



The puzzling affinity between modularity and dependence asymmetry[☆]



Gilberto Corso^{a,*}, N.F. Britton^b

^aDepartamento de Biofísica e Farmacologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, 59072-970 Natal-RN, Brazil

^bDepartment of Mathematical Sciences and Centre for Mathematical Biology, University of Bath, Bath BA2 7AY, UK

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ABSTRACT

We discuss the relationship between two patterns found in interaction networks (**INs**) of community ecology: modularity and asymmetric specialisation. These two patterns express two opposite features: asymmetric specialisation suggests an interplay of generalists and specialists forming an entangled web of interconnected species, while modularity brings the idea of groups of species interacting in isolated cliques. We perform the analysis using Dependence Asymmetry (**DA**), which is the simplest way to quantify asymmetric specialisation. We construct an algorithm that finds the pattern of maximal **DA**, and we estimate the upper bound of **DA** analytically. We study the symmetric modular structure that has zero **DA**, and then force an asymmetric mismatch in this pattern to generate high **DA**, allowing us to compare it with a random pattern and with the maximal possible value. We conclude that, despite the opposite notions suggested by the studied patterns, if a modular pattern has enough asymmetry it resembles a specialised asymmetric pattern.

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1. Introduction

The network approach to ecology focuses on patterns of interactions among species, and how links are structured in the network, more than on the species composing a community. The research on Interaction Networks (**INs**) in community ecology is an emerging field of theoretical ecology (Bascompte and Jordano, 2007; Vázquez et al., 2009) that is closely related to food webs and antagonistic networks, but we shall focus on bipartite mutualistic networks. The area is characterised by the famous MacArthur quotation (MacArthur, 1972): “To do science is to search for patterns, not just to accumulate facts”. Perhaps, for **IN** studies, the priority task is not to search for patterns, but to clarify their meaning and mathematical basis. We consider in this paper two patterns that are used to analyse **INs**: modularity and asymmetric specialisation. The puzzling situation is that these patterns may be either exclusive or complementary.

Modular patterns, or compartmentalisation in species interactions, are widespread phenomena in **INs**, that are present in plant–pollinator networks (Guimarães et al., 2007; Olesen, 2007), host–parasite networks (Vacher et al., 2008), and food webs (Bascompte

and Stouffer, 2011). Compartmentalisation can appear due to spatial or temporal co-occurrence of species in a community (Vázquez et al., 2009). Some authors also claim that modular patterns may be associated with groups of species that specialise on other groups due to adaptation in a coevolutionary game, of which a prototypical example is a predator–prey arms race (Thompson, 2005). To quantify modularity the most used algorithm is by (Guimerá et al., 2007), which gives the optimal number of modules and an index of modularity with a confidence interval.

Asymmetric specialisation is a pattern that expresses the following rule: species interact preferentially with species that have the maximum difference in their number or weight of interactions. Specialists prefer generalists, and neither generalists nor specialists tend to interact with each other. Asymmetric specialisation does not have a unique index; in this work we use the Dependence Asymmetry **DA** because it is the simplest way to quantify asymmetric specialisation in **INs**. The **DA** was explored initially by (Jordano, 1987) and (Vázquez and Aizen, 2004) in plant–pollinator networks. Most research in **DA** is connected to the idea that asymmetric specialisation increases stability of **INs** (Bascompte et al., 2006), an important issue in the complexity–stability debate (MacCann, 2000; May, 1974).

Modularity and asymmetric specialisation are patterns that suggest opposite tendencies. Modularity evokes the idea of closed groups of species that interact among themselves and exclude other species (Bascompte and Jordano, 2007). Asymmetric specialisation, on the other hand, points in an opposite direction,

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* Corresponding author. Tel.: +55 84 3215 3419.

E-mail addresses: corso@cb.ufrn.br, gfcorso@gmail.com (G. Corso), n.f.britton@bath.ac.uk (N.F. Britton).

where species with a large number of interactions associate with species with few interactions. A game that gives origin to an entangled ensemble that exclude groups and strongly integrates species in the web of interactions (Vázquez and Aizen, 2004).

We explore differences and convergences between modularity and **DA**, a topic that is specially relevant for the characterisation of mutualistic **INs** (Bascompte and Jordano, 2007). We shall see that the most symmetrical modular structures indeed have zero **DA**, but a mismatch in the modular structure generates a substantial alteration in the **DA**, easily surpassing the **DA** of a random network. The paper starts by defining dependence asymmetry and the related connectivity asymmetry. The algorithm of maximal **DA** is then introduced and we exemplify patterns of maximal **DA**. An analytic estimate of the average **DA** for a modular structure with an asymmetry is found, and this result is compared with a random and a maximal average **DA**. Finally we discuss the results in connection with the concept of nestedness, in particular the implications of this result for the debate on modularity versus nestedness.

2. Dependence asymmetry

Consider a mutualistic plant–pollinator community consisting of L_P plants and L_A animal (usually insect) pollinators. The central concept of this work is the $L_P \times L_A$ 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 the case of a binary (or qualitative) networks, and $a_{i,j} = w_{i,j}$ or 0 for a quantitative network. For the qualitative network, $a_{i,j} = 1$ indicates the presence of an interaction between plant species i and pollinator species j , while $a_{i,j} = 0$ indicates the absence of such an interaction. For quantitative networks, $w_{i,j}$ is the weight of the interaction between species i and j ; this quantity is measured by the frequency of visits of the pollinator species j to the plant species i . In both cases, we can project the information of the matrix onto connectivities of plants, k^P , and animals, k^A , given by

$$k_i^P = \sum_{j=1}^{L_A} a_{i,j} \quad \text{and} \quad k_j^A = \sum_{i=1}^{L_P} a_{i,j} \quad (1)$$

For a binary network the quantity k_i^P gives the number of pollinator species that pollinate plant species i , and k_j^A the number of plant species pollinated by pollinator species j ; in the case of the quantitative network k_i^P is the total number of observations of pollinators pollinating plant species i , and k_j^A the counterpart for pollinator species j . For simplicity of the mathematical analysis, we shall focus on binary networks from now on.

The dependence of a plant species i on any pollinator species is a measure of how much the plant species depends on that particular species for pollination. In a binary network the dependence d_i^P of plant species i on any one of its pollinating species is defined to be the reciprocal of the total number of its pollinating species. The dependence of d_j^A of a pollinator species j on any one of the plant species that it pollinates is defined in a similar way. Hence,

$$d_i^P = \frac{1}{k_i^P} \quad \text{and} \quad d_j^A = \frac{1}{k_j^A}. \quad (2)$$

In this way, a specialist plant species i that interacts with just one pollinator species has a maximal dependence on this species, $d_i^P = 1$. In the opposite case we have a generalist, a plant species i that depends on a large number N of pollinator species, and as a consequence its dependence on any one of these species is minimal, $d_i^P = 1/N \rightarrow 0$.

The dependence asymmetry $d_{i,j}$ between plant species i and pollinator species j is a quantity that expresses the difference

between the two dependences in the interaction. In this work we employ a measure adapted from (Bascompte et al., 2006). For noninteracting species we define $d_{i,j} = 0$, and for interacting species we define $d_{i,j}$ by

$$d_{i,j} = \frac{|d_i^P - d_j^A|}{(d_i^P + d_j^A)}. \quad (3)$$

The modulus is taken since we are not interested in the sign of the difference between species i and j , but only on its relative value. We note that the index $d_{i,j}$ is normalised, since $0 \leq d_{i,j} < 1$.

The connectivity asymmetry index $c_{i,j}$ is also defined in the literature, and is given by

$$c_{i,j} = \frac{|k_i^P - k_j^A|}{(k_i^P + k_j^A)}. \quad (4)$$

It is not difficult to prove that $d_{i,j} = c_{i,j}$ (Blüthgen et al., 2006). Throughout this paper we use the term **DA** because it is more often used in the literature. However, for mathematical simplicity, all proofs in the manuscript will be based on Eq. (4).

The average **DA** of a network is therefore equal to its average connectivity asymmetry \bar{c} , given by averaging $c_{i,j}$ over all the occupied sites of the matrix:

$$\bar{c} = \frac{1}{N} \sum_{i,j} c_{i,j}, \quad (5)$$

where N is the number of non-zero sites in the matrix. In this way \bar{c} is non-trivially related to the occupation $\rho = N/(L_P L_A)$ of the matrix. As we shall see, there is a considerable dependence of maximal \bar{c} and random \bar{c} on ρ , and this fact expresses a true correlation among these quantities and not an artifact of normalisation.

3. Algorithm of maximal DA for a square lattice

One of the objectives of this paper is to determine the maximal **DA**, c_{\max} , for a given occupation of a square lattice. We accomplish this task using an appropriate algorithm, employing a recursive equation that optimises $c_{i,j}$. The algorithm for c_{\max} is summarised as follows.

1. Choose sites on a square lattice of size $L \times L$ uniformly at random until it is filled with occupancy ρ .
2. Compute the function $H_{i,j}$ for every site according to the rule:

$$\text{if } \begin{cases} a_{i,j} = 1, & H_{i,j} = c_{i,j} \\ a_{i,j} = 0, & H_{i,j} = -c_{i,j} \end{cases}$$
3. Choose uniformly at random one occupied site among the 10% smallest positive $H_{i,j}$ and erase it. This choice guarantees that we are erasing a site whose **DA** is low.
4. Choose uniformly at random one empty site among the smallest negative $H_{i,j}$ and occupy this site. In this way sites whose occupancy maximally increases the **DA** are systematically occupied.
5. The last two steps guarantee that the overall occupation of the matrix remains constant. Repeat the three previous steps until $\sum_{H_{i,j} > 0} H_{i,j}$ converges to an optimal value.

We use the algorithm of maximal **DA** to plot c_{\max} against ρ , as in Fig. 1. Here we took $L = 20$ and iterated the algorithm for 20,000 steps. The first behaviour to notice in this plot is that c_{\max} decreases with occupancy; indeed, this is a probabilistic effect. High c is

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