1 **Trophic interaction models predict interactions across ~~ecosystems~~regions, not food web**

2 **propertiess~~.~~**

3

4 **Running title:** Interaction models transferability

5

6 **Abstract**

7 **Aim:** Trophic interactions are central to our understanding of essential ecosystem functions as

8 well as their stability. Predicting these interactions has become increasingly common due to the

9 lack of empirical data on trophic interactions for most taxa in most ecosystems. We aim to

10 determine whether and how accurately we can extrapolate to new communities both in terms of

11 pairwise predator-prey interactions and higher level food web attributes (i.e., species position,

12 food web-level properties).

13 **Location:** Canada, Europe, Tanzania.

14 **Time period:** Current.

15 **Major taxa studied:** Terrestrial vertebrates

16 **Methods:** We use a trait-based model of pairwise trophic interactions, ~~calibrated~~trained

17 independently on four different terrestrial vertebrate food webs (Canadian tundra, Serengeti,

18 alpine south-eastern Pyrenees, and entire Europe) and assess the ability of each ~~calibrated~~

19 instance of the model to predict alternative food webs. We test how well predictions recover

20 individual predator-prey interactions as well as higher level food web properties across

21 geographical locations.

22 **Results:** We find that, given enough phylogenetic and environmental similarities between food

23 webs, trait-based models predict most interactions and their absence correctly (AUC > 0.82),

24    even across highly contrasting environments. However, network metrics were less well-predicted

25    than single interactions by our models. Predicted food webs were more connected, less modular,

26    and had higher mean trophic levels than observed.

27    **Main conclusions:** Theory predicts that the variability observed in food webs can be explained

28    by differences in trait distributions and trait-matching relationships. Trait-based models can

29    predict potential interactions amongst species in a region~~n ecosystem~~ when ~~calibrated~~trained

30    using food web data from reasonably similar ~~ecosystems~~region. This suggests that food webs

31    vary spatially primarily through changes in trait distributions. These models, however, are less

32    good at predicting system level food web properties. We thus highlight the need for

33    methodological advances to simultaneously address trophic interactions and the structure of food

34    webs across time and space.

35

36    **Key Words:** ecological predictions; food web; model transferability; terrestrial vertebrates; trait

37    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). 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 extremely 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~~Fortunately, the predator-prey interaction that compose food webs 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

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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 they can serve as

proxy for trait relationships, and because 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). ~

2022) 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.,Strydom et al.(

It is, however, still unclear how well predictive models of trophic interactions can transfer

knowledge across different regions. (In Strydom et al., (2022) , recently tested model

transferability using 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. 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 results raise the

following question: it is hard to know how inferences would transfer to more contrasting

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84  environments?. ~~Europe and Canada share similar bioclimatic conditions and, despite the few~~

85  ~~species common to both regions, more than half of Canadian mammals have congeneric species~~

86  ~~in Europe.~~

87

88  It is also unclear how well trophic interaction models can predict the underlying structure of

89  entire food webs emerging from individual trophic interactions. Food web structure encompasses

90  system-level properties such as connectivity or number of trophic levels, as well as species traits

91  such as number of prey or their position within the food web. Most studies are aimed at

92  predicting either the properties of food webs (e.g., Williams and Martinez 2008) or their

93  interactions (e.g., Laigle et al. 2018; Pomeranz et al. 2019). They rarely assess how well

94  predicted interactions can recover food web structure. Despite being able to recover most trophic

95  interactions among European tetrapods, Caron et al. (2022) found that food web connectance

96  was systematically overpredicted across Europe by 2-4 times. ~~However, the authors did not~~

97  ~~explore how~~However, to our knowledge, how well trophic interaction models predict other food

98  web properties (e.g., maximum trophic level, modularity) or species positions (e.g., trophic level,

99  centrality) ~~predictedwere~~ have never been tested.

100

101 Here, we test whether predictive models ~~calibrated~~trained using a network of predator-prey

102 interactions (i.e. a food web) from one geographical region of the world can reliably predict

103 interactions, species role, and food web structure in other ~~ecosystems~~regions ~~across the world~~.

104 Using terrestrial vertebrate food webs from Europe, the Pyrenees, Northern Québec and

105 Labrador, and the Serengeti, we develop trait-based Bayesian hierarchical models to study

106 prediction efficiency of species interactions and food web properties across regions. We aim to

107 (1) identify the factors (i.e., geographic, environmental, functional, or phylogenetic distances)

108 influencing the transferability of models across ~~ecosystems and~~ geographical regions, (2) predict

109 trophic roles across species and (3) quantify the predicted food web properties. First, ~~W~~we

110 expect more similar food webs will yield better transferability since the similarity of the

111 functional relationships driving interactions should depend on the similarity of the environment

112 and species composition of the respective food webs (Gravel et al., 2016). ~~and, b~~Second, ~~ased on~~

113 ~~previous results~~, we expect the prediction of pairwise interactions to be superior to that of food

114 web properties. Some processes constrain food webs properties (e.g., the number of feasible

115 interactions) act at scales different than the processes driving interactions that are encompassed

116 by trophic interaction models (Strydom et al., 2021). This mismatch between the scale of

117 processes modelled and the processes influencing food web properties are likely to create

118 discrepancies between the predicted and observed food webs.

119

120 **Methods**

121 *Food web data*

122 We extracted predator-prey interactions among terrestrial vertebrates (mammals, birds,

123 amphibians and reptiles) from four well-resolved food webs (Table 1, Figure 1): the European

124 food webs of tetrapods (Maiorano et al., 2020), the Pyrenees vertebrate food webs (Lurgi et al.,

125 2012), the Northern Québec and Labrador food web (Berteaux et al., 2018), and the Serengeti

126 food web (de Visser et al., 2011). All four food webs are compiled from literature review and

127 completed by expert knowledge. The four food webs document the predator-prey interactions

128 ~~(i.e., the predator could feed on the prey species)~~ between all known terrestrial vertebrates in

their respective location. 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. Since each food web document *potential* interactions (i.e., the predator could feed on the prey species), and uses expert knowledge, we assume that they are less sensitive to incomplete sampling than observation-based food webs (i.e., interactions and non-interactions are similarly uncertain). 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. Thus, we can expect more false positives (i.e., non-interactions documented as interactions) in the Serengeti than in the other three food webs. We describe each food web in Appendix S1.

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). Here, the first trophic level (i.e., basal species) are defined as species not feeding on any other terrestrial vertebrates. 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.

152 *Trait data*

153 We extracted terrestrial vertebrate species ecological traits from the database compiled by Etard

154 et al. (2020). This dataset combines species-level information from large freely available

155 secondary trait databases (e.g., EltonTraits: Wilman et al. (2014), AmphiBIO: Oliveira et al.

156 (2017)). Overall, the database includes traits for 6 990 amphibian, 11 634 bird, 5 380 mammal,

157 and 10 612 reptile species. We extracted the available body mass (mean: 11 kg; range: 0.001–4

158 220 kg), longevity (mean: 5 885 days; range: 91–46 386 days), litter or clutch size (mean: 131

159 offsprings; range: 1–20 000 offsprings), habitat breadth (number of habitats a species uses, using

160 level 2 of the IUCN Habitat Classification Scheme; mean: 10 habitats, range: 1-90 habitats),

161 trophic level (3 levels: herbivore, omnivore, carnivore), activity time (2 categories: nocturnal,

162 non-nocturnal) and habitat use (12 categories: forest, savanna, shrubland, grassland, wetland,

163 rocky areas/cave/subterranean, desert, marine, marine/intertidal or coastal/supratidal, artificial,

164 introduced vegetation) for ~~all~~every species considered in our study.

165

166 To match species in the trait databases to the species in the food webs, we standardized their

167 names following the taxonomic backbone of the Global Biodiversity Information Facility (GBIF)

168 using the function *name_backbone* from the package *rgbif* **(Chamberlain et al., 2022)** in the R

169 statistical language (R Core Team, 2022). In each food web, we excluded species for which no

170 taxonomic information or none of the traits were available. The trait coverage was excellent for

171 each species with more than 80% available traits in any of the food webs (Table 1; Appendix S2).

172 ~~For species that have one or more of the traits documented, w~~We imputed missing traits with the

173 MissForest algorithm using the *missForest* R package (Stekhoven & Buehlmann, 2012) for

174 amphibians, birds, mammals and reptiles separately. MissForest uses random forests to

8

175 iteratively predict missing data from the known data. Each random forest uses a different trait as

176 response variable and the remaining traits as predictors.

177

178 *Phylogeny data*

179 We used phylogenetic data to measure how model transferability was influenced by phylogenetic

180 relatedness. We used published global phylogenies for birds (Jetz et al. 2012), amphibians (Jetz

181 and Pyron 2018), squamates (Tonini et al., 2016), turtles (Thomson et al., 2021), and mammals

182 (Upham et al., 2019). All five phylogenies ~~are dated,~~ were built from molecular data~~,~~ and

183 delivered as a posterior distribution of trees. We sampled 100 trees from the posterior of each

184 phylogeny and calculated the mean cophenetic distance from these samples between all species

185 of the four food webs. Following Letten & Cornwell (2015), we square root transformed

186 cophenetic distances to better ~~represent functional dissimilarity~~relate with ecological processes

187 like trophic interactions.

188

189 *Predictive models*

190 We ~~calibrated~~trained a Bayesian hierarchical generalized linear model on each of the four food

191 webs (Figure 1a). The response data are trophic interactions we modelled as Bernoulli

192 distributed. Because Caron et al. (2022) found that trait-interaction relationships vary between

193 predator groups, we added varying slope and intercept terms for the taxonomic order of

194 predators. For each model, we randomly drew 30% of the data for validation to keep the

195 prevalence of trophic interaction in the validation subset equal to the prevalence of the entire

196 food web. We used all predator-prey interactions of the remaining 70% of the data and an equal

197 number of absence of interactions for calibration.

$$198 \qquad\qquad L_{ij} \sim Bernouilli(p_{ij}),$$

$$199 \qquad logit(p_{ij}) = \alpha + \alpha_{predator[j]} + \sum_{k=1}^{13}(\beta_k \times T_k + \beta_{k,predator[j]} \times T_k),$$

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

201  probability of interaction, $\alpha$ and $\beta_k$ are the fixed intercept and slopes of the linear model, ~~and~~

202  $\alpha_{predator[j]}$ and $\beta_{k,predator[j]}$ are the random intercepts and slopes for the order of predator $j$, and

203  $T_k$ are the trait-based predictors.

204

205  We used 13 trait-based predictors in the models: five predator traits (trophic level, body mass,

206  habitat breadth, longevity, and clutch size), five prey traits (trophic level, body mass, habitat

207  breadth, longevity, and clutch size), and three trait-match predictors (match in activity time,

208  habitat use and body mass). Since the activity time trait is binary (nocturnal and non-nocturnal)

209  in Etard et al. (2020), activity time match is also a binary variable where a 1 means the predator

210  and the prey share the same activity time trait. Habitat match is the Jaccard similarity index

211  between the habitat used by the prey and the predator across the 12 habitat categories, which

212  takes into account overlap in habitat and specialization to shared habitats. Body mass match is

213  the squared difference between the log-transformed body mass of the prey and the predator,

214  because we expect predators to eat prey within a given body mass interval (small enough to be

215  handled, but large enough to be profitable. We log-transformed body mass, longevity and clutch

216  size, and scaled each continuous predictor (after transformation) by subtracting out the mean and

217  dividing by two times the standard deviation so coefficients of continuous predictors are

218  comparable to unscaled binary predictors (Gelman, 2008).

219

10

220   Fixed effects were drawn from a normal distribution with a mean of 0 and a standard deviation of

221   1. Random effects were drawn from normal distributions. We used a normal distribution with a

222   mean of 0 and a standard deviation of 1 as prior for the mean and a Half-Cauchy distribution

223   with a scale parameter of 5 as prior for the standard deviation of the random effects:

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

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

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

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

228   Model parameters were estimated with Hamiltonian Monte Carlo (Neal, 2011). To fit the models,

229   we ran four chains, each with 2000 warm-up iterations, followed by 2000 iterations for

230   inference. We diagnosed convergence and adequacy with trace rank plots, posterior predictive

231   checks, and we calculated the rank-normalized potential scale reduction factor on split chains for

232   all runs (Vehtari et al. 2021; Appendix S56). We conducted the analyses using Stan (Carpenter et

233   al., 2017) through the package *brms* in R (Bürkner 2017).

234

235   *Predicting species interactions*

236   To quantify model transferability, we used each model to predict the food web fitted with that

237   modelon which it was trained and that of the other regions considered (Figure 1a). For each

238   possible predator-prey pair, we extracted the mean of the posterior as the probability of

239   interaction, and the standard deviation of the posterior as the uncertainty around the predicted

240   probability of interaction. When predicting the food web on which the model was

241   calibratedtrained (i.e., within food web predictions), we compared the predicted interaction

242   probabilities to the validation subset of the food web. When predicting food webs other than the

243    one on which the model was ~~calibrated~~trained (i.e., between food web predictions), we compared

244    the predicted interaction probabilities to the entire empirical food web. We measured

245    performance with the area under the receiver operating characteristic curve (AUC; Hanley and

246    McNeil 1982). AUC varies from 0 to 1 where 0.5 indicates that the model failed to rank

247    interactions higher than absences of interactions (i.e., random predictions), and 1 indicates that

248    the model systematically ranked interactions higher than non-interactions (i.e., perfect

249    predictions). We also measured the area under the precision-recall-gain curve (AUPRG; Flach &

250    Kull, 2015). AUPRG is independent of the true negative rate, making it useful for highly

251    imbalanced datasets, like food webs (many more non-interactions than interactions to predict;

252    Saito & Rehmsmeier, 2015). AUPRG takes a value of 0 for random predictions, and a value of 1

253    for perfect predictions. ~~, and directly used posterior draws to get distributions for the true~~

254    ~~positive rate, true negative rate, positive predictive value and negative predictive value~~

255    ~~(Appendix S6).~~(Davis & Goadrich, 2006)

256

257    To explore factors influencing model transferability, we assessed the performance of models to

258    predict each food web using three distance measures: geographic distance, environmental

259    dissimilarity, and phylogenetic relatedness. We measured geographic distance as the

260    ~~Euclidean~~great-circle distance distance between the polygon centroid delimiting the spatial

261    domain of each food web. Environmental dissimilarity was quantified using all 19 bioclimatic

262    variables in WorldClim (Hijmans, 2021). ~~We randomly drew 500 points within each polygon~~

263    ~~corresponding to the spatial domain of our food webs, extracted bioclimatic data for these~~

264    ~~points~~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 repeated this step 10 times (10 sets of 500 random points) to make sure the environmental distance estimates are robust to random sampling (Appendix S4).~~ 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 on which the model was ~~calibrated~~trained.

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~~against how connected the focal species is and how distinct the focal species is to the species pool used to ~~calibrate~~train 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

288 distance between the focal species and the closest relative in the species in the food web used for

289 model calibration.

290

291 *Predicting species' functional role*s

292 Next, we were interested in how well species functional roles were predicted by our models. The

293 functional role of a species is determined by its position in the food web (Cirtwill et al., 2018),

294 which we quantified using five metrics related to the species centrality within the food webs

295 (number of prey, number of predators, betweenness, closeness, eigenvector centrality), two

296 metrics related to their trophic position (trophic levels and omnivory), two module-based metrics

297 (within-module degree and participation coefficient; Guimerà & Amaral, 2005), and the motif

298 profile of each species (Stouffer et al., 2012). We detail each metric, their relation to functional

299 role, and how they were calculated in Appendix S34.

300

301 To measure how well species roles were predicted, we compared each species position metric in

302 empirical food webs to the species position in predicted food webs. For predicted food webs, we

303 measured each role metric on 100 samples of the posterior distribution of the entire food web

304 with the mean as the best point estimate for the metric and the standard deviation as measure of

305 uncertainty. For each combination of model, predicted food web, and species role metric, we

306 fitted a linear regression between the predicted position and the empirical position and used the

307 coefficient of determination ($R^2$). We also explored prediction biases (e.g., systematic

308 overestimation/underestimation) using the simple linear models' coefficients. We expect an

309 intercept of zero for perfectunbiased predictions of species role. An intercept, and deviation from

310 greater than zero would suggest an systematicoverall biasoverestimation of the role metric across

14

311 the range of the role metric, whereas an intercept less than zero would suggest a systematic

312 underestimation of the role metric. We expect a slope of one for perfect predictions. A slope less

313 than one would suggest that the role metric of speciesvalues at the lower range are overpredicted,

314 whereas the role metric of speciesvalues at the upper range are underpredicted (i.e., more

315 homogeneous rolevalues across species than in the empirical food web). A slope greater than one

316 would suggest the opposite (i.e., more heterogeneous rolevalues across species than in the

317 empirical food web).

318

319 *Predicting food web properties*

320 Finally, we investigated how well the global properties of food webs were predicted. We selected

321 a range of metrics commonly used to quantify food web structure and which have been shown to

322 influence food web functioning and stability: connectance, mean trophic level, maximum trophic

323 level, motifs distribution, food web diameter, number of clusters, and modularity (Borrelli, 2015;

324 Vermaat et al., 2009). As for species position, we evaluated these properties on the empirical

325 food webs and compared them to the properties predicted using the mean of 100 samples of the

326 posterior food web prediction. We detail each metric, their relation to food web function, and

327 how they were calculated in Appendix S34.

328

329 *Boosted regression trees*

330 To make sure results are general and not dependent on the model framework chosen (Bayesian

331 hierarchical generalized linear model), we fitted boosted regression trees (BRT) on each food

332 web and ran the same analyses (Appendix S5). BRT are a machine learning algorithm that allows

333 non-linear relationships between predictors and the response variable (Friedman, 2001). To make

15

334 results comparable, we used the exact same training/validation splits and same predictor

335 variables to train and measure performance of the BRT and the Bayesian hierarchical generalized

336 linear models.

337

338 **Results**

339 *Predicting trophic interactions*

340 For all food webs, trophic interactions were better predicted by the model ~~calibrated~~trained on

341 the same food web (within food web predictions) than by models ~~calibrated~~trained on other food

342 webs (between food web predictions; Table 2). For within food web predictions, AUC varied

343 between 0.92 and 0.96 and AUPRG varied between 0.93 and 0.96. Model performance was also

344 good (AUC > 0.82; AUPRG > 0.84) for transfer between the Europe, Pyrenees, and Northern

345 Québec and Labrador food webs, except for the model trained on the Pyrenees predicting

346 Europe. For this case, AUC was good (0.89) but not AUPRG (0.63), suggesting that the model

347 was much better to discriminate non-interactions than interactions. Models did not transfer as

348 well from and to the Serengeti food web, but performance was still good (AUC > 0.75); AUPRG

349 > 0.73). The area under the precision-recall-~~-~~gain curve, true positive rate, true negative rate,

350 positive predictive value, and negative predictive value were all positively correlated with AUC

351 and showed the same overall pattern (Appendix S6).

352

353 To explore the factors influencing the transferability of interaction models, we modelled their

354 performance relative ~~to~~against the geographic, environmental, and phylogenetic distances

355 between the ~~calibrated and~~ predicted food web and the food web used for training (Figure 2).

356 Overall, performance tended to decrease with environmental (direct effect estimate: -0.~~52~~29,

357  95%CrI = [-0.~~89~~91, ~~-0.11~~0.33]) and phylogenetic distance (direct effect estimate: -0.3~~9~~1, 95%CrI

358  = [-0.~~78~~68, 0.05~~-0.03~~]). Performance also tended to decrease~~d~~ with geographic distance (total

359  effect estimate: -0.5~~7~~4, 95%CrI = [-0.7~~9~~8, -0.3~~0~~5]), but this effect largely disappeared after

360  controlling for phylogenetic and environmental distances (direct effect estimate: -0.~~07~~24,

361  95%CrI = [-0.~~48~~84, 0.3~~4~~6]). Overall, these results suggest that the transferability of our model of

362  trophic interactions decreases with geographic distances, but mainly through the differences in

363  the environmental and phylogenetic domain between the food web predicted and the food web

364  used to train the model.

365

366  ~~We also~~To identif~~yied~~ the factors influencing transferability at the species ~~for which the~~

367  ~~interactions were incorrectly predicted between food web~~level. ~~We~~, we modelled species-specific

368  performance to the phylogenetic and functional distance between the focal species and the

369  species pool used to train the models (Figure 3). As expected, species with phylogenetically close

370  relatives in the species pool used for calibration were, on average, better predicted than distant

371  relatives (Figure 3a). Species-specific performance slightly decreased at low and intermediate

372  phylogenetic distances, and then dropped significantly at large distances. Models

373  ~~calibrated~~trained and predicted across classes (e.g. mammals to amphibians) had the lowest

374  performance, as expected. This situation only occurs with the Northern Québec and Labrador

375  model predicting the other three food webs as there are no amphibians or reptiles in Northern

376  Québec and Labrador. Surprisingly, predictive performance remained qualitatively unchanged by

377  functional distance (Figure 3b). We also found that interactions of specialist (i.e., species with

378  few interactions) and generalist species (i.e., species with many interactions) were, on average,

379  better predicted than interactions of species of intermediate specialization (Figure 3c).

380

*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.

387

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 S7, slopes less than 1).

395

*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 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.

18

403

*Boosted regression trees*

We found the same general results with BRT (Appendix S5). Overall, BRT performed similarly
to our linear model to predict interactions within and across food webs (AUC between ; AUCPR
between ). Species functional role and food web properties were be slightly better predicted by
the BRT, but we still found similar biases in predictions (Appendix S5).

**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~~First, we showed that our
trait-based trophic interaction models can predict interactions across ~~ecosystems~~regions. We
found that, given enough phylogenetic and environmental similarities between the system on
which the model is ~~calibrated~~trained and the system for which the predictions are made, models
predicted most interactions reasonably well (AUC > 0.82). Our results suggest that, for terrestrial
vertebrate food webs, trait relationships driving interactions appear to be relatively general even
in highly contrasting environments. Second, ~~A~~although models ~~were successful at~~
~~predicting~~predicted correctly most interactions, they ~~were less successful at~~failed to predict~~ing~~
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 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). Both these findings do not seem to be specific to Bayesian

19

426   hierarchical generalized linear models since we found the same overall patterns using boosted

427   regression trees (Appendix S5)(Friedman, 2001)

428

429   The trait-matching framework of trophic niche theory assumes that variation across food webs

430   arises through differences in the trait-matching rules driving interactions (e.g., body mass

431   relationships between the predator and its prey) and the distribution of traits in different systems

432   (Gravel et al., 2016). Spatial transferability of trait-based models depend on the generality of the

433   trait-matching rules driving interactions. Therefore, Oour ability to predict food web interactions

434   across contrasting environments partially agrees with this framework by suggesting suggests that

435   spatial food web variation is mainly driven by changes in the distribution of functional traits, and

436   less so by the variation of trait-matching relationships. These results are in line with previous

437   research finding generalities made on trait-interactions relationships across European bioregions

438   (Caron et al., 2022), the predator-prey body-size ratios within habitat, predator, and prey types

439   (Brose et al., 2006), and the trait-interactions relationships in soil invertebrates across three forest

440   areas in Germany (Laigle et al. 2018). Given that trait-matching rules driving species interactions

441   seem general in reasonably similar environments, it should be possible to use data from well-

442   studied areas to predict interactions in areas we know very little about or forecast (and hindcast)

443   food webs given new trait distributions.

444

445   We also highlighted a major limitation of trophic interaction models: trophic interaction models

446   predict interactions, not food webs. Even if most interactions and absences of interactions are

447   well predicted (high true positive and negative rates), there are many more absences of

448   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 S7). 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.

Food webs are more than a collection of independent trophic interactions (Strydom et al., 2021).

Some factors constrains food web on their global network properties (e.g., connectance), other

the position species occupy within the food web (e.g., trophic level). Here, predicting individual

links to predict higher-level properties, suggesting that trophic interactions models cannot capture 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). Area also influences the structural properties of food webs (Galiana et al., 2018). 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 the predictions of food web webs between systems. However, within food-webs predictions produced similarly biased higher-level properties, so area does not seem to be the major constraint explaining model failure to predict realistic networks.

Correcting biases in higher-level property predictions presents an opportunity to improve species interaction predictions. In sStacked species distribution models have similar challenges, where models can predict well the distribution of individual species but less higher-level properties of the community (e.g., species richness). , mMethods 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. For example, (Leung et al., (2019)T combined predicted species distributions and expected species richness to quantify species and spatial biases. They then correlated those biases to species traits and environmental co-variates to improve predicted species distribution. Therefore,Similar methods that would combine predictions of interactions and networks have the potential to provide better food web predictions. For Bayesian interaction models, we could penalize posterior food web predictions resulting into improbable food web structure based on predictions of structural food web models (Williams & Martinez, 2008) to update pairwise

495 interaction probabilities. ~~tructural food web models can predict the probability distribution of~~

496 ~~many food web properties (Williams & Martinez, 2008). Information on probable food web~~

497 ~~structure could be used to correct posterior predictive distributions of species interactions. S~~

498

499 Our study suffers from a few limitations that, if overcome, could move us closer to a

500 comprehensive framework for ecological interactions and networks prediction. First, our study

501 relied on terrestrial vertebrates. Although there is no clear *a priori* reason not to be applicable in

502 other systems, our results are unlikely to be general across all taxa and types of interactions. We

503 are not aware of another other test of interaction model transferability, but it would be interesting

504 to investigate if our results hold for systems where trait-matching relationships are stronger or

505 weaker. The exclusion of non-vertebrates (e.g., plants, invertebrates, parasites) also influence the

506 empirical and predicted species role and food web properties. For example, the first trophic

507 levels in our food webs were not primary producers, but species not feeding on terrestrial

508 vertebrates (e.g., herbivores, invertivores). However, extension of trait-matching models to also

509 include invertebrates can be achieved with a coarser resolution (Li et al., 2023) or with additional

510 traits (Laigle et al., 2018). Second, the food webs we used were potential and binary food webs.

511 Trait-matching models predict the probabilities that a species could eat another species given

512 they are encountering each other. Additional data, such as co-occurrence and abundance data, are

513 needed to make predictions of realized and quantitative interactions. Finally, due to the scarcity

514 of food web data, we only had four food webs to work with. This means we only had four sets of

515 within food web predictions, and 12 sets of between food web predictions. This explains the

516 large uncertainty for some of our results (e.g., Figure 2). ~~Despite the low sample size, we still~~

517 ~~detected significant relationship between model transferability and geographic, phylogenetic, and~~

518 ~~environmental distances.~~

519

520 Overall, we found that our trait-based interaction models can transfer knowledge relatively well

521 given enough phylogenetic and environmental similarities between systems. They are useful for

522 producing initial expectations even in contrasting ecosystems. This, and other recent research

523 (Brose et al., 2006; Caron et al., 2022; Laigle et al., 2018), suggests there are ~~f~~ fundamental trait-

524 based constraints on trophic interactions that are generalizable to some extent. The nature of this

525 constraint also appears to result from species traits rather than the 'match' between a predator

526 and its prey, which has interesting ties to the broader question of how traits vary between

527 ~~ecosystems~~regions and along gradients (Gravel et al., 2016). Future research could better link

528 subfields within trait-based ecology for a comprehensive understanding of how species relate to

529 their environment and to other species, and to enable better predictions of the responses of

530 species and ecosystems to threats and global change.

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532 **References**

Albouy, C., Velez, L., Coll, M., Colloca, F., Loc'h, F. L., Mouillot, D., & Gravel, D. (2014).
From projected species distribution to food-web structure under climate change. *Global Change Biology*, *20*(3), 730–741. https://doi.org/10.1111/gcb.12467

Baiser, B., Gravel, D., Cirtwill, A. R., Dunne, J. A., Fahimipour, A. K., Gilarranz, L. J., Grochow, J. A., Li, D., Martinez, N. D., McGrew, A., Poisot, T., Romanuk, T. N., Stouffer, D. B., Trotta, L. B., Valdovinos, F. S., Williams, R. J., Wood, S. A., & Yeakel, J. D. (2019). Ecogeographical rules and the macroecology of food webs. *Global Ecology and Biogeography*, *28*(9), 1204–1218. https://doi.org/10.1111/geb.12925

Berteaux, D., Ropars, P., & Casajus, N. (2018). Toundra Nunavik: Matrice des relations trophiques entre espèces du Labrador et du Québec nordique, v. 1.0 (1980-2010). *Nordicana D36*. https://doi.org/10.5885/45555CE-DA1FF11FA4254703

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, *23*(7), 1050–1063. https://doi.org/10.1111/ele.13525

Borrelli, J. J. (2015). Selection against instability: Stable subgraphs are most frequent in empirical food webs. *Oikos*, *124*(12), 1583–1588. https://doi.org/10.1111/oik.02176

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., … Cohen, J. E. (2006). Consumer–Resource Body-Size Relationships in Natural Food Webs. *Ecology*, *87*(10), 2411–2417. https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2

Bürkner, P.-C. (2017). **brms**: An *R* Package for Bayesian Multilevel Models Using *Stan*. *Journal of Statistical Software*, *80*(1). https://doi.org/10.18637/jss.v080.i01

Canard, E., Mouquet, N., Marescot, L., Gaston, K. J., Gravel, D., & Mouillot, D. (2012). Emergence of Structural Patterns in Neutral Trophic Networks. *PLOS ONE, 7*(8), e38295. https://doi.org/10.1371/journal.pone.0038295

Caron, D., Maiorano, L., Thuiller, W., & Pollock, L. J. (2022). Addressing the Eltonian shortfall with trait-based interaction models. *Ecology Letters*, ele.13966. https://doi.org/10.1111/ele.13966

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). *Stan*: A Probabilistic Programming Language. *Journal of Statistical Software, 76*(1). https://doi.org/10.18637/jss.v076.i01

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., & Ram, K. (2022). *rgbif: Interface to the global biodiversity information facility API* [Manual]. https://CRAN.R-project.org/package=rgbif

Cirtwill, A. R., Dalla Riva, G. V., Gaiarsa, M. P., Bimler, M. D., Cagua, E. F., Coux, C., & Dehling, D. M. (2018). A review of species role concepts in food webs. *Food Webs, 16*, e00093. https://doi.org/10.1016/j.fooweb.2018.e00093

Davis, J., & Goadrich, M. (2006). The relationship between Precision-Recall and ROC curves. *Proceedings of the 23rd International Conference on Machine Learning - ICML '06*, 233–240. https://doi.org/10.1145/1143844.1143874

de Visser, S. N., Freymann, B. P., & Olff, H. (2011). The Serengeti food web: Empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology, 80*(2), 484–494. https://doi.org/10.1111/j.1365-2656.2010.01787.x

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E., & Loreau, M. (2007). The functional role of biodiversity in ecosystems: Incorporating trophic complexity. *Ecology Letters, 10*(6), 522–538. https://doi.org/10.1111/j.1461-0248.2007.01037.x

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R.,
Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T.,
Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., …
Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. *Science*, *333*(6040), 301–
306. https://doi.org/10.1126/science.1205106

Etard, A., Morrill, S., & Newbold, T. (2020). Global gaps in trait data for terrestrial vertebrates.
*Global Ecology and Biogeography*, *29*(12), 2143–2158.
https://doi.org/10.1111/geb.13184

Flach, P., & Kull, M. (2015). Precision-Recall-Gain Curves: PR Analysis Done Right. In C.
Cortes, N. Lawrence, D. Lee, M. Sugiyama, & R. Garnett (Eds.), *Advances in Neural
Information Processing Systems* (Vol. 28). Curran Associates, Inc.
https://proceedings.neurips.cc/paper_files/paper/2015/file/33e8075e9970de0cfea955afd4
644bb2-Paper.pdf

Fricke, E. C., Hsieh, C., Middleton, O., Gorczynski, D., Cappello, C. D., Sanisidro, O., Rowan,
J., Svenning, J.-C., & Beaudrot, L. (2022). Collapse of terrestrial mammal food webs
since the Late Pleistocene. *Science*, *377*(6609), 1008–1011.
https://doi.org/10.1126/science.abn4012

Friedman, J. H. (2001). Greedy Function Approximation: A Gradient Boosting Machine. *The
Annals of Statistics*, *29*(5), 1189–1232. JSTOR.

Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., Gravel, D.,
& Montoya, J. M. (2018). The spatial scaling of species interaction networks. *Nature
Ecology & Evolution*, *2*(5), Article 5. https://doi.org/10.1038/s41559-018-0517-3

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics
in Medicine*, *27*(15), 2865–2873. https://doi.org/10.1002/sim.3107

Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, *465*(7300), Article 7300. https://doi.org/10.1038/nature09113

Gower, J. C. (1971). A General Coefficient of Similarity and Some of Its Properties. *Biometrics*, *27*(4), 857–871. https://doi.org/10.2307/2528823

Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1694), 20150268. https://doi.org/10.1098/rstb.2015.0268

Gravel, D., Baiser, B., Dunne, J. A., Kopelke, J.-P., Martinez, N. D., Nyman, T., Poisot, T., Stouffer, D. B., Tylianakis, J. M., Wood, S. A., & Roslin, T. (2019). Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, *42*(3), 401–415. https://doi.org/10.1111/ecog.04006

Guimerà, R., & Amaral, L. A. N. (2005). Cartography of complex networks: Modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment*, *2005*(02), P02001. https://doi.org/10.1088/1742-5468/2005/02/P02001

Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, *143*(1), 29–36. https://doi.org/10.1148/radiology.143.1.7063747

Harvey, E., Gounand, I., Ward, C. L., & Altermatt, F. (2017). Bridging ecology and conservation: From ecological networks to ecosystem function. *Journal of Applied Ecology*, *54*(2), 371–379. https://doi.org/10.1111/1365-2664.12769

Hijmans, R. J. (2021). *raster: Geographic data analysis and modeling* [Manual]. https://CRAN.R-project.org/package=raster

Jetz, W., & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology & Evolution*, *2*(5), Article 5. https://doi.org/10.1038/s41559-018-0515-5

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity

of birds in space and time. *Nature*, *491*(7424), Article 7424.

https://doi.org/10.1038/nature11631

Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, *30*(12),

1883–1893. https://doi.org/10.1111/1365-2435.12763

Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I., & Gravel, D. (2018). Species traits as

drivers of food web structure. *Oikos*, *127*(2), 316–326. https://doi.org/10.1111/oik.04712

Letten, A. D., & Cornwell, W. K. (2015). Trees, branches and (square) roots: Why evolutionary

relatedness is not linearly related to functional distance. *Methods in Ecology and*

*Evolution*, *6*(4), 439–444. https://doi.org/10.1111/2041-210X.12237

Leung, B., Hudgins, E. J., Potapova, A., & Ruiz-Jaen, M. C. (2019). A new baseline for

countrywide α-diversity and species distributions: Illustration using >6,000 plant species

in Panama. *Ecological Applications*, *29*(3), e01866. https://doi.org/10.1002/eap.1866

Li, J., Luo, M., Wang, S., Gauzens, B., Hirt, M. R., Rosenbaum, B., & Brose, U. (2023). A size-

constrained feeding-niche model distinguishes predation patterns between aquatic and

terrestrial food webs. *Ecology Letters*, *26*(1), 76–86. https://doi.org/10.1111/ele.14134

Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, *23*(4), 399–417.

https://doi.org/10.2307/1930126

Lurgi, M., Galiana, N., López, B. C., Joppa, L. N., & Montoya, J. M. (2014). Network

complexity and species traits mediate the effects of biological invasions on dynamic food

webs. *Frontiers in Ecology and Evolution*, *2*.

https://www.frontiersin.org/articles/10.3389/fevo.2014.00036

Lurgi, M., López, B. C., & Montoya, J. M. (2012). Climate change impacts on body size and

food web structure on mountain ecosystems. *Philosophical Transactions of the Royal*

*Society B: Biological Sciences*, *367*(1605), 3050–3057.

https://doi.org/10.1098/rstb.2012.0239

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F.,
Maire, E., Mouillot, D., & Villéger, S. (2022). mFD: An R package to compute and
illustrate the multiple facets of functional diversity. *Ecography, 2022*(1).
https://doi.org/10.1111/ecog.05904

Maiorano, L., Montemaggiori, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-
EU 1.0: A species-level trophic metaweb of European tetrapods. *Global Ecology and
Biogeography*, geb.13138. https://doi.org/10.1111/geb.13138

Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic
interactions from proxies. *Trends in Ecology & Evolution, 30*(6), 347–356.
https://doi.org/10.1016/j.tree.2015.03.014

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity
measures: An overview of their redundancy and their ability to discriminate community
assembly rules. *Functional Ecology, 24*(4), 867–876. https://doi.org/10.1111/j.1365-
2435.2010.01695.x

Neal, R. M. (2011). MCMC Using Hamiltonian Dynamics. In *Handbook of Markov Chain
Monte Carlo* (pp. 113–162). CRC Press. https://doi.org/10.1201/b10905-7

Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C., & Costa, G. C. (2017).
AmphiBIO, a global database for amphibian ecological traits. *Scientific Data, 4*(1),
Article 1. https://doi.org/10.1038/sdata.2017.123

Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet,
C., Vissault, S., & Chapman, D. (2021). Global knowledge gaps in species interaction
networks data. *Journal of Biogeography*, jbi.14127. https://doi.org/10.1111/jbi.14127

Pomeranz, J. P. F., Thompson, R. M., Poisot, T., & Harding, J. S. (2019). Inferring predator–prey
interactions in food webs. *Methods in Ecology and Evolution, 10*(3), 356–367.
https://doi.org/10.1111/2041-210X.13125

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation

    for Statistical Computing. https://www.R-project.org/

Saito, T., & Rehmsmeier, M. (2015). The Precision-Recall Plot Is More Informative than the

    ROC Plot When Evaluating Binary Classifiers on Imbalanced Datasets. *PLOS ONE*,

    *10*(3), e0118432. https://doi.org/10.1371/journal.pone.0118432

Stekhoven, D. J., & Buehlmann, P. (2012). MissForest—Non-parametric missing value

    imputation for mixed-type data. *Bioinformatics (Oxford, England)*, *28*(1), 112–118.

Stouffer, D. B., Sales-Pardo, M., Sirer, M. I., & Bascompte, J. (2012). Evolutionary Conservation

    of Species' Roles in Food Webs. *Science*, *335*(6075), 1489–1492.

    https://doi.org/10.1126/science.1216556

Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M. J., Fortin, M.-J.,

    Hemming, V., Mercier, B., Pollock, L. J., Runghen, R., Dalla Riva, G. V., & Poisot, T.

    (2022). Food web reconstruction through phylogenetic transfer of low-rank network

    representation. *Methods in Ecology and Evolution*, *13*(12), 2838–2849.

    https://doi.org/10.1111/2041-210X.13835

Strydom, T., Catchen, M. D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P.,

    Forero-Muñoz, N. R., Higino, G., Mercier, B., Gonzalez, A., Gravel, D., Pollock, L., &

    Poisot, T. (2021). A roadmap towards predicting species interaction networks (across

    space and time). *Philosophical Transactions of the Royal Society of London. Series B,*

    *Biological Sciences*, *376*(1837), 20210063. https://doi.org/10.1098/rstb.2021.0063

Thomson, R. C., Spinks, P. Q., & Shaffer, H. B. (2021). A global phylogeny of turtles reveals a

    burst of climate-associated diversification on continental margins. *Proceedings of the*

    *National Academy of Sciences*, *118*(7), e2012215118.

    https://doi.org/10.1073/pnas.2012215118

Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, *204*, 23–31. https://doi.org/10.1016/j.biocon.2016.03.039

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M., & Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, *92*(2), 698–715. https://doi.org/10.1111/brv.12252

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology*, *17*(12), e3000494. https://doi.org/10.1371/journal.pbio.3000494

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P.-C. (2021). Rank-Normalization, Folding, and Localization: An Improved R̂ for Assessing Convergence of MCMC (with Discussion). *Bayesian Analysis*, *16*(2), 667–718. https://doi.org/10.1214/20-BA1221

Vermaat, J. E., Dunne, J. A., & Gilbert, A. J. (2009). Major dimensions in food-web structure properties. *Ecology*, *90*(1), 278–282. https://doi.org/10.1890/07-0978.1

Wang, S., & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: The vertical diversity hypothesis. *Ecology Letters*, *21*(1), 9–20. https://doi.org/10.1111/ele.12865

Williams, R. J., & Martinez, N. D. (2008). Success and Its Limits among Structural Models of Complex Food Webs. *Journal of Animal Ecology*, *77*(3), 512–519.

Wilman, H., Belmaker, J., Simpson, J., Rosa, C. de la, Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027–2027. https://doi.org/10.1890/13-1917.1

533 **Data Accessibility Statement**

534     All data sources have been previously published. All data used in the analyses and relevant code

535     will be archived on a Open Science Framework repository.

*Table 1: Summary statistics~~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 |

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*Table 2: Food webs are better predicted by their own ~~calibrated~~trained model. Area under the receiver operating curve (AUC) and area under the precision-recall-gain curve (AUPRG) of each model predicting every food web.* -

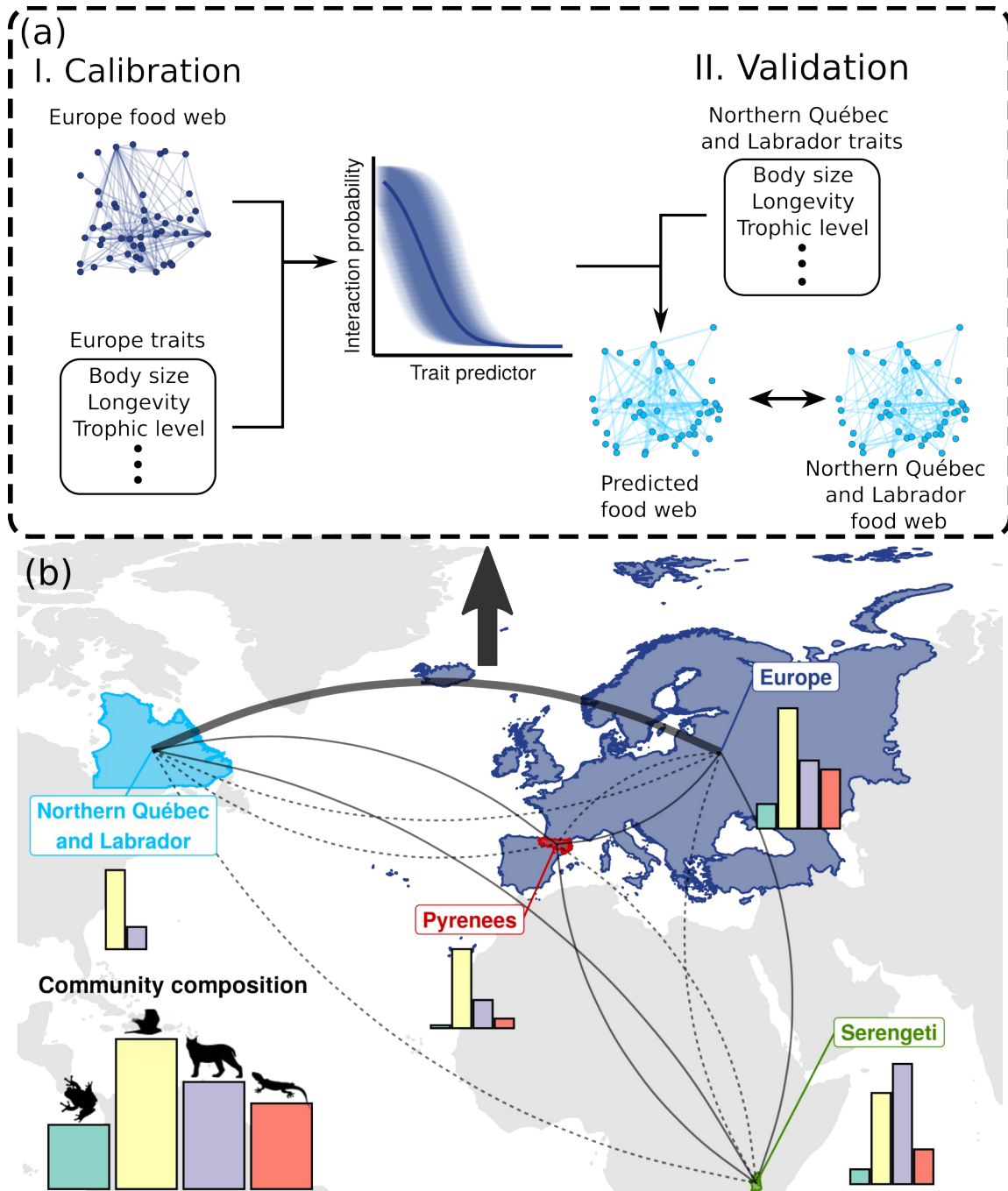| | Food web | | | |
|---|---|---|---|---|
| Model | Europe | Pyrenees | North Québec and Labrador | Serengeti |
| AUC | | | | |
| Europe | **0.96** | 0.89 | 0.9 | 0.8 |
| Pyrenees | 0.86 | **0.95** | 0.85 | 0.79 |
| North Québec And Labrador | 0.82 | 0.9 | **0.95** | 0.75 |
| Serengeti | 0.85 | 0.78 | 0.77 | **0.92** |
| AUPRG | | | | |
| Europe | **0.96** | 0.63 | 0.91 | 0.84 |
| Pyrenees | 0.9 | **0.95** | **0.94** | 0.84 |
| North Québec And Labrador | 0.88 | 0.9 | 0.93 | 0.8 |
| Serengeti | 0.84 | 0.73 | 0.77 | **0.93** |

*Figure 1:* **Trophic interactions model transferability analysis workflow.** *We* ~~*calibrated*~~*trained a trophic interaction model using each food web considered in this study* ~~*separately*~~ *(panel a.I). We* ~~*validated*~~*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 (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.** *~~Each P~~points ~~are~~is the predictive performance (AUC) of ~~the sixteen~~a model-food web predicted combination ~~of model-food web prediction~~ (16 combination; ~~(~~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 (includes the indirect effects of environmental and phylogenetic distances; turquoise) and partial (controls for environmental and phylogenetic distances; 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.*
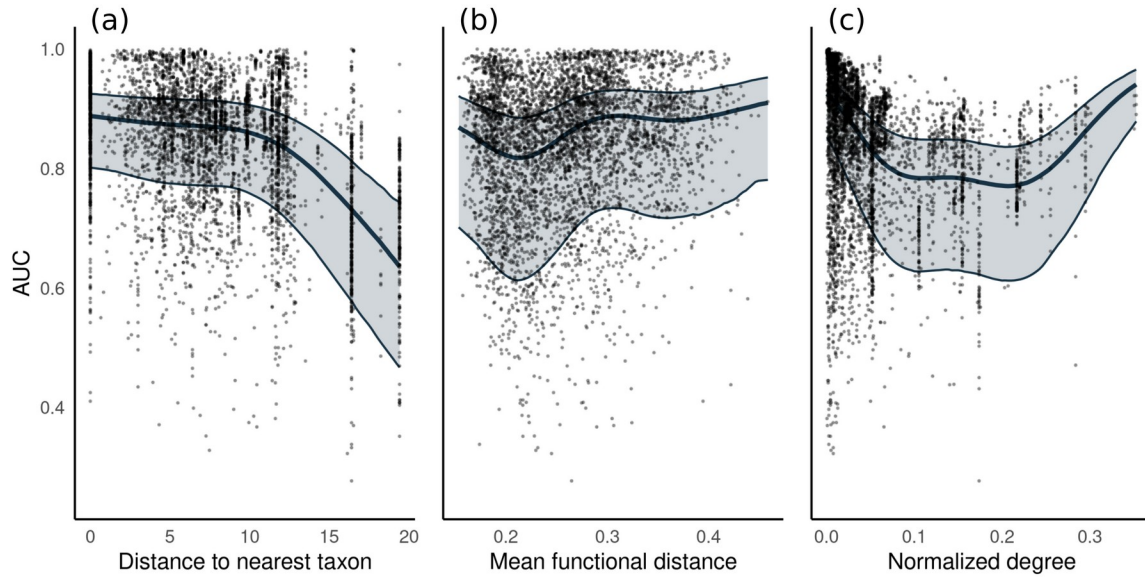
*Figure 3: **Predicting species interactions**. Performance of the models to predict the interactions of species in the ~~other~~alternative food webs. Each point is the performance to predict the prey and predators of a single species. The trend lines are the median effects with their 95% credible interval 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.*
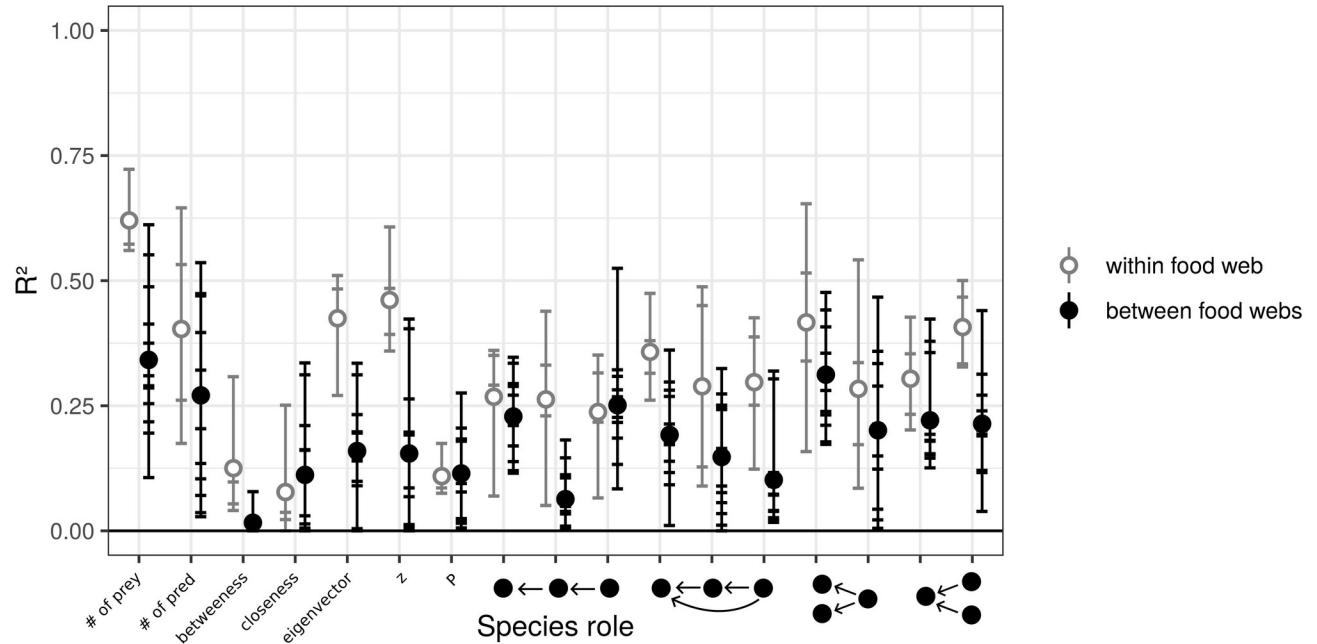
*Figure 4: **Predicting species functional role**. Performance of models to predict species functional role measured as the proportion of the variance in trophic positions explained by the models ($R^2$). From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, 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~~between -food web predictions.*
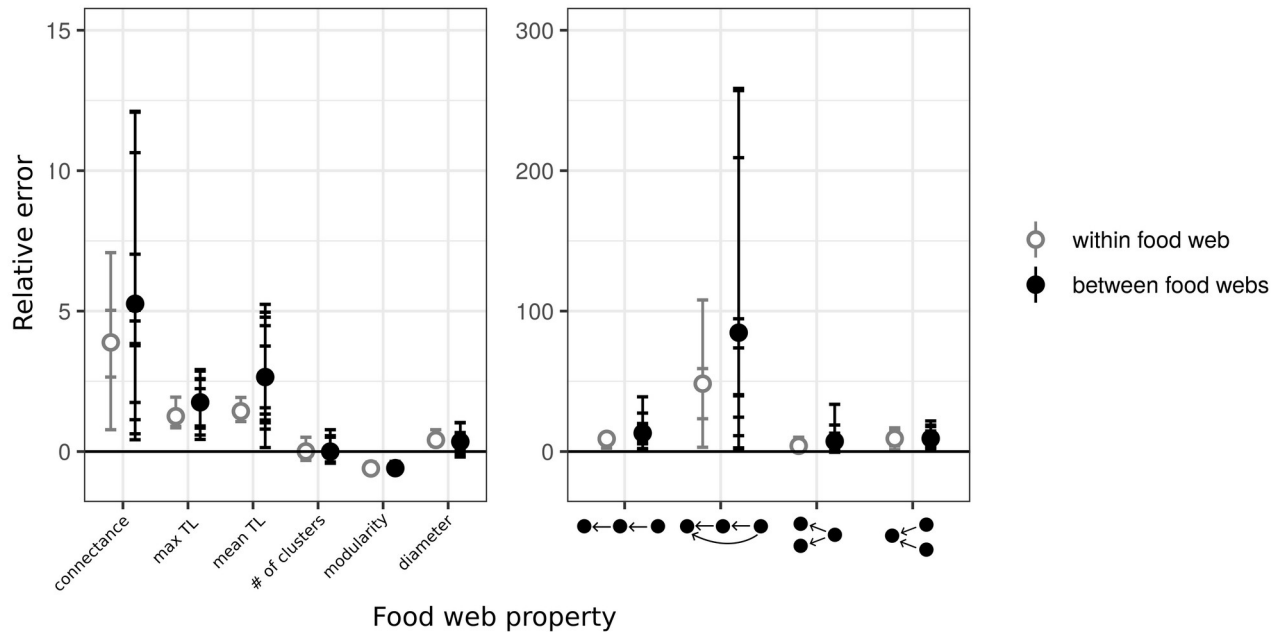
*Figure 5:* **Prediction error of global food web properties**. ~~The relative error of the predicted food web properties.~~ *Relative error is the difference between the predicted and <u>the</u> empirical estimates divided by the empirical estimate. From left to right, the figure shows the relative 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 <u>(1 consumer – 2 resources)</u> 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.~~*