# THINKING OUTSIDE THE BOX PREDICTING BIOTIC INTERACTIONS IN DATA-POOR ENVIRONMENTS

DAVID BEAUCHESNE<sup>1\*</sup>, PHILIPPE DESJARDINS-PROULX<sup>2</sup>, PHILIPPE ARCHAMBAULT<sup>3</sup>, and DOMINIQUE GRAVEL<sup>2</sup>

\* email: david.beauchesne@uqar.ca

<sup>1</sup> Université du Québec à Rimouski

<sup>2</sup> Université de Sherbrooke

<sup>3</sup> Université Laval

10

September 19, 2016

RUNNING TITLE: PREDICTING BIOTIC INTERACTIONS IN DATA-POOR ENVIRONMENTS

### 1 Abstract

Large networks of ecological interactions, such as food webs, are complex to 12 characterize, be it empirically or theoretically. The former requires exhaustive 13 observations, while the latter generally requires ample data to be validated. 14 We therefore wondered whether readily available data, namely empirically de-15 scribed interactions in a variety of ecosystems, could be combined to predict 16 species interactions in data deficient ecosystems. To test this, we built a bi-17 otic interactions catalogue from a collection of 94 empirical food webs, detailed predator-prey interaction databases and interactions from the Global Biotic In-19 teractions (GloBI) database. We used an unsupervised machine learning method 21 to predict interactions between any given set of taxa, given pairwise taxonomic proximity and known consumer and resource sets found in the interaction catalogue. Initial results suggest that pairwise interactions can be predicted with 23 high accuracy. Although results are seemingly dependent on the comprehensiveness of the catalogue knowledge of taxonomy was found to complement well 25 the catalogue and improve predictions, especially as empirical information available diminished. Given it's high accuracy, this methodology could democratize 27 the use of food webs and network level descriptors in remote location where empirical data is hard to gather. Network characteristics could then be effi-29 ciently evaluated and correlated to levels of environmental stressors in order 30 to improve vulnerability assessments of ecosystems to global changes, opening 31 promising avenues for further research and for management initiatives. 32

**Keywords:** Interactions, machine learning, food webs, K-nearest neighbour, taxonomy, St. Lawrence

# 2 Introduction

33

34

47

50

Large networks of ecological interactions, such as food webs, are complex to characterize (Martinez, 1992; Pascual and Dunne, 2006). Empirical descriptions require exhaustive observations, while theoretical inference generally requires ample data to be validated. For this reason, studies focusing on communities of interacting species remain understudied, even though we acknowledge the importance of considering the reticulated nature of complex networks (Ings et al., 2009; Tylianakis et al., 2008). When time is of the essence, the long term studies required quickly become impractical and the use of network level approaches is relegated to the sideline.

Alternatively, a currently evolving approach is to predict interactions using proxies such as functional traits, phylogenies and spatial distributions (e.g. Gravel et al., 2013; Morales-Castilla et al., 2015; Bartomeus et al., 2016). For example, multiple traits can play a significant role in community dynamics and influence the presence and intensity of biotic interactions, like the influence of body size on predator-prey interactions, a literal take on big fish eats small fish (Cohen et al., 2003; Brose et al., 2006; Gravel et al., 2013). However, the time

required to gather the necessary data to apply those methods may still be restrictive, or the data be unavailable altogether, so much so that other methods have been developed to fill the gaps in knowledge (e.g. Schrodt et al., 2015).

We therefore wondered whether more readily available data could be used to infer interactions in data deficient ecosystems. There is an increasing amount 57 of data describing worldwide species interactions, some freely available through the Global Biotic Interactions (GloBI) database (Poelen et al., 2014). Another readily available piece of information on species is their taxonomy, through initiatives like the World Register of Marine Species (WoRMS; Bailly et al., 61 2016). More than simple nomenclature, evolutionary processes are thought to influence consumer-resource relationships (Mouquet et al., 2012; Rohr and Bascompte, 2014) so that taxonomically related species would be more likely to share similar types of both consumers and resources (Eklöf et al., 2012; 65 Morales-Castilla et al., 2015; Gray et al., 2015). Based on that assumption, taxonomy might be useful in predicting interactions for species lacking detailed information on their biology, but which have a taxonomically related species for which such information is available. The objective of this work is thus to combine empirical biotic interactions originating from a variety of ecosystems with taxonomic relatedness to predict interactions in data deficient ecosystems. As an example, we compare the observed interactions in the southern Gulf of 72 St. Lawrence (SGSL; Savenkoff et al., 2004) with predictions made using our approach. 74

# 3 Methods

55

The objective of our methodology is to predict the interactions between all pairs of taxa within an arbitrary set  $N_1$ , using a set of taxa  $N_0$  with empirically described interactions from which we can extract pairs of consumers and resources and their taxonomy. We couple the use of empirical data with an unsupervised machine learning method to achieve this.

#### 3.1 Biotic interaction catalogue

We built a biotic interaction catalogue to serve as a set of taxa  $N_0$  for training the algorithm with empirically described interactions. The empirical data used to construct the interaction catalogue was gathered in two successive steps. The first consisted of gathering data from a collection of 94 empirical food webs in marine and coastal ecosystems from which we extracted pairwise taxa interactions (see Brose et al., 2005; Kortsch et al., 2015; GlobalWeb database for more information). We also used a detailed predator-prey interaction database describing trophic relationships between XX predators and their prey (Barnes et al., 2008). From these datasets, only interactions between taxa at the taxonomic scale of the family or higher were selected for inclusion in the catalogue.

As empirical food webs are vastly dominated by non-interactions, these datasets yielded a highly skewed distribution of interactions vs non-interactions.

To counterbalance this, the second step of data compilation consisted of extracting observed interactions from the Global Biotic Interaction (GloBI) database (Poelen et al., 2014), which describes binary interactions for a wide range of taxa worldwide. We extracted all interactions available on GloBI for species belonging to the families of taxa identified through step 1. Interactions were extracted using the rGloBI package in R (Poelen et al., 2015). As per step 1, only interactions between taxa at the taxonomic scale of the family or higher were retained

The nomenclature used between datasets and food webs varied substantially. Taxa names thus had to be verified, modified according to the scientific nomenclature and validated. This process was performed using the Taxize package in R (Chamberlain and Szöcs, 2013; Chamberlain et al., 2014) and manually verified for errors. The same package was used to extract the taxonomy of all taxa for which interactions were obtained in previous steps. The complete R code and data used to build the catalogue is available at https://github.com/davidbeauchesne/Interaction\_catalog.

#### 3.2 Unsupervised machine learning

We use the K-nearest neighbor (KNN) algorithm (**ref**) to predict pairwise interactions for a set of taxa S. The KNN algorithm predicts missing entries or proposes additional entries by a majority vote based on the K nearest (i.e. most similar) entries (see Box 1 for an example). In this case, taxa are described by a set of resources when considered as a consumer, a set of consumers when considered as a resource and their taxonomy (i.e. kingdom, phylum, class, order, family, genus, species). Similarity between taxa was evaluated using the Tanimoto similarity measure (**ref**), which compares two vectors with i elements based on the number of elements they share and contain:

$$tanimoto(\mathbf{x}, \mathbf{y}) = \frac{\sum_{i} x_i \wedge y_i}{\sum_{i} x_i \vee y_i},$$
(1)

where  $\land$  is bitwise *and*, while  $\lor$  is the bitwise *or* operators. Adding a weighting scheme, we can measure the similarity using two different sets of vectors with i and j elements, respectively.

$$tanimoto_t(\mathbf{x}, \mathbf{y}, w_t) = w_t tanimoto(\mathbf{x_i}, \mathbf{y_i}) + (1 - w_t) tanimoto(\mathbf{x_j}, \mathbf{y_j}),$$
(2)

where  $w_t$  is the weight given to vector i,  $\mathbf{x_i}$ ,  $\mathbf{y_i}$  are the resource or consumer sets of the two taxa and  $\mathbf{x_j}$  and  $\mathbf{y_j}$  are the vectors for the taxonomy of two taxa. When  $w_t = 0$  only resource or consumer sets are used to compute similarity, while  $w_t = 1$  solely uses taxonomy.

# 3.3 Predicting interactions, Biotic predictor algorithm, Twoway Tanimoto algorithm, Feng shui name algorithm, Find a name for the algorithm

The XXX algorithm is built on a series of logical steps that ultimately predicts a candidate resources list  $C_R$  for each taxon in  $N_1$  (Figure 1). For all consumer taxa  $T_C$  in  $N_1$ , the algorithm first verifies whether it has empirical resources  $T_R$  listed in the catalogue (Step S1, Figure 1). When it does, if  $T_R$  are also in  $N_1$ , they are added as predicted resources for  $T_C$  (S2, S3). This corresponds to what we refer to as the catalogue contribution to resource predictions. Two taxa in  $N_1$  that are known to interact through the catalogue are automatically assumed to interact in  $N_1$ .

Otherwise, the algorithm passes to what we refer to as the predictive contribution to resource predictions (S4 to S16), with candidate resources for  $T_C$  identified with the KNN algorithm. If  $T_R$  are absent from  $N_1$ , K most similar resources  $T_{R'}$  are identified in  $N_1$  to add to  $C_R$  (S4 to S7). Then for all  $T_C$  in  $N_1$ , the algorithm identifies K most similar consumers  $T_{C'}$  in  $N_0$  and extracts their resource sets (S8). As before, if those resources are found in  $N_1$  (S9) they are added to  $C_R$  (S10 to S12), otherwise K most similar resources  $T_{R'}$  are identified in  $N_1$  (S13) to add to  $C_R$  (S14 to S16). A simple working example is presented at Box 1. Note that other parameters are used in the algorithm, but not presented here for the sake of message clarity. A more comprehensive mathematical description of the algorithm and the parameters used is however available through Figure 1 and the complete R code and data used for the algorithm is available at https://github.com/david-beauchesne/Predict\_interactions.

#### 3.4 Algorithm prediction accuracy

We used the most extensive and taxonomically detailed datasets included in the catalogue (ref) to assess the prediction accuracy of the algorithm. Testing accuracy of a particular dataset was done by first removing from the catalogue all pairwise interacting taxa originating from that dataset. Accuracy was evaluated using three different statistics:

1.  $Score_y$  is the fraction of interactions correctly predicted:

$$Score_y = \frac{a}{a+c} \tag{3}$$

2.  $Score_{\neg y}$  is the fraction of non-interactions correctly predicted:

$$Score_{\neg y} = \frac{d}{b+d} \tag{4}$$

3. TSS, The True Skilled Statistics (TSS) evaluated prediction success by considering both true and false predictions, returning a value ranging from 1 (prefect predictions) to -1 (inverted predictions; Allouche et al., 2006):

$$TSS = \frac{(ad - bc)}{(a+c)(b+d)} \tag{5}$$

where a is the number of links predicted and observed, b is the number predicted but not observed, c is the number of non-interaction predicted but interactions observed and d is the number of non-interaction predicted absent and observed. These three statistics give a different perspective on prediction accuracy, focusing in turn on true interactions and non-interactions, and on both true and false predictions.

We evaluated the three statistics for the complete algorithm and for the catalogue and the predictions individually to evaluate their respective contribution to the algorithm predictive accuracy. Multiple  $w_t$  values were also tested to evaluate whether taxa similarity measured as a function of resource/consumer sets or taxonomy contributed more significantly towards increased predictive accuracy. The same was done with multiple K values.

Finally, we evaluated the influence of the comprehensiveness of the catalogue on prediction accuracy. We selected the arctic food web from Kortsch et al. (2015) as a test. This food web was selected as it is highly detailed taxonomically. Furthermore, once removed from the catalogue, almost 100% of its taxa still had information available on sets of consumers and resources, which necessary for testing the impact of catalogue comprehensiveness on prediction accuracy. We iteratively and randomly (n = 50 randomizations) removed a percentage of empirical data describing the food web taxa from the catalogue before generating new predictions with the algorithm. We also tested  $w_t$  values of 0.5 and 1 to evaluate whether taxonomic similarity could support predictive accuracy in cases when empirical data for species in  $N_1$  in the catalogue is unavailable.

# 6 4 Results

#### 4.1 Biotic interaction catalogue

The data compilation process allowed us to build an interaction catalogue composed of 276708 pairwise interactions (interactions = 72110; non-interactions = 204598). A total of 9712 taxa (Superfamily = 15; Family = 591; Subfamily = 29; Tribe = 8; Genus = 1972; Species = 7097) are included in the catalogue, 4159 of which have data as consumers and 4375 as resources.

#### 4.2 Algorithm predictive accuracy

The overall predictive accuracy of the algorithm ranges between 80% to almost 100% in certain cases (Figure 2). Both interactions and non-interactions are well predicted by the algorithm. TSS scores are lower than  $Score_y$  and  $Score_{\neg y}$  due to misclassified interactions and non-interactions. This can also be observed through the effect of varying K values, which increases the number of potential candidate resources for each taxa in the predictive portion of the algorithm. Prediction accuracy increases for interactions, while it decreases for non-interactions, as K values increase.

Similarity being predominantly measured with resource/consumer sets ( $w_t$  closer to 0) yielded better predictions than when measured with taxonomy ( $w_t$  closer to 1; Figure 2). Resource/consumer sets therefore appears to serve as a better predictor of similarity between taxa for interactions predictions. It is nonetheless interesting to note that although the predictive contribution of the algorithm decreases as  $w_t$  increases, an increased mean and decreased variability values for the TSS and  $Score_y$  statistics is also observed (Figure 2). This suggests that while using taxonomy for similarity measurements yields lower predictive accuracy, it may also complement the catalogue contribution by predicting interactions not captured through empirical data, effectively increasing the predictive accuracy of the complete algorithm.

The partitioning of the catalogue and predictive portions of the algorithm shows that it is dependent on the comprehensiveness of the catalogue for high prediction accuracy (Figures 2, 3). As the amount of empirical data available in the catalogue decreases so does the overall accuracy of the algorithm (Figures 3). The predictive contribution of the algorithm however slows down the decrease in the prediction efficiency of the algorithm. Prediction accuracy still remains around 75% with only 40% of  $N_1$  taxa found in the catalogue (Figures 3). Furthermore, the use of taxonomy for similarity measurements is more efficient as empirical data becomes scarcer and no different than resource/consumer sets for the complete algorithm when ample data is available (Figures 3).

#### 4.3 Southern Gulf of St. Lawrence

202

204

206

207

208

209

210

211

212

213

214

215

217

218

219

221

222

223

224

226

228

229

230

231

232

233

234

235

236

237

239

240

241

243

As an example, we used the XXX algorithm to predict interactions in the southern Gulf of St. Lawrence (SGSL) in eastern Canada. The empirical data and taxa list come from Savenkoff et al. (2004). They present a list of 29 functional groups for a total of 80 taxa presented at least at taxonomical scale of the family. Other coarser taxa families were not used for this example (see Table S1 in Supplementary information (SI) and Savenkoff et al. (2004) for a complete description of functional groups). As their analysis was performed on the functional groups rather than the taxa themselves, we used the algorithm to predict interactions between all 80 taxa selected. We then aggregated them back to their original functional groups to compare with interactions presented in Savenkoff et al. (2004). In total, there were empirical data available in the catalogue for 78% of SGSL taxa (62/80). The algorithm correctly predicted close to 80% of interactions (a = 135/170) and non-interactions (d = 354/455) extracted from Savenkoff et al. (2004). It also predicted an additional 101 interactions (c) that were not noted in Savenkoff et al. (2004) and failed to predict 36 observed interactions that were (c), resulting in a TSS score of 0.57. A visual comparison of results obtained from the algorithm with interactions noted in Savenkoff et al. (2004) is available at Figure 4. The network presented is centered on the observed and predicted interactions of the capelin (Mallotus villosus) and piscivorous small pelagic feeders (e.g. Scomber scombrus and Illex illecebrosus).

### 5 Discussion

#### 5.1 Algorithm accuracy

We show that out of the box interaction inference for a set of taxa with incomplete or unavailable preexisting information can be achieved with high accuracy using a combination of empirical data describing biotic interactions and tax-onomic relatedness. Although the efficiency of the algorithm is dependent on the comprehensiveness of the interactions catalogue, taxonomic proximity acts as a complement to increase the number of observed interactions correctly predicted. Taxonomic proximity also supports the efficiency of the algorithm when catalogue comprehensiveness decreases.

#### 5.2 Usefulness of taxonomic relatedness

While we found that taxonomy could be useful as a complement to predictions made using empirical data, the accuracy of predictions made using the KNN algorithm could be improved. Other uses of this machine learning approach have achieved much higher prediction rates (e.g. ?), which suggests that taxonomy may not be the optimal proxy for predicting interactions. While evolutionary history plays a significant role in influencing consumer-resource trait matching and food web structure (Mouquet et al., 2012; Rohr and Bascompte, 2014), phylogenetic constraints do not account efficiently for certain traits such as body size (Eklöf and Stouffer, 2016). Including traits like body size and metabolism as an additional component of this algorithm could thus help increasing overall prediction accuracy, especially in cases where the catalogue lacks data on taxa for which interactions have to be predicted. Although promising, such an approach would undermine the premise under which this method was built and which constitutes its main strength, *i.e.* predicting interactions in data deficient environments using readily available data.

#### 5.3 Interactions classification

That  $Score_y$  and  $Score_{\neg y}$  are inversely proportional means that non-interactions are misclassified as interactions in the process of increasing  $Score_y$ , consequently decreasing  $Score_{\neg y}$ . This could either stem from the algorithm poorly predicting non-interactions or from the empirical data itself. Accuracy evaluation assumes that non-interactions from empirical food web are observed data, yet it is usually not the case. Most empirical webs have a strong focus attributed to higher order consumer species and very little attention given to other taxa (?). Furthermore, the methodologies used to obtain consumer-resource data usually relies on gut content analyses, which is efficient at observing interactions, but not so for absence of interactions (?). Misclassified interactions could thus be real, albeit unobserved through empirical data available.

#### 5.4 Southern Gulf of St. Lawrence

The St Lawrence example (Figure 4 and SI) provides great material to discuss predictions in greater detail. The algorithm fails to predict 20% of interactions presented in Savenkoff et al. (2004). Interactions that failed to be predicted were mainly centered on invertebrate species (e.g. polychaetes and mollusks) and large functional groups described by coarse taxonomic categories (e.g. diatoms) alongside few species in Savenkoff et al. (2004) (e.g. piscivorous small pelagic feeders; Table S3). As we focused on the taxa at least at the scale of family, it is likely that their functional groups had a broader range of possible interactions included than what the algorithm could predict using only a few taxa. Furthermore, the efficiency of the algorithm greatly depends on the underlying empirical data that defines the catalogue. If the empirical data used to build the catalogue focuses on higher order consumers, it should come as no surprise that the algorithm would be afflicted by the same limitations.

The algorithm also predicts substantially more interactions than those presented in Savenkoff et al. (2004) (Figure 4; Table S2). The catalogue is not currently built to take into account life stages of species. Considering life stages and the fact that they are not explicitly considered in the catalogue could explain additional interactions that seem suspicious at first, like the surprise amount of additional interactions predicted for small piscivorous pelagic feeders as consumers (Figure 4). Due to the aggregated nature of the SGSL web, we believe the TSS score to be an underestimate of the efficiency of the algorithm.

#### 5.5 Perspectives

284

285

286

287

288

290

291

292

293

294

295

297

298

299

301

302

303

305

306

308

310

311

312

313

314

315

316

317

318

319

320

321

323

Overall, we believe our method performs well and offers promising avenues for further applied research and management initiatives. Interaction strength and species co-occurrence are major attributes affecting the probability of observing interactions. Interaction strength is instrumental to understanding community dynamics, stability and robustness (Laska and Wootton, 1998; Morales-Castilla et al., 2015), while the co-occurrence of species encloses valuable information on interactions and is a pre-requisite for them to exist (Cazelles et al., 2016). Considering them in our methodology would be highly valuable to correctly assess interactions in a given ecosystem and predict the spatial distribution of interaction networks. Given its high efficiency and simplicity, our methodology could broaden the use and the accessibility of food webs and network level descriptors for integrative management initiatives such as cumulative impacts assessments and systematic planning (Giakoumi et al., 2015; Beauchesne et al., 2016), especially for remote locations where empirical data is hard to gather. Network characteristics could be efficiently evaluated and correlated to levels of multiple environmental stressors to assess the vulnerability of ecosystems to global changes. We believe that the development of such predictive approaches could represent the first much needed steps towards the use of ecological networks in systematic impacts assessments.

# 6 Acknowledgements

We thank the Fond de Recherche Québécois Nature et Technologie (FRQNT) and the Natural Science and Engineering Council of Canada (CRSNG) for financial support. This project is also supported by Québec Océan, the Quebec Centre for Biodiversity Science (QCBS), and the Notre Golfe and CHONeII networks. We also wish to thank K. Cazelles for the help, constructive comments and suggestions.

# References

364

```
Allouche, Omri, Asaf Tsoar, and Ronen Kadmon (2006). "Assessing the ac-
333
       curacy of species distribution models: prevalence, kappa and the true skill
334
       statistic (TSS)". In: Journal of Applied Ecology 43.6, pp. 1223–1232. ISSN:
335
       00218901. DOI: 10.1111/j.1365-2664.2006.01214.x. URL: http://doi.
       wiley.com/10.1111/j.1365-2664.2006.01214.x.
337
   Bailly, N et al. (2016). World Register of Marine Species (WoRMS). \url=http://www.marinespecies.org.
338
       URL: http://www.marinespecies.org.
339
   Barnes, C., D. M. Bethea, R. D. Brodeur, J. Spitz, V. Ridoux, C. Pusineri,
       B. C. Chase, M. E. Hunsicker, F. Juanes, A. Kellermann, J. Lancaster, F.
341
       Ménard, F.-X. Bard, P. Munk, J. K. Pinnegar, F. S. Scharf, R. A. Rountree,
342
       K. I. Stergiou, C. Sassa, A. Sabates, and S. Jennings (2008). "Predator and
343
       prey body sizes in marine food webs". In: Ecology 89.3, pp. 881–881. DOI:
       10.1890/07-1551.1. URL: http://doi.wiley.com/10.1890/07-1551.1.
345
   Bartomeus, Ignasi, Dominique Gravel, Jason M. Tylianakis, Marcelo A. Aizen,
346
       Ian A. Dickie, and Maud Bernard-Verdier (2016). "A common framework for
347
       identifying linkage rules across different types of interactions". In: Functional
       Ecology, n/a-n/a. ISSN: 02698463. DOI: 10.1111/1365-2435.12666. URL:
349
       http://doi.wiley.com/10.1111/1365-2435.12666.
   Beauchesne, David, Cindy Grant, Dominique Gravel, and Philippe Archambault
351
       (2016). "L'évaluation des impacts cumulés dans l'estuaire et le golfe du Saint-
       Laurent : vers une planification systémique de l'exploitation des ressources".
353
       In: Le Naturaliste canadien 140.2, p. 45. ISSN: 0028-0798. DOI: 10.7202/
       1036503ar. URL: http://id.erudit.org/iderudit/1036503ar.
355
   Brose, Ulrich, Lara Cushing, Eric L. Berlow, Tomas Jonsson, Carolin Banasek-
356
       Richter, Louis-Felix Bersier, Julia L. Blanchard, Thomas Brey, Stephen
357
       R. Carpenter, Marie-France Cattin Blandenier, Joel E. Cohen, Hassan Ali
358
       Dawah, Tony Dell, Francois Edwards, Sarah Harper-Smith, Ute Jacob, Roland
       A. Knapp, Mark E. Ledger, Jane Memmott, Katja Mintenbeck, John K.
360
       Pinnegar, Björn C. Rall, Tom Rayner, Liliane Ruess, Werner Ulrich, Philip
361
       Warren, Rich J. Williams, Guy Woodward, Peter Yodzis, and Neo D. Mar-
362
```

//doi.wiley.com/10.1890/05-0379.

tinez (2005). "Body sizes of consumers and their resources". In: *Ecology* 86.9, pp. 2545–2545. ISSN: 0012-9658. DOI: 10.1890/05-0379. URL: http:

Brose, Ulrich, Tomas Jonsson, Eric L. Berlow, Philip Warren, Carolin Banasek-Richter, Louis-Félix Bersier, Julia L. Blanchard, Thomas Brey, Stephen R. Carpenter, Marie-France Cattin Blandenier, Lara Cushing, Hassan Ali Dawah, Tony Dell, Francois Edwards, Sarah Harper-Smith, Ute Jacob, Mark E. Ledger, Neo D. Martinez, Jane Memmott, Katja Mintenbeck, John K. Pinnegar, Björn C. Rall, Thomas S. Rayner, Daniel C. Reuman, Liliane Ruess, Werner Ulrich, Richard J. Williams, Guy Woodward, and Joel E. Cohen (2006). "Consumer-resource body-size relationships in natural food webs". In: Ecology 87.10, pp. 2411–2417. DOI: 10.1890/0012-9658(2006) 87[2411:CBRINF]2.0.CO;2. URL: http://doi.wiley.com/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CD;2. 

Cazelles, Kévin, Miguel B. Araújo, Nicolas Mouquet, and Dominique Gravel (2016). "A theory for species co-occurrence in interaction networks". In: *Theoretical Ecology* 9.1, pp. 39-48. ISSN: 1874-1738. DOI: 10.1007/s12080-015-0281-9. URL: http://link.springer.com/10.1007/s12080-015-0281-9.

Chamberlain, Scott A. and Eduard Szöcs (2013). "taxize: taxonomic search and retrieval in R". In: F1000Research 2. ISSN: 2046-1402. DOI: 10.12688/f1000research.2-191.v1. URL: http://f1000research.com/articles/2-191/v1.

Chamberlain, Scott A., Eduard Szocs, Carl Boettiger, Karthik Ram, Ignasi Bartomeus, and John Baumgartner (2014). taxize: Taxonomic information from around the web. URL: https://github.com/ropensci/taxize.

Cohen, Joel E, Tomas Jonsson, and Stephen R Carpenter (2003). "Ecological community description using the food web, species abundance, and body size." In: Proceedings of the National Academy of Sciences of the United States of America 100.4, pp. 1781-6. ISSN: 0027-8424. DOI: 10.1073/pnas. 232715699. URL: http://www.ncbi.nlm.nih.gov/pubmed/12547915% 20http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=PMC149910.

Eklöf, Anna, Matthew R. Helmus, M. Moore, and Stefano Allesina (2012). "Relevance of evolutionary history for food web structure". In: *Proceedings of the Royal Society of London B: Biological Sciences* 279.1733.

Eklöf, Anna and Daniel B. Stouffer (2016). "The phylogenetic component of food web structure and intervality". In: *Theoretical Ecology* 9.1, pp. 107–115. ISSN: 1874-1738. DOI: 10.1007/s12080-015-0273-9. URL: http://link.springer.com/10.1007/s12080-015-0273-9.

Giakoumi, Sylvaine, Benjamin S. Halpern, Loïc N. Michel, Sylvie Gobert, Maria Sini, Charles-François Boudouresque, Maria-Cristina Gambi, Stelios Katsanevakis, Pierre Lejeune, Monica Montefalcone, Gerard Pergent, Christine Pergent-Martini, Pablo Sanchez-Jerez, Branko Velimirov, Salvatrice Vizzini, Arnaud Abadie, Marta Coll, Paolo Guidetti, Fiorenza Micheli, and Hugh P. Possingham (2015). "Towards a framework for assessment and management of cumulative human impacts on marine food webs". In: Conservation Biology 29.4, pp. 1228–1234. ISSN: 08888892. DOI: 10.1111/cobi.12468. URL: http://doi.wiley.com/10.1111/cobi.12468.

```
Mouillot (2013). "Inferring food web structure from predator-prey body size
413
       relationships". In: Methods in Ecology and Evolution 4.11. Ed. by Robert
414
       Freckleton, pp. 1083-1090. ISSN: 2041210X. DOI: 10.1111/2041-210X.
       12103. URL: http://doi.wiley.com/10.1111/2041-210X.12103.
416
    Gray, Clare, David H. Figueroa, Lawrence N. Hudson, Athen Ma, Dan Perkins,
417
       and Guy Woodward (2015). "Joining the dots: An automated method for
       constructing food webs from compendia of published interactions". In: Food
419
       Webs 5, pp. 11-20. ISSN: 23522496. DOI: 10.1016/j.fooweb.2015.09.001.
420
   Ings, Thomas C., José M. Montoya, Jordi Bascompte, Nico Blüthgen, Lee Brown,
421
       Carsten F. Dormann, François Edwards, David Figueroa, Ute Jacob, J. Iwan
422
       Jones, Rasmus B. Lauridsen, Mark E. Ledger, Hannah M. Lewis, Jens M.
423
       Olesen, F.J. Frank van Veen, Phil H. Warren, and Guy Woodward (2009).
424
       "Review: Ecological networks - beyond food webs". In: Journal of Ani-
425
       mal Ecology 78.1, pp. 253–269. ISSN: 00218790. DOI: 10.1111/j.1365-
       2656.2008.01460.x. URL: http://doi.wiley.com/10.1111/j.1365-
427
       2656.2008.01460.x.
428
   Kortsch, Susanne, Raul Primicerio, Maria Fossheim, Andrey V. Dolgov, and
429
       Michaela Aschan (2015). "Climate change alters the structure of arctic ma-
       rine food webs due to poleward shifts of boreal generalists". In: Proceedings
431
       of the Royal Society of London B: Biological Sciences 282.1814.
   Laska, Mark S. and J. Timothy Wootton (1998). "Theoretical concepts and
433
       empirical approaches to measuring interaction strength". In: Ecology 79.2,
       pp. 461–476. DOI: 10.1890/0012-9658(1998)079[0461:TCAEAT]2.0.CO;2.
435
       URL: http://doi.wiley.com/10.1890/0012-9658(1998)079[0461:
436
       TCAEAT] 2.0.CO; 2.
437
   Martinez, Neo D. (1992). "Constant connectance in community food webs". In:
438
       American Naturalist 139.6, pp. 1208-1218. URL: http://www.jstor.org/
439
       stable/2462337.
440
   Morales-Castilla, Ignacio, Miguel G. Matias, Dominique Gravel, and Miguel B.
441
       Araújo (2015). "Inferring biotic interactions from proxies". In: Trends in
442
       Ecology & Evolution 30.6, pp. 347–356. ISSN: 01695347. DOI: 10.1016/j.
443
       tree.2015.03.014.
444
   Mouquet, Nicolas, Vincent Devictor, Christine N. Meynard, Francois Munoz,
445
       Louis-Félix Bersier, Jérôme Chave, Pierre Couteron, Ambroise Dalecky, Colin
446
       Fontaine, Dominique Gravel, Olivier J. Hardy, Franck Jabot, Sébastien Lavergne,
447
       Mathew Leibold, David Mouillot, Tamara Münkemüller, Sandrine Pavoine,
448
       Andreas Prinzing, Ana S.L. Rodrigues, Rudolf P. Rohr, Elisa Thébault, and
       Wilfried Thuiller (2012). "Ecophylogenetics: advances and perspectives". In:
450
       Biological Reviews 87.4, pp. 769–785. ISSN: 14647931. DOI: 10.1111/j.1469-
451
       185X.2012.00224.x. URL: http://doi.wiley.com/10.1111/j.1469-
452
       185X.2012.00224.x.
   Pascual, M and JA Dunne (2006). Ecological networks: linking structure to dy-
454
       namics in food webs. URL: https://books.google.ca/books?hl=en%
455
```

Gravel, Dominique, Timothée Poisot, Camille Albouy, Laure Velez, and David

412

456

7B%5C&%7Dlr=%7B%5C&%7Did=YpQRDAAAQBAJ%7B%5C&%7Doi=fnd%7B%5C&

```
%7Dpg=PP1%7B%5C&%7Ddq=Pascual+and+Dunne+2006+interactions%7B%
457
       5C\&\%7Dots=K4a5d62r9X\%7B\%5C\&\%7Dsig=01fs\%7B\%5C\_\%7DfXV1pgP6IeP1jBIb3B61rU.
458
    Poelen, Jorrit H., Stephen Gosnell, and Sergev Slyusarev (2015). rglobi: R In-
459
       terface to Global Biotic Interactions. URL: https://cran.r-project.org/
       package=rglobi.
461
    Poelen, Jorrit H., James D. Simons, and Chris J. Mungall (2014). "Global biotic
462
       interactions: An open infrastructure to share and analyze species-interaction
463
       datasets". In: Ecological Informatics 24, pp. 148–159. ISSN: 15749541. DOI:
464
       10.1016/j.ecoinf.2014.08.005.
465
    Rohr, Rudolf P. and Jordi Bascompte (2014). "Components of Phylogenetic Sig-
466
       nal in Antagonistic and Mutualistic Networks". In: The American Naturalist
467
       184.5, pp. 556-564. DOI: 10.1086/678234. URL: http://www.journals.
468
       uchicago.edu/doi/10.1086/678234.
469
    Savenkoff, Claude, Hugo Bourdages, Douglas P. Swain, Simon-Pierre Despatie,
470
       J. Mark Hanson, Red Méthot, Lyne Morissette, and Mike O. Hammil (2004).
       Input data and parameter estimates for ecosystem models of the southern
472
       Gulf of St. Lawrence (mid-1980s and mid-1990s). Tech. rep. Mont-Joli, Québec,
473
       Canada: Canadian Technical Report of Fisheries, Aquatic Sciences 2529, De-
474
       partment of Fisheries, and Oceans, p. 105.
    Schrodt, Franziska, Jens Kattge, Hanhuai Shan, Farideh Fazayeli, Julia Joswig,
476
       Arindam Banerjee, Markus Reichstein, Gerhard Bönisch, Sandra Díaz, John
       Dickie, Andy Gillison, Anuj Karpatne, Sandra Lavorel, Paul Leadley, Chris-
478
       tian B. Wirth, Ian J. Wright, S. Joseph Wright, and Peter B. Reich (2015).
       "BHPMF - a hierarchical Bayesian approach to gap-filling and trait predic-
480
       tion for macroecology and functional biogeography". In: Global Ecology and
481
       Biogeography 24.12, pp. 1510-1521. ISSN: 1466822X. DOI: 10.1111/geb.
482
       12335. URL: http://doi.wiley.com/10.1111/geb.12335.
    Tylianakis, Jason M., Raphael K. Didham, Jordi Bascompte, and David A.
484
       Wardle (2008). "Global change and species interactions in terrestrial ecosys-
485
       tems". In: Ecology Letters 11.12, pp. 1351-1363. ISSN: 1461023X. DOI: 10.
486
       1111/j.1461-0248.2008.01250.x. URL: http://doi.wiley.com/10.
487
       1111/j.1461-0248.2008.01250.x.
488
```

#### 6.1 Box 1

489

492

494

497

498

499

500

501 502

The XXX algorithm follows a series of logical steps to predict resources for all taxa in an arbitrary set of taxa  $N_1$  using a set of taxa  $N_0$  with empirically 491 described interactions from which we can extract sets of consumers and resources and their taxonomy. In this example, we are predicting interactions for a fictitious  $N_1 = \{T_1, T_9, T_{10}, T_{11}, T_{12}\}$  using  $N_0$  with information on 12 taxa. This catalogue holds information on consumer or resource for 10 taxa and the taxonomy for all 12 taxa in the list.

$N_0$ taxa ID	taxonomy	resource	consumer
$\overline{T_1}$	$\{a,b,c\}$	$\{T_2, T_3, T_{12}\}$	$\{T_4\}$
$T_2$	$\{e,f,g\}$		$\{T_1,T_5\}$
$T_3$	$\{i,j,k\}$		$\{T_5\}$
$T_4$	$\{m,n,o\}$	$\{T_1, T_5\}$	
$T_5$	$\{a,b,d\}$	$\{T_8,T_9\}$	$\{T_4\}$
$T_6$	$\{i,q,r\}$	$\{T_2, T_8\}$	$\{T_4\}$
$T_7$	$\{e,f,h\}$		$\{T_1, T_6\}$
$T_8$	$\{s,t,u\}$		$\{T_5, T_6\}$
$T_9$	$\{s,t,v\}$		$\{T_5\}$
$T_{10}$	$\{i,j,l\}$		
$T_{11}$	$\{m,n,p\}$		
$T_{12}$	$\{q,r,s\}$		$\{T_1\}$

Similarity between all pairs of taxa in  $N_0$  is measured for consumer, resource and taxonomic proximity using equation 1. The upper triangular matrix represents similarity measured with taxa sets of resources/consumers, while the lower triangular represents taxonomic similarities. For consumer/resource set similarities, values of 0 mean that similarity equals 0 for both similarity measurements.

 $tanimoto(T_Cx, T_Cy) / tanimoto(T_Rx, T_Ry)$ 

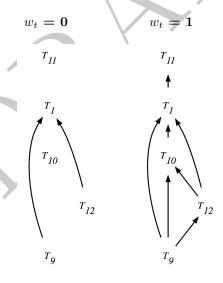
	$T_1$	$T_2$	$T_3$	$T_4$	$T_5$	$T_6$	$T_7$	$T_8$	$T_9$	$T_{10}$	$T_{11}$	$T_{12}$
$\overline{T_1}$	-	0	0	0	0/1	0.3/1	0	0	0	0	0	0
$T_2$	0	-	0/0.5	0	0	0	0/0.3	0/0.3	0/0.5	0	0	0/0.5
$T_3$	0	0	-	0	0	0	0	0/0.5	0/1	0	0	0
$T_4$	0	0	0	-	0	0	0	0	0	0	0	0
$T_5$	0.5	0	0	0	-	0.3/1	0	0	0	0	0	0
$T_6$	0	0	0.2	0	0	-	0	0	0	0	0	0
$T_7$	0	0.5	0	0	0	0	-	0/0.3	0	0	0	0/0.5
$T_8$	0	0	0	0	0	0	0	-	0	0	0	0
$T_9$	0	0	0	0	0	0	0	0.5	-	0	0	0
$T_{10}$	0	0	0.5	0	0	0.2	0	0	0	-	0	0
$T_{11}$	0	0	0	0.5	0	0	0	0	0	0	-	0
$T_{12}$	0	0	0	0	0	0.5	0	0.2	0.2	0	0	-

 $tanimoto(T_Tx, T_Ty)$ 

From these, the algorithm goes through logical steps (Figure 1) to identify a candidate resource list  $C_R$  for each taxon in  $N_1$  using either empirical data directly or K most similar taxa with equation 2. Going through the process for  $T_1$ , using K = 1 and  $w_t = 1$ :

Steps	1	Catalogue	Prediction
1	$I(T_1, T_R)$ in $N_0$ ?		
2	$T_R$ in $N_1$ ?		
4-7	$T_2 = \text{no} \rightarrow t(T_2, T_{R'}, w_t) = \text{NA}$	{}	{}
4-7	$T_3 = \text{no} \rightarrow t(T_2, T_{R'}, w_t) = T_{10} = 0.5$	{}	$\{T_{10}\}$
3	$T_{12} = \text{yes}$	$\{T_{12}\}$	$\{T_{10}\}$
8	$t(T_1, T_{C'}, w_t) = T_5 = 0.5$		
9	$I(T_5,T_R)$ in $N_1$ ?		
13-16	$T_8 = \text{no} \rightarrow t(T_8, T_{R'}, w_t) = T_9 = 0.5$	$\{T_{12}\}$	$\{T_9, T_{10}\}$
10-12	$T_9 = \text{yes}$	$\{T_9, T_{12}\}$	$\{T_9, T_{10}\}$

The logical steps allow us to predict a set of resources for  $T_1=\{T_9,\,T_{10},\,T_{12}\}$ . Doing it for all taxa in  $N_1$  with  $w_t=0$  and 1 predicts the following networks:



### 10 6.2 Figures

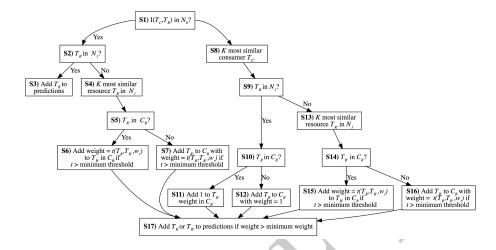


Figure 1: Description of logical steps used by the algorithm to suggest a list of candidate resources  $(C_R)$  for each consumer taxa  $(T_C)$  in an arbitrary set of  $N_1$  for which interactions are predicted, using a set of taxa  $N_0$  with empirically described interactions. Interactions between consumer and resource taxa are denoted as  $I(T_C,T_R)$ . K is the number of most similar neighbours selected for the KNN algorithm, t stands for tanimoto in equation 1,  $w_t$  is the weight given to sets of resources and consumers in equation 2, the minimum threshold is an arbitrary value setting the minimal similarity value accepted for taxa to be considered as close neighbours in the KNN algorithm, the weight is the value added to a candidate resource each time it is added to  $C_R$  and the minimum weight is the minimal weight value accepted for candidate resources to be selected as predicted sources in the algorithm.

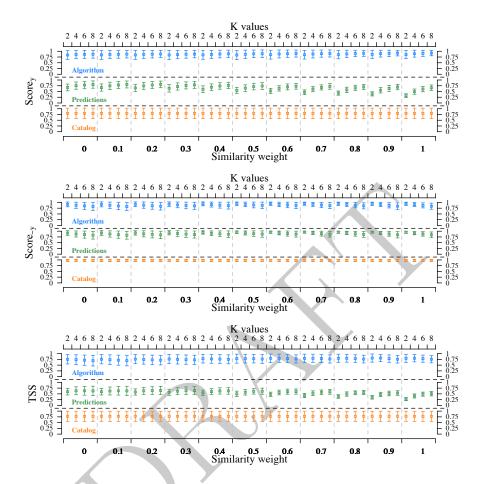


Figure 2: The graph presents the three statistics (i.e.  $Score_y$ ,  $Score_{\neg y}$  and TSS) used to evaluate the accuracy of the algorithm as a function of as a function of K values tested (i.e. 2, 4, 6 and 8 most similar seighbours, top x-axis) and trait weight (bottom x-axis), which varies between 0 and 1, and . A weight of 0 means that similarity is measured only using set of resources/consumers for each taxa, while a weight of 1 means that similarity is based solely on taxonomy. For each statistics, the topmost graph presents prediction accuracy for the complete algorithm, the middle graph corresponds to predictions made through the predictive portion of the algorithm (Steps S4-S16; Figure 1) and the bottom graph presents the catalogue contribution for the algorithm (Steps S1-S3; Figure 1). Note that the sum of the predictive and catalogue contributions can be over 100% as there is overlap between predictions made through both. The 7 datasets used for this analysis contained over 50 taxa (Christian1999; Link2002; Thompson2005; Brose et al., 2005; Barnes et al., 2008; Kortsch et al., 2015)

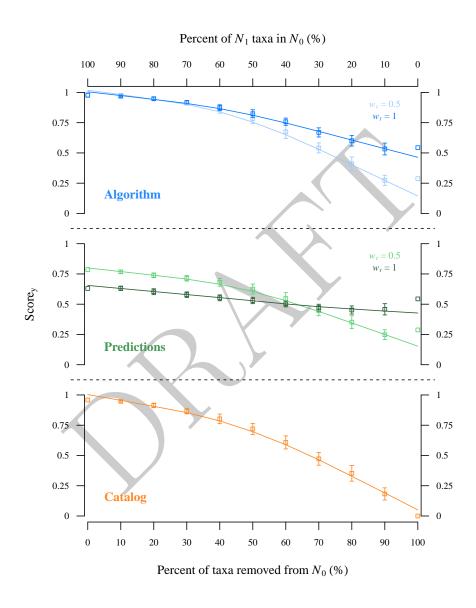


Figure 3: Caption on next page.

Figure 3: Graph presenting  $Score_y$  as a function of catalogue comprehensiveness, i.e. the amount of information on sets of consumer and resources available in the catalogue. We tested this on the arctic food web from Kortsch et al. (2015). This food web was highly detailed taxonomically. Once removed from the catalogue, almost 100% of its taxa still had information available on sets of consumers and resources, which necessary for testing the impact of catalogue comprehensiveness on prediction accuracy. A random percentage of data available in the catalogue for taxa in the food web (i.e. 0 to 100%) was iteratively removed (n = 50 randomizations) before generating new predictions with the algorithm.  $w_t$  values of 0.5 and 1 were evaluated to verify the usefulness of taxonomy in supporting predictive accuracy. The topmost graph presents prediction accuracy for the complete algorithm, the middle graph corresponds to predictions made through the predictive portion of the algorithm (Steps S4-S16; Figure 1) and the bottom graph presents the catalogue contribution for the algorithm (Steps S1-S3; Figure 1). Note that the sum of the predictive and catalogue contributions can be over 100% as there is overlap between predictions made through both.

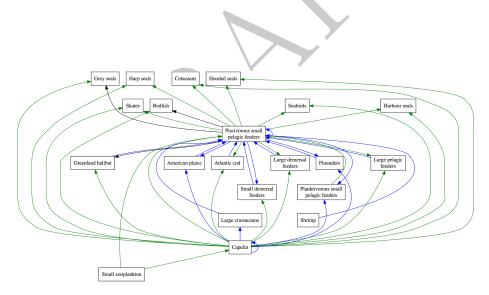


Figure 4: Example of results from the algorithm with the Network of the southern Gulf of St. Lawrence (Savenkoff et al., 2004) centered on interactions of the capelin (*Mallotus villosus*) and piscivorous small pelagic feeders (*e.g. Scomber scombrus and Illex illecebrosus*). Edge with colors green were both predicted and observed (26), black were observed only (3) and blue were predicted only (19). Arrows are pointed towards consumers.