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

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# 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

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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

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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 83 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 85 marine and coastal ecosystems from which we extracted pairwise taxa interactions (see Brose et al., 2005; Kortsch et al., 2015; University of Canberra, 87 2016 for more information). We also used a detailed predator-prey interaction database describing trophic relationships of 68 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. 91 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 (Murphy, 2012) 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, 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  $\wedge$  is bitwise *and*, while  $\vee$  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 datasets including more than 50 taxa (Christian and Luczkovich, 1999; Link, 2002; Thompson et al., 2004; Brose et al., 2005; Barnes et al., 2008; Kortsch et al., 2015) 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.

# 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

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 taxonomic 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. 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 often uneven effort made to thoroughly detail species interactions (**Dunne2006**). Furthermore, the methodologies used to obtain consumer-resource data, often relying on gut content analyses, which is efficient at observing interactions, may be inefficient to detect absence of interactions in natural systems (**Dunne2006**). This is especially true with our methodology,

where we predict interactions between species whose co-occurrence may have been observed in the other ecosystems we are using to predict 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

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 326 much needed steps towards the use of ecological networks in systematic impacts assessments. 328

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#### References 336

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```
Allouche, Omri, Asaf Tsoar, and Ronen Kadmon (2006). "Assessing the ac-
337
       curacy of species distribution models: prevalence, kappa and the true skill
338
       statistic (TSS)". In: Journal of Applied Ecology 43.6, pp. 1223–1232. ISSN:
330
       00218901. DOI: 10.1111/j.1365-2664.2006.01214.x. URL: http://doi.
       wiley.com/10.1111/j.1365-2664.2006.01214.x.
341
   Bailly, N et al. (2016). World Register of Marine Species (WoRMS). \url=http://www.marinespecies.org.
342
       URL: http://www.marinespecies.org.
   Barnes, C., D. M. Bethea, R. D. Brodeur, J. Spitz, V. Ridoux, C. Pusineri,
344
       B. C. Chase, M. E. Hunsicker, F. Juanes, A. Kellermann, J. Lancaster, F.
345
       Ménard, F.-X. Bard, P. Munk, J. K. Pinnegar, F. S. Scharf, R. A. Rountree,
346
       K. I. Stergiou, C. Sassa, A. Sabates, and S. Jennings (2008). "Predator and
       prey body sizes in marine food webs". In: Ecology 89.3, pp. 881–881. DOI:
348
       10.1890/07-1551.1. URL: http://doi.wiley.com/10.1890/07-1551.1.
   Bartomeus, Ignasi, Dominique Gravel, Jason M. Tylianakis, Marcelo A. Aizen,
350
       Ian A. Dickie, and Maud Bernard-Verdier (2016). "A common framework for
351
       identifying linkage rules across different types of interactions". In: Functional
352
       Ecology, n/a-n/a. ISSN: 02698463. DOI: 10.1111/1365-2435.12666. URL:
       http://doi.wiley.com/10.1111/1365-2435.12666.
354
   Beauchesne, David, Cindy Grant, Dominique Gravel, and Philippe Archambault
355
       (2016). "L'évaluation des impacts cumulés dans l'estuaire et le golfe du Saint-
356
       Laurent : vers une planification systémique de l'exploitation des ressources".
357
       In: Le Naturaliste canadien 140.2, p. 45. ISSN: 0028-0798. DOI: 10.7202/
       1036503ar. URL: http://id.erudit.org/iderudit/1036503ar.
359
   Brose, Ulrich, Lara Cushing, Eric L. Berlow, Tomas Jonsson, Carolin Banasek-
360
       Richter, Louis-Felix Bersier, Julia L. Blanchard, Thomas Brey, Stephen
```

R. Carpenter, Marie-France Cattin Blandenier, Joel E. Cohen, Hassan Ali Dawah, Tony Dell, Francois Edwards, Sarah Harper-Smith, Ute Jacob, Roland A. Knapp, Mark E. Ledger, Jane Memmott, Katja Mintenbeck, John K. Pinnegar, Björn C. Rall, Tom Rayner, Liliane Ruess, Werner Ulrich, Philip Warren, Rich J. Williams, Guy Woodward, Peter Yodzis, and Neo D. Martinez (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: //doi.wiley.com/10.1890/05-0379.

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407

408

- Brose, Ulrich, Tomas Jonsson, Eric L. Berlow, Philip Warren, Carolin Banasek-370 Richter, Louis-Félix Bersier, Julia L. Blanchard, Thomas Brey, Stephen R. Carpenter, Marie-France Cattin Blandenier, Lara Cushing, Hassan Ali 372 Dawah, Tony Dell, Francois Edwards, Sarah Harper-Smith, Ute Jacob, Mark 373 E. Ledger, Neo D. Martinez, Jane Memmott, Katja Mintenbeck, John K. 374 Pinnegar, Björn C. Rall, Thomas S. Rayner, Daniel C. Reuman, Liliane 375 Ruess, Werner Ulrich, Richard J. Williams, Guy Woodward, and Joel E. 376 Cohen (2006). "Consumer-resource body-size relationships in natural food 377 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/10.1890/0012-379 9658(2006)87[2411:CBRINF]2.0.CO;2. 380
- Cazelles, Kévin, Miguel B. Araújo, Nicolas Mouquet, and Dominique Gravel 381 (2016). "A theory for species co-occurrence in interaction networks". In: Theoretical Ecology 9.1, pp. 39-48. ISSN: 1874-1738. DOI: 10.1007/s12080-383 015-0281-9. URL: http://link.springer.com/10.1007/s12080-015-0281-9. 385
- Chamberlain, Scott A. and Eduard Szöcs (2013). "taxize: taxonomic search and retrieval in R". In: F1000Research 2. ISSN: 2046-1402. DOI: 10.12688/ 387 f1000research.2-191.v1. URL: http://f1000research.com/articles/ 388 2-191/v1. 389
  - 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.
  - Christian, Robert R. and Joseph J. Luczkovich (1999). "Organizing and understanding a winter's seagrass foodweb network through effective trophic levels". In: Ecological Modelling 117.1, pp. 99–124. ISSN: 03043800. DOI: 10. 1016/S0304-3800(99)00022-8.
- Cohen, Joel E, Tomas Jonsson, and Stephen R Carpenter (2003). "Ecological community description using the food web, species abundance, and body 398 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. 400 232715699. URL: http://www.ncbi.nlm.nih.gov/pubmed/12547915% 20http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid= 402 PMC149910. 403
  - 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.
- Gravel, Dominique, Timothée Poisot, Camille Albouy, Laure Velez, and David Mouillot (2013). "Inferring food web structure from predator-prey body size relationships". In: *Methods in Ecology and Evolution* 4.11. Ed. by Robert Freckleton, pp. 1083–1090. ISSN: 2041210X. DOI: 10.1111/2041-210X. 12103. URL: http://doi.wiley.com/10.1111/2041-210X.12103.
- Gray, Clare, David H. Figueroa, Lawrence N. Hudson, Athen Ma, Dan Perkins, and Guy Woodward (2015). "Joining the dots: An automated method for constructing food webs from compendia of published interactions". In: Food Webs 5, pp. 11–20. ISSN: 23522496. DOI: 10.1016/j.fooweb.2015.09.001.
- Ings, Thomas C., José M. Montoya, Jordi Bascompte, Nico Blüthgen, Lee Brown,
  Carsten F. Dormann, François Edwards, David Figueroa, Ute Jacob, J. Iwan
  Jones, Rasmus B. Lauridsen, Mark E. Ledger, Hannah M. Lewis, Jens M.
  Olesen, F.J. Frank van Veen, Phil H. Warren, and Guy Woodward (2009).
  "Review: Ecological networks beyond food webs". In: Journal of Animal Ecology 78.1, pp. 253–269. ISSN: 00218790. DOI: 10.1111/j.13652656.2008.01460.x. URL: http://doi.wiley.com/10.1111/j.1365-
  - Kortsch, Susanne, Raul Primicerio, Maria Fossheim, Andrey V. Dolgov, and Michaela Aschan (2015). "Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists". In: *Proceedings of the Royal Society of London B: Biological Sciences* 282.1814.
  - Laska, Mark S. and J. Timothy Wootton (1998). "Theoretical concepts and empirical approachesto measuring interaction strength". In: *Ecology* 79.2, pp. 461–476. DOI: 10.1890/0012-9658(1998)079[0461:TCAEAT]2.0.CO;2. URL: http://doi.wiley.com/10.1890/0012-9658(1998)079[0461:TCAEAT]2.0.CO;2.
- Link, J (2002). "Does food web theory work for marine ecosystems?" In: Marine Ecology Progress Series 230, pp. 1-9. ISSN: 0171-8630. DOI: 10.3354/ meps230001. URL: http://www.int-res.com/abstracts/meps/v230/p1-9/.
- Martinez, Neo D. (1992). "Constant connectance in community food webs". In:
   American Naturalist 139.6, pp. 1208-1218. URL: http://www.jstor.org/stable/2462337.
- Morales-Castilla, Ignacio, Miguel G. Matias, Dominique Gravel, and Miguel B.
   Araújo (2015). "Inferring biotic interactions from proxies". In: Trends in

```
Ecology & Evolution 30.6, pp. 347–356. ISSN: 01695347. DOI: 10.1016/j.
455
       tree.2015.03.014.
456
    Mouquet, Nicolas, Vincent Devictor, Christine N. Meynard, François Munoz,
457
       Louis-Félix Bersier, Jérôme Chave, Pierre Couteron, Ambroise Dalecky, Colin
       Fontaine, Dominique Gravel, Olivier J. Hardy, Franck Jabot, Sébastien Lavergne,
459
       Mathew Leibold, David Mouillot, Tamara Münkemüller, Sandrine Pavoine,
460
       Andreas Prinzing, Ana S.L. Rodrigues, Rudolf P. Rohr, Elisa Thébault, and
461
       Wilfried Thuiller (2012). "Ecophylogenetics: advances and perspectives". In:
       Biological Reviews 87.4, pp. 769–785. ISSN: 14647931. DOI: 10.1111/j.1469-
463
       185X.2012.00224.x. URL: http://doi.wiley.com/10.1111/j.1469-
       185X.2012.00224.x.
465
    Murphy, Kevin P. (2012). Machine learning: a probabilistic perspective. MIT
466
       Press, p. 1067. ISBN: 9780262018029.
467
    Pascual, M and JA Dunne (2006). Ecological networks: linking structure to dy-
468
       namics in food webs. URL: https://books.google.ca/books?hl=en%
       7B%5C&%7Dlr=%7B%5C&%7Did=YpQRDAAAQBAJ%7B%5C&%7Doi=fnd%7B%5C&
470
       %7Dpg=PP1%7B%5C&%7Ddq=Pascual+and+Dunne+2006+interactions%7B%
471
       5C&%7Dots=K4a5d62r9X%7B%5C&%7Dsig=01fs%7B%5C_%7DfXV1pgP6IeP1jBIb3B61rU.
472
    Poelen, Jorrit H., Stephen Gosnell, and Sergey Slyusarev (2015). rglobi: R In-
       terface to Global Biotic Interactions. URL: https://cran.r-project.org/
474
       package=rglobi.
    Poelen, Jorrit H., James D. Simons, and Chris J. Mungall (2014). "Global biotic
476
       interactions: An open infrastructure to share and analyze species-interaction
       datasets". In: Ecological Informatics 24, pp. 148–159. ISSN: 15749541. DOI:
478
       10.1016/j.ecoinf.2014.08.005.
479
    Rohr, Rudolf P. and Jordi Bascompte (2014). "Components of Phylogenetic Sig-
480
       nal in Antagonistic and Mutualistic Networks". In: The American Naturalist
       184.5, pp. 556-564. DOI: 10.1086/678234. URL: http://www.journals.
482
       uchicago.edu/doi/10.1086/678234.
483
    Savenkoff, Claude, Hugo Bourdages, Douglas P. Swain, Simon-Pierre Despatie,
484
       J. Mark Hanson, Red Méthot, Lyne Morissette, and Mike O. Hammil (2004).
485
       Input data and parameter estimates for ecosystem models of the southern
486
       Gulf of St. Lawrence (mid-1980s and mid-1990s). Tech. rep. Mont-Joli, Québec,
487
       Canada: Canadian Technical Report of Fisheries, Aquatic Sciences 2529, De-
       partment of Fisheries, and Oceans, p. 105.
489
    Schrodt, Franziska, Jens Kattge, Hanhuai Shan, Farideh Fazayeli, Julia Joswig,
490
       Arindam Banerjee, Markus Reichstein, Gerhard Bönisch, Sandra Díaz, John
491
       Dickie, Andy Gillison, Anuj Karpatne, Sandra Lavorel, Paul Leadley, Chris-
       tian B. Wirth, Ian J. Wright, S. Joseph Wright, and Peter B. Reich (2015).
493
       "BHPMF - a hierarchical Bayesian approach to gap-filling and trait predic-
       tion for macroecology and functional biogeography". In: Global Ecology and
       Biogeography 24.12, pp. 1510-1521. ISSN: 1466822X. DOI: 10.1111/geb.
       12335. URL: http://doi.wiley.com/10.1111/geb.12335.
497
    Thompson, Ross M., Kim N. Mouritsen, and Robert Poulin (2004). "Importance
       of parasites and their life cycle characteristics in determining the structure
499
       of a large marine food web". In: Journal of Animal Ecology 74.1, pp. 77–85.
500
```

```
DOI: 10.1111/j.1365-2656.2004.00899.x. URL: http://doi.wiley.com/
501
       10.1111/j.1365-2656.2004.00899.x.
502
    Tylianakis, Jason M., Raphael K. Didham, Jordi Bascompte, and David A.
503
       Wardle (2008). "Global change and species interactions in terrestrial ecosys-
       tems". In: Ecology\ Letters\ 11.12,\ pp.\ 1351–1363.\ ISSN:\ 1461023X.\ Doi:\ 10.
505
       1111/j.1461-0248.2008.01250.x. URL: http://doi.wiley.com/10.
506
       1111/j.1461-0248.2008.01250.x.
507
    University of Canberra (2016). Food Web Database - University of CANBERRA.
508
       URL: http://globalwebdb.com/.
509
```



#### 6.1 Box 1

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

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.

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

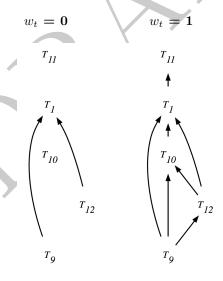
	$T_1$	$T_2$	$T_3$	$T_4$	$T_5$	$T_6$	$T_7$	$T_8$	$T_9$	$T_{10}$	$T_{11}$	$T_{12}$
$\overline{T_1}$	-	0	0	0	0/1	0.3/1	0	0	0	0	0	0
$T_2$	0	-	0/0.5	0	0	0	0/0.3	0/0.3	0/0.5	0	0	0/0.5
$T_3$	0	0	-	0	0	0	0	0/0.5	0/1	0	0	0
$T_4$	0	0	0	-	0	0	0	0	0	0	0	0
$T_5$	0.5	0	0	0	-	0.3/1	0	0	0	0	0	0
$T_6$	0	0	0.2	0	0	-	0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



## $_{\circ}$ 6.2 Figures

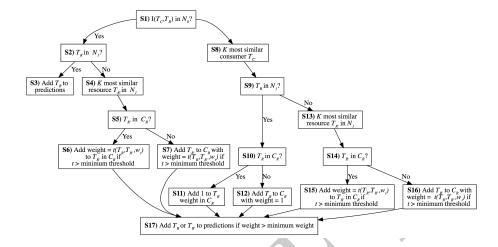


Figure 1: Description of logical steps used by the algorithm to suggest a list of candidate resources  $(C_R)$  for each consumer taxa  $(T_C)$  in an arbitrary set of  $N_1$  for which interactions are predicted, using a set of taxa  $N_0$  with empirically described interactions. Interactions between 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.

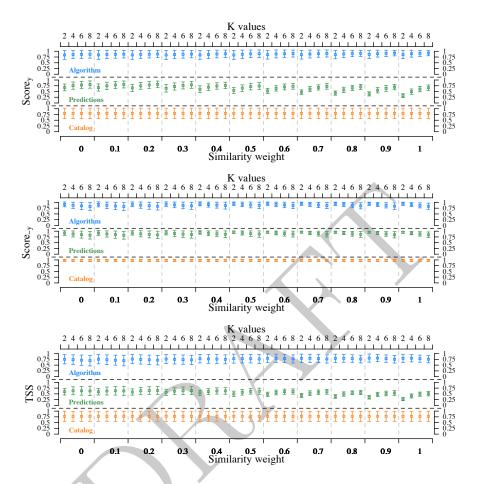


Figure 2: The graph presents the three statistics (i.e.  $Score_y$ ,  $Score_{\neg y}$  and TSS) used to evaluate the accuracy of the algorithm as a function of as a function of K values tested (i.e. 2, 4, 6 and 8 most similar seighbours, top x-axis) and trait weight (bottom x-axis), which varies between 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 (Christian and Luczkovich, 1999; Link, 2002; Thompson et al., 2004; Brose et al., 2005; Barnes et al., 2008; Kortsch et al., 2015)

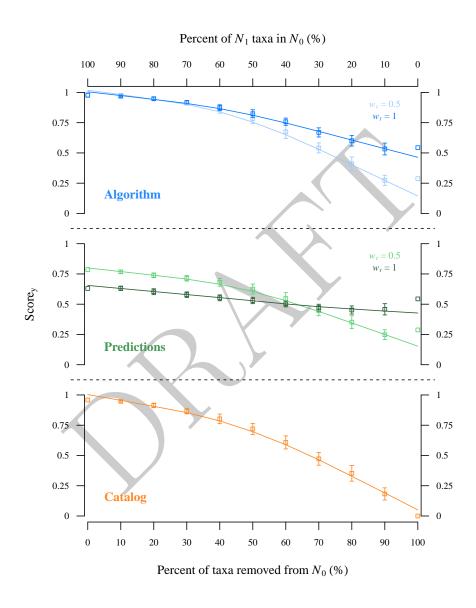


Figure 3: Caption on next page.

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.

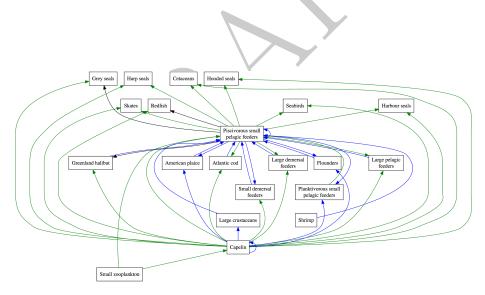


Figure 4: Example of results from the algorithm with the Network of the southern Gulf of St. Lawrence (Savenkoff et al., 2004) centered on interactions of the capelin (*Mallotus villosus*) and piscivorous small pelagic feeders (*e.g. Scomber scombrus and Illex illecebrosus*). Edge with colors green were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