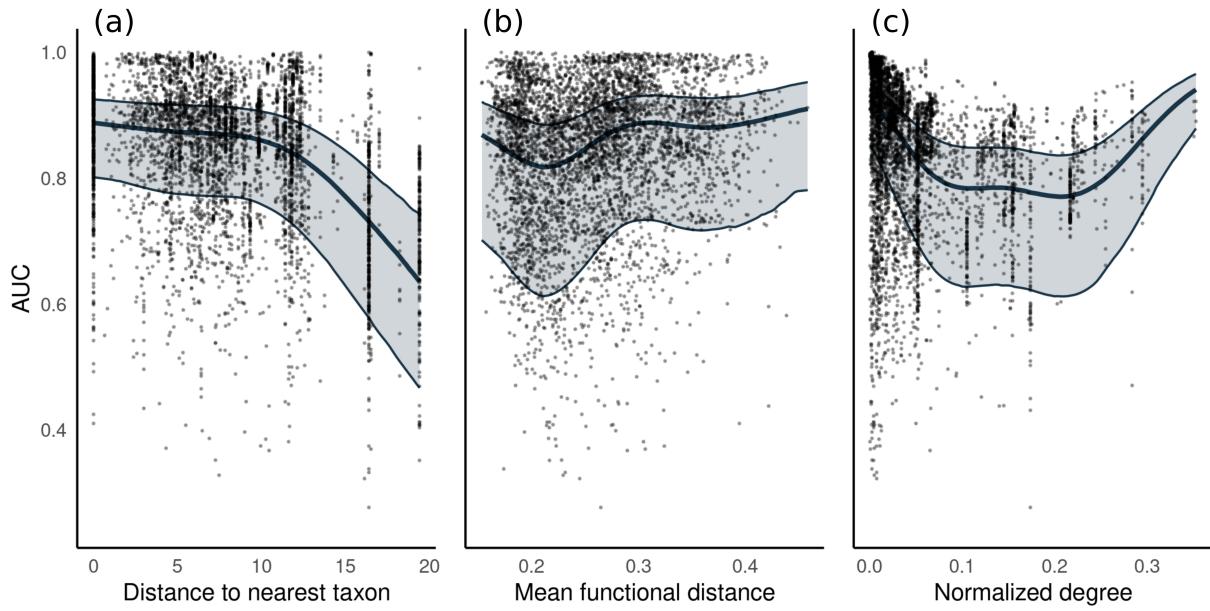


Figure 3: Predicting species interactions. Model predictive performance for the species interactions in alternative food webs. Each point shows the model performance in predicting the prey and predators of a single species using area under the receiver operating curve (AUC) as a metric. For each panel, 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.

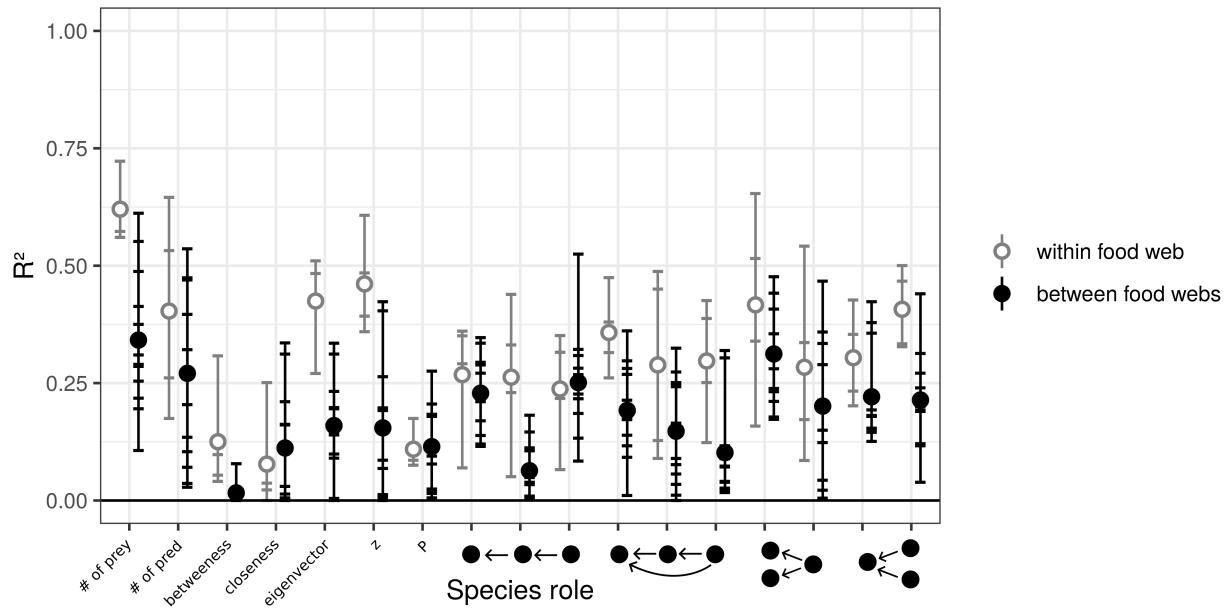


Figure 4: Predicting species functional role. Performance of models to predict species functional role measured as the proportion of the variance in trophic positions explained by the models (R^2). From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, eigenvector 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.

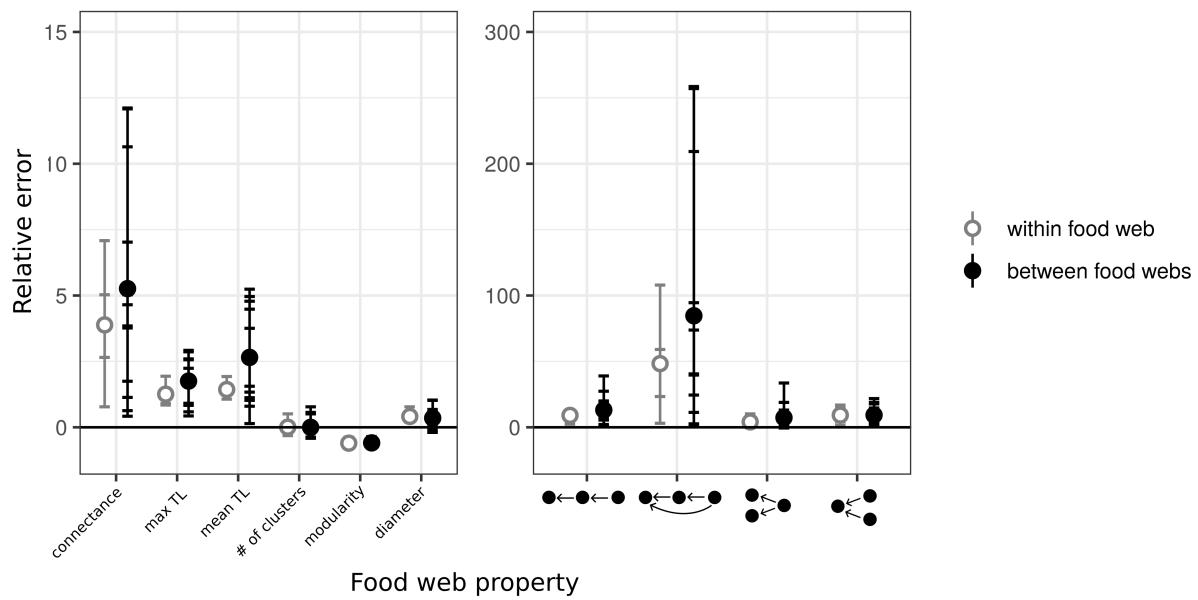


Figure 5: Prediction error of global food web properties. Relative error is the difference between the predicted and the empirical estimates divided by the empirical estimate. From left to right, the figure shows the relative error for connectance, maximum trophic level, mean trophic level, number of 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.