

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

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21 **Abstract**

22 Trophic interactions between species are central to our understanding of biodiversity functions
23 such as stability, nutrient cycling, and productivity. Yet, we lack data on predator-prey
24 relationships for most taxa and systems. A promising avenue for tackling this knowledge gap is
25 through predictions of trophic interactions. These predictions can fill gaps in existing food webs
26 (i.e. within food web predictions) or transfer knowledge between areas (i.e. across food web
27 predictions). Here, we used four trait-based models of trophic interactions, each calibrated on a
28 different food web of terrestrial vertebrates from contrasting environments to ask what limit
29 across food web predictions and how well they predict higher-level properties of food webs
30 (species position and entire food web properties). We found that given enough phylogenetic and
31 environmental similarities between food webs, trait-based models predict most interactions and
32 non-interactions correctly in new environments. However, when we collated predicted trophic
33 interactions to recover food webs, species trophic position and food web properties were not well
34 predicted. Predicted food webs tended to be more connected, less modular, and with higher mean
35 trophic levels. Our results show that trait-based models can predict pools of potential interactions
36 in environments we know nothing. We also highlight the need for methodological advances to
37 simultaneously study trophic interactions and the structure of food webs across time and space.

38 **Introduction**

39 Many ecosystem functions (e.g., energy flows, material cycling, and stability) depend on the
40 trophic relationships that link species of a community (Harvey et al. 2017; Thompson et al.
41 2012). These trophic relationships form the food web. Despite recognizing the central role of
42 food webs in ecosystems for over 80 years (Lindeman 1942), we still lack food web data for
43 most places and taxa (Cameron et al. 2019; Hortal et al. 2015; Poisot et al. 2021). The reason for
44 this knowledge gap is two-fold. First, the number of possible interactions grows quadratically
45 with the number of species. Second, observing (and even more quantifying) interactions between
46 two individuals is inherently hard as we need to detect simultaneously two species and the
47 interactions (Jordano 2016). Having more widespread food web data and at larger scales would
48 open research opportunities by integrating the Grinnellian and Eltonian niche into biogeography
49 (Braga et al. 2019; Gravel et al. 2019), incorporating trophic interactions into meta-community
50 ecology (Guzman et al. 2019), and describing the functional role of species in biodiversity-
51 ecosystem functioning (Dehling and Stouffer 2018; Gonzalez et al. 2020).

52

53 A promising first step towards filling this knowledge gap about food webs is by predicting
54 potential trophic interactions. This should be possible since predator and prey tend to respond to
55 a predictable set of geographic, phylogenetic and functional relationships (Morales-Castilla et al.
56 2015). The neutral model predicts that the probability and strength of interactions respond only
57 to the co-occurrences and abundances of species (Canard et al. 2012). Although co-occurrence
58 patterns and species interactions influence each other, they are not evidence of one another
59 (Blanchet, Cazelles, and Gravel 2020). Niche theory predicts that the match between the

functional traits of predators and their prey should improve these predictions by identifying which interactions are feasible (Williams and Martinez 2000). These trait-based models have been used to predict food webs in freshwater streams (Pomeranz et al. 2019), of marine fishes (Albouy et al. 2014), terrestrial invertebrates (Laigle et al. 2018), and vertebrates (Caron et al. 2022; Fricke et al. 2022), among others. Phylogenetic relationships are also informative since interactions and species positions tend to be evolutionarily conserved (Gómez, Verdú, and Perfectti 2010; Stouffer et al. 2012). For example, Strydom et al. (2021) recently used the mammal phylogeny to map latent traits extracted from the European mammal food web to predict the Canadian mammal food web.

However, some questions remain about the potential of trophic interaction models to predict food webs. The first question is how well can predictive models transfer knowledge across different regions. Strydom et al. (2021) successfully recovered over 90% of known interactions among Canadian mammals without any information about the food web, but they had very little information on non-interactions. It is hard to evaluate how well their predictions can recover the entire food web (interactions and non-interactions) since they could only evaluate performance on known interactions. Also, despite the little overlap in species, they transferred knowledge between two systems with large shared evolutionary history (one order unique to each in Canada and Europe). Given that their method uses phylogeny as a medium to transfer knowledge, it is unclear how well their methods would perform for more contrasting systems. The second question is how well can models of trophic interactions predict the structure of food webs? By structure, we mean the properties of food webs (e.g., connectance, number of trophic levels) and

the position of species (e.g., number of prey, centrality) in food webs. Most studies aimed to predict either the properties of food webs (e.g., Allesina et al., 2008; Allesina & Pascual, 2009; Cattin et al., 2004; Williams & Martinez, 2000) or interactions (e.g., Gravel et al., 2013; Laigle et al., 2018; Pomeranz et al., 2019), but rarely assessed if predicting interactions also recover the structure of food webs. Caron et al. (2022) found that connectance of terrestrial food webs tended to be systematically overpredicted across Europe by 2-4 times, but did not explore other food web properties or species positions. This is an important knowledge gap as many ecosystem functions and the functional role of species are controlled by the global shape of food webs and species positions within the food web (Cirtwill et al. 2018; Dunne, Williams, and Martinez 2002; Smith-Ramesh, Moore, and Schmitz 2016; Thompson et al. 2012).

Here, we trained a set of trait-based predictive models on four contrasting food webs of terrestrial vertebrates: the trophic food web of European tetrapods, the Nunavik food web, the Pyrenees vertebrate food web, and the Serengeti food web. The models are Bayesian generalized hierarchical models that we calibrated on each food web and validated on the other food webs. We used these models to determine how well trait-based models of trophic interactions can transfer across systems. More specifically, we ask: (1) What are the factors (i.e., geographic, environmental, functional, or phylogenetic distances) influencing the transferability of models? (2) How well the trophic role of species are predicted? and (3) How well food web properties are predicted?

Methods

104 *Food web data*

105 We extracted trophic interactions between terrestrial vertebrates (terrestrial mammals, birds,
106 amphibians and reptiles) from four well-resolved food webs (Table 1):

107

108 1. *Europe food web*: The trophic food web of European tetrapods was assembled by
109 Maiorano et al. (2020). The Europe food web contains the potential trophic interactions
110 and non-interactions between all terrestrial vertebrates in Europe based on data from
111 guide books, published papers, and expert opinions. The authors originally reported
112 interactions between predators and prey at different life-stage (eggs, larvae/young, or
113 adult). Here, we only extracted interactions between predators and adult prey.

114

115 2. *Pyrenees food web*: The Pyrenees vertebrate food web was assembled indenpendently
116 from the Europe food web by Lurgi et al. (2012). The authors compiled all known
117 interactions between vertebrate species in the southeastern Pyrenees mountain range. To
118 keep the same taxonomic coverage between food webs, we excluded fish species.

119

120 3. *Nunavik food web*: The trophic tundra food web of Labrador and northern Quebec
121 (Canada) was compiled by Berteaux et al. (2018). The Nunavik food web is a binary
122 matrix documenting the trophic relationships between all birds, mammals, and some
123 groups of plants and arthropods whose distribution overlaps Labrador and Quebec north
124 of the 50°N. The documented area is dominated by the Canadian tundra ecosystem.

Trophic interactions were collated from a literature review, combined with data from existing databases, and expert opinions. We excluded all non-vertebrate species.

4. *Serengeti food web*: The Serengeti food web compiles all interactions between the different trophic groups in the Serengeti National Park (Tanzania) and was assembled from a literature review (Baskerville et al. 2011; de Visser, Freymann, and Olff 2011). We assumed that species within a trophic group share the same predator and prey. We excluded all non-terrestrial vertebrate species.

Table 1: Summary of the food webs after excluding species for which no match were found in the GBIF Backbone Taxonomy or 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	Nunavik	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

Trait data

We used the database of ecological traits for terrestrial vertebrates compiled by Etard et al. (2020). Etard et al. (2020) combined the information on species-level body size, longevity, clutch size, trophic level, activity time and habitat use from large freely available secondary trait

138 databases. The database includes traits for 6 990 amphibians, 11 634 birds, 5 380 mammals, and
139 10 612 reptiles.

140

141 To match species in the trait databases to the species in the food webs, we standardized their
142 names following the taxonomic backbone of GBIF. To do so, we used the function
143 *name_backbone* from the package *rgbif* (Chamberlain et al. 2022; Chamberlain and Boettiger
144 2017) in R. In each food web, we excluded all species for which no match was found in the
145 taxonomic backbone of GBIF or the trait database. We imputed missing traits using the
146 missForest algorithm (Stekhoven and Buehlmann 2012) for amphibians, birds, mammals and
147 reptiles separately.

148

149 *Predictive models*

150 We calibrated a Bayesian hierarchical linear model (GLMM) on each of the four food webs. The
151 response data are trophic interactions that we modelled as Bernouilli distributed. For each model,
152 we used 70% of all interactions, and an equal number of non-interactions for calibration. We
153 used the remaining of the data for validation. Because we previously found that trait-interaction
154 relationships vary between predator groups (Caron et al. 2022), we used the order of the predator
155 as random effect on the intercept and slopes in each model.

156

157 The models used 13 trait-based predictors: the trophic level, body mass, habitat breadth,
158 longevity, and clutch size of the predator and the prey, and the match between their activity time,
159 habitat use and body mass. Activity time match is a binary variable where one means the

predator and the prey are active at the same time of the day. Habitat match is the Jaccard similarity index between the habitat used by the prey and the predator across the 13 habitat categories in the trait database. Body mass match is the squared difference between the log-transformed body mass of the prey and the predator. We log-transformed body mass, longevity and clutch size. We also scaled each continuous predictor by subtracting it by the mean and dividing by two times the standard deviation, so that the coefficients of the scaled continuous predictors are directly comparable to coefficients of unscaled binary predictors (Gelman 2008).

We used weakly informative priors for the intercept and the slopes of each model. The random effects (intercepts and slopes) were drawn from normal distributions. We used a normal distribution with a mean of 0 and a standard deviation of 1 as prior for the mean and a half Cauchy distribution with a scale parameter of 5 as prior for the standard deviation of the random effects. We describe the models in more detail in appendix XX.

We ran four chains, each with 1000 warm-up iterations, followed by 1000 iterations for inference. We diagnosed convergence and adequacy with trace plots, posterior predictive checks, and calculated the potential scale reduction factor for all runs (Gelman & Rubin, 1992; Appendix XX). We conducted the Bayesian analyses using Stan through the package *brms* in R (Bürkner 2017; Carpenter et al. 2017).

Predicting species interactions

181 To measure how well models transfer, we used each model to predict the other three food webs
182 (Figure 1). For each possible predator-prey pair, we extracted the mean of 100 posterior draws to
183 get the probability of interaction. We compared these probabilities of interactions to the empirical
184 food web interactions to measure how well species interactions are predicted. We measured
185 performance with the area under the receiver operating characteristic curve (AUC). AUC varies
186 from 0.5 to 1 where 0.5 indicates that the model failed to rank interactions higher than non-
187 interactions (i.e., random prediction), and 1 indicates that the model systematically ranked
188 interactions higher than non-interactions (i.e., perfect prediction). We also measured the area
189 under the precision-recall curve, and directly used the posterior draws to get distributions for the
190 true positive rate, true negative rate, positive predictive value and negative predictive value
191 (Appendix XX).

192

193 To explore factors influencing model transferability, we modelled the performance of models to
194 predict each food webs with three distance measures: geographic distance, environmental
195 dissimilarity, and phylogenetic relatedness. We measured geographic distance with the euclidean
196 distance between the centroid of the polygon delimiting each food web. We measured
197 environmental dissimilarity using all bioclimatic variables (Hijmans 2021). We randomly drew
198 500 points within each polygons and extracted bioclimatic data for these points. We then ran a
199 principal component analysis on the extracted bioclimatic variables and calculated the euclidean
200 distance between the centroid of the principal components (Appendix XX). We measured
201 phylogenetic relatedness with the mean phylogenetic distance to the nearest taxon of every
202 species in the predicted food web. In other words, we averaged over all species in the predicted

203 food web the phylogenetic distance to the closest related species in the food web used for
204 calibration. This measures the amount of evolutionary history in the predicted food web
205 undocumented by the food web the model was calibrated on. We used the published phylogeny
206 for birds (W. Jetz et al. 2012), amphibians (Walter Jetz and Pyron 2018), squamates (Tonini et al.
207 2016), turtles (Thomson, Spinks, and Shaffer 2021), and mammals (Upham, Esselstyn, and Jetz
208 2019). Following the recommendations by Letten & Cornwell (2015), we square root
209 transformed phylogenetic distances to better represent functional dissimilarity.

210

211 We further explored the factors influencing model transfer by analyzing species-specific
212 performance. For each combination of predicted food web-model (i.e., curves in Figure 1), we
213 measured how well the prey and predators of each species were predicted using the AUC. We
214 modelled the species-specific performance to how distinct the focal species is to the species pool
215 used to calibrate the predictive model. We used the functional mean pairwise distance (Mouchet
216 et al. 2010) and distance to nearest taxon (Tucker et al., 2017). Functional mean pairwise
217 distance is the average Gower distance (Gower 1971) between the focal species and all species in
218 the food web used for calibration. To calculate Gower distances, we used all traits available in
219 Etard (2020) through the function *funct.dist* from the package mFD in R (Magneville et al.
220 2022). Distance to nearest taxon distance is the square root of the phylogenetic distance between
221 the focal species and the closest relative in the species in the food web used for model
222 calibration.

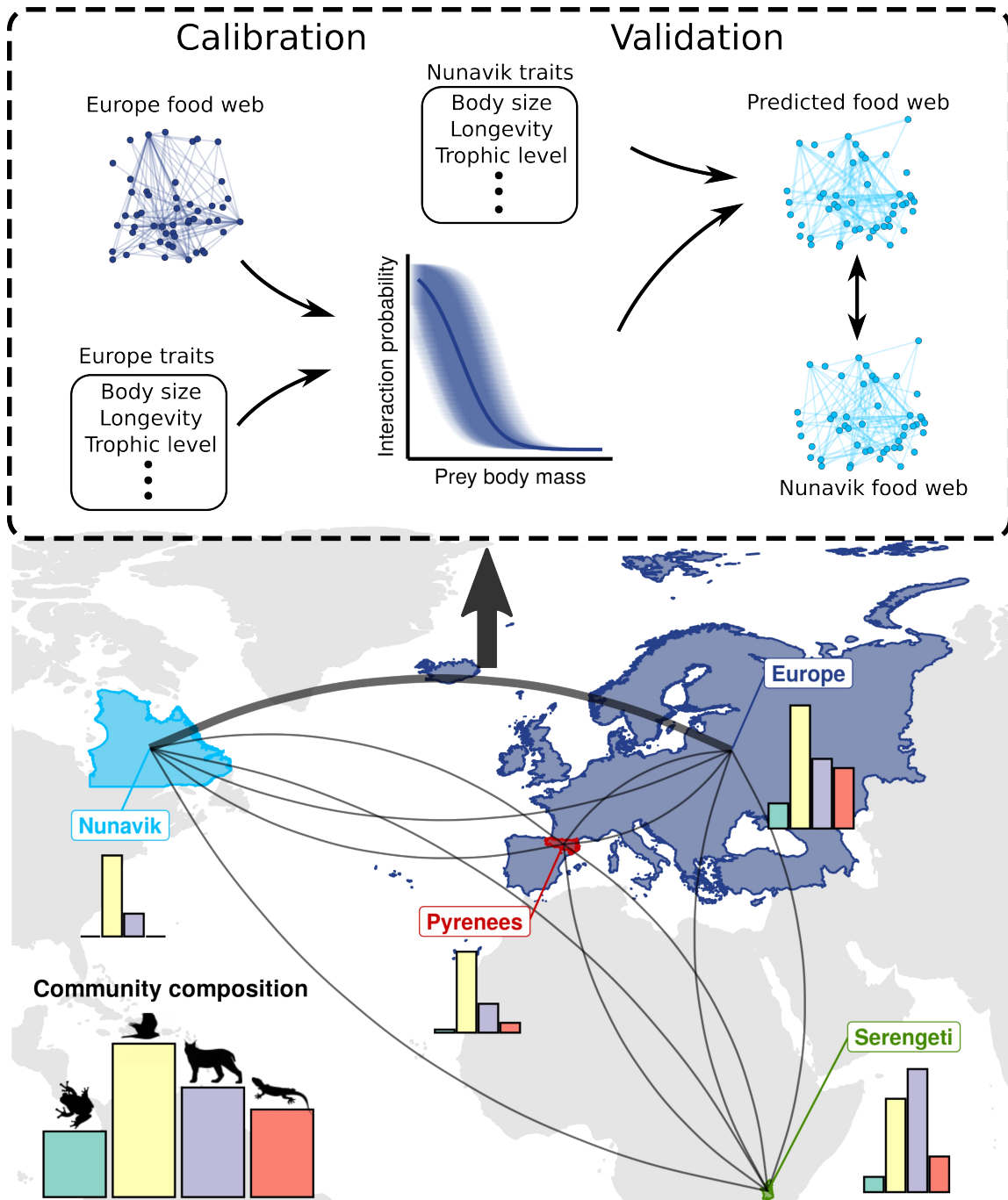


Figure 1: Trophic interactions model transferability analysis workflow. We calibrated a trophic interaction model on a calibration subset of each food webs. We validated the four models on a validation subset for within food web predictions, and the entire food webs for across food web predictions (grey curves). The bar plots show the proportion of amphibians (green), birds (yellow), mammals (purple), and reptiles (red) in each food web. The upper panel shows an example workflow for the across food web predictions (model calibrated in Europe predicting the Nunavik food web).

224 *Predicting species' functional roles*

225 Next, we were interested in how well species trophic role was predicted. The trophic role of a
226 species is determined by its position in the food web (Cirtwill et al. 2018). Here, we used 5
227 metrics related to how central the species is (number of prey, number of predators, betweenness,
228 closeness, eigenvector centrality), 2 metrics related to trophic level (trophic levels and
229 omnivory), 2 module-based metrics (within-module degree and participation coefficient;
230 Guimerà & Amaral, 2005), and the motif profile of species (Stouffer et al. 2012). We detail each
231 metric, their relation to functional role, and how they were calculated in Appendix XX.

232

233 We measured how well each trophic position metric we compared the species roles in empirical
234 food webs to the species roles in predicted food webs. For predicted food webs, we measured
235 each role metric on 100 posterior predictions of the entire food web and took the mean to get the
236 best point estimate for the metric. For each combination of model, food web predicted, and
237 species role metric, we fitted a linear regression between the predicted position and the empirical
238 position. We used the coefficient of determination (R^2) to measure how well species roles were
239 predicted, and the models' coefficients to determine biases in the predictions.

240

241 *Predicting food web properties*

242 Finally, we investigated how well the global properties of food webs were predicted. Again,
243 several metrics describe the structure of food webs. We chose food web properties that influence
244 food web functioning and stability: connectance, mean trophic level, maximum trophic level,
245 motif distribution, food web diameter, number of clusters, and modularity. As for species

position, we evaluated these properties on the empirical food webs and compared them to the properties predicted using 100 posterior predictions. We detail each metric, their relation to food web function, and how they were calculated in Appendix X.

Results

Predicting trophic interactions

For all food webs, trophic interactions were better predicted by the model calibrated on the same food web (“within food web” predictions) than by model calibrated on other food webs (“across food web” predictions; Table 2). Similarly, all models performed better in predicting the food web they were calibrated on, than other food webs. For within food web predictions, AUC varied between 0.92 and 0.96. The model performance were also good ($AUC > 0.82$) for across food web predictions between the Europe, Pyrenees, and Nunavik food webs. Compared to other food webs, models did not transferred as well from and to the Serengeti food web. The area under the precision-recall curve, true positive rate, true negative rate, positive predictive value, and negative predictive value were all positively correlated with AUC and showed the same overall pattern (Appendix X).

Table 2: Area under the receiver operating curve (AUC) of each models predicting every food webs.

	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

263 To explore the factors influencing the transferability of interaction models, we modelled their
 264 performance to the geographic, environmental, and phylogenetic distances between the food web
 265 the model was calibrated on and the food web predicted (Figure 2). Overall, performance tend to
 266 decrease with environmental (direct effect estimate: -0.54, 95%CrI = [-0.95, -0.13]) and
 267 phylogenetic distance (direct effect estimate: -0.44, 95%CrI = [-1.01, 0.06]). Performance also
 268 decreased with geographic distance (total effect estimate: -0.56, 95%CrI = [-0.80, -0.30]), but not
 269 after controlling for phylogenetic and environmental distances (direct effect estimate: -0.03,
 270 95%CrI = [-0.47, 0.39]).

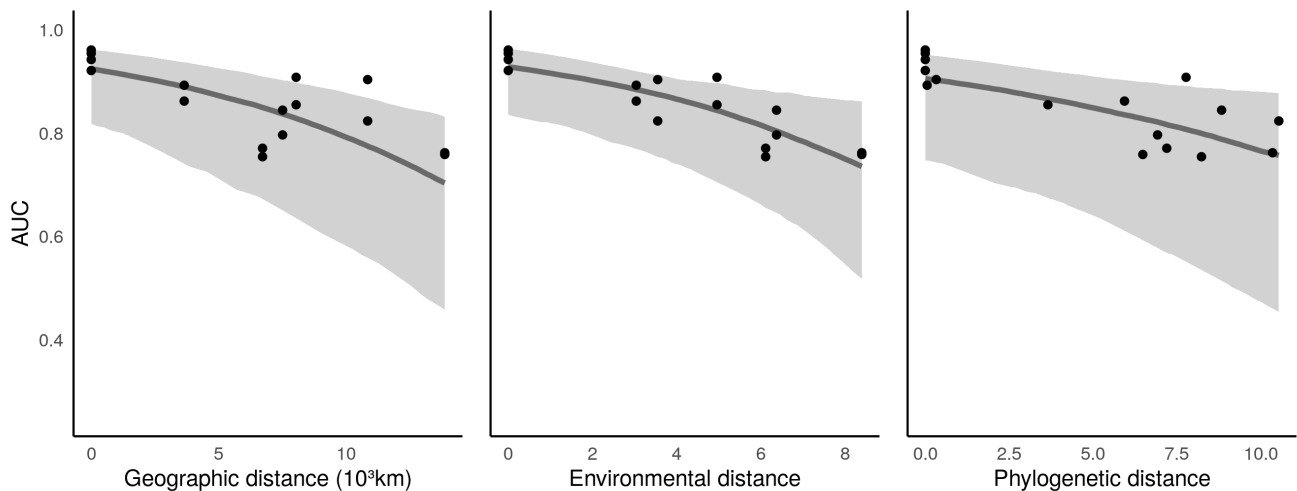


Figure 2 : Transferability of predictive models. Points are the predictive performance (area under the receiver operating curve) of the sixteen combination of model-food web prediction (Table 2). The trend lines are the median effects with their 95% credible interval of geographic, environmental, and phylogenetic distances on predictive performance. We showed the total effect of geographic distance (not controlling for environmental and phylogenetic distances), and the direct (controlling for geographic distance) effects of environmental and phylogenetic distances.

272 We also tested the interactions of which species were less well predicted by across food web
 273 predictions. We modelled the species-specific performance to the phylogenetic and functional

distance between the focal species and the species pool used to train the models (Figure 3). As expected, species with phylogenetically closed relatives in the species pool used for calibration were, on average, better predicted. Species-specific performance slightly decrease at low phylogenetic distances, and then drops significantly at large phylogenetic distances. We found that these large phylogenetic distances represent species for which its class (e.g., amphibians), was not present in the species pool on which the model was calibrated (Appendix X). This situation only occurs with the Nunavik model predicting the other three food webs as there are no amphibians or reptiles in Nunavik. Surprisingly, predictive performance remained qualitatively unchanged by functional distance. We also found that interactions of specialist (i.e., species with few prey and predators) and generalist species (i.e., species with many prey and predators) were, on average, better predicted than interactions of species of intermediate specialization.

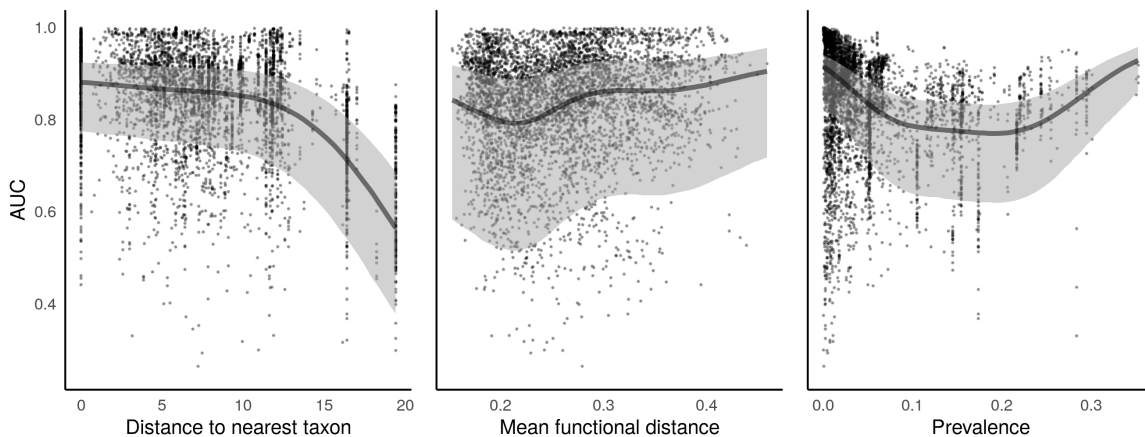


Figure 3: Predicting species interactions. Performance of the model calibrated on each food web to predict the interactions of species in the other food webs. Each point is the performance to predict the prey and predators of a single species. The trend lines are the median effects with their 95% credible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

288 *Predicting species functional role*

289 We found a lot of variation in how well species trophic positions were predicted (Figure 4).

290 Species roles were slightly better predicted by within food web predictions than by across food
291 web predictions. Interestingly, some measures of centrality (betweenness and closeness) were not
292 well predicted, whereas others (number of prey and predators, eigenvector centrality) were
293 relatively well predicted.

294

295 We also found important biases in the predictions of species roles when we modelled the
296 predicted roles to the empirical roles. For example, the number of prey, number of predators,
297 trophic level, omnivory, and most motif roles tended to be systematically overpredicted
298 (Appendix X). These biases tended to be constant for all species (slopes close to 1). For other
299 roles, like eigenvector centrality, betweenness, closeness, and module-based roles, species had
300 more similar values in predicted food webs than empirical food webs (Appendix X, slopes lower
301 than 1).

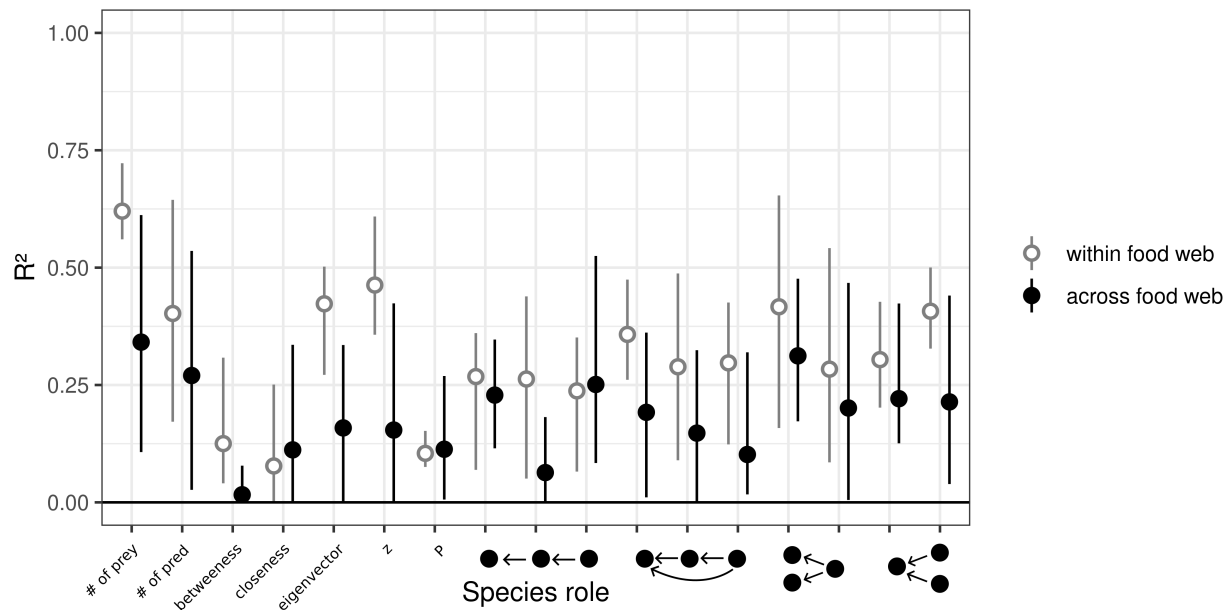


Figure 4: Predicting species functional role. The variance explained of the predicted trophic position by the empirical trophic position. From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, eigenvector centrality, within-module centrality, among-module connector, times the species is at a specific position in the linear chain, intraguild predation, direct competition, and apparent competition motifs. White dots are the mean R^2 with the minimum and maximum values for within food web predictions. Black dots are the mean R^2 with the minimum and maximum values for within food web predictions.

303 Predicting food web properties

304 Many food web properties were not well predicted by our interaction models (Figure 5).

305 Connectance, mean and max trophic levels, and the frequency of most motifs were

306 overpredicted, whereas the number of clusters and modularity were slightly underpredicted by

307 our models. The mean and variance of relative errors were greater for between food web

308 predictions compared to within food web predictions. In all, predicted food webs were more

309 connected, increasing the frequency of most motifs, and resulting in a less modular food web and

310 with less basal species which increased the trophic level of most species.

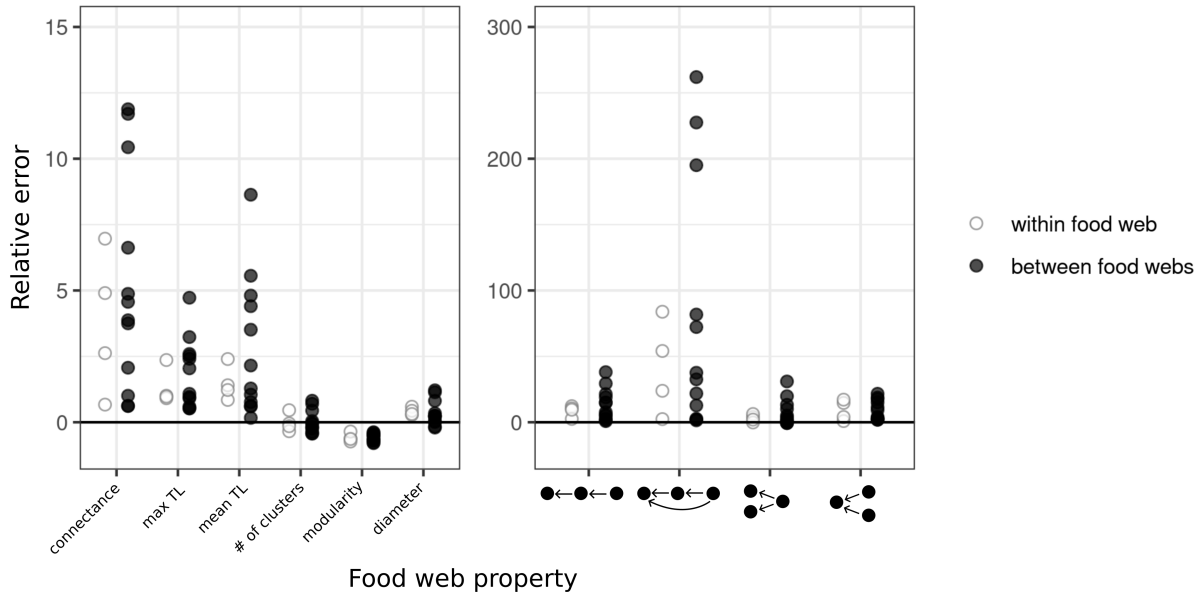


Figure 5: Predicting global food web properties. The relative error of the predicted food web properties. Relative error is the difference between the predicted and empirical estimates divided by the empirical estimate. From left to right, the figure shows, connectance, maximum trophic level, mean trophic level, number of clusters, modularity, diameter, number of linear chain, intraguild predation, direct competition, and apparent competition motifs. White dots are the relative errors for within food web predictions, and black dots are the relative errors for across food web predictions.

312 Discussion

313 Predictive models of trophic interactions will be central in filling knowledge gaps about how
 314 predator and prey interact across space and time. Here, we showed that trait-based trophic
 315 interaction models can predict interactions across systems. We found that, given enough
 316 phylogenetic and environmental similarities between the system on which the model is calibrated
 317 and the system for which the predictions are made, models predicted most interactions
 318 reasonably well. Our results suggest that, for terrestrial vertebrate food webs, the trait
 319 relationships driving interactions appear to be relatively general even in highly contrasting
 320 environments. Although most interactions were well predicted, higher-level properties of the
 321 food webs were not as well predicted. We found systematic biases in the species position and

322 food web properties predictions. Biases varied across metrics, but overall, the predicted food
323 webs were better connected, less modular, had more trophic levels, and species were more
324 equally connected. These higher-level properties of food webs were especially poorly predicted
325 when making across food web predictions (i.e., knowledge transfer).

326

327 The trait-matching framework of trophic niche theory assumes that spatial variation in food webs
328 arises either through variation in the trait-matching rules driving interactions, the distribution of
329 traits in different systems, or both (Gravel, Albouy, and Thuiller 2016). Our ability to predict
330 food web interactions across contrasting environment suggests that spatial food web variation is
331 mainly driven by changes in the distribution of functional traits, and less so by the variation of
332 trait-matching relationships. These are in line with previous results finding generalities in trait-
333 interactions relationships across European bioregions (Caron et al. 2022), the predator-prey
334 body-size ratios within habitat, predator, and prey types (Brose et al. 2006), trait-interactions
335 relationships in soil invertebrates across three forest areas in Germany (Laigle et al. 2018). The
336 finding that trait-matching rules driving species interactions seem general in reasonably similar
337 environments opens the opportunity to use data from well-studied areas to predict interactions in
338 areas we know very little about or forecast (and hindcast) food webs given new trait
339 distributions. Strydom et al. (2021) also found that latent trait models could accurately transfer
340 knowledge through phylogenetic relationships. In the future, different predictors (e.g., trait-based
341 models, phylogeny-based models), and models (e.g., linear models, machine learning) could be
342 combined into ensemble models. Ensemble models have the potential to make better predictions

by cancelling the noise created by the specific data and models (Araújo and New 2007; Dormann et al. 2018), but do not always outperform individual models. (Hao et al. 2020).

We also highlighted a major limitation of trophic interaction models: trophic interaction models predict interactions, not food webs. Food webs are more than the sum of their parts (Cohen et al. 2009). The structural properties of food webs (i.e., connectance, number of trophic levels, modularity) influence the stability, invasibility, and productivity of ecosystems (Baiser, Russell, and Lockwood 2010; Duffy et al. 2007; Wang and Brose 2018), whereas the position of species within food webs determine their functional role, and can help identify keystone species and prevent cascading effects of extinction (Cirtwill et al. 2018; Estes et al. 2011; McDonald-Madden et al. 2016). Here, predicting individual links failed to predict higher-level properties, suggesting that there are constraints acting on the structures of food webs that trophic interaction models cannot capture. Spatial and temporal variation of ecological network structure has gained a lot of interest recently (Baiser et al. 2019; Gravel et al. 2019). Because sampling interactions at large scales is difficult, predictions by interaction models could help to investigate the variation of interactions and network structures simultaneously (e.g., Albouy et al., 2014). This would be possible only if the biases in predicted network structure are constant across the gradient of interest (e.g., spatial, temporal, environmental gradients). In the future, testing this assumption should be necessary to robustly test the variation in ecological network structure. Alternatively, we propose to use food web structural models (e.g., trophic niche models; Williams & Martinez, 2000) which can predict higher-level properties relatively well.

365 We can also view the failure to predict higher-level properties as an opportunity to improve
366 species interaction predictions. Methods that would combine predictions of interactions and
367 networks have the potential to provide better food web predictions. Different models can predict
368 the number of links that we expect from the number of species (MacDonald, Banville, and Poisot
369 2020). With the number of links and species, structural food web models can predict the
370 probability distribution of many food web properties (Allesina, Alonso, and Pascual 2008;
371 Allesina and Pascual 2009; Cattin et al. 2004; Williams and Martinez 2000). Information on
372 probable food web structure could be used to correct posterior predictive distributions of species
373 interactions. In species distribution models, methods are already developed to use higher-level
374 properties (e.g., species richness) to correct distribution prediction (e.g., Leung et al., 2019).
375 These models correct systematic biases in prediction, such as those we found in our study.
376

377 We need to mention a few limitations for our study. First, we used four food webs of terrestrial
378 vertebrates. Although there is no clear *a priori* reason not to be applicable in other systems, our
379 results are unlikely to be general across all taxa and types of interactions. We don't know any
380 other test of interaction model transferability, but it would be interesting to investigate if our
381 results hold for systems where trait-matching relationships are stronger or weaker. Second, the
382 food webs we used are potential and binary food webs. Trait-matching models predict the
383 probabilities that a species could eat another species given they are encountering. Additional data,
384 such as co-occurrence and abundance data, are needed to make predictions of realized and
385 quantitative interactions. Finally, due to the scarcity of food web data, we only had four food
386 webs to work with. This means we only had four within food web predictions, and 12 across

food web predictions. This explains the large uncertainty for some of our results (e.g., Figure 2).

Despite the low sample size, we still detected significant signal in model transferability.

In all, we found that trait-based interaction models can transfer knowledge relatively well given

enough phylogenetic and environmental similarities between systems. These models can predict

pools of potential interactions even in contrasting environments, suggesting that changes in food

webs are more explain by changes in trait distribution than by changes in the trait-interaction

relationships. However, the resulting food webs should be viewed as a preliminary set of

interactions, asking for refinement since the structure and trophic positions of species are not

correctly predicted. These refinements could take the form of bias correction methods using

predictions of higher-level food web properties, or by combining predictions to other types of

data (i.e., expert knowledge, co-occurrences, abundances, etc). Such methodological

advancements would allow better prediction of both interactions and food webs across space and

time, which in turn, play a large role in filling the large knowledge gaps on how species interact

and allow to investigate how global changes may impact ecosystems (Albouy et al. 2014;

Cameron et al. 2019; Fricke et al. 2022).

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Author contributions

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