

THE STRUCTURE OF PROBABILISTIC NETWORKS

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INTRODUCTION

Ecological networks are an efficient way to represent the interactions between individual, populations, or species. Historically, their study has focused on (i) linking their structure to community or ecosystem-level properties such as stability (McCann 2014), the maintenance of species richness (Bastolla *et al.* 2009; Haerter *et al.* 2014), ecosystem functioning (Duffy 2002; Thébaud & Loreau 2003), and (ii) describing the overall structure of networks, with a particular attention on food webs (Dunne 2006) and plant-pollinator interactions (Jordano 1987; Bascompte *et al.* 2003). To a large extent, the description of network structure enabled questions about how it ties into functional properties, and it is no surprise that the methodology to describe networks is large.

Most measures of network structure function in the following way. Given a network as input, they return a *property* based on one or several *units* within this network. Some of the properties are *direct* properties (they only require knowledge of the unit on which they are applied), and some others are *emerging* properties (they require knowledge of higher-order structures). For example, connectance, the proportion of realized 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, whereas the degree distribution is an emerging property of all nodes. Establishing a difference between direct and emerging properties is important when interpreting their values: direct properties are conceptually equivalent to means, whereas emerging properties are conceptually equivalent to variances.

In the recent years, the interpretation of the values of network structure (as indicators of the action of ecological or evolutionary processes) has been somewhat complicated by the observation that network structure varies through space, and time; species from the same pool do not interact in a consistent way (Poisot *et al.* 2012). Empirical and theoretical studies suggest that the network is not the right

unit to understand this variation; rather, network variation is an emerging property of the response of ecological interactions to environmental factors and chance events (Poisot *et al.* 2014). Interactions can vary because of local mis-matching in phenology (Olesen *et al.* 2011), populations fluctuations preventing the interaction (Canard *et al.* 2014), or a combination of both (Chamberlain *et al.* 2014; Olito & Fox 2014). Olito & Fox (2014) show that accounting for neutral (population-size driven) and trait-based effects allows predicting the cumulative change in network structure, but not the change at the level of individual interactions.

Taken together, these considerations highlight the need to amend our current methodology on ecological network to give more importance to the variation at the interaction level. Because the methodology to describe networks has first been crafted at a time when assuming that interactions did not vary, it is unsuited to address the questions that probabilistic networks allows asking. In this paper, we show that several direct and emerging core properties of ecological networks (both bipartite and unipartite) can be re-formulated in a probabilistic context; we conclude by showing how this methodology can be applied to exploit the information contained in the variability and networks, and reduce the computational burden of current methods in network analysis.

METRICS

Throughout this section, we will assume the following notation. \mathbf{A} is a matrix wherein A_{ij} is $P(ij)$, *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 the probabilities of each species interacting with itself. If \mathbf{A} represents a bipartite network (*e.g.* a pollination network), it will most likely not 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 unipartite transformation of a bipartite matrix \mathbf{A} is the block matrix

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

2

1 where $0_{(C,R)}$ is a matrix of C rows and R columns filled with 0s, etc.

2 We assume that all interactions are independent (so that $P(ij|kl) = P(ij)P(kl)$ for any species), and
 3 can be represented as Bernoulli trials (so that $0 \leq P(ij) \leq 1$). The later condition allows to derive
 4 estimates for the *variance* of the measures, since (i) the variance of a single event X_i of probability p
 5 is $\text{var}(X) = p(1 - p)$, its expected value is $E(X) = p$, (ii) the variance of additive independent events is
 6 the sum of their individual variances, and (iii) the variance of multiplicative independent events is

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

7 As a final note, all of the measures described below can be applied on the binary (0/1) versions of the
 8 networks, and will give the exact value of the non-probabilistic measure. And ain't that nice?

9 **Direct properties.**

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

$$(3) \quad \hat{L} = \sum A_{ij},$$

13 and $\hat{Co} = \hat{L}/(R \times C)$.

14 The variance of the number of interactions is $\text{var}(\hat{L}) = \sum (A_{ij}(1 - A_{ij}))$.

15 *Node degree.* The degree distribution of a network is the distribution of the number of interactions
 16 established and received by each node. The expected degree of species i is

$$(4) \quad \hat{k}_i = \sum_j (A_{ij} + A_{ji})$$

1 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
 2 as expected, $\sum \hat{k}_i = 2\hat{L}$.

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

5 **Emerging properties.**

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

$$(5) \quad n_{ij}^{(2)} = (\mathbf{A}^k)_{ij},$$

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

12 It is possible to calculate the probability of having at least one path between the two species: this
 13 can be done by calculating the probability of having 0 paths, then multiplying the resulting array of
 14 probabilities. For the example of length 2, species i and j are connected through k with probability
 15 $A_{ik}A_{kj}$, and so this path does not exist with probability $1 - A_{ik}A_{kj}$. For any pair i, j , let \mathbf{m} be the
 16 vector such as $m_k = A_{ik}A_{kj}$ for all $k \notin (i, j)$ (Mirchandani 1976). The probability of not having any
 17 path of length 2 is $\prod (1 - \mathbf{m})$. Therefore, the probability of having a path of length 2 between i and j
 18 is

$$(6) \quad \hat{p}_{ij}^{(2)} = 1 - \prod_4 (1 - \mathbf{m}).$$

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

$$(7) \quad \hat{p}_{ij}^{(3)} = (1 - A_{ij})(1 - \hat{p}_{ij}^{(2)})(1 - \prod_{x,y} (1 - \mathbf{m})) \prod_{x,y} ((1 - A_{ix})(1 - A_{xy})(1 - A_{yj})),$$

4 where \mathbf{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
 5 one path from i to j , passing through any pair of nodes x and y , without having any shorter path.
 6 In theory, this approach can be generalized up to an arbitrary path length, but it becomes rapidly
 7 untractable.

8 *Nestedness.* We use the formula for nestedness proposed by Bastolla et al. (2009). They define nest-
 9 edness for each margin of the matrix, as $\eta^{(R)}$ and $\eta^{(C)}$ for, respectively, rows and columns. As per
 10 Almeida-Neto et al. (2008), we define a global statistic for nestedness as $\eta = (\eta^{(R)} + \eta^{(C)})/2$.

11 Nestedness, in a probabilistic network, is defined as

$$(8) \quad \eta^{(R)} = \sum_{i < j} \frac{\sum_k A_{ik}A_{jk}}{\min(g_i, g_j)},$$

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

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

15 *Katz centrality.* Although a rough estimate of centrality is the node degree, as described above, it is
 16 often needed to measure centrality within the context of a larger neighborhood. In addition, we derive
 17 the expected value of centrality according to Katz (1953). This measures generalizes to directed acyclic
 18 graphs. Although eigenvector centrality is often used in ecology, it cannot be measured on probabilis-
 19 tic graphs. Eigenvector centrality requires that the matrix has its largest eigenvalues real, which is not
 20 the case for *all* probabilistic matrices. Katz's centrality is nonetheless a useful replacement, because it
 21 uses the paths of all lengths between two species instead of focusing on the shortest path.

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

$$(9) \quad C_i = \sum_{k=1}^{\infty} \sum_{j=1}^n \alpha^k (\mathbf{A}^k)_{ji}.$$

3 The parameter $\alpha \in [0; 1]$ regulates how important long paths are. When $\alpha = 0$, only first-order paths
 4 count. When $\alpha = 1$, all paths are equally important. As C_i is sensitive to the size of the matrix, we
 5 suggest to normalise it so that

$$(10) \quad C_i = \frac{C_i}{C}.$$

6 This results in the *expected relative centrality* of each node in the probabilistic network. Note that
 7 when using only $k = 1$, and $\alpha = 1$, the raw value of Katz's centrality is the species generality.

8 *Number of primary producers.* Primary producers, in a food web, are species with no successors, includ-
 9 ing themselves. Biologically, they are autotrophic organisms, or organisms whose preys or substrates
 10 have been remove from the network. A species is a primary producer if it manages *not* to establish
 11 any outgoing interaction, which for species i happens with probability

$$(11) \quad \prod_j (1 - A_{ij}).$$

12 The number of expected primary producers is therefore the sum of the above across all species:

$$(12) \quad \hat{P}P = \sum_i \left(\prod_j (1 - A_{ij}) \right).$$

1 The variance in the number of expected primary producers is

$$(13) \quad \text{var}(\hat{P}P) = \sum_i \left(\prod_j (1 - A_{ij}^2) - \prod_j (1 - A_{ij})^2 \right)$$

2 *Number of top predators.* Top-predators can loosely be defined as species that have no predecessors in
 3 the network: they are establishing links with other species, but no species are establishing links with
 4 them. Using the same approach than for the number of primary producers, the expected number of
 5 top-predators is therefore

$$(14) \quad \hat{T}P = \sum_i \left(\prod_{j \neq i} (1 - A_{ji}) \right)$$

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

7 *Number of species with no interactions.* Predicting the number of species with no interaction (or whether
 8 any species will have at least one interaction) is useful to predict whether species will be able to inte-
 9 grate themselves in an existing network, for example.

10 A species has no interactions with probability

$$(15) \quad \prod_{j \neq i} (1 - A_{ij})(1 - A_{ji})$$

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

$$(16) \quad \hat{F}S = \sum_i \prod_{j \neq i} (1 - A_{ij})(1 - A_{ji})$$

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

$$(17) \quad \text{var}(\hat{FS}) = \sum_i \left(A_{ij}(1-A_{ij})A_{ji}(1-A_{ji}) + A_{ij}(1-A_{ij})A_{ji}^2 + A_{ji}(1-A_{ji})A_{ij}^2 \right)$$

2 Note that from a methodological point of view, this can be a helpful *a priori* measure to determine
 3 whether null models of networks will have a lot of species with no interactions, and so will require
 4 intensive sampling.

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

9 *Motifs.* Motifs are sets of pre-determined interactions between a fixed number of specie (Milo *et al.*
 10 2002), such as for example one predator sharing two preys. As there is an arbitrarily large number of
 11 motifs, we will illustrate the formulae with only two examples.

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

$$(18) \quad P(i, j, k \in \text{app. comp}) = A_{ij}(1-A_{ji})A_{ik}(1-A_{ki})(1-A_{jk})(1-A_{kj})$$

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

$$(19) \quad P(i, j, k \in \text{omniv.}) = A_{ij}(1-A_{ji})A_{ik}(1-A_{ki})A_{jk}(1-A_{kj})$$

1 The probability of the number of *any* motif m in a network is given by

$$(20) \quad \hat{N}_m = \sum_i \sum_{j \neq i} \sum_{k \neq j} P(i, j, k \in m)$$

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

5 *Unipartite projection of bipartite networks.* As the unipartite projection of a bipartite network is ob-
 6 tained by assigning an edge between any two nodes that are connected through at least one node of
 7 the other mode, it is readily obtained using the formula in the *Path length* section. This yields either
 8 the probability of an edge in the unipartite projection (of the upper or lower nodes), or if using the
 9 matrix multiplication, the expected number of such nodes.

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

17 Within our framework, these measures can be applied to probabilistic networks. The expected values
 18 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}
 19 is measured requires to alter the matrices \mathbf{A}_1 and \mathbf{A}_2 . To measure β_{OS} , one must remove all unique
 20 species; to measure β_{WN} , one must expand the two matrices so that they have the same species at the
 21 same place, and give a weight of 0 to the added interactions.

In this section, we will provide an overview of the applications of probabilistic network measures. The current way of dealing with probabilistic interactions is (i) to ignore it entirely or (ii) to generate random networks. Probabilistic metrics are an alternative to that. When ignoring the probabilistic nature of interactions, what we call *Binary* from here on, every non-zero element of the network is assumed to be 1. This leads to over-representation of some rare-events, and increases the number of interactions.

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 is problematic because (i) higher order structures involving rare events will be under-represented in the sample, and (ii) naive approaches are likely to generate free species, especially in sparsely connected networks frequently encountered in ecology (Milo *et al.* 2003; Poisot & Gravel 2014).

Comparison of probabilistic networks. In this sub-section, we apply the above measures to a bacteria-phage interaction network. Poullain et al. (2008) have measured the probability that 24 phages can infect 24 strains of bacteria of the *Pseudomonas fluorescens* species (group SBW25). Each probability has been observed through three independent infection assays, and can take values of 0, 0.5, and 1.0. Measuring the structure of the Binary, Bernoulli trials, and Probabilistic network gives the following result:

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

As these results show, transforming the probabilistic matrix into a binary one (i) overestimates nestedness by ≈ 0.02 , and (ii) overestimates the number of links by 115. For the number of links, both the

1 probabilistic measures and the average and variance of 10^4 Bernoulli trials were in strong agreement
2 (they differ only by the second decimal place).

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

12 **Null-model based hypothesis testing.** In this section, we analyse 59 pollination networks from the
13 literature using two “classical” null models of network structure, and two intermediate models. These
14 data cover a wide range a situations, from small to large, and from densely to sparsely connected
15 networks. They provide a good demonstration of the performance of probabilistic metrics.

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

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

1 We measured the nestedness of the 59 networks, then generated the random networks under the four
 2 null models, and calculated the expected nestedness. For each null model i , the difference $\Delta_N^{(i)}$ in
 3 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 .
 4 Our results are presented in Figure 1.

5 There are two striking results. First, null models consistently *underestimate* the nestedness of the 59
 6 pollination networks, as evidence by the fact that all Δ_N values are strictly positive. Second, this
 7 underestimation is *linear* between null models I and II, although null model II is always closer to the
 8 *actual* nestedness value. The markedly non-random value of the null nestednesses when compared
 9 to the empirical values calls for a closer evaluation of how the results of null models are interpreted
 10 (especially since Bernoulli simulations revealed a very low variance in the simulated nestedness). In-
 11 terestingly, models III in and III out made overall *less* mistakes at estimating nestedness – resp. 0.129
 12 and 0.123, compared to resp. 0.219 and 0.156 for model I and II. Although the error is overall sensible
 13 to model type (Kruskal-Wallis $\chi^2 = 35.80$, d.f. = 3, $p \leq 10^{-4}$), the three pairs of models that were
 14 significantly different after control for multiple comparison are I and II, I and III in, and I and III out
 15 (model II is not different from either models III).

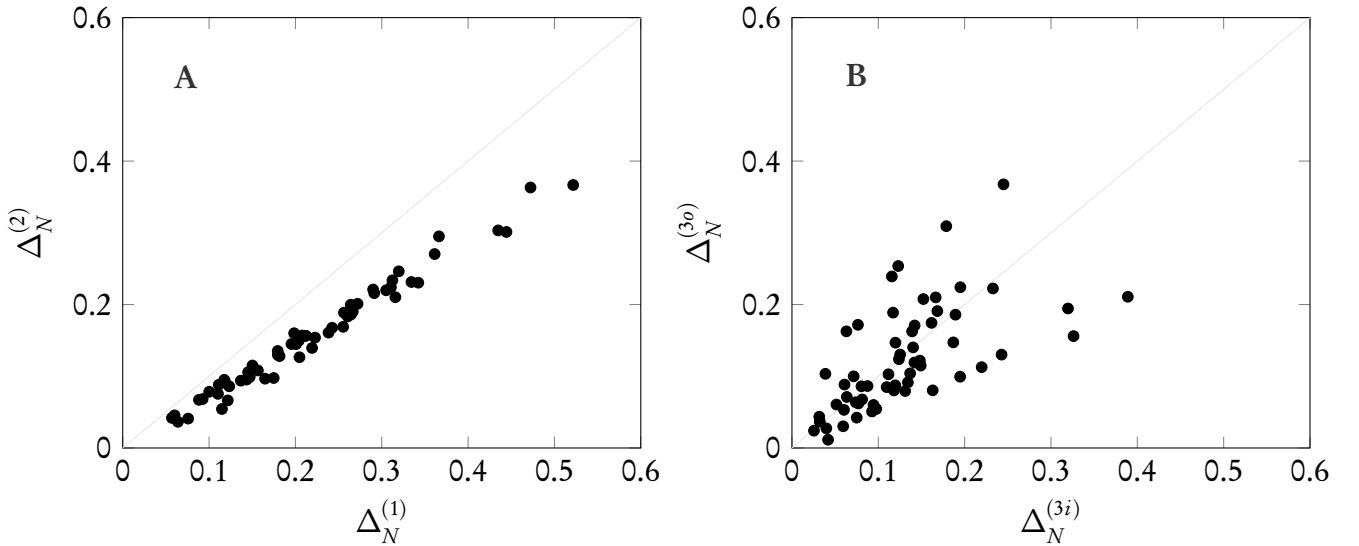


FIGURE 1. Results of the null model analysis of 59 plant-pollination networks. **A.** There is a consistent tendency for (i) both models I and II to estimate less nestedness than in the empirical network, although null model II yields more accurate estimates. **B.** Models III in and III out also estimate less nestedness than the empirical network, but neither has a systematic bias.

1 In short, this analysis reveals that (i) the estimated value of a network measure under randomisation
2 scenarios can be obtained through the analysis of the probabilistic matrix, instead of the analysis of
3 simulated Bernoulli networks; (ii) Different models have different systematic biases, with models of
4 the type III performing overall better for nestedness than any other models. This can be explained by
5 the fact that nestedness of a network, as expressed by Bastolla et al. (2009), is the average of a row-wise
6 and column-wise nestedness. These depend on the species degree, and as such should be well predicted
7 by models III.

8 DISCUSSION

- 9 • What does it mean for probabilities to be independent
- 10 • Consequences for null models now that we have direct estimates
- 11 • Synthesis - works for all types of matrices, not just interactions

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