A quantitative framework for investigating the reliability of network construction

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Statement of authorship

DG designed the analytical approach. AC and DG wrote the code. AC performed statistical analyses. All authors contributed to writing and revising the manuscript.

Data accessibility

All data used in this study have been independently published and are accessible following the references provided in text.

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1

Abstract

Descriptions of ecological networks typically assume that the same interspecific interactions occur each time a community is observed. This contrasts with the known stochasticity of ecological communities: community composition, species abundances, and link structure all vary in space and time. Moreover, finite sampling generates variation in the set of interactions actually observed. Here we develop the conceptual and analytical tools needed to capture uncertainty in the estimation of pairwise interactions. To define the problem, we identify the different contributions to the uncertainty of an interaction and its implications for the estimation of network properties. We then outline a framework to quantify the uncertainty around each interaction. We illustrate this framework using the most extensively sampled network to date. We found significant uncertainty in estimates for the probability of most pairwise interactions which we could, however, limit with informative priors. Through these efforts, we demonstrate the utility of our approach and the importance of acknowledging the uncertainty inherent in network studies. Most importantly, we stress that networks are best thought of as systems constructed from random variables, the stochastic nature of which must be acknowledged for an accurate representation. Doing so will fundamentally change networks analyses and yield greater realism.

1 Introduction

2 Representing an assemblage of species as a network offers a convenient summary of how

3 the community is constructed as networks simultaneously describe species composition and

4 interactions between species. A tabulation of the nodes (species) and their relative

5 abundances forms the basis for traditional metrics of community composition such as alpha

6 diversity. To move from these simpler metrics to a network framework, the tabulation of

7 nodes is combined with interactions (links between nodes) so that networks provide

8 additional, higher-order information on community structure. While this additional

9 information is useful (as, for example, interactions can affect changes in species abundances

10 over time), empirical descriptions of ecological networks are still limited because they are

11 usually considered to be static representations of the communities and interactions they

12 describe. That is, whether the network is assembled based on aggregated data, a single

13 intensive "snapshot" sample, or expert knowledge, interactions are assumed to occur

14 deterministically wherever and whenever the community is observed (Olesen *et al.*, 2011).

15 The assumption of static communities contrasts significantly with the widely recognised

16 stochasticity of ecological communities (Gotelli, 2000). Community composition and

17 species abundances vary from site to site (Baiser *et al.*, 2012) and over time within a

18 site (Olesen *et al.*, 2011). Likewise, interactions vary over space (Kitching & Kitching,

19 1987; Baiser *et al.*, 2012), time (Kitching & Kitching, 1987; Olesen *et al.*, 2011), and

20 between individuals of a given species (Pires *et al.*, 2011a; Fodrie *et al.*, 2015;

21 Novak & Tinker, 2015). We emphasise that variability in community composition and

22 interactions may or may not be closely related. The removal of a species from a site will

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23 obviously also remove its interactions but, conversely, the co-occurrence of potentially

24 interacting species does not in itself guarantee that they will interact at a given place and

25 time. Interactions can be lost if the interaction partners remain present but are separated

26 in time or are too rare to detect each other (Tylianakis *et al.*, 2010). Interactions can also

27 fail to occur because of environmental contingencies (Poisot *et al.*, 2015), or through

28 changes to individual preferences (Fodrie *et al.*, 2015).

29 Beyond "true" variation in network structure, several researchers have pointed to the

30 importance of sampling intensity for the assessment of network structure

31 (e.g., Martinez *et al.*, 1999; Blüthgen *et al.*, 2006, 2007). An assessment of the

32 accumulation of interactions with increasing sampling effort suggests that it is even more

33 challenging to document interactions than species (Poisot *et al.*, 2012). As a result, it has

34 been proposed that interactions should be described probabilistically and network metrics

35 computed accordingly (Poisot *et al.*, 2016). Early work in this vein includes food-web

36 models using likelihood-based approaches (Allesina *et al.*, 2008) or

37 Gaussian (Williams *et al.*, 2010) or binomial (Rohr *et al.*, 2016) probability functions for

38 each possible interaction. These models may include information about species'

39 traits (Rohr *et al.*, 2016) or may attempt to reproduce empirical network structures using a

40 set of simple rules (Allesina *et al.*, 2008; Williams *et al.*, 2010).

41 Despite these preliminary efforts, to date we lack the quantitative methodology to deal

42 with the uncertainty generated by spatiotemporal variation in ecological interactions and

43 by sampling. Even in extremely well-sampled networks, uneven sampling across species (or

44 pairs of species) can lead to the erroneous inference that some species do not interact

45 because they co-occur rarely or have not yet been observed together - even if they do

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⁴⁶ interact when they do co-occur (see Box 1 for an example). Nearly all network studies will

⁴⁷ thus neglect some interactions, necessitating an approach that acknowledges this

⁴⁸ uncertainty.

⁴⁹   In this study, we formalise the description of interactions between species as

⁵⁰ probabilities and develop analytical tools to capture the uncertainty in the estimation of

⁵¹ these interactions. We focus on binary interactions as a first step, but the framework could

⁵² be expanded to deal with interaction frequencies and strength. To define the problem, we

⁵³ first identify the different contributions to the uncertainty of an interaction and discuss the

⁵⁴ implications of each source of uncertainty for the properties of ecological networks. Next,

⁵⁵ we develop an analytical framework to quantify the uncertainty around interactions in an

⁵⁶ empirical web. We illustrate this framework using the most extensively sampled network to

⁵⁷ date (Box 1). Finally, we offer tangible recommendations for improved descriptors of

⁵⁸ ecological interactions. Through these efforts, we demonstrate both the utility of our

⁵⁹ approach and the importance of acknowledging the uncertainty inherent in network studies.

⁶⁰ Why do some interactions *not* occur?

⁶¹ To define the problems associated with quantifying ecological interaction networks, we will

⁶² start from the perspective of an empirical community ecologist faced with the task of

⁶³ describing a previously unknown interaction network. This ecologist will be interested in

⁶⁴ generating a description of the species/nodes present and the links between

⁶⁵ them (Roslin & Majaneva, 2016). Importantly, the information sought is conveyed by both

⁶⁶ the presence and *absence* of links. Presences and absences are not, however, equally

67 certain. An observed link will always remain an observed link but there are multiple

68 reasons why a given link may not be observed. Thus, the detection of any interaction is a

69 stochastic process. We define three nested levels of uncertainty contributing to this

70 stochasticity: interaction uncertainty, process uncertainty, and detection uncertainty.

71 Interaction uncertainty

72 First, and most fundamentally, we do not know whether or not a pair of species have the

73 appropriate characteristics (or traits) to interact. We define the probability of an

74 interaction L given those characteristics $\mathbf{T}$ as $P(L|\mathbf{T}) = \lambda$. Obviously, if k (the number of

75 observed interactions) is 0, it is possible that the two species would not interact even if

76 there were no external constraints (e.g., temporal or environmental separation) preventing

77 the interaction from co-occurring. As a simple example, a prey species may be too large to

78 be consumed by a particular predator. In such cases, λ would take a value of 0 and there

79 would be no uncertainty.

80 Nevertheless, it is also possible that the interaction is a rare phenomenon with $\lambda > 0$

81 that has not yet been documented. This source of uncertainty is the one documented by

82 trait-matching models (Bartomeus *et al.*, 2016). It arises because every model is imperfect

83 and lacks information (i.e. about traits) that could be used to define constraints on the

84 interaction (Dormann *et al.*, 2017). Further study may, however, eventually reveal the

85 traits of interest and allow us to reduce interaction uncertainty. In other words, with

86 sufficient sampling and all information accessible, this interaction probability λ should

87 either tend to 0 or to 1.

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Process uncertainty

Even when an interaction is feasible, i.e. $L = 1$, it may not occur at a given location or moment in time because of local constraints such as inclement weather or the lack of suitable habitat. We define the realisation of the interaction process with the variable X, given that the interaction is feasible, as a stochastic process with associated probability $P(X|L = 1) = \chi$. This phenomenon of interaction contingencies is usually not considered in network studies, but there is a rich literature in community ecology about the contingencies of interactions. Phenological matching (Miller-Rushing *et al.*, 2010; Gezon *et al.*, 2016), species preferences (Pires *et al.*, 2011b; Novak & Tinker, 2015; Coux *et al.*, 2016), and fear effects of other species (Luttbeg & Kerby, 2005; Wirsing & Heithaus, 2008) are just some of the factors contributing to variation in the frequency of interactions between a given pair of species. Although some of the factors leading to process uncertainty can be addressed in mesocosm studies of networks (e.g., environmental conditions can be held stable), process uncertainty is likely inevitable in the field.

Detection uncertainty

Lastly, measurement errors are a pervasive source of uncertainty in the observation of ecological processes. Given that an interaction is feasible and occurs under the local conditions (L=1 and X=1), we may define the detection of an interaction, D, as a stochastic process with the associated probability $P(D|X = 1, L = 1) = \delta$. Detection failure could happen for several reasons including failure to rear a parasitoid, species mis-identification, or because the interaction is very rare (see Wirta *et al.* (2014) for

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109 examples of some of these difficulties and partial solutions to them). Some sources of

110 detection error can be minimised with appropriate sampling effort (δ will converge to one

111 with increasing number of samples), but other sources are often difficult to reduce (e.g. the

112 occurrence of cryptic species might require molecular analysis for appropriate taxonomic

113 identification as in Wirta *et al.* 2014; Frost *et al.* 2016).

114 Estimating detection and process uncertainty

115 Together, the combination of these three sources of uncertainty –interaction uncertainty,

116 process uncertainty, and detection uncertainty– results in a range of potential explanations

117 for the observation of an absence of interaction (D, X, and/or $L = 0$). The ecologist

118 wanting to describe the network, however, is specifically interested in the situation where

119 $L = 0$ (i.e., in true absences). Thus, while there is no difficulty interpreting the observation

120 of an interaction, the observation of an absence of an interaction offers more of a challenge

121 since it must be decomposed into different quantities. It is particularly important to rule

122 out the situations where $D = 0 \cup X = 1 \cup L = 1$, i.e. where the interaction occurred at the

123 location but was not observed, and $D = 1 \cup X = 0 \cup L = 1$, i.e., where the interaction is

124 feasible and would have been detected but did not occur at the local site. The occurrence

125 of a true absence, our quantity of interest, corresponds to the joint event

126 $L = 0 \cup X = 1 \cup D = 1$ but in reality an empirical ecologist will measure the marginal

127 probability $P(L) = k/n$ where k is again the number of observed interactions and n the

128 number of observed co-occurrences.

129 The considerations above raise a major challenge: when faced with empirical data, how

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130 may we infer whether unobserved interactions went undetected due to sampling or whether

131 they truly do not occur? How then may we refine our sampling approaches to reduce

132 uncertainties, and do we gain insights into the impact of multiple processes on field

133 observations? Importantly, some sources of uncertainty can be minimised with appropriate

134 sampling design and efforts while other sources are difficult or impossible to reduce since

135 they are generated by chance variation created by the very process in which we are

136 interested. Given this multifaceted problem of uncertainty, what can we do to separate the

137 different types of variation and reduce those that can be reduced?

138 The obvious rule of thumb is to "sample more" (see Fig. 2 for a demonstration of the

139 power of increasing sample size). Sampling more will clearly reduce uncertainty regarding

140 the upper bound of the probability of interaction and it will also increase the probability of

141 detecting unlikely interactions (e.g.,. interactions where $L{=}1$ but process uncertainty is

142 high). Despite these benefits, we note that there are limits to the utility of increased

143 sampling. Since the probability of observing the co-occurrence of two species will always be

144 higher than the probability of observing their interaction (since the probability of

145 interaction is conditional on both interaction partners being present; see Fig. 1E-F), we

146 will accumulate observations of co-occurrences faster than we will accumulate observations

147 of interactions. Thus, the more we sample, the more zeros will appear in our interaction

148 matrix.

149 In one endeavour to determine whether unobserved interactions were undetected due to

150 sampling, or whether they truly do not occur, Weinstein & Graham (2017) used repeated

151 sampling rounds to estimate the daily probability of detecting a hummingbird interaction,

152 and to thereby model detection and process uncertainty. While conceptually attractive,

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153 this approach is unsuitable for interactions occurring over longer time scales (e.g.,

154 associations between hosts and parasitoids with a single generation per year), or very rare

155 interactions which might not occur on any of the sampling days or might involve

156 individuals of a species that is not under observation. What is worse, the problem persists

157 that the absence of an interaction of a given day could either be because it was impossible

158 on that day despite being otherwise feasible $[P(X|D = 1, L = 1) = 0]$, because interaction

159 did occur but could not be observed $[P(D|X = 1, L = 1) = 0]$, or any combination of the

160 two. From a conceptual perspective, this approach therefore fails to satisfactorily

161 distinguish between sources of uncertainty. Most importantly, if two species are never

162 observed co-occurring during several days of sampling then we have learned nothing about

163 their probability of interacting if they should ever co-occur. In other words, there is no

164 information about interactions without co-occurrence.

165   An added complication is that not all sources of uncertainty are proportional to sample

166 size. To record an interaction between A and B, we need to identify both partners correctly

167 (a non-trivial problem in many food webs; e.g. Kaartinen & Roslin, 2011;

168 Roslin & Majaneva, 2016) and be able to resolve all interactions with a similar likelihood.

169 For both molecular and rearing techniques, certain types of interactions may go unnoticed

170 due to technical challenges (Wirta *et al.*, 2014). This can bias the set of recorded

171 interactions. The bottom line is that separating different sources of uncertainty is difficult

172 indeed. As an alternative to abandoning empirical networks or continuing to ignore the

173 uncertainty inherent in undetected observations, we propose that some insight regarding

174 the detectability of interactions between species not found co-occurring in a focal system

175 may be gained from data on other species pairs in the same or a similar system.

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A naive quantification of uncertainty

To progressively dissect the different contributions to uncertainty, we will start by considering how we could naively quantify interaction probability and its associated uncertainty *for an interaction that has not yet been observed*. We consider the case where a pair of species have been observed co-occurring n times, of which they have been observed to interact in $k = 0$ cases. We now aim to evaluate the uncertainty of this interaction. We consider the occurrence of an interaction as a Bernoulli trial. Consequently, the number of successes k over n trials will follow a binomial distribution:

$$X \sim Bin(n, \lambda), \tag{1}$$

$$P(X = k|\lambda, n) = \binom{n}{k}\lambda^k(1 - \lambda)^{n-k}. \tag{2}$$

The parameter λ, the probability of observing an interaction over an infinite time interval and area, is the quantity we want to estimate from empirical data. The maximal likelihood estimate (MLE) of λ is straightforward to find given k and n:

$$\lambda_{MLE} = \frac{k}{n}. \tag{3}$$

The variance of a Bernoulli experiment is $n\lambda(1\text{-}\lambda)$. It is important to remember that this variance describes the variability of the number of successes k for n trials and is not the variance associated with the estimation of λ. Given this variance, it is possible to compute the confidence interval for the MLE of λ using any of several methods, including

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the *Wilson score interval*, the *Clopper-Pearson interval*, and the *Agresti-Coull interval* (for details, see [Brown *et al.*, 2001]). Finding this estimate is therefore quite straightforward, but it nonetheless has two drawbacks. First, λ is not a single point estimate but rather a random variable with an unknown distribution. This means that if $k = 0$ in a given sample, this does not necessarily imply that the two species will never interact. Rather, $k = 0$ implies that 'no interaction' is the most likely outcome when the species do co-occur but there is nonetheless a substantial chance that the two species *could* interact. In the situation where $k > 0$, in contrast, we are sure that the interaction is feasible ($L = 1$) but still cannot be sure of the cause if the interaction is not observed at some sites/times (i.e., we cannot say why $k < n$). There may be local constraints ($X = 0$) or we might simply not observe the interaction in every sample ($D < 1$).

Second, where the number of samples n is very low (some pairs of species may never have been documented as co-occurring), there will be considerable uncertainty around our estimate of λ. In Fig. 2 and Box 2, we derive the Clopper-Pearson interval to explore how the estimate of λ varies with sample size. At a small sample size, the 95% confidence interval spans all values of λ. To establish that species are not interacting with any acceptable certainty requires tens of observations of the two species co-occurring but not interacting. As most data sets will lack such extensive sampling across all species pairs, we can use a Bayesian approach to supplement what data we do have with other sources of information.

Bayesian approach to infer interaction probabilities

Posterior distribution of the interaction probability

Here we adopt a Bayesian approach to estimate the posterior distribution of the parameter λ:

$$\underbrace{P(\lambda|k,n)}_{Posterior} = \frac{\overbrace{P(k|\lambda,n)}^{Likelihood}\overbrace{P(\lambda)}^{Prior}}{\underbrace{P(k|N)}_{Normaliser}}. \tag{4}$$

According to the above description, the likelihood is simply the binomial distribution (Eq. 2). Since λ is a probability, it is bounded between 0 and 1 and the most appropriate prior distribution is the beta:

$$\lambda \sim Beta(\alpha, \beta), \tag{5}$$

which has two shape parameters, α and β.

The beta-binomial distribution is a conjugate distribution of the binomial distribution. This allows us to analytically compute the posterior distribution of a binomial model with a beta prior distribution. We can re-write the posterior distribution of λ as:

$$P(\lambda|k,n) = \frac{\lambda^{\alpha+k-1}(1-\lambda)^{\beta+n-k-1}}{B(\alpha+k, \beta+n-k)}, \tag{6}$$

where the function B is the beta function. The posterior distribution of λ therefore follows the beta distribution with new parameters $\alpha' = \alpha + k$ and $\beta' = \beta + n - k$. The weight of the prior on the posterior distribution can be understood from these parameter definitions:

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225 the difference between the posterior and the prior will increase with k and $n - k$. In other

226 words, the distribution of λ for better-sampled pairs of species will rely less on the

227 information used to build the prior distribution and depend more on the observed data.

228 When plotted, we find the shape of the distribution gets narrower with k and n (Fig. 3).

229 Moments and other properties

230 It is common to preform analyses that require calculating higher-order network properties

231 in interaction networks. The fact that the posterior distribution of λ follows a beta

232 distribution makes it straightforward to compute moments and other properties needed for

233 this.

234 The **average** of λ is:

$$\bar{\lambda} = \frac{\alpha + k}{\alpha + \beta + n}, \tag{7}$$

235 and its **variance** is:

$$Var(\lambda|k) = \frac{(\alpha + k)(\beta + n - k)}{(\alpha + \beta + n)^2(\alpha + \beta + n + 1)} \tag{8}$$

236 The **mode** of the distribution is:

$$\hat{\lambda} = \frac{\alpha + k - 1}{\alpha + \beta + n - 2}. \tag{9}$$

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The prior distribution

Parameters α and β determine the shape of the prior distribution, which follows a beta

distribution. These are called hyper parameters. Below we identify four ways to formulate

the prior distribution of λ.

Uninformative prior

In the absence of any external information, an uninformative prior is the most conservative

hypothesis for the distribution of λ. The beta distribution is in this case a uniform

distribution, specified with hyper parameters $\alpha = 1$ and $\beta = 1$.

Distribution of connectance

The ecological network literature boasts a collection of networks for which connectance has

been calculated and for which we can thus define the connectance distribution.

Connectance is measured as $C = L/S^2$, where L is the number of interactions and S is the

number of species. It measures the filling of an interaction matrix and thereby expresses

the average probability that any two species interact with each other. If we know only the

mean $\overline{C}$ and the variance σ_C^2 of the distribution of C, then the beta parameters could be

computed as follows using the method of moments:

$$\alpha = \overline{C}(\frac{\overline{C}(1 - \overline{C})}{\sigma_C^2} - 1), \tag{10}$$

$$\beta = (1 - \overline{C})(\frac{\overline{C}(1 - \overline{C})}{\sigma_C^2} - 1). \tag{11}$$

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Degree distribution or interaction probabilities

The degree of a node in a network is defined as its number of connections to other nodes. The degree distribution of a network is then the probability distribution of these degrees over the whole network and the standardised degree could therefore be interpreted as an interaction probability. It is consequently possible to use the degree distribution to inform the prior distribution. The degree distribution could come from several networks, from a similar network (e.g. a known network at slightly different location) or from the network of interest if interaction probabilities for some species are already documented. The latter approach allows researchers to apply information from known, abundant species to the rarest species for which interactions are less frequently documented.

If our focal network describes a system similar to that in a known network, we can use the distribution of interaction probabilities in that network to inform our prior. The probability of any interaction L_{ij} depends on the degrees of species i and j. Using normalised degrees Δ_i and Δ_j (i.e., degrees divided by the number of species in the network), we can obtain the probability of interaction $L_{ij} = \Delta_i \times \Delta_j$. Similar to the procedure for degree distribution, the distribution of these interaction probabilities can be used to establish a prior distribution before any data from the focal network are collected. For distributions of either degrees or interaction probabilities, the procedure for the estimation of the hyper parameters follows the same approach as described above for connectance except that each measurement is at the individual interaction level instead of the network level.

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274 Trait-matching function

275 As a fourth and final approach, it may be possible to obtain the prior distribution of λ

276 using the outcome of a trait-matching model, provided such a model has been

277 parameterised using external data and relevant traits are available. In such a case, the

278 prior distribution would follow the function $P(\lambda|\mathbf{T}) = f(\mathbf{T})$ based on a set of traits for

279 both species $\mathbf{T}$. There are several techniques available to perform this inference of

280 interaction probability, some of which are Bayesian, and we refer to Bartomeus $et\ al.$

281 (2016) and Weinstein & Graham (2017) for recent reviews about this topic. Note that in

282 this case the prior might not be beta-distributed and numerical methods might be required

283 to compute the posterior distribution.

284 A quantitative example

285 The Bayesian framework can be illustrated with a simple quantitative example. Suppose

286 we have $n = 10$ observations of co-occurrence between species i and species j in a given

287 time interval and area, and $k = 3$ observations of interactions. The maximum likelihood

288 estimate of the interaction probability is simply $\lambda_{MLE} = 3/10 = 0.3$.

289 Now consider we know that species i is known to interact with 10 species (other than

290 species j), which have the following degrees:

291 *degree=c(14, 4, 2, 3, 17, 6, 2, 15, 1, 1) .*

292 If the network has 20 species total, this gives the normalised degrees:

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293   *norm_degree=c(0.65, 0.20, 0.10, 0.15, 0.85, 0.30, 0.10, 0.75, 0.05, 0.05).*

294   Species i has a normalised degree of 0.55 (it interacts with species j and 10 other

295   species). We can combine the normalised degree of i with the normalised degrees of its

296   interaction partners to obtain the following set of interaction probabilities for species i and

297   each of its interaction partners:

298   *int_probs = c(0.358, 0.110, 0.055, 0.082, 0.468, 0.165, 0.055, 0.412, 0.028, 0.028) .*

299   The mean of these interaction probabilities is 0.176, approximately two-thirds the λ_{MLE}

300   obtained from the observed data. We can use the distribution of these interaction

301   probabilities as our prior distribution and estimate the uncertainty surrounding our λ_{MLE}.

302   With some simple R code (function "calculate_parameters", *Appendix S1*), we obtain prior

303   parameters α=0.998 and β=4.63. Using these priors in equations 7 and 8 above (or in the

304   R function "calculate_distribution" in *Appendix S1*), we find a prior $\bar{\lambda}$=0.177 and

305   var(λ)=0.026. Adding the observed data ($n = 10$, $k = 3$) and using the same code, we

306   obtain posterior parameters α'=4.00 and β'=11.6 and a posterior $\bar{\lambda}$=0.256 and

307   var(λ)=0.012. Comparing the posterior distribution to the prior, we see that the posterior

308   is closer to the observed data and that the additional data about interactions between

309   species i and j has reduced the variance. We may also wish to calculate a credible interval

310   (analogous to the frequentist confidence interval). This is also quite straightforward in R

311   (see function "credible_interval" in *Appendix S1*). In this case, a 95% credible interval for $\bar{\lambda}$

312   is (0.080, 0.491).

313   Now, consider the case where the two species have never been observed interacting

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314 across n trials, i-e. $k = 0$. The question is then "what is the probability that these two

315 species do not interact"? Since it is not possible to prove that the two species could never

316 interact (strictly speaking, in a Bayesian approach $\lambda = 0$ is impossible), we must fix a

317 threshold below which we consider that there is no interaction ($\lambda \sim 0$). We call this

318 threshold probability $\lambda*$. We then use the cumulative distribution function to estimate

319 $P(\lambda < \lambda * | L = 0, n)$ for different n. The function "samples_for_threshold" in *Appendix S1*

320 calculates distribution function for $\lambda*$ with an increasing number of trials. This yields a

321 surprising result: it requires >24 observations of no interactions to be 95% sure that the

322 interaction probability is smaller than $\lambda*=0.1$ (recall Fig. 2, Box 2). Note the special case

323 where there is no observation of the two species co-occurring, $n = 0$. In this situation, the

324 posterior distribution converges to the prior distribution since the data include no

325 information on the probability with which species might interact should they co-occur.

Scaling up to networks - an empirical example

327 In the following section, we will provide an empirical example based on the well-sampled

328 system of *Salix* plants, herbivorous gallers, and their natural enemies described

329 by Kopelke *et al.* (2017); see Box 1 or *Appendix S2* for a description). Using this dataset,

330 we will demonstrate the derivation of prior distributions for the *Salix*-galler and

331 galler-natural enemy components of these networks and the differences between these

332 priors and posterior distributions which include all information available in this

333 dataset (Kopelke *et al.*, 2017). Finally, we will calculate network properties using a suite of

334 networks sampled from these posterior distributions and show how the uncertainty around

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335 interactions that have not been observed impact these metrics.

Computing the posterior distribution

337 In a strict Bayesian framework, we wish to use a prior distribution that does not rely on

338 any information from the study at hand. Network data for a similar study system may,

339 however, not be available. In that case, one might use the first sub-network collected as

340 "training data" to guide future sampling. To simulate this situation, we created priors

341 using a single sub-network from the middle of the geographical distribution of

342 the Kopelke *et al.* (2017) dataset. To demonstrate how the use of data from a different

343 system can affect the prior distribution and conclusions based on it, we repeated our

344 analyses using priors derived from a much smaller *Salix*-galler-natural enemy

345 system (Barbour *et al.*, 2016, Data available from the Dryad Digital Repository:

346 https://doi.org/10.5061/dryad.g7805). This smaller system was much more

347 densely-connected than that described in Kopelke *et al.* (2017) and provided unreasonable

348 distributions for interaction probabilities (*Appendix S4*).

349   To obtain the priors based on the Zillis sub-network, we estimated frequencies of

350 *Salix*-galler interactions based on the normalised degree of each species in each network

351 component (see *Appendix S3* for details and code). Specifically, we obtained prior

352 parameters of $\alpha=8.72$, $\beta=305$ for the *Salix*-galler component and $\alpha=0.700$, $\beta=8.49$ for the

353 galler-natural enemy components of the network. After calculating these prior parameters,

354 we were then able to estimate the posterior distribution of interaction probabilities given

355 the additional information in our dataset.

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356   For species where no co-occurrences were observed ($n = 0$), we can calculate the

357   estimates for the mean and variance of λ_{ij} directly from the prior parameters following

358   equations 7 and 8 (see *Appendix S1* for R implementation). For the *Salix*-galler network,

359   the prior distribution was: $\bar{\lambda}$=0.028, var(λ)=8.60×10^{-5}. The prior distribution for the

360   galler-natural enemy network was: $\bar{\lambda}$=0.076, var(λ)=0.008. The posterior interaction

361   probabilities obtained based on the Zillis sub-network were much lower than those obtained

362   based on Barbour *et al.* (2016, Data available from the Dryad Digital Repository:

363   https://doi.org/10.5061/dryad.g7805); this emphasises the importance of using an

364   appropriate study system when constructing a prior (*Appendix S4*).

365   For a pair of species with some observed co-occurrences ($n > 0$), we can update the

366   prior distribution with these data. If we consider only pairs of species which were observed

367   to co-occur but not to interact, k_{ij} is always 0 and only n_{ij} will vary between species pairs,

368   giving α'=α and β'=$\beta + n_{ij}$. As the most extreme case, consider a pair of species which

369   co-occurred at all 374 sites and was never observed to interact. Using the priors described

370   above, our distribution for the *Salix*-galler network would become $\bar{\lambda}_{ij}$=1.27 × 10^{-2},

371   var(λ_{ij})=1.82 × 10^{-5} while our distribution for the galler-natural enemy network would

372   become $\bar{\lambda}_{ij}$=1.83 × 10^{-3}, var(λ_{ij})=4.76. Distributions for both network components were

373   very close to 0 with small variance about our estimate of λ; species i and j are extremely

374   unlikely to interact at sites or times not included in our sample.

375   For most pairs of species i and j, however, n_{ij} was much less than 374 and our posterior

376   mean and variance therefore retain more of the influence of the prior. We can see this in

377   the increasing means and variances as we decrease n_{ij} (Fig. 3). The change in distribution

378   as n_{ij} decreases can also be shown by calculating 95% credible intervals for λ (see the

379 function "credible_interval" in *Appendix S2*). The 95% credible interval around the

380 estimate of λ also widens as n_{ij} decreases from (0.001, 0.017) and (<0.001, 0.11) for

381 hypothetical *Salix*-galler and galler-natural enemy pairs that might be observed

382 co-occurring at all 374 sites without any observed interaction to (0.152, 0.931) and (0.008,

383 0.364) for *Salix*-galler and galler-natural enemy pairs that were never observed

384 co-occurring. The 95% credible interval for hypothetical *Salix*-galler pairs widened from

385 (0.006, 0.022) if the pair co-occurred at all sites to (0.013, 0.049) if they co-occurred at

386 none. The 95% credible interval for hypothetical galler-natural enemy pairs, meanwhile,

387 widened from (0.00001, 0.008) to (0.0005, 0.304).

How many samples are required to reach a minimal precision

389 Rather than calculating credible intervals for a posterior distribution after collecting data,

390 we may wish to know how many data points are necessary to obtain a given level of

391 confidence that two co-occurring species do not interact. The number of samples needed

392 will depend on both our desired level of confidence and the threshold below which we

393 assume that two species are unlikely to ever interact (Fig. 4; see function

394 samples_for_threshold in *Appendix S1*). In our dataset, the entire 95% credible interval was

395 (0.013, 0.049). We may therefore be 95% confident that the interaction probability for

396 *Salix* and galler species that have not been observed co-occurring is below 0.05. As the

397 peak of the prior distribution for the probability of interaction between *Salix* and galler

398 probabilities is around 0.02 (Fig. 3), to be 95% confident that the interaction probability

399 for these species is below 0.01 would require 1029 observed co-occurrences with no

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400 interaction - far more than the number of sites in the (Kopelke *et al.*, 2017) dataset.

401 The number of samples required to be 95% confident that the interaction probability

402 between galler and natural enemy species is below a threshold also increases quickly as the

403 threshold decreases. The 95% credible interval is (<0.001, 0.303) for the probability of

404 interaction between two species observed to co-occur but never interact. To be 95%

405 confident that the probability of interaction is below 0.1, 0.05, or 0.01 would require 15, 39,

406 and 229 observed co-occurrences, respectively.

407 Given the low levels of replication in most network studies, this implies that we should

408 have fairly low confidence in many "non-interacting" pairs of species. Even in the

409 extensively replicated *Salix*-galler-natural enemy dataset, very few species pairs were

410 observed co-occurring frequently enough to reach these thresholds. Regardless of our choice

411 of prior, no species pairs were observed to co-occur frequently enough to reach the

412 threshold for an interaction probability of 0.01. Discounting potential interactions, then,

413 requires either a stronger prior expectation of no interaction (e.g. for forbidden

414 interactions) or very extensive sampling. For all we know, most links absent from current

415 descriptions of network structure may be so not because the species do not interact, but

416 because we have not sampled deeply enough to detect them.

Scaling up to network metrics

418 It is fairly straightforward to compute most network metrics when the different λ of the

419 adjacency matrix are known and assumed not to vary without variance (Poisot *et al.*,

420 2016). Several of these metrics derive directly from quantitative indices of network

23

421 structure which are equivalent to λ. The remainder, originally defined for binary networks,

422 can be adjusted to account for interaction probabilities between zero and one. It is not as

423 easy, however, to understand how the uncertainty in these estimated interaction

424 probabilities influences network metrics. Computation of these metrics involves non-linear

425 functions. Since Jensen's inequality states that the average of a non-linear function of a

426 stochastic variable differs from the function of the average of that variable, any uncertainty

427 in the values of λ could bias both the mean and variance of a network metric. One way to

428 avoid potentially biased analytical calculation of network properties is to calculate the

429 properties of a suite of simulated networks.

430   Using the prior distributions and procedures described above, we calculated posterior

431 probability distributions for *Salix*-galler or galler-natural enemy pairs that were not

432 observed interacting. Using these posterior distributions and assuming probabilities of 1 for

433 pairs of species that were observed interacting, we created a suite of 100 webs of each

434 network type by randomly sampling from each posterior distribution. After obtaining these

435 posterior networks, we calculated the connectance of each web, as well as the number of

436 links per resource (*Salix* in the *Salix*-galler networks or galler in the galler-natural enemy

437 networks) and links per consumer. To demonstrate how these network metrics will be

438 affected by detection uncertainty, we then created a suite of filtered networks for each

439 posterior network. Networks were filtered by randomly sampling 99%, 95%, 90%, 80%,

440 70%, 60%, and 50% of the interactions included in each posterior network. This gradient is

441 akin to a gradient of sampling effort. For each level of detection accuracy, we created 100

442 randomly-sampled networks per posterior-probability network (giving 100 posterior

443 networks and 1000 detection-filtered networks each for the *Salix*-galler and galler-natural

24

444 enemy networks). We then calculated the same network properties as described above.

445 We find, perhaps not surprisingly, that the posterior webs for the Salix-galler network

446 had higher connectances than the original, observed web (C=0.028 for the observed web

447 and $0.082 \leq C \leq 0.096$ for the posterior webs; Fig. 5A). The number of links per $Salix$

448 species in the observed web (L_{Salix}=2.71) was similar to those in the posterior webs (2.53

449 $\leq L_{Salix} \leq 3.19$; Fig 5C). The number of links per galler, however, was lower in the

450 observed web (L_{galler}=1.47) than in the posterior webs, accounting for the increased

451 connectance ($4.67 \leq L_{galler} \leq 5.88$; Fig. 5E). There was a more substantial difference in the

452 nestedness of the observed and posterior webs: the observed network had NODF=0.560

453 while the posterior networks were more nested ($1.39 \leq NODF \leq 1.94$). Even the networks

454 sampled with a detection filter of 50% had non-zero nestedness (Fig. 5G). This last result

455 highlights the potential for the possibility for network structure to vary when considering

456 the possibility that unobserved species pairs may interact.

457 Considering the galler-natural enemy networks, the connectance, mean links per galler,

458 and mean links per natural enemy were also much lower in the observed web (C=0.078,

459 L_{galler}=9.99, and $L_{naturalenemy}$=7.45, respectively) than in the posterior webs ($0.186 \leq C \leq$

460 0.198, $13.4 \leq L_{galler} \leq 14.6$, and $23.4 \leq L_{naturalenemy} \leq 25.0$). When the detection

461 probability was relatively low (i.e., 50%), however, the properties of randomised networks

462 became similar to those in the observed webs (Fig. 5B,D,F). Nestedness was higher in the

463 observed network (NODF=6.85) than in the posterior webs ($6.31 \leq NODF \leq 6.82$;

464 Fig. 5H); in this case, the stronger the detection filter the farther apart were the observed

465 and posterior webs.

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Conclusions/recommendations

Real interaction networks vary over several dimensions (Kitching & Kitching, 1987; Olesen *et al.*, 2011; Pires *et al.*, 2011a; Baiser *et al.*, 2012; Fodrie *et al.*, 2015; Novak & Tinker, 2015) and to capture this variation we must turn from static descriptions of network structure to probabilistic descriptions. In this study, we have developed the analytical tools to capture the uncertainty in the estimation of pairwise interactions and a conceptual framework for its individual components: interaction uncertainty, process uncertainty, and detection uncertainty. Using this framework leads us to offer tangible recommendations for improved descriptors of ecological interactions. First, our analyses point to detection uncertainty as a major contributor to overall uncertainty of is establishing the absence of interaction. To counter this and establish true absences of interactions requires comparatively large sample size on the order of 30-50 observations per species pair. Second, where such extensive sampling is not feasible, researchers should still acknowledge the varying levels of confidence surrounding the presence or absence of interactions between different pairs of species. Including the n and k values for each interaction will clearly indicate which unobserved interactions are most likely to be observed with further sampling and which estimates are more reliable. Third, the uncertainty around interactions (especially interactions that were not observed) should be incorporated in calculations of network properties like connectance or nestedness. Re-sampling networks based on a probabilistic understanding of networks is straightforward and gives distributions for network properties rather than point estimates. This not only acknowledges the fact that interactions vary over time and space but will

26

488 also facilitate comparisons between networks. With confidence intervals around network

489 metrics, we can not only say that one network is more connected than another but also

490 whether the networks are more different than we would expect based on imperfect

491 sampling of interactions. To facilitate these recommendations, we provide all code used in

492 this paper in the supplementary material.

Acknowledgements

Boxes and figures

Box 1: *Salix*-galler-natural enemy dataset.

As a case study, we use an extensively sampled *Salix*-galler-natural enemy meta-network. This dataset consists of a single community type sampled across Europe: willow (*Salix*) species, willow-galling sawflies, and their natural enemies. The data were collected over 29 years at 374 unique locations across Europe with a total of 641 site visits. Each site visit or each unique site can be considered as a network in its own right or as an independent sample from which to build the meta-network. Here we take the more conservative approach and pool visits to the same site for a sample size of 374 sub-networks. The meta-network consists of 1,173 different interactions between 52 *Salix* nodes, 92 herbivore nodes, and 126 natural enemy nodes. The high spatiotemporal resolution of this network and the unusually high sampling effort implemented at the site level makes this dataset particularly well suited for illustrating the difficulties in completely sampling a network and testing Bayesian approaches to overcome these difficulties.

We may begin by comparing the frequency of co-occurrences for pairs of species in each part of the network to reveal the challenge of having sufficient sampling to be confident that an interaction does not occur. Most pairs of species (3,986/4,992 *Salix*-galler pairs and 9,794/12,096 galler-natural enemy pairs) are never found co-occurring and, for species that did occur together, the total number of co-occurrences was generally low (mean=4.24, variance=36.3 for *Salix*-galler pairs; mean=3.87, variance=28.8 for galler-natural enemy pairs; Fig. 1A-B). The bulk of these co-occurring species pairs were never observed to interact: only 2.82% of *Salix*-galler pairs and 7.76% of galler-natural enemy pairs were observed interacting at one or more sites. Of those pairs that did interact, the incidence of interaction was also low (mean=12.0, variance=155 for *Salix*-galler pairs; mean=4.04, variance=29.3 for galler-natural enemy pairs; Fig. 1C-D). Thus, even in the most extensive data set that we could find, there was very little empirical data for each species pair. This suggests that limited sampling is a major source of uncertainty in all empirical networks. This dataset also illustrates the potential for increased sampling to not necessarily reveal more interactions as a pair of species that is able to interact may not be observed interacting in all samples where the pair co-occurs (Fig. 1E-F).

Box 2: Calculating the credible interval around a probability estimate

Here we describe the derivation of the Clopper-Pearson credible interval for the estimated probability of interaction λ of a pair of species observed co-occurring n times and interacting k times. As we are most interested in the probability of interaction between species pairs that have never been observed co-occurring, we consider only the case where $k = 0$ over a variety of n. This is straightforward to do in R (see the function "credible_interval" in *Appendix S1*).

First, we must obtain the α and β parameters for the prior distribution. In this study we obtained these parameters using the R (R Core Team, 2016) function fitdist from the package fitdistrplus (Delignette-Muller & Dutang, 2015). Once α and β are known, we can update them using our observed data. Specifically, we are interested in $\alpha' = \alpha + k$ and $\beta' = \beta + n - k$. These parameters can then be used to calculate a credible interval using the R (R Core Team, 2016) function qbeta. In the table below, we present the 95% credible intervals for *Salix*-galler and galler-natural enemy pairs with different numbers of observed co-occurrences (n) and no observed interactions ($k = 0$), calculated using prior information derived from the Zillis sub-network (Kopelke *et al.*, 2017).

Table 1: Here we give the lower and upper bounds of 95% credible intervals for the probability of interaction λ between *Salix*-galler or galler-natural enemy pairs that have been observed co-occurring n times but have never been observed interacting.

n	*Salix*-galler		galler-natural enemy	
	Lower bound	Upper bound	Lower bound	Upper bound
0	0.013	0.049	5.39×10^{-4}	0.304
1	0.013	0.048	4.82×10^{-4}	0.276
2	0.013	0.048	4.35×10^{-4}	0.253
5	0.012	0.048	3.37×10^{-4}	0.203
10	0.012	0.047	2.45×10^{-4}	0.152
15	0.012	0.046	1.93×10^{-4}	0.121
20	0.012	0.046	1.59×10^{-4}	0.101
25	0.012	0.045	1.35×10^{-4}	0.087
50	0.011	0.042	7.72×10^{-5}	0.050
100	0.010	0.037	4.16×10^{-5}	0.027
150	0.009	0.033	2.84×10^{-5}	0.019
200	0.008	0.030	2.16×10^{-5}	0.014
374	0.006	0.022	1.18×10^{-5}	0.008

Figure 1: A-B) Most pairs of *Salix* and gallers or gallers and natural enemies were never observed co-occurring despite the high levels of replication in our example dataset. For those pairs that were observed together at least once ($n_{ij} > 0$), the number of observed co-occurrences was generally small (<10). Here we show a histogram of the number of pairs of species observed co-occurring at least once. 3986 *Salix*-galler and 9794 galler-enemy pairs were never observed co-occurring: these pairs are omitted from the histogram. **C-D)** Most pairs of species that were observed at the same site were never observed interacting. Here we show a histogram of the number of observed interactions within pairs of co-occurring species. Species which co-occurred but never interacted are included in these histograms. **E-F)** Here we show, for each species pair, the number of observed interactions plotted against the number of observed co-occurrences. *Salix*-galler pairs either are never observed interacting or interact almost every time they co-occur, while galler-enemy pairs had more variable frequencies of interaction. In panels E and F the red, dashed line indicates a 1:1 relationship between interactions and co-occurrences.
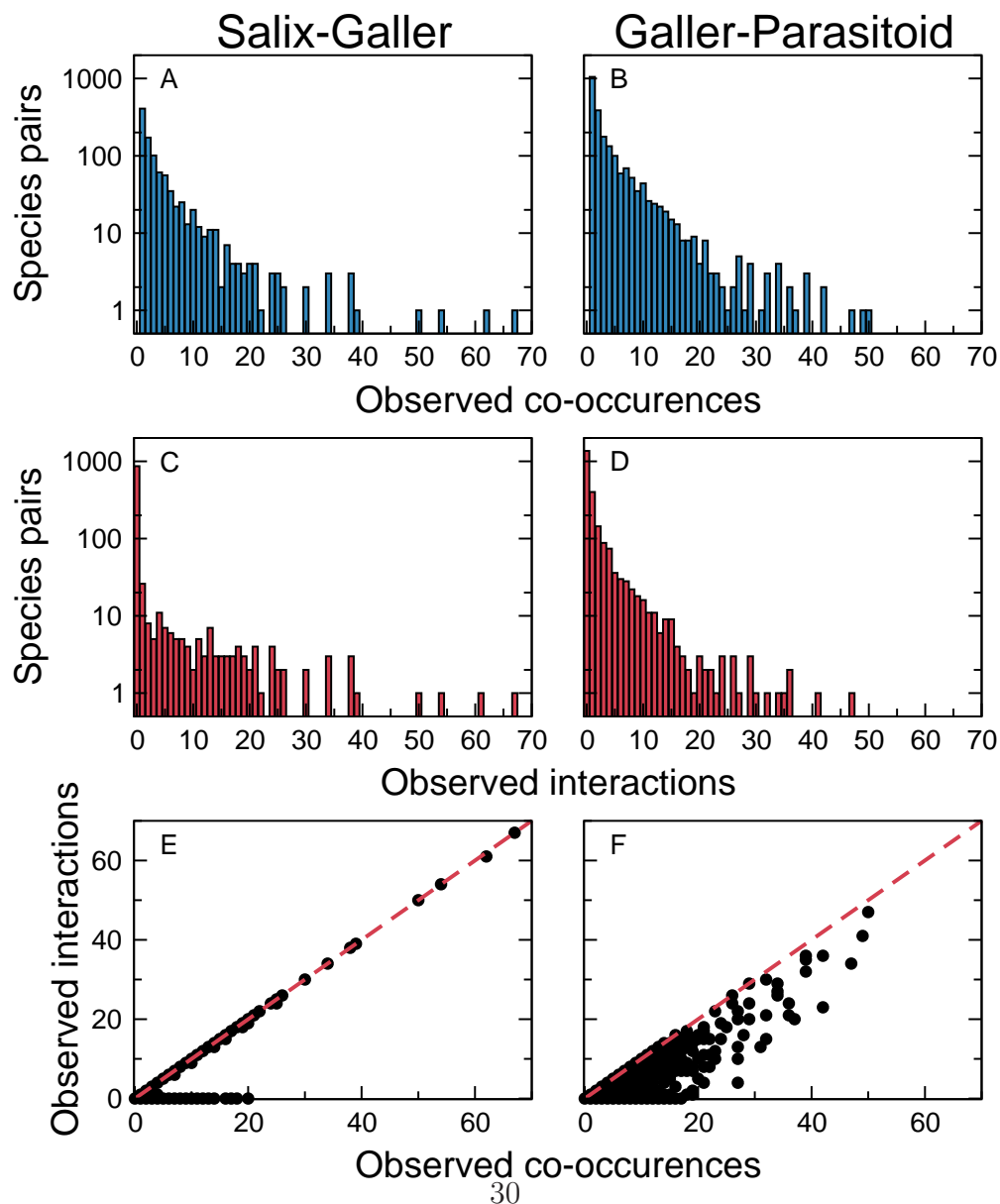
Figure 2: A simple example will illustrate the problem of imperfect detection of interactions. Assume that we want to infer the probability of an interaction between two species, i and j. Now assume that in reality, interaction between i and j is completely impossible (i.e. the true $\lambda = 0$) but the observer does not know this and seeks to estimate this interaction probability (λ). The number of observed interactions will follow a binomial distribution with number of interactions k and number of observations n. Using this distribution, we can compute the credible interval of the estimated probability λ. Even assuming no added detection error in observing the incidence of the interaction, a single observation of species co-occurrence reveals very little regarding the probability of the interaction as the credible interval for a pair of species with one observation essentially spans from 0 to 1. Only with 35 observations will the upper limit of the credible interval be lowered to 0.1. Thus, adding more observations is certainly useful in controlling uncertainty, but the number of observations added needs to be very high. Here we show the upper bound (solid black line) of a 95% Clopper-Pearson true credible interval for λ when $k = 0$ (i and j have not been observed interacting) for a variety of n (observed co-occurrences of i and j). Using a Bayesian approach with an informative prior can reduce the confidence interval about λ for a given sample size. A threshold interaction probability of 0.1 is indicated by the dashed red line.
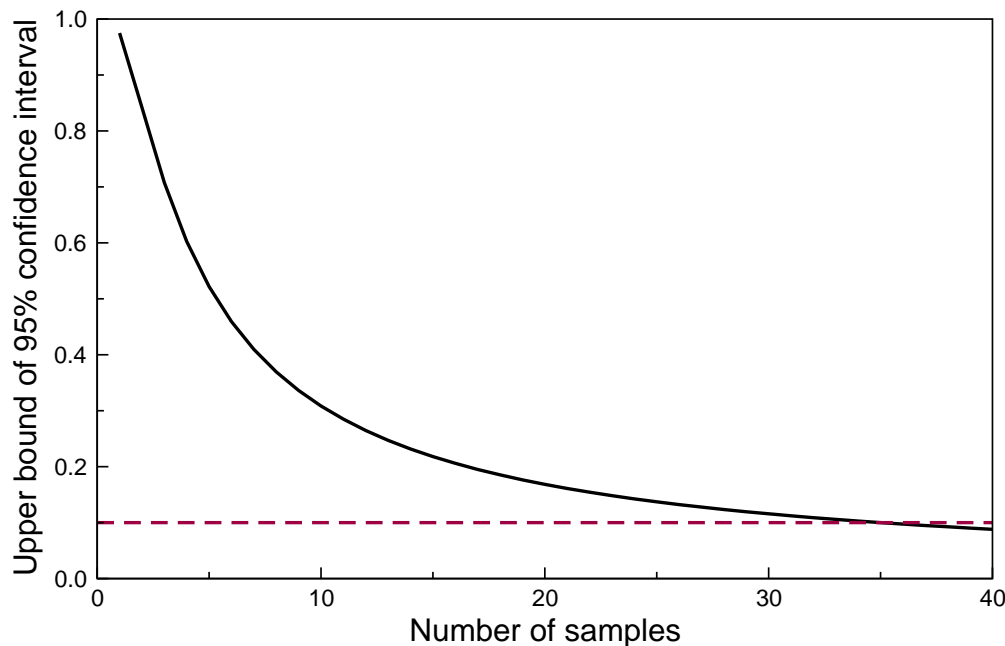
Figure 3: Using prior distributions based on the *Salix*-galler and galler-natural enemy networks sampled at a single site in Kopelke *et al.* (2017), we can calculate posterior distributions for the probability of interaction (λ) between two species that have not yet been observed interacting. Here we show posterior distributions for λ in each network component ranging from the prior distribution ($n = 0$ observed co-occurrence) to the distribution obtained when the pair of species has been observed co-occurring 100 times. The distribution narrows and approaches zero as the sample size increases. Likewise, the maximum likelihood estimator for the mean probability of interaction (diamonds at top of each panel) approaches zero and the 95% credible interval (lines at top of each panel) narrows as sample size increases. **A)** The posterior distributions for λ in the *Salix*-galler component are narrower at low n but shrink less with increased sampling than those for **B)** the distributions of λ in the galler-natural enemy component.
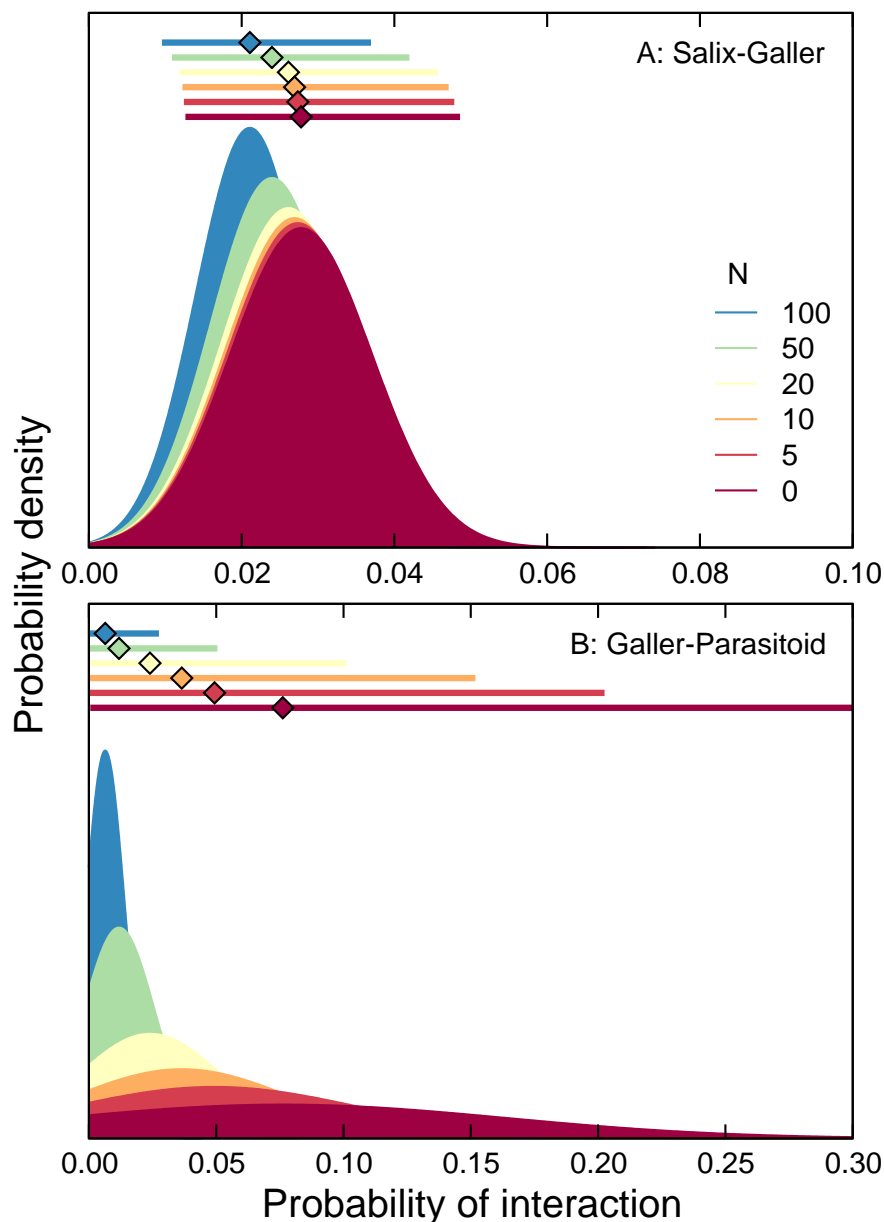
Figure 4: The number of samples required to achieve a given level of confidence that an interaction probability λ_{ij} is below a given threshold varies with both parameters. With a low threshold, our confidence that λ_{ij} is below the threshold increases rapidly with repeated observation of co-occurrence without interaction. Here we show the cumulative density functions for threshold probabilities of 0.5 (solid line), 0.25 (dashed line), 0.1 (dash-dot line), and 0.05 (dotted line) as well as the points at which the cdf reaches 0.90 (orange square), 0.95 (red circle), and 0.975 (blue diamond) for each threshold value. The large ticks along the x-axis indicate the number of samples associated with each of these points. **A)** In the *Salix*-galler network component, the 95% credible interval for λ_{ij} when $n=0$ was (0.013, 0.049). We can therefore be at least 95% confident that λ_{ij} is below thresholds of 0.1 or 0.05 without any observed co-occurrence of species i and j. To be confident that λ_{ij} is less than 0.01, however, would require more observed co-occurrences than there are sites in our dataset. **B)** In the galler-parasitoid network component, the 95% credible interval for λ_{ij} was substantially broader and many observed co-occurrences ($\approx$ 15-35) are required to be 95% confident that λ_{ij} is below thresholds of 0.1 or 0.05.
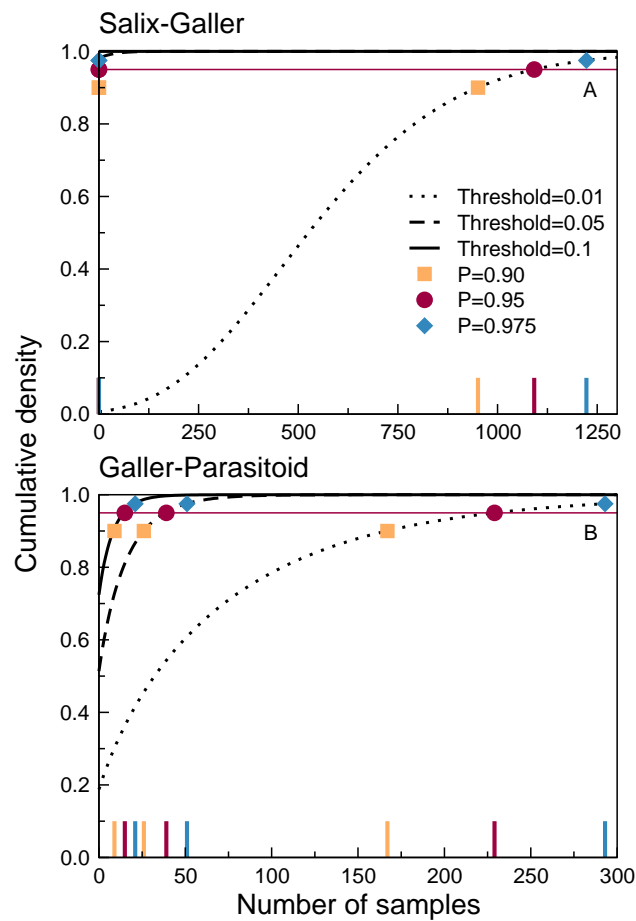
Figure 5: Here we show the mean connectance, links per resource (*Salix* in the *Salix*-galler networks and gallers in the galler-natural enemy networks), links per consumer, and nestedness (NODF) for networks assembled using posterior distributions based on a single sub-network in the Kopelke *et al.* (2017) dataset (Zillis). We created 100 "posterior-sampling" networks and then, for each of these, created 100 "detection-filter" networks by randomly sampling 50%-99% of the interactions included in the posterior-sampling network. This simulates imperfect detection of interactions in the field. Each point represents the mean network property (e.g., connectance) obtained from a set of 100 detection-filter networks, plotted against the value of the network property in the posterior-sampling network used to create the detection-filter networks. For each property and both network types, the posterior-sampling networks cover a relatively small range of network properties than the range covered by networks with varying detection probabilities. The value of each property decreases with the proportion of links included in the detection-filter networks.

34
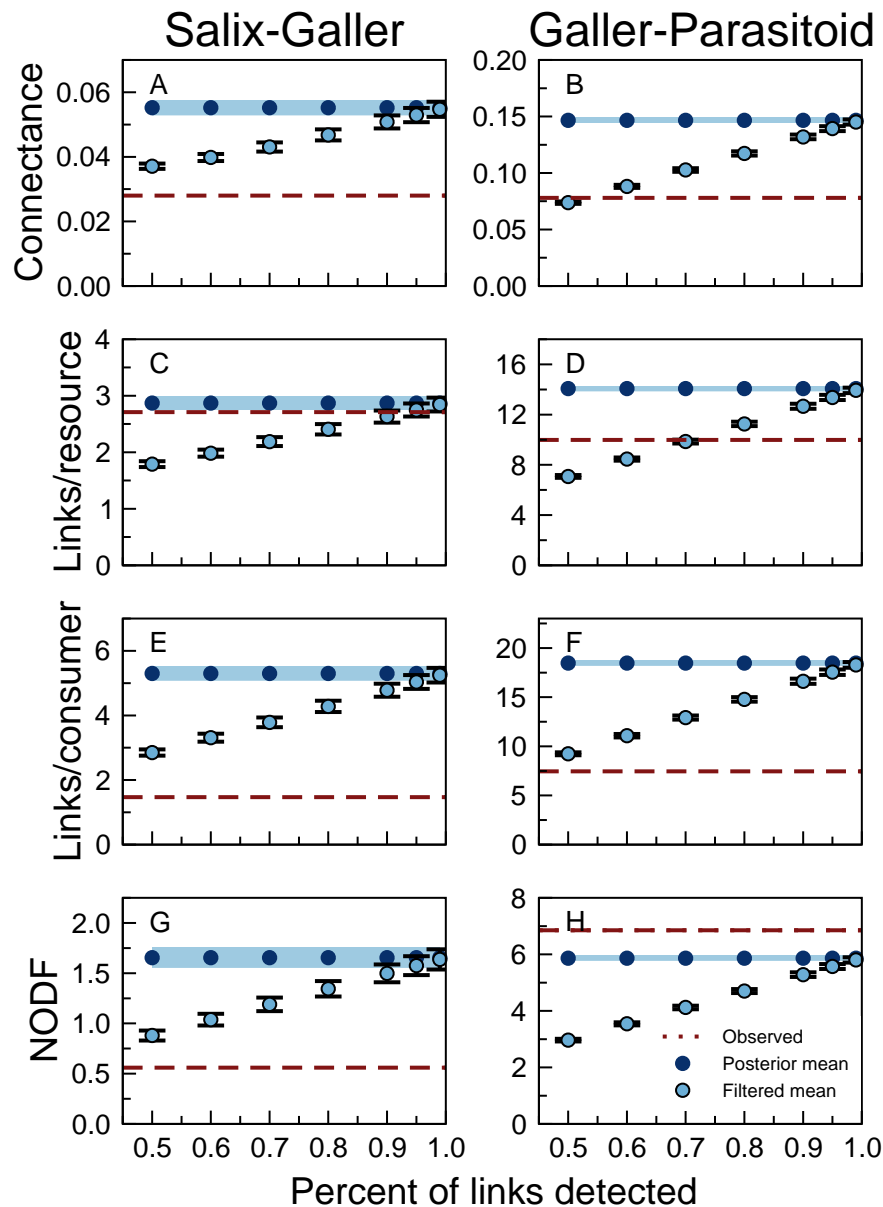
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