

1           **Trophic interaction models predict interactions across space, not food webs.**

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

23 **Abstract**

24 **Aim:** Trophic interactions are central to our understanding of essential ecosystem functions such  
25 as nutrient cycling and productivity as well as their stability. While empirical data on trophic  
26 interactions remains unavailable for most taxa in most ecosystems, predicting these interactions  
27 has become increasingly common. We aim at determining how far we can extrapolate with these  
28 trophic interaction models and how well can they recover higher level properties of food webs  
29 (species position and entire food web properties).

30 **Location:** Canada, Europe, Tanzania.

31 **Time period:** Current.

32 **Major taxa studied:** Terrestrial vertebrates

33 **Methods:** We use four trait-based models of trophic interactions, each calibrated on a different  
34 food web of terrestrial vertebrates (list them), to predict to the remaining food webs. We test how  
35 well predictions recover individual predator-prey pairs and higher level properties of food webs.

36 **Results:** We find that, given enough phylogenetic and environmental similarities between food  
37 webs, trait-based models predict most interactions and non-interactions correctly ( $AUC > 0.82$ )  
38 even in highly contrasting environment. However, network metrics were less well-predicted with  
39 predicted food webs being more connected, less modular, and having higher mean trophic levels.

40 **Main conclusions:** Trophic niche theory predicts that food webs vary through either changes in  
41 trait distributions and trait-matching relationships. Trait-based models can predict pools of  
42 potential interactions from reasonably similar food webs, suggesting that food webs vary  
43 spatially primarily through changes in trait distributions. We also highlight the need for  
44 methodological advances to simultaneously address trophic interactions and the structure of food  
45 webs across time and space.

46 **Introduction**

47 Many ecosystem functions (e.g., energy flows and material cycling) and community stability  
48 depend on the trophic relationships that link species within a community (Harvey et al. 2017).  
49 Despite the recognized importance of food webs in ecosystems over the last 80 years (Lindeman  
50 1942), we still face major challenges to develop accurate descriptions of food webs. The lack of  
51 trophic interactions data across most locations and taxa (Poisot et al. 2021) lie at the core of the  
52 fundamental technical and practical challenges in food web ecology. Observing interactions is  
53 more challenging than observing species because two individuals need to be simultaneously  
54 detected while they are interacting (Jordano 2016), and the number of possible interactions webs  
55 grows quadratically with the number of species. Determining all possible interactions among  
56 species within a network is difficult even in species-poor ecosystems. Quantifying the strength  
57 and type (e.g. predator vs mutualism vs competition) of interactions, a common goal of  
58 ecological network studies, adds even more complexity to this already difficult problem.

59

60 A first step towards constructing food webs is to focus on a single type of interaction, predator-  
61 prey relationships, which are the most commonly recorded one, and have been shown to respond  
62 to a predictable set of neutral and niche processes (Morales-Castilla et al. 2015). A neutral model  
63 for trophic interactions suggests that the probability and strength of interactions respond only to  
64 the co-occurrences and abundances of species (Canard et al. 2012). Recent studies have shown  
65 however, that even if co-occurrence is a requirement for species to interact, it is not evidence for  
66 realized trophic interactions (Blanchet, Cazelles, and Gravel 2020). We must thus be careful  
67 when making assertions about trophic interactions based solely on co-occurrence data. Niche  
68 theory predicts that the association between the functional traits of predators and those of their

69 prey should improve predictions by identifying interactions that are feasible (Morales-Castilla et  
70 al. 2015). Trait-based models have been used to predict food webs in freshwater streams  
71 (Pomeranz et al. 2019), marine fishes (Albouy et al. 2014), terrestrial invertebrates (Laigle et al.  
72 2018), and vertebrates (Caron et al. 2022; Fricke et al. 2022), among others. Phylogenetic  
73 relationships are also informative since interactions and species role (i.e., the position the species  
74 has in the food web) tend to be evolutionary conserved (Gómez, Verdú, and Perfectti 2010;  
75 Stouffer et al. 2012). Strydom et al. (2021) recently used a mammal phylogeny to map latent  
76 traits extracted from the European mammalian food web to predict its Canadian counterpart.  
77 Using this approach the authors were able to recover 90% of known trophic interactions among  
78 Canadian mammals without any prior information on the food web.

79

80 The question remains however, of how well can predictive models of trophic interactions transfer  
81 knowledge across different regions? In Strydom et al. (2021), it is challenging to know how  
82 inferences would transfer to more contrasting environments. Europe and Canada share similar  
83 bioclimatic conditions and, despite the little overlap in species, more than half of Canadian  
84 mammals have congeneric species in Europe. Another outstanding question is how well can  
85 trophic interaction models predict the underlying structure of the predator-prey relationships  
86 within a food web? Food web structure encompasses system-level properties such as  
87 connectivity or number of trophic levels, as well as species traits such as number of prey or their  
88 position within the food web. Most studies are aimed at predicting either the properties of food  
89 webs (e.g., Williams and Martinez 2008) or their interactions (e.g., Laigle et al. 2018; Pomeranz  
90 et al. 2019). They rarely assess how well predicted interactions can recover food web structure.  
91 Despite being able to recover most trophic interactions among European tetrapods, Caron et al.

92 (2022) found that food web connectance was systematically overpredicted across Europe by 2-4  
93 times. However, the authors did not explore how other food web properties (e.g., maximum  
94 trophic level, modularity) or species positions (e.g., trophic level, centrality) were predicted.

95

96 Here we test whether predictive models calibrated with a predator-prey network from one  
97 geographical region of the world can reliably predict interactions, species role and food web  
98 structure in similar ecosystems across the world. Using terrestrial vertebrate food webs from  
99 Europe, the Pyrenees, Northern Québec and Labrador, and the Serengeti we develop trait-based  
100 Bayesian hierarchical models to study how well can species interactions and food web properties  
101 be predicted across regions. We aim at (1) identifying the factors (i.e., geographic,  
102 environmental, functional, or phylogenetic distances) influencing the transferability of models  
103 across ecosystems and geographical regions, (2) predicting trophic roles across species and (3)  
104 quantifying the predicted food web properties.

105

## 106 **Methods**

### 107 *Food web data*

108 We extracted predator-prey interactions among terrestrial vertebrates (mammals, birds,  
109 amphibians and reptiles) from four well-resolved food webs (Table 1):

110

- 111 1. *Europe food web*: The food web comprising European tetrapods was assembled by  
112 Maiorano et al. (2020). The Europe food web contains the potential trophic interactions  
113 between all terrestrial vertebrates in Europe based on data from atlases, field guides,  
114 published papers, and expert knowledge. Maiorano et al. (2020) originally reported

115 interactions between predators and their prey at different life-stage (eggs, larvae/young,  
116 or adult). In this study, we focused on interactions between predators and adult prey.  
117

118 2. *Pyrenees food web*: The Pyrenees vertebrate food web was assembled independently  
119 from the European food web by Lurgi et al. (2012) who compiled all known interactions  
120 between vertebrate species in the southeastern Pyrenees mountain range. For this study,  
121 we excluded fish species.

122

123 3. *Northern Québec and Labrador food web*: The trophic tundra food web of Labrador and  
124 northern Quebec (Canada) was compiled by Berteaux et al. (2018). The Northern Québec  
125 and Labrador food web documents the presence (absence) of trophic relationships  
126 between all birds, mammals, and groups of plants (e.g., moss, ferns, grass) and  
127 arthropods (e.g., Lepidoptera, Diptera, Arachnida) whose distribution overlap Labrador  
128 and Quebec north of 50°N (Nunavik region). Trophic interactions were collated from a  
129 literature review, data from existing databases, and expert knowledge. For our study, we  
130 focused on the bird and mammal species (i.e. the vertebrates) of this network.

131

132 4. *Serengeti food web*: The Serengeti food web compiles all interactions between resource  
133 categories (e.g., seeds, shrubs, fruits and nectar), invertebrate groups (e.g., thrips, bees,  
134 moths, crickets), and vertebrate species in the Serengeti National Park (Tanzania) and  
135 was assembled from a literature review (de Visser, Freymann, and Olff 2011). The nodes  
136 of the original food webs are resource categories, or trophic groups including one or more  
137 invertebrate groups and vertebrate species. In this study, we focused on vertebrate

138 species, and assumed that species within a trophic group share the same predator and  
139 prey species.

140

141 In all food webs, trophic interaction is a binary variable where 0 is the absence of predator-prey  
142 interaction and 1 is the presence of predator-prey interaction between two species (i.e., the  
143 predator could feed on the prey species). The species composition of the four food webs are  
144 different (Table 1). There are no amphibians or reptiles in Northern Québec and Labrador, the  
145 Pyrenees food web is dominated by birds (67%) and mammals (23%), with very few reptiles  
146 (8%), the European food web has a comparable number of reptiles (21%) and mammals (25%),  
147 and almost half (46%) of Serengeti food web are mammals. The Europe, Pyrenees, and Northern  
148 Québec and Labrador food webs all have comparable mean trophic levels (between 1.24 and 1.3)  
149 and connectance (between 0.02 and 0.05) compared to the Serengeti food web (mean trophic  
150 level: 1.61; connectance: 0.12). Most species are basal species (e.g., insectivores, herbivores,  
151 piscivores) in Europe, Pyrenees and Northern Québec and Labrador, whereas many more species  
152 are eating terrestrial vertebrates (non-basal species) in the Serengeti.

153

#### 154 *Trait data*

155 We extracted terrestrial vertebrate species ecological traits from the database compiled by Etard  
156 et al. (2020). This dataset combines species-level information from large freely available  
157 secondary trait databases (e.g., EltonTraits: Wilman et al. (2014), AmphiBIO: Oliveira et al.  
158 (2017)). Overall, the database includes traits for 6 990 amphibian, 11 634 bird, 5 380 mammal,  
159 and 10 612 reptile species. We extracted the body mass (mean: 11 kg; range: 1 g–4 220 kg),  
160 longevity (mean: 5 885 days; range: 91–46 386 days), litter or clutch size (mean: 5 885

161 offsprings; range: 1–20 000 offsprings), habitat breadth (mean: 10, range: 1–90), trophic level (3  
162 levels: herbivore, omnivore, carnivore), activity time (2 categories: nocturnal, non-nocturnal) and  
163 habitat use (12 categories: forest, savanna, shrubland, grassland, wetland, rocky  
164 areas/cave/subterranean, desert, marine, marine/intertidal or coastal/supratidal, artificial,  
165 introduced vegetation) for species present in at least one of the four food webs of our study.

166

167 To match species in the trait databases to the species in the food webs, we standardized their  
168 names following the taxonomic backbone of the Global Biodiversity Information Facility (GBIF)  
169 using the function *name\_backbone* from the package *rgbif* (Chamberlain et al. 2022) in the R  
170 statistical language (R Core Team 2022). In each food web, we excluded all species for which no  
171 taxonomic information or traits were available. We imputed missing traits using the MissForest  
172 algorithm (Stekhoven and Buehlmann 2012) for amphibians, birds, mammals and reptiles  
173 separately. MissForest first imputes all missing data with the mean (for quantitative variables) or  
174 the mode (for categorical variables). For each variable, MissForest then calibrates a random  
175 forest on the known data and predicts the missing data.

176

#### 177 *Phylogeny data*

178 We used phylogeny data to measure how model transferability was influenced by phylogenetic  
179 relatedness. We used the published global phylogeny for birds (Jetz et al. 2012), amphibians (Jetz  
180 and Pyron 2018), squamates (Tonini et al. 2016), turtles (Thomson, Spinks, and Shaffer 2021),  
181 and mammals (Upham, Esselstyn, and Jetz 2019). All five phylogeny are dated and were built  
182 with molecular data. Species with missing molecular data in the birds, amphibians, squamates,  
183 and mammals phylogeny were imputed, whereas the turtles phylogeny only includes species for

184 which molecular data was available (80% of all turtle species). We sampled 100 trees from the  
185 posterior of each phylogeny and calculated the mean cophenetic distance from these samples  
186 between all species of the four food webs. Following the recommendations by Letten &  
187 Cornwell (2015), we square root transformed cophenetic distances to better represent functional  
188 dissimilarity.

189

#### 190 *Predictive models*

191 We calibrated a Bayesian hierarchical generalized linear model on each of the four food webs  
192 (Figure 1a.I). The response data are trophic interactions that we modelled as Bernoulli  
193 distributed. Because Caron et al. (2022) found that trait-interaction relationships vary between  
194 predator groups, we used the order of the predator as varying intercepts and slopes. For each  
195 model, we randomly drew 70% of the predator-prey interactions and an equal number of absence  
196 of interaction for calibration and used remaining data for validation. To make our results are  
197 robust to the random calibration-validation split, we compared the predictions made by ten  
198 random calibration subsets and ten random validation subsets for each models.

199 
$$L_{ij} \sim \text{Bernouilli}(p_{ij}),$$

200 
$$\text{logit}(p_{ij}) = \alpha + \alpha_{\text{predator}[j]} + \sum_{k=1}^{13} (\beta_k \times T_k + \beta_{k,\text{predator}[j]} \times T_k),$$

201 where  $L_{ij}$  is the occurrence of interaction between predator  $j$  and prey  $i$ ,  $p_{ij}$  is the associated  
202 probability of interaction,  $\alpha$  and  $\beta$  are the fixed intercept and slopes of the linear model, and  
203  $\alpha_{\text{predator}[j]}$  and  $\beta_{\text{predator}[j]}$  are the random intercepts and slopes for the order of predator  $j$ .

204

205 We used 13 trait-based predictors in the models: five predator traits (trophic level, body mass,  
206 habitat breadth, longevity, and clutch size), five prey traits (trophic level, body mass, habitat  
207 breadth, longevity, and clutch size), and three trait-match predictors (match in activity time,  
208 habitat use and body mass). Since the activity time trait is binary (nocturnal and non-nocturnal)  
209 in Etard et al. (2020), the activity time match is a binary variable where a one means the predator  
210 and the prey share the same activity time trait. Habitat match is calculated as the Jaccard  
211 similarity index between the habitat used by the prey and the predator across the 12 habitat  
212 categories available in the trait database. The Jaccard similarity index takes into account the  
213 overlap in habitat used by both species and how specialized they are to these shared habitats  
214 (e.g., the habitat match of two habitat specialists species sharing their only habitat category is  
215 higher than the habitat match of two habitat generalists sharing one of their respective habitat  
216 categories). Body mass match is the squared difference between the log-transformed body mass  
217 of the prey and the predator. We used the squared difference between log-transformed body mass  
218 because we expect predators to eat prey within a given body mass interval (small enough to be  
219 handled by the predator, but big enough to be profitable; Petchey et al. (2008)). We log-  
220 transformed body mass, longevity and clutch size, because we expect the probability of  
221 interaction to respond more linearly with relative change in these variables (e.g., increase of 10%  
222 of body mass) than absolute change (e.g., increase of 10 grams). We also scaled each continuous  
223 predictor (after transformation) by subtracting out the mean and dividing by two times the  
224 standard deviation, so that the coefficients of the scaled continuous predictors are directly  
225 comparable to coefficients of unscaled binary predictors (Gelman 2008).

226

227 We used weakly informative priors for the intercept and the slopes of each model. Fixed effects  
228 were drawn from a normal distribution with a mean of 0 and a standard deviation of 1. Random  
229 effects (intercepts and slopes) were drawn from normal distributions. We used a normal  
230 distribution with a mean of 0 and a standard deviation of 1 as prior for the mean and a Half-  
231 Cauchy distribution with a scale parameter of 5 as prior for the standard deviation of the random  
232 effects:

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

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

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

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

237 To fit the models, we ran four chains, each with 1000 warm-up iterations, followed by 1000  
238 iterations for inference. We diagnosed convergence and adequacy with rank plots, posterior  
239 predictive checks, and we calculated the rank-normalized potential scale reduction factor on split  
240 chains for all runs (Vehtari et al. 2021; Appendix XX). We conducted the analyses using Stan  
241 (Carpenter et al. 2017) through the package *brms* in R (Bürkner 2017).

242

243 *Predicting species interactions*

244 To quantify model transferability, we used each model to predict the food web fitted with that  
245 model and that of the other regions considered (Figure 1a.II). For each possible predator-prey  
246 pair, we extracted the mean of the posterior as the probability of interaction, and the standard  
247 deviation of the posterior as the uncertainty around the predicted probability of interaction. When  
248 predicting the food web on which the model was calibrated (i.e., within food web predictions),  
249 we compared the predicted interaction probabilities to the validation subset of the food web.

250 When predicting food webs other than the one on which the model was calibrated (i.e., between  
251 food web predictions), we compared the predicted interaction probabilities to the entire empirical  
252 food web. We measured performance with the area under the receiver operating characteristic  
253 curve (AUC; Hanley and McNeil 1982). AUC varies from 0 to 1 where 0.5 indicates that the  
254 model failed to rank interactions higher than absences of interactions (i.e., random predictions),  
255 and 1 indicates that the model systematically ranked interactions higher than non-interactions  
256 (i.e., perfect predictions). We also measured the area under the precision-recall curve (Davis and  
257 Goadrich 2006), and directly used the posterior draws to get distributions for the true positive  
258 rate, true negative rate, positive predictive value and negative predictive value (Appendix XX).

259

260 To explore factors influencing model transferability, we assessed the performance of models to  
261 predict each food webs using three distance measures: geographic distance, environmental  
262 dissimilarity, and phylogenetic relatedness. We measured geographic distance as the Euclidean  
263 distance between the polygon centroid delimiting the spatial domain of each food web.  
264 Environmental dissimilarity was quantified using all 19 bioclimatic variables in WorldClim  
265 (Hijmans 2021). We randomly drew 500 points within each polygon corresponding to the spatial  
266 domain of our food webs and extracted bioclimatic data for these points. We used the mean of  
267 each bioclimatic variables to calculate the bioclimatic centroid of each food web. We calculated  
268 environmental distance as the Euclidean distance between the food web bioclimatic centroids.  
269 We repeated this step 10 times (10 sets of 500 random points) to make sure the environmental  
270 distance estimates are robust to random sampling (Appendix X). To measure phylogenetic  
271 relatedness, we used the mean cophenetic distance to the nearest taxon of every species in the  
272 predicted food web. We averaged over all species in the predicted food web the cophenetic

273 distance to the phylogenetically closest species in the food web used for calibration. This  
274 approach measures the amount of evolutionary history in the predicted food web undocumented  
275 by the food web the model was calibrated on.

276

277 Another test of the factors influencing model transferability focuses on analyzing predictive  
278 performance at the species level. For each combination of predicted food web models (i.e.,  
279 curves in Figure 1), we measured how accurately the set of prey and predators of each species  
280 were predicted also using the AUC. We modelled species-specific performance in terms of how  
281 connected the focal species is and how distinct the focal species is to the species pool used to  
282 calibrate the predictive model. To do this, we used species normalized degree (number of  
283 interactions divided by the maximum possible number of interactions), the functional mean  
284 pairwise distance (Mouchet et al. 2010) and distance to nearest taxon (Tucker et al., 2017).  
285 Functional mean pairwise distance is the average Gower distance (Gower 1971) between the  
286 focal species and all species in the food web used for calibration. To calculate Gower distances,  
287 we used all traits available in Etard (2020) through the function *funct.dist* from the R package  
288 mFD (Magneville et al. 2022). Distance to nearest taxon was quantified as the cophenetic  
289 distance between the focal species and the closest relative in the species in the food web used for  
290 model calibration.

291

## 292 *Predicting species' functional roles*

293 Next, we were interested in how well species functional roles were predicted by our models. The  
294 functional role of a species is determined by its position in the food web (Cirtwill et al. 2018),  
295 which we quantified using five metrics related to the position of the species within the food webs

296 (number of prey, number of predators, betweenness, closeness, eigenvector centrality), two  
297 metrics related to their trophic position (trophic levels and omnivory), two module-based metrics  
298 (within-module degree and participation coefficient; Guimerà & Amaral, 2005), and the motif  
299 profile of each species (Stouffer et al. 2012). We detail each metric, their relation to functional  
300 role, and how they were calculated in Appendix XX.

301

302 To measure how well species roles were predicted, we compared each species position metric in  
303 empirical food webs to the species position in predicted food webs. For predicted food webs, we  
304 measured each role metric on 100 samples of the posterior distribution of the entire food web  
305 with the mean as the best point estimate for the metric and the standard deviation as measure of  
306 uncertainty. For each combination of model, predicted food web, and species role metric, we  
307 fitted a linear regression between the predicted position and the empirical position. We used the  
308 coefficient of determination ( $R^2$ ) to measure how well species roles were predicted. We also  
309 explored prediction biases using the simple linear models' coefficients. We expect an intercept of  
310 zero for perfect predictions of species role, and deviation from zero would suggest systematic  
311 bias across the range of the role metric. We expect a slope of one for perfect predictions. A slope  
312 less than one would suggest that the role metric of species at the lower range are overpredicted,  
313 whereas the role metric of species at the upper range are underpredicted (i.e., more homogeneous  
314 role across species than in the empirical food web). A slope greater than one would suggest the  
315 opposite (i.e., more heterogeneous role across species than in the empirical food web).

316

317 *Predicting food web properties*

318 Finally, we investigated how well the global properties of food webs were predicted. We selected  
319 a range of metrics commonly used to quantify food web structure and which have been shown to  
320 influence food web functioning and stability: connectance, mean trophic level, maximum trophic  
321 level, motifs distribution, food web diameter, number of clusters, and modularity (Vermaat,  
322 Dunne, and Gilbert 2009; Borrelli 2015). As for species position, we evaluated these properties  
323 on the empirical food webs and compared them to the properties predicted using the mean of 100  
324 sample of the posterior food web prediction. We detail each metric, their relation to food web  
325 function, and how they were calculated in Appendix X.

326

## 327 **Results**

### 328 *Predicting trophic interactions*

329 For all food webs, trophic interactions were better predicted by the model calibrated on the same  
330 food web (within food web predictions) than by model calibrated on other food webs (between  
331 food web predictions; Table 2). For within food web predictions, AUC varied between 0.92 and  
332 0.96. Model performance was also good ( $AUC > 0.82$ ) for transfer between the Europe,  
333 Pyrenees, and Northern Québec and Labrador food webs. Models did not transfer as well from  
334 and to the Serengeti food web, but performance was still good ( $AUC > 0.75$ ). The area under the  
335 precision-recall curve, true positive rate, true negative rate, positive predictive value, and  
336 negative predictive value were all positively correlated with AUC and showed the same overall  
337 pattern (Appendix X).

338

339 To explore the factors influencing the transferability of interaction models, we modelled their  
340 performance relative to the geographic, environmental, and phylogenetic distances between the

341 calibrated and predicted food web (Figure 2). Overall, performance tended to decrease with  
342 environmental (direct effect estimate: -0.54, 95%CrI = [-0.96, -0.12]) and phylogenetic distance  
343 (direct effect estimate: -0.45, 95%CrI = [-0.84, -0.07]). Performance also decreased with  
344 geographic distance (total effect estimate: -0.56, 95%CrI = [-0.80, -0.30]), but not after  
345 controlling for phylogenetic and environmental distances (direct effect estimate: -0.06, 95%CrI =  
346 [-0.46, 0.34]).

347

348 We also identified the species for which the interactions were incorrectly predicted by between  
349 food web predictions. We modelled species-specific performance to the phylogenetic and  
350 functional distance between the focal species and the species pool used to train the models  
351 (Figure 3). As expected, species with phylogenetically close relatives in the species pool used for  
352 calibration were, on average, better predicted than distant relatives. Species-specific performance  
353 slightly decreased at low and intermediate phylogenetic distances, and then dropped significantly  
354 at large distances. Models calibrated and predicted across classes (e.g. mammals to amphibians)  
355 had the lowest performance as expected (Appendix X). This situation only occurs with the  
356 Northern Québec and Labrador model predicting the other three food webs as there are no  
357 amphibians or reptiles in Northern Québec and Labrador. Surprisingly, predictive performance  
358 remained qualitatively unchanged by functional distance. We also found that interactions of  
359 specialist (i.e., species with few interactions) and generalist species (i.e., species with many  
360 interactions) were, on average, better predicted than interactions of species of intermediate  
361 specialization (Figure 3c).

362

363 *Predicting species functional role*

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

369

370 We also found important biases in the predictions of species roles when we fitted linear  
371 regressions between species roles in predicted food webs to their roles in the empirical food  
372 webs. The number of prey, predators, trophic level, omnivory, and the frequency of motif  
373 positions tended to be similarly overestimated across species (slopes close to 1, and intercept  
374 greater than 0). For other measures such as eigenvector centrality, betweenness, closeness, and  
375 module-based roles, species had more similar values between predicted and empirical food webs  
376 (Appendix X, slopes less than 1).

377

### 378 *Predicting food web properties*

379 The majority of food web properties were not well predicted by our interaction models (Figure  
380 5). Connectance, mean and max trophic levels, and the frequency of most motifs were  
381 overpredicted, whereas the number of clusters and modularity were slightly underpredicted.  
382 Mean and variance of relative errors were greater for between- compared to within-food web  
383 predictions. In general, predicted food webs were more connected, displayed a higher frequency  
384 of most motifs, and were less modular and with less basal species. This increased the trophic  
385 level of most species.

386

387 **Discussion**

388 Predictive models of trophic interactions have recently become central in filling knowledge gaps  
389 about how predators and prey interact across space and time. Here, we showed that trait-based  
390 trophic interaction models can predict interactions across ecosystems. We found that, given  
391 enough phylogenetic and environmental similarities between the system on which the model is  
392 calibrated and the system for which the predictions are made, models predicted most interactions  
393 reasonably well. Our results suggest that, for terrestrial vertebrate food webs, trait relationships  
394 driving interactions appear to be relatively general even in highly contrasting environments.

395 Although models were successful at predicting interactions, they were less successful higher-  
396 level food web properties. We found systematic biases in the species position and food web  
397 properties predictions. Biases varied across metrics, but overall, the predicted food webs were  
398 better connected, less modular, had more trophic levels, and species were more equally  
399 connected. These higher-level properties of food webs were especially poorly predicted when  
400 making between food web predictions (i.e., knowledge transfer).

401

402 The trait-matching framework of trophic niche theory assumes that spatial variation in food webs  
403 arises through variation in the trait-matching rules driving interactions and the distribution of  
404 traits in different systems (Gravel, Albouy, and Thuiller 2016). Our ability to predict food web  
405 interactions across contrasting environment suggests that spatial food web variation is mainly  
406 driven by changes in the distribution of functional traits, and less so by the variation of trait-  
407 matching relationships. These are in line with previous results finding generalities in trait-  
408 interactions relationships across European bioregions (Caron et al. 2022), the predator-prey  
409 body-size ratios within habitat, predator, and prey types (Brose et al. 2006), and the trait-

410 interactions relationships in soil invertebrates across three forest areas in Germany (Laigle et al.  
411 2018). Given that trait-matching rules driving species interactions seem general in reasonably  
412 similar environments, it should be possible to use data from well-studied areas to predict  
413 interactions in areas we know very little about or forecast (and hindcast) food webs given new  
414 trait distributions. Strydom et al. (2021) also found that latent trait models could accurately  
415 transfer knowledge through phylogenetic relationships. In the future, different predictors (e.g.,  
416 trait-based models, phylogeny-based models), and models (e.g., linear models, machine learning)  
417 could be combined into ensemble models. Ensemble models have the potential to make better  
418 predictions by cancelling the noise created by the specific data and models (Araújo and New  
419 2007). However, model comparison studies are needed since ensemble models do not always  
420 outperform individual models (Hao et al. 2020).

421

422 We also highlighted a major limitation of trophic interaction models: trophic interaction models  
423 predict interactions, not food webs. Even if most interactions and absences of interactions are  
424 well predicted (high true positive and negative rates), there are much more absences of  
425 interactions to predict than presences in real food webs (low connectance). This might explain  
426 why our models systematically overpredicted the number of interactions (number of prey and  
427 predators) across species (Appendix X). This bias probably propagated through the food webs,  
428 explaining why the centrality of species was more evenly distributed, and the predicted food  
429 webs were more connected, less modular, and with higher trophic levels.

430

431 The structural properties of food webs (i.e., connectance, number of trophic levels, modularity)  
432 influence the stability, invasibility, and productivity of ecosystems (Duffy et al. 2007; Wang and

433 Brose 2018; Lurgi et al. 2014), whereas the position of species within food webs determine their  
434 functional role, and can help identify keystone species and prevent cascading effects of  
435 extinction (Cirtwill et al. 2018; Estes et al. 2011). Here, predicting individual links failed to  
436 predict higher-level properties, suggesting that there are constraints acting on the structures of  
437 food webs that trophic interaction models cannot capture. Spatial and temporal variation of  
438 ecological network structure has gained a lot of interest recently (Baiser et al. 2019; Gravel et al.  
439 2019). Because sampling interactions at large scales is difficult, predictions by interaction  
440 models could help to investigate the variation of interactions and network structures  
441 simultaneously (e.g., Albouy et al., 2014). This would be possible only if the biases in predicted  
442 network structure are constant across the gradient of interest. Given our results, testing this  
443 assumption should be necessary to robustly test the variation in network structure.

444

445 Correcting biases in higher-level property predictions is possibly an opportunity to improve  
446 species interaction predictions. In species distribution models, methods are already developed to  
447 use biases in higher-level properties (e.g., species richness) to correct distribution predictions  
448 (e.g., Leung et al., 2019). These models correct systematic biases in predictions similar to those  
449 we found in our study. Therefore, methods that would combine predictions of interactions and  
450 networks have the potential to provide better food web predictions. Different models can predict  
451 the number of links that we expect from the number of species (MacDonald, Banville, and Poisot  
452 2020). With the number of links and species, structural food web models can predict the  
453 probability distribution of many food web properties (Williams and Martinez 2008). Information  
454 on probable food web structure could be used to correct posterior predictive distributions of  
455 species interactions.

456

457 Our study suffers from a few limitations that if overcome can move us closer to a comprehensive  
458 framework for ecological interactions and networks prediction. First, we used four food webs of  
459 terrestrial vertebrates. Although there is no clear *a priori* reason not to be applicable in other  
460 systems, our results are unlikely to be general across all taxa and types of interactions. We don't  
461 know any other test of interaction model transferability, but it would be interesting to investigate  
462 if our results hold for systems where trait-matching relationships are stronger or weaker. The  
463 exclusion of non-terrestrial vertebrates (e.g., plants, invertebrates, parasites) also influence the  
464 empirical and predicted species role and food web properties. For example, the first trophic  
465 levels in our food webs were not primary producers, but species not feeding on terrestrial  
466 vertebrates (e.g., herbivores, invertivores). Second, the food webs we used are potential and  
467 binary food webs. Trait-matching models predict the probabilities that a species could eat another  
468 species given they are encountering. Additional data, such as co-occurrence and abundance data,  
469 are needed to make predictions of realized and quantitative interactions. Finally, due to the  
470 scarcity of food web data, we only had four food webs to work with. This means we only had  
471 four sets of within food web predictions, and 12 sets of between food web predictions. This  
472 explains the large uncertainty for some of our results (e.g., Figure 2). Despite the low sample  
473 size, we still detected significant relationship between model transferability and geographic,  
474 phylogenetic, and environmental distances.

475

476 Overall, we found that trait-based interaction models can transfer knowledge relatively well  
477 given enough phylogenetic and environmental similarities between systems. These models can  
478 predict pools of potential interactions even in contrasting environments, suggesting that changes

479 in food webs are mainly explain by changes in trait distribution, and less by changes in the trait-  
480 interaction relationships. However, the resulting food webs should be viewed as a preliminary set  
481 of interactions, asking for refinement since the structure and trophic positions of species are not  
482 correctly predicted. These refinements could take the form of bias correction methods using  
483 predictions of higher-level food web properties, combination of predictions to other types of data  
484 (e.g., expert knowledge, co-occurrences, abundances), or combination of types of models (e.g.,  
485 trait-matching, phylogenetic matching, machine learning). Such methodological advancements  
486 would allow better prediction of both interactions and food webs across space and time, which in  
487 turn, play a large role in filling the large knowledge gaps on how species interact and allow to  
488 investigate how global changes may impact ecosystems (Albouy et al. 2014; Fricke et al. 2022).

489

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491

492 **Author contributions**

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*Table 1: Summary of properties 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

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*Table 2: Food webs are better predicted by their own calibrated model. Area under the receiver operating curve (AUC) of each model predicting every food web.*

Model	Food web			
	Europe	Pyrenees	Nunavik	Serengeti
Europe	<b>0.96</b>	0.89	0.9	0.8
Pyrenees	0.86	<b>0.94</b>	0.86	0.75
Nunavik	0.82	0.91	<b>0.95</b>	0.76
Serengeti	0.84	0.77	0.76	<b>0.92</b>

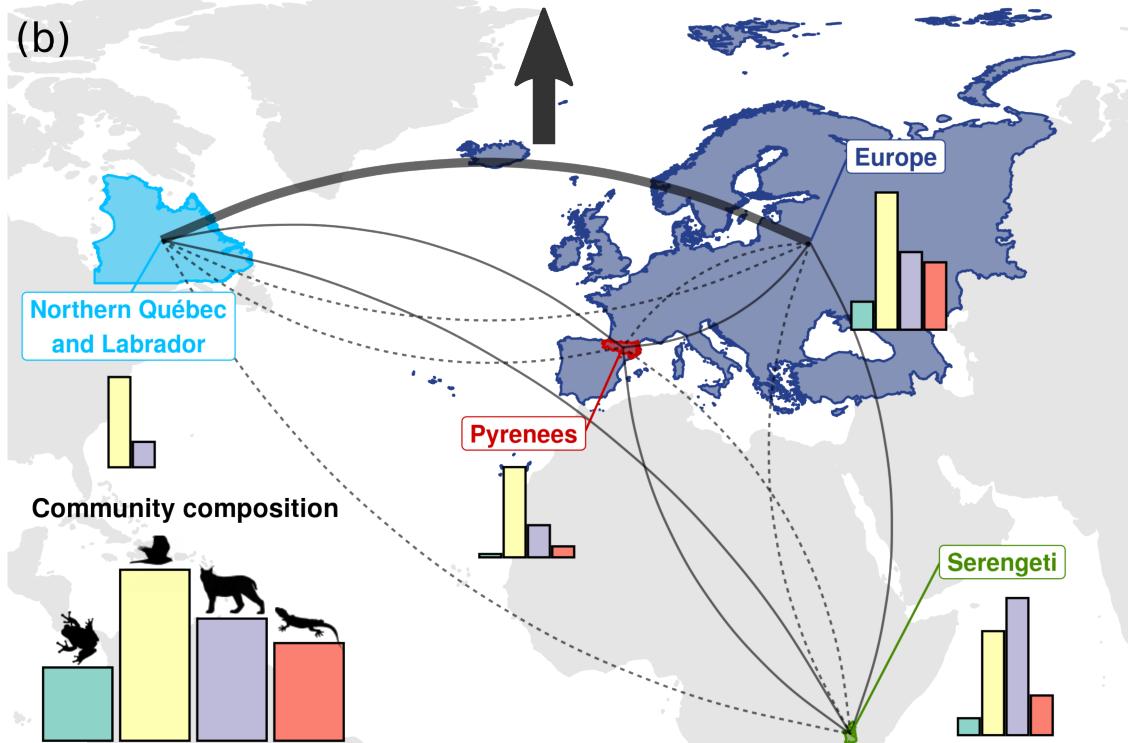
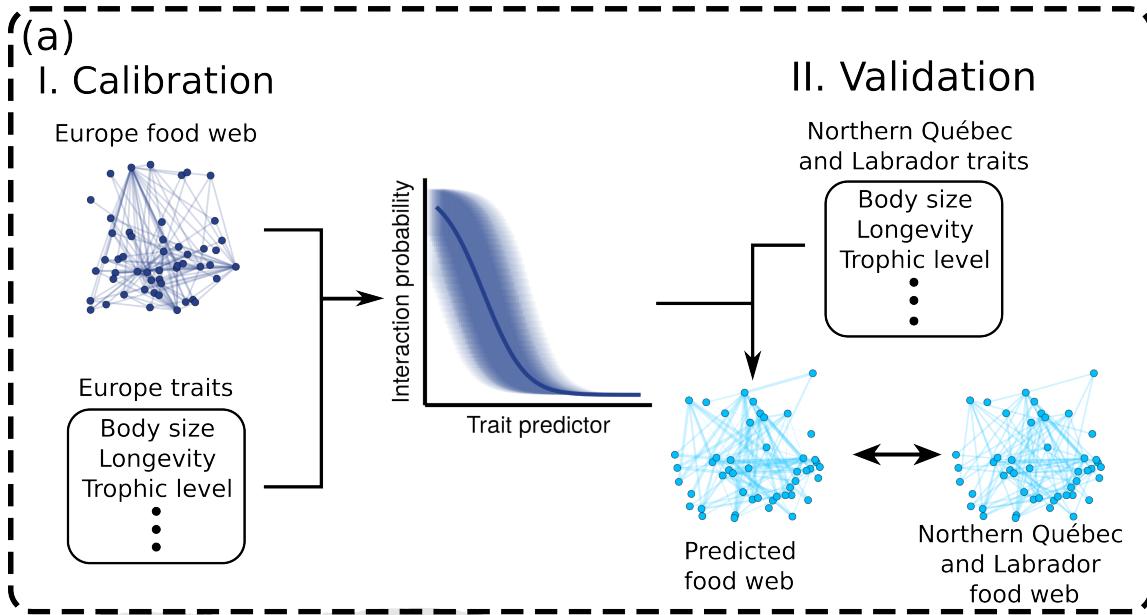
*Figure 1: Trophic interactions model transferability analysis workflow.* We calibrated trophic interaction model on using each food web considered in this study separately (panel a.I). We validated the four models on a validation subset for within-food web predictions (not shown in the figure), and the entire set of food webs for between-food web predictions (panel a.II). Panel (a) shows an example workflow for the between food web predictions. Panel (b) is a map of the spatial domain of each food web. The 12 curves are the model-food web pairs for between food web predictions. The within food web predictions are not shown in the figure. Bar plots show the proportion of amphibians (green), birds (yellow), mammals (purple), and reptiles (red) in each food web.

*Figure 2: Transferability of predictive models.* Points are the predictive performance (area under the receiver operating curve) of the sixteen combination of model-food web prediction (Table 2). The trend lines are the median effects with their 95% credible interval of geographic, environmental, and phylogenetic distances on predictive performance. Shown are the direct effect of geographic distance (controlling for environmental and phylogenetic distances), and the direct (controlling for geographic distance) effects of environmental and phylogenetic distances.

*Figure 3: Predicting species interactions.* Performance of the model calibrated on each food web to predict the interactions of species in the other food webs. Each point is the performance to predict the prey and predators of a single species. The trend lines are the median effects with their 95% credible interval of distance to the nearest taxon, mean functional pairwise distance, and normalized degree on predictive performance.

*Figure 4: Predicting species functional role.* The variance in predicted trophic positions explained by the empirical trophic position. From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, eigenvector centrality, within-module degree, participation coefficient, times the species is at a specific position in the linear chain, intraguild predatrion, direct competition, and apparent competition motifs. The horizontal lines are the  $R^2$  for each role, model, and food web predicted combination. White dots are the mean  $R^2$  with for within food web predictions. Black dots are the mean  $R^2$  for across food web predictions.

*Figure 5: Predicting global food web properties.* The relative error of the predicted food web properties. Relative error is the difference between the predicted and 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, intraguild predation, direct competition, and apparent competition motifs. Horizontal lines are the relative errors for each property, model, and food web predicted combination. White dots are the mean relative errors for within- and black dots are the mean relative errors for between-food web predictions.



*Figure 1: Trophic interactions model transferability analysis workflow.*

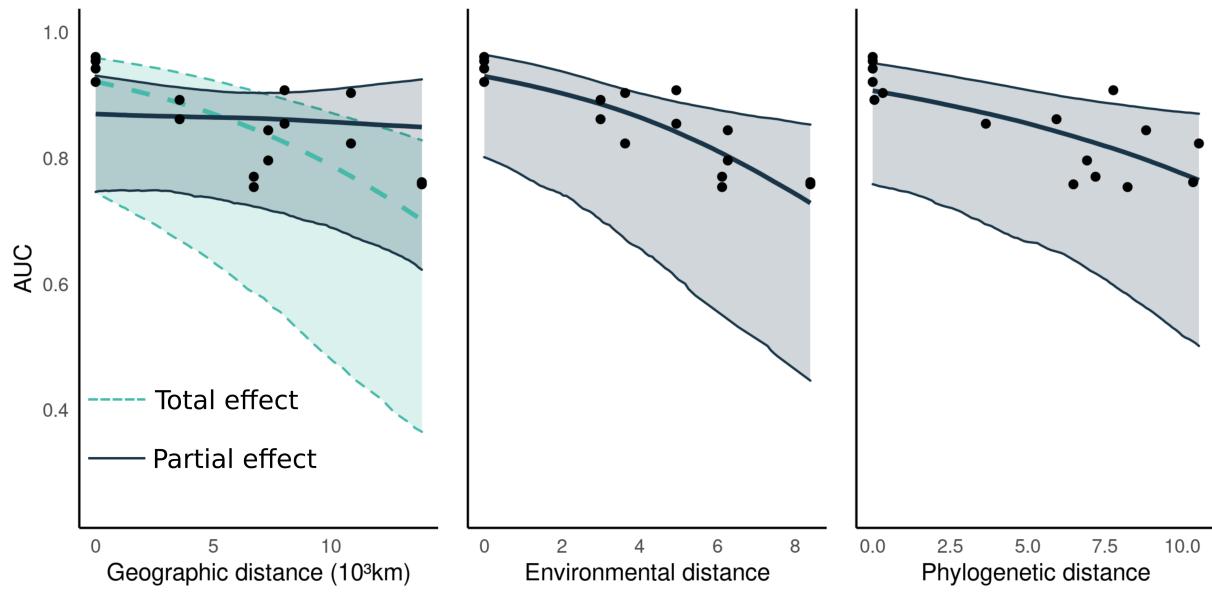


Figure 2: *Transferability of predictive models.*

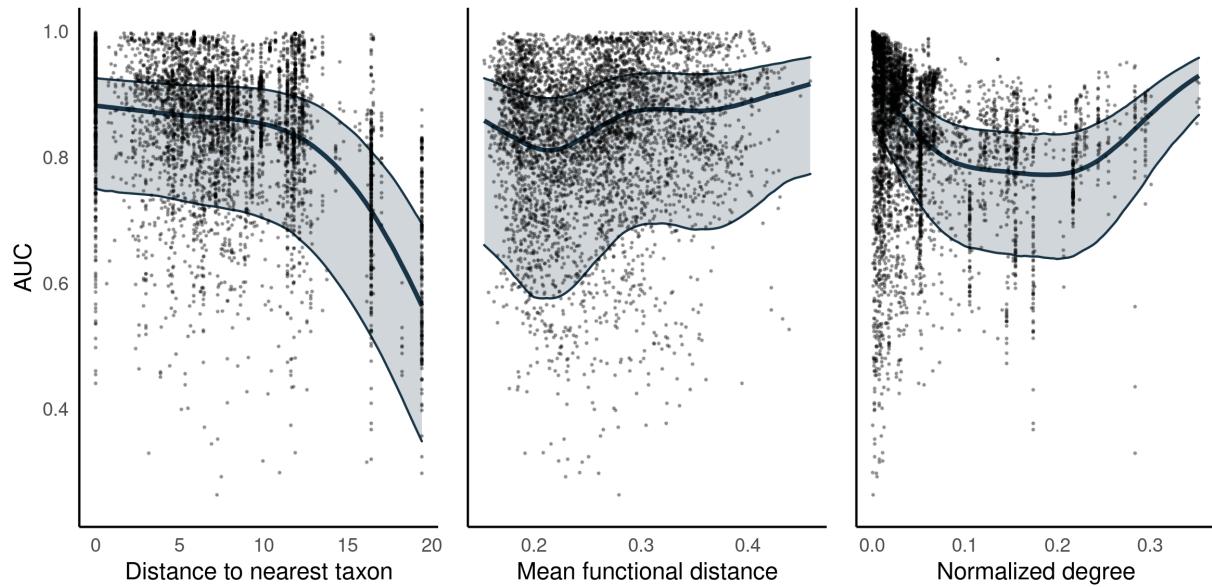
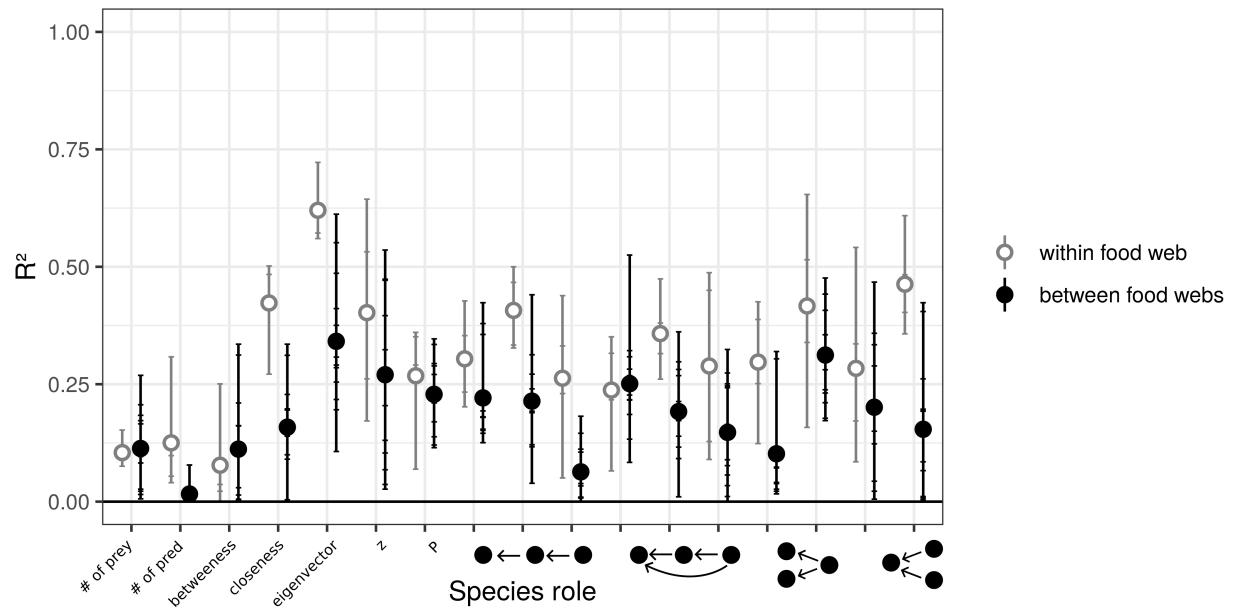
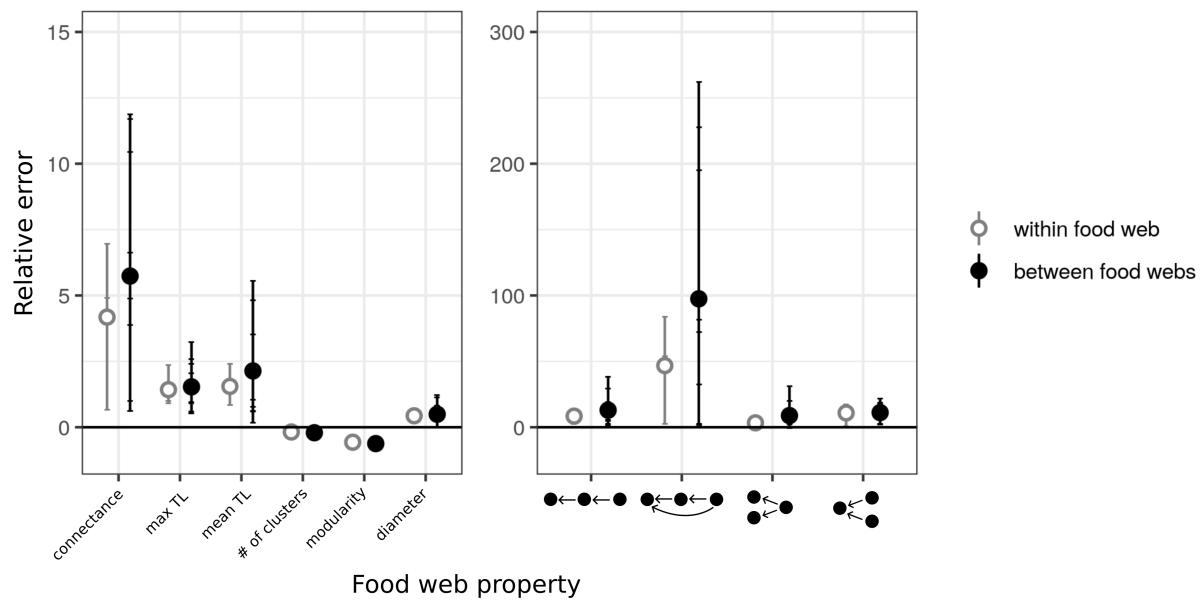


Figure 3: *Predicting species interactions.*



*Figure 4: Predicting species functional role.*



*Figure 5: Predicting global food web properties.*