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

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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.

Introduction

Many ecosystem functions (e.g., energy flows and material cycling) and community stability

depend on the trophic relationships that link species within a community (Harvey et al. 2017).

Despite the recognized importance of food webs in ecosystems over the last 80 years (Lindeman

1942), we still face major challenges to develop accurate descriptions of food webs. The lack of

trophic interactions data across most locations and taxa (Poisot et al. 2021) lie at the core of the

fundamental technical and practical challenges in food web ecology. Observing interactions is

more challenging than observing species because two individuals need to be simultaneously

detected while they are interacting (Jordano 2016), and the number of possible interactions webs

grows quadratically with the number of species. Determining all possible interactions among

species within a network is difficult even in species-poor ecosystems. Quantifying the strength

and type (e.g. predator vs mutualism vs competition) of interactions, a common goal of

ecological network studies, adds even more complexity to this already difficult problem.

A first step towards constructing food webs is to focus on a single type of interaction, predator-

prey relationships, which are the most commonly recorded one, and have been shown to respond

to a predictable set of neutral and niche processes (Morales-Castilla et al. 2015). A neutral model

for trophic interactions suggests that the probability and strength of interactions respond only to

the co-occurrences and abundances of species (Canard et al. 2012). Recent studies have shown

however, that even if co-occurrence is a requirement for species to interact, it is not evidence for

realized trophic interactions (Blanchet, Cazelles, and Gravel 2020). We must thus be careful

when making assertions about trophic interactions based solely on co-occurence data. Niche

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., insectives, 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.

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

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

201 where L_{ij} is the occurrence of interaction between predator *j* and prey *i*, p_{ij} is the associated

202 probability of interaction, α and β are the fixed intercept and slopes of the linear model, and

203 $\alpha_{predator[j]}$ and $\beta_{predator[j]}$ 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 role*s

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

13

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*

14

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*

16

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

Discussion

Predictive models of trophic interactions have recently become central in filling knowledge gaps about how predators and prey interact across space and time. Here, we showed that trait-based trophic interaction models can predict interactions across ecosystems. We found that, given enough phylogenetic and environmental similarities between the system on which the model is calibrated and the system for which the predictions are made, models predicted most interactions reasonably well. Our results suggest that, for terrestrial vertebrate food webs, trait relationships driving interactions appear to be relatively general even in highly contrasting environments. Although models were successful at predicting interactions, they were less successful higher-level food web properties. We found systematic biases in the species position and food web properties predictions. Biases varied across metrics, but overall, the predicted food webs were better connected, less modular, had more trophic levels, and species were more equally connected. These higher-level properties of food webs were especially poorly predicted when making between food web predictions (i.e., knowledge transfer).

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

18

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**

493 **References**

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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

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.

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

*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.*
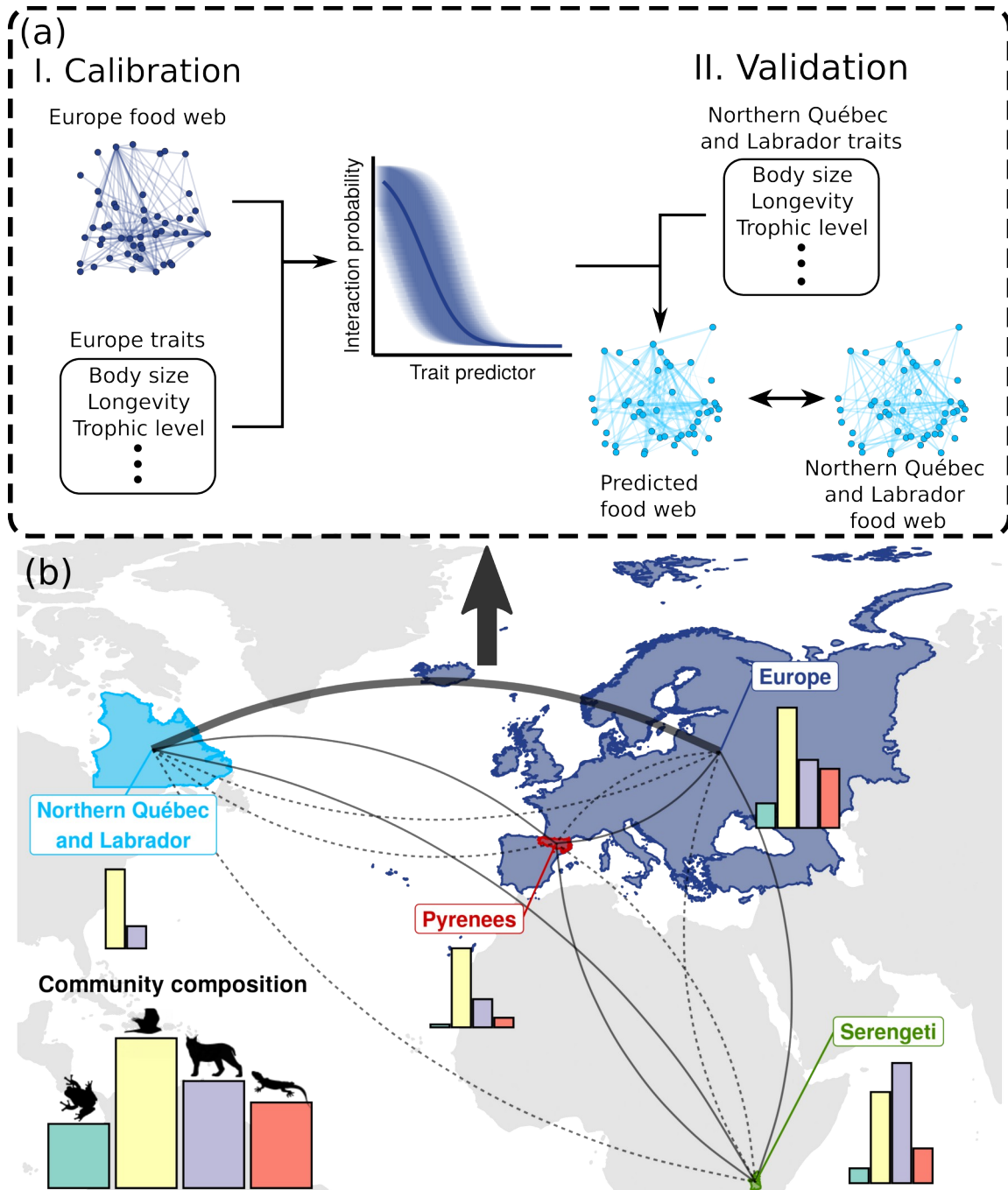
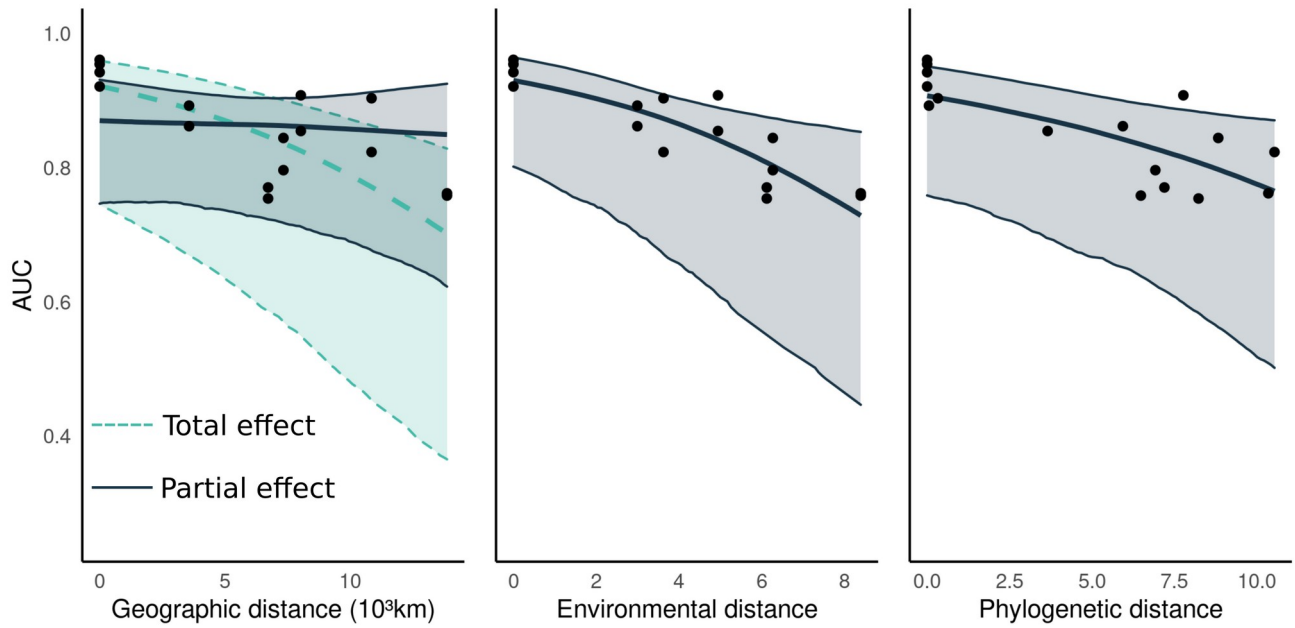*Figure 2:* **Trophic interactions model transferability analysis workflow.**

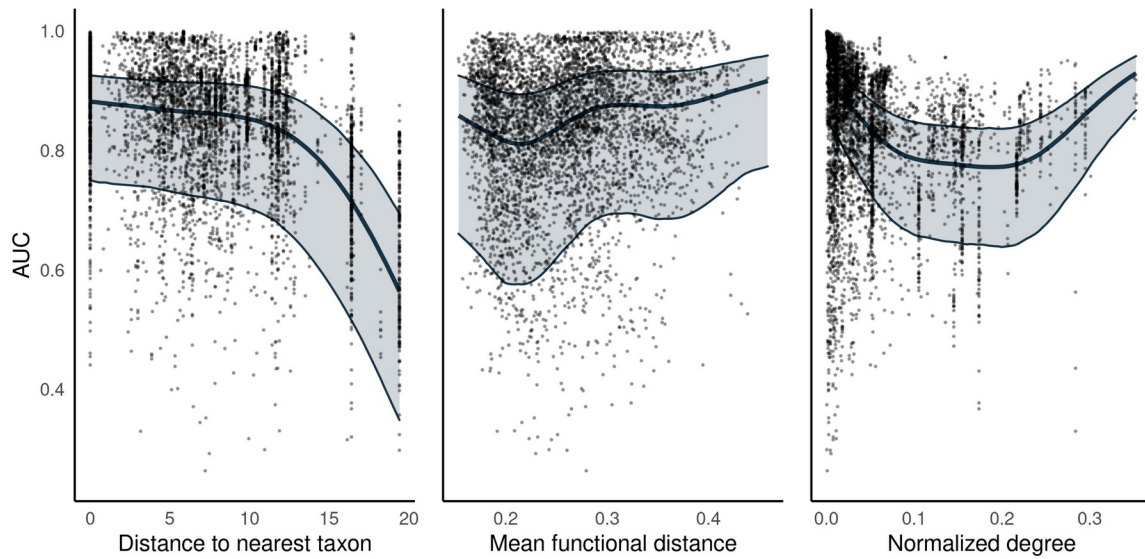*Figure 2 :* **Transferability of predictive models.**
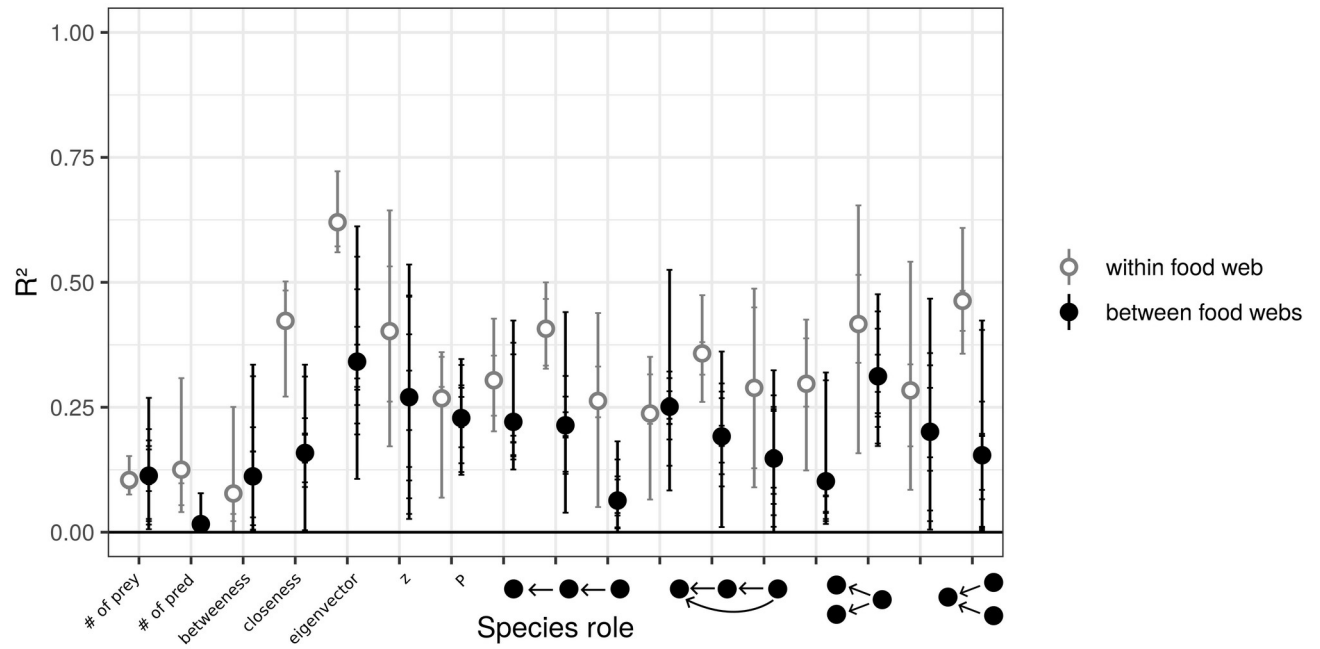

Figure 3: **Predicting species interactions.**
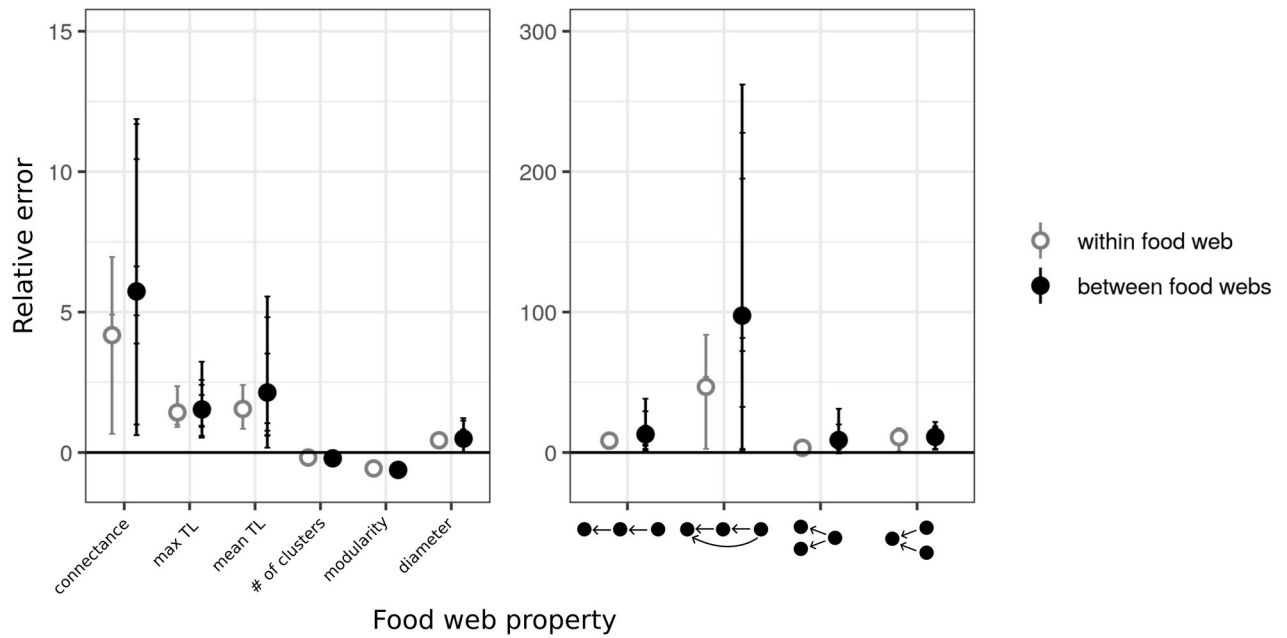
Figure 4: **Predicting species functional role**.

Figure 5: **Predicting global food web properties**.