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

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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 how far and accurately trophic interaction models 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, calibrated independently on four different terrestrial vertebrate food webs (Canadian tundra, Serengeti, alpine south-eastern Pyrenees, and entire Europe) and assess the ability of each calibrated 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 than single interactions by our models. Predicted food webs were more connected, less modular, and had higher mean trophic levels than observed.

Main conclusions: Theory predicts that the variability observed in food webs can be explained by differences in trait distributions and trait-matching relationships. Trait-based models can predict potential interactions amongst species in an ecosystem when calibrated using food web data from reasonably similar ecosystems. This suggests that food webs vary spatially primarily through changes in trait distributions. These models however, are less good at predicting system level food web properties. We thus highlight the need for methodological advances to simultaneously address trophic interactions and the structure of food webs across time and space.

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). This challenge is exacerbated by the fact that the number of possible interactions in food webs increases quadratically with the number of species, making the potential set of observations to be made dramatically large. Determining all possible interactions among species within a food web is thus difficult even in species-poor ecosystems, which calls for a systematic approach to predict links.

A first step towards constructing food webs is to focus on predator-prey relationships because they are the most commonly recorded type of ecological interaction, and have been shown to respond to a predictable set of neutral and niche processes (Morales-Castilla et al., 2015). A neutral model for trophic interactions suggests that the probability and strength of interactions depend only onto the co-occurrences and abundances of species (Canard et al., 2012). However, recent studies have shown that even if co-occurrence is a requirement for species to interact, it is not evidence for realized trophic interactions (Blanchet et al., 2020). We must thus be careful when making assertions about trophic interactions based solely on co-occurrence data. Niche theory predicts that the matching between the functional traits of predators and those of their prey (e.g., smaller predators eat smaller prey) should improve predictions by identifying interactions that are feasible (Morales-Castilla et al. 2015). Trait-based models have been used to predict food webs in 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 interactions and species role (i.e., species positions in the food web) tend to be evolutionary conserved (Gómez et al., 2010; Stouffer et al., 2012). Strydom et al. (2021) recently used a mammal phylogeny to map latent traits extracted from the European mammalian food web to predict its Canadian counterpart. Using this approach, the authors were able to recover 90% of known trophic interactions among Canadian mammals without any prior information on the food web.

It is however still unclear how well can predictive models of trophic interactions transfer knowledge across different regions. In Strydom et al. (2021), it is hard to know how inferences would transfer to more contrasting environments. 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. It is also unclear how well trophic interaction models can predict the underlying structure of entire food webs emerging from individual 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. Most studies are aimed at predicting either the properties of food webs (e.g., Williams and Martinez 2008) or their 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. However, the authors did not explore how other food web properties (e.g., maximum trophic level, modularity) or species positions (e.g., trophic level, centrality) were predicted.

Here we test whether predictive models calibrated using a network of predator-prey interactions (i.e. a food web) from one geographical region of the world can reliably predict interactions, species role, and food web structure in other ecosystems across the world. Using terrestrial vertebrate food webs from Europe, the Pyrenees, Northern Québec and Labrador, and the Serengeti, we develop trait-based Bayesian hierarchical models to study prediction efficiency of species interactions and food web properties across regions. We aim at (1) identifying the factors (i.e., geographic, environmental, functional, or phylogenetic distances) influencing the transferability of models across ecosystems and geographical regions, (2) predicting trophic roles across species and (3) quantifying the predicted 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 Europe food webs of tetrapods (Maiorano et al., 2020), the Pyrenees vertebrate food webs (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 are compiled from literature review and completed by expert knowledge. The four food webs document the predator-prey interactions (i.e., the predator could feed on the prey species) between all terrestrial vertebrates. Trophic interaction is a binary variable where 0 defines the absence of predator-prey interaction and 1 the presence of predator-prey interaction between two species. The nodes in the original Serengeti food web are 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. We describe each food web in Appendix 1.

The species composition of the four food webs are different (Table 1). There are no amphibians or reptiles in Northern Québec and Labrador, the Pyrenees food web is dominated by birds (67%) and mammals (23%), with very few reptiles (8%), the European food web has a comparable number of reptiles (21%) and mammals (25%), and almost half (46%) of the Serengeti food web are mammals. The Europe, Pyrenees, and Northern Québec and Labrador food webs all have comparable mean trophic levels (between 1.24 and 1.3) and connectance (between 0.02 and 0.05) compared to the Serengeti food web (mean trophic level: 1.61; connectance: 0.12). In Europe, the Pyrenees and Northern Québec and Labrador most species are basal species (e.g., insectivores, herbivores, piscivores), whereas many more species feed on terrestrial vertebrates (non-basal species) in the Serengeti.

Trait data

We extracted terrestrial vertebrate species ecological traits from the database compiled by Etard et al. (2020). This dataset combines species-level information from large freely available secondary trait databases (e.g., EltonTraits: Wilman et al. (2014), AmphiBIO: Oliveira et al. (2017)). Overall, the database includes traits for 6 990 amphibian, 11 634 bird, 5 380 mammal, and 10 612 reptile species. We extracted the body mass (mean: 11 kg; range: 0.001–4 220 kg), longevity (mean: 5 885 days; range: 91–46 386 days), litter or clutch size (mean: 131 offsprings; range: 1–20 000 offsprings), habitat breadth (number of habitats a species uses, using level 2 of the IUCN Habitat Classification Scheme; mean: 10 habitats, range: 1-90 habitats), trophic level (3 levels: herbivore, omnivore, carnivore), activity time (2 categories: nocturnal, non-nocturnal) and habitat use (12 categories: forest, savanna, shrubland, grassland, wetland, rocky areas/cave/subterranean, desert, marine, marine/intertidal or coastal/supratidal, artificial, introduced vegetation) for all species considered in our study.

To match species in the trait databases to the species in the food webs, we standardized their names following the taxonomic backbone of the Global Biodiversity Information Facility (GBIF) using the function *name_backbone* from the package *rgbif (Chamberlain et al., 2022)* in the R statistical language (R Core Team, 2022). In each food web, we excluded species for which no taxonomic information or none of the traits were available. For species that have one or more of the traits documented, we imputed missing traits with the MissForest algorithm using the *missForest* R package (Stekhoven & Buehlmann, 2012) for amphibians, birds, mammals and reptiles separately. MissForest uses random forests to iteratively predict missing data from the known data. Each random forest uses a different trait as response variable and the remaining traits as predictors.

Phylogeny data

We used phylogeny data to measure how model transferability was influenced by phylogenetic relatedness. We used published global phylogeniesy for birds (Jetz et al. 2012), amphibians (Jetz and Pyron 2018), squamates (Tonini et al., 2016), turtles (Thomson et al., 2021), and mammals (Upham et al., 2019). All five phylogenies are dated, were built from molecular data, and delivered as posterior distribution of trees. We sampled 100 trees from the posterior of each phylogeny and calculated 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 represent functional dissimilarity.

Predictive models

We calibrated a Bayesian hierarchical generalized linear model on each of the four food webs (Figure 1a.I). The response data are trophic interactions we modelled as Bernoulli distributed. Because Caron et al. (2022) found that trait-interaction relationships vary between predator groups, we used the order of the predator as varying intercepts and slopes. 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.

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

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

where L_{ij} is the occurrence of interaction between predator *j* and prey i, p_{ij} is the associated probability of interaction, α and β are the fixed intercept and slopes of the linear model, and $\alpha_{predator[j]}$ and $\beta_{predator[j]}$ are the random intercepts and slopes 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) in Etard et al. (2020), activity time match is a binary variable where a 1 means the predator and the prey share the same activity time trait. Habitat match is calculated as the Jaccard similarity index between the habitat used by the prey and the predator across the 12 habitat categories available in the trait database. The Jaccard similarity index takes into account the overlap in habitat used by both species and how specialized they are to these shared habitats (e.g., the habitat match of two habitat specialist species sharing their only habitat category is higher than the habitat match of two habitat generalists sharing one of their respective habitat categories). Body mass match is the squared difference between the log-transformed body mass of the prey and the predator. We used the squared difference between log-transformed body mass because we expect predators to eat prey within a given body mass interval (small enough to be handled by the predator, but big enough to be profitable). We log-transformed body mass, longevity and clutch size, because we expect the probability of interaction to respond more linearly with relative change in these variables (e.g., increase of 10% of body mass) than absolute change (e.g., increase of 10 grams). We scaled each continuous predictor (after transformation) 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).

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:

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

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

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

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

Model parameters were estimated with Hamiltonian Monte Carlo (Neal, 2011). To fit the models, we ran four chains, each with 2000 warm-up iterations, followed by 2000 iterations for inference. We diagnosed convergence and adequacy with 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 XX). We conducted the analyses using Stan (Carpenter et al., 2017) through the package *brms* in R (Bürkner 2017).

Predicting species interactions

To quantify model transferability, we used each model to predict the food web fitted with that model and that of the other regions considered (Figure 1a.II). 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. 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; Hanley and McNeil 1982). 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). We also measured the area under the precision-recall curve (Davis & Goadrich, 2006), and directly used 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 assessed the performance of models to predict each food webs using three distance measures: geographic distance, environmental dissimilarity, and phylogenetic relatedness. We measured geographic distance as the Euclidean distance between the polygon centroid delimiting the spatial domain of each food web. Environmental dissimilarity was quantified using all 19 bioclimatic variables in WorldClim (Hijmans, 2021). We randomly drew 500 points within each polygon corresponding to the spatial domain of our food webs and extracted bioclimatic data for these points. We used the mean of each bioclimatic variables to calculate the bioclimatic centroid of each food web. We calculated environmental distance as the Euclidean distance between the food web bioclimatic centroids. We repeated this step 10 times (10 sets of 500 random points) to make sure the environmental distance estimates are robust to random sampling (Appendix X). To measure phylogenetic relatedness, we used the mean cophenetic distance to the nearest taxon of every species in the predicted food web. 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 the model was calibrated on.

Another test of the factors influencing model transferability focuses on analyzing 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. We modelled species-specific performance in terms of how connected the focal species is and how distinct the focal species is to the species pool used to calibrate the predictive model. 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). 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 R package mFD (Magneville et al., 2022). Distance to nearest taxon was quantified as the cophenetic distance between the focal species and the closest relative in the species in the food web used for model calibration.

*Predicting species' functional role*s

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

To measure how well species roles were predicted, we compared each species position metric in empirical food webs to the species position in predicted food webs. For predicted food webs, we measured each role metric on 100 samples of the posterior distribution of the entire food web with the mean as the best point estimate for the metric and the standard deviation as measure of uncertainty. For each combination of model, predicted food web, and species role metric, we fitted a linear regression between the predicted position and the empirical position. We used the coefficient of determination (R^2) to measure how well species roles were predicted. We also explored prediction biases using the simple linear models' coefficients. We expect an intercept of zero for perfect predictions of species role, and deviation from zero would suggest systematic bias across the range of the role metric. We expect a slope of one for perfect predictions. A slope less than one would suggest that the role metric of species at the lower range are overpredicted, whereas the role metric of species at the upper range are underpredicted (i.e., more homogeneous role across species than in the empirical food web). A slope greater than one would suggest the opposite (i.e., more heterogeneous role 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, 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 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). For within food web predictions, AUC varied between 0.92 and 0.96. Model performance was also good (AUC > 0.82) for transfer between the Europe, Pyrenees, and Northern Québec and Labrador food webs. Models did not transfer as well from and to the Serengeti food web, but performance was still good (AUC > 0.75). 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).

To explore the factors influencing the transferability of interaction models, we modelled their performance relative to the geographic, environmental, and phylogenetic distances between the calibrated and predicted food web (Figure 2). Overall, performance tended to decrease with environmental (direct effect estimate: -0.50, 95%CrI = [-0.90, -0.09]) and phylogenetic distance (direct effect estimate: -0.39, 95%CrI = [-0.76, 0.00]). Performance also decreased with geographic distance (total effect estimate: -0.54, 95%CrI = [-0.78, -0.30]), but this effect disappeared after controlling for phylogenetic and environmental distances (direct effect estimate: -0.07, 95%CrI = [-0.49, 0.34]).

We also identified the species for which the interactions were incorrectly predicted between food web. We modelled 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 (Figure 3a). Species-specific performance slightly decreased at low and intermediate phylogenetic distances, and then dropped significantly at large 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 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 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. 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 similarly overestimated across species (slopes close to 1, and intercept greater than 0). For other measures such as eigenvector centrality, betweenness, closeness, and module-based roles, species had more similar values between predicted and empirical food webs (Appendix X, slopes less than 1).

Predicting food web properties

The majority of 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 were 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.

Discussion

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

Although models were successful at predicting interactions, they were less successful at predicting higher-level food web properties. We found systematic biases in the species position and food web properties predictions. Biases varied across metrics, but overall, the predicted food webs were better more highly connected, less modular, had more trophic levels, with species within them being more homogeneously connected than their observed counterparts. 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 variation across food webs arises through differences in the trait-matching rules driving interactions and the distribution of traits in different systems (Gravel et al., 2016). Our ability to predict food web interactions across contrasting environments partially agrees with this framework by suggesting 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 results are in line with previous finding generalities made on 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.

We also highlighted a major limitation of trophic interaction models: trophic interaction models predict interactions, not food webs. Even if most interactions and absences of interactions are well predicted (high true positive and negative rates), there are many more absences of interactions to predict than presences in real food webs (low connectance). This might explain why our models systematically overpredicted the number of interactions (number of prey and predators) across species (Appendix X). This bias 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.

The structural properties of food webs (i.e., connectance, number of trophic levels, modularity) influence the stability, invasibility, and productivity of ecosystems (Duffy et al., 2007; Lurgi et al., 2014; Wang & 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). 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. 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). Because sampling interactions at large scales is difficult, predictions by interaction models could help investigate the variation of interactions and network structures simultaneously (e.g., Albouy et al., 2014), which would be possible only if the biases in predicted network structure are constant across the gradient of interest. Given our results, testing the assumption that the bias is constant should be necessary to robustly measure the variation in network structure.

Correcting biases in higher-level property predictions presents an opportunity to improve species interaction predictions. In species distribution models, methods have been developed to harness 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. Structural food web models can predict the probability distribution of many food web properties (Williams & Martinez, 2008). Information on probable food web structure could be used to correct posterior predictive distributions of species interactions.

Our study suffers from a few limitations that, if overcome, can move us closer to a comprehensive framework for ecological interactions and networks prediction. First, our study relied on 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 are not aware of another 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. The exclusion of non-vertebrates (e.g., plants, invertebrates, parasites) also influence the empirical and predicted species role and food web properties. For 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). Despite the low sample size, we still detected significant relationship between model transferability and geographic, phylogenetic, and environmental distances.

Overall, 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. This ability to transfer predictions suggests that there are fundamental trait-based constraints on trophic interactions that are generalizable to some extent (within reasonably similar ecosystems). However, these trait-based relationships appear to be driven more by the traits of the respective predator-prey pair rather than the ‘match’ between them. This finding has interesting ties to the broader question of how traits vary between ecosystems and along gradients (Gravel et al., 2016). Future research could better link these two fields for a comprehensive understanding of how species relate to their environment and to other species, and to enable better predictions of the responses of species and ecosystems to threats and global change.

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Author contributions

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

	Europe	Pyrenees	North Québec and Labrador	Serengeti
No. of species	1135	196	200	298
Prop of amphibians	0.09	0.02	0	0.06
Prop of birds	0.45	0.67	0.78	0.35
Prop of mammals	0.25	0.23	0.22	0.46
Prop of reptiles	0.21	0.08	0	0.13
No. of interactions	57 746	831	1 098	11 038
Connectance	0.05	0.02	0.03	0.12
Mean trophic level	1.24	1.25	1.3	1.61
Trait coverage (%)	83.9	92.1	96.3	81.9

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

	Food web			
	Europe	Pyrenees	North Québec and Labrador	Serengeti
Model				
Europe	**0.96**	0.89	0.9	0.8
Pyrenees	0.86	**0.95**	0.85	0.79
North Québec and Labrador	0.82	0.9	**0.95**	0.75
Serengeti	0.85	0.78	0.77	**0.92**

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

Figure 2: ***Transferability of predictive models.*** *Points are the predictive performance (AUC) of the sixteen combination of model-food web prediction (Table 2). The trend lines are the median effects with their 95% credible interval constructed with the posterior predictive distribution of geographic, environmental, and phylogenetic distances on predictive performance. Shown are the total (turquoise) and partial (dark blue) effects of geographic distance (controlling for environmental and phylogenetic distances), and the direct (controlling for geographic distance) effects of environmental and phylogenetic distances.*

Figure 3: ***Predicting species interactions****. Performance of the model calibrated on each food web to predict the interactions of species in the other food webs. Each point is the performance to predict the prey and predators of a single species. The trend lines are the median effects with their 95% credible interval constructed from 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 are the R^2 for each role, model, and food web predicted combination. Grey open dots are the mean R^2 with for within food web predictions. Full black dots are the mean R^2 for across food web predictions.*

Figure 5: ***Prediction error of 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 (predator – consumer - resource), intraguild predation (omnivore – consumer - resource), direct competition (2 consumers – 1 resource), and apparent competition motifs (1 consumer – 2 resources). Short horizontal lines are the relative errors for each property, model, and food web predicted combination. Grey open dots are the mean relative errors for within- food web predictions and full black dots are the mean relative errors for between-food web predictions. The relative errors were presented in two panels to highlight the important difference in relative error between network properties and species roles.*

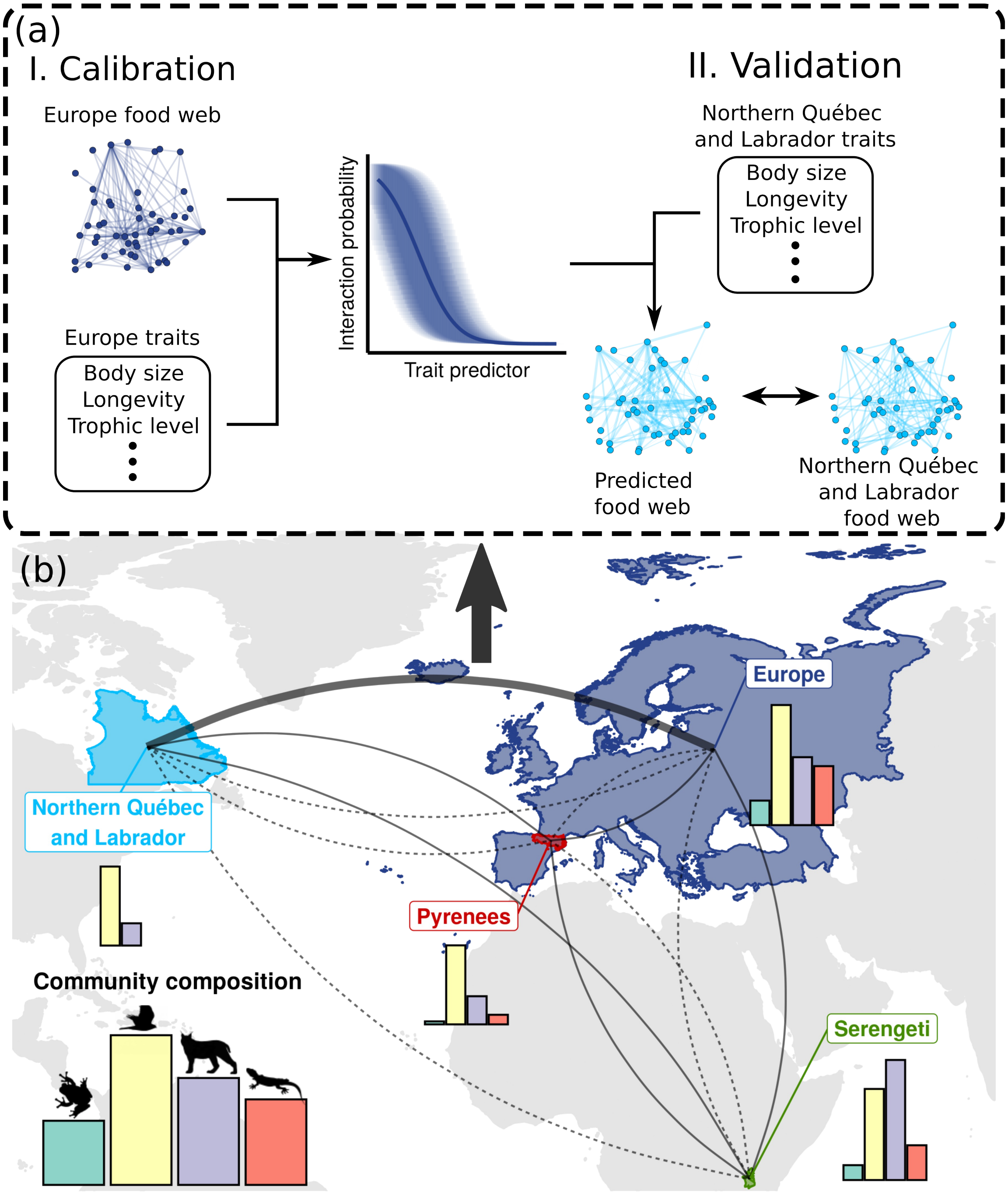

Figure 1: ***Trophic interactions model transferability analysis workflow.***

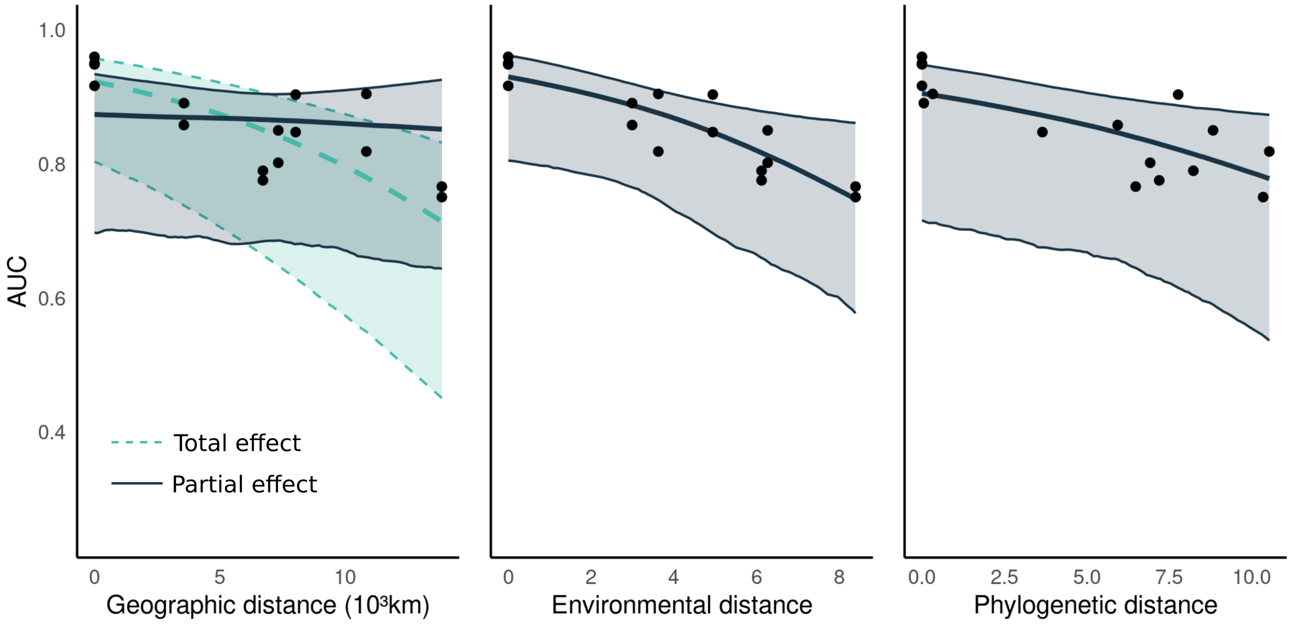

Figure 2 : ***Transferability of predictive models.***

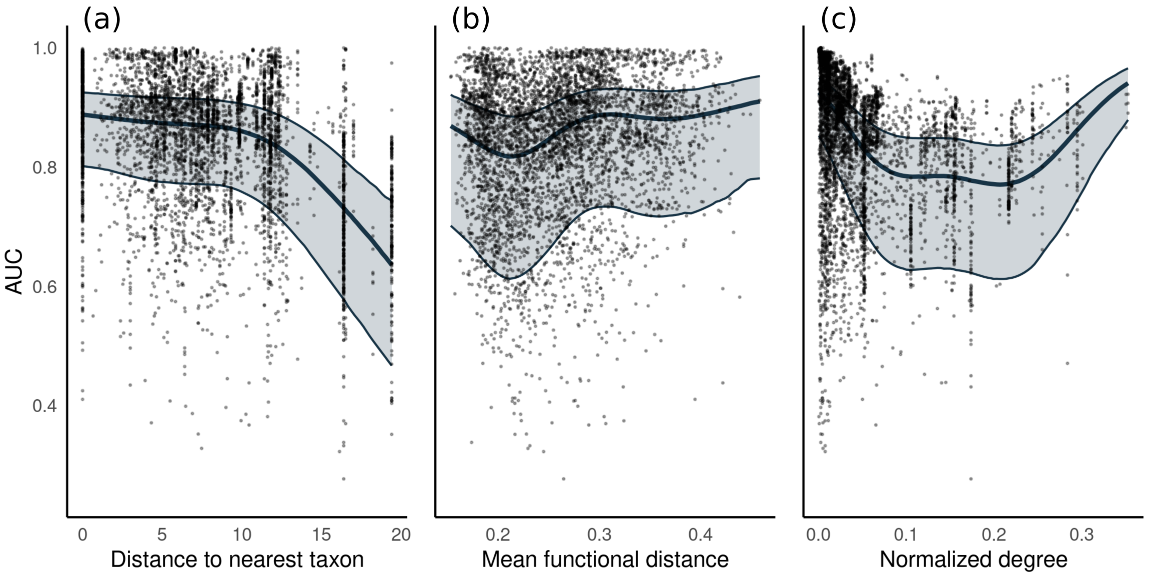

Figure 3: ***Predicting species interactions****.*

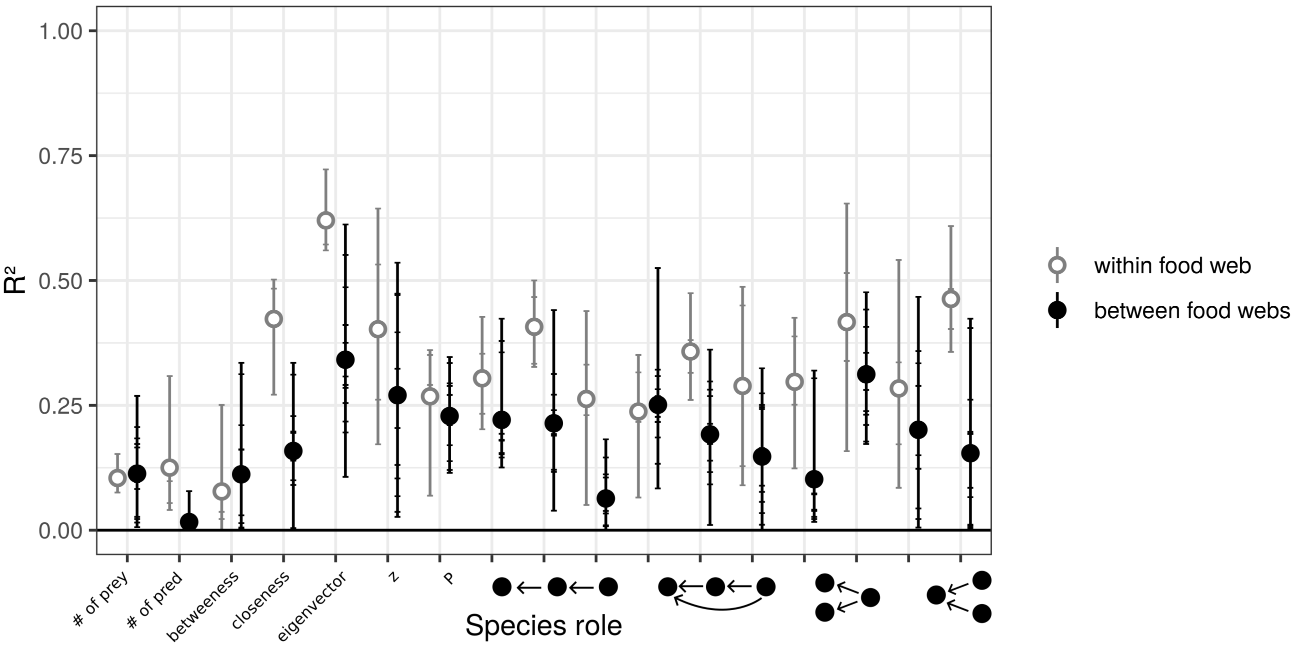

Figure 4: ***Predicting species functional role***.

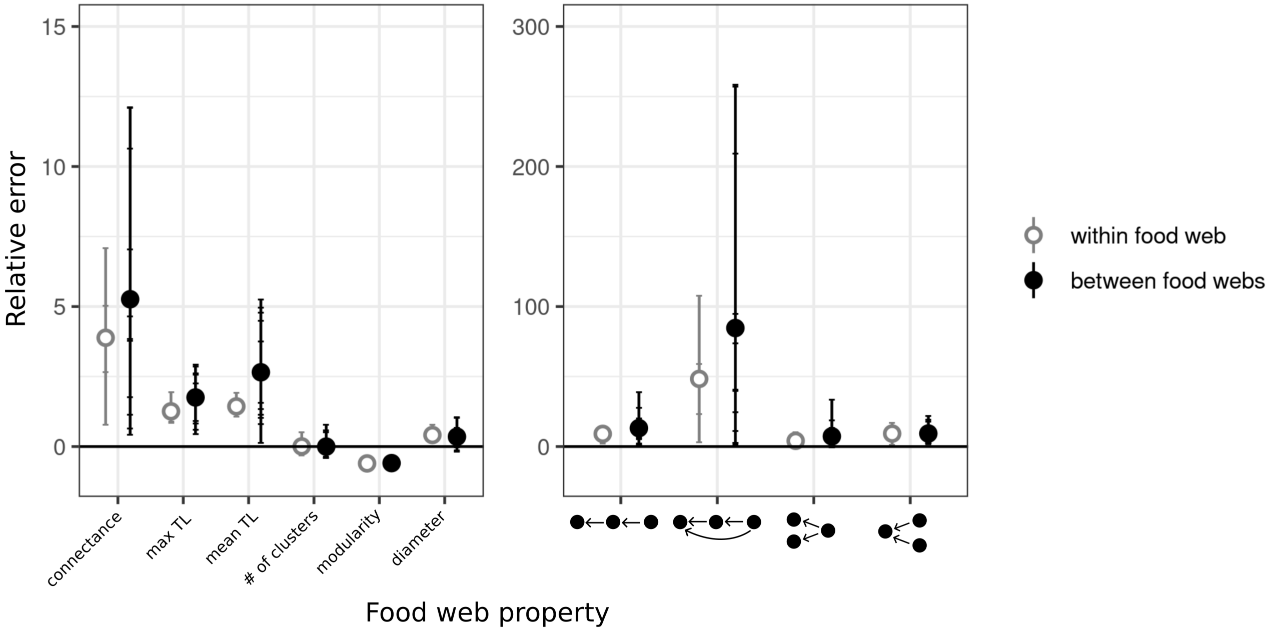

Figure 5: ***Prediction error of global food web properties.***