

# Quantitative prediction of interactions in bipartite networks based on traits, abundances, and phylogeny

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## Abstract

Ecological interactions link species in networks. Loss of species from, or introduction of new species into, an existing network may have substantial effects for interaction patterns. Predicting changes in interaction frequency while allowing for rewiring of existing interactions, and hence estimating the consequences of community compositional changes is thus a central challenge for network ecology.

Interactions between species groups, such as pollinators and flowers or parasitoids and hosts, are moderated by matching morphological traits or sensory clues, most of which are unknown to us. If these traits are phylogenetically conserved, however, we can use phylogenetic distances to construct latent, surrogate traits and try to match those across groups, in addition to observed traits. Understanding how important traits and trait-matching are, relative to abundances and chance, is crucial to estimate the fundamental predictability of network interactions.

Here we present a statistically sound approach (“tapnet”) to fitting abundances, traits and phylogeny to observed network data in order to predict interaction frequencies. We thereby expand existing approaches to quantitative bipartite networks, which so far failed to correctly represent the non-independence of network interactions. Furthermore, we use simulations and cross-validation on independent data to evaluate the predictive power of the fit. Our results show that tapnet is on a par with abundance-only, matching-centrality and machine learning approaches. This approach also allows us to evaluate how well current concepts of trait matching work. Based on our results, we expect that interactions in well-sampled networks can be well predicted if traits and abundances are the main driver of interaction frequency.

Keywords: community, morphological trait, mutualist network, phylogeny, pollination

## 25 **Introduction**

26 Network ecology has vastly increased our knowledge of ecosystems, delivered fascinating in-  
27 sights into their organization (e.g. the slow-and-fast-energy channels in Rooney et al. 2006),  
28 and fostered speculation about co-evolution (e.g. Guimarães Jr et al., 2011). While arguably the  
29 litmus test of any ecological understanding is a test of its predictive power (Houlihan et al.,  
30 2017), only recently have predictive models of network interactions started to emerge (e.g. Ives  
31 and Godfray, 2006; Petchey et al., 2008; Crea et al., 2016; Rohr et al., 2016; Brousseau et al., 2018;  
32 Pichler et al., 2020). After several decades of research on ecological networks we have learned  
33 a lot about their patterns (e.g. along latitudinal or elevational gradients, across different types  
34 of interactions) and their stability (see, e.g. Bascompte and Jordano, 2014; Moore et al., 2017),  
35 yet so far we have had limited success in predicting interaction intensities or even aggregate  
36 network structure (as pointed out by Vázquez et al. 2009; Olito and Fox 2015; Poisot et al. 2016;  
37 Valdovinos et al. 2018, but see Pomeranz et al. 2019; Vizentin-Bugoni et al. 2020).

38 Some of the most successful attempts at predicting network structure were made in studies  
39 of food webs, where body size ratios were found to be a good predictor of presence or absence  
40 of predator-prey interactions (e.g. Allesina, 2011; Gravel et al., 2013; Pomeranz et al., 2019), and  
41 allometric scaling of parameters allowed to fit a mechanistic model of optimal foraging theory  
42 (the contingency model: Stephens and Krebs, 1986) to large networks (Beckerman et al., 2006;  
43 Petchey et al., 2008). However, body size is not a suitable predictor for most other interaction  
44 types, for example host–parasitoid interactions or interactions involving plants (Bascompte  
45 and Jordano, 2014; Dormann and Blüthgen, 2017). Moreover, while network predictions should  
46 ideally be based on theory, existing theoretical models such as the contingency model make  
47 strongly simplifying assumptions (e.g. sequential encounter of resources, maximising of av-  
48 erage resource intake, ideal knowledge of resource availability, no within-guild interference:  
49 Pyke, 1984; Stephens and Krebs, 1986), but still require large numbers of parameter values as  
50 input, which are difficult to provide without a shortcut such as allometric scaling. Thus, we still  
51 lack a general approach to predict various types of ecological networks. In addition, whereas  
52 most existing models of ecological networks only predict binary network structure, models

53 that allow to estimate the intensity of interspecific interactions can glean more information  
54 from the data.

55 While a theoretical model encompassing all types of interaction networks does not yet  
56 exist, there are obvious candidate factors for predicting interaction intensities, some at the level  
57 of the individual species (such as their abundance), some at the interplay of species, such as the  
58 match of interaction-relevant traits (Junker et al., 2010, 2013; Dehling et al., 2016). Since some  
59 of the relevant traits are difficult to measure, but show a phylogenetic signal, phylogeny can  
60 be used as a proxy for such unmeasured traits (Ives and Godfray, 2006; Pearse and Altermatt,  
61 2013; Morales-Castilla et al., 2015; Peralta, 2016).

62 There are several previous approaches to include traits, abundance and phylogeny into a  
63 statistical method to analyze and possibly predict interactions. They differ in their scope (bi-  
64 nary vs quantitative networks), the type of network (bipartite vs. unipartite) and the statistical  
65 method. For example, Ives and Godfray (2006), Pearse and Altermatt (2013), Rohr et al. (2016)  
66 and Crea et al. (2016) all used regression models to predict binary networks based on phy-  
67 logeny and measured traits. Brousseau et al. (2018) improved on the model of Rohr et al. (2016)  
68 by adding a larger number of traits as predictors and using a more flexible Generalized Addi-  
69 tive Model (GAM). Vázquez et al. (2009) and Olito and Fox (2015) chose a different statistical  
70 approach in which they constructed matrices of interaction probabilities based on traits and  
71 abundances and assumed that the observed interaction intensities are drawn from a multino-  
72 mial distribution with these probabilities. Most recently, Desjardins-Proulx et al. (2017) and  
73 Pichler et al. (2020) modelled interaction networks using machine-learning algorithms, which  
74 are highly flexible, but provide little information on the underlying mechanisms of the inter-  
75 actions.

76 While the above-mentioned approaches have had some success in describing ecological  
77 networks, they are faced with two issues, one statistical, the other ecological. First, most meth-  
78 ods treat the interactions in a network as statistically independent (except Vázquez et al., 2009;  
79 Olito and Fox, 2015; Crea et al., 2016), although this assumption is likely to be violated. Any  
80 interaction with one species precludes the interaction with other species at the same time;  
81 thus, one more observation here inevitably means one less there. Furthermore, depending on

82 the type of interaction and method of data collection, the same individual may be observed  
83 multiple times, again violating the independence assumption. Finally, interactions of differ-  
84 ent consumer species may be non-independent due to intraguild competition for resources,  
85 which can cause shifts in species' preferences (e.g. Loeuille and Loreau, 2005; Spiesman and  
86 Gratton, 2016). Such non-independence must be accounted for in order not to yield biased and  
87 overconfident model estimates.

88 An ecological issue is how to represent the role of species traits and their matching. Models  
89 based on linear regression assume that all traits and trait combinations have linear effects on  
90 interaction probabilities, while machine-learning algorithms do not provide any information  
91 on the mechanisms connecting traits to interactions. In reality, interaction intensities may  
92 depend on the matching of quantitative trait values in nonlinear and possibly asymmetric  
93 ways. For instance, large billed birds can feed on small seeds, but small billed ones not on  
94 large seeds (e.g. Muñoz et al., 2017). Ideally, models of ecological networks should allow to  
95 explicitly incorporate such trait-matching mechanisms, to correctly represent the ecological  
96 mechanisms and provide accurate predictions (but see Sebastián-González et al., 2016, for an  
97 implicit approach).

98 In this paper we present a statistical approach to analyzing and predicting interaction in-  
99 tensity, based on observed and phylogeny-based latent traits and their matching, alongside  
100 abundances of each species. Unlike previous analyses, which were mostly explorative, we  
101 assess our model's performance on independent network data that were not used for fitting.  
102 For more ecological realism, and in extension to previous approaches, we provide symmetric  
103 and asymmetric trait-matching functions. In contrast to all previous approaches for traits and  
104 phylogeny, we account for the non-independence of observations in the network, using the  
105 multinomial probability approach of Vázquez et al. (2009) and Olito and Fox (2015). Finally, we  
106 assess the quality of our approach at the level of the individual link, not only at the level of  
107 network patterns, as the aim is to predict a specific interaction.

108 Our approach can be used for prediction of, say, introduction or loss of species from a  
109 community, which may lead to a "rewiring" of interactions, or for predicting the effects of  
110 changes in abundances. Moreover, it can be used to quantify the importance of observed trait

111 pairs for such predictions, such as the morphological compatibility of a plant’s flower corolla  
112 and a pollinator’s proboscis, or the beak size of a frugivorous bird and the size of a fruit (see  
113 also Pichler et al., 2020).

114 We first outline the idea and details behind our approach, then demonstrate its validity  
115 with simulated data, and finally use three hummingbird-flower networks to make predictions  
116 across habitats. In that case study, we also use alternative published approaches to gauge their  
117 performances on real-world validation data.

## 118 **Methods**

119 We call our approach “tapnet”, as it uses traits, abundance-activity and phylogeny to predict  
120 network interactions. Our background in pollination ecology makes it natural for us to think  
121 of bipartite interaction networks, where one group’s members (e.g. pollinators) interact with  
122 members of another group (e.g. plants), but not within each group. However, the approach can  
123 be similarly applied to functional group- or individual-based networks and probably extended  
124 to one-mode networks, but that is beyond the scope of our study. In the case of analysing  
125 individuals, species’ average traits would be replaced by individual trait values. Abundances  
126 could either be removed completely or replaced by some measure of individual activity.

127 Before explaining our approach in detail, here is an outline (Fig. 1): We developed a model  
128 that outputs expected interaction probabilities based on traits, abundances and phylogenies.  
129 We can now compare the output with an observed network and optimize model parameters so  
130 as to maximize fit. In this way we estimate several (largely) ecologically interpretable param-  
131 eters. For prediction, we can use the fitted model together with new abundances (including  
132 previously unobserved species) and yield expected interaction probabilities. While the role of  
133 traits is probably clear, phylogenies are used to construct so-called latent traits to be matched  
134 across groups. As a side effect, new species entering a community can be positioned in the  
135 phylogeny and this position then feeds through to the actual predictions, in addition to the  
136 (optional) observed traits.

137 Traits refer to species-specific characteristics that have a counterpart in a trait of the other

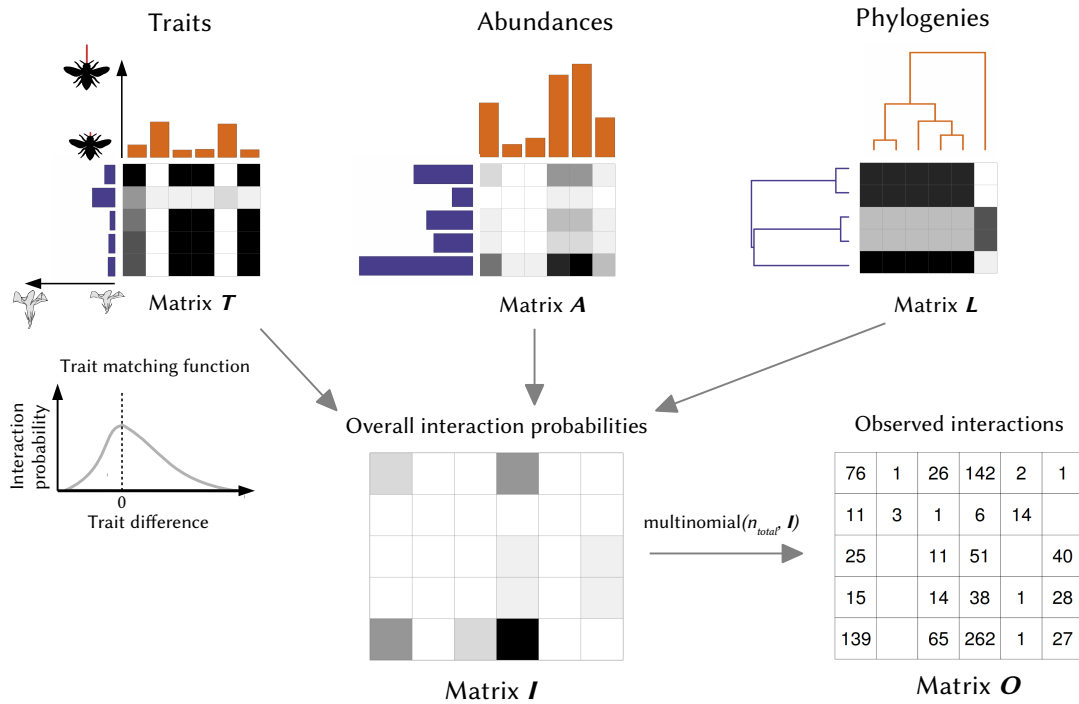


Figure 1: Conceptual overview of the tapnet approach. Tapnet combines information on trait matching (**T**), abundances (**A**) and phylogeny-derived matching latent traits (**L**) (top row) into a single matrix **I** of predicted interaction probabilities. The observed interaction network **O** is assumed to be drawn from a multinomial distribution with probabilities given by **I** and total number of interactions  $n_{total}$  equaling the observed number of interactions. Traits have to be provided in pairs across the two levels, which are then compared using a possibly asymmetric trait-matching function. Each input yields an independent matrix of interaction probabilities, which are then multiplied and re-scaled to yield the final interaction matrix **I**. Matrix cells are filled in different shades of gray to indicate interaction probabilities from zero (white) to one (black). Some values which are close to zero appear white.

138 group, and the analyst must provide these traits in matching format (i.e. corolla and proboscis  
139 length, or phenologies during a season, quantified in such a way that the same value for both  
140 would imply a perfect match). The model can be employed without trait information.

141 Abundance-activity (henceforth abundances) can be any measure proportional to the prob-  
142 ability of encountering a species in the field. For instance, a plant with an attractive scent would  
143 be more conspicuous to a pollinator than a non-odorant one. And an abundant bee would be  
144 encountered more often than a rare one, if they move at the same rate (hence abundance-  
145 activity). If the trait-pairs responsible for interaction activity are known and provided to tap-  
146 net, the role of actual abundances can be quantified, otherwise the two will remain confounded  
147 (as in any other analysis).

148 Phylogenies for each group are used as building blocks for unobserved (latent) traits mod-  
149 erating species interactions. They add complementary information to the observed traits (Pearse  
150 et al., 2013), and may be able to suggest possible additional traits that underlie the observed  
151 interactions.

152 We present the approach starting with the statistical goal and then going into ever more  
153 detail. We provide R-code for simulating “tapnet” data, for fitting observed networks, for as-  
154 sessing model fit and for predicting to new abundances and traits in the package tapnet.<sup>1</sup>

## 155 Likelihood

156 Our approach is to fit a (non-standard) statistical model to observed data on interaction net-  
157 works. While we can use several networks simultaneously to fit the model, we restrict our  
158 outline here to the simplest case of only one observed network. Let us call the observed inter-  
159 action matrix  $\mathbf{O}$  of dimension  $m \times n$  ( $m$  rows by  $n$  columns).

160 We compare  $\mathbf{O}$  with our model predictions  $\mathbf{P}$  by means of a multinomial distribution  
161 (eqn 1), as entries in that interaction matrix are non-independent. (Entries in  $\mathbf{O}$  are integers,  
162 typically number of observed interactions per standardized observation effort. For continuously-  
163 valued observations, a Dirichlet distribution could probably be employed: Crea et al. 2016.) To  
164 do so, we represent  $\mathbf{O}$  as a vector of length  $mn$ , rather than a matrix. Formally, we predict the

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<sup>1</sup><https://github.com/biometry/tapnet>



165 entries in  $\mathbf{O}$ ,  $o_i$ , based on the total number of observed interactions,  $n_{\text{total}} = \sum_{i=1}^{mn} o_i$ , and the  
 166 vector of predicted interaction probabilities,  $\hat{p}_i$ , which are the output of our model:

$$f(o_1, \dots, o_{mn}; n_{\text{total}}, \hat{p}_1, \dots, \hat{p}_{mn}) = \frac{n_{\text{total}}!}{\prod_i o_i!} \prod_{i=1}^{mn} \hat{p}_i^{o_i} \quad (1)$$

## 167 **Model components**

168 Our model yields a matrix of predicted interactions,  $\mathbf{P} = (\hat{p}_{i,j}) \in \mathbb{R}^{m \times n}$ , as (re-scaled) Hadamard  
 169 (= element-wise) product of three prediction components: abundance-based expected proba-  
 170 bilities  $\mathbf{A}$ , trait-matching based expected probabilities  $\mathbf{T}$ , and latent-trait-based expected prob-  
 171 abilities  $\mathbf{L}$ , each scaled to sum to 1:

$$\mathbf{P} = \mathbf{A} \circ \frac{(\mathbf{T} \circ \mathbf{L})^\delta}{\sum (\mathbf{T} \circ \mathbf{L})^\delta}. \quad (2)$$

172  $\mathbf{A}$  is the matrix of abundance-based interaction probabilities based on the cross-product of  
 173 normalized species abundances vectors for the lower  $o_A^l$  and higher  $o_A^h$  trophic level (note that  
 174 we reserve capital letters for matrices):  $\mathbf{A} = \frac{o_A^l}{\sum o_A^l} \times \frac{o_A^h}{\sum o_A^h}$ . Thus,  $\mathbf{A}$  represents the probability  
 175 of an interaction for each cell based only on the relative abundances of the different species:  
 176 we would expect more interactions among common species than among rare species.  $o_A^{l,h}$  is  
 177 based on independently measured abundances, not simply the marginal totals of the observed  
 178 matrix  $\mathbf{O}$ . The free exponent,  $\delta \in (0, 1)$ , allows the optimization to give more or less weight to  
 179 traits relative to abundance, and thereby also serves as a quantification of the importance of  
 180 abundance within the fit. As a side-effect, the abundance-only predictions are a limiting case  
 181 of tapnet, for  $\delta = 0$ . The denominator summing over  $(\mathbf{T} \circ \mathbf{L})^\delta$  is necessary to re-normalize this  
 182 term to sum to 1, on a par with  $\mathbf{A}$ .

183  $\mathbf{T}$  is the matrix of expected interaction probabilities based on the degree to which observed  
 184 traits match between species of the different groups. If, say, the proboscis of a pollinator is a  
 185 bit too short or too long compared to the depth of the corolla of a plant species, then inter-  
 186 actions become less likely than perfectly matching lengths. We define a (single parameter)  
 187 trait-matching function for a pair  $(i, j)$  of trait values  $f_i(t_i^l, t_j^h)$  by the Gaussian function:

$$f_t(t_i^l, t_j^h, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(t_j^h - t_i^l)^2}{2\sigma^2}}. \quad (3)$$

188 Alternatively, we can define an asymmetric matching function (a log-normal with its mode  
189 shifted to 0), as too long a proboscis is no obstacle to an interaction, while one too short is:

$$f_t(t_i^l, t_j^h, \mu) = \frac{1}{(t_j^h - t_i^l + e^{\mu-1})\sqrt{2\pi}} e^{-\frac{1}{2}(\ln(t_j^h - t_i^l + e^{\mu-1}) - \mu)^2}, \quad (4)$$

190 where  $e^{\mu-1}$  is a parameter determining the shape of the function, in a similar way to  $\sigma$  in eqn 3.  
191 It is fit during the model optimization (see further below). Other functions could of course  
192 be used, especially when the relationship between trait values and interaction probability is  
193 known. The trait-matching functions is computed for all species, i.e. the inputs are in fact  
194 vectors of trait values for the lower ( $\mathbf{t}^l$ ) and higher level ( $\mathbf{t}^h$ ). The elements of  $\mathbf{T}$ , ( $\tau_{ij}$ ), are the  
195  $f_t$ -values computed using eqns. 3 or 4: ( $\tau_{ij}$ ) =  $f_t(t_i^l, t_j^h)$ .

196 Latent-trait-based interaction probability matrix  $\mathbf{L}$ , finally, is the most complex matrix of  
197 expected interaction probabilities. Its function is primarily to improve predictions, as abun-  
198 dances and observed traits are unlikely to be sufficient to capture the information present in  
199 the observed interaction matrix. Just like  $\mathbf{T}$ , also  $\mathbf{L}$  is found by matching traits of one level  
200 to those of the other by optimizing the  $\sigma$ -parameter of its Gaussian trait-matching function  
201 (eqn 3). In this case, however, these traits are unobserved (latent) and are constructed as part  
202 of the optimization process from phylogenetic eigenvectors, as explained in the next section.

## 203 **Constructing matching latent trait values**

204 The reasons why a species from one group interacts with one from another may be extremely  
205 complex. Bees, for example, may rely on visual and olfactorial signals, as well as innate pref-  
206 erences and learned behavior, for selecting a flower to visit (Chittka and Raine, 2006). On the  
207 other hand, plants may increase nectar production in response to sensing pollinator's wing-  
208 beats (Veits et al., 2019). If these traits can be measured, they can be used in tapnet as observed  
209 traits. In many cases, however, we may have little chance to identify, let alone measure, the

210 traits involved. In such cases, one can “invent” trait values with the sole aim of improving the  
211 fit of the model.

212 Computationally it is more efficient, and ecologically more satisfactory, if there is a basis  
213 for computing such latent trait values (similar to geographic distances in spatial models used  
214 in joint species distribution models: Warton et al., 2015). In our case, we assume latent traits  
215 to summarize traits correlated with phylogeny. These latent traits typically exhibit no phy-  
216 logenetic signal anymore, and the phylogenies are only used as an efficient way to generate  
217 orthogonal vectors. This approach has several benefits. Firstly, it allows us to introduce new  
218 species when predicting from the fitted tapnet model, as we can compute their phylogenetic  
219 position relative to the other species in the group, and hence also the value of their latent  
220 trait. Secondly, the resulting latent trait may, upon mapping it to the phylogeny, suggest a  
221 hypothesis about an actual trait behind it.

222 Technically, constructing a latent trait within a group is straightforward if a phylogeny  
223 is available. Alternatively, a taxonomy can be used (Clarke and Warwick, 1999). From such a  
224 phylogeny one can compute phylogenetic eigenvectors (Guénard et al., 2013), i.e. for  $k$  species  
225  $k - 1$  vectors that are orthogonal to each other and represent the information of the phylogeny  
226 (similar to the way a Principal Component Analysis summarizes the information in a data set):  
227 the first phylogenetic eigenvector accounts for the largest genetic differences in the tree, the  
228 second for the largest in the remaining variation, and so forth. Mathematically, a phylogenetic  
229 tree can be represented as a (cophenetic) distance matrix, and an eigenvalue decomposition of  
230 said distance matrix yields the phylogenetic eigenvectors.

231 For each group, we can now define a latent trait vector  $\mathbf{l}$  as a linear combination of the  
232 phylogenetic eigenvectors  $\mathbf{p}_1, \dots, \mathbf{p}_{k-1}$ , one for each trophic level:

$$\begin{aligned}\mathbf{l}^l &= a_1\mathbf{p}_1^l + a_2\mathbf{p}_2^l + a_3\mathbf{p}_3^l + \dots + a_{m-1}\mathbf{p}_{m-1}^l \\ \mathbf{l}^h &= b_0 + b_1\mathbf{p}_1^h + b_2\mathbf{p}_2^h + b_3\mathbf{p}_3^h + \dots + b_{n-1}\mathbf{p}_{n-1}^h\end{aligned}\quad (5)$$

233 For computational reasons, we will only use the first few (3-5) phylogenetic eigenvectors.  
234 When  $\mathbf{l}^l$  and  $\mathbf{l}^h$  match, the probability of an interaction is high, just like for observed traits

235  $\mathbf{t}^l$  and  $\mathbf{t}^h$  above. The values of  $a_i$  and  $b_i$  have to be found by optimisation. Since the values of  
236  $\mathbf{l}$  are void of meaning, one cannot assume that the latent vectors align optimally. Therefore,  
237 a shift parameter is fitted for the higher trophic level ( $b_0$ ). Analogous to  $\mathbf{T}$ , the elements of  
238  $\mathbf{L}$ ,  $(\ell_{ij})$ , are the  $f_i$ -values computed using eqn 3 based on the latent traits:  $(\ell_{ij}) = f_t(l_i^l, l_j^h)$ .

## 239 **Fitting the model**

240 The tapnet model outlined above can now be fitted to the observed interaction network by ad-  
241 justing several parameters. As input the model requires the paired observed traits (0 to many);  
242 the phylogeny of each group; the abundance vector for each group, and for computation of  
243 the likelihood, the observed interaction matrix. The model parameters are

- 244 1. the width of the trait matching function ( $\sigma$  in eqn 3) for each pair of traits;
- 245 2. the width of the trait matching function for the latent traits; and,
- 246 3. two vectors of parameters for the construction of the latent trait (eqn 5).

247 In the optimization using the standard Nelder-Mead algorithm, we used a few tricks to  
248 increase the reliability of the model. To ensure identifiability, we constrained  $a_1$  to be positive  
249 (i.e. defined it as  $e^{a_1}$ ). Otherwise the exact same values with inverted signs would yield the  
250 same fit. Furthermore, any multiple of  $\mathbf{a}^l, \mathbf{a}^h$  would yield the same prediction. Therefore we  
251 standardized both  $\mathbf{l}^l$  and  $\mathbf{l}^h$  before entering them into the trait-matching function (eqn 3).

252 When fitting multiple networks simultaneously or when using different networks for op-  
253 timization and prediction, we run into the problem of having different species present in each  
254 network. In such cases we first calculate the eigenvectors of the phylogenetic tree containing  
255 all species from all networks. In a second step, we select from these eigenvectors those that  
256 are most relevant for the respective network, i.e. the eigenvectors most closely correlated with  
257 each of the eigenvectors of the tree containing only the species of this particular network. We  
258 then fit parameters only for the selected relevant eigenvectors.

## 259 **Assessing model quality**

260 Optimizing the model parameters immediately yields the model’s likelihood. Additionally, we  
261 may be interested in the latent variables, as they code the (combination of) trait(s) missing  
262 in our observed data. For simulated data, we can compare the reconstructed latent traits with  
263 those actually simulated. Predicted and observed interactions were additionally compared us-  
264 ing other distance measures, such as the Pearson correlation or Bray-Curtis distance, or by  
265 summarizing the network structure by indices (such as nestedness or specialization). For net-  
266 work indices, we drew 1000 realizations from the fitted multinomial distribution of each sim-  
267 ulated network (see below) and computed network indices for these. Then, we computed on  
268 which quantile of these 1000 realization the observed network’s index lay (sometimes called  
269 the ‘posterior p-value’: Gelman, 2005). Ideally, this value should be 0.5, indicating no bias in  
270 indices in the fitted network.

## 271 **Simulations**

272 To assess how performance of the tapnet model varies with the characteristics of the data  
273 used for fitting, we performed two simulation experiments. The first aimed to evaluate the  
274 model’s goodness of fit to the interaction network used for estimating parameters, while the  
275 second was designed to test the model’s accuracy of prediction to a new network. In both  
276 experiments we varied six parameters (Table 1) using Latin hypercube sampling (McKay et al.,  
277 1979). Ranges of numerical parameters were divided into 500 equally spaced intervals, and a  
278 single random value was drawn from each interval. For parameters with integer values (e.g.  
279 number of observed traits), drawn values were rounded to the nearest integer. In the case  
280 of categorical parameters, we randomly sampled 500 times with replacement from the set of  
281 possible values. (A pre-run with only 100 samples yielded virtually identical results, indicating  
282 that 500 runs are sufficient.) Since the number of observed traits varied between zero and  
283 four, we drew four sets of 500 values for the width parameter of the trait matching function.  
284 Depending on the number of observed traits of the respective parameter combination, we used  
285 only a subset of the four values to calculate matrix  $\mathbf{T}$  (or none at all with zero traits).

Table 1: Parameters varied in the simulation experiments used to assess the model’s goodness of fit. The “width” parameter defines the sensitivity of the probability of an interaction to mismatches between traits; small values demand very neat matching for an interaction to be likely.

Parameter	Type	Range or possible values
Total number of observed interactions $n_{\text{total}}$	integer	50 - 1000
Number of observed traits	integer	0 - 4
Type of trait-matching function for observed traits	categorical	normal or shifted log-normal
Shape of abundance distribution	categorical	uniform or log-normal
Width parameter of trait matching function for observed traits	continuous	0.05 - 1
Width parameter of trait matching function for latent traits	continuous	0.05 - 2

286 For each of the 500 parameter combinations, we simulated a data set consisting of relative  
 287 abundances, phylogenetic trees and pairs of matching traits. Species abundances were either  
 288 all set to the same value ( $1/m$  or  $1/n$ , respectively) or drawn from a log-normal distribution  
 289 with parameters  $\mu = 0$  and  $\sigma^2 = 1$  and standardized to a sum of one. Trait values were likewise  
 290 drawn from a log-normal distribution with  $\mu = 0$  and  $\sigma^2 = 1$ . We simulated phylogenetic trees  
 291 using the function “pbtree” from R package “phytools” (Revell, 2012) with a speciation rate of  
 292 1 and extinction rate of 0.

293 For both experiments, we simulated phylogenies and traits of 30 and 60 lower- and higher-  
 294 trophic level species, respectively, for each parameter combination. These data were used to  
 295 construct a matrix of interaction probabilities  $\mathbf{P}$  according to the “tapnet” model as described  
 296 above. While the width parameters of the trait matching functions for observed and latent  
 297 traits were systematically varied between simulations, the latent trait linear combination pa-  
 298 rameters  $a_i$  were set to a value of 1 in all simulations. From the interaction probabilities we  
 299 constructed a network of simulated interactions with total number of interactions  $n_{\text{total}}$  by  
 300 drawing from a multinomial distribution with probabilities  $\hat{p}_{i,j}$ .

301 For the first experiment, we then randomly selected 15 (lower trophic level) and 30 (higher  
 302 trophic level) species. To these data, we fit tapnet and assess goodness of fit.

303 For the second experiment, we randomly drew *twice* a random set of  $15 \times 30$  species.  
 304 Again, tapnet was fit to the first, but then predicted to the second set. On average, these two

305 sets share half of their species and 25% of their interactions. It thus represents a strong test of  
306 predicting to new data. As measures of goodness of fit, we calculated the Bray-Curtis similarity  
307 and Spearman rank-correlation between the entries of simulated and predicted networks.

## 308 **Independently observed vs network-derived abundances**

309 The majority of published interactions networks does not provide independent estimates of  
310 the abundances of each species ( $o_A^l$  and  $o_A^h$  for lower and higher trophic level, respectively;  
311 see eqn 2). In current network analyses, it is thus customary to use network-derived, marginal  
312 totals of the network matrix ( $\mathbf{O}_{\cdot i}$  and  $\mathbf{O}_{\cdot j}$ , respectively) as plugin instead (e.g. to formulate null  
313 model expectations: Vázquez and Aizen, 2003; Barber, 2007; Blüthgen et al., 2007; Dormann  
314 et al., 2009). However, these marginal totals carry the imprint of network structure. In one ex-  
315 treme, pollinators in the region may simply not be attracted by the flowers in the patch under  
316 consideration and hence are not present in the network. Or, in the case of antagonistic net-  
317 works, a parasite may reduce the population size of its host to such a degree that interactions  
318 are hardly observed, although their intensity is very high (e.g. Barbosa et al., 2017).

319 We investigated the consequences of using independent vs network-derived abundances  
320 on prediction quality with the simulated data. For the same simulated data, we once fit tapnet  
321 with the simulated independent abundances and once with the marginal totals of the simulated  
322 interaction network. We then predict to either the independent abundances of the second sim-  
323 ulated network vs its marginal totals. We expect that network-derived abundances will lead  
324 to a better model prediction, simply because they contain information on the structure of the  
325 test network.

## 326 **Case study**

327 As a demonstration, we use the case study of Tinoco et al. (2017), who compiled data on  
328 hummingbird-pollination networks in three different habitats (forest, shrubland and a cat-  
329 tle farm) in the southern Ecuadorian Andes. The data published alongside the paper<sup>2</sup> include  
330 traits for both plants and hummingbirds, as well as external abundance data. These networks

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<sup>2</sup><http://dx.doi.org/10.5061/dryad.j860>

331 are unusually intensively sampled, with 1288, 3979 and 2405 interactions in each of the three  
332 habitats, respectively, across 32 plant and 14 hummingbird species, some occurring only in one  
333 habitat.

334 In the case study, we additionally compare the predictive performance of tapnet with  
335 three different alternative approaches: abundance-only, trait-matching-and-phylogeny GAM  
336 following the ideas of Brousseau et al. (2018), and a similar model using random forest (see  
337 supplementary material for R-code and detailed results).

338 The abundance-only model can be seen as a baseline: it uses only the information on the  
339 activity/abundance of the  $m$  lower level and  $n$  higher level species in the validation data  $v$ ,  
340 specifying the estimated probability of interactions:  $\widehat{\mathbf{P}}_v = \frac{\mathbf{o}_v^l}{\sum_{i=1}^m o_{v,i}^l} \times \frac{\mathbf{o}_v^h}{\sum_{j=1}^n o_{v,j}^h}$ . Multiplying this  
341 with the number of observed interactions,  $N_{\text{total}} = \sum o^l = \sum o^h$ , yields the predicted interaction  
342 intensity. Only improving on this model demonstrates explanatory power of traits and their  
343 matching.

344 Following the approach of Brousseau et al. (2018), we fitted a negative-binomial GAM us-  
345 ing 2-D-splines on the first phylogenetic eigenvectors of each group, the same for the second  
346 eigenvectors, the observed trait values per species of each group and the squared difference  
347 between traits (representing trait matching). While the original approach used traits and phy-  
348 logenies to predict binary networks, here we predicted quantitative interaction matrices and  
349 additionally used the abundances as predictors. Spline complexity was set to  $k = 3$  for uni-  
350 variate and  $k = 20$  for 2D-splines, and an additional shrinkage was imposed by setting gamma  
351 to 1.4, both following Brousseau et al. (2018). Note that this approach, as well as the next,  
352 implicitly assumes entries of the interaction matrix to be (conditionally) independent (see dis-  
353 cussion).

354 The random forest approach was run using default setting (i.e. 500 trees, trying the rounded  
355 down square root of number of predictors at each split). It was provided with the same infor-  
356 mation as the previous GAM but using all phylogenetic eigenvectors; it serves as a comparison  
357 of the algorithm's flexibility, as it allows for interactions among the predictors.

358 While tapnet can fit several networks simultaneously (see supplementary material), we  
359 employed it akin to the other approaches in a cross-validation setting: the models were fitted



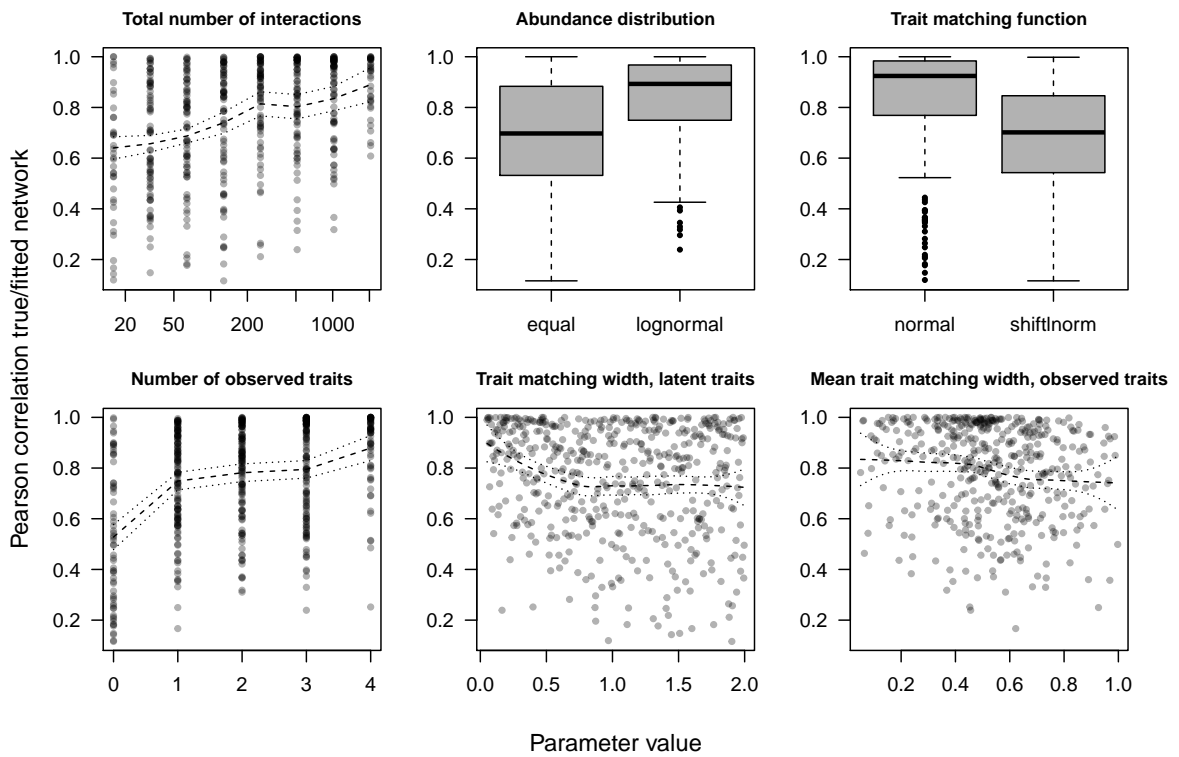


Figure 2: Pearson correlation between fitted model prediction and the simulated interaction network. Scatter plots show the correlation coefficient  $\rho$  as a function of six model parameters whose values were varied simultaneously using Latin Hypercube sampling. Data were simulated for 500 parameter combinations. Networks were of size  $15 \times 30$  species. Lines represent local weighted smoothers and their 95% confidence interval to indicate trends in the simulations.

360 to one network, and then predicted to the two others in turn. Results were compared using  
 361 the correlation between predicted and observed interactions.

362 Models were fit in R using packages `mgcv` (Wood, 2006) and `ranger` (Wright and Ziegler,  
 363 2017); see supplement for R-code of simulations and case study.

## 364 Results

### 365 Simulations

366 In the first simulation experiment, the correlation between observed and fit networks was  
 367 overall only moderate (mean value  $r = 0.76$  across all 500 parameter combinations). A strong  
 368 effect of the number of observations was detectable, yielding high correlations between ob-

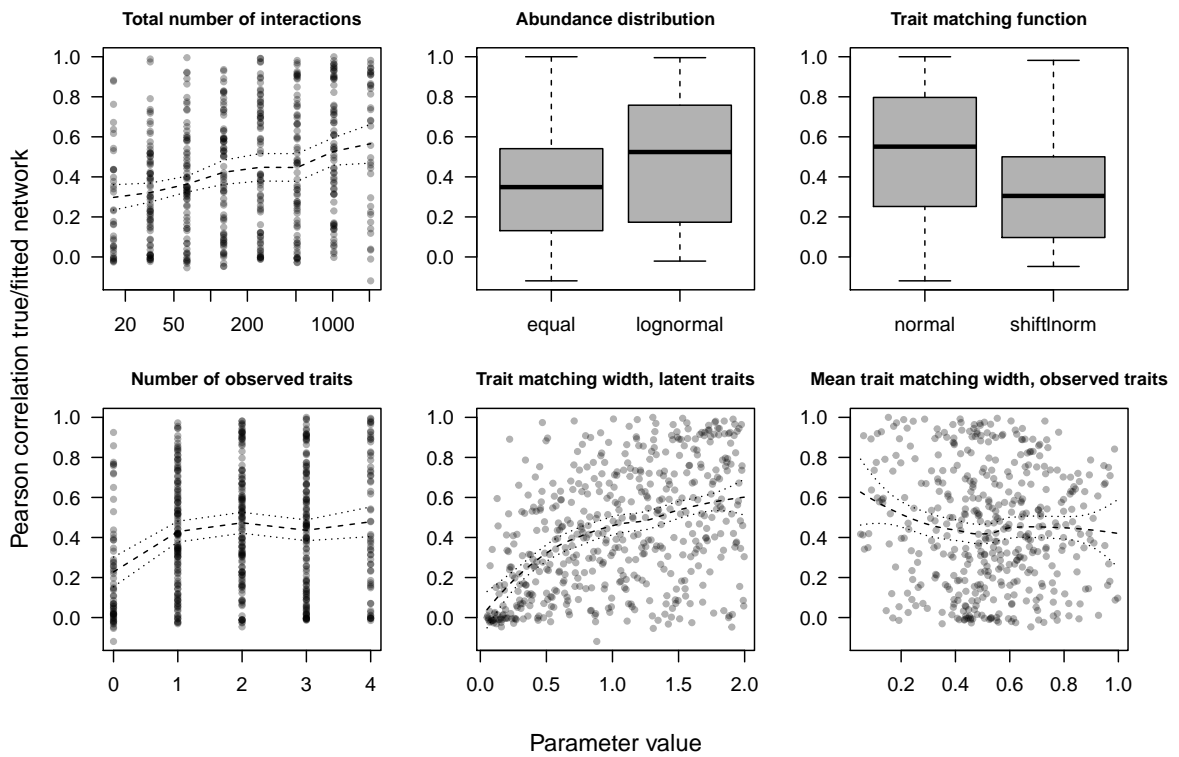


Figure 3: Pearson correlation between model predictions and a new interaction network simulated with identical parameter values. Scatterplots show the correlation coefficient  $\rho$  as a function of six model parameters whose values were varied simultaneously using Latin Hypercube sampling. Data were simulated for 500 parameter combinations. Lines represent local weighted smoothers and their 95% confidence interval to indicate trends in the simulations.

369 served and fit networks ( $\bar{r} > 0.83$ ) for networks with more than 0.5 (i.e. 250 interactions in a  
 370 network with  $15 \cdot 30 = 450$  cells) observations per number of cells (Fig. 2, top left). Correlation  
 371 coefficients were lower for networks with equal than for log-normal abundances of all species,  
 372 and higher for the ‘normal’ trait-matching functions than shifted log-normal. With increasing  
 373 number of observed traits, correlation coefficients also increased, indicating the usefulness  
 374 of observed traits for thinly sampled networks. The two trait-matching function parameters  
 375 (trait matching width of latent and of observed traits) did not seem to have a clear effect on  
 376 the correlation between observed and predicted networks. Patterns of variation in Bray-Curtis  
 377 similarity of observed and predicted networks were similar to those for Pearson’s  $r$  (results not  
 378 shown).

379 In the second simulation experiment, with prediction to a new network, patterns were  
 380 very similar to those in the fitting-evaluation, with overall lower correlations ( $\bar{r} = 0.42$ , and

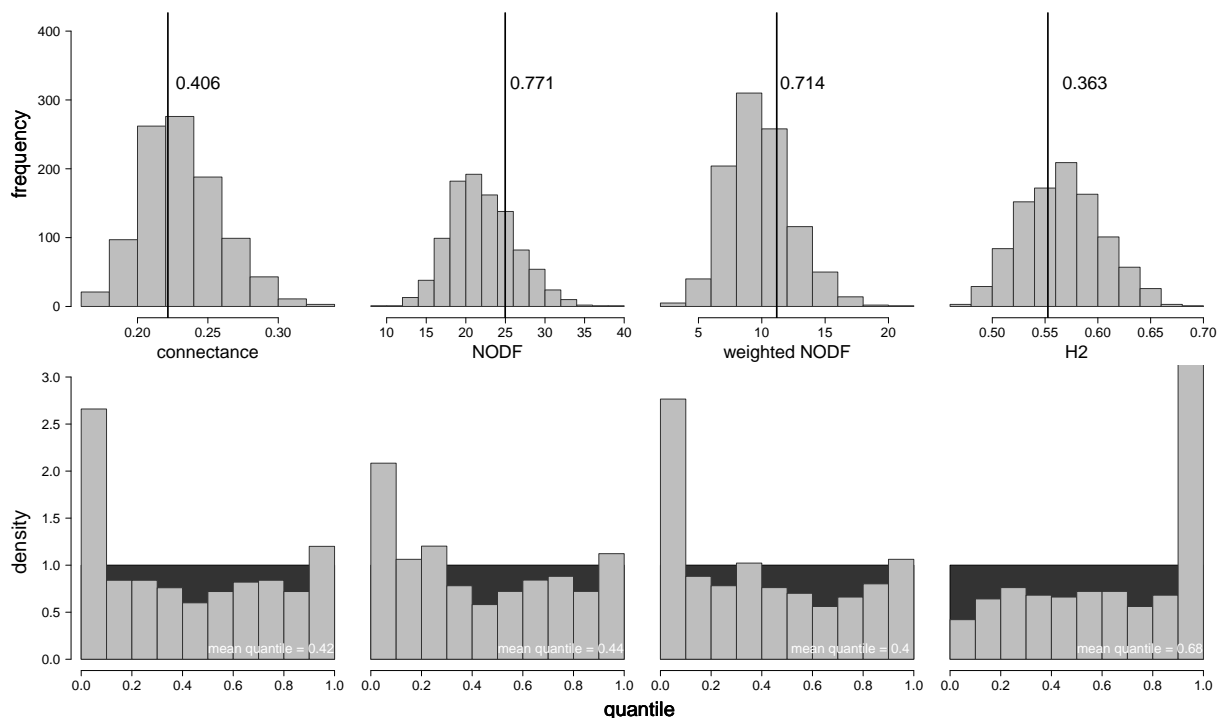


Figure 4: *Top row*: Example of network indices for 1000 realizations of one fitted network, compared with the simulated true value (vertical line; number gives quantile of true value within this frequency distribution). *Bottom row*: Quantiles of true network index values across the 500 simulations of experiment 1. Black background indicates ideal, uniform distribution. Despite a good overall match, spikes indicate a consistent underestimation of specialisation and hence lower connectance, lower nestedness and higher specialisation in the observed network.

381 for densely sampled networks  $\bar{r} = 0.49$ ). Correlation coefficients depended strongly on the  
 382 number of observations, abundance distribution and type of trait-matching function employed  
 383 (Fig. 3). All other parameters had much less effect, and the difference between the two trait-  
 384 matching functions can thus be seen as two almost separate sets of points in all plots apart  
 385 from the categorical abundances.

386 Network indices for random realizations of the fitted network were very similar to those of  
 387 the observed, usually falling within the 95% confidence interval of the null model (Fig. 4). To  
 388 assess the coverage of the fits and their potential bias, we computed posterior  $p$ -values for each  
 389 index as mean quantile (see methods: Assessing model quality). Across the 500 simulations of  
 390 the first experiment, mean posterior  $p$ -values were: connectance 0.42; NODF 0.44; weighted  
 391 NODF 0.40; and  $H_2'$  0.68, all indicating a slightly too generalist estimation of network structure  
 392 (Fig. 4, bottom row).

Table 2: Pearson correlation coefficients between fitted and observed hummingbird-flower network (Tinoco et al., 2017) for the four approaches, and their mean across the three habitats. Approaches are sorted by ranking in their cross-validation performance (Table 3).

Approach	Forest	Shrub	Farm	Mean
abundance-only	0.25	0.09	0.49	0.28
random forest	0.93	0.93	0.91	0.92
tapnet	0.57	0.60	0.65	0.61
GAM	0.56	0.29	0.40	0.42

### 393 **Difference between independent and network-derived abundances**

394 The fit of tapnet to the simulated data was slightly improved by using the marginal totals,  
 395 rather than the independently “observed” abundances ( $\bar{r} = 0.76 \pm 0.22$  (1 sd) for independent  
 396 abundances compared to  $\bar{r} = 0.83 \pm 0.15$  with marginal totals). Also the prediction to the  
 397 second simulated network, where half of the species were previously unobserved, improved  
 398 markedly from  $\bar{r} = 0.41 \pm 0.30$  for independent abundances to  $\bar{r} = 0.62 \pm 0.25$  with marginal  
 399 totals of the new network. Note that using *only* the marginal totals of the test network (with-  
 400 out traits or phylogeny) to predict interactions already fitted and predicted well, with a high  
 401 correlation between marginals and the new network interactions ( $\bar{r} = 0.66 \pm 0.17$ ).

### 402 **Case study**

403 The tapnet model fitted the three hummingbird-flower networks better than the abundance-  
 404 only model and the GAM, but worse than the random forest approach (Table 2). On cross-  
 405 validation, when fitting to one and predicting to the other two networks in turn, the tapnet  
 406 approach was no better or worse than the abundance-only and the random forest approach,  
 407 but substantially better than the GAM (Table 3). Interestingly, all approaches except the trait-  
 408 neutral, abundance-only lost dramatically in performance from train to test data. The GAM,  
 409 for example, fitted the data moderately, but held no predictive power for the test data. Ran-  
 410 dom forest, although reporting an extremely good fit, decreased to the level of tapnet and  
 411 abundance-only on the test data. This drop in performance from fitting to predicting suggests  
 412 that all statistical approaches overfitted, sometimes heavily.

Table 3: Pearson correlation of cross-validating by predicting with a model fitted to one habitat on the other habitats (indicated by  $\rightarrow$ ). F, S and C are for forest, shrubland and cattle farm, respectively. For cross-validation log-likelihoods, which show the same result, see supplementary material.

<b>Approach</b>	<b>F<math>\rightarrow</math>S</b>	<b>F<math>\rightarrow</math>C</b>	<b>S<math>\rightarrow</math>F</b>	<b>S<math>\rightarrow</math>C</b>	<b>C<math>\rightarrow</math>F</b>	<b>C<math>\rightarrow</math>S</b>	<b>Mean</b>
abundance-only	0.09	0.49	0.25	0.49	0.25	0.09	0.28
random forest	0.23	0.36	0.33	0.14	0.40	0.17	0.27
tapnet	0.21	0.46	0.12	0.53	0.15	0.11	0.26
GAM	-0.01	0.33	0.26	0.13	-0.01	-0.02	0.11

## 413 Discussion

414 Over the last years, two main, not mutually exclusive lines of modeling approaches to predict  
 415 network structure have emerged (as reviewed in Valdovinos, 2019). *Neutral models* assume all  
 416 species to be similar and generalist, and hence describe an expectation for network structure  
 417 primarily based on sampling intensity and abundance distributions. Indeed, such approaches  
 418 are often used as null model against which to gauge the effect of interaction preferences (e.g.  
 419 Vázquez and Aizen, 2003; Blüthgen et al., 2006; Dormann et al., 2009). In contrast, *interaction*  
 420 *constraint models* focus on why some links are not present, typically using species traits and  
 421 their match across the groups as explanatory features (Santamaría and Rodríguez-Gironés,  
 422 2007; Bartomeus et al., 2016). In the approach presented here, we combine both by allowing  
 423 abundances to contribute or even entirely dominate the prediction, but use matching between  
 424 observed traits and between latent traits as constraints.

425 The results so far are both promising and sobering. On the one hand we demonstrated that  
 426 we can fit the observed data well with the tapnet approach, and predict reasonably in sim-  
 427 ulated data. We can also predict with moderate accuracy networks from other habitats, and  
 428 that the tapnet approach did that better than some previous attempts to combine observed  
 429 and latent traits (Brousseau et al., 2018). On the other hand, by far the most important pre-  
 430 dictor for our case study was species abundance, which makes it easy for any approach and  
 431 prevents the trait-matching strength of tapnet to play out. Thus, a neutral model, using only  
 432 abundances, was as good in prediction (but not fit), and at the same time much simpler, than  
 433 tapnet or random forest. We think that at least two factors contribute to this finding: (1) the  
 434 hummingbird-flower-network is not very specialized, despite featuring the most spectacular

435 sword-billed hummingbird (*Ensifera ensifera*), whose pollination-adapted bill is longer than its  
436 body, and (2) when abundance is very important, the log-likelihood becomes very shallow and  
437 difficult to improve upon. Also, abundance may be correlated with a trait relevant for inter-  
438 actions, although in this case there was no correlation between bill/seed size and abundances  
439 ( $r = 0.019$  and  $-0.15$ , respectively; see supplement).

440 In simulations with many ( $> 500$ ) observations, tapnet predictions were very reasonable,  
441 while in the case study all approaches fared relatively poorly. Our simulations included pro-  
442 cesses deemed to be most important for determining network structure (compared to the list  
443 in Valdovinos, 2019). This suggests that either mutualist networks may simply be extremely  
444 noisy and under low evolutionary pressure, or that the current trait-matching concepts are  
445 not good enough for describing, across networks, the processes that drive interactions. This  
446 suggests a strong context-dependence of interactions, depending probably substantially on in-  
447 traspecific trait variation (Laughlin et al., 2012), behavioral complexity (Kaiser-Bunbury et al.,  
448 2010; Morán-López et al., 2020), competition within guilds (Vandermeer, 2004; Saavedra et al.,  
449 2013), non-linear frequency-dependence (Benadi and Pauw, 2018) and environmental condi-  
450 tions more generally (see Valdovinos, 2019, for review). Future research across many different  
451 networks has to show whether abundance is consistently such an important predictor for in-  
452 teraction frequencies.

## 453 **The chicken-and-egg problem of abundances and network structure**

454 Not all studies record independent abundances, e.g. by estimating floral cover, sweep-netting  
455 insects or alike, and this is more common for birds than for insects. Without such independent  
456 abundance data, its role for determining interaction frequencies cannot be determined. One  
457 frequent “solution” is to use the observed interactions of each species (the marginal totals of  
458 the interactions matrix) as surrogate for its abundance. This approach has been rightly criti-  
459 cized as confounding the effect of abundances on network interactions with the effect of net-  
460 work structure on abundances, i.e. the chicken-and-egg problem of network interactions (Fort  
461 et al., 2016; Dormann et al., 2017). This conflict was also detectable in our simulations, where  
462 the tapnet-prediction to the test data was substantially improved by using the test network’s

463 marginal total as predictor. Clearly, these surrogate abundances carry some information, be-  
464 yond abundance, on network structure and hence interaction intensity.

465 Flower-visitation networks are, in general, only moderately “ecologically specialized” (sensu  
466 Armbruster, 2017) (see, e.g., Blüthgen et al., 2007; Schleuning et al., 2012; Zanata et al., 2017),  
467 suggesting that neither plants nor pollinators depend crucially on a specific (set of) species to  
468 interact with. As a consequence, network structure and species abundances are strongly linked.  
469 In these cases, marginal totals may arguably be used in lieu of independent abundances. Our  
470 case study on a plant-pollinator system shows that this is not the correct approach. Indeed,  
471 when predicting the fitted model once with the external and once with the marginal abun-  
472 dances, we find a dramatically better performance for the marginal abundances (across the  
473 three habitats, predictive correlation is  $\bar{r} = 0.75$ , compared to a meager  $\bar{r} = 0.26$  with inde-  
474 pendent abundances: see supplementary material). Clearly, marginal abundances contain an a  
475 priori unknown amount of information, representing the outcome of within-guild interactions,  
476 variable activity of individuals, selection cues (scent, visual signals) and so forth.

## 477 **How independent are observed interactions?**

478 We believe that treating observed interactions as independent data is statistically incorrect  
479 (see introduction), thus questioning the likelihood used by Rohr et al. (2016) and Brousseau  
480 et al. (2018), as well as the implicit independence assumption in Pichler et al. (2020).

481 Therefore, we here used a (network-wide) multinomial distribution, as had been suggested  
482 by Vázquez et al. (2009), accommodating the compositional nature of the data. While it rec-  
483 ognizes the non-independence of observations, it does not thereby automatically capture the  
484 processes behind it. That means, while the inference based on this distribution is probably  
485 correct, our multinomial approach may not result in better predictions until the drivers of  
486 non-independence are represented in the model (e.g. intra-guild competition). Additionally  
487 this approach has two statistically relevant implications. First, we only get a single likelihood  
488 value for a network, rather than  $nm$ . As a consequence, secondly, we assess the fit of the entire  
489 model, without any chance of adapting only the fits of some specific species or interaction,  
490 as is the case for the GAM and random forest approaches used here for comparison. While

491 we regard it as a more correct representation of the data, it also severely limits the type of  
492 statistical approaches that can be used for predicting network interactions.

493 Olito and Fox (2015) focus on a comparison of network indices produced by their predictive  
494 approach with those of the observed network. They conclude that even similar networks may  
495 have rather different index values, and different networks similar indices, making such indices  
496 a poor target for optimization. In our simulated networks, we were able to fit networks so that  
497 their index values centered on the observed value. This illustrates that tapnet did manage to  
498 fit network indices in line with the observations as a by-product of the multinomial likelihood  
499 *in principle*.

## 500 **Traits, observed and latent**

501 Following the lead of previous studies (in particular Rohr et al., 2016), tapnet uses phylogenetic  
502 information to construct (not necessarily phylogenetically conserved) latent traits to improve  
503 fit to data. Clearly these are only a statistical placeholder for actual but unobserved ecologi-  
504 cal traits. Beyond the obvious but difficult to measure sensory interaction cues (Junker et al.,  
505 2013), also traits related to optimal foraging should be considered here – from both groups  
506 of interacting species. As Pyke (2016) exemplifies, the fitness benefit of pollination for plants  
507 depends on pollen-transfer efficiency of pollinators, and too high nectar rewards may give an  
508 incentive to inefficient visitors. Latent traits may thus reflect a complex and fine-tuned pair of  
509 matching sets of traits, without obvious interpretation.

510 A corollary of the possibility of fitting trait-pairs is also risk of identifying spurious char-  
511 acteristics of species (Mlambo, 2014). At present, interaction traits are almost exclusively mor-  
512 phological (see Junker et al., 2013, for an exception), but phenology can be incorporated simi-  
513 larly. In the future, both ecophysiological and genetic sampling may become sensitive enough  
514 to extend research into interaction traits for example related to vision in the ultraviolet (e.g.  
515 Rae and Vamosi, 2013), scent (e.g. Wright and Schiestl, 2009), or ultrasonic sound (e.g. Simon  
516 et al., 2019). Until such devices become available, latent traits are a statistical stand-in for what  
517 really makes species interact.



## 518 **Conclusion**

519 The approach we presented here predicts network interactions for new networks, conditional  
520 on trait, abundance/activity and phylogenetic data for the new network. It is flexible enough  
521 to include any type of function translating trait-matches into interaction probabilities. As a  
522 side-effect, it quantifies the importance of abundance relative to traits for network interac-  
523 tions. Future applications will have to assess the importance of traits across different types of  
524 networks, testing the assumption of many network studies that traits are the driving force of  
525 network interactions.

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## 532 **Author contributions**

533 Conceptualisation: GB, CFD, JF, DPV; method and software development: GB, CFD, RS; code  
534 review: GB, CFD, JF, RS; simulations and analyses: GB, CFD; writing original draft: GB and  
535 CFD; reviewing and editing: GB, CFD, JF, RS, DPV.

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