Measuring Asymmetry in Insect-Plant Networks

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Abstract. In this work we focus on interaction networks between insects and plants and in the characterization of insect plant asymmetry, an important issue in coevolution and evolutionary biology. We analyze in particular the asymmetry in the interaction matrix of animals (herbivorous insects) and plants (food resource for the insects). Instead of driving our attention to the interaction matrix itself we derive two networks associated to the bipartite network: the animal network, \( D_1 \), and the plant network, \( D_2 \). These networks are constructed according to the following recipe: two animal species are linked once if they interact with the same plant. In a similar way, in the plant network, two plants are linked if they interact with the same animal. To explore the asymmetry between \( D_2 \) and \( D_1 \) we test for a set of 23 networks from the ecologic literature networks: the difference in size, \( \Delta L \), clustering coefficient difference, \( \Delta C \), and mean connectivity difference, \( \Delta \langle k \rangle \). We used a nonparametric statistical test to check the differences in \( \Delta L \), \( \Delta C \) and \( \Delta \langle k \rangle \). Our results indicate that \( \Delta L \) and \( \Delta \langle k \rangle \) show a significative asymmetry.

1. INTRODUCTION

In ecology, networks are mainly used to visualize and describe food webs [1]. In the last two decades, scientists have shown a growing interest in networks in order to study other ecological interactions such as pollination, parasitism [2], seed dispersion or detrivory [3]. Plants and their pollinators or animals and their parasites are examples of interaction networks in community ecology. All these community ecology systems can be described by interaction matrices, or bipartite graphs. In pollinator networks, for example, the two functional groups are pollinators and flowering plants. The pollinators and flowering plants are the vertices of the bipartite network and observed interactions are drawn as links. In this context a species (pollinator or plant) that interacts with many species is called a generalist, while a species that have exclusive interactions or with few species is called specialist. In Ecology, the field data corresponding to the digraph is composed by two sets of species and the corresponding links (interactions) between them.

Some metrics over the interaction matrices have been used to characterize its order or structure, for instance, the modularity, the connectivity, the nestedness and the asymmetry [3].
The main objective of this manuscript is to explore the asymmetry of the interaction matrix using a new tool. Instead of driving our attention to the interaction matrix itself we focus the analysis on the two networks derived from the bipartite network: the animal network, $D_1$, and the plant network, $D_2$. These networks are built in the standard way in network analysis [4]. This work is organized as follows: in section 2 we outline the interaction matrix, where we show the mathematical background and presented the biological data set; in section 3 we present our results; finally in section 4 we discuss the results of the work.

2. INTERACTION MATRIX

2.1. MATHEMATICAL BACKGROUND

In order to fix the notation we call digraph an object $D$ formed by two sets of vertices $V_1$ and $V_2$ and a set of links between these two sets. The digraph is completely described by the adjacency matrix, $M$, of order $L_1 \times L_2$, where $L_1$ and $L_2$ are the number of elements of $V_1$ and $V_2$, respectively. By definition:

$$M_{i,j} = \begin{cases} 
0, & \text{if } i \text{ and } j \text{ are not linked.} \\
1, & \text{if there is a link between vertices } i \text{ of } V_1 \text{ and } j \text{ of } V_2 
\end{cases} \quad (1)$$

![Figure 1](image1.png)

**Figure 1.** In (a) we have a example of an adjacency matrix, $M$, with zeros and ones sites; In (b) we have the representation of bipartite graph of the adjacency matrix, $M$, and, in (c) we have the two networks, $D_1$ and $D_2$, derived from the interaction network.

Moreover, the number of links of a vertex $l$ is $k_l$ and the distribution of links of $D_1$ and $D_2$ is $P_{l_1}$ and $P_{l_2}$ respectively. We define the occupancy number $\rho$ as the fraction of ones in the adjacency matrix. For $N$, the total number of ones in $M$, we have

$$\rho = \frac{N}{L_1L_2} \quad (2)$$

We study the asymmetry of a bipartite graph $M$ using the two associated networks of $M$: the animal network, $D_1$, and the plant network, $D_2$. These networks are constructed according to...
the following recipe: two animal species are linked once if they interact with the same plant. In a similar way, in the plant network, two plants are linked if they interact with the same animal. In figure 2.1 we show the formation of two associated networks from a source bipartite graph.

2.2. ECOLOGICAL DATA SET

In the present paper we select a set of 23 plant-insect matrices of herbivorous insects and its host plants, which is characterized as antagonist interactions [4]. All the analyzed matrices consist of insects observed feeding on vegetal tissues of host plants. We used this data set by convenience, but the same study conducted here could be performed with mutualistic interactions, as well as with other antagonist interactions. In table 1 we show the main characteristics of the 23 interaction matrices used in this work: the number of plants (flowering plants) $D_2$, the number of animals (insects) in the matrix $D_1$, the occupancy of the matrix $\rho$ and the reference of the data in the literature.

| Matrix | $L_2$ | $L_1$ | $\rho$ | Reference |
|--------|-------|-------|--------|-----------|
| CJ     | 33    | 21    | 0.13   | [5]       |
| PO     | 13    | 12    | 0.44   | [6]       |
| AN     | 33    | 29    | 0.05   | [7]       |
| MG     | 53    | 92    | 0.02   | [8]       |
| AP     | 27    | 22    | 0.09   | [9]       |
| SR     | 15    | 8     | 0.49   | [10]      |
| CW     | 33    | 55    | 0.09   | [11]      |
| JM     | 54    | 24    | 0.13   | [12]      |
| RA     | 13    | 9     | 0.23   | [13]      |
| CP     | 18    | 15    | 0.16   | [14]      |
| BF     | 43    | 14    | 0.14   | [15]      |
| PD     | 55    | 43    | 0.04   | [16]      |
| FJ     | 107   | 104   | 0.01   | [17]      |
| FG     | 18    | 57    | 0.43   | [18]      |
| NE     | 46    | 22    | 0.06   | [19]      |
| BL     | 63    | 25    | 0.08   | [15]      |
| DW     | 10    | 18    | 0.11   | [20]      |
| CE     | 21    | 32    | 0.20   | [21]      |
| JS     | 51    | 27    | 0.05   | [22]      |
| PP     | 8     | 11    | 0.15   | [23]      |
| PN     | 11    | 11    | 0.35   | [6]       |
| BJ     | 30    | 34    | 0.08   | [9]       |
| JA     | 52    | 22    | 0.16   | [24]      |
3. RESULTS

In this section we analyze asymmetry between plant and animal interaction network. To explore the asymmetry between $D_2$ and $D_1$ we test for the set of 23 antagonist networks the following quantities: the difference in size, $\Delta L$, clustering coefficient difference, $\Delta C$, and mean connectivity difference, $\Delta <k>$. 

We start our analysis with the size difference to test for size bias. The clustering coefficient $C$ quantifies how much the vertices connected with a given vertex are connected among them. Indeed, $C$ counts the number of triangles in the network [4]. Finally $<k>$ measures the average number of connections of the vertices, $<k> = \frac{2L}{N}$.

Figures 2, 3 and 4 summarize the differences between animal and plant networks. In this set of figures we show in the horizontal axis the 23 matrices. In figure 2 we show size difference, $\Delta L = L_2 - L_1$. In figure 3 we show the clustering coefficient difference, $\Delta C = C_2 - C_1$ and, finally, in figure 4 we have the mean connectivity difference, $\Delta <k> = <k>_2 - <k>_1$.

Figure 2. Normalized size difference, $\Delta L = \frac{L_2 - L_1}{L_2 + L_1}$, for the 23 networks depicted in table 1. This figure reveals an asymmetry between the two sets, the size of the insect set is statistically larger than the plants. This visual result is supported by statistical inference in the text.

In figure 2 we ranked the networks according to size difference to better visualize the results. The figures 2, 3 and 4 have the studied quantities for the set of the 23 networks, in all these figures we plot the networks in the same order to compare the results. In the inset of figures 3 and 4 the same result ranked. The figure in the inset allows direct visual check for asymmetry while the main figure is useful to compare the differences among specific networks. A simple visual inspection of the figures reveals that the $\Delta L$ is not responsible for the behavior of $\Delta C$ or $\Delta <k>$. That means, a potential asymmetry in $\Delta C$ or $\Delta <k>$ is not due to the most obvious asymmetry in $\Delta L$.

In figure 2 is possible to see that the size distribution is asymmetric. This result is not surprising considering that the number (abundance and diversity) of insect exceed the number of plants in nature, and that interaction networks usually present more animals than plants. Otherwise, there is a paper in the literature has found, for a set of mutualist interaction networks, that there is an asymmetry between animal and plant sizes [2]. In figure 3 is plotted the clustering coefficient difference, $\Delta C$. A simple inspection in the data show an almost symmetric
Figure 3. Clustering coefficient difference, $\Delta C = L_2 - L_1$, for the 23 networks depicted in table 1. We use in this picture the same network order of figure 2. In the inset we show the same data, but ranked to visualize the asymmetry. Indeed, the statistical test reveals no significative difference between the sets, $\Delta C$ do not reveals asymmetry.

Figure 4. Mean connectivity difference, $\Delta \langle k \rangle = \langle k \rangle_2 - \langle k \rangle_1$, for the 23 networks depicted in table 1. We use in this picture the same network order of figure 2. In the inset we show the same data set, but ranked to highligth the asymmetry between the two sets. In the text we confirm the assymetry of the figure using a statistical test.

distribution of $\Delta C$. This result indicates that $\Delta C$ is not an index appropriate to measure asymmetry in this class of bipartite networks. In the next section we discuss the possible use of the normalized clustering coefficient. In figure 4 is plotted the mean connectivity difference, $\Delta \langle k \rangle$. This result seems to indicate that the $\Delta \langle k \rangle$ is a good candidate to be used as an
asymmetry index in matrices networks.

We use the Wilcoxon test and the signal test to compare the difference between the properties of the two sets (plants and insects). The two tests produce the same result. For a significance level \( p < 0.05 \), we verified asymmetry for \( L(L_1 > L_2) \), \( <k> (\leq k \leq k_2) \) but not for \( C(C_1 < C_2) \).

4. CONCLUSION

In this work we developed a simple and effective way to measure the differences between two groups of ecological actors in a community context. We project the bipartite interaction network into two sets of vertices and construct two new networks. We use the difference between the indices of these new networks to characterize the asymmetry between these groups. We tested our technique in a set of 23 antagonist interaction networks insect and flowers. We observed for a significant level \( (p < 0.05) \) difference between the groups for the network size \( \Delta L \) and the mean connectivity \( \Delta k \). The clustering coefficient \( C \) have not shown difference between the sets.

We have two perspectives in mind. The first is to use other network indices to evaluate the asymmetry. The second point is not related to asymmetry, but to apply the same technique of this work to characterize the difference between nested and modular interaction networks.

We have explored the clustering coefficient which shows a distribution almost symmetric for the studied group of matrices. In the network literature it is common to use the normalized clustering coefficient, \( C_{\text{norm}} = \frac{C}{C_{\text{rand}}} \), where \( C_{\text{rand}} = \frac{<k>}{N} \) is the clustering coefficient of an associated random network with number of vertices \( N \). This quantity is used when we compare a network with its random counterpart. This normalized index expresses directly how far a network is from the random model and it is used to measure the complexity of a network [4]. The quantity \( C_{\text{norm}} \) is as asymmetric as \( <k> \) (we have not shown this result in this paper), but its asymmetry comes from \( <k> \). Nevertheless, we point that our interaction matrix problem is asymmetric for \( C \), a common measure of network science.

In a future work we will explore other network indices in the search for asymmetry in community networks. Indeed, there is a large set of indices to test, we have not explored, for instance, neither any centrality or betweenness index, nor the degree distribution \( P(k) \) of the networks. There is an important study on the subject that claims that \( P(k) \) of animals and plants in mutualistic interaction networks follow power-law distributions, or truncated power-law [29]. This result was criticized by Okuyama, T. [30], that remark that \( P(k) \) of interaction networks are not easily classified into a single distribution class. The question we pose, otherwise, is other, we are not interested in \( P(k) \) of the interaction network, but of animal and plant networks, which is not the same. By construction the networks \( D_2 \) and \( D_1 \) present much higher \( <k> \) values than the interaction matrices, a fact that has deep consequences on \( P(k) \). Finally, the road to achieve a good index to quantify asymmetry in interaction networks is only at the beginning. What is clear in this project is that the understanding of asymmetry in mutualistic and antagonistic networks is a major challenge in communities ecology and evolutionary biology.

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