

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

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21 **Abstract**

22 Trophic interactions are central to our understanding of essential ecosystem functions such as
23 stability, nutrient cycling and productivity. While empirical data on trophic interactions remains
24 unavailable for most taxa in most ecosystems, predicting these interactions has become
25 increasingly common. Here, we ask how far we can extrapolate with these models (e.g. how well
26 can the arctic tundra be predicted by the Serengeti?). We use four trait-based models of trophic
27 interactions, each calibrated on a different food web of terrestrial vertebrates (list them), to
28 predict to the remaining food webs. We test how well predictions recover individual predator-
29 prey pairs and higher level properties of food webs (species position and entire food web
30 properties). We find that, given enough phylogenetic and environmental similarities between
31 food webs, trait-based models predict most interactions and non-interactions correctly (AUC >
32 0.82) even in highly contrasting environment. However, network metrics were less well-
33 predicted with predictions being more connected, less modular, and having higher mean trophic
34 levels. This result highlights the need for methodological advances to simultaneously address
35 trophic interactions and the structure of food webs across time and space. Overall, our results
36 show that trait-based models can predict pools of potential interactions from reasonably similar
37 food webs, even when data is entirely lacking.

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) an interaction
46 between two individuals is inherently hard as we need to detect simultaneously both species and
47 their interaction (Jordano 2016). Having more widespread food web data and at larger scales
48 would open research opportunities by integrating the Grinnellian and Eltonian niche into
49 biogeography (Braga et al. 2019; Gravel et al. 2019), incorporating trophic interactions into
50 meta-community ecology (Guzman et al. 2019), and describing the functional role of species in
51 biodiversity-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-prey relationships respond
55 to a predictable set of neutral and niche processes (Morales-Castilla et al. 2015). The neutral
56 model predicts that the probability and strength of interactions respond only to the co-
57 occurrences and abundances of species (Canard et al. 2012). Although co-occurrences is a
58 requirements for two species to interact, they are not evidence for trophic interactions (Blanchet,
59 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 evolutionary 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. First, 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 it is impossible to know how well their predictions recovered non-interactions. Also, it is hard to know what how their model would transfer contrasting environment since, 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). Second, how well can models of trophic interactions predict the structure of food webs? By structure, we are referring to 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 have 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 studies have rarely assessed if predicting interactions can 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 test whether trophic interactions and network properties known from one region can be used to reliably predict interactions in other ecosystems. We trained a set of trait-based predictive models on four contrasting food webs of terrestrial vertebrates from: Europe, the Pyrenees, Nunavik, and the Serengeti. The models are Bayesian generalized hierarchical models that we sequentially calibrated on each food web and validated on all others. 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 are the trophic roles of species predicted? and (3) How well are food web properties predicted?

Methods

Food web data

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

1. *Europe food web*: The trophic food web of European tetrapods was assembled by Maiorano et al. (2020). The Europe food web contains the potential trophic interactions and non-interactions between all terrestrial vertebrates in Europe based on data from guide books, published papers, and expert knowledge. The authors originally reported interactions between predators and prey at different life-stage (eggs, larvae/young, or adult). Here, we only extracted interactions between predators and adult prey.
2. *Pyrenees food web*: The Pyrenees vertebrate food web was assembled independently from the Europe food web by Lurgi et al. (2012). The authors compiled all known interactions between vertebrate species in the southeastern Pyrenees mountain range. To keep the same taxonomic coverage between food webs, we excluded fish species.
3. *Nunavik food web*: The trophic tundra food web of Labrador and northern Quebec (Canada) was compiled by Berteaux et al. (2018). The Nunavik food web is a binary matrix documenting the trophic relationships between all birds, mammals, and some groups of plants and arthropods whose distribution overlap Labrador and Quebec north of 50°N. Trophic interactions were collated from a literature review, 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 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	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 databases. The database includes traits for 6 990 amphibians, 11 634 birds, 5 380 mammals, and 10 612 reptiles.

To match species in the trait databases to the species in the food webs, we standardized their names following the taxonomic backbone of GBIF. To do so, we used the function `name_backbone` from the package `rgbif` (Chamberlain et al. 2022; Chamberlain and Boettiger

2017) in R. In each food web, we excluded all species for which no match was found in the taxonomic backbone of GBIF or the trait database. We imputed missing traits using the missForest algorithm (Stekhoven and Buehlmann 2012) for amphibians, birds, mammals and reptiles separately.

Predictive models

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

We used 13 trait-based predictors in the models: the trophic level, body mass, habitat breadth, longevity, and clutch size of the predator and the prey, and the match between their activity time, habitat use and body mass. Activity time match is a binary variable where a 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 out 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 we calculated the potential scale reduction factor for all runs (Gelman & Rubin, 1992; Appendix XX). We conducted the analyses using Stan through the package *brms* in R (Bürkner 2017; Carpenter et al. 2017).

Predicting species interactions

To measure how well models transfer, we used each model to predict all four food webs (Figure 1). For each possible predator-prey pair, we extracted the mean of 100 posterior draws as the probability of interaction. When predicting the food web on which the model was calibrated (i.e., within food web predictions), we compared the predicted interaction probabilities to the validation subset of the food web. When predicting food webs other than the one on which the model was calibrated (i.e., between food web predictions), we compared the predicted interaction

probabilities to the entire empirical food web. We measured performance with the area under the receiver operating characteristic curve (AUC). AUC varies from 0 to 1 where 0.5 indicates that the model failed to rank interactions higher than non-interactions (i.e., random predictions), and 1 indicates that the model systematically ranked interactions higher than non-interactions (i.e., perfect predictions). We also measured the area under the precision-recall curve, and directly used the posterior draws to get distributions for the true positive rate, true negative rate, positive predictive value and negative predictive value (Appendix XX).

To explore factors influencing model transferability, we modelled the performance of models to predict each food webs with three distance measures: geographic distance, environmental dissimilarity, and phylogenetic relatedness. We measured geographic distance with the euclidean distance between the centroid of the polygon delimiting each food web. We measured geographic distance with the euclidean distance between the centroid of the polygon delimiting each food web. We measured environmental dissimilarity using all 19 bioclimatic variables in WorldClim (Hijmans 2021). We randomly drew 500 points within each polygons and extracted bioclimatic data for these points. We then calculated the euclidean distance between the food web centroids in the entire bioclimatic space (Appendix XX). We measured phylogenetic relatedness with the mean phylogenetic distance to the nearest taxon of every species in the predicted food web. In other words, we averaged over all species in the predicted food web the phylogenetic distance to the closest related species in the food web used for calibration. This measures the amount of evolutionary history in the predicted food web undocumented by the food web the model was calibrated on. Following the recommendations by Letten & Cornwell (2015), we square root

transformed phylogenetic distances to better represent functional dissimilarity. We used the published phylogeny for birds (W. Jetz et al. 2012), amphibians (Walter Jetz and Pyron 2018), squamates (Tonini et al. 2016), turtles (Thomson, Spinks, and Shaffer 2021), and mammals (Upham, Esselstyn, and Jetz 2019).

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

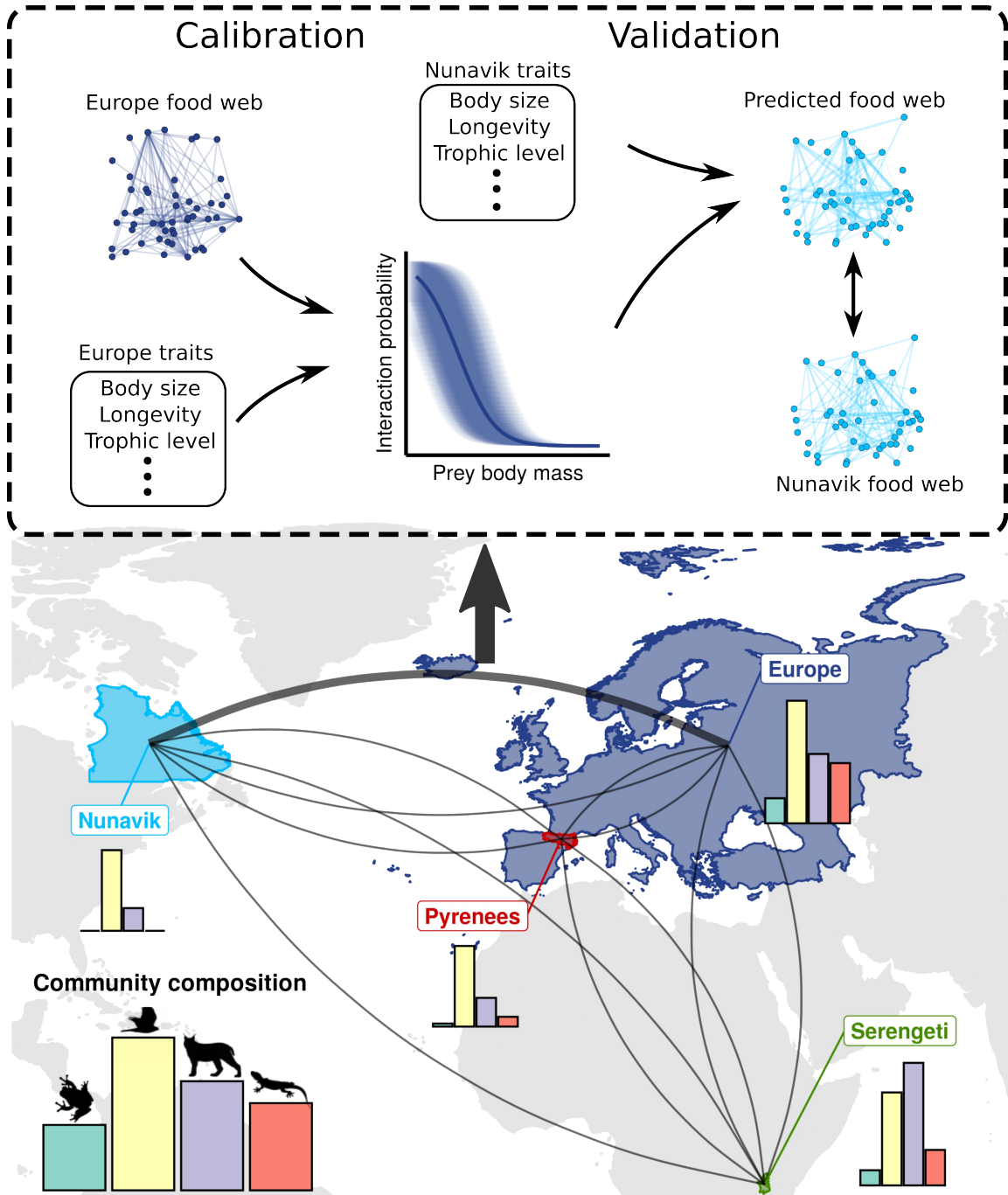


Figure 1: Trophic interactions model transferability analysis workflow. We calibrated a trophic interaction model on a calibration subset of each food webs. We validated the four models on a validation subset for within food web predictions, and the entire food webs for between food web predictions (grey 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 between food web predictions (model calibrated in Europe predicting the Nunavik food web).

223 *Predicting species' functional roles*

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

232

233 To measure how well species roles were predicted, we compared each species position metric in
234 empirical food webs to the species position in predicted food webs. For predicted food webs, we
235 measured each role metric on 100 posterior predictions of the entire food web with the mean as
236 the best point estimate for the metric. For each combination of model, predicted food web, 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. We selected
243 a range of metrics that influence food web functioning and stability: connectance, mean trophic
244 level, maximum trophic level, motifs 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 (between food web predictions; Table 2). Similarly, all models performed better in predicting the food web in which they were calibrated, compared to other food webs. For within food web predictions, AUC varied between 0.92 and 0.96. The model performances were also good ($AUC > 0.82$) for transfer between the Europe, Pyrenees, and Nunavik food webs. Compared to other food webs, models did not transfer 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

262 To explore the factors influencing the transferability of interaction models, we modelled their
 263 performance relative to the geographic, environmental, and phylogenetic distances between the
 264 calibrated and predicted food web (Figure 2). Overall, performance tended to decrease with
 265 environmental (direct effect estimate: -0.54, 95%CrI = [-0.96, -0.12]) and phylogenetic distance
 266 (direct effect estimate: -0.45, 95%CrI = [-0.84, -0.07]). Performance also decreased with
 267 geographic distance (total effect estimate: -0.56, 95%CrI = [-0.80, -0.30]), but not after
 268 controlling for phylogenetic and environmental distances (direct effect estimate: -0.06, 95%CrI =
 269 [-0.46, 0.34]).

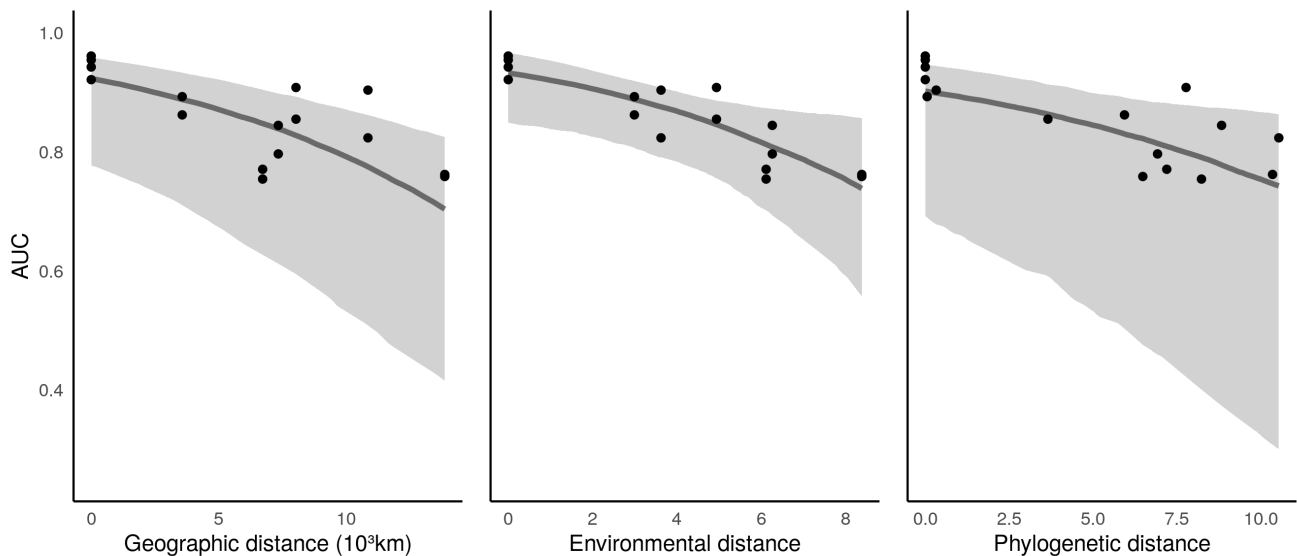


Figure 2 : Transferability of predictive models. Points are the predictive performance (area under the receiver operating curve) of the sixteen combination of model-food web prediction (Table 2). The trend lines are the median effects with their 95% credible interval of geographic, environmental, and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

271 We also identified the species for which the interactions were incorrectly predicted by between
 272 food web 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 close relatives in the species pool used for calibration were, on average, better predicted than distant relatives. Species-specific performance slightly decreased at low and intermediate phylogenetic distances, and then drops significantly at large phylogenetic distances. Models calibrated and predicted across classes (e.g. mammals to amphibians) had the lowest performance as expected (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.

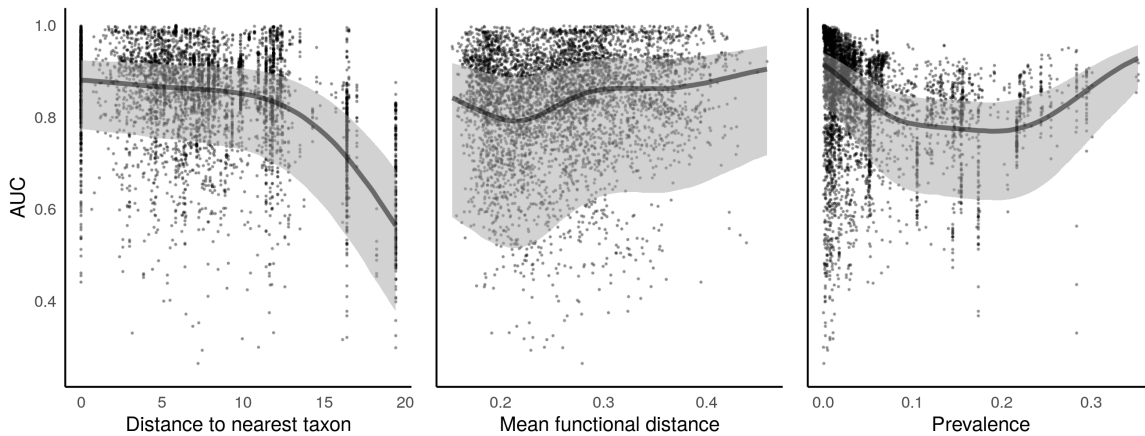


Figure 3: Predicting species interactions. Performance of the model calibrated on each food web to predict the interactions of species in the other food webs. Each point is the performance to predict the prey and predators of a single species. The trend lines are the median effects with their 95% credible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

286 *Predicting species functional role*

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

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

292

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

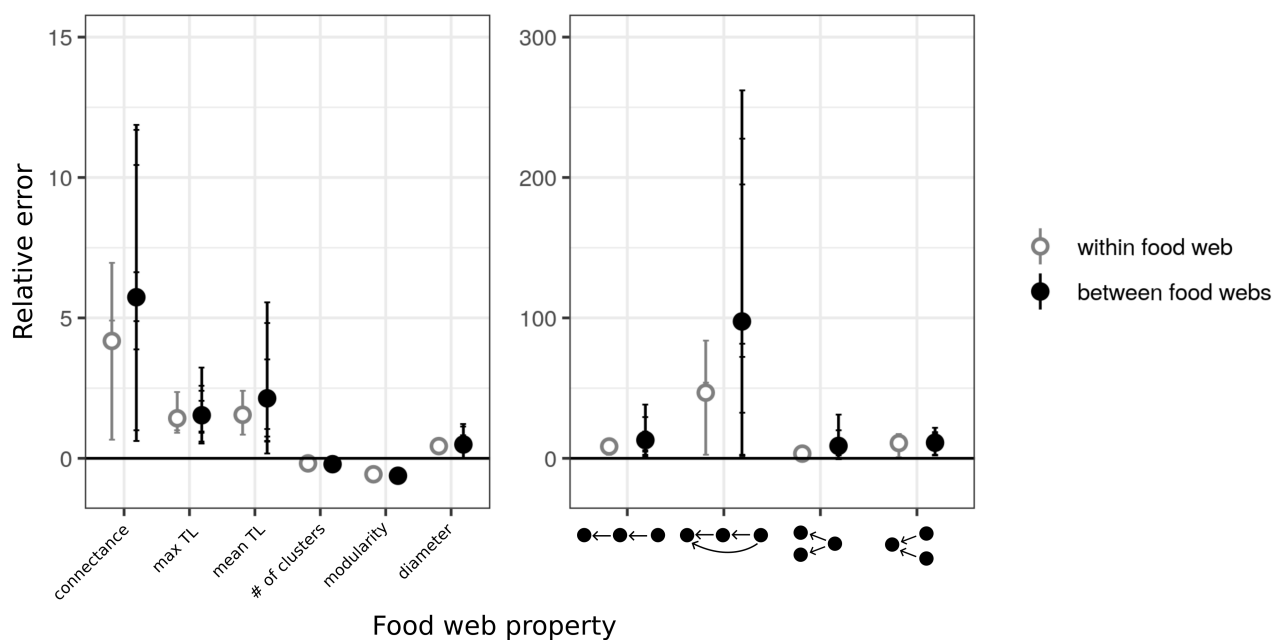


Figure 5: Predicting global food web properties. The relative error of the predicted food web properties. Relative error is the difference between the predicted and empirical estimates divided by the empirical estimate. From left to right, the figure shows the relative error for connectance, maximum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

310 Discussion

311 Predictive models of trophic interactions will be central in filling knowledge gaps about how
 312 predators and prey interact across space and time. Here, we showed that trait-based trophic
 313 interaction models can predict interactions across ecosystems. We found that, given enough
 314 phylogenetic and environmental similarities between the system on which the model is calibrated
 315 and the system for which the predictions are made, models predicted most interactions
 316 reasonably well. Our results suggest that, for terrestrial vertebrate food webs, the trait
 317 relationships driving interactions appear to be relatively general even in highly contrasting

environments. Although most interactions were well predicted, higher-level properties of the food webs were not as well predicted. 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-interactions relationships in soil invertebrates across three forest areas in Germany (Laigle et al. 2018). Given that trait-matching rules driving species interactions seem general in reasonably similar environments, it should be possible to use data from well-studied areas to predict interactions in areas we know very little about or forecast (and hindcast) food webs given new trait distributions. Strydom et al. (2021) also found that latent trait models could accurately transfer knowledge through phylogenetic relationships. In the future, different predictors (e.g., trait-based models, phylogeny-based models), and models (e.g., linear models, machine learning)

340 could be combined into ensemble models. Ensemble models have the potential to make better
341 predictions by cancelling the noise created by the specific data and models (Araújo and New
342 2007; Dormann et al. 2018). However, model comparison studies are needed since ensemble
343 models do not always outperform individual models (Hao et al. 2020).

344

345 We also highlighted a major limitation of trophic interaction models: trophic interaction models
346 predict interactions, not food webs. Food webs are more than the sum of their parts (Cohen et al.
347 2009). The structural properties of food webs (i.e., connectance, number of trophic levels,
348 modularity) influence the stability, invasibility, and productivity of ecosystems (Baiser, Russell,
349 and Lockwood 2010; Duffy et al. 2007; Wang and Brose 2018), whereas the position of species
350 within food webs determine their functional role, and can help identify keystone species and
351 prevent cascading effects of extinction (Cirtwill et al. 2018; Estes et al. 2011; McDonald-
352 Madden et al. 2016). Here, predicting individual links failed to predict higher-level properties,
353 suggesting that there are constraints acting on the structures of food webs that trophic interaction
354 models cannot capture. Spatial and temporal variation of ecological network structure has gained
355 a lot of interest recently (Baiser et al. 2019; Gravel et al. 2019). Because sampling interactions at
356 large scales is difficult, predictions by interaction models could help to investigate the variation
357 of interactions and network structures simultaneously (e.g., Albouy et al., 2014). This would be
358 possible only if the biases in predicted network structure are constant across the gradient of
359 interest (e.g., spatial, temporal, environmental gradients). Given our results, testing this
360 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.

Correcting the biases in higher-level property predictions is possibly an opportunity to improve species interaction predictions. In species distribution models, methods are already developed to use biases in higher-level properties (e.g., species richness) to correct distribution predictions (e.g., Leung et al., 2019). These models correct systematic biases in predictions similar to those we found in our study. Therefore, methods that would combine predictions of interactions and networks have the potential to provide better food web predictions. Different models can predict the number of links that we expect from the number of species (MacDonald, Banville, and Poisot 2020). With the number of links and species, structural food web models can predict the probability distribution of many food web properties (Allesina, Alonso, and Pascual 2008; Allesina and Pascual 2009; Cattin et al. 2004; Williams and Martinez 2000). Information on probable food web structure could be used to correct posterior predictive distributions of species interactions.

We need to mention a few limitations for our study. First, we used four food webs of terrestrial vertebrates. Although there is no clear *a priori* reason not to be applicable in other systems, our results are unlikely to be general across all taxa and types of interactions. We don't know any other test of interaction model transferability, but it would be interesting to investigate if our results hold for systems where trait-matching relationships are stronger or weaker. Second, the food webs we used are potential and binary food webs. Trait-matching models predict the

probabilities that a species could eat another species given they are encountering. Additional data, such as co-occurrence and abundance data, are needed to make predictions of realized and quantitative interactions. Finally, due to the scarcity of food web data, we only had four food webs to work with. This means we only had four sets of within food web predictions, and 12 sets of between 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 relationship between model transferability and geographic, phylogenetic, and environmental distances.

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 mainly explain by changes in trait distribution, and less 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, combination of predictions to other types of data (e.g., expert knowledge, co-occurrences, abundances), or combination of types of models (e.g., trait-matching, phylogenetic matching, machine learning). 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).

405

406 **Acknowledgements**

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408 **Author contributions**

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