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Binary versus weighted interaction networks

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ABSTRACT

Interaction networks (**IN**) have been used in ecology to model different kinds of interactions in ecological communities. Historically there are two basic ways to construct an **IN**: binary networks (**BN**) that represent unweighted links among species in the web, and weighted networks (**WN**) that weight each interaction among species by its relative or absolute frequency in the web. We call binary reduction the transition from **WN** to **BN** which obviously entails loss of information. We performed an analysis with 69 **WN** on which we worked the binary reduction. For both **WN** and **BN** we computed: the coefficient of variation, skewness, kurtosis, Shannon entropy and the Gini coefficient on the population statistics. We also computed the dependence asymmetry, the pairwise Jaccard distance and two different measures of nestedness, (W)NODF and τ-temperature, for the **WN** and **BN**. From correlations between the values for **WN** and **BN** we concluded that, for most of the indices, the loss of information due to the binary reduction is not significant. Using a statistical evaluation, for most indices, **BN** give similar results to their corresponding **WN**.

1. Introduction

In the last decade interaction networks have become an important research field in community ecology (Lewinsohn et al., 2006; Bascompte, 2009; Guimarães et al., 2007; Fontaine et al., 2011). From early studies of frugivory by animals (Jordano, 1987) and pollination webs (Olesen, 2007; Guimarães et al., 2007) the area expanded to analyse plants and their inhabiting ants (Fonseca and Ganade, 1996), interactions of herbivorous animals and their food plants (Prado and Lewinsohn, 2004), the network of carcass visits by scavenger animals (Selva and Fortuna, 2007), the interactions between sea anemones and their associated fish species (Ollerton et al., 2007) and host–parasite networks (Vázquez et al., 2005). Interaction networks (**IN**) according to the data represented can be classified as either: qualitative (or binary) or quantitative (or weighted) networks. In binary networks (**BNs**) only the presence or absence of interactions between every two species in the network is represented, whereas for the Weighted Networks (**WNs**) the strength of each interaction is represented by a continuous or frequency measure (Bascompte, 2009).

Several authors have voiced reservations as to **BNs** compared to **WNs** (Blüthgen et al., 2006; Ings et al., 2009) and the reason for that is manifest. Suppose for instance a pollination web in which an animal species *i* is observed visiting a flower of species *l* forty times and a flower *m* just once. When we reduce this **WN** to a **BN** the visitor frequency is equalized, so that 40 and 1 are reduced to 1 in the **BN**. We call the compression of information in the passage from **WN** to **BN** a binary reduction (Fig. 1). In the hypothetical example the binary reduction seems to entail a substantial loss of information that may jeopardize any analysis performed over a **BN**. In a recent review paper on ecological networks (Ings et al., 2009) the **BN** is declared a "dead end" in comparison to **WN** which is considered as a "fruitful avenue".

Much effort has been spent in the last decade to find patterns in **INs** such as the recurrence of asymmetric specialization, nestedness and modularity (Lewinsohn et al., 2006; Olesen, 2007; Bascompte and Stouffer, 2011). **INs** formed by antagonistic relations tend to be more modular while mutualistic **INs** tend to be nested (Bascompte et al., 2003; Thébault and Fontaine, 2010);

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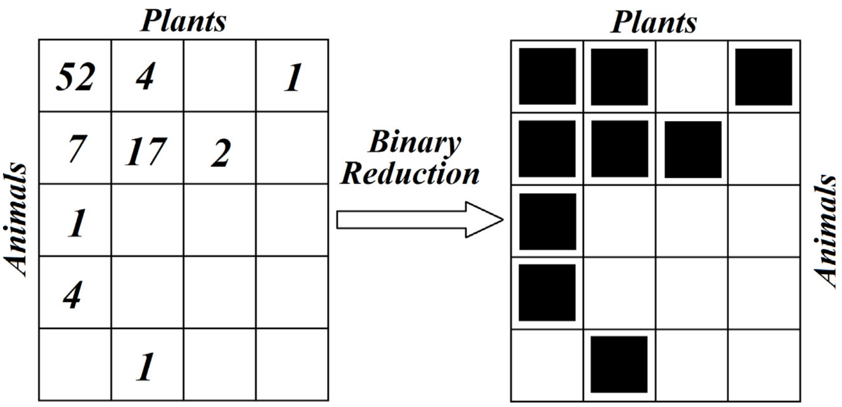

Fig. 1. Sketch of the binary reduction of an interaction network from a weighted network **WN** to a binary network **BN**. The data of this picture are artificial, but they illustrate the heterogeneity and asymmetry of real communities.

antagonistic webs coevolve in an arms race that favours the formation of cliques whereas mutualistic webs seem to follow a rule: "the maximum number of interactions is the best" (Guimarães et al., 2007). Asymmetry has been found in mutualistic networks, if a plant depends strongly on a given animal species, that animal depends only weakly on the plant (Bascompte et al., 2006; Vázquez and Aizen, 2004). These results were based on a statistical analysis of dozens of **INs**, some of which were **WNs** but most were **BNs**. A question that follows is: what is the validity of these results and how valid is a meta-analysis using **BNs**, in combination with **WNs** or not? This question is relevant to the use of many **BN** data sets available in the literature that represent a valuable legacy of biological knowledge.

In this study we devise a statistical strategy to compare **BNs** and **WNs**. We start with a set of empirical **WNs** obtained from the literature and operate a binary reduction to produce their corresponding **BNs**. We then select several indices that are well defined for both **BN** and **WN** and analyse their correlation. A high correlation of indices from **BNs** with their corresponding **WNs** would indicate that the loss of information in the binary reduction is not significant. The objective of this work is to examine differences between **BNs** and **WNs** from a statistical perspective, i.e. to test several indices of **BN** and **WN** to ascertain their correlation.

2. Methodology

This section is comprised of two parts. Initially we present the biological data used to explore the effect of the binary reduction. The second part is devoted to describe the statistical treatment we used to evaluate the differences between **BNs** and **WNs**.

2.1. The biological data set

We employed a set of ecological weighted interaction webs obtained from our own data and the literature. We used a total of 69 weighted webs (N_{total}) comprised of the following kinds of interaction: pollination ($N_{poll} = 22$), frugivory ($N_{frug} = 21$), herbivory ($N_{herb} = 22$) and ant–plant networks ($N_{ant} = 4$). Mutualistic networks include pollination webs formed by flowering plants and pollinator animal species (Jordano, 1987; Memmott, 1999), frugivory webs of fruiting plants and frugivorous animal species that disperse their seeds (Jordano, 1985; Schleuning et al., 2011; Mello et al., 2011), and ant–plants networks formed by ant species that inhabit trees and defend them against herbivory (Fonseca and Ganade, 1996). Antagonistic webs are represented by herbivory webs formed by herbivorous insect species and their respective host plants (Nascimento et al., 2014). The empirical data used in this work are listed in Tables 1, 2 and 3 of the supplementary material, with the number of plant N_P and animal species N_A, and also the total number of links among plant and animals N_L, and the reference in the literature for each network.

2.2. Statistical treatment

Each network is set up as a $N_P \times N_A$ adjacency matrix, the mathematical object that represents the **IN**. The structure of the **IN** is summarised in the matrix elements $a_{i,j} = 1$ or 0 for **BN** and $a_{i,j} = w_{i,j}$ for **WN**. For **BN**, $a_{i,j} = 1$ indicates that an interaction between plant species i and animal species j is recorded, while $a_{i,j} = 0$ indicates that this interaction was not observed. For **WN**, $w_{i,j}$ is the weight of the interaction between species i and j; this value is usually measured as visit frequency of species j to the species i, but it may also represent individuals or biomass consumed. In both cases, we can project the information of the matrix into connectivities of plants, k^P, and animals, k^A, given by

$$k_i^P = \sum_{j=1}^{N_A} a_{i,j} \quad \text{and} \quad k_j^A = \sum_{i=1}^{N_P} a_{i,j} \tag{1}$$

The marginal totals of the **BN** matrix are respectively k_i^P, the number of animals interacting with a plant species i and k_j^A the quantity of plant species interacting with each animal species j; in the case of the **WN** k_i^P is the total number of observations of animals interacting with plant species i, and k_j^A the counterpart for animal species j. The k_i^P and k_j^A values can be regarded as a rough estimate of the effectively interacting population distributions.

2.2.1. Correlation analysis

In our analyses we compared the average behaviour of a set of **WNs** with their respective **BNs**. We first performed a binary reduction for each **WN**, creating two sets **WN** and **BN** to compare, (Fig. 1). For these two sets we computed population (for plants and animals) and community-level statistics. We then performed a correlation analysis for each statistics. Here we used the Pearson correlation; an analysis with the Spearman correlation test gave similar results. Given that we are examining a set of correlations for different indices, without inspecting each index separately, correction for simultaneous multiple tests (e.g. stepwise Bonferroni correction), which in any case are arguable, does not apply (Sokal and Rohlf, 1994). We also used covariance analysis to verify