THE STRUCTURE OF PROBABILISTIC NETWORKS

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Abstract

1. There is a growing realization among community ecologists that interactions between species vary in space and time, and that this variation needs be quantified. Yet, our current numerical framework to analyze the structure of species interactions, largely based on graph-theoretical approaches, is unsuited to ~~this type of data~~probabilistic approaches. Since the variation of species interactions holds ~~much~~ valuable ecological information, there is a need to develop new metrics to exploit it.
2. We present analytical expressions of key network metrics, using a probabilistic framework. Our approach is based on modeling each interaction as a Bernoulli event, and using basic calculus to express the expected value, and when mathematically tractable, its variance. We provide a free and open-source implementation of these measures.
3. We show that our approach allows us to overcome limitations of both neglecting the variation of interactions (over-estimation of rare events) and using simulations (extremely high computational demand). We present a few case studies that highlight how these measures can be used.
4. We conclude ~~this contribution~~ by discussing how the sampling and data representation of ecological ~~network~~ networks can be adapted to better allow the application of a fully probabilistic numerical network framework.

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

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INTRODUCTION

Ecological networks are an efficient way to represent biotic interactions between individuals, populations, or species. Historically, their study focused on describing their structure, with a particular attention on food webs (Dunne 2006) and plant-pollinator interactions (Bascompte et al. 2003; Jordano 1987). The key result of this line of research was linking ~~this~~ network structure to community or ecosystem-level properties such as stability (McCann 2014), coexistence (Bastolla et al. 2009; Haerter, Mitarai, and Sneppen 2014), or ecosystem functioning (~~Thébault and Loreau 2003;~~ Duffy 2002~~; Poisot 2012~~). To a large extent, the description of ecological networks resulted in the emergence of questions about how functions ~~emerged from~~ and properties of communities emerged from their structure, and this stimulated the development of a rich methodological literature (see *e.g.* Jordano and Bascompte 2013), defining a wide array of structural properties.

Given a network (*i.e.* a structure where nodes, most often species, are linked by edges, representing ecological interactions) as input, measures of network structure return a *property* based on one or several *units* (*e.g.* nodes, links, or groups thereof) from this network. Some of the properties are *direct* properties (they only require knowledge of the unit on which they are applied), whereas others are *emergent* (they require knowledge of, and describe, higher-order structures). For example, connectance, the realized proportion of potential interactions, is a direct property of a network. The degree of a node (how many interactions it is involved in) is a direct property of the node. The nestedness of a network (that is, the extent to which specialists and generalists overlap), on the other hand, is an emergent property that is not directly predictable from the degree of all nodes. Though the difference may appear to be semantics, establishing a difference between direct and emergent properties is important when interpreting their values; direct properties are conceptually equivalent to means, in that they tend to be the first moment of network units, whereas emergent properties are conceptually equivalent to variances~~or other~~, higher-order moments, or probability distributions.

In the recent years, the interpretation of the properties of network structure (as indicators of the action of ecological or evolutionary processes) has been ~~somewhat complicated~~ challenged by the observation that network structure varies through space and time. This happens because, contrary to a long-standing assumption of network studies, species from the same pool do not interact in a consistent way (Poisot et al. 2012; Trøjelsgaard et al. 2015). Empirical and theoretical studies suggest that the network is not the right unit to understand this variation; rather, network variation is an emergent property of the response of ecological interactions to environmental factors and chance events (~~???~~see Poisot, Stouffer, and Gravel 2015 for a review). Interactions can vary because of local mismatching in phenology (~~J. M.~~ Olesen et al. 2011; P. K. Maruyama et al. 2014; Vizentin-Bugoni, Maruyama, and Sazima 2014), populations fluctuations preventing the interaction (E. F. Canard et al. 2014), or a combination of both (Olito and Fox 2014; Chamberlain et al. 2014). For example, Olito and Fox (2014) ~~show~~ showed that accounting for neutral (population-size driven) and trait-based effects allows the prediction of the cumulative change in network structure, but not of the change at the level of individual interactions. In addition, Carstensen et al. (2014) ~~show that within a meta-community,~~ showed that not all interactions are equally variable within a meta-community: some are highly consistent, whereas others are extremely rare. These empirical results all point to the fact that species interactions cannot always be adequately ~~modeled~~ represented as yes-no events; since it is well established that they do vary, it is necessary to represent them as probabilities. ~~To the question of *Do these two species interact?*, we should substitute~~ We should therefore replace the question of *Do these two species interact?* by *How likely is it that they will interact?*.

The current way of dealing with probabilistic interactions are either to ignore variability entirely or to generate random networks. Probabilistic ~~metrics~~ measures of network structure are a mathematically rigorous alternative to both. When ignoring the probabilistic nature of interactions (henceforth *binary* networks), every non-zero element of the network is ~~assumed to be~~ explicitly assumed to occur with probability 1. This leads to over-representation of some rare events, and increases the number of interactions~~.~~; as a result, this changes the estimated value of different network properties, in a way that remains poorly understood. Issues are most likely to arise for the range of connectances where the topological (Chagnon 2015) or permutational (Poisot and Gravel 2014) space of random network is small, leading to over-replication or uncharacterized biases. An alternative is to consider only the interactions above a given threshold, which ~~leads to an~~ unfortunately leads to under-representation of rare events and decreases the effective number of interactions ~~.~~ (in addition to the problem that there is no robust criterion to decide on a threshold). More importantly, the use of thresholds introduces the risk of removing species that have a lot of interactions that individually have a low probability of occurring. Taken together, these considerations highlight the need to amend our current methodology for the description of ecological networks, in order to give more importance to the variation of individual interactions — current measures neglect the variability of interactions, and are therefore discarding valuable ecological information. Because the methodological corpus available to describe ecological networks had first been crafted at a time when it was assumed that interactions were ~~invariants, it is~~ invariant, extent measures of network structure are unsuited to address the questions that probabilistic networks would allow us to ~~ask~~address.

~~In~~ The elements discussed above requires the considerable methodological adjustment of re-writing measures of network structure to account for the fact that interactions are not consistent; in this paper, we ~~show that several~~ re-develop a unified toolkit of measures to characterize the structure of probabilistic interaction networks. Several direct and emergent core properties of ecological networks (both bipartite and unipartite) can be re-formulated in a probabilistic context~~(Yeakel et al. 2012; **???**); we~~. We conclude by showing how this methodology can be applied to exploit the information contained in the variability of networks, and to reduce the computational burden of current methods in network analysis. ~~We also provide a free and open-source (MIT license) implementation of this suite of measures in a library for the `julia` language, available at `http://github.com/PoisotLab/ProbabilisticNe`~~

Suite of probabilistic network metrics

Throughout this paper, we use the following notation. $\mathbf{A}$ is a matrix ~~wherein~~ where each element A_{ij} ~~is~~ gives $\mathrm{P}(ij)$, *i.e.* the probability that species i establishes an interaction with species j. If $\mathbf{A}$ represents a unipartite network (*e.g.* a food web), it is a square matrix and contains the probabilities of each species interacting with all others, including itself. If $\mathbf{A}$ represents a bipartite network (*e.g.* a pollination network), it will not necessarily be square. We call S the number of species, and R and C respectively the number of rows and columns. $S = R = C$ in unipartite networks, and $S = R + C$ in bipartite networks.

Note that all of the measures defined below can be applied on a bipartite network that has been made unipartite~~; the~~ .

The unipartite transformation of a bipartite matrix **A** is the block matrix **A**:

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

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 to be relevant in bipartite networks, this matrix should be made symmetric: $\mathbf{B}_{ij} = \mathbf{B}_{ji}$.

We will also assume that all interactions are independent (so that ~~$\mathrm{P}(ij|kl) = \mathrm{P}(ij)\mathrm{P}(kl)$~~ $\mathrm{P}(ij \cap kl) = \mathrm{P}(ij)\mathrm{P}(kl)$ for any species), and can be represented as a series of Bernoulli trials (so that $0 \leq \mathrm{P}(ij) \leq 1$). A Bernoulli trial is the realization of a probabilistic event that gives 1 with probability $\mathrm{P}(ij)$ and 0 otherwise. The latter condition allows us to derive estimates for the *variance* ($\mathrm{var}(X) = p(1-p)$), and expected values ($\mathrm{E}(X) = p$), of the network metrics. We can therefore estimate the variance of most network properties, using the fact that the variance of additive independent events is the sum of their individual variances, and that the variance of multiplicative independent events is

$$\mathrm{var}(X_1 X_2 \ldots X_n) = \prod_i \left(\mathrm{var}(X_i) + [\mathrm{E}(X_i)]^2\right) - \prod_i [\mathrm{E}(X_i)]^2 \tag{2}$$

As all X_i are Bernouilli random variables ,

$$\mathrm{var}(X_1 X_2 \ldots X_n) = \prod_i p_i - \prod_i p_i^2 \tag{3}$$

As a final note, all of the measures described below can be applied on the binary (0/1) versions of the networks ~~and will give the exact value of the non-probabilistic measure~~ in which case they converge on the non-probabilistic version of the measure as usually calculated. This property is particularly desirable as it allows our framework to be used on any network, whether they are represented in a probabilistic or binary way. Nonetheless, the approach outlined here differs from using *weighted* networks, in that it answers a completely different question (**???**). Probabilistic networks describe the probability that any interaction will happen, whereas weighted networks describe the effect of the interaction when it happens (**???**). Although there are several measures for *quantitative* networks (Bersier, Bana\vsek-Richter, and Cattin 2002), in which interactions happen but with different outcomes, these are not relevant for probabilistic networks, which require accounting for the fact that interactions are probabilistic event, *i.e.* they display a variance that will cascade up to the network level. Instead, the weight of each interaction is best viewed as a second modeling step that focuses solely on the non-zero cases (*i.e.* the interactions that are realized); this is similar to the method now frequently used in species distribution models, where the species presence is modeled first, and its abundance second, using a (possibly) different set of predictors (Boulangeat, Gravel, and Thuiller 2012).

Direct network properties.

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

$$\hat{L} = \sum_{i,j} A_{ij} \,, \tag{4}$$

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

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

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

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 ~~as expected,~~ $\sum \hat{k}_i = 2\hat{L}$~~.~~ , as expected

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

~~emergent~~ Emergent network properties.

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

$$n_{ij}^{(\hat{k})} = \left(\mathbf{A}^k\right)_{ij} \; , \qquad (6)$$

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

It is possible to calculate the probability of having at least one path of length k between the two species: this can be done by calculating the probability of having no path of length k, then taking the running product of the resulting array of probabilities. For the example of length 2, species i and j are connected 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 i, j, let $\mathbf{m}$ be the vector such ~~as~~ that $m_g = A_{ig}A_{gj}$ for all $g \notin (i, j)$ (Mirchandani

1976). The probability of not having any path of length 2 is $\prod(1-\mathbf{m})$. Therefore, the probability of having a path of length 2 between i and j is

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

which can also be noted

$$\hat{p}^{(2)}_{ij} = 1 - \prod_{g}(1 - A_{ig}Agj). \tag{8}$$

In most situations, one would be interested in knowing the probability of having a path of length 2 *without* having a path of length 1; this is simply expressed as ~~$(1-A_{ij})\hat{p}^{(2)}_{ij}$. One can~~ $\hat{p}^{(2)*}_{ij} = (1-A_{ij})\hat{p}^{(2)}_{ij}$. These results can be expanded to any length k in $[2, n-1]$. First one can, by the same logic, generate the expression for having at least one path of length ~~3~~ k:

$$\hat{p}^{(3)(k)}{}_{ij} = (1-A_{ij})(1-{}^{(2)}_{ij})1 - \prod_{(g_1,g_2,...,g_{k-1})}(1-\mathbf{m})\prod_{x,y}(1 - A_{iyig_1}A_{g_1g_2}...A_{g_{k-1}j})(1-A_{xj}), \tag{9}$$

where ~~**m** is the vector of all $A_{ix}A_{xy}A_{yj}$ for $x \notin (i,j), y \neq x$. This gives the probability of having at least one path from i to j, passing through any pair of nodes x and y,~~ $(g_1, g_2,..., g_{k-1})$ are all the $(k-1)$-permutations of $1, 2, ..., n\backslash(i,j)$. Then having a path of length k without having any ~~shorter path . In theory, this approach can be generalized up to an arbitrary path length, but it becomes rapidly untractable.~~ smaller path is

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

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

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

Nestedness, in a probabilistic network, is defined as

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

where g_i is the expected generality of species i. The reciprocal holds for $\eta^{(C)}$ when using v_i (the vulnerability) instead of g_i.

The values returned are within [0; 1], with $\eta = 1$ indicating complete nestedness.

Modularity. Modularity represents the extent to which networks are compartmentalized, *i.e.* the tendency for subsets of species to be strongly connected together, while they are weakly connected to the rest of the network (~~Daniel B.~~ Stouffer and Bascompte 2011). Modularity is measured as the proportion of interactions between nodes of an arbitrary number of modules, as opposed to the random expectation. Assuming a vector $\mathbf{s}$ which, for each node in the network, holds the value of the module it belongs to (an integer in $[1, c]$), Newman (2004) proposed a general measure of modularity, which is

$$Q = \sum_{m=1}^{c} \left(e_{mm} - a_m^2 \right)$$

$$Q = \sum_{m=1}^{c} \left(e_{mm} - a_m^2 \right) \,, \tag{12}$$

~~,~~where c is the number of modules,

$$e_{mm} = \sum_{ij} \frac{\mathbf{A}_{ij}}{2c} \delta(\mathbf{s}_i, \mathbf{s}_j)$$

$$e_{mm} = \sum_{ij} \frac{\mathbf{A}_{ij}}{2c} \delta(\mathbf{s}_i, \mathbf{s}_j) \,, \tag{13}$$

~~,~~and

$$a_m = \sum_{n} e_{mn}$$

~~,~~

$$a_m = \sum_{n} e_{mn} \,, \tag{14}$$

with δ being Kronecker's function, returning 1 if its arguments are equal, and 0 otherwise. This formula can be *directly* applied to probabilistic networks. Modularity takes values in [0; 1], where 1 indicates perfect modularity.

Centrality. Although node degree is a rough first order estimate of centrality, other measures are often needed. ~~We~~ Here, we derive the expected value of centrality according to Katz (1953). This

~~measures~~ measure generalizes to directed acyclic graphs (whereas other do not). For example, although eigenvector centrality is often used in ecology, it cannot be measured on probabilistic graphs. Eigenvector centrality requires the matrix's largest eigenvalues to be real, which is not the case for all probabilistic matrices. The measure proposed by Katz is a useful replacement, because it accounts for the paths of all length between two species instead of focusing on the shortest path.

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

$$C_i = \sum_{j=1}^{n} \sum_{k=1}^{\cancel{\infty}\, n-1} \alpha^k (\mathbf{A}^k)_{ji} \,. \tag{15}$$

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

$$C_i = \frac{C_i}{\mathbf{C}} \,. \tag{16}$$

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

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

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

$$\prod_j (1 - A_{ij})\,. \tag{17}$$

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

$$\hat{PP} = \sum_i \left(\prod_j (1 - A_{ij}) \right) \cancel{.}\,, \tag{18}$$

and its variance is

$$\mathrm{var}(\hat{PP}) = \sum_i \left(\prod_j (1 - A_{ij}^2) - \prod_j (1 - A_{ij})^2 \right) . \tag{19}$$

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

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

$$\hat{TP} = \sum_i \left(\prod_{j \neq i} (1 - A_{ji}) \right) . \tag{20}$$

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

Number of species with no interactions. Predicting the number of species with no interactions (or whether any species will have at least one interaction) is useful when predicting whether species will be able to integrate into an existing network, for example. ~~Note that from~~ From a methodological point of view, this can also be a helpful *a priori* measure to determine whether null models of networks will have a lot of species with no interactions, and so will require intensive sampling.

A species has no interactions with probability

$$\prod_{j \neq i}(1 - A_{ij})(1 - A_{ji}) \,. \tag{21}$$

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

$$\hat{FS} = \sum_i \prod_{j \neq i}(1 - A_{ij})(1 - A_{ji}) \,. \tag{22}$$

The variance of the number of species with no interactions is

$$\mathrm{var}(\hat{FS}) = \sum_i \left(A_{ij}(1 - A_{ij})A_{ji}(1 - A_{ji}) + A_{ij}(1 - A_{ij})A_{ji}^2 + A_{ji}(1 - A_{ji})A_{ij}^2 \,. \right) \tag{23}$$

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

Motifs. Motifs are sets of pre-determined interactions between a fixed number of species (R Milo et al. 2002; ~~Daniel B~~D. B. Stouffer et al. 2007), such as ~~for example~~ apparent competition with one predator sharing two ~~preys~~prey. As there are an arbitrarily large number of motifs, we will illustrate the approach with only two examples.

The probability that three species form an apparent competition motif ~~(one predator, two prey)~~ where i is the predator, j and k are the prey, is

$$\text{(24)} \qquad \mathrm{P}(i,j,k \in \text{app. comp}) = A_{ij}(1-A_{ji})A_{ik}(1-A_{ki})(1-A_{jk})(1-A_{kj}).$$

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

$$\text{(25)} \qquad \mathrm{P}(i,j,k \in \text{omniv.}) = A_{ij}(1-A_{ji})A_{ik}(1-A_{ki})A_{jk}(1-A_{kj}).$$

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

$$\text{(26)} \qquad \hat{N}_\mathrm{m} = \sum_i \sum_{j\neq i} \sum_{k\neq j} P(i,j,k \in \mathrm{m}).$$

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

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

Within our framework, these measures can be applied to probabilistic networks. The expected values of $\bar{a}$, $\bar{c}$, 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 measured requires to alter the matrices $\mathbf{A}_1$ and $\mathbf{A}_2$. To measure β_{OS}, one must remove all unique species; to measure β_{WN}, one must expand the two matrices so that they have the same species at the same place, and give a weight of 0 to the added interactions.

APPLICATIONS

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

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

Measuring the structure of the Binary, Bernoulli trials, and Probabilistic network gives the following ~~result~~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

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

Using Bernoulli trials had the effect of slightly over-estimating nestedness. The overestimation is statistically significant from a purely frequentist point of view, but significance testing is rather meaningless when the number of replicates is this large and can be increased arbitrarily; what is important is that the relative value of the error is small enough that Bernoulli trials are able to adequately reproduce the probabilistic structure of the network. It is not unexpected that Bernoulli trials are this close to the analytical expression of the measures; due to the experimental design of the Poullain et al. (2008) study, probabilities of interactions are bound to be high, and so variance is minimal (most elements of $\mathbf{A}$ have a value of either 0 or 1, and so their individual variance is 0 – though their confidence interval varies as a function of the number of observations from which the probability is derived). Still, despite overall low variance, the binary approach severely mis-represents the structure of the network.

Null-model based hypothesis testing. In this section, we analyse 59 pollination networks from the literature using two usual null models of network structure, and two models with intermediate constraints. These data cover a wide range a situations, from small to large, and from densely to sparsely connected networks. They provide a good demonstration of the performance of probabilistic metrics. Data come from the *InteractionWeb Database*, and were queried on Nov. 2014.

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

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

We measured the nestedness of the 59 (binary) networks, then generated the random networks under the four null models, and calculated the expected nestedness using the probabilistic measure. ~~For each null model i, the difference $\Delta_N^{(i)}$ in nestedness N is expressed as $\Delta_N^{(i)} = N - \mathcal{N}^{(i)}(N)$, where $\mathcal{N}^{(i)}(N)$ is the nestedness of null model i.~~ Our results are presented in Figure 1.

~~group style=columns=2, horizontal sep=2cm, xmin=0, xmax=0.6, ymin=0, ymax=0.6black!10, no markerscoordinates (0,0) (0.6,0.6); only markstable x = d1, y = d2figures/app2.dat; at (axis~~

~~cs:0.1,0.55)**A**; black!10, no markerscoordinates (0,0) (0.6,0.6); only markstable x = d3i, y = d3ofigures/app2.dat; at (axis cs:0.1,0.55)**B**;~~

~~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.~~

There are two striking results. First, empirical data are consistently *more* nested than the null expectation, as evidenced by the fact that all Δ_N values are strictly positive. Second, this underestimation is *linear* between null models I and II~~(in that it does not depends on how nested the empirical network is)~~, although null model II is always closer to the nestedness of the empirical network (which makes sense, since null model II incorporates the higher order constraint of ~~respecting~~ approximating the degree distribution of both levels). That the nestedness of the null model probability matrix is so strongly determined by the nestedness of the empirical networks calls for a closer evaluation of how

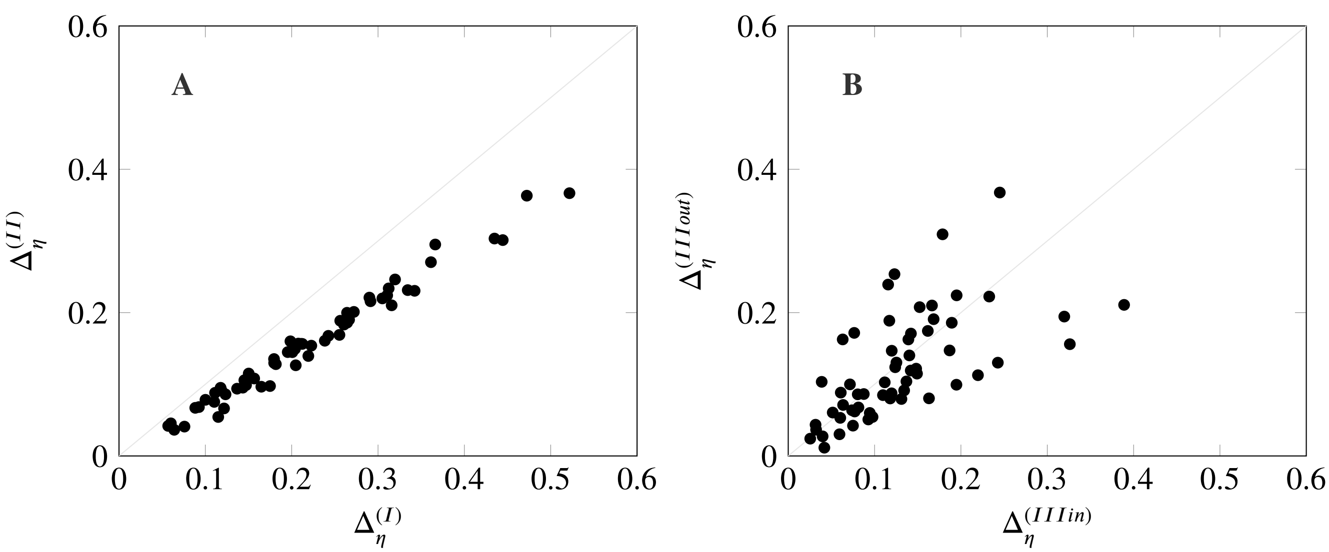

FIGURE 1. Results of the null model analysis of 59 plant-pollination networks. **A**. There is a consistent tendency for (i) both models I and II to estimate less nestedness than in the empirical network, although null model II yields more accurate estimates. **B**. Models III in and III out also estimate 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.

the results of null models are interpreted (especially since ~~Bernoulli simulations~~ networks generated using Bernoulli trials revealed a very low variance in ~~the simulated~~ their nestedness).

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

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

~~IMPLICATIONS FOR DATA COLLECTION~~

Spatial-variation predicts local network structure. In this final application, we re-analyze data from a previous study by Trøjelsgaard et al. (2015), to investigate how spatial information can be used to derive probability of interactions. In the original dataset, fourteen locations have been sampled to describe the local plant-pollination network. This dataset exhibits both species and interaction variability across sampling locations. We define the overall probability of an interaction in the following way,

$$\mathrm{P}(i \rightarrow j) = \frac{\mathbf{N}_{ij}}{\mathbf{O}_{ij}}, \tag{27}$$

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 number of sampling locations in which they interact. This takes values between 0 (no co-occurence *or* no interactions) and 1 (interaction observed every time there is co-occurrence). This represents a simple probabilistic model, in which it is assumed that our ability to observe the interaction is a proxy of how frequent it is.

Based on this information, we compare the connectance, nestedness, and modularity, of each sampled network, to the expected values if interactions are well predicted by the probability given above. The results are presented in Figure 2. There is a clear linear, positive correlation (coeff. 0.89 for

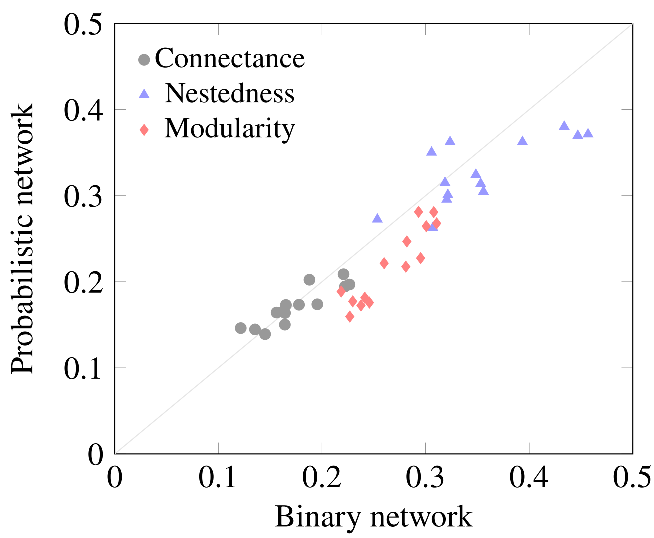

FIGURE 2. Local network structure infered from the locally observed interactions (x-axis) or the spatial probabilistic model (y-axis) in the Canaria Island dataset. Although the binary networks slightly under-estimate the properties studied here, there is a positive and linear relationship between the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

connectance, 0.76 for η, and 0.92 for modularity) between the observed network properties (binary matrices) and the predictions based on the probabilistic model. This analysis, although simple, suggest that the *local* structure of ecological networks can represent the outcome of a filtering of species interactions, the signature of which can be detected at the regional level by a variation in the probabilities of interactions.

Discussion

Understanding the structure of ecological networks, and whether it relates to emergent ecosystem properties, is a key challenge for community ecology. A proper estimation of this structure requires tools that address all forms of complexity, the most oft-neglected yet pervasive of which is the fact that interactions are variable. Through the suite of measures we present here, we allow future analyses of network structure to account for this phenomenon. There are two main considerations highlighted by this methodological development. First, in what way are probabilistic data are actually independent, and second, what are the implications for data collection.

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

Estimates of interaction probabilities. Estimating interaction probabilities based on species abundances (E. F. Canard et al. 2014; Olito and Fox 2014) do not ~~, for example,~~ yield independent probabilities: changing the abundance of one species changes all probabilities in the network. They are not Bernoulli events either, as the sum of all probabilities derived this way sums to unity. On the other hand, "cafeteria experiments" (in which individuals from two species are directly exposed to one another to observe whether or not an interaction occurs) give truly independent probabilities of interactions; even a simple criteria, such as the frequency of interactions when the two species are put together, is a way of estimating probability. Using the approach ~~outline by **(???)**, both~~ outlined by Poisot, Stouffer, and Gravel (2015), different sources of information (species abundance, trait distribution, and the outcome of experiments) can be combined to estimate the probability that interactions will happen in empirical communities. ~~This effort requires improved communications between scientists collecting data and scientists developing methodology to analyze them.~~

Another way to obtain approximation of the probability of interactions is to use spatially replicated sampling. Some studies (Tylianakis, Tscharntke, and Lewis 2007; Carstensen et al. 2014; Olito and Fox 2014; Trøjelsgaard et al. 2015) surveyed the existence of interactions at different locations, and a simple approach of dividing the number of observations of an interaction by the number of co-occurence of the species involved will provide a (somewhat crude) estimate of the probability of this interaction. This approach requires extensive sampling, especially since interactions are harder to observe than species (Poisot et al. 2012; Gilarranz et al. 2014), yet it enables the re-analysis of existing datasets in a probabilistic context.

~~Understanding the structure of ecological networks, and whether it relates to ecosystem properties, isemergent as a key challenge for community ecology. A proper estimation of this structure requires tools that address all forms of complexity, the most oft-neglected yet pervasive of which is~~

Implications for data collection. An important outcome is that, when estimating probabilities from observational data, it becomes possible to have an estimate of how robust the sampling is. How completely a network is sampled is a key, yet often-overlooked, driver of some measures of structure (Nielsen and Bascompte 2007; Chacoff et al. 2011). The probabilistic approach allows to estimate the *confidence interval* of the interaction probability, knowing the number of samples used for the estimation. Assuming normally distributed observational error (this can be generalized for other structure of error), the confidence interval around a probability p estimated from n samples is

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

For a 95% confidence interval, $z \approx 1.96$. If an interaction is estimated to happen at $p = 0.3$, its 95% confidence interval is $[0; 0.74]$ when estimated from four samples, $[0.01; 0.58]$ when estimated from ten, and $[0.21; 0.38]$ when estimated from a hundred. This points out to a fundamental issue with the sampling of networks: a correct estimate of the probability of interaction from observational data is tremendously difficult to achieve, and the development of predictive models should be a research priority since it partly alleviates this difficulty. Note also that the above formula tends to perform poorly when $n < 30$, or when $p \in \{0, 1\}$; it nevertheless provides an *estimate*, in other situations, of how robust the probability estimate is.

Implementation. We provide these measures of probabilistic network structure in a free and open-source (MIT license) library for the ~~fact that interactions are variable. By developing these metrics, we allow future analyses of network structure to account for this phenomenon.~~ `julia` language, available at `http://github.com/PoisotLab/ProbabilisticNetwork.jl`. The code can be cited using the following DOI: **TODO**. A user guide, and API reference, can be found at `http://probabilisticnetworkjl.rea` The code library undergoes automated testing and coverage analysis, the results of which can be accessed from the *GitHub* page given above.

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