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

2 **properties**

3

4 **Running title:** Interaction models transferability

5

6 **Abstract**

7 **Aim:** Trophic interactions are essential for understanding how ecosystems function, but

8 empirical data on interactions is lacking for most taxa in most ecosystems. Fortunately, trophic

9 interactions can be estimated with trait-based models to some degree. We test how well these

10 models can extrapolate to new ecological communities (necessary for the success of these

11 models to fill data gaps) both in terms of pairwise predator-prey interactions and higher-level

12 food web attributes (i.e., species position, food web-level properties).

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

14 **Time period:** Current.

15 **Major taxa studied:** Terrestrial vertebrates.

16 **Methods:** We train trait-based models of pairwise trophic interactions on four independent

17 vertebrate food webs (Canadian tundra, Serengeti, alpine south-eastern Pyrenees, and entire

18 Europe) and evaluate how well these models predict pairwise interactions and network properties

19 for each of the set of food webs.

20 **Results:** We find that, overall, trait-based models predict most interactions and their absence

21 correctly, even across highly contrasting environments. Performance declined with

22 environmental and phylogenetic distance from within food webs (AUC > 0.90) to the strong

23 contrast of the tundra-Serengeti (AUC > 0.75). Network metrics were less well-predicted than

24   single interactions by our models with predicted food webs being more connected, less modular,

25   and with higher mean trophic levels than observed.

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

27   by differences in trait distributions and trait-matching relationships. The finding that trait-based

28   models can predict many trophic interactions, even in contrasting environments, suggests that

29   there are general constraints on interactions and that trait-based methods can serve as a first

30   approximation of food webs in unknown areas. However, food webs are more than the sum of

31   their parts, and predicting network attributes will likely require models that simultaneously

32   predict individual interactions and community constraints.

33

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

35   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 in developing accurate descriptions of natural food webs. One major obstacle is the lack of trophic interaction data across most locations and taxa (Poisot et al., 2021). The difficulty is that, to detect an interaction, you must first observe individuals of both species simultaneously, and then observe an interaction between the species (Jordano, 2016). This means that trophic interactions are substantially more difficult to observe than species, which is in itself a biodiversity shortfall. Adding to the detection issues, the number of possible interactions within food webs increases quadratically with the number of species resulting in extremely large sets of potential interactions in realistic communitites. Observing all possible interactions among species within a food web is very difficult even in species-poor ecosystems, so a systematic approach for predicting interactions with available data is essential.

In response to this need, models have been developed that predict interactions based on food web theory (Strydom et al., 2021). These models identify feasible interactions based on some combination of the traits of predators, the traits of prey, and the 'match' of traits between predator and prey (e.g., smaller predators eat smaller prey; Bartomeus et al., 2016). Such trait-based models have been used to predict food webs for freshwater streams (Pomeranz et al., 2019), marine fishes (Albouy et al., 2014), terrestrial systems comprising vertebrate (Caron et al., 2022; Fricke et al., 2022) and invertebrate species (Laigle et al., 2018), among others.

59 Phylogenetic relationships are also informative since they can serve as proxy for trait

60 relationships, and because interactions and species' roles (i.e., species' positions in the food web)

61 tend to be evolutionary conserved (Gómez et al., 2010; Stouffer et al., 2012).

62

63 While trait-based models have been shown to predict food webs for a given ecosystem, a more

64 challenging, yet largely untested, proposition is whether trait-based models fit on one ecosystem

65 could predict the food web of another. If trait-matching rules determining interactions are

66 general, then i) we should observe the same trait-interaction relationships across regions and ii) a

67 model trained in one location should be transferable. Also, given the strong data deficiency,

68 many ecosystems may require extrapolation from other ecosystems. Initial results suggest that

69 this is possible in the case of terrestrial mammals. Strydom et al. (2022) used a mammal

70 phylogeny to map latent traits extracted from a European mammalian food web to predict its

71 Canadian counterpart and were able to recover 90% of known trophic interactions among

72 Canadian mammals without any prior information on the food web. This demonstrates the

73 potential for transferability between vast regions, where trait-interaction relationships are

74 expected to be general, with relatively similar bioclimatic conditions and somewhat related

75 species (more than half of Canadian mammals have congeneric species in Europe). Given

76 transferability should depend on the similarity of the environment and species composition of the

77 respective food webs (Gravel et al., 2016), this raises the question of how well trait-based models

78 could extrapolate to more contrasting environments.

79

80 A second question is whether these trait-based trophic interaction models can estimate aggregate

81 food web properties such as network connectance, number of trophic levels and species position

82   within the food web. These higher-level properties emerge from the joint effect of trait-matching

83   between interacting partners, the trait distribution of species composing the food web (Gravel et

84   al., 2016), and are influenced by the spatial scale of the network (Galiana et al., 2018). Most

85   studies are aimed at predicting either the properties of food webs (e.g., Williams & Martinez,

86   2008) or their pairwise interactions (e.g., Laigle et al., 2018; Pomeranz et al., 2019), but initial

87   results that combine the two show that food web connectance was systematically over-estimated

88   across Europe by 2-4 times (Caron et al., 2022). While this result is not particularly surprising

89   given the model is calibrated for predicting pairwise interactions, not network properties, it is

90   still interesting to understand whether this is the case more generally and, if so, begin to

91   hypothesize whether there are fundamental differences in the scale of ecological processes that

92   constrain food web properties (e.g., the number of feasible interactions) from those that drive

93   pairwise interactions, which is commonly the focus of trophic interaction models (Strydom et al.,

94   2021). This requires more knowledge of how well trait-matching models can be used to estimate

95   a range of food web properties.

96

97   Here, we first ask whether predictive trait-based models from one region of the world can

98   reliably predict the predator-prey interactions of other regions. We estimate transferability (how

99   well a model fit in one region predicts the other) between regions (Europe, the Pyrenees,

100   Northern Québec and Labrador, and the Serengeti) with trait-based Bayesian hierarchical

101   models. We expect better transferability between food webs that are more similar. To test this, we

102   determine how transferability changes with geographic, environmental, trait, and phylogenetic

103   distances. Second, we evaluate how well these models can be used to estimate a species' role in

104   the network and food web structure. Given previous findings and the fact that the models only

105   indirectly estimate these metrics, we expect that the models are better at predicting pairwise

106   interactions than estimating the role of a species in a network and food web properties. We

107   similarly expect a decline in performance when models are trained and tested on different

108   ecosystems.

109

110   **Methods**

111   *Food web data*

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

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

114   food web of tetrapods (Maiorano et al., 2020), the Pyrenees vertebrate food web (Lurgi et al.,

115   2012), the Northern Québec and Labrador food web (Berteaux et al., 2018), and the Serengeti

116   food web (de Visser et al., 2011). All four food webs were compiled from literature reviews and

117   completed with expert knowledge. The four food webs document the predator-prey interactions

118   between all known terrestrial vertebrates in their respective geographical region. Trophic

119   interaction is defined as a binary variable where 0 represents the absence and 1 the presence of a

120   predator-prey interaction between two species. Since all food webs document *potential*

121   interactions (i.e., the predator could feed on the prey species), and use expert knowledge to

122   define these trophic relations, we assume that they are less sensitive to incomplete sampling than

123   observation-based food webs (i.e., interactions and non-interactions are similarly uncertain).

124   Nodes in the original Serengeti food web represent trophic groups including one or more

125   vertebrate species. In this study, we assumed that species within a trophic group share the same

126   predator and prey species. Thus, we can expect more false positives (i.e., non-interactions

6

127   documented as interactions) in the Serengeti than in the other three food webs. Food webs are

128   fully described in Appendix S1.

129

130   The species composition of the four food webs is different (Table 1). There are no amphibians or

131   reptiles in Northern Québec and Labrador; the Pyrenees food web is dominated by birds (67%)

132   and mammals (23%), with very few reptiles (8%); the European food web has a comparable

133   number of reptiles (21%) and mammals (25%), and almost half (46%) of the Serengeti food web

134   are mammals. The Europe, Pyrenees, and Northern Québec and Labrador food webs all have

135   comparable mean trophic levels (between 1.24 and 1.3) and connectance (between 0.02 and

136   0.05) but the Serengeti differed (mean trophic level: 1.61; connectance: 0.12). Here, the first

137   trophic level (i.e., basal species) is defined as species not feeding on any other terrestrial

138   vertebrate. In Europe, the Pyrenees, and Northern Québec and Labrador most species are basal

139   species (e.g., insectivores, herbivores, piscivores), whereas many more species feed on terrestrial

140   vertebrates (non-basal species) in the Serengeti.

141

142   *Trait data*

143   We extracted traits from the database compiled by Etard et al. (2020). This dataset combines

144   species-level information from large freely available secondary trait databases (e.g., EltonTraits:

145   Wilman et al. (2014), AmphiBIO: Oliveira et al. (2017)). Overall, the database includes traits for

146   6 990 amphibian, 11 634 bird, 5 380 mammal, and 10 612 reptile species. We extracted the

147   available body mass (mean: 11 kg; range: 0.001–4 220 kg), longevity (mean: 5 885 days; range:

148   91–46 386 days), litter or clutch size (mean: 131 offspring; range: 1–20 000 offspring), habitat

149   breadth (number of habitats a species uses, using level 2 of the IUCN Habitat Classification

150   Scheme; mean: 10 habitats, range: 1-90 habitats), trophic level (3 levels: herbivore, omnivore,

151   carnivore), activity time (2 categories: nocturnal, non-nocturnal) and habitat use (12 categories:

152   forest, savanna, shrubland, grassland, wetland, rocky areas/cave/subterranean, desert, marine,

153   marine/intertidal or coastal/supratidal, artificial, introduced vegetation) for every species

154   considered in our study.

155

156   We standardized species names following the taxonomic backbone of the Global Biodiversity

157   Information Facility (GBIF) using the function *name_backbone* from the package *rgbif*

158   (Chamberlain et al., 2022) in the R statistical language (R Core Team, 2022). We excluded

159   species for which no taxonomic information or none of the traits were available. More than 80%

160   of traits were available across species of all food webs (Table 1; Appendix S2). For remaining

161   species, we imputed missing traits using the MissForest algorithm implemented in the *missForest*

162   R package (Stekhoven & Buehlmann, 2012) for amphibians, birds, mammals and reptiles

163   separately. MissForest uses random forests to iteratively predict missing data from the known

164   data. Each random forest uses a different trait as response variable and the remaining traits as

165   predictors.

166

167   *Phylogeny data*

168   We used published global phylogenies for birds (Jetz et al., 2012), amphibians (Jetz & Pyron,

169   2018), squamates (Tonini et al., 2016), turtles (Thomson et al., 2021), and mammals (Upham et

170   al., 2019). All five phylogenies were built from molecular data and delivered as a posterior

171   distribution of trees. We sampled 100 trees from the posterior of each phylogeny and calculated

172   the mean cophenetic distance from these samples between all species of the four food webs.

173   Following Letten & Cornwell (2015), we square root transformed cophenetic distances to better

174   relate to ecological processes such as trophic interactions.

175

176   *Predictive models*

177   We trained a Bayesian hierarchical generalized linear model on each of the four food webs

178   (Figure 1a) with trophic interactions following a Bernoulli distribution. Because Caron et al.

179   (2022) found that trait-interaction relationships vary between predator groups, we added varying

180   slope and intercept terms for the taxonomic order of predators. For each model, we randomly

181   drew 30% of the data for validation to keep the prevalence of trophic interaction in the validation

182   subset equal to the prevalence of the entire food web. We used all predator-prey interactions of

183   the remaining 70% of the data and an equal number of absences of interaction for calibration to

184   have a more optimal balance of presences and absences for calibration (i.e., random

185   undersampling).

186
$$L_{ij} \sim Bernoulli(p_{ij}),$$

187

188
$$logit(p_{ij}) = \alpha + \alpha_{predator[j]} + \sum_{k=1}^{13}\left(\beta_k \times T_k + \beta_{k,predator[j]} \times T_k\right),$$

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

190   probability of interaction, α is the fixed intercept and β_k the slope corresponding to the trait-

191   based predictor T_k in the linear model. Similarly, $\alpha_{predator[j]}$ is the random intercept and

192    $\beta_{k,predator[j]}$ the random slope corresponding to the trait-based predictor T_k for the order of

193   predator j.

194

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

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

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

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

199　activity time match is also a binary variable where a 1 means the predator and the prey share the

200　same activity time trait. Habitat match is the Jaccard similarity index between the habitat used by

201　the prey and the predator across the 12 habitat categories, which considers overlap in habitat and

202　specialization to shared habitats. Body mass match is the squared difference between the log-

203　transformed body mass of the prey and the predator because we expect predators to eat prey

204　within a given body mass interval (small enough to be handled, but large enough to be

205　profitable). We log-transformed body mass, longevity, and clutch size, and scaled each

206　continuous predictor (after transformation) by subtracting out the mean and dividing by two

207　times the standard deviation so coefficients of continuous predictors are comparable to unscaled

208　binary predictors (Gelman, 2008).

209

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

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

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

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

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

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

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

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

10

218 Model parameters were estimated with Hamiltonian Monte Carlo (Neal, 2011). We ran four

219 chains, each with 2000 warm-up iterations, followed by 2000 iterations for inference. We

220 diagnosed convergence and adequacy with trace rank plots, posterior predictive checks, and we

221 calculated the rank-normalized potential scale reduction factor on split chains for all runs

222 (Vehtari et al., 2021; Appendix S6). We conducted the analyses using Stan (Carpenter et al.,

223 2017) through the package *brms* in R (Bürkner, 2017).

224

225 *Predicting species interactions*

226 We used each model to predict the food web on which it was trained and that of the other regions

227 considered (Figure 1a). For each possible predator-prey pair, we extracted the mean of the

228 posterior as the probability of interaction, and the standard deviation of the posterior as the

229 uncertainty around the predicted probability of interaction. We compared the predicted

230 interaction probabilities to the validation subset of the same food web (within-food web

231 predictions) and compared the predicted interaction probabilities to entire empirical food webs

232 (between-food web predictions). We measured performance with the area under the receiver

233 operating characteristic curve (AUC; Hanley & McNeil, 1982) and the area under the precision-

234 recall-gain curve (AUPRG; Flach & Kull, 2015). AUC varies from 0 to 1 where 0.5 indicates

235 that the model failed to rank interactions higher than absences of interactions (i.e., random

236 predictions), and 1 indicates that the model systematically ranked interactions higher than non-

237 interactions (i.e., perfect predictions). AUPRG is independent of the true negative rate, making it

238 useful for highly imbalanced datasets, like food webs where there are many more absences than

239 presences of interaction to predict (Saito & Rehmsmeier, 2015). AUPRG takes a value of 0 for

240 random predictions and a value of 1 for perfect predictions.

241

242   We assessed the performance of models to predict each food web using three distance measures:

243   geographic distance, environmental dissimilarity, and phylogenetic relatedness. To do so, we

244   fitted hierarchical linear models with logit-transformed AUC as a function of distance measures,

245   with random intercepts for the food web predicted and used for calibration (Appendix S7). We

246   measured geographic distance as the great-circle distance between the polygon centroid

247   delimiting the spatial domain of each food web. We quantified environmental dissimilarity using

248   all 19 bioclimatic variables in WorldClim (Hijmans, 2021). We extracted the bioclimatic data for

249   all pixels (10' resolution) falling within the spatial domain of the food webs and used the mean of

250   each bioclimatic variable to calculate the bioclimatic centroid of each food web. We calculated

251   environmental distance as the Euclidean distance between the food web bioclimatic centroids.

252   We used the mean cophenetic distance to the nearest taxon of every species in the predicted food

253   web to measure phylogenetic relatedness. We averaged over all species in the predicted food web

254   the cophenetic distance to the phylogenetically closest species in the food web used for

255   calibration. This approach measures the amount of evolutionary history in the predicted food

256   web undocumented by the food web on which the model was trained.

257

258   We also analyzed predictive performance at the species level. For each combination of predicted

259   food web models (curves in Figure 1b), we measured how accurately the set of prey and

260   predators of each species was predicted also using the AUC and AUPRG. We fitted a hierarchical

261   linear model with species-specific performance as a function of how connected the focal species

262   is and how distinct the focal species is to the species pool used to train the predictive model

263   (Appendix S7). To do this, we used species normalized degree (number of interactions divided

264   by the maximum possible number of interactions), the functional mean pairwise distance

265   (Mouchet et al., 2010) and distance to nearest taxon (Tucker et al., 2017). We quantified

266   functional mean pairwise distance using the average Gower distance (Gower, 1971) between the

267   focal species and all species in the food web used for calibration. To calculate Gower distances,

268   we used all traits available in Etard (2020) through the function *funct.dist* from the R package

269   mFD (Magneville et al., 2022). We quantified distance to nearest taxon as the cophenetic

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

271   model calibration.

272

273   *Predicting species' role*s

274   Next, we were interested in how well species' roles were predicted. The role of a species is

275   determined by its position in the food web (Cirtwill et al., 2018), which we quantified using five

276   metrics related to the species' centrality within the food web (number of prey, number of

277   predators, betweenness, closeness, eigenvector centrality), two metrics related to their trophic

278   position (trophic levels and omnivory), two module-based metrics (within-module degree and

279   participation coefficient; Guimerà & Amaral, 2005), and the motif role of each species (Stouffer

280   et al., 2012). We detail each metric, their relation to species' role, and how they were calculated

281   in Appendix S4.

282

283   We compared each species' role metric in empirical food webs to the species' role in predicted

284   food webs. We measured each role metric on 100 draws of the posterior predictive distribution of

285   predicted food webs. We used the mean across posterior draws as the best point estimate for the

286   metric and the standard deviation as the measure of uncertainty. For each combination of model,

287   predicted food web, and species' role metric, we fitted a linear regression between the predicted

288   role and the empirical role and calculated the coefficient of determination (R^2). We also explored

289   prediction biases (e.g., systematic overestimation/underestimation) using the simple linear

290   models' coefficients. We expect an intercept of zero for unbiased predictions of species' role. An

291   intercept greater than zero would suggest an overall overestimation of the role metric, whereas

292   an intercept less than zero would suggest a systematic underestimation of the role metric. We

293   expect a slope of one for perfect predictions. A slope less than one would suggest that the role

294   values at the lower range are overpredicted, whereas the role values at the upper range are

295   underpredicted (i.e., more homogeneous values across species than in the empirical food web). A

296   slope greater than one would suggest the opposite (i.e., more heterogeneous values across species

297   than in the empirical food web).

298

299   *Predicting food web properties*

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

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

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

303   level, motif profile, food web diameter, number of clusters, and modularity (Borrelli, 2015;

304   Vermaat et al., 2009). As for species' role, we evaluated these properties on the empirical food

305   webs and compared them to the properties predicted using the mean of 100 draws of the

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

307   how they were calculated in Appendix S4.

308

309   *Boosted regression trees*

14

310   To make sure our esults are general and not dependent on the model framework chosen

311   (Bayesian hierarchical generalized linear models), we fitted boosted regression trees (BRTs) on

312   each food web and ran the same analyses (Appendix S5). BRTs are a machine learning algorithm

313   that allows non-linear relationships between predictors and the response variable (Friedman,

314   2001). To make results comparable, we used the exact same training/validation splits and the

315   same predictor variables to train and measure performance of BRTs and Bayesian hierarchical

316   generalized linear models.

317

318   **Results**

319   *Predicting pairwise interactions*

320   For all food webs, pairwise interactions were better predicted by the model trained on the same

321   food web (within-food web predictions) than by models trained on other food webs (between-

322   food web predictions; Table 2). For within-food web predictions, AUC ranged from 0.92 and

323   0.96 and AUPRG ranged from 0.93 and 0.96. Model performance was also good (AUC > 0.82;

324   AUPRG > 0.84) for transfer between the Europe, Pyrenees, and Northern Québec and Labrador

325   food webs, except for the model trained on the Pyrenees web when predicting the Europe web.

326   For this case, AUC was high (0.89) whereas AUPRG (0.63) was comparatively small, suggesting

327   that the model was much better at discriminating the absences than presences of interactions.

328   Models did not transfer as well from and to the Serengeti food web, but performance was still

329   good (AUC > 0.75; AUPRG > 0.73). The transferability of the Serengeti food web was expected

330   to be more challenging because nodes do not represent species (as is the case for the other food

331   webs), but trophic groups, as mentioned in the *Food web data* subsection. The area under the

332   precision-recall-gain curve, true positive rate, true negative rate, positive predictive value, and

15

333   negative predictive value were all positively correlated with AUC and showed the same overall

334   pattern (Appendix S7).

335

336   Model performance tended to decline for ecologically different food webs (Figure 2).

337   Specifically, performance tended to decrease with environmental (direct effect estimate: -0.30,

338   95%CrI = [-0.90, 0.32]) and phylogenetic distance (direct effect estimate: -0.31, 95%CrI = [-

339   0.69, 0.06]). Performance also tended to decrease with geographic distance (total effect estimate:

340   -0.57, 95%CrI = [-0.78, -0.36]), but this effect largely disappeared after controlling for

341   phylogenetic and environmental distances (direct effect estimate: -0.26, 95%CrI = [-0.87, 0.35]).

342   Therefore, transferability likely decreases with geographic distance mainly because the

343   environment and phylogeny diverged between the predicted food webs and those used to train

344   the model.

345

346   We also found that species-specific model performance tended to decline when a focal species

347   was ecologically different than the species pool used to train models (Figure 3). As expected,

348   species with phylogenetically close relatives in the species pool used for calibration were, on

349   average, better predicted than distant relatives (Figure 3a). Species-specific performance slightly

350   decreased at low to intermediate phylogenetic distances and then dropped significantly at large

351   distances. Models trained and predicted across classes (e.g., mammals to amphibians) had the

352   lowest performance, as expected. This situation only occurs when the Northern Québec and

353   Labrador model predicts the other three food webs as there are no amphibians or reptiles in

354   Northern Québec and Labrador. Surprisingly, predictive performance remained qualitatively

355   unchanged by trait distance (Figure 3b). We also found that interactions of specialist (i.e., species

16

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

357   average, better predicted than interactions of species of intermediate specialization (Figure 3c).

358

359   *Predicting species' role*

360   Species' roles were slightly better predicted by within-food web predictions than by between-

361   food web predictions (Figure 4). Interestingly, some measures of centrality (betweenness and

362   closeness) were not well predicted, whereas others (number of prey and predators, eigenvector

363   centrality) were relatively well predicted.

364

365   We also found important biases in the predictions of species' roles when we fitted linear

366   regressions between species' roles in predicted food webs to their roles in the empirical food

367   webs. The number of prey, predators, trophic level, omnivory, and the frequency of motif

368   positions tended to be overestimated across species (intercept greater than 0). For other measures

369   such as eigenvector centrality, betweenness, closeness, and module-based roles, species had

370   more similar values in the predicted than in the empirical food webs (Appendix S8, slopes less

371   than 1).

372

373   *Predicting food web properties*

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

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

376   overpredicted, whereas modularity was slightly underpredicted. The frequency of the omnivory

377   motif was particularly overpredicted, with the motif being often 50 times more prevalent in the

378   predicted food webs than in the observed food webs. The mean and variance of relative errors

17

379 were greater for between- compared to within-food web predictions. In general, predicted food

380 webs were more connected, less modular, with fewer basal species, and increased, but less

381 distinct (more omnivory), trophic levels.

382

383 *Boosted regression trees*

384 We found the same general results with BRTs (Appendix S5). Overall, BRTs performed similarly

385 to Bayesian linear model to predict interactions within and across food webs (AUC between 0.69

386 and 0.98; AUPRG between 0.73 and 0.96). Species' role and food web properties were also not

387 well predicted by BRTs, and we found similar biases in predictions (Appendix S5).

388

389 **Discussion**

390 Predictive models of trophic interactions have recently become central in filling the substantial

391 knowledge gaps of how food webs vary across space and time. In the most comprehensive test so

392 far, we evaluate how well these models can transfer to other ecosystems (i.e., can make

393 predictions for an ecosystem using only data from another). Overall, we found that: (1) our

394 models were able to predict pairwise interactions across ecosystems reasonably well (AUC >

395 0.82), (2) pairwise interactions were well predicted (AUC > 0.80) for most novel species unless

396 no species of the same class was present in the food web used for training, and (3) as expected,

397 models were not as good at predicting food web properties, over-estimating some metrics (e.g.

398 connectance, trophic level, omnivory) and under-estimating others (e.g. modularity), especially

399 when extrapolating to new regions. Results suggest both optimism for the use of these models

400 when data for some regions are lacking or future communities with no current analog, and the

18

401 need for novel approaches that combine pairwise interactions with higher-order food web

402 metrics.

403

404 Theory describes how the variation in food webs arises from two key processes: trait-interaction

405 rules (e.g., body mass relationships between predators and their prey) and the distribution of

406 traits in different systems (Gravel et al., 2016). Our ability to predict food web interactions

407 across contrasting environments suggests that spatial food web variation is mainly driven by

408 changes in the distribution of functional traits, and less so by the variation of trait-interaction

409 relationships. These results are in line with previous research finding generalities made on trait-

410 matching relationships across European bioregions (Caron et al., 2022), predator-prey body-size

411 ratios within habitat, predator, and prey types (Brose et al., 2006), and the trait-interaction

412 relationships in soil invertebrates across three forest areas in Germany (Laigle et al., 2018). The

413 generalities we found in trait-matching relationships within major taxonomic groups (order and

414 class) also add to previous research indicating evolutionary conservation of species interactions

415 (Gómez et al., 2010) and role (Stouffer et al., 2012). These generalities in the trait-interaction

416 relationships across space and within taxonomic groups demonstrate the potential for using data

417 from well-studied areas to predict interactions in areas we know very little about or forecast (and

418 hindcast) food webs given new trait distributions.

419

420 As expected, pairwise trophic interaction models predict interactions, not necessarily food web

421 properties, and here this is shown for a much wider set of metrics than previous comparisons

422 (e.g., Caron et al., 2022). The explanation could be biological, methodological, or both. Food

423 webs are more than a collection of independent pairwise interactions (Strydom et al., 2021) and

19

424 could be constrained by ecological processes such as dispersal limitation or even area (Galiana et

425 al., 2018), which are not included in our models. How these constraints lead to the spatial and

426 temporal variation of ecological networks is gaining interest recently (Baiser et al., 2019; Gravel

427 et al., 2019). While a process-based understanding of ecological constraints is beyond the scope

428 of this study, our findings can offer some hints as to what might be causing the differences

429 between predicted and observed network properties.

430

431 In particular, our study adds to the previous findings that connectance is over-estimated with

432 these models, often with the number of interactions two-fold greater than observed. Caron et al.

433 (2022) previously found similar results for the European web and showed how the over-

434 estimation increased with species richness. Our study additionally shows that the over-estimation

435 is even more exaggerated with extrapolation (predicting to novel conditions), in which the

436 models are even less likely to contain the relevant ecological constraints. For example, if there is

437 a different structure of specialists and generalists in the training and testing ecosystem, then we

438 would expect differences in network properties. The Serengeti contained more generalist and less

439 basal species than others, so models trained there are more likely to overestimate connectance in

440 other regions. Our results also show that prey and predators of intermediate specialization were

441 less well-predicted, which suggests that their trophic niches are harder to define by functional

442 traits and would ask for more attention when sampling interactions. Finally, our results show that

443 predicted food web have more, but less distinct (more omnivory), trophic levels. Again, adding

444 better species trophic level information, or giving special attention to omnivorous interactions

445 during sampling, would help refine predicted food webs.

446

447   The overall overestimation of the number of prey and predators (Appendix S8), probably

448   propagated through the food webs, explaining why the centrality of species was more evenly

449   distributed, and why the predicted food webs were more connected, less modular, and with

450   higher trophic levels. Statistically speaking, even if most interactions and absences of

451   interactions are well predicted (high true positive and negative rates), there are often an order of

452   magnitude more absences of interactions to predict than presences in real food webs (low

453   connectance). Another explanation recently proposed is constraints on food webs due to the area

454   of the food web (Galiana et al., 2018). This could influence our findings as we compared food

455   webs with very different areas (ranging from 36 thousand km² for Serengeti to 11 million km² for

456   Europe). However, in this case, area does not seem to be a major constraint given within-food

457   web predictions were also biased. Additional research is needed to understand how realized food

458   webs differ from feasible trophic interactions.

459

460   There are also many methodological possibilities for correcting biases in higher-level properties

461   that arise from aggregating sets of independent models. This problem has been addressed

462   extensively in the field of species distribution modelling, where individual models predict

463   species well, but not necessarily species richness in communities (Zurell et al., 2020). Methods

464   have been developed to harness biases in higher-level properties to correct distribution

465   predictions. For example, Leung et al. (2019) combined predicted species distributions and

466   expected species richness to quantify species and spatial biases. They correlated biases to species

467   traits and environmental co-variates to improve predicted species distribution. Similar methods

468   integrating predictions of interactions and networks have the potential to provide better food web

469   predictions (Isaac et al., 2020).

470

471 Until then, these food webs remain very useful first-order approximations of food webs when

472 there is little to no data in these ecosystems. Most food webs, even expert-based, are missing

473 some interactions (e.g., cryptic and opportunistic interactions). And one could argue that over-

474 estimating connections is better than under-estimating given these are candidate interactions,

475 which can then be refined through geographic subsets, expert opinion or additional data.

476

477 Future studies could address other limitations of our study, such as the reliance on terrestrial

478 vertebrates. It would be interesting to compare whether models are better where trait-matching

479 relationships are weaker or stronger, such as in marine food webs. The exclusion of non-

480 vertebrates (e.g., plants, invertebrates, parasites) meant the first trophic levels were vertebrates,

481 not primary producers, but the extension of trait-matching models to also include invertebrates

482 can be achieved with a coarser resolution (Li et al., 2023) or with additional traits (Laigle et al.,

483 2018). Second, the food webs we used were binary food webs. Trait-matching models predict the

484 probabilities that a species could eat another species given they are encountering each other.

485 Additional data, such as co-occurrence and abundance data, are needed to make predictions of

486 realized and quantitative interactions. Finally, due to the scarcity of food web data, we only had

487 four food webs to work with. This means we only had four sets of within-food web predictions

488 and 12 sets of between-food web predictions. This explains the large uncertainty for some of our

489 results (e.g., Figure 2).

490

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

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

493   producing initial expectations even in contrasting ecosystems and for future communities. This,

494   and other recent research (Brose et al., 2006; Caron et al., 2022; Laigle et al., 2018), suggests

495   there are fundamental trait-based constraints on trophic interactions that are generalizable to

496   some extent. Food web variation thus results from species traits rather than the 'match' between

497   a predator and its prey, which has interesting ties to the broader question of how traits vary

498   between regions and along gradients (Gravel et al., 2016). Future research could better link

499   subfields within trait-based ecology for a comprehensive understanding of how species traits and

500   network structure relate to their environment and enable trait-matching approach to inform

501   restoration and re-wilding initiatives on the choice of appropriate species to re-establish former

502   links and potentially ecosystem functions related to these interactions.

503

504 **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

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M.

(2016). A common framework for identifying linkage rules across different types of

interactions. *Functional Ecology*, *30*(12), 1894–1903. https://doi.org/10.1111/1365-

2435.12666

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/33e8075e9970de0cfea955afd4644bb2-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

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 Rˆ 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

Zurell, D., Zimmermann, N. E., Gross, H., Baltensweiler, A., Sattler, T., & Wüest, R. O. (2020).

Testing species assemblage predictions from stacked and joint species distribution

models. *Journal of Biogeography*, *47*(1), 101–113. https://doi.org/10.1111/jbi.13608

505

506 **Data Accessibility Statement**

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

508 are archived on the Open Science Framework repository OSF | Interaction model Transferability.

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

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

	Food web			
Model	Europe	Pyrenees	North Québec and Labrador	Serengeti
AUC				
Europe	**0.96**	0.89	0.9	0.8
Pyrenees	0.87	**0.95**	0.86	0.76
North Québec And Labrador	0.81	0.91	**0.95**	0.76
Serengeti	0.84	0.87	0.78	**0.95**
AUPRG				
Europe	**0.97**	0.66	0.86	0.84
Pyrenees	0.9	**0.98**	0.95	0.84
North Québec And Labrador	0.88	0.91	**0.96**	0.8
Serengeti	0.84	0.86	0.83	**0.97**

511
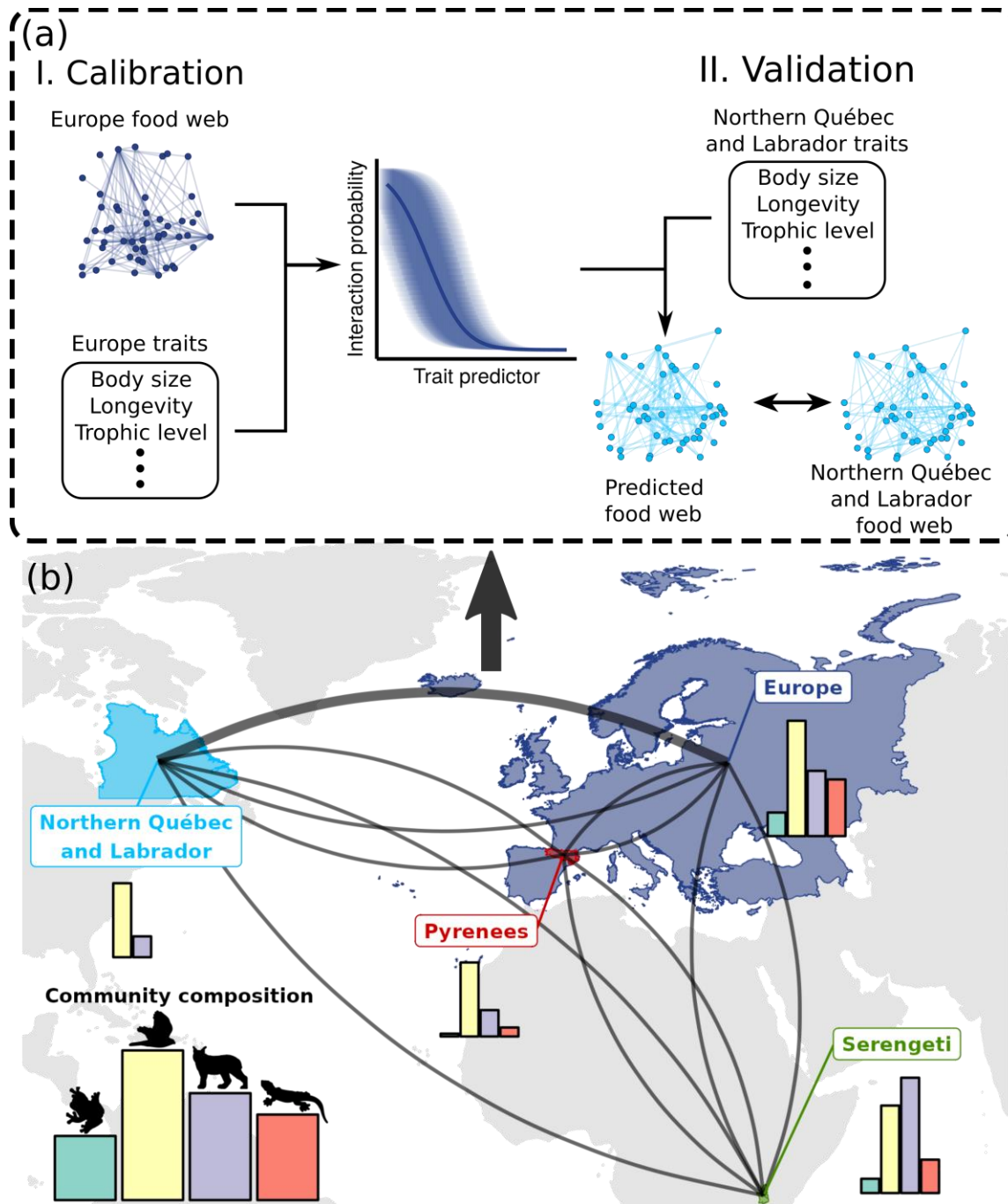
Figure 1: Trophic interactions model transferability analysis workflow. *Panel (a) shows an example workflow for between-food web predictions. We trained a trophic interaction model using each food web considered in this study (panel a.I). We measured the performance of the four models on a validation subset for within-food web predictions, and the entire food webs for between-food web predictions (panel a.II). Panel (b) maps the spatial domain of each food web. The curves present the pairs of food web model used to make between-food web predictions. Within-food web predictions are not shown in the figure. Bar plots illustrate the proportion of amphibians (green), birds (yellow), mammals (purple), and reptiles (red) in each food web.*

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

Figure 3: Predicting species interactions. *Model predictive performance for the species interactions in alternative food webs. Each point shows the model performance in predicting the prey and predators of a single species using area under the receiver operating curve (AUC) as a metric. For each panel, the thick line is the median effect while the enveloppe is the 95% credible interval on predictive performance built using the posterior predictive distribution of (a) distance to the nearest taxon, (b) mean functional pairwise distance, and (c) normalized degree on predictive performance.*
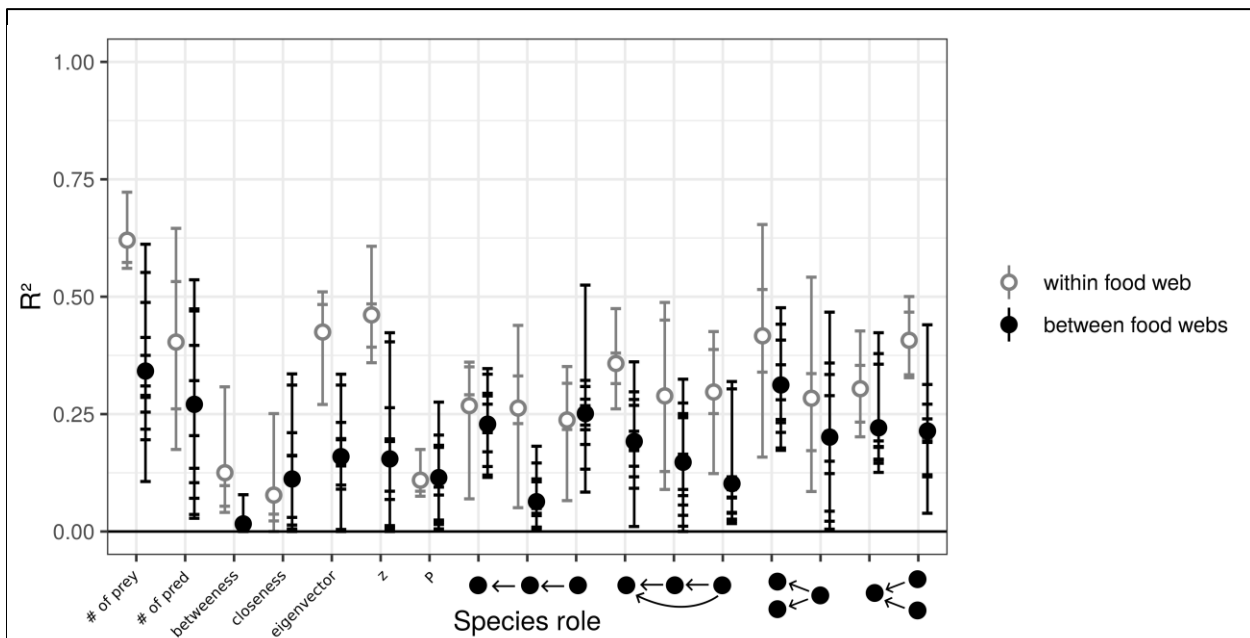
514

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 (R²). From left to right, the figure shows the number of prey, number of predators, betweenness, closeness, eigenvector centrality, within-module degree (z), participation coefficient (P), times the species is at a specific position in the linear chain (predator – consumer - resource), intraguild predation (omnivore – consumer - resource), direct competition (2 consumers – 1 resource), and apparent competition motifs (1 consumer – 2 resources). The short horizontal lines highlight the R² for each role, model, and food web predicted combination. Grey open dots are the mean R² for within-food web predictions. Full black dots are the mean R² for between-food web predictions.*

515

Figure 5: Prediction error of global food web properties. *Relative error is the difference between the predicted and the 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 (1 consumer – 2 resources) motifs. 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. We divided the figure in two panels because the food web properties in panels (a) and (b) had widely different relative errors.*

516