

Trait-matching models predict pairwise interactions across regions, not food web properties

Running title: Interaction models transferability

Abstract

Aim: Trophic interactions are central to our understanding of essential ecosystem functions as well as their stability. Predicting these interactions has become increasingly common due to the lack of empirical data on trophic interactions for most taxa in most ecosystems. We aim to determine whether and how accurately we can extrapolate to new communities both in terms of pairwise predator-prey interactions and higher-level food web attributes (i.e., species position, food web-level properties).

Location: Canada, Europe, Tanzania.

Time period: Current.

Major taxa studied: Terrestrial vertebrates.

Methods: We use a trait-based model of pairwise trophic interactions, trained independently on four different terrestrial vertebrate food webs (Canadian tundra, Serengeti, alpine south-eastern Pyrenees, and entire Europe) and assess the ability of each instance of the model to predict alternative food webs. We test how well predictions recover individual predator-prey interactions as well as higher level food web properties across geographical locations.

Results: We find that, given enough phylogenetic and environmental similarities between food webs, trait-based models predict most interactions and their absence correctly ($AUC > 0.82$), even across highly contrasting environments. However, network metrics were less well-predicted

24 than single interactions by our models. Predicted food webs were more connected, less modular,
25 and had higher mean trophic levels than observed.

26 **Main conclusions:** Theory predicts that the variability observed in food webs can be explained
27 by differences in trait distributions and trait-matching relationships. The generality of trait-
28 matching relationships across regions and ecosystems suggests that food webs vary spatially
29 primarily through changes in trait distributions. However, food webs are more than the sum of
30 their parts, and predicting ecological networks will require a modelling approach that
31 simultaneously address trophic interactions and the structure of food webs across time and space.

32

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

Introduction

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 importance of food webs for understanding ecosystem structure and dynamics, recognized over the last 80 years (Lindeman, 1942), we still face major challenges to develop accurate descriptions of natural food webs. The lack of trophic interactions data across most locations and taxa (Poisot et al., 2021) lies 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 interacting (Jordano, 2016). Not only is detection more difficult than for species, the number of possible interactions to detect in food webs increases quadratically with the number of species resulting in extremely large sets of potential interactions. Therefore, observing all possible interactions among species within a food web is very difficult even in species-poor ecosystems, which calls for a systematic approach to predict interactions even when data from some regions are sparse or non-existent.

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

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

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

It is also unclear how well trophic interaction models can predict the underlying structure of entire food webs emerging from pairwise trophic interactions. Food web structure encompasses system-level properties such as connectivity or number of trophic levels, as well as species traits such as number of prey or their position within the food web. These higher-level properties emerge from the joint effect of trait-matching between interacting partners, the trait distribution of species composing the food web (Gravel et al., 2016), and are influenced by the spatial scale

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

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

transferability. Second, given the models' focus on pairwise interactions and based on previous results, we expect the prediction of pairwise interactions to be better than that of food web properties.

Methods

Food web data

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

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

139

140 *Trait data*

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

149 herbivore, omnivore, carnivore), activity time (2 categories: nocturnal, non-nocturnal) and
150 habitat use (12 categories: forest, savanna, shrubland, grassland, wetland, rocky
151 areas/cave/subterranean, desert, marine, marine/intertidal or coastal/supratidal, artificial,
152 introduced vegetation) for every species considered in our study.

153

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

164

165 *Phylogeny data*

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

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

Predictive models

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

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

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

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

We used 13 trait-based predictors in the models: five predator traits (trophic level, body mass, habitat breadth, longevity, and clutch size), five prey traits (trophic level, body mass, habitat breadth, longevity, and clutch size), and three trait-match predictors (match in activity time,

habitat use and body mass). Since the activity time trait is binary (nocturnal and non-nocturnal), activity time match is also a binary variable where a 1 means the predator and the prey share the same activity time trait. Habitat match is the Jaccard similarity index between the habitat used by the prey and the predator across the 12 habitat categories, which considers overlap in habitat and specialization to shared habitats. Body mass match is the squared difference between the log-transformed body mass of the prey and the predator, because we expect predators to eat prey within a given body mass interval (small enough to be handled, but large enough to be profitable. We log-transformed body mass, longevity, and clutch size, and scaled each continuous predictor (after transformation) by subtracting out the mean and dividing by two times the standard deviation so coefficients of continuous predictors are comparable to unscaled binary predictors (Gelman, 2008).

Fixed effects were drawn from a normal distribution with a mean of 0 and a standard deviation of 1. Random effects 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:

$$\alpha, \beta \sim \text{Normal}(0, 1)$$

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

$$\mu \sim \text{Normal}(0, 1)$$

$$\sigma \sim \text{HalfCauchy}(0, 5)$$

Model parameters were estimated with Hamiltonian Monte Carlo (Neal, 2011). We ran four chains, each with 2000 warm-up iterations, followed by 2000 iterations for inference. We diagnosed convergence and adequacy with trace rank plots, posterior predictive checks, and we

calculated the rank-normalized potential scale reduction factor on split chains for all runs (Vehtari et al., 2021; Appendix S6). We conducted the analyses using Stan (Carpenter et al., 2017) through the package *brms* in R (Bürkner, 2017).

Predicting species interactions

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

We assessed the performance of models to predict each food web using three distance measures: geographic distance, environmental dissimilarity, and phylogenetic relatedness. To do so, we fitted hierarchical linear models with logit-transformed AUC as a function of distance measures, with random intercepts for the food web predicted and used for calibration (Appendix S7). We measured geographic distance as the great-circle distance between the polygon centroid delimiting the spatial domain of each food web. We quantified environmental dissimilarity using all 19 bioclimatic variables in WorldClim (Hijmans, 2021). We extracted the bioclimatic data for all pixels (10' resolution) falling within the spatial domain of the food webs and used the mean of each bioclimatic variable to calculate the bioclimatic centroid of each food web. We calculated environmental distance as the Euclidean distance between the food web bioclimatic centroids. We used the mean cophenetic distance to the nearest taxon of every species in the predicted food web to measure phylogenetic relatedness. We averaged over all species in the predicted food web the cophenetic distance to the phylogenetically closest species in the food web used for calibration. This approach measures the amount of evolutionary history in the predicted food web undocumented by the food web on which the model was trained.

We also analyzed predictive performance at the species level. For each combination of predicted food web models (i.e., curves in Figure 1b), we measured how accurately the set of prey and predators of each species were predicted also using the AUC and AUPRG. We ~~modelled~~fitted a hierarchical linear model with species-specific performance ~~against~~as a function of how connected the focal species is and how distinct the focal species is to the species pool used to train the predictive model (Appendix S7). To do this, we used species normalized degree (number of interactions divided by the maximum possible number of interactions), the functional

mean pairwise distance (Mouchet et al., 2010) and distance to nearest taxon (Tucker et al., 2017). We quantified functional mean pairwise distance using 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 R package mFD (Magneville et al., 2022). We quantified distance to nearest taxon as the cophenetic distance between the focal species and the closest relative in the species in the food web used for model calibration.

268

269 | Predicting species' *functional* roles

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

278

279 | We compared each species' *positionrole* metric in empirical food webs to the species'
280 | *positionrole* in predicted food webs. We measured each role metric on 100 samples of the
281 | posterior distribution of predicted food webs with the mean as the best point estimate for the
282 | metric and the standard deviation as measure of uncertainty. For each combination of model,
283 | predicted food web, and species' role metric, we fitted a linear regression between the predicted

~~position~~role and the empirical ~~position~~role and ~~used the~~calculated coefficient of determination (R^2). We also explored prediction biases (e.g., systematic overestimation/underestimation) using the simple linear models' coefficients. We expect an intercept of zero for unbiased predictions of species' role. An intercept greater than zero would suggest an overall overestimation of the role metric, whereas an intercept less than zero would suggest a systematic underestimation of the role metric. We expect a slope of one for perfect predictions. A slope less than one would suggest that the role values at the lower range are overpredicted, whereas the role values at the upper range are underpredicted (i.e., more homogeneous values across species than in the empirical food web). A slope greater than one would suggest the opposite (i.e., more heterogeneous values across species than in the empirical food web).

Predicting food web properties

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

Boosted regression trees

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

Results

Predicting pairwise interactions

For all food webs, pairwise interactions were better predicted by the model trained on the same food web (within-food web predictions) than by models trained on other food webs (between-food web predictions; Table 2). For within-food web predictions, AUC varied between 0.92 and 0.96 and AUPRG varied between 0.93 and 0.96. Model performance was also good (AUC > 0.82; AUPRG > 0.84) for transfer between the Europe, Pyrenees, and Northern Québec and Labrador food webs, except for the model trained on the Pyrenees web when predicting the Europe web. For this case, AUC was high (0.89) whereas AUPRG (0.63) was comparatively small, suggesting that the model was much better at discriminating the absences than presences of interaction. Models did not transfer as well from and to the Serengeti food web, but performance was still good (AUC > 0.75; AUPRG > 0.73). The transferability of the Serengeti food web was expected to be more challenging because nodes do not represent species (as is the case for the other food webs), but trophic groups, as mentioned in the *Food web data* subsection. The area under the precision-recall-gain 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 S7).

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

We also analyzed transferability at the species level with comparison of species-specific performance as a function of phylogenetic and [functional trait](#) 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 (Figure 3a). Species-specific performance slightly decreased at low and intermediate phylogenetic distances, and then dropped significantly at large distances. Models trained and predicted across classes (e.g., mammals to amphibians) had the lowest performance, as expected. This situation only occurs with the Northern Québec and Labrador model predicting the other three food webs as there are no amphibians or reptiles in Northern

Québec and Labrador. Surprisingly, predictive performance remained qualitatively unchanged by ~~functional~~trait distance (Figure 3b). We also found that interactions of specialist (i.e., species with few interactions) and generalist species (i.e., species with many interactions) were, on average, better predicted than interactions of species of intermediate specialization (Figure 3c).

Predicting species' ~~functional~~ role

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

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

Predicting food web properties

Most food web properties were not well predicted by our interaction models (Figure 5). Connectance, mean and max trophic levels, and the frequency of most motifs were overpredicted, whereas modularity was slightly underpredicted. Mean and variance of relative

errors were greater for between- compared to within-food web predictions. In general, predicted food webs were more connected, displayed a higher frequency of most motifs, and were less modular and with less basal species, which increased the trophic level of most species.

Boosted regression trees

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

Discussion

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

397 | Theory describes how the variation in food webs arises from two key processes: trait-interaction
398 rules (e.g., body mass relationships between predators and their prey) and the distribution of
399 traits in different systems (Gravel et al., 2016). Our ability to predict food web interactions
400 across contrasting environments suggests that spatial food web variation is mainly driven by
401 changes in the distribution of functional traits, and less so by the variation of trait-interaction
402 relationships. These results are in line with previous research finding generalities made on trait-
403 matching relationships across European bioregions (Caron et al., 2022), predator-prey body-size
404 ratios within habitat, predator, and prey types (Brose et al., 2006), and the trait-interaction
405 relationships in soil invertebrates across three forest areas in Germany (Laigle et al., 2018). The
406 generalities we found in trait-matching relationships within major taxonomic groups (order and
407 class) also add to previous research indicating evolutionary conservation of species interactions
408 (Gómez et al., 2010) and trophic role (Stouffer et al., 2012). These generalities in the trait-
409 interaction relationships across space and within taxonomic groups demonstrate the potential for
410 using data from well-studied areas to predict interactions in areas we know very little about or
411 forecast (and hindcast) food webs given new trait distributions.

412

413 | We also highlighted a major limitation of trophic interaction models: trophic interaction models
414 predict interactions, not food webs properties. Even if most interactions and absences of
415 interactions are well predicted (high true positive and negative rates), there are many more
416 absences of interactions to predict than presences in real food webs (low connectance). This
417 might explain why our models systematically overpredicted the number of interactions (number
418 of prey and predators) across species (Appendix S8). Most food webs, even expert-based, are
419 missing some interactions (e.g., cryptic and opportunistic interactions), so the additional

interactions predicted by our models could be candidates for further investigation. However, our models overestimated the number of interactions by two-fold even for the Serengeti food web which probably already overestimates interactions since species are grouped into trophic groups. The prey and predators of species of intermediate specialization were also less well-predicted, which suggest that their trophic niches are harder to define by functional traits and could be influenced by other factors like abundances and co-occurrences. The overall overestimation of the number of prey and predators, and the bias against species of intermediate specialization, probably propagated through the food webs, explaining why the centrality of species was more evenly distributed, and why the predicted food webs were more connected, less modular, and with higher trophic levels.

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

442 failure to predict realistic networks, and additional research is needed to understand the
443 constraints differentiating realized food webs from feasible trophic interactions.
444

445 Correcting biases in higher-level property predictions presents an opportunity to improve species
446 interaction predictions. Stacked species distribution models have similar challenges, where
447 models can predict well the distribution of individual species ~~but less~~better than higher-level
448 properties of the community (Zurell et al., 2020). Methods have been developed to harness
449 biases in higher-level properties to correct distribution predictions. For example, Leung et al.
450 (2019) combined predicted species distributions and expected species richness to quantify
451 species and spatial biases. They correlated biases to species traits and environmental co-variables
452 to improve predicted species distribution. Similar methods combining predictions of interactions
453 and networks have the potential to provide better food web predictions. For example, we could
454 penalize posterior food web predictions resulting into improbable food web structure to update
455 pairwise interaction probabilities.
456

457 Our study suffers from a few limitations that, if overcome, could move us closer to a
458 comprehensive framework for ecological interactions and networks prediction. First, our study
459 relied on terrestrial vertebrates. Although there is no clear *a priori* reason not to be applicable in
460 other systems, our results are unlikely to be general across all taxa and types of interactions. It
461 would be interesting to investigate if our results hold for systems where trait-matching
462 relationships are stronger or weaker. The exclusion of non-vertebrates (e.g., plants, invertebrates,
463 parasites) also influences the empirical and predicted species roles and food web properties. For
464 example, the first trophic levels in our food webs were not primary producers, but species not

feeding on terrestrial vertebrates (e.g., herbivores, invertivores). However, extension of trait-matching models to also include invertebrates can be achieved with a coarser resolution (Li et al., 2023) or with additional traits (Laigle et al., 2018). Second, the food webs we used were ~~potential and~~ binary food webs. Trait-matching models predict the probabilities that a species could eat another species given they are encountering each other. 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).

Overall, we found that our trait-based interaction models can transfer knowledge relatively well given enough phylogenetic and environmental similarities between systems. They are useful for producing initial expectations even in contrasting ecosystems and for future communities. This, and other recent research (Brose et al., 2006; Caron et al., 2022; Laigle et al., 2018), suggests there are fundamental trait-based constraints on trophic interactions that are generalizable to some extent. Food web variation thus result from species traits rather than the ‘match’ between a predator and its prey, which has interesting ties to the broader question of how traits vary between regions and along gradients (Gravel et al., 2016). Future research could better link subfields within trait-based ecology for a comprehensive understanding of how species traits and network structure relate to their environment and enable trait-matching approach to inform restoration and re-wilding initiatives on the choice of appropriate species to re-establish former links and potentially ecosystem functions related to these interactions.

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491 **Data Accessibility Statement**

492 All data sources have been previously published. All data used in the analyses and relevant code
493 are archived on the Open Science Framework repository [OSF | Interaction model Transferability](#).

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Table 1: Summary statistics of the food webs used in this study after excluding species for which no match was found in the GBIF Backbone Taxonomy or was not documented in the trait database. Trait coverage is the percentage of traits documented in Etard et al. (2020) before imputing missing traits.

	Europe	Pyrenees	North Québec and Labrador
No. of species	1135	196	200
Prop of amphibians	0.09	0.02	0
Prop of birds	0.45	0.67	0.78
Prop of mammals	0.25	0.23	0.22
Prop of reptiles	0.21	0.08	0
No. of interactions	57 746	831	1 098
Connectance	0.05	0.02	0.03
Mean trophic level	1.24	1.25	1.3

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

	Food web		
Model	Europe	Pyrenees	North Québec and Labrador
AUC			
Europe	0.96	0.89	0.9
Pyrenees	0.86	0.95	0.85
North Québec And Labrador	0.82	0.9	0.95
Serengeti	0.85	0.78	0.77
AUPRG			
Europe	0.96	0.63	0.91
Pyrenees	0.9	0.95	0.94
North Québec And Labrador	0.88	0.9	0.93

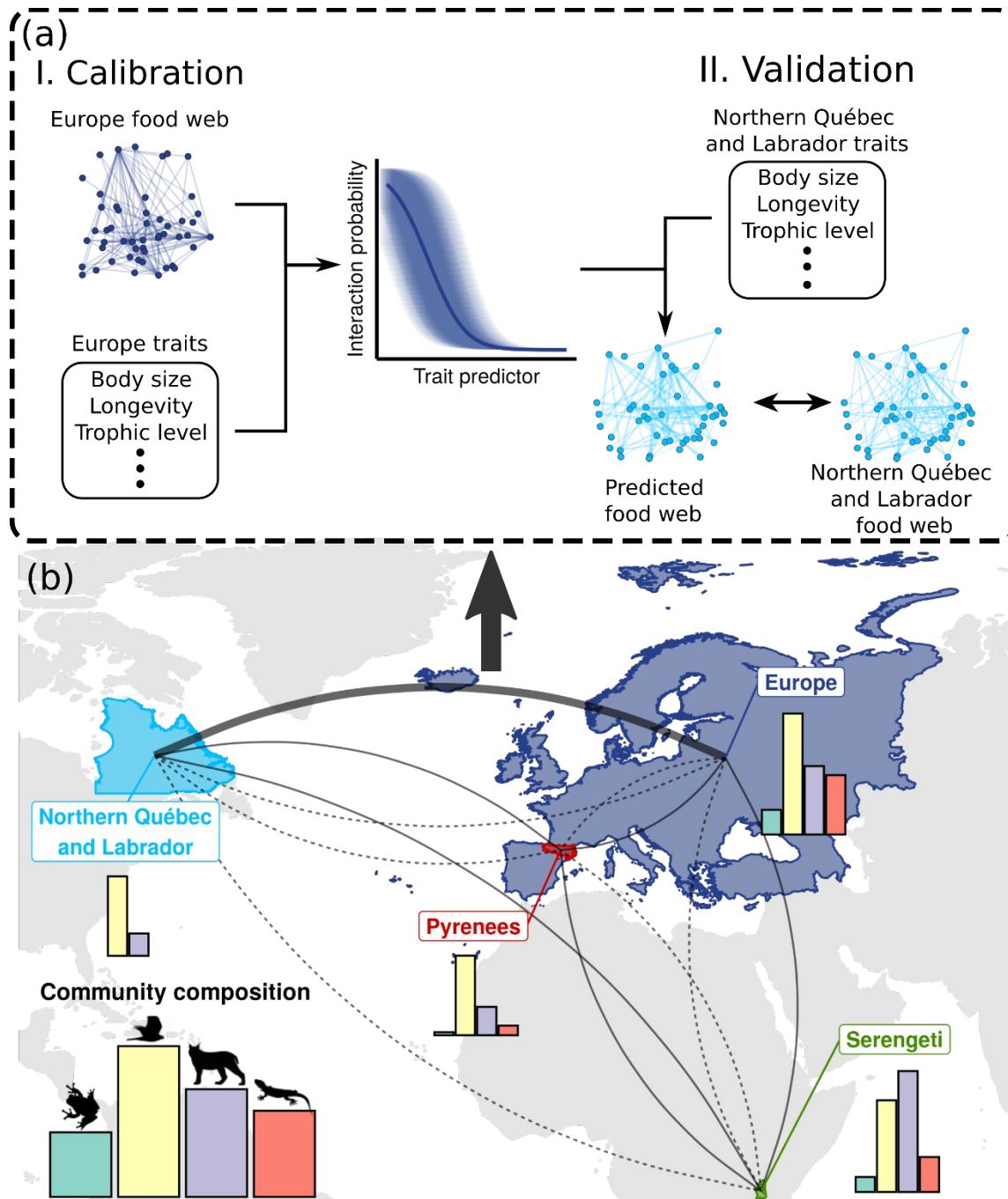


Figure 1: Trophic interactions model transferability analysis workflow. Panel (a) shows an example workflow for between-food web predictions. We trained a trophic interaction model using each food web considered in this study (panel a.I). We measured the performance of the four models on a validation subset for within-food web predictions, and the entire food webs for between-food web predictions (panel a.II). Panel (b) maps the spatial domain of each food web. The curves present the pairs of food web model used to make between-food web predictions. Within-food web predictions are not shown in the figure. Bar plots illustrate the proportion of amphibians (green), birds (yellow), mammals (purple), and reptiles (red) in each food web.

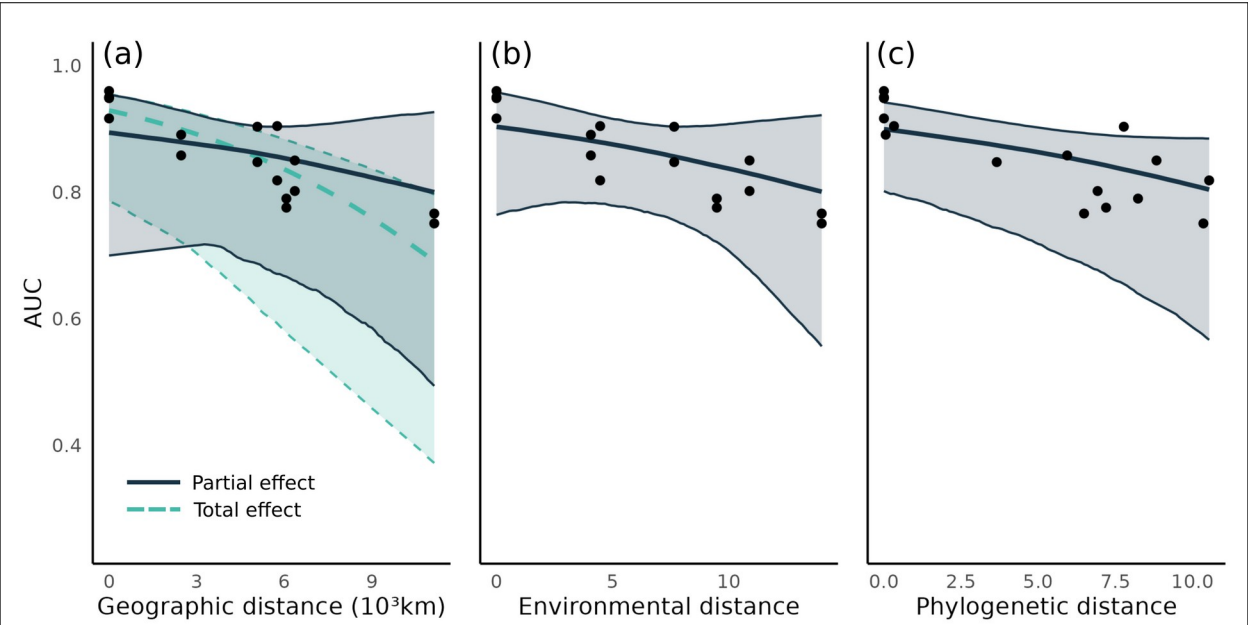


Figure 2: Transferability of predictive models across geographic, environmental and phylogenetic distance. In each panel, the points present the predictive performance (as area under the receiver operating curve, AUC) of a model food web prediction combination (16 combination; Table 2). For each panel, the thick line is the median effects while the envelope is the 95% credible interval on predictive performance built using the posterior predictive distribution of geographic, environmental, and phylogenetic distances. Panel (a) illustrates the total (includes the indirect effects of environmental and phylogenetic distances; turquoise) and partial (controlling for environmental and phylogenetic distances; dark blue) effects of geographic. Panel (b) shows the effect of environmental distance after controlling for geographic distance. Panel (c) presents the effect of phylogenetic distance after controlling for geographic distance.

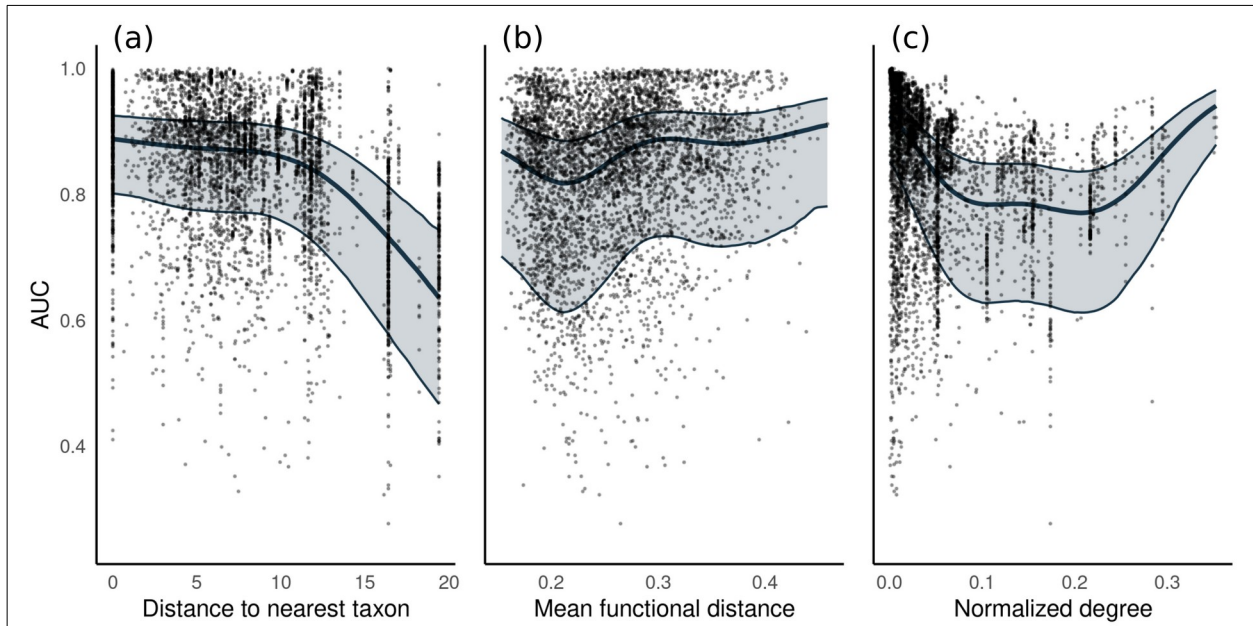


Figure 3: Predicting species interactions. Model predictive performance for the species interactions in alternative food webs. Each point shows the model performance in predicting the prey and predators of a single species using area under the receiver operating curve (AUC) as a metric. For each panel, the thick line is the median effects while the shaded area envelope is the 95% credible interval on predictive performance built using the posterior predictive distribution of (a) distance to the nearest taxon, (b) mean functional pairwise distance, and (c) normalized degree on predictive performance.

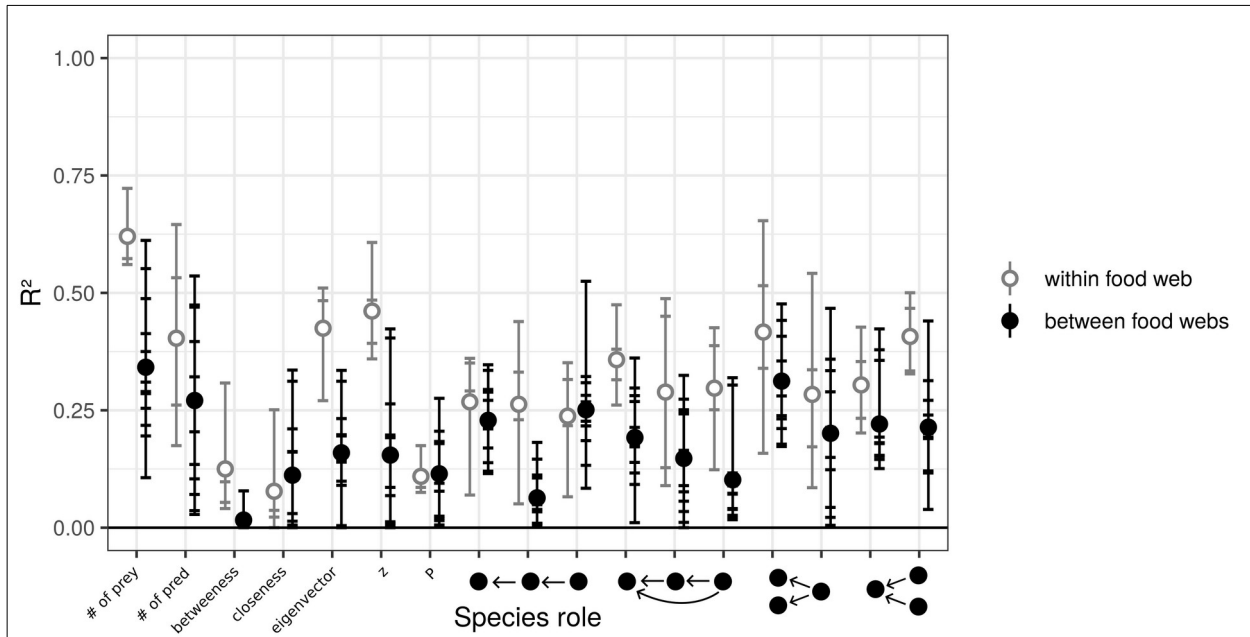


Figure 4: Predicting species functional role. Performance of models to predict species functional role measured as the proportion of the variance in trophic positions explained by the models (R^2). From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, eigenvector centrality, within-module degree (z), participation coefficient (P), times the species is at a specific position in the linear chain (predator – consumer – resource), intraguild predation (omnivore – consumer – resource), direct competition (2 consumers – 1 resource), and apparent competition motifs (1 consumer – 2 resources). The short horizontal lines highlight the R^2 for each role, model, and food web predicted combination. Grey open dots are the mean R^2 for within-food web predictions. Full black dots are the mean R^2 for between-food web predictions.

