

The nested assembly of plant–animal mutualistic networks

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Most studies of plant–animal mutualisms involve a small number of species. There is almost no information on the structural organization of species-rich mutualistic networks despite its potential importance for the maintenance of diversity. Here we analyze 52 mutualistic networks and show that they are highly nested; that is, the more specialist species interact only with proper subsets of those species interacting with the more generalists. This assembly pattern generates highly asymmetrical interactions and organizes the community cohesively around a central core of interactions. Thus, mutualistic networks are neither randomly assembled nor organized in compartments arising from tight, parallel specialization. Furthermore, nestedness increases with the complexity (number of interactions) of the network: for a given number of species, communities with more interactions are significantly more nested. Our results indicate a nonrandom pattern of community organization that may be relevant for our understanding of the organization and persistence of biodiversity.

Studies of plant–animal mutualisms have traditionally focused on highly specific interactions among a few species, such as a plant and its pollinators or seed dispersers (1, 2). On the other hand, some systems seem to involve a much larger number of species, and some authors have used the term “diffuse coevolution” to describe the coevolutionary process in such communities (3–5). The approach of diffuse coevolution, however, has not provided any insight on the structural organization of species-rich communities (6), yet this is a fundamental property to understand coevolution in these species-rich assemblages.

Mutualistic networks can be depicted by a matrix of plant species in rows and animal species in columns (ref. 7; Fig. 1). An element a_{ij} of such a matrix is 1 if plant i and animal j interact, and zero otherwise. In a perfectly nested matrix (8), each species would interact only with proper subsets of those species interacting with the more generalist species (Fig. 1a). On the other hand, a mutualistic network would be assembled randomly if each plant (animal) species interacts with a random set of the total pool of animals (plants) (Fig. 1b). Nestedness entails a nonrandom pattern of structure beyond the topological pattern of connectedness frequently assessed in networks of ecological interactions (9–11).

Here we analyzed 27 plant–frugivore networks and 25 plant–pollinator networks illustrating a wide range of conditions of species richness, taxonomy, latitude, and ecology (Table 1). Our goal is to understand how mutualistic networks are assembled. We report on the highly nested organization of mutualistic networks and discuss the implications of nestedness for their persistence and coevolution.

Materials and Methods

Measure of Nestedness. We estimated an index of matrix nestedness (N) by using NESTEDNESS CALCULATOR software. This software was originally developed by W. Atmar and B. D. Patterson in 1995 (AICS Research, University Park, NM; see ref. 8) to characterize how species are distributed among a set of islands (8, 12, 13).

NESTEDNESS CALCULATOR first reorganizes the matrix by ar-

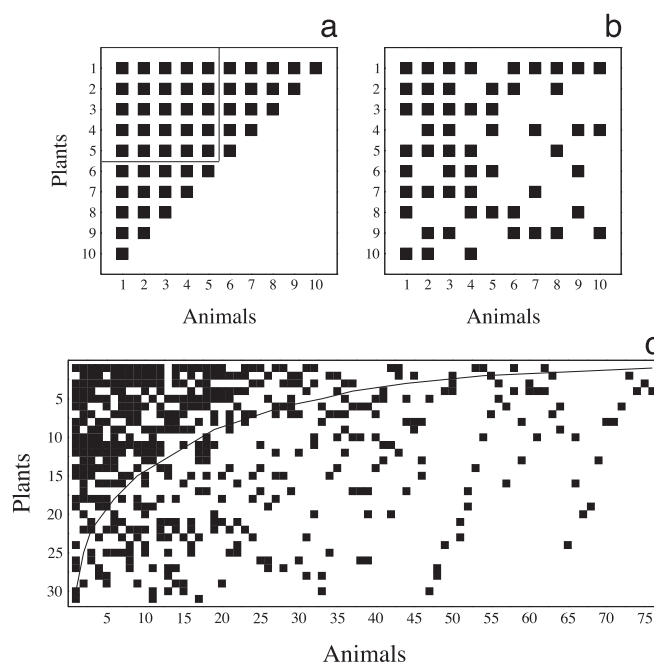


Fig. 1. Plant–animal mutualistic interaction matrices. Numbers label plant and animal species, which are ranked in decreasing number of interactions per species. A filled square indicates an observed interaction between plant i and animal j . a–c correspond to perfectly nested, random, and real mutualistic matrices [plant–pollinator network of Zackenberg (J.M.O. and H. Elberling, unpublished work)], respectively. Values of nestedness are $N = 1$ (a), $N = 0.55$ (b), and $N = 0.742$ ($P < 0.01$) (c). The box outlined in a represents the central core of the network, and the line in c represents the isocline of perfect nestedness. On a perfectly nested scenario, all interactions would lie before the isocline (on the left side).

ranging rows (plants) and columns (animals) from the most generalist to the most specialist in the way that maximizes nestedness (8). Given a particular number of plants (P), animals (A), and interactions (L), an isocline of perfect nestedness is calculated for each matrix (Fig. 1c). For each plant species (row) all of the absences of pairwise interactions before the isocline and all of the observed interactions beyond the isocline are recorded as unexpected. For each of these unexpected presences or absences, a normalized measure of global distance to the isocline is calculated (8), and these values are averaged. By using an analogy with physical disorder, this measure is called temperature, T (8), with values ranging from 0^0 to 100^0 . Because in this paper we emphasize nestedness or order instead of disorder, we define the level of nestedness, N , as: $N = (100 - T)/100$, with values ranging from 0 to 1 (maximum nestedness).

Null Models and Significance. To assess the significance of nestedness we have to compare the observed value with a benchmark

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Table 1. Data sets analyzed in this article

| Type | Nestedness | No. of species | Latitude | Ref. |
|----------------|---------------------|----------------|---------------|---|
| Seed dispersal | 0.762 ^{NS} | 28 | Temperate | 32 |
| Seed dispersal | 0.806 ^{**} | 40 | Tropical | 33 |
| Seed dispersal | 0.944 [*] | 54 | Mediterranean | 34 |
| Seed dispersal | 0.842 ^{**} | 78 | Tropical | 35 |
| Seed dispersal | 0.847 [*] | 26 | Subtropical | 36 |
| Seed dispersal | 0.679 ^{NS} | 19 | Temperate | 37 |
| Seed dispersal | 0.857 ^{**} | 33 | Mediterranean | P.J., unpublished |
| Seed dispersal | 0.771 [*] | 32 | Tropical | 38 |
| Seed dispersal | 0.768 ^{**} | 86 | Tropical | 39 |
| Seed dispersal | 0.932 ^{**} | 209 | Tropical | 40 |
| Seed dispersal | 0.878 ^{**} | 46 | Mediterranean | P.J., unpublished |
| Seed dispersal | 0.565 ^{NS} | 27 | Tropical | 41 |
| Seed dispersal | 0.936 ^{**} | 23 | Temperate | 42 |
| Seed dispersal | 0.848 ^{NS} | 13 | Temperate | 43 |
| Seed dispersal | 0.748 [*] | 25 | Tropical | 44 |
| Seed dispersal | 0.877 ^{**} | 64 | Tropical | 44 |
| Seed dispersal | 0.651 ^{**} | 64 | Tropical | 45 |
| Seed dispersal | 0.999 ^{NS} | 9 | Mediterranean | 34 |
| Seed dispersal | 0.853 ^{**} | 18 | Mediterranean | 34 |
| Seed dispersal | 0.984 ^{**} | 14 | Mediterranean | 34 |
| Seed dispersal | 0.866 ^{**} | 25 | Mediterranean | 34 |
| Seed dispersal | 0.921 ^{**} | 17 | Mediterranean | 34 |
| Seed dispersal | 0.996 ^{NS} | 10 | Mediterranean | 34 |
| Seed dispersal | 0.884 ^{NS} | 11 | Mediterranean | 34 |
| Seed dispersal | 0.897 ^{**} | 24 | Mediterranean | 46 |
| Seed dispersal | 0.958 ^{**} | 317 | Tropical | 47 and unpublished |
| Seed dispersal | 0.716 ^{NS} | 25 | Temperate | 48 |
| Pollination | 0.960 ^{**} | 185 | Temperate | 49 |
| Pollination | 0.910 ^{**} | 107 | Temperate | 49 |
| Pollination | 0.925 ^{**} | 61 | Temperate | 49 |
| Pollination | 0.860 [*] | 142 | Arctic | 50 |
| Pollination | 0.742 ^{**} | 107 | Arctic | J.M.O. and H. Elberling, unpublished |
| Pollination | 0.945 ^{**} | 110 | Arctic | 51 |
| Pollination | 0.911 ^{**} | 205 | Mediterranean | 52 |
| Pollination | 0.671 ^{NS} | 22 | Tropical | J.M.O., unpublished |
| Pollination | 0.594 ^{NS} | 50 | Temperate | J.M.O., unpublished |
| Pollination | 0.952 ^{**} | 84 | Tropical | J.M.O., unpublished |
| Pollination | 0.828 ^{**} | 108 | Temperate | J.M.O., unpublished |
| Pollination | 0.955 ^{**} | 251 | Temperate | 53 |
| Pollination | 0.955 ^{**} | 111 | Arctic | 54 |
| Pollination | 0.628 ^{NS} | 50 | Temperate | J.M.O., unpublished |
| Pollination | 0.702 ^{NS} | 32 | Tropical | 55 |
| Pollination | 0.781 ^{NS} | 29 | Arctic | 56 |
| Pollination | 0.925 ^{**} | 97 | Tropical | 57 |
| Pollination | 0.940 ^{**} | 167 | Temperate | 58 |
| Pollination | 0.925 ^{**} | 180 | Temperate | 58 |
| Pollination | 0.736 ^{**} | 78 | Temperate | 58 |
| Pollination | 0.867 ^{**} | 40 | Temperate | 59 |
| Pollination | 0.874 ^{**} | 27 | Tropical | L. I. Eskildsen <i>et al.</i> , unpublished |
| Pollination | 0.871 [*] | 93 | Tropical | 60 |
| Pollination | 0.904 [*] | 117 | Temperate | 61 |
| Pollination | 0.975 ^{**} | 446 | Temperate | 62 |
| Food web | 0.678 ^{NS} | 20 | Temperate | 63 |
| Food web | 0.670 ^{NS} | 22 | Temperate | 63 |
| Food web | 0.507 ^{NS} | 16 | Subtropical | 64 |
| Food web | 0.607 ^{NS} | 12 | Subtropical | 64 |
| Food web | 0.724 ^{**} | 75 | Temperate | 65 |
| Food web | 0.774 ^{NS} | 78 | Temperate | 65 |
| Food web | 0.522 ^{NS} | 28 | Temperate | 66 |
| Food web | 0.772 ^{NS} | 59 | Temperate | 66 |
| Food web | 0.737 ^{NS} | 32 | Temperate | 66 |
| Food web | 0.856 ^{**} | 104 | Tropical | 67 |
| Food web | 0.547 ^{NS} | 64 | Tropical | 67 |
| Food web | 0.554 ^{NS} | 37 | Temperate | 68 |
| Food web | 0.942 ^{**} | 76 | Temperate | 68 |
| Food web | 0.826 ^{**} | 25 | Temperate | 69 |

No. of species, sum of animal and plant species. Food webs were decomposed in resource–consumer, bipartite graphs, so two or three different graphs can be obtained from the same food web. The level of significance was tested against null model 2 (results are qualitatively similar for null model 1). *, $P < 0.05$; **, $P < 0.01$; NS, not significant.

provided by a **null model**. The goal is to test whether the observed level of structure (in our case nestedness) can be explained by simple rules (e.g., a derived probability of cell occupancy). An intensive discussion has revolved around null models and how conclusions on community structure may depend on our choice of a null model (14–16).

NESTEDNESS CALCULATOR uses a null model in which each cell in the interaction matrix has the same probability of being occupied. **This probability is estimated as the number of “1s” in the original matrix divided by the number of cells ($A \times P$). We will refer to this as null model 1.** This null model is very general, and so deviations from this homogeneous benchmark could be due to multiple factors, such as a different degree (some species have more connections than others) (14, 16). Previous work has shown that mutualistic networks have a variation in the number of connections per species (degree) much larger than expected by random (11). Because we want to look at a deeper level of structure beyond the one depicted by the degree distribution, we have considered a **second null model**. In our null model 2, the probability of each cell being occupied is the **average of the probabilities of occupancy of its row and column**. Biologically, this means that the probability of drawing an interaction is proportional to the level of generalization (degree) of both the animal and the plant species. Interestingly enough, the results here provided are very robust, and there are not strong qualitative differences for both null models (only 6 of 52 networks changed in significance status from one model to the other). Throughout the paper, we will present the results for null model 2, which yields the most conservative inference about the significance of nestedness (16).

For each mutualistic matrix, we generated a population of $n = 50$ random networks for each null model. **Our statistic was P , the probability of a random replicate being equally or more nested than the observed matrix.** To allow across-network comparisons, that is, to account for variation in species richness and number of interactions, relative nestedness is defined as $N^* = (N - \bar{N}_R) / \bar{N}_R$, where N and \bar{N}_R are the value of nestedness for the actual matrix and the average nestedness of the random replicates, respectively.

Results

Most mutualistic webs were highly nested (Fig. 2). The average \pm SE nestedness was $\bar{N} = 0.844 \pm 0.043$ for seed dispersal and $\bar{N} = 0.853 \pm 0.047$ for pollination (Fig. 2a). There were no significant differences between both systems ($F = 0.098$, $df = 1, 50$, $P = 0.75$), which suggests a common assembly process regardless of the different nature of these mutualisms.

The fraction of networks that departed significantly ($P < 0.05$) from randomly assembled webs was 0.70 for seed dispersal and 0.80 for pollination. These percentages, however, increased dramatically beyond a minimum number of species. For example, all seed-dispersal networks >28 species (40.7%) and all pollination networks >50 species (72.0%) were significantly nested (Fig. 2b).

To assess the generality of our results and to put them within the context of other ecological webs, we also studied nestedness in a set of 14 resource–consumer bipartite graphs extracted from several detailed food webs (Table 1). Their level of nestedness ($\bar{N} = 0.694 \pm 0.077$) was significantly lower than for mutualistic networks (their residual nestedness, after accounting for variation in species richness, differed significantly from both pollinator and seed-dispersal webs; $F = 7.71$, $df = 1, 60$, $P = 0.007$; Tukey's honestly significant difference test; Fig. 2a). It is not clear whether this difference reflects a different biological organization or differences in sampling resolution.

Is the level of nestedness independent of the complexity of the network? To answer this question, we begin by considering the relationship between the number of species ($S = A + P$) and

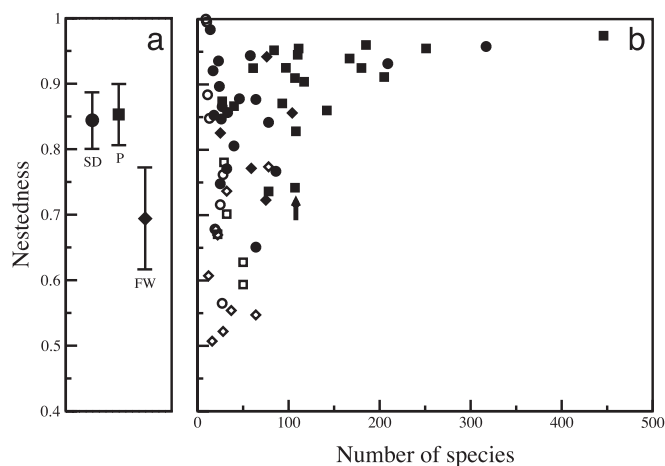


Fig. 2. Nestedness values for seed dispersal (SD, circles), pollination (P, squares), and food webs (FW, diamonds). (a) Mean and SE of nestedness for the three types of networks. Seed-dispersal and pollination matrices have similar nestedness, significantly higher than consumer–resource webs. (b) Nestedness vs. species richness for all data sets. Each point corresponds to a specific community and is solid if the level of nestedness is significant at the $P < 0.05$ level and empty otherwise. The arrow indicates the plant–pollinator network shown in Fig. 1c.

the number of interactions (L), a question widely discussed in food web studies (17–24). As shown in Fig. 3, our mutualistic data fit a power-law relationship between L and S ; that is, $\log(L) = 0.132 + 1.139 \log(S)$, $r = 0.943$, and $P < 0.0001$. The slope of the log–log plot (1.139) is slightly higher than 1. This means that L increases slightly faster than S , confirming early results for food webs (24).

We calculated the residuals from the regression in Fig. 3. Positive and negative residuals correspond to those matrices that have more and fewer connections, respectively, than expected from their number of species. We compared the average relative

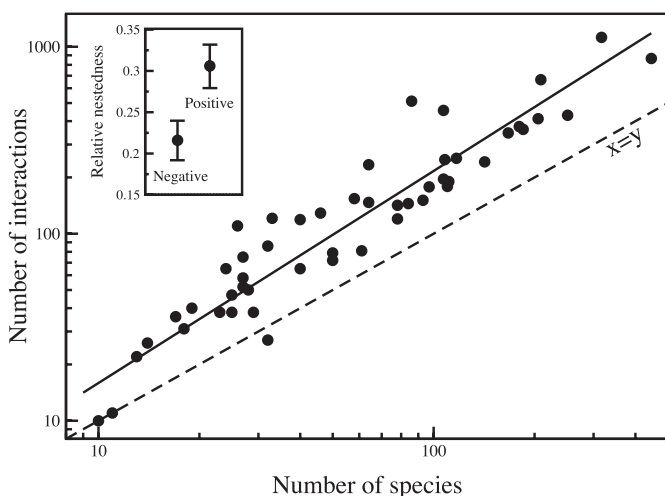


Fig. 3. Number of interactions (L) vs. number of species (S) for the mutualistic networks (pollination and seed dispersal). The continuous line is the best fit to data. The broken line represents the $x = y$ axis. As noted, L increases slightly faster than S (slope = 1.139). All communities can be classified in two groups: networks with fewer interactions than expected (negative residuals) and networks with more interactions than expected (positive residuals). (Inset) The average and SE of relative nestedness (N^*) for the communities with positive and negative residuals. Networks with positive residuals, that is, with more interactions than expected for a specific number of species, are significantly more nested than networks with fewer interactions than expected.

value of nestedness (\bar{N}^*) for both groups of residuals. Interestingly enough, there are significant differences between them ($F = 6.59$, $df = 1, 50$, $P = 0.013$). For a given species richness, communities with a larger than expected number of interactions are significantly more nested than communities with a lower than expected number of interactions. The mutualistic webs become relatively more structured as their complexity (number of links for a given number of species) increases.

Discussion

A long-standing challenge in food web theory has been to detect the level of structure of food webs (21, 24–28). There is not enough empirical support on how food webs are structured. For example, attempts to find compartmentalization in food webs have failed (refs. 25 and 27; see, however, refs. 28 and 29). The question remains on whether this is due to the incompleteness of the data or to the fact that complex networks are organized in a different way. By analyzing the best resolved data set on ecological networks, we have unambiguously shown that mutualistic webs are neither randomly assembled nor compartmentalized, but are highly nested.

Some potential implications of nestedness for community persistence can be drawn. First, nested networks are highly cohesive; that is, the most generalist plant and animal species interact among them generating a dense core of interactions to which the rest of the community is attached (Fig. 1). Together with highly heterogeneous distributions of the number of interactions per species (11), this cohesive pattern can provide alternative routes for system responses to perturbations. For example, a species is more unlikely to become isolated of the network after the elimination of other species when embedded on a highly cohesive network. Second, nestedness organizes the community in a highly asymmetrical way (Fig. 1), with specialist species interacting only with generalist (and so less fluctuating

(30) species. This asymmetrical pattern can provide pathways for rare species to persist (7).

In relation to coevolution, previous studies have traditionally focused on interactions between pairs of species. But, as noted by Thompson, “studies of pair-wise interactions alone are insufficient for understanding the evolution of interactions in general and the coevolutionary process in particular” (ref. 6, p. 286; see also ref. 31). In this paper we have presented empirical evidence for a highly significant structural pattern with far-reaching consequences for coevolutionary interactions in species-rich communities. Nestedness organizes complex coevolving networks in a specific way between highly specialized pairwise coevolution and highly diffuse coevolution. It results in both a core of taxa that may drive the evolution of the whole community, and in asymmetric interactions among species with different specialization levels. Our data do not indicate the presence of compartments suggestive of tight, parallel specialization. Rather, our results show that specialized species are frequently dependent on a core of generalist taxa. This macroscopic organization of coevolutionary interactions can be reduced neither to a collection of pairs of coevolving species, nor to a collection of subwebs made up of tightly integrated species. A nontrivial question that deserves further study is how the assembly pattern described in this paper affects the coevolutionary process in species-rich networks.

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