Reducing the Eltonian shortfall with trophic interaction models

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28 **Abstract**

29 While species interactions are fundamental for linking biodiversity to ecosystem functioning and for

30 conservation, large-scale empirical data are lacking for most species and ecosystems. Accumulating

31 evidence suggests that trophic interactions are predictable from available functional trait information,

32 but we have yet to understand how well we can predict interactions across large spatial scales and food

33 webs. Here, we built a model predicting predator-prey interactions based on functional traits for

34 European vertebrates. We found that even models calibrated with very few known interactions (100 out

35 of 71k) estimated the entire food web reasonably well. However, predators were easier to predict than

36 prey, with prey in some clades being particularly difficult to predict (e.g., fowls and storks). Local food

37 web connectance was also consistently over-estimated. Our results demonstrate the potential for filling

38 gaps in sparse food webs, an important step towards a better description of biodiversity with strong

39 implications for conservation planning.

Introduction

Food webs are collections of trophic interactions describing both the composition and structure of communities. Trophic interactions influence ecosystems at all levels including how energy flows through ecosystems (Thompson *et al.* 2012), how populations respond to perturbations through time (Zhao *et al.* 2019), and how species are distributed in space (Wisz *et al.* 2013). Trophic interactions are disrupted by human pressures, with interactions being lost at a higher rate than species, which lead to simplified food webs that have fewer trophic levels, are more homogeneous and less redundant (Laliberté & Tylianakis 2010; Estes et al. 2011; Valiente-Banuet et al. 2015). Therefore, knowing the structure of a food web is critical to maintain ecosystem functions (Harvey *et al.* 2017) and anticipate species extinctions (McDonald-Madden *et al.* 2016). Despite these key roles and threats on food webs, empirical data on trophic interactions remain particularly limited.

The Eltonian shortfall – "*the lack of knowledge about interactions among species or among groups of species*" – is perhaps the biggest of all biodiversity shortfalls (Hortal *et al.* 2015). Available data on food webs are mostly restricted to the United States and Europe similar to other types of species interaction networks (Hortal *et al.* 2015; Cameron *et al.* 2019; Poisot *et al.* 2021). Compounding the problem even further, the sampling effort to detect interactions far exceeds the effort needed to detect species (Chacoff *et al.* 2012; Jordano 2016), meaning that rare interactions are often missed while those of dominant species are overestimated. So, even when available, food web datasets are often incomplete and biased. It is possible to fill gaps in empirical food webs with expert knowledge and literature review (e.g., Maiorano et al., 2020; Piechnik et al., 2008). While this solution is promising, it remains limited to well-studied systems, prone to biases, time-consuming and expensive. Ultimately, these gaps and biases in food web datasets limit the scale of food web research and are major hurdles

63   toward the needed shift in focus from species to interaction networks in conservation (Harvey *et al.*

64   2017; Pollock *et al.* 2020).

65

66   Despite the size of the problem, there is reason to be optimistic about the potential for predicting

67   species interactions to fill gaps in food web databases. In some cases, trophic interactions can be

68   reasonably well predicted if they conform to a predictable set of phylogenetic and functional traits

69   (Morales-Castilla *et al.* 2015). Niche theory predicts that two species interact if the foraging traits of

70   the predator match the vulnerability traits of the prey (Williams & Martinez 2000; Gravel *et al.* 2016).

71   This trait-matching framework serves as the basis for most studies aiming to predict interactions (e.g.,

72   Bartomeus et al., 2016; Gravel et al., 2013; Pichler et al., 2020), which have shown promising results.

73   Notably, Eklöf et al., (2013) found that 3-5 traits suffice to predict most trophic interactions, whereas

74   Gravel et al., (2013) showed that predictions of trophic interactions in marine ecosystems are robust to

75   sampling effort. These findings suggest that we can potentially predict missing trophic interactions

76   even when data are sparse.

77

78   Yet, there has been no large-scale, multi-clade test of predictive models of species interactions. Most

79   studies have used trait-matching models in systems where the relationships between the traits of

80   predators and their prey are expected to be strong, such as marine food webs (e.g., Albouy et al., 2019;

81   Gravel et al., 2013; Laigle et al., 2018). Other studies built more complex models which outperform

82   simpler models (e.g., Rohr et al., 2016). Although these more complex models are often more realistic,

83   they have many more parameters and are more sensitive to sampling biases, thus relying on large

84   amounts of data, which are rarely available. Therefore, only models based on relatively simple trait-

85   matching relationships are now possible for a wide range of taxa that have available trait data, but are

86 they realistic enough to make good predictions across a diverse set of taxa and ecosystems? We need a

87 better understanding of the amount data needed to make reliable predictions and how general the

88 matching rules are across clades and space.

89

90 Here, we build a model to predict trophic interactions based on functional traits that are widely

91 available. We designed our model to be useful even when data are sparse as it is a Bayesian linear

92 model relating trophic interaction (and non-interactions) to a small number of predictor variables

93 describing the foraging ability of the predator, the vulnerability of the prey, and the trait-match of

94 interacting species. We test our model using the recently assembled food web of all terrestrial

95 vertebrates in Europe (Maiorano *et al.* 2020) and use the model to determine: (1) how much data are

96 needed to accurately predict the entire European food web, (2) which traits make the best predictions,

97 (3) how input data (empirical versus multi-sourced data) influence predictions, (4) which taxa are

98 easier or harder to make predictions for, and (5) how well the properties of local food webs can be

99 predicted across space.

100

101 **Materials and methods**

102 *Study area, species, and functional traits*

103 Our study focuses on trophic interactions among all terrestrial vertebrates of Europe: mammals,

104 breeding birds, reptiles, and amphibians. For each species, we extracted five functional traits from

105 Thuiller et al. (2015): diet (17 binary variables), nesting habitat (10 binary variables), activity time (4

106 binary variables), foraging behavior (4 binary variables), and body mass (continuous). Because body

107 mass was missing for many amphibians - 52% missing for frogs (*Anura*) and 46% for salamanders

108 (*Caudata*) - we imputed missing body mass from available body length information for these two

6

111 groups separately. These imputations were justified by the strong relationship between body mass and

112 length in our study (r^2 = 0.75 and 0.84 for frogs and salamanders respectively; Appendix S1), and

113 others (Deichmann *et al.* 2008). In all, we gathered these five functional traits for 1055 species: 101

114 amphibians, 507 birds, 267 mammals, and 180 reptiles.

115

116 Using diet, nesting habitat, activity time, foraging behavior, and body mass, we calculated ten predictor

117 variables for each species pair (Table 1). These predictors of predator-prey interactions can be

118 categorized into three types: foraging traits, vulnerability traits, and matching traits (Gravel *et al.* 2016;

119 Rohr *et al.* 2016). Foraging traits (body mass of the predator and its foraging behavior) influence the

120 number of prey of a given predator, whereas vulnerability traits (body mass of the prey) influence the

121 number of predators of a given prey. Matching traits influence the feasibility of the interaction

122 (difference in body mass and diet match) or the encounter rate of species (activity time and habitat

123 match).

124

125 *Interaction data*

126 We extracted interaction data from the trophic metaweb of European terrestrial vertebrates (referred

127 later as the Metaweb; Maiorano et al., 2020). A metaweb documents all potential interactions between

128 all species at the regional scale (Dunne 2006). The Metaweb was built from multiple sources and

129 contains all potential trophic interactions and non-interactions between all terrestrial vertebrates of

130 Europe. The interactions were compiled by Maiorano et al. (2020) from guide books, published papers,

131 and completed by expert opinion. We extracted the interactions and non-interactions between all of the

132 1 055 species for which we had functional traits. This represents 71 417 potential interactions and 1

133 041 608 non-interactions.

134

135 Because the Metaweb documents *potential* trophic interactions, we also used a database of empirical

136 observations of species interactions. We extracted all interactions reported in the Global Biotic

137 Interactions (GloBI) platform (Poelen *et al.* 2014). The Metaweb and GloBI are very different in terms

138 of data coverage. While the Metaweb documents only trophic interactions in Europe, GloBI aggregates

139 trophic (and non-trophic) interactions from anywhere in the world. The absences of interactions in the

140 Metaweb can be interpreted as true absences (i.e., low false negative rate), whereas absences of

141 interactions in GloBI cannot (i.e., high false negative rate). Conversely, the presences of interactions in

142 the Metaweb are more uncertain (i.e., higher false positive rate) than in GloBI. We used the package

143 rglobi of the R software to extract all trophic interactions between any of the focal 1 055 species. In all,

144 we extracted 291 trophic interactions from GloBI involving 194 different species (75 predator species

145 and 146 prey species).

146

147 *Predictive model*

148 We modelled the occurrence of a food web interaction for each pair of species as a function of their

149 traits (see Table 1 for predictors) using Bayesian generalized linear models (GLM). We assumed that

150 the occurrence of interaction between species i and j, L_{ij}, is Bernouilli distributed. The corresponding

151 probability of interaction was modelled as the inverse *logit* of a linear function with a common

152 intercept, α, and a set of linear coefficients β associated with predictors T_{ij}:

$$logit(P(L_{ij} = 1) = \alpha + \sum_{k=1}^{n} \beta_k T_{ijk}$$

153   (Eq. 1)

154 We measured the predictive performance of each model on independent validation datasets using the

155 area under the receiver operating characteristic curve (AUC). AUC varies from 0.5 to 1 where 0.5

156   indicates that the model failed to rank interactions higher than non-interactions (i.e., random

157   prediction), and 1 indicates that the model systematically ranked interactions higher than non-

158   interactions (i.e., perfect prediction).

159

160   Before fitting the GLMs, we scaled each continuous predictor by subtracting it by its mean and

161   dividing by two times its standard deviation, so that the coefficients of the scaled continuous predictors

162   are directly comparable to coefficients of unscaled binary predictors (Gelman 2008). We used Bayesian

163   inference and Markov chain Monte Carlo algorithm to estimate the model parameters (α and β_k). We

164   used weakly informative priors for the parameters:

$$\alpha \sim Normal(mean = 0, sd = 10)$$ (Eq. 2)

$$\beta_k \sim Normal(mean = 0, sd = 1)$$ (Eq. 3)

167   where *sd* is the standard deviation of the prior distribution. We ran 3 chains, each with 1000 warm-up

168   iterations, followed by 5 000 iterations for inference. We diagnosed convergence visually of a few test

169   runs, and calculated the potential scale reduction factor, $\hat{R}$, for all runs (Gelman & Rubin, 1992;

170   Appendix S2). We conducted the Bayesian analyses using the package greta in R (Golding 2019).

171

172   *Predicting trophic interactions with models trained on the Metaweb*

173   We used the model described above to make predictions for predator-prey pairs in the Metaweb, and

174   determine the information needed to make reliable predictions. More specifically, we determined (1)

175   which of the predictors (Table 1) made the most important contribution, and (2) the number of trophic

176   interactions needed to calibrate models that could recover most of the Metaweb. First, we used the

177   estimated mean coefficient value to assess variable importance, which we could do as we scaled

178   predictor variables (Gelman 2008). Second, we trained the model described above with progressively

179   more trophic interactions from the Metaweb going from 2 to 5000 pairwise interactions, with 10 000

180   non-interactions. We then measured how well these models predicted the Metaweb by comparing the

181   predictions generated by the model to an independent validation dataset (Metaweb validation dataset).

182   We created the Metaweb validation dataset by sampling 1% of the entire Metaweb.

183

184   We also measured how well each of the models described above predict the empirical interactions in

185   GloBi. To do so, we compared predictions generated by each model to the 291 trophic interactions we

186   extracted from GloBi. Because GloBI only includes interactions, we added 3 845 non-interactions

187   extracted from the Metaweb to the GloBI validation dataset. This number of non-interactions makes the

188   prevalence of interactions in the GloBI validation dataset comparable to the prevalence in the Metaweb

189   validation dataset.

190

191   *Predicting trophic interactions with models trained on GloBI*

192   We were also interested in how well we could predict the entire European Metaweb without using any

193   information from the Metaweb itself (i.e., species traits and interactions from GloBI). Similar to the

194   models described in the previous paragraph, we fitted predictive models using a progressively

195   increasing number of trophic interactions extracted from GloBI: from 2 to 291 trophic interactions

196   combined with 10 000 pseudo-absences. We randomly drew pseudo-absences among the pairs of

197   species for which no interaction was documented in GloBI. We used pseudo-absences to avoid using

198   any information from the European Metaweb. We measured performance of these models with respect

199   to the Metaweb validation dataset, and to the GloBI validation dataset.

200

201   *Predictions of interactions for different taxa*

202   In addition to the overall predictive performance of the models, we wanted to identify whether

203   interactions between certain species, certain clades and different types of species (e.g., specialists

204   versus generalists) were more or less predictable with our model. To do this, we first trained a model

205   (*master* model) with 10% of the European Metaweb (sufficient based on the results of previous

206   sections) and predicted all trophic interactions and non-interactions in the entire food web. We

207   measured the performance of the model to predict all interactions (i.e., the prey and predators) of every

208   species. We further compared these performances for individual species to the position of that species

209   in the food web to ask whether interactions of specialists (i.e., species interacting with few species)

210   were harder to predict than interactions of generalists (i.e., species interacting with many species).

211   Specifically, we modelled the performance for each species (the AUC value) as a function of the

212   species generality using generalized linear mixed models (GLMMs) with random intercepts and slopes

213   for the species group (i.e., order), and a logit-link function. All species were included in each model,

214   but different representations of generality (the number of total interactions, the number of prey and of

215   predators for each species) were included as fixed effects in three separate models. The fixed effects

216   were log-transformed and scaled before running the GLMMs. We conducted the GLMMs using the

217   package lme4 in R.

218

219   Finally, we performed a miscalibration analysis to investigate the ecological differences making the

220   trophic interactions of some groups less predictable than others. We first trained group-specific models

221   for each order of predators. For example, considering frogs (*Anura*), we trained a predictive model only

222   using interactions (and non-interactions) involving a frog species as predator. For many order, most

223   species shared very similar foraging behaviors. This caused some group-specific models not to

224 converge or to over-fit the data. For this reason, we excluded foraging behaviors from the predictors in

225 the miscalibration analysis. We compared the group-specific models to a *general* model trained on the

226 entire Metaweb. Specifically, we calculated the differences between the parameters inferred for the

227 *general* model to the parameters inferred for the group-specific models to measure the miscalibration of

228 the *general* model for each group. By doing so, we identified the miscalibrated coefficients causing the

229 general model to incorrectly predict the prey of specific predator groups. Conversely to the *master*

230 model, the *general* model did not include foraging behaviors as predictors to make it comparable to

231 group-specific models.

232

233 *Predictions of interactions across space*

234 In addition to predicting interactions for the entire set of species, it is also possible to predict trophic

235 interactions for any local or regional food web with a species list or occurrence data. This a separate but

236 important test of these models because it investigates whether predictive models are useful to recover

237 potential food webs at a finer scale, and whether environmental gradients might influence the

238 ecological constraints driving local and regional trophic interactions. To do this, we used the *master*

239 model described above to make predictions for: 1- regional food webs based on species occurrences in

240 bioregions and 2- 'local' food webs based on distribution data for each 5km pixel across Europe. In

241 both cases, we used the distribution data from Maiorano et al. (2013). Here, species distributions are

242 determined by the presence of primary habitat within the known species distribution range, and

243 validated by field data. Species habitat relationships are based on expert knowledge, and species ranges

244 are extracted from atlases. The original data are 300-m cell range maps with three levels: unsuitable,

245 secondary and primary habitat. We upscaled the distributions data to a 5km pixel equal-area grid, and

246 considered a species present in a cell if it had at least one occurrence of primary habitat.

247

We created bioregional food webs by extracting the species from the European metaweb for which the

range intersected in at least 1 % of the European bioregions (see O'Connor et al., 2020). Using these

bioregional food webs, we trained models for each bioregion. To investigate the transferability of

predictive models across bioregions, we compared the parameters of the models trained in each

bioregion, and how well they could predict the food webs of other bioregions.

253

In addition to bioregional food webs, we created 'local' food webs for each 5km pixel across Europe.

We pruned the European metaweb in every pixel using the species present in that pixel. We compared

the pruned local webs to the predicted local webs given the *master* model described earlier to look at

how the predictability of food webs varies across space.

258

Results

How much data are needed to accurately predict the entire European food web?

Most pairwise interactions in the Metaweb were predicted reasonably well by models trained on few

interactions. Predictive performance increased when more interactions were used to train the model,

but performance stabilized around AUC=0.92 at 100 training interactions (0.14% of the total number

of interactions in the Metaweb; Fig 1a). Even with as low as 10 interactions (0.014% of all interactions

in the Metaweb; Fig 1a), the AUC was over 0.90. Training the model on a lot more presences and

absences did not improve substantially model performance. The *master* model, which we trained on

10% of the entire Metaweb to predict the interactions of every species, resulted in an AUC of 0.92, well

above the 0.5 expected from a null model.

269

270 *Which traits best predict interactions?*

271 All of the traits used as predictor variables in the models were important for predicting interactions: all

272 corresponding linear coefficients were significantly different from 0 (i.e., 95% credible interval did not

273 include 0). The most important predictors were the match between the diet of the predator and the type

274 of prey (median = 2.29, 95%CI = [2.27, 2.32]), the body mass of the predator (median = 2.08, 95%CI =

275 [2.04, 2.12]), the body mass of the prey (median = -2.00, 95%CI = [-2.03, -1.96]), and the match

276 between the body mass of the predator and the body mass of the prey (median = -1.75, 95%CI = [-1.79,

277 -1.70]). All parameter estimates with their 95% credible interval are available in Appendix S4.

278

279 *How input data (empirical versus multi-sourced data) influences predictions?*

280 We found that results from models trained on the European Metaweb were consistent with models

281 trained on interactions from GloBI. Models fitted using all GloBI interactions (291 interactions)

282 predicted the metaweb well (AUC=0.91; Fig 1a). Also, all models performed similarly in predicting the

283 realized interactions from GloBI compared to the potential interactions of the European Metaweb (Fig

284 1b).

285

286 *Which taxa are easier or harder to make predictions for?*

287 Overall, the *master* model performed well for all groups (AUC > 0.75 for all groups; Fig 2). The

288 variation between groups was mostly due to variation in the ability of the model to predict prey (Fig 2).

289 For example, prey of carnivorans (*Carnivora*), fowls (*Galliformes* and *Anseriformes*), pelicans

290 (*Pelicaniformes*), storks (*Ciconiformes*), and birds of prey (*Falconiformes, Charadriformes,* and

291 *Strigiformes*) were harder to predict on average (Fig 2). In contrast, predicting predators was similarly

292 easy across all prey groups (AUC > 0.9). One exception to this pattern was amphibians (both *Caudata*

293   and *Anura*). Predictive models performed better than average when amphibians were the predator, but

294   worse when amphibians were the prey.

295

296   Interactions of specialists tended to be more predictable than interactions of generalists (Fig 3). After

297   controlling for the group-level variation, the number of interactions explained 25% (marginal R^2_{GLMM})

298   of the variation in the logit-AUC (fixed effect estimate = -0.48; 95%CI = [-0.63, -0.32]). In general, it

299   is easier to predict species predators than its prey (Fig 3). Prey of generalist predators tended to be

300   harder to predict (fixed effect estimate = -0.15), although not significantly (95%CI = [-0.31, 0.04]).

301   Conversely, predators of generalist prey tended to be easier to predict (fixed effect estimate = 0.10), but

302   again not significantly (95%CI = [-0.08, 0.27]).

303

304   For most groups in which potential prey were difficult to predict, the group-specific model performed

305   much better, with the AUC increasing by 0.1 or more (Appendix S5). Our models highlight how some

306   bird groups (e.g., *Galliformes, Anseriformes, Pelicaniformes*) tend to feed on prey active at different

307   times during the day and nest in different habitats than the focal predator. This contrasts with the

308   *general* model, for which species are more likely to interact when they share similar habitat and

309   activity time. It also contrasts with woodpeckers (*Piciformes*). For this group, the matches of activity

310   times and nesting habitats of the prey and the predator are especially important. For other groups (e.g.,

311   *Rodentia, Eulipotyphla, Strigiformes, Passeriformes*) the relation between the body mass of the

312   predator and the prey is more important to explain interactions than average. We also found that, for

313   carnivorans (*Carnivora*), the predictive performance of the group-specific model remained low (AUC

314   = 0.63). The coefficients of the different predictors were mostly lower than the *general* model (i.e.,

315 closer to 0), suggesting that the interactions of carnivorans are difficult to predict from our set of traits.

316 The complete results of the miscalibration analysis are available in the Appendix S5.

317

318 *How well the properties of local food webs can be predicted across space?*

319 Overall, local food webs with more trophic interactions were less predictable than simpler ones (Fig 4).

320 This trend resulted in a slight latitudinal gradient in the predictability of local food webs (Fig 4). True

321 positive rates were higher than true negative rates across the entire continent which caused the

322 predicted connectance (i.e., proportion of possible links that are realized) to be systematically

323 overestimated (Fig 4). All bioregional food webs were similarly predictable (0.89 < AUC < 0.92) by the

324 *master* model and models transferred from one bioregion to another were also well predicted

325 (Appendix S6). Similarly, trait parameters of each bioregional predictive models did not diverge greatly

326 from the *master* model (Appendix S6).

327

328 **Discussion**

329 In this study, we recovered a large-scale food web with minimal data and widely available species

330 traits. We were able to recover most trophic interactions (~71k) between terrestrial vertebrates of

331 Europe from a model calibrated on less than 100 known species interactions. In general, the most

332 important predictors were the body masses of the prey and the predator, and the diet category of the

333 predator. Our predictive model performed similarly well when trained using interactions from a

334 combination of data sources (i.e., European Metaweb) or from empirical data (i.e., GloBI). Our

335 predictive model was as successful for predicting potential interactions (i.e., European Metaweb) as for

336 realized interactions (i.e., GloBI). However, not all interactions were well-predicted, especially the prey

337 of some predator orders, and trophic interactions of generalist species. Finally, the models tended to

16

338   predict more interactions than observed - an effect that scaled up to result in over-estimating

339   connectance in local food webs, especially in areas with more complex food webs.

340

341   Our results are further evidence of the promise of predictive models to help fill the Eltonian shortfall,

342   but they also highlight taxa and situations in which we likely will need more information to make

343   accurate predictions. This is important as directly monitoring interactions is especially hard, and it is

344   virtually impossible to inventory all of them (Chacoff *et al.* 2012; Jordano 2016). Trophic interaction

345   data remain scarce, but initiatives are emerging to make species interactions data more accessible (e.g.,

346   Poelen et al., 2014; Poisot et al., 2016). Given that we made relatively accurate predictions of a large-

347   scale and diverse food web with only a small fraction of all interactions and a few predictors, we

348   should already be able to make initial predictions even in data-poor systems. Many trait databases

349   already exist for a large array of organisms and functional traits (e.g., Kattge et al., 2011; Myhrvold et

350   al., 2015; Oliveira et al., 2017; Schneider et al., 2019; Wilman et al., 2014). When functional traits are

351   not available, many methods exist to impute missing data (Penone et al., 2014; Pollock et al., 2020).

352   Although imputation models are generally robust (Debastiani *et al.* 2021), they should be used with

353   caution as they can bias predictions, especially for taxa that are rare, poorly studied, or with extreme

354   traits. Alternatively, phylogenies, which are also available for many taxa, can be useful proxies to

355   predict interactions (e.g., Jetz et al., 2012; Jetz & Pyron, 2018; Tonini et al., 2016; Upham et al., 2019).

356   However, this phylogenetic approach does not allow the interpretation of the ecological constraints that

357   drive the trophic interactions and miss variation between closely related species, making it less

358   generalizable across taxa (Morales-Castilla *et al.* 2015; Gravel *et al.* 2016).

359

360　We also found that ecological constraints driving trophic interactions did not vary greatly in space. For

361　example, the parameters of all bioregional models were all similar, and the predictive performance of

362　bioregional models did not decrease when used to predict other bioregional food webs. So, our

363　predictive models could be used to transfer information from data-rich bioregions to data-poor

364　bioregions. Similar to our results, Wenger & Olden (2012) previously found that simpler models, such

365　as our generalized linear model, tended to have better out-of-sample performance than more complex

366　ones for modelling species distributions. In this study, we showed how models can transfer information

367　at one scale (i.e., bioregion food webs) and within one continent, but we need more studies on the

368　factors influencing model transferability in food web interactions to fully appreciate the potential of

369　trait-based models to predict interactions in data-poor system or under future conditions (Yates *et al.*

370　2018).

371

372　While the generality and overall performance of these models is promising, we also highlight some

373　systematic biases and needed improvements. For example, our predictive model systematically

374　overestimated the number of links in local food webs (Fig 4). Our models were better at predicting

375　interactions (true positive rate ≈ 0.9) than non-interactions (true negative rate ≈ 0.8; Appendix S7),

376　meaning most interactions that are realized in the system are among the predicted interactions.

377　However, among the predicted interactions are also a large number of incorrectly predicted non-

378　interactions. This is caused by the lower true negative rate combined with the typical low connectance

379　of food webs, meaning there is a lot more non-interactions than interactions to predict. Thus, our

380　predictive model should be viewed as a first step toward a correct description of a regional and local

381　food webs by reducing the millions of possible interactions to thousands of feasible ones. Our

382   predictions could be used to inform targeted sampling or initiate expert elicitation approaches to get a

383   more accurate picture of the true food web.

384

385   We also show that not all taxonomic groups are equivalent. The prey of some taxonomic groups were

386   harder to predict than others using a general model (Fig 2). Our miscalibration analysis helped

387   understand where the general model failed for these groups and highlighted some ecological

388   differences in how predator groups choose their prey (Appendix S5). For example, while the match in

389   nesting habitat and activity time of the predator and the prey were not among the important predictors

390   in the general model, these predictors were particularly important for some groups. Woodpeckers

391   (*Piciformes*) tend to feed on prey that share similar nesting habitats and are active at similar times.

392   Conversely, fowls (*Galliformes* and *Anseriformes*), pelicans (*Pelicaniforms*) and storks (*Ciconiformes*)

393   tend to feed on prey that nest in different habitats and active at different times during the day. These are

394   not surprising results: woodpeckers generally both forage and nest in and on trees, while many fowls

395   and storks forage on water but nest in different habitats (Svensson & Grant 2009). We also found that

396   the prey of other predator groups, such as carnivorans (*Carnivora*), falcons (*Falconiformes*), and owls

397   (*Strigiformes*), were harder to predict on average. These groups include many relatively generalist

398   predators that feed on many prey types (small herbivores, but also ungulates, birds, or other carnivores)

399   (Svensson & Grant 2009; Hackländer & Zachos 2020). The functional diversity of the diet of generalist

400   predators is larger which make it harder to find general matching rules that explain how these generalist

401   predators choose their prey. Alternatively, other traits excluded from our model (e.g., speed, physical or

402   chemical defences) may be important in how species of these groups choose their prey.

403

404 So how could we improve the predictive model we presented here? Because we showed that predators

405 tend to vary in how they choose their prey between taxonomic groups, hierarchical models are good

406 candidates to improve predictions. Hierarchical models allow some variation in the regression

407 coefficients between groups (Gelman et al., 2020; Ovaskainen et al., 2017). These coefficients are

408 drawn from a common distribution, and we can include external information to specify how the

409 coefficients vary across groups. Because how species choose their prey results from evolution,

410 phylogenetic relationships could inform how regression coefficients correlate across clades (Gómez *et*

411 *al.* 2010). Other options are machine learning algorithms which already have been used to predict

412 interactions and oftentimes outperformed linear models (e.g., Desjardins-Proulx et al., 2017; Pichler et

413 al*.,* 2020). Hierarchical and nonlinear models typically have more parameters to infer, therefore rely on

414 a larger volume of data. The scarcity of species interaction data limits these complex models to well-

415 studied or smaller-scale systems.

416

417 *Conclusion*

418 Predictive models have a role in filling the Eltonian shortfall. By predicting a large-scale, multi-clade

419 food web, we were able to identify which interactions are feasible and which are not. Having potential

420 food web interactions that can be spatially explicit could serve as a basis for a better understanding of

421 community and ecosystem dynamics. One promising avenue of research is to combine predictive

422 models of trophic interactions to other methods, such as expert elicitation or bio-energetic models, to

423 downscale regional metaweb into local quantitative food webs. This would allow us to investigate how

424 food webs and species interactions vary in space and time, and to forecast the consequences of global

425 changes on the composition and structure of ecosystems. Ultimately, predicting large-scale food webs

426 of potential interactions is the first step toward a better understanding of how ecosystems function and

427 can help to maximize conservation outcomes, even in a scenario of extremely sparse data.

428

429 **Aknowledgements**

438

439 **References**

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440

441 *Table 1: Variables used to predict trophic interactions between all species pairs. The variables are*

442 *grouped as foraging traits, vulnerability traits and matching traits. BM stands for body mass.*

	Foraging		Vulnerability	Matching				
	Predator body mass	Predator foraging behavior	Prey body mass	Diet	Activity time	Nesting habitat	Body mass difference
Operation	log		log	Does the diet of the predator match the type of prey (1) or not (0) ?	Jaccard similarity*	Jaccard similarity*	$(\log(BMpredator) - \log(BMprey))^2$
Variable type	Continuous	4 binary variables	Continuous	Binary	Continuous	Continuous	Continuous

443 * We calculated the Jaccard similarity coefficient for the activity time and nesting habitat of the

444 predator and the prey. Activity time and nesting habitat are a set of binary variables.

445
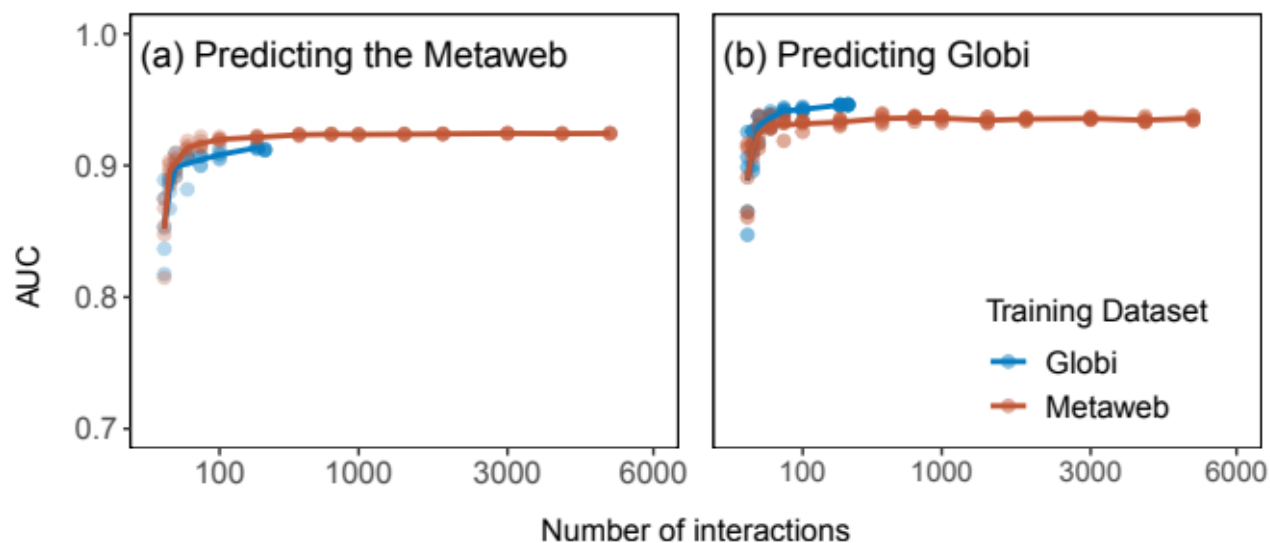
Figure 1: Effect of the number of interactions sampled on the predictive performance of the model. In

(a), we measured performance using the European Metaweb validation dataset. In (b), we measured

performance with interactions using the GloBI validation dataset. In red and blue are the predictive

*models trained with interactions sampled from the European metaweb and GloBI, respectively.*
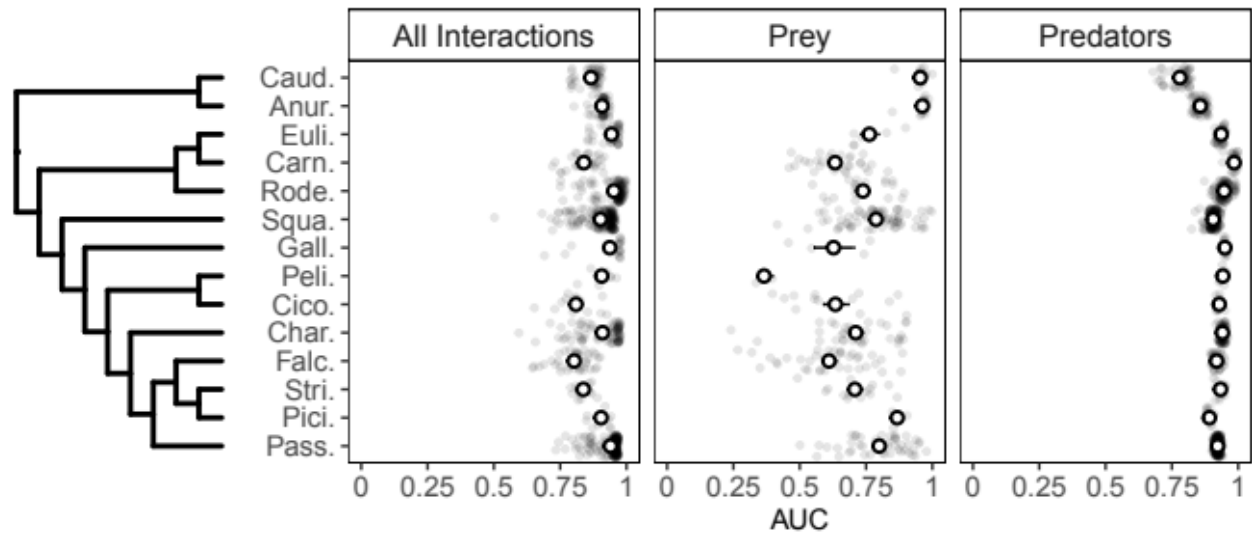
Figure 2: Differences in predictive performance among groups. Predictive performance is measured with the AUC. Each grey point is the predictive performance of the general model for a single species. The white points are the group mean, with the associated standard error. From left to right, the panels represent the performance of the general model to predict all trophic interactions, the prey, and the predators of the focal species. From top to bottom, the groups are Caudata, Anura, Eulipotyphla, Carnivora, Rodentia, Squamata, Galliformes, Pelecaniformes, Ciconiiformes, Charadriiformes, Falconiformes, Strigiformes, Piciformes, and Passeriformes.
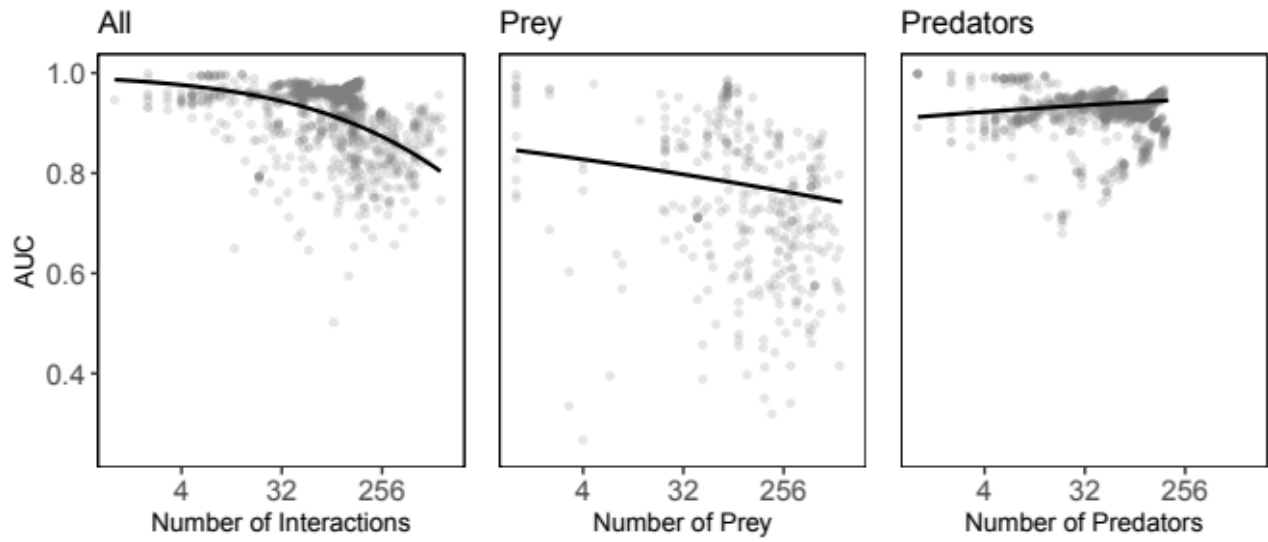
461 *Figure 3: Effect of generality on model performance. Each grey point is the predictive performance of*

462 *the master model to predict all interactions (left), the prey (center), and the predators (right) of a*

463 *single species. We measured generality as the number of interactions (left), the number of prey*

464 *(center), and the number of predators (right) of a given species. The trend lines are the mean effect of*

465 *the scaled generality (log transformed) on the logit-AUC.*
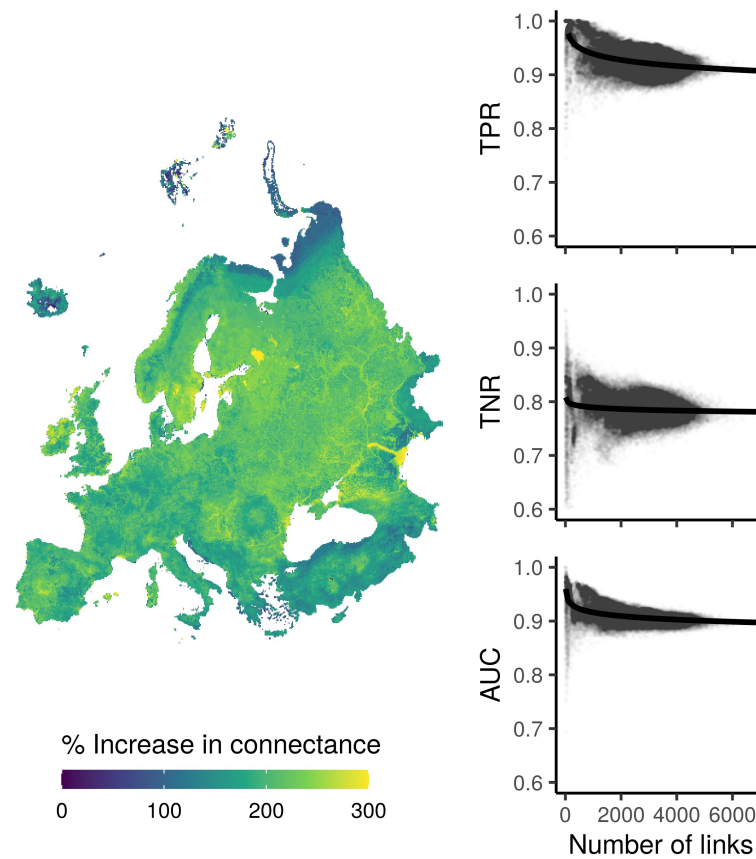
Figure 4: Spatial variation in predictability of local food webs. The left panel shows the overestimation of connectance of each 5km-cell food web. The right panels show the true positive rate (TPR; top), the true negative rate (TNR; middle), and area under the receiver operating curve (AUC; bottom) in relation to the complexity of the local web.