

The structure of probabilistic networks

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1 Abstract

2 1. There is a growing realization among community ecologists that interactions between species vary across
3 space and time, and that this variation needs be quantified. Our current numerical framework to analyze the
4 structure of species interactions, based on graph-theoretical approaches, usually do not consider the variabil-
5 ity of interactions. Since this variability has been show to hold valuable ecological information, there is a
6 need to adapt the current measures of network structure so that they can exploit it.

7 2. We present analytical expressions of key measures of network structured, adapted so that they account for
8 the variability of ecological interactions. We do so by modeling each interaction as a Bernoulli event; using
9 basic calculus allows expressing the expected value, and when mathematically tractable, its variance. When
10 applied to non-probabilistic data, the measures we present give the same results as their non-probabilistic
11 formulations, meaning that they can be generally applied.

12 3. We present three case studies that highlight how these measures can be used, in re-analyzing data that exper-
13 imentally measured the variability of interactions, to alleviate the computational demands of permutation-
14 based approaches, and to use the frequency at which interactions are observed over several locations to infer
15 the structure of local networks. We provide a free and open-source implementation of these measures.

16 4. We discuss how both sampling and data representation of ecological networks can be adapted to allow the
17 application of a fully probabilistic numerical network approach.

18 **Keywords:** ecological networks, species interactions, connectance, degree distribution, nestedness, modularity

1 Introduction

2 Ecological networks efficiently represent biotic interactions between individuals, populations, or species.
3 Historically, their study focused on describing their structure, with a particular attention on food webs
4 (???[Dunne 2006](#)) and plant-pollinator interactions (???; ???[Jordano 1987](#); [Bascompte et al. 2003](#)). This
5 established that network structure is linked to community or ecosystem-level properties such as stability
6 (???[McCann 2014](#)), coexistence (???; ???[Bastolla et al. 2009](#); [Haerter et al. 2014](#)), or ecosystem func-
7 tioning (???[Duffy 2002](#)). The description of ecological networks resulted in the emergence of questions
8 about how functions and properties of communities emerged from their structure, and this stimulated the
9 development of a wide array of measures for key network properties (???; ???; ???[Bersier et al. 2002](#);
10 [Banašek-Richter et al. 2004](#); [Jordano & Bascompte 2013](#)).

11 Given a network (*i.e.* a structure where nodes, most often species, are linked by edges, representing eco-
12 logical interactions) as input, measures of network structure return a *property* based on one or several
13 *units* (*e.g.* nodes, links, or groups thereof) from this network, either directly measured, ~~ef~~[or](#) after an opti-
14 mization process. Some of the properties are *direct* properties (they only require knowledge of the unit on
15 which they are applied), whereas others are *emergent* (they require knowledge of, and describe, higher-
16 order structures). For example, connectance, the realized proportion of potential interactions, is a direct
17 property of a network, since it can be derived from the number of nodes and edges only. The degree of a
18 node (how many interactions it is involved in) is a direct property of the node. The nestedness of a network
19 (that is, the extent to which specialists and generalists overlap), is an emergent property, as it is not directly
20 predictable from the degree of all nodes. The difference is no mere semantics: the difference between
21 direct and emergent properties is important when interpreting their values. Direct properties are concep-
22 tually equivalent to means, in that they tend to be the first moment of network units, whereas emergent
23 properties are conceptually equivalent to variances, higher-order moments, or probability distributions.

24 The interpretation of the measures of network structure as indicators of the action of ecological or evolu-
25 tionary processes must now account for the numerous observations that network structure varies through
26 space and time. In addition to the already well-established variation in the composition of the local
27 species ~~poll~~ (???[pool](#) ([Havens 2015](#))), networks vary because species do not interact in a consistent way

1 ([Poisot et al. 2012](#)). Empirical evidence suggests that the network is not the right unit to under-
2 stand this variation; rather, network variation emerges from the response of interactions to environmental
3 factors and chance events (see [Poisot et al. 2015](#) for a review). Interactions can vary for multiple
4 (non-exclusive) reasons. Local mismatching in phenology creates *forbidden links* ([Poisot et al. 2011](#); [Vizentin-Bugoni et al. 2014](#); [Maruyama et al. 2014](#)). Local variations in abundance prevent
5 the species from encountering one another ([Canard et al. 2014](#)). The joint action of neutral, pheno-
6 logic, and behavioral effects, creates complex and hard to predict responses ([Poisot et al. 2011](#); [Poisot et al. 2015](#); [Chamberlain](#)
7 [et al. 2014](#); [Olito & Fox 2015](#); [Trøjelsgaard et al. 2015](#)). For example, ([Olito & Fox \(2015\)](#)) showed
8 that accounting for neutral (population-size driven) and trait-based effects allows the prediction of the
9 cumulative change in network structure, but not of the change at the level of individual interactions. In
10 addition, ([Carstensen et al. \(2014\)](#)) showed that not all interactions are equally variable within a meta-
11 community: some are highly consistent, whereas others are extremely rare. These results suggest that
12 species interactions, because they vary, cannot be adequately represented as yes-no events; it is therefore
13 necessary to represent them as probabilities. We should replace the question of *Do these two species*
14 *interact?* by *How likely is it that they will interact?*

16 Yet the current way of dealing with probabilistic interactions are either to ignore variability entirely, or to
17 generate networks with yes/no interactions based on the measured probabilities. Both approaches incur
18 a net loss of information, and measures of network structure that explicitly account for interaction vari-
19 ability are a much needed mathematically rigorous alternative. When ignoring the probabilistic nature of
20 interactions (henceforth *binary* networks), every non-zero element of the network is explicitly assumed
21 to occur with probability 1. This over-represents rare events, and increases the number of interactions;
22 as a result, this changes the estimated value of different network properties, in a way that remains poorly
23 understood. The generation of random binary networks based on probabilities also suffers from biases,
24 especially in the range of connectance within which most ecological systems [hieslie](#). These biases are (i)
25 pseudo-replication when the permutational space is small ([Poisot & Gravel 2014](#)), and (ii) systematic
26 biases in the emergent properties at low connectances ([Chagnon 2015](#)). An alternative is to consider
27 only the interactions above a given threshold, which unfortunately leads to under-representation of rare
28 events and decreases the effective number of interactions. The use of thresholds also notably introduces

1 the risk of removing species that have a lot of interactions that individually have a low probability of
 2 occurring. These considerations highlight the need to amend our current methodology for the description
 3 of ecological networks, in order to give more importance to the variation of individual interactions.

4 Yet the extant methodological corpus is well accepted, and the properties it describes are well understood.
 5 Rather than suggesting measures, we argue that it is more productive to re-express those we already have,
 6 in a way that ~~do not loses~~ does not lose information when applied to probabilistic networks. We contribute
 7 to this effort by re-developing a unified toolkit of measures to characterize the structure of probabilistic
 8 interaction networks. Several direct and emergent core properties of ecological networks (both bipartite
 9 and unipartite) can be re-formulated in a probabilistic context. We illustrate this toolkit through several
 10 case studies, and discuss how the current challenges in the (i) measurement and (ii) analysis of probabilistic
 11 interaction networks.

12 Suite of probabilistic network metrics

13 We use the following notation throughout the paper. \mathbf{A} is a matrix where each element A_{ij} gives $P(ij)$,
 14 *i.e.* the probability that species i establishes an interaction with species j . If \mathbf{A} represents a unipartite
 15 network (*e.g.* a food web), it is a square matrix and contains the probabilities of each species interacting
 16 with all others, including itself. If \mathbf{A} represents a bipartite network (*e.g.* a pollination network), it will not
 17 necessarily be square. We call S the number of species, and R and C respectively the number of rows
 18 and columns. $S = R = C$ in unipartite networks, and $S = R + C$ in bipartite networks. Note that all of
 19 the measures defined below can be applied on a bipartite network that has been made unipartite.

20 The unipartite transformation of a bipartite matrix \mathbf{A} is the block matrix \mathbf{B} :

$$\mathbf{B} = \begin{pmatrix} 0_{(R,R)} & \mathbf{A} \\ 0_{(C,R)} & 0_{(C,C)} \end{pmatrix}, \quad (1)$$

21 where $0_{(C,R)}$ is a matrix of C rows and R columns (noted $C \times R$) filled with 0s, etc. Note that for centrality
 22 to be relevant in bipartite networks, this matrix should be made symmetric: $\mathbf{B}_{ij} = \mathbf{B}_{ji}$.

1 We assume that all interactions are independent (so that $P(ij \cap kl) = P(ij)P(kl)$ for any species), and can
 2 be represented as a series of Bernoulli trials (so that $0 \leq P(ij) \leq 1$). A Bernoulli trial is the realization
 3 of a probabilistic event that gives 1 with probability $P(ij)$ and 0 otherwise. The latter condition allows
 4 us to derive estimates for both the *variance* ($\text{var}(X) = p(1 - p)$) and expected values ($E(X) = p$) of the
 5 network measures. The variance of additive independent events is the sum of their individual variances,
 6 and the variance of multiplicative independent events is

$$\text{var}(X_1 X_2 \dots X_n) = \prod_i (\text{var}(X_i) + [E(X_i)]^2) - \prod_i [E(X_i)]^2. \quad (2)$$

7 As all X_i are Bernoulli random variables ,

$$\text{var}(X_1 X_2 \dots X_n) = \prod_i p_i - \prod_i p_i^2. \quad (3)$$

8 As a final note, all of the measures described below can be applied on the binary (0/1) versions of the net-
 9 works in which case they converge on the non-probabilistic version of the measure as usually calculated.
 10 This property is particularly desirable as it allows our framework to be used on any unweighted network
 11 represented in a probabilistic or binary way. The approach outlined here differs from using *weighted* net-
 12 works, in that it answers a different ecological question. Probabilistic networks describe the probability
 13 that any interaction will happen, whereas weighted networks describe some measure of the effect of the
 14 interaction when it happens ([Berlow et al. 2009](#)); weighted networks therefore assume that the inter-
 15 action happen. Although there are several measures for weighted ecological networks ([Bersier et al. 2002](#)), in which interactions happen but with different outcomes, these are not relevant for probabilistic
 16 networks; they do not account for the fact that interactions display a variance that will cascade up to the
 17 network level. Instead, the weight of each interaction is best viewed as a second modeling step focusing
 18 on the non-zero cases (*i.e.* the interactions that are realized); this is similar to the method now frequently
 19 used in species distribution models, where the species presence is modeled first, and its abundance second,
 20 using a (possibly) different set of ecological predictors ([Boulangeat et al. 2012](#)).

1 Direct network properties

2 Connectance and number of interactions

3 Connectance (or network density) is the proportion of possible interactions that are realized, defined as
4 $Co = L/(R \times C)$, where L is the total number of interactions. As all interactions in a probabilistic network
5 are assumed to be independent, the expected value of L , is

$$\hat{L} = \sum_{i,j} A_{ij}, \quad (4)$$

6 and $\hat{Co} = \hat{L}/(R \times C)$. Likewise, the variance of the number of interactions is $\text{var}(\hat{L}) = \sum (A_{ij}(1 - A_{ij}))$.

7 Node degree

8 The degree distribution of a network is the distribution of the number of interactions established (number
9 of successors) and received (number of predecessors) by each node. The expected degree of species i is

$$\hat{k}_i = \sum_j (A_{ij} + A_{ji}). \quad (5)$$

10 The variance of the degree of each species is $\text{var}(\hat{k}_i) = \sum_j (A_{ij}(1 - A_{ij}) + A_{ji}(1 - A_{ji}))$. Note also that
11 $\sum \hat{k}_i = 2\hat{L}$, as expected

12 Generality and vulnerability

13 By simplification of the above, generality \hat{g}_i and vulnerability \hat{v}_i are given by, respectively, $\sum_j A_{ij}$ and
14 $\sum_j A_{ji}$, with their variances $\sum_j A_{ij}(1 - A_{ij})$ and $\sum_j A_{ji}(1 - A_{ji})$.

1 Emergent network properties

2 Path length

3 Networks can be used to describe indirect interactions between species through the use of paths. The
4 existence of a path of length 2 between species i and j means that they are connected through at least one
5 additional species k . In a probabilistic network, unless some elements are 0, all pairs of species i and j
6 are connected through a path of length 1, with probability A_{ij} . The expected number of paths of length k
7 between species i and j is given by

$$n_{ij}^{(k)} = (\mathbf{A}^k)_{ij}, \quad (6)$$

8 where \mathbf{A}^k is the matrix multiplied by itself k times.

9 It is possible to calculate the probability of having at least one path of length k between the two species:
10 this can be done by calculating the probability of having no path of length k , then taking the running
11 product of the resulting array of probabilities. For the example of length 2, species i and j are connected
12 through g with probability $A_{ig}A_{gj}$, and so this path does not exist with probability $1 - A_{ig}A_{gj}$. For any pair
13 i, j , let \mathbf{m} be the vector such that $m_g = A_{ig}A_{gj}$ for all $g \notin (i, j)$ (???[Mirchandani 1976](#)). The probability
14 of not having any path of length 2 is $\prod (1 - \mathbf{m})$. Therefore, the probability of having a path of length 2
15 between i and j is

$$\hat{p}_{ij}^{(2)} = 1 - \prod (1 - \mathbf{m}), \quad (7)$$

16 which can also be noted

$$\hat{p}_{ij}^{(2)} = 1 - \prod_g (1 - A_{ig}A_{gj}). \quad (8)$$

17 In most situations, one would be interested in knowing the probability of having a path of length 2 *without*
18 having a path of length 1; this is simply expressed as $\hat{p}_{ij}^{(2)*} = (1 - A_{ij})\hat{p}_{ij}^{(2)}$. These results can be expanded

1 to any length k in $[2, n - 1]$. First one can, by the same logic, generate the expression for having at least
 2 one path of length k :

$$\hat{p}_{ij}^{(k)} = 1 - \prod_{(g_1, g_2, \dots, g_{k-1})} (1 - A_{ig_1} A_{g_1 g_2} \dots A_{g_{k-1} j}) \quad (9)$$

3 where $(g_1, g_2, \dots, g_{k-1})$ are all the $(k - 1)$ -permutations of $1, 2, \dots, n \setminus (i, j)$. Then having a path of length k
 4 without having any smaller path is

$$\hat{p}_{ij}^{(k)*} = (1 - A_{ji})(1 - \hat{p}^{(2)}) \dots (1 - \hat{p}^{(k-1)}) \hat{p}^{(k)}. \quad (10)$$

5 Unipartite projection of bipartite networks

6 The unipartite projection of a bipartite network is obtained by linking any two nodes of one mode (“side”
 7 of the network) that are connected through at least one node of the other mode; for example, two plants
 8 are connected if they share at least one pollinator. It is readily obtained using the formula in the *Path*
 9 *length* section. This yields either the probability of an edge in the unipartite projection (of the upper or
 10 lower nodes), or if using the matrix multiplication, the expected number of such nodes.

11 Nestedness

12 Nestedness is an important measure of (bipartite) network structure that tells the extent to which the inter-
 13 actions of specialists and generalists overlap. We use the formula for nestedness proposed by [\(Bastolla et al. 2009\)](#)
 14 [\(2009\)](#); this measure is a modification of NODF [\(Almeida-Neto et al. 2008\)](#) for ties in species
 15 degree that removes the constraint of decreasing fill. Nestedness for each margin of the matrix is defined
 16 as $\eta^{(R)}$ and $\eta^{(C)}$ for, respectively, rows and columns. As per [\(Almeida-Neto et al. 2008\)](#), we define a
 17 global statistic for nestedness as $\eta = (\eta^{(R)} + \eta^{(C)})/2$.

18 Nestedness, in a probabilistic network, is defined as

$$\eta^{(R)} = \sum_{i < j} \frac{\sum_k A_{ik} A_{jk}}{\min(g_i, g_j)}, \quad (11)$$

1 where g_i is the expected generality of species i . The reciprocal holds for $\eta^{(C)}$ when using v_i (the vulnera-
 2 bility) instead of g_i . The values returned are within $[0; 1]$, with $\eta = 1$ indicating complete nestedness.

3 **Modularity**

4 Modularity represents the extent to which networks are compartmentalized, *i.e.* the tendency for subsets
 5 of species to be strongly connected together, while they are weakly connected to the rest of the network
 6 (???[Stouffer & Bascompte 2011](#)). Modularity is measured as the proportion of interactions between nodes
 7 of an arbitrary number of modules, as opposed to the random expectation. The modularity as derived by
 8 (???[Newman \(2004\)](#)) can be expressed as

$$Q = \sum \left[\left(\frac{\mathbf{A}}{2 \sum \mathbf{A}} - \frac{\sum_i \mathbf{A} \sum_j \mathbf{A}}{2 \sum \mathbf{A}^2} \right) \delta \right] \quad (12)$$

9 where $\sum_i \mathbf{A}$ and $\sum_j \mathbf{A}$ are the sums of rows and columns of \mathbf{A} , and δ is a matrix, wherein δ_{ij} is 1 if i
 10 and j belong to the same module, and 0 otherwise. This formula can be *directly* applied to probabilistic
 11 networks. Modularity takes values in $[0; 1]$, where 1 indicates perfect modularity.

12 **Centrality**

13 Although node degree is a rough first order estimate of centrality, other measures are often needed. Here,
 14 we derive the expected value of centrality according to (???[Katz \(1953\)](#)). This measure generalizes to
 15 directed acyclic graphs (whereas other do not). For example, although eigenvector centrality is often used
 16 in ecology, it cannot be measured on probabilistic graphs. Eigenvector centrality requires the matrix's
 17 largest eigenvalues to be real, which is not the case for all probabilistic matrices. The measure proposed
 18 by Katz is a useful replacement, because it accounts for the paths of all length between two species instead
 19 of focusing on the shortest path.

20 As described above, the expected number of paths of length k between i and j is $(\mathbf{A}^k)_{ij}$. Based on this,

1 the expected centrality of species i is

$$C_i = \sum_{j=1}^n \sum_{k=1}^{n-1} \alpha^k (\mathbf{A}^k)_{ji}. \quad (13)$$

2 The parameter $\alpha \in [0; 1]$ regulates how important long paths are. When $\alpha = 0$, only first-order paths
 3 are accounted for (and the centrality is equal to the degree). When $\alpha = 1$, paths of all length are equally
 4 important. As C_i is sensitive to the size of the matrix, we suggest normalizing by $\mathbf{C} = \sum C$ so that

$$\langle C_i \rangle = \frac{C_i}{\mathbf{C}}. \quad (14)$$

5 This results in the *expected relative centrality* of each node in the probabilistic network, which sums to
 6 unity.

7 **Species with no outgoing links**

8 Estimating the number of species with no outgoing links (successors) can be useful when predicting
 9 whether, *e.g.*, predators will go extinct. Alternatively, when prior information about traits are available,
 10 this can allow predicting the invasion success of a species in a novel community.

11 A species has no successors if it manages *not* to establish any outgoing interaction, which for species i
 12 happens with probability

$$\prod_j (1 - A_{ij}). \quad (15)$$

13 The number of expected such species is therefore the sum of the above across all species,

$$\hat{P}P = \sum_i \left(\prod_j (1 - A_{ij}) \right), \quad (16)$$

1 and its variance is

$$\text{var}(\hat{P}) = \sum_i \left(\prod_j (1 - A_{ij}^2) - \prod_j (1 - A_{ij})^2 \right). \quad (17)$$

2 Note that in a non-probabilistic context, species with no outgoing links would be considered primary
3 producers. This is not the case here: if interactions are probabilistic events, then even a top predator may
4 have no preys, and this clearly doesn't imply that it will become a primary producer in the community.
5 For this reason, the trophic position of the species may be measured better with the binary version of the
6 matrix.

7 **Species with no incoming links**

8 Using the same approach as for the number of species with no outgoing links, the expected number of
9 species with no incoming links is therefore

$$\hat{T}P = \sum_i \left(\prod_{j \neq i} (1 - A_{ji}) \right). \quad (18)$$

10 Note that we exclude self-interactions, as top-predators in food webs can, and often do, engage in canni-
11 balism.

12 **Number of species with no interactions**

13 Predicting the number of species with no interactions (or whether any species will have at least one in-
14 teraction) is useful when predicting whether species will be able to integrate into an existing network,
15 for example. From a methodological point of view, this can also be a helpful *a priori* measure to deter-
16 mine whether null models of networks will have a lot of species with no interactions, and so will require
17 intensive sampling.

1 A species has no interactions with probability

$$\prod_{j \neq i} (1 - A_{ij})(1 - A_{ji}). \quad (19)$$

2 As for the above, the expected number of species with no interactions (*free species*) is the sum of this
3 quantity across all i :

$$\hat{FS} = \sum_i \prod_{j \neq i} (1 - A_{ij})(1 - A_{ji}). \quad (20)$$

4 The variance of the number of species with no interactions is

$$\text{var}(\hat{FS}) = \sum_i \left(A_{ij}(1 - A_{ij})A_{ji}(1 - A_{ji}) + A_{ij}(1 - A_{ij})A_{ji}^2 + A_{ji}(1 - A_{ji})A_{ij}^2 \right) \quad (21)$$

5 Self-loops

6 Self-loops (the existence of an interaction of a species onto itself) is only meaningful in unipartite net-
7 works. The expected proportion of species with self-loops is very simply defined as $\text{Tr}(\mathbf{A})$, that is, the sum
8 of all diagonal elements. The variance is $\text{Tr}(\mathbf{A} \diamond (1 - \mathbf{A}))$, where \diamond is the element-wise product operation
9 (Hadamard product).

10 Motifs

11 Motifs are sets of pre-determined interactions between a fixed number of species (~~???~~, ~~???~~ [Milo et al. 2002](#);
12 [Stouffer et al. 2007](#)), such as apparent competition with one predator sharing two prey. As there
13 are an arbitrarily large number of motifs, we will illustrate the approach with only two examples.

14 The probability that three species form an apparent competition motif where i is the predator, j and k are
15 the prey, is

$$P(i, j, k \in \text{app. comp}) = A_{ij}(1 - A_{ji})A_{ik}(1 - A_{ki})(1 - A_{jk})(1 - A_{kj}). \quad (22)$$

1 Similarly, the probability that these three species form an omnivory motif, in which i and j consume k
 2 and i consumes j , is

$$P(i, j, k \in \text{omniv.}) = A_{ij}(1 - A_{ji})A_{ik}(1 - A_{ki})A_{jk}(1 - A_{kj}). \quad (23)$$

3 The probability of the number of *any* three-species motif m in a network is given by

$$\hat{N}_m = \sum_i \sum_{j \neq i} \sum_{k \neq j} P(i, j, k \in m). \quad (24)$$

4 It is indeed possible to have an expression of the variance of this value, or of the variance of any three
 5 species forming a given motif, but their expressions become rapidly untractable and are better computed
 6 than written.

7 Network comparison

8 The dissimilarity of a pair of (ecological) networks can be measured using the framework set forth by
 9 [\(Koleff et al. \(2003\)\)](#) using β -diversity measures. Measures of β -diversity compute the dissimilarity
 10 between two networks based on the cardinality of three sets, a , c , and b , which are respectively the shared
 11 items, items unique to superset (network) 1, and items unique to superset 2 (the identity of which network
 12 is 1 or 2 matters for asymmetric measures). Supersets can be the species within each network, or the
 13 interactions between species. Following [\(Poisot et al. \(2012\)\)](#), the dissimilarity of two networks can
 14 be measured as either β_{WN} (all interactions), or β_{OS} (interactions involving only common species), with
 15 $\beta_{OS} \leq \beta_{WN}$.

16 Within our framework, these measures can be applied to probabilistic networks. The expected values of
 17 \bar{a} , \bar{c} , and \bar{b} are, respectively, $\sum \mathbf{A}_1 \diamond \mathbf{A}_2$, $\sum \mathbf{A}_1 \diamond (1 - \mathbf{A}_2)$, and $\sum (1 - \mathbf{A}_1) \diamond \mathbf{A}_2$. Whether β_{OS} or β_{WN} is
 18 measured requires to alter the matrices \mathbf{A}_1 and \mathbf{A}_2 . To measure β_{OS} , one must remove all unique species;
 19 to measure β_{WN} , one must expand the two matrices so that they have the same species at the same place,
 20 and give a weight of 0 to the added interactions.

1 Implementation

2 We provide these measures of probabilistic network structure in a free and open-source (MIT licensed) li-
3 brary for the julia language, available at <http://github.com/PoisotLab/ProbabilisticNetworkEcological>
4 The code can be cited using the following DOI: ~~(given-upon-acceptance)~~[10.5281/zenodo.28317](https://doi.org/10.5281/zenodo.28317) (version
5 [1.0.1](#)). A user guide, including examples, resides at <http://probabilisticnetworkjl.ecologicalnetworkjl.re>

6 Case studies

7 In this section, we contrast the use of probabilistic measures to the current approaches of either using
8 binary networks, or working with null models through simulations. When generating random networks,
9 what we call *Bernoulli trials* from here on, a binary network is generated by doing a Bernoulli trial with
10 probability A_{ij} , for each element of the matrix. This generates networks that have only 0/1 interactions,
11 and are realizations of the probabilistic network. This is problematic because higher order structures
12 involving rare events will be under-represented in the sample, and because most naive approaches (*i.e.* not
13 controlling for species degree) are likely to generate species with no interactions, especially in sparsely
14 connected networks frequently encountered in ecology (~~???~~~~???~~~~???~~[Milo et al. 2003](#); [Poisot & Gravel](#)
15 [2014](#); [Chagnon 2015](#)) – on the other hand, non-naive approaches (*e.g.* based on swaps or quasi-swaps)
16 break the assumption of independence between interactions.

17 Comparison of probabilistic networks

18 In this sub-section, we apply the above probabilistic measures to a bacteria–phage interaction network.
19 ~~???~~[Poullain et al. \(2008\)](#) measured the probability that 24 phage can infect 24 strains of bacteria of the
20 *Pseudomonas fluorescens* species (group SBW25). The (probabilistic) adjacency matrix was constructed
21 by estimating the probability of each phage–bacteria interaction through independent infection assays, and
22 can take values of 0, 0.5 (interaction is variable), and 1.0. We have generated a “Binary” network by
23 setting all interactions with a probability higher than 0 to unity, to simulate the results that would have
24 been obtained in the absence of estimates of interaction probability.

1 Measuring the structure of the Binary, Bernoulli trials, and Probabilistic network gives the following
2 results (average, and variance when there is an analytical expression):

Measure	Binary	Bernoulli trials	Probabilistic
links	336	221.58 ± 57.57	221.52 ± 57.25
η	0.73	0.528	0.512
$\eta^{(R)}$	0.72	0.525	0.507
$\eta^{(C)}$	0.75	0.531	0.518
one consumer, two resources motif	4784	2089	2110
two consumers, one resource motif	4718	2116	2120

3 As these results show, treating all interactions as having the same probability, *i.e.* removing the informa-
4 tion about variability, (i) overestimates nestedness by ≈ 0.2 , (ii) overestimates the number of links by 115,
5 and (iii) overestimates the number of motifs (we have limited our analysis to the two following motifs:
6 one consumer sharing two resources, and two consumers competing for one resource). For the number of
7 links, both the probabilistic measures and the average and variance of 10^4 Bernoulli trials were in strong
8 agreement (they differ only by the second decimal place). For the number of motifs, the difference was
9 larger, but not overly so. It should be noted that, especially for computationally demanding operations
10 such as motif counting, the difference in runtime between the probabilistic and Bernoulli trials approaches
11 can be extremely important.

12 Using Bernoulli trials had the effect of slightly over-estimating nestedness. The overestimation is statis-
13 tically significant from a purely frequentist point of view, but significance testing is rather meaningless
14 when the number of replicates is this large and can be increased arbitrarily; what is important is that the
15 relative value of the error is small enough that Bernoulli trials are able to adequately reproduce the prob-
16 abilistic structure of the network. It is not unexpected that Bernoulli trials are this close to the analytical
17 expression of the measures; due to the experimental design of the [\(Poullain et al. \(2008\)\)](#) study, proba-
18 bilities of interactions are bound to be high, and so variance is minimal (most elements of **A** have a value
19 of either 0 or 1, and so their individual variance is 0 – though their confidence interval varies as a function

1 of the number of observations from which the probability is derived). Still, despite overall low variance,
2 the binary approach severely mis-represents the structure of the network.

3 **Null-model based hypothesis testing**

4 In this section, we analyse 59 pollination networks from the literature using two usual null models of net-
5 work structure, and two models with intermediate constraints. These data cover a wide range a situations,
6 from small to large, and from densely to sparsely connected networks. They provide a good demonstra-
7 tion of the performance of probabilistic metrics. Data come from the *InteractionWeb Database*, and were
8 queried on Nov. 2014.

9 We use the following null models. First (Type I, (???Fortuna & Bascompte (2006))), any interaction
10 between plant and animals happens with the fixed probability $P = Co$. This model controls for con-
11 nectance, but removes the effect of degree distribution. Second, (Type II, (???Bascompte et al. (2003))),
12 the probability of an interaction between animal i and plant j is $(k_i/R + k_j/C)/2$, the average of the
13 richness-standardized degree of both species. In addition, we use the models called Type III in and out
14 (???Poisot et al. 2013), that use the row-wise and column-wise probability of an interaction respectively,
15 as a way to understand the impact of the degree distribution of upper and lower level species.

16 Note that these null models will take a binary network and, through some rules turn it into a probabilistic
17 one. Typically, this probabilistic network is used as a template to generate Bernoulli trials and measure
18 some of their properties, the distribution of which is compared to the empirical network. This approach
19 is computationally inefficient (???Poisot & Gravel 2014), especially using naive models (???Milo et al.
20 2003), and as we show in the previous section, can yield biased estimates of the true average of nestedness
21 (and presumably other properties).

22 We measured the nestedness of the 59 (binary) networks, then generated the random networks under the
23 four null models, and calculated the expected nestedness using the probabilistic measure. Our results are
24 presented in Figure 1.

25 There are two striking results. First, empirical data are consistently *more* nested than the null expectation,
26 as evidenced by the fact that all $\Delta_N - \Delta_n$ values are strictly positive. Second, this underestimation is *linear*

1 between null models I and II, although null model II is always closer to the nestedness of the empirical
2 network (which makes sense, since null model II incorporates the higher order constraint of approximating
3 the degree distribution of both levels). That the nestedness of the null model probability matrix is so
4 strongly determined by the nestedness of the empirical networks calls for a closer evaluation of how the
5 results of null models are interpreted (especially since networks generated using Bernoulli trials revealed
6 a very low variance in their nestedness).

7 There is a strong, and previously unaccounted for, circularity in this approach: empirical networks are
8 compared to a null model which, as we show, has a systematic bias *and* a low variance (in the properties
9 of the networks it generates), meaning that differences in nestedness that are small (thus potentially eco-
10 logically irrelevant) have a good chance of being reported as significant. Interestingly, models III in and
11 III out made overall *fewer* mistakes at estimating nestedness – respectively 0.129 and 0.123, compared to
12 resp. 0.219 and 0.156 for model I and II. Although the error is overall sensitive to model type (Kruskal-
13 Wallis $\chi^2 = 35.80$, d.f. = 3, $p \leq 10^{-4}$), the three pairs of models that were significantly different after
14 controlling for multiple comparisons are I and II, I and III in, and I and III out (model II is not different
15 from either models III in or out).

16 In short, this analysis reveals that (i) the null expectation of a network property under randomization
17 scenarios can be obtained through the analysis of the probabilistic matrix, instead of the analysis of sim-
18 ulated Bernoulli networks; (ii) different models have different systematic biases, with models of the type
19 III performing ~~overall~~ better for nestedness than any other models. This can be explained by the fact that
20 nestedness of a network, as expressed by ~~(???)~~[Bastolla et al. \(2009\)](#), is the average of a row-wise and
21 column-wise nestedness. These depend on the species degree, and as such should be well predicted by
22 models III. The true novelty of the approach outlined here is that, rather than having to calculate the mea-
23 sure for thousands of replicates, an *unbiased* estimate of its mean can be obtained in a fraction of the time
24 using the measures described here. This is particularly important since, as demonstrated by ~~(???)~~[Chagnon](#)
25 [\(2015\)](#), the generation of null randomization is subject to biases in the range of connectance where most
26 ecological networks fall. Our approach aims to provide a bias-free, time-effective way of estimating the
27 expected value of a network property.

1 Spatial-variation predicts local network structure

2 In this final application, we re-analyze data from a previous study by ~~(???Trøjelsgaard~~ [Trøjelsgaard et al. \(2015\)](#), to in-
3 vestigate how spatial information can be used to derive probability of interactions. In the original dataset,
4 fourteen locations have been sampled to describe the local plant-pollination network. This dataset exhibits
5 both species and interaction variability across sampling locations. We define the overall probability of an
6 interaction in the following way,

$$P(i \rightarrow j) = \frac{\mathbf{N}_{ij}}{\mathbf{O}_{ij}}, \quad (25)$$

7 where \mathbf{O}_{ij} is the number of sampling locations in which both pollinator i and plant j co-occur, and \mathbf{N}_{ij} is the
8 number of sampling locations in which they interact. This takes values between 0 (no co-occurrence *or* no
9 interactions) and 1 (interaction observed every time there is co-occurrence, including single observations
10 of an interacting species pair). This represents a simple probabilistic model, in which it is assumed that
11 our ability to observe the interaction is a proxy of how frequent it is.

12 Based on this information, we compare the connectance, nestedness, and modularity, of each sampled
13 (binary) network, to the expected values if interactions are well predicted by the probability given above.
14 The results are presented in [Figure 2](#). There is a clear linear, positive correlation (coeff. 0.89 for con-
15 nectance, 0.76 for η , and 0.92 for modularity) between the observed network properties (binary matrices)
16 and the predictions based on the probabilistic model. This analysis, although simple, suggest that the
17 *local* structure of ecological networks can represent the outcome of a filtering of species interactions, the
18 signature of which can be detected at the regional level by a variation in the probabilities of interactions.
19 Note however that this approach *does not* ~~allows~~ [allow](#) predicting the structure of any arbitrary species
20 pool, since it cannot know the probability of an interaction between two species that never co-occured.

21 Discussion

22 Understanding the structure of ecological networks, and whether it relates to emergent ecosystem prop-
23 erties, is a strong research agenda for community ecology. A proper estimation of this structure requires

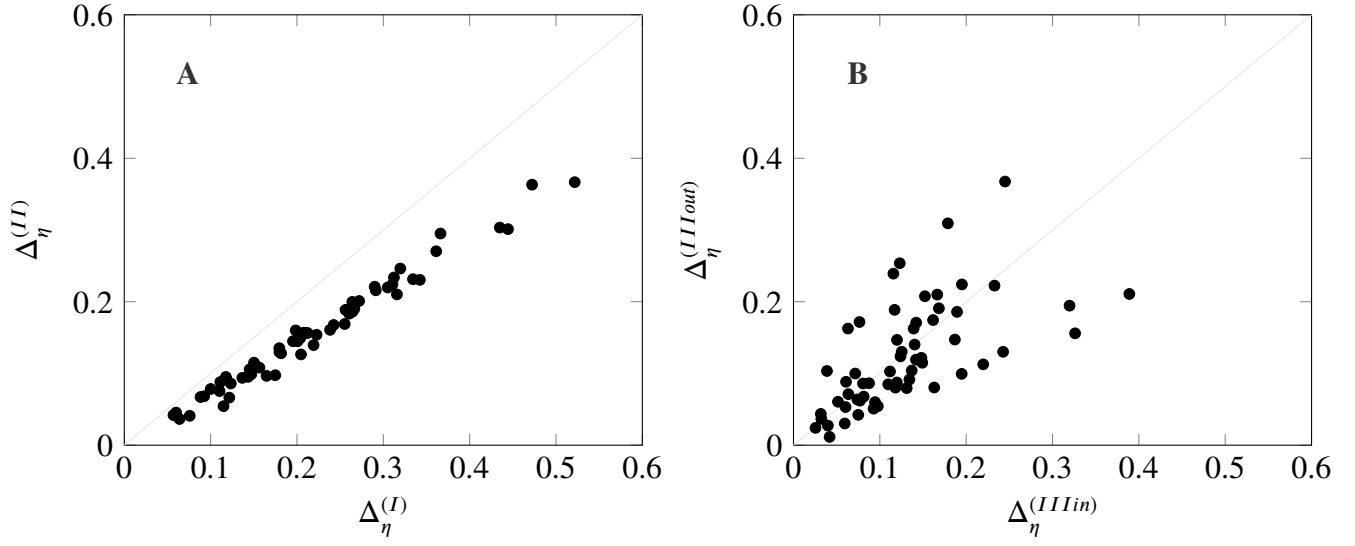


Figure 1: Results of the null model analysis of 59 plant-pollination networks. **A.** There is a consistent tendency for (i) both models I and II to estimate less nestedness than in the empirical network, although null model II yields more accurate estimates. **B.** Models III in and III out also estimate less nestedness than the empirical network, but neither has a systematic bias. For each null model i , the difference $\Delta_{\eta}^{(i)}$ in nestedness η is expressed as $\Delta_{\eta}^{(i)} = \eta - \mathcal{N}^{(i)}(\eta)$, where $\mathcal{N}^{(i)}(\eta)$ is the nestedness of null model i .

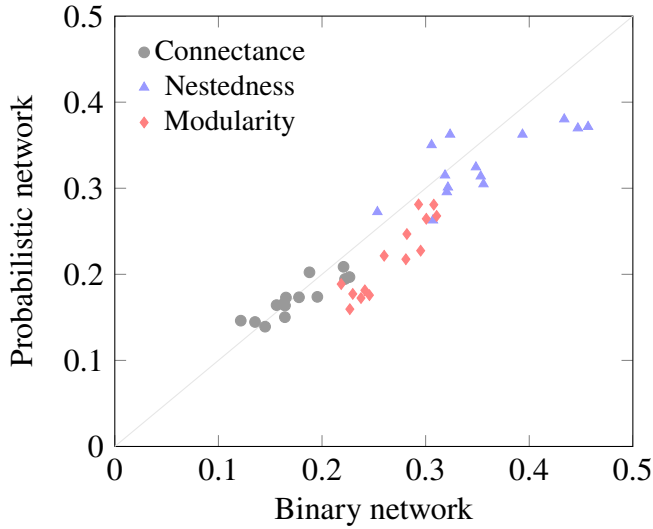


Figure 2: Local network structure inferred from the locally observed interactions (x-axis) or the spatial probabilistic model (y-axis) in the Canaria Island dataset. Although the binary networks slightly underestimate the properties studied here, there is a positive and linear relationship between the empirical structure, and the structure predicted based on probabilities of interactions derived from occurrence information.

1 tools that address all forms of complexity, the most oft-neglected yet pervasive of which is the fact that
2 interactions are variable. Through the suite of measures we present here, we allow future analyses of
3 network structure to account for this phenomenon. There are two main considerations highlighted by this
4 methodological development. First, in what way are probabilistic data are actually independent? Second,
5 what are the implications for data collection?

6 **Non-independance of interactions**

7 We developed and presented a set of measures to quantify the expected network structure, using the prob-
8 ability that each interaction is observed or happens, in a way that does not require time-consuming sim-
9 ulations. Our framework is set up in such a way that the probabilities of interactions are considered to
10 be independent. This is an over-simplification of what we understand of ecological reality, where inter-
11 actions have effects on one another (~~???~~; ~~???~~; ~~???~~ [Golubski & Abrams 2011](#); [Sanders & Veen 2012](#); [Ims](#)
12 [et al. 2013](#)). Yet we feel that, as a first approximation, this assumption is reasonable. There is a strong
13 methodological argument for which the non-independance of interactions cannot currently be robustly
14 accounted for: analytical expectations for non-independant Bernoulli events require knowledge of the full
15 dependence structure. Not only does this severely limit the ability to provide measures of network struc-
16 ture, it requires a far more extensive sampling that what is needed to obtain an estimate of the probability
17 of interactions one by one.

18 **Estimates of interaction probabilities**

19 Estimating interaction probabilities based on species abundances (~~???~~; ~~???~~ [Canard et al. 2014](#); [Olito](#)
20 [& Fox 2015](#)) do not yield independent probabilities: changing the abundance of one species changes
21 all probabilities in the network. They are not Bernoulli events either, as the sum of all probabilities
22 derived this way sums to unity. On the other hand, “cafeteria experiments” (in which individuals from
23 two species are directly exposed to one another to observe whether or not an interaction occurs) give truly
24 independent probabilities of ~~interactions; even a simple criteria, such as the frequency of interactions when~~
25 ~~the two species are put together, is a way of estimating probability~~ [interactions—although this approach is](#)

1 limited to systems with a small number of species, and that are amenable to microcosms or mesocosms
2 experiments. Using the approach outlined by (???Poisot *et al.* (2015)), different sources of information
3 (species abundance, trait distribution, and the outcome of experiments) can be combined to estimate the
4 probability that interactions will happen in empirical communities.

5 Another way to obtain approximation of the probability of interactions is to use ~~replicated sampling~~ spatially
6 and temporally replicated sampling (assuming that replicates are done in environments that can be assumed
7 to be comparably homogeneous); in this context, it is not the interactions that are repeatedly sampled, but
8 the network as a whole. Some studies (~~???~~ ~~???~~ ~~???~~ ~~???~~ Tylianakis *et al.* 2007; Carstensen *et al.*
9 2014; Olito & Fox 2015; Trøjelsgaard *et al.* 2015) surveyed the existence of interactions at different lo-
10 cations, and a simple approach of dividing the number of observations of an interaction by the number of
11 co-occurrence of the species involved will provide a (somewhat crude) estimate of the probability of this
12 interaction. This approach requires extensive sampling, especially since interactions are harder to observe
13 than species (~~???~~ ~~???~~ Poiset *et al.* 2012; Gilarranz *et al.* 2015), yet it enables the re-analysis of existing
14 datasets in a probabilistic context.

15 **Implications for data collection**

16 An important outcome is that, when estimating probabilities from observational data, it becomes possible
17 to have an estimate of how robust the sampling is. How completely a network is sampled is a key, yet
18 often-overlooked, driver of some measures of structure (~~???~~ ~~???~~ Nielsen & Bascompte 2007; Chacoff *et*
19 *al.* 2012; Fründ *et al.* 2015). The probabilistic approach allows to estimate the *confidence interval* of
20 the interaction probability, knowing the number of samples used for the estimation. Assuming normally
21 distributed observational error (this can be generalized for other ~~structure-of-error~~ error distributions), the
22 confidence interval around a probability p estimated from n samples is

$$\epsilon = z \sqrt{\frac{1}{n} p(1 - p)}. \quad (26)$$

23 For a 95% confidence interval, $z \approx 1.96$. If an interaction is estimated to happen at $p = 0.3$, its 95%
24 confidence interval is $[0; 0.74]$ when estimated from four samples, $[0.01; 0.58]$ when estimated from ten,

1 and [0.21; 0.38] when estimated from a hundred. ~~This points out~~ Note that the above formula tends to
2 perform poorly when $n < 30$, and do not applies when $p \in \{0, 1\}$; it nevertheless provides an *estimate* of
3 how robust the probability estimate is.

4 The quantification, and integration, of uncertainty in the probability of interaction, is a subject that remains
5 to be worked out. To develop a coarse understanding of how it affects the estimate of network properties,
6 one can (for example) sample the interaction probability within its 95% confidence interval. This points
7 to a fundamental issue with the sampling of networks: a ~~correct~~ precise estimate of the probability of
8 interactions from observational data is tremendously difficult to achieve, ~~and~~. Although the development
9 of predictive models ~~should be a research priority since it~~ partly alleviates this difficulty. ~~Note also that the~~
10 ~~above formula tends to perform poorly when $n < 30$, and do not applies when $p \in \{0, 1\}$; it nevertheless~~
11 ~~provides an *estimate* of how robust the probability estimate is,~~ estimating confidence intervals around the
12 probability of an interaction guide empirical research efforts to (i) either collect additional replicates or
13 (ii) provide additional data to improve the performance of predictive models.

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19 Montpellier in 2012.

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