Competition-induced increase of species abundance in mutualistic networks

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Abstract. Nutrients from a flowering plant are shared by its pollinators, giving rise to competition in the latter. Such exploitative competition of pollinators can limit their abundance and affect the global organization of the mutualistic partnership in the plant-pollinator mutualistic community. Here we investigate the effects of the exploitative competition between pollinators on the structure and the species abundance of the mutualistic networks which evolve by changing mutualistic partnership towards higher abundance of species. Simulations show different emergent network characteristics between plants and animals; hub plants connected to many pollinators are very rare while a few super-hub pollinators appear with the exploitative competition included, in contrast to equally many hubs of both types without the exploitative competition. More interestingly, the abundance of plant species increases with increasing the exploitative competition strength. We analyze the inverse of the generalized interaction matrix in the weak-interaction limit to identify the leading structural factors relevant to the species abundance, which are shown to be instrumental in optimizing the network structure to increase the mutualistic benefit and lower the cost of exploitative competition.

Keywords: co-evolution, evolution models, population dynamics, random graphs, networks
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1. Introduction

The organization of intra- and interspecific interaction strongly affects the stability of an ecological community and its response to perturbations [1–3]. The ecological networks have been recently investigated to reveal their different structural characteristics depending on the nature of interactions and differentiating the dynamic behaviors of the corresponding communities [4]. In case of flowering plants and animal pollinators that interact mutualistically, their network is characterized by high nestedness, meaning high likelihood of sharing mutualistic partners [5, 6]. Such nested structure has been shown to enhance stability and biodiversity [7–9]. On the other hand, trophic networks develop modular structure to reduce competition in sharing a common prey [8].

Structural characteristics serving for functional benefits such as high species abundance can be selected and enhanced during evolution. If certain organisms of a species form a mutualistic relationship with a new partner and thereby achieve a significantly high abundance and reproduction rate, then the species will be soon dominated by the descendants of these mutant organisms and their new partner will be among the list of mutualistic partners of the species. In accordance with the study revealing the advantage of the nested organization of mutualistic partnership for increasing the species
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abundance [7], researchers have shown that the link rewiring conditioned towards increasing the species abundance can indeed generate highly nested structure in mutualistic networks [10].

Yet, in reality, various types of interactions may be present simultaneously in a given community [11, 12], which complicates the problem of what structural characteristics will emerge in the community. What interests us the most is that species in a mutualistic community can be subject to a competition similar to the one found in trophic networks; the benefit gained by an insect in pollinating a plant can be reduced if there are many other pollinators occupying the same plant, as they should share its finite nutrient resource. This type of competition, which we call here exploitative competition, is different from the random interactions assumed between every pair of species in previous studies [13–15] in that it exists only between the species sharing a common mutualistic partner. Therefore the organization of mutualistic relationship is coupled with that of exploitative competition. The exploitative competition between pollinators sharing common plant partners has been incorporated in a growing network model to explain the empirically observed asymmetric degree distributions between plants and animals [16–18]. Compared with the introduction of new species, as considered in the growing network model, a change in the mutualistic partnership can occur on a shorter time scale facilitating the enhancement or suppression of selected network characteristics to serve for increasing the species abundance.

In this paper we investigate numerically and analytically the effects of the exploitative competition arising between the pollinators sharing the same plant species on the structure and the species abundance of the evolving plant-pollinator mutualistic network. To this end, we use the co-evolution model [10] in which the abundance of each species is determined by the interspecific interaction encoded in the network structure and the network evolves by selective link rewiring towards abundance increase. The interaction matrix ruling the species abundance is here generalized to incorporate the exploitative competition.

We find that the iterative feedback between the species abundance and the network structure leads to the optimal organization of mutualistic partnership that fully extracts the benefit of mutualism while lowers the cost of exploitative competition. Hub plant nodes are made rare, not to induce high competition between many pollinators sharing a plant. On the contrary, super-hub animals connected to all plants appear, gaining large mutualistic benefit exceeding the exploitative competition cost at the expense of leaving many animals isolated. Interestingly, as the exploitative competition strength increases, the abundance of animals fast decreases but that of plants, counter-intuitively, increases. Given that the species abundance is determined by the inverse of the generalized interaction matrix in the co-evolution model, we expand it in the powers of interaction strength to identify the structural factors relevant to the species abundance in the weak-interaction limit. The study of those leading structural factors uncovers the combinatorial effects of the interspecific interactions of different nature, mutualism and competition, on the evolution of ecological networks.

The studied model is described in section 2 and the simulation results for the species abundance and the connectivity patterns emerging in the evolved network are presented in section 3. We derive and examine the analytic relation between the
species abundance and the structural factors in section 4 and summarize our findings in section 5.

2. Model

2.1. Abundance dynamics with the intrinsic competition and mutualistic interaction

We consider a model system consisting of $N^P$ plant species and $N^A$ animal species. In the initial stage ($t = 0$), the system has the interaction matrix $M(0)$ mediating the quadratic intra- and interspecific interaction ruling the time-evolution of the abundance of each species $x_i$ as [7, 10]

$$\frac{dx_i}{d\tau} = \alpha_i x_i + x_i \sum_{j=1}^S M_{ij}(0) x_j$$

with $S = N^P + N^A$, $\tau$ the microscopic time, a much shorter scale than the macroscopic time or stage $t$, and $\alpha_i$ the intrinsic growth rate. The $S \times S$ interaction matrix is represented as

$$M(0) = -I - \begin{pmatrix} W^{(P)} & 0 \\ 0 & W^{(A)} \end{pmatrix} + \begin{pmatrix} 0 & \Gamma(0) \\ \Gamma^T(0) & 0 \end{pmatrix},$$

where the identity $I_{ij} = \delta_{ij}$ represents the unit rate of self-regulation. The intrinsic competitions between the species of the same type, plant or animal, are encoded in the $N^P \times N^P$ matrix $W^{(P)}$ and the $N^A \times N^A$ matrix $W^{(A)}$, the elements of which are random but fixed against time or stage; $W_{pp}'(W_{aa}')$ is a positive random number with probability $C$ or 0 with probability $1 - C$. The mutualistic interaction between plant and animal species is represented by the $N^P \times N^A$ matrix $\Gamma(0)$, and its elements are positive random numbers with probability $C$ or 0 with probability $1 - C$. Here $C$ controls the fraction of interacting pairs, both mutualism and intrinsic competition, and will be called the connectance.

If there were no interspecific interaction $W^{(P,A)} = 0$ and $\Gamma(0) = 0$, equation (1) would be reduced to a single-species equation $dx_i/d\tau = \alpha_i x_i - x_i^2$, with which the abundance $x_i$ converges to the only stable fixed point $x_i = \alpha_i$. This fixed point can be shifted by introducing non-zero interspecific interaction. We remark that if equation (1) contains a cubic term $x_i^3$, then two stable fixed points may emerge and the corresponding system becomes stable conditionally [19].

The mutualistic interaction matrix and the whole interaction matrix as well evolve as stage $t$ changes, denoted by $\Gamma(t)$ and $M(t)$. The mutualistic interaction is assumed to be symmetric such that $M_{ap}(t) = M_{pa}(t)$. A bipartite network of $N^P$ plant-type nodes and $N^A$ animal-type nodes will be called the mutualistic network in this work, which has the $N^P \times N^A$ adjacency matrix $A(t)$ with $(A_{pa})(t_1) = 1$ if $\Gamma_{pa}(t) > 0$ and 0 otherwise. Note that the interaction and adjacency matrices depend only on $t$ while the species abundance is a function of both $t$ and $\tau$, denoted by $x_i(\tau; t)$ with $\tau$ running from

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0 to infinity for each stage $t \geq 0$. We will use simply $x_i$ instead of $x_i(\tau; t)$ and use $x_i(t)$ to represent the stationary abundance in each stage $\lim_{\tau \to \infty} x_i(\tau; t)$.

### 2.2. Inclusion of exploitative competition for $t \geq 1$

As introduced in section 1, we are particularly interested in the possibility that the mutualistic benefit of a pollinator is reduced by the competition with other animal species pollinating the same plants. To quantify such reduction of benefit and incorporate it into the interaction matrix, we consider the effective mutualistic benefit and use it to construct the interaction matrix for stage $t \geq 1$.

For $t = 1$, the mutualistic interaction matrix and the adjacency matrix are identical to those at $t = 0$, i.e. $\Gamma(1) = \Gamma(0)$ and $A(1) = A(0)$, respectively. In equation (1) for $t = 0$, we consider $M_{ap}(0)x_p$ as the mutualistic benefit of an animal species $a$ in pollinating a plant species $p$ and $M_{aa'}(0)x_{a'}$ as its cost of intrinsic competition with another animal species $a'$. They have the same dimension as the growth rate $\alpha_a$, effectively modifying the latter. Given that they are proportional to the abundance of mutualistic partner and other animal species, we can naturally assume that the reduction of mutualistic benefit caused by other pollinators at the same plant species is proportional to their abundances, leading us to represent the effective mutualistic benefit of $a$ in pollinating $p$ as

$$M_{ap}(1)x_p = M_{ap}(0)x_p - \sum_{a'} A_{pa}(1)A_{pa'}(1)\ell_{aa'; p} x_{a'},$$  \hspace{1cm} (3)$$

where $M_{ap}(0) = \Gamma_{pa}(0) = \Gamma_{pa}(1)$ and $\ell_{aa'; p}$ is the strength of the competition between two animal species $a$ and $a'$ in pollinating $p$. Summing equation (3) over $p$, we find the whole benefit of $a$ from mutualistic interaction to be represented as

$$\sum_p M_{ap}(1)x_p = \sum_p M_{ap}(0)x_p - \sum_{a'} U_{aa'}(1)x_{a'},$$ \hspace{1cm} (4)$$

where

$$U_{aa'}(1) = \sum_p A_{pa}(1)A_{pa'}(1)\ell_{aa'; p} = k_{aa'}(1)\langle \ell_{aa'; p} \rangle_p$$ \hspace{1cm} (5)$$

is the sum of $\ell_{aa'; p}$ over $k_{aa'}(1) \equiv \sum_p A_{pa}(1)A_{pa'}(1)$ distinct plant species co-pollinated by $a$ and $a'$, representing the strength of the exploitative competition of $a$ and $a'$. Note that $\langle \ell_{aa'; p} \rangle_p = \sum_p A_{pa}(1)A_{pa'}(1)\ell_{aa'; p}/\sum_p A_{pa}(1)A_{pa'}(1)$ is the average of $\ell_{aa'; p}$ over $p$, the co-pollinated plant species. Using equation (4) in the time-evolution equation of the species abundance for $t = 1$ like equation (1), one finds that the whole interaction matrix is represented as

$$M(1) = M(0) - \begin{pmatrix} 0 & 0 \\ 0 & U(1) \end{pmatrix}$$

$$= -I + \begin{pmatrix} -W^{(P)} & \Gamma(1) \\ \Gamma(1) & -W^{(A)} - U(1) \end{pmatrix}.$$ \hspace{1cm} (6)$$
The mutualistic interaction $\Gamma(t)$ and the adjacency matrix $A(t)$ change with $t$ as will be detailed below, and we constitute the interaction matrix in the same form as in equation (6) not only for $t = 1$ but for all $t \geq 1$:

$$M(t) = -I + \begin{pmatrix} -W^{(P)} & \Gamma(t) \\ \Gamma^r(t) & -W^{(A)} - U(t) \end{pmatrix}. \tag{7}$$

Here, like equation (5), the exploitative competition matrix $U(t)$ has elements

$$U_{aa'}(t) = \rho u_{aa'} k_{aa'}(t), \tag{8}$$

where $k_{aa'}(t) = \sum_{a'} A_{pa}(t) A_{pa'}(t)$, called here the overlap of $a$ and $a'$, and $\rho$ and $u_{aa'}$ are constants satisfying

$$\rho u_{a,a'} = \langle \ell_{aa';p} \rangle_p \tag{9}$$

under the assumption that the average $\langle \ell_{aa';p} \rangle_p$ is independent of time. The latter assumption is reasonable, considering that $k_{aa'}(t)$ will change more significantly with $t$ than $\langle \ell_{aa';p} \rangle_p$, which is an averaged quantity usually following a narrow distribution as stated in the central limit theorem. $u_{aa'}$ is a random positive constant and $\rho$ is a control parameter. Note that $U(t)$ depends on the mutualistic interaction $\Gamma(t)$ or the adjacency matrix $A(t)$ by equation (8).

### 2.3. Co-evolution of the interaction matrix and the species abundance for $t \geq 2$

From equation (1) with the interaction matrix $M_i(t)$ used in place of $M_i(0)$, one can expect the abundance $x_i(\tau; t)$ of species $i$ to converge in the limit $\tau \to \infty$ to $x_i(t)$ in stage $t$ given by

$$x_i(t) = -\sum_{j=1}^{N} M_{ij}^{-1}(t) \alpha_j. \tag{10}$$

This is expected to be stable against slight perturbation $\delta x = \{x_i(\tau; t) - x_i(t)\}$ as long as the magnitude of off-diagonal elements of $M$ are sufficiently small [3, 10, 20]. Since a complicated $\tau$-dependent behavior of the species abundance in case of equation (10) being unstable or in general cases [21] is not the main concern of the present study, we restrict out study to the case of weak interaction, i.e. the characteristic strength of intrinsic and exploitative competition and mutualism set to be small. Then, according to equation (10), a change in the interaction matrix $M$ may induce the increase or decrease of the species abundance. Given $M(1)$ as in equation (7) with $t = 1$, the interaction matrix $M(t)$ for $t \geq 2$ is generated recursively as follows. At each stage $t$, we randomly choose a species $i$, plant or animal type, and change one of its partner $j$ by a new one $j'$ to form a trial mutualistic interaction matrix $\Gamma'$ that is equal to $\Gamma(t)$ except for the elements $\Gamma'_{ij'} = \Gamma_{ij}(t)$ and $\Gamma'_{ij} = \Gamma_{ij}(t) = 0$ (or $\Gamma'_{j'i} = \Gamma_{j'i}(t)$ and $\Gamma'_{ji} = \Gamma_{ji}(t) = 0$). Computing the trial exploitative competition matrix $U'$ by using equation (8) with $\Gamma'$ and then the whole interaction matrix $M'$ by equation (7), we obtain the new abundance $x_i'$ of the selected species $i$ by equation (10) with $M'$. If $x_i'$
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from $M'$ is not smaller than the original abundance $x_i(t)$ from $M(t)$, then the considered link rewiring is accepted and we take $M'$ as the interaction matrix at the next stage $t + 1$, i.e. $M(t + 1) = M'$. Otherwise, the link rewiring is disallowed and the interaction matrix remains unchanged; $M(t + 1) = M(t)$. To summarize,

$$M(t + 1) = \begin{cases} M' & \text{if } x'_i \geq x_i(t), \\ M(t) & \text{otherwise}; \end{cases}$$

(11)

Such conditional rewiring is repeated every stage to generate a series of the interaction matrix $\{M(t)|1 \leq t \leq T\}$ and that of the species abundance $\{x_i(t)|1 \leq i \leq S, 1 \leq t \leq T\}$ with $T$ the total simulation stage.

The absolute value of a random number obeying the Gaussian distribution with zero mean and standard deviation $\sigma$ is assigned to $u_{aa'}$ for each pair of $a \neq a'$ in equation (8) and to each non-zero positive element of $W^{(P,A)}$ and $\Gamma(1)$ in equation (7). Note that the elements of $\Gamma(1)$ are continually exchanged with one another to form $\Gamma(t)$ for $t \geq 2$. The parameter $\sigma$ characterizes the strength of the intrinsic competition and mutualism, and $\rho\sigma$ is the strength of the exploitative competition. We choose a small value of $\sigma$ such that equation (10) is a stable fixed point for equation (1). The control parameter $\rho$ represents the characteristic relative strength of the exploitative competition compared to the mutualism or the intrinsic competition.

While it is possible that the intrinsic growth rates $\alpha_i$’s are altered by environmental effects or various types of perturbations, suggesting the volume of the $\alpha$ domain sustaining all species’ survival as a stability measure [2], we assume here that the mutations altering the intrinsic growth rate of a species occur on a much longer time scale than those leading to the change of its mutualistic partners. Also we assume that $\alpha_i$’s are not much different from species to species in a given mutualistic community. Given these considerations, we set the growth rate to $\alpha_i = -\sum_j M_{ij}(0)$, which is close to 1 as the off-diagonal terms of $M$ are small, such that the abundance $x_i(0)$ at the initial stage ($t = 0$) is 1 for all $i$. This constitutes the initial condition of our model mutualistic network characterized by random interactions and an identical abundance for all species, helping us to see clearly the co-evolution of network structure and species abundance.

3. Effects of exploitative competition: simulation results

In this section we present and analyze our simulation results for the evolution of the model mutualistic network for the period $0 \leq t \leq T = 5 \times 10^6$ with the number of species of each type $N^{(A)} = N^{(P)} = N = 25$, the interaction strength $\sigma = 0.025$, the connectance $C = 0.175$ following the empirical relation $C \simeq 4/S^{0.8}$ [10], and the relative strength of the exploitative competition $\rho$ varied between 0 and 0.7. Simulations with different numbers of species $N^{(A)} = N^{(P)} = 15, 40, 50$, different numbers of species between animal and plant, e.g. $\{N^{(A)}, N^{(P)}\} = \{16, 34\}$ or a different value of $\sigma = 0.0125$ have been performed, but do not change qualitatively the results and discussions presented in this section.
3.1. Species abundance

The average abundance of a plant and an animal species increases as stage $t$ increases after a drop at $t = 1$ due to the inclusion of the exploitative competition for $t \geq 1$ (figure 1(a)). The abundance in the stationary stage $t \to \infty$ shows big difference between plants and animals. Animal’s stationary-stage abundance $x^{(A)}(\infty)$ rapidly decreases with the exploitative competition strength $\rho$, but the abundance of plant $x^{(P)}(\infty)$ increases with increasing $\rho$ over a range $\rho \lesssim 0.1$ (figure 1(b)). This anomalous increase of the plant abundance is interesting and must be related to the optimal structure of the mutualistic network obtained by evolution under different $\rho$’s. The increase of the species abundance $x(\infty) - x(1)$ during evolution is much larger in plants than animals for $\rho$ small as shown in the inset of figure 1(b).
3.2. Network structure

The standard deviation of the node degree varies with time as shown in figure 2(a), implying a significant change in the network structure during evolution. The initial mutualistic network is a random bipartite network (figure 2(b)). In the stationary stage of evolution, the mutualistic network comes to exhibit quite different characteristics from the initial network depending on $\rho$ as shown in figures 2(c)–(f). Without exploitative competition ($\rho = 0$), a number of hub nodes of both plant and animal type exist, the abundance of which are high. The plant and animal hubs are connected to each other and isolated nodes are very rare. Under the exploitative competition between animals ($\rho > 0$), the evolved network exhibits asymmetry between plants and animals; plant nodes are homogeneous whereas animal nodes are strongly heterogeneous in their connectivity pattern. Hub plants or isolated plants are very rare. Plant nodes have similar degrees and abundance. In contrast, a large number of animal nodes become isolated for $\rho > 0$. Also there appear a few super-hub animal nodes that are connected to

Figure 2. Structural evolution of the mutualistic networks under exploitative competition. (a) Time-evolution of the standard deviation of node degree for different $\rho$'s. (b) An example of the mutualistic network in the initial stage $t = 0$. It is a random bipartite network. Plant- and animal-type nodes are shown as a green triangle and red circle, respectively. (c)–(f) An evolved network in the final stage for (c) $\rho = 0$, (d) $\rho = 0.02$, (e) 0.1, and (f) 0.5. Node size varies with the abundance.
all plant nodes. Such heterogeneity of animal nodes is weakened when the exploitative competition is sufficiently strong ($\rho \gtrsim 0.5$) as shown in figure 2(f).

### 3.3. Degree distribution

The structure of the mutualistic networks varying with $\rho$ can be quantitatively described in terms of the degree distribution. We find that the degree distribution in Poisson form at $t = 0$ changes to a power-law $P(k) \sim k^{-\gamma}$ with $\gamma \approx 1.6$ in the stationary stage both for plants and animals with $\rho = 0$ as shown in figures 3(a) and (b). With $\rho > 0$, the degree distribution of plants is no more in a power-law form; it gets narrower with increasing $\rho$ as shown in figure 3(a) such that it is narrower even than the initial Poisson degree distribution for $\rho$ sufficiently large. The standard deviation of plants’ degree decreases with $\rho$ (figure 3(c)), indicating that plants have increasingly similar numbers of partners with increasing $\rho$. On the other hand, the animals’ degree distribution develops a peak at the maximum possible degree $k = N^{(P)}$ (figure 3(b)), indicating the appearance of the animal species pollinating all plant species. The appearance of such super-hub pollinators is made possible at the expense of leaving many animal nodes isolated. The presence of the animal nodes of such extreme connectivity, all or nothing, leads to the large values of the standard deviation of the animals’ degree in the range $\rho \lesssim 0.1$ (figure 3(c)). For $\rho \gtrsim 0.1$, even the degree distribution of animals loses its power-law form and becomes narrower with increasing $\rho$ (figures 3(b) and (c)).

### 3.4. Evolution strategy

The large variation of the network structure with $\rho$ shown in figures 2(c)–(f) and 3 reflects that the structural evolution strategy for maximizing species abundance strongly depends on the exploitative competition. Furthermore, the anomalous behavior of the plants’ abundance (figure 1(b)) and the non-monotonic behavior of the standard deviation of the animals’ degree (figure 3(c)) suggest the nontrivial combinatorial effects of the mutualistic interaction and the exploitative competition on the optimal network structure. The abundance and the degree of individual species are in general positively correlated as shown in figure 4. Hub nodes benefit greatly from many partners and thus their abundance can be large. Given that the preferential link attachment to nodes with many links can generate hubs and power-law degree distributions in growing networks [17, 18, 22], similar preferential link rewiring is expected to play a role during evolution to generate hubs and broad, power-law-like, degree distributions for $\rho = 0$. Such heterogeneous connectivity pattern common to plant and animals is no more optimal if the exploitative competition is present. For $\rho > 0$, if many distinct animal species pollinated a common plant species, it would induce high exploitative competition between those pollinators and the abundance would be greatly reduced. Therefore the pollinators are redistributed uniformly over as many plant species as possible, which is the origin of the narrow degree distribution of plants and the disappearance of isolated plant nodes. The number of plant partners of an individual animal species is governed by the benefit of mutualistic interaction and the cost of exploitative competition. The super-hubs have their mutualistic benefit exceeding well the competition cost, due to the most partners possible. Their partners may have been taken from small-degree animals seeing little possibility to have such high abundance as super hubs.
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with their just few partners. For sufficiently large \( \rho \), the cost of exploitative competition is so large that many pollinators come to have small degrees. The abundance of plant species stops to increase with \( \rho \) but decreases for such large \( \rho \).

These arguments help us understand how the exploitative competition induces heterogeneity for animals and homogeneity for plants in the evolving mutualistic network.
However, they are still qualitative and it still remains open how much a variation of structural characteristics changes the species abundance and what structural features are relevant to the abundance. The mechanism enabling the plant abundance to increase with $\rho$ is in question. Quantitative answers to these questions can greatly advance our understanding of the interplay between the mutualistic benefit and the exploitative competition in the evolution of mutualistic community, which is the subject of the next section.

4. Structural factors relevant to species abundance: analytic approach

The mechanism optimizing the network structure for maximizing the species abundance can be quantitatively understood by analyzing the relation between the species abundance and the interaction matrix in equation (10). The analysis can rely on the

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linearization or the expansion of the quantities of interest in powers of the characteristic strength $\sigma$ if $\sigma$ is small. We first study the accepted link rewiring to illustrate how the model network evolves with time and then obtain the stationary-stage abundance in terms of network properties.

4.1. Change of species abundance by rewiring a link

When a randomly selected species $i$ attempts to replace one of its partners by another, this rewiring will be accepted if the abundance of $i$ is not decreased by this replacement, as in equation (11). In the weak interaction limit ($\sigma \to 0$), the resulting variation of the abundance $\delta x_i$ is related linearly to the change of the interaction matrix $\delta M$ caused by the considered rewiring as [10]

$$\delta x_i = \sum_j \delta M_{ij} x_j.$$  \hfill (12)

When a plant node $p$ replaces one of its partners $a_1$ by a new partner $a_2$, the mutualistic interaction for the new pair $(p,a_2)$ becomes $\Gamma_{pa_1}$ and that for the old pair $(p,a_1)$ is changed to 0. Using $\delta M_{pa_1} = -\Gamma_{pa_1}$ and $\delta M_{pa_2} = \Gamma_{pa_1}$, one finds the variation of the abundance of $p$ given by

$$\delta x_p = (x_{a_2} - x_{a_1})\Gamma_{pa_1}. \hfill (13)$$

This rewiring will be accepted if the new partner $a_2$ is not less abundant than $a_1$. Assuming a linear relation between the abundance and the degree of an animal species, $x^{(A)}_a \simeq c^{(A)} k_a + b^{(A)}$ with $c^{(A)}$ and $b^{(A)}$ constants as suggested in figure 4 and taking the constant-interaction approximation $\Gamma_{pa} = \sigma A_{pa}$, we obtain

$$\delta x_p \simeq \sigma c^{(A)} (k_{a_2} - k_{a_1}). \hfill (14)$$

This result shows the direction of the structural evolution: a plant can increase its abundance by replacing its animal partner by the one with a larger degree. Accordingly, hub animal nodes can be created along with the broadened degree distribution (figure 3(b)). Such preferential rewiring is underlying the increase of the standard deviation $\sigma^{(A)}_{k}$ of animals’ with the evolution stage (figure 2(a)).

When an animal species $a$ replaces its plant partner $p_1$ by $p_2$, not only the mutualistic benefit but also the exploitative competition cost can be changed, resulting in the change of the abundance of $a$ given by

$$\delta x_a = (x_{p_2} - x_{p_1})\Gamma_{p_1a} - \sum_{a'}(A_{a'p_2} - A_{a'p_1})\rho u_{a'a} x_{a'}. \hfill (15)$$

Introducing the approximation $x^{(P)}_p \simeq c^{(P)} k_p + b^{(P)}$ and assuming $\Gamma_{pa} = \sigma A_{pa}$ and $u_{a'a} = \sigma$, we have

$$\delta x_a \simeq \sigma \left[ c^{(P)} - \rho \langle x \rangle' \right] \langle k_p \rangle - b^{(P)}/ \hfill (16)$$

where $\langle x \rangle' \equiv c^{(A)} \langle k \rangle' + b^{(A)}$ and $\langle k \rangle' \equiv \frac{\sum_p \sum_a A_{pa} k_a}{\sum_p \sum_a A_{pa} k_a} = \frac{\sum_a k^2_a}{\sum_a k_a}$ are the average abundance and the degree, respectively, of a pollinator connected to a randomly-selected plant and $\sum_a A_{pa} k_a \simeq k_p \langle k \rangle'$ is assumed for any $p$. Let us define $\tilde{\rho}$ as

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\[ \tilde{\rho} \equiv c(P) \langle x \rangle' \]  (17)

Equation (16) indicates that animal nodes will tend to replace their partners by the ones having large (small) degrees, broadening (narrowing) the degree distribution of plants if \( \rho < \tilde{\rho} \) (\( \rho > \tilde{\rho} \)). The inequality between \( \rho \) and \( \tilde{\rho} \) should be related to which is dominant of the mutualistic benefit and the exploitative competition cost. By using the estimated parameters and the second moments from simulation results, we can evaluate \( \tilde{\rho} \) as a function of \( \rho \), which is shown in figure 5. It turns out that \( \rho \) remains smaller than \( \tilde{\rho} \) for \( \rho \lesssim 0.1 \), which explains why the degree distribution of plants in the stationary stage is broader for \( \rho = 0.02 \) but narrower with \( \rho = 0.1 \) or 0.5 than the initial Poisson distribution in figure 3(a). The standard deviation \( \sigma_k^{(P)}(\infty) \) of plants’ degree decreases with \( \rho \) passing the initial-stage value \( \sigma_k^{(P)}(0) \approx 2.1 \) around \( \rho \approx 0.03 \) which is comparable to the threshold 0.1 at which \( \tilde{\rho} = \rho \).

Although obtained by approximations, equations (14) and (16) explain well the evolution of the connectivity pattern of the mutualistic network; the degree distribution of animals is broadened for all \( \rho \) while that of plants is broadened only for \( \rho \) small.

4.2. Structural factors mediating direct and indirect interactions

Here we obtain the inverse of the interaction matrix \( M^{-1} \) up to the second order of \( \sigma \), which reveals all direct and indirect interactions between two species connected by a link or a path of length two. The mechanism enabling the anomalous increase of the plant abundance under increasing exploitative competition will be illuminated by this analysis.

Let us take the constant-interaction approximation for the intrinsic competition, \( W_{ij}^{(P,A)} = C\sigma(1 - \delta_{ij}) \) for all \( i \) and \( j \) as well as for the mutualism and the exploitative competition, \( \Gamma = \sigma A \), and \( U = \rho \sigma A^\dagger A \). Then the sum of the self-regulation and the

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intrinsic competition \( M_0 = -I - \begin{pmatrix} W^{(P)} & 0 \\ 0 & W^{(A)} \end{pmatrix} \) has its inverse exactly obtained as \( M_0^{-1} = - \begin{pmatrix} G_0 & 0 \\ 0 & G_0 \end{pmatrix} \) with [10]

\[
(G_0)_{ij} = \delta_{ij} - \frac{C\sigma}{1 - C\sigma(1 + C\sigma(N - 1))}.
\] (18)

The inverse of the whole interaction matrix \( M^{-1} = (M_0 + V)^{-1} \) can be expanded in terms of the network-dependent interaction \( V \equiv \sigma \begin{pmatrix} 0 & A \\ A^\top & \rho A^\top A \end{pmatrix} \) as \( M^{-1} = M_0^{-1} - M_0^{-1} V M_0^{-1} + M_0^{-1} V M_0^{-1} V M_0^{-1} + O(V^3) \). Up to the second order of \( \sigma \), the inverse \( M^{-1} \) is represented as

\[
-M^{-1} = \begin{pmatrix} G_0 & 0 \\ 0 & G_0 \end{pmatrix} + \sigma \begin{pmatrix} 0 & G_0 A^\top G_0 \\ G_0 A^\top G_0 & -\rho G_0 A^\top A G_0 \end{pmatrix} + \sigma^2 \begin{pmatrix} AA^\top & -\rho AA^\top A \\ -\rho A^\top AA^\top & A^\top A + \rho^2 A^\top AA^\top A \end{pmatrix} + O(\sigma^3).
\] (19)

Using equations (18) and (19) into (10) with \( \alpha_j = 1 \), we obtain the average abundance of plants

\[
x^{(P)} \simeq 1 + \sigma^2 \left\{ \kappa_2^{(P)} - (CN)^2 - \rho \kappa_3 \right\},
\] (20)

and the average abundance of animals

\[
x^{(A)} = 1 - \rho \sigma \kappa_2^{(A)} + \sigma^2 \left\{ (1 + 2\rho (CN))\kappa_2^{(A)} - (CN)^2 - \rho \kappa_3 + \rho^2 \kappa_4^{(A)} \right\},
\] (21)

where \( N \) is the number of plant or animal species set equal for simplicity. Note that the benefit of the direct mutualistic interaction \( \sigma \sum_{pa} (G_0 A^\top G_0)_{pa} \simeq CN\sigma \) in the first order of \( \sigma \) is canceled out by the intrinsic competition included in \( \sum_p (G_0)_{pp} = \frac{1}{CN(1-N)} \simeq 1 - CN\sigma \).

On the other hand, the exploitative competition survives in the \( \sigma \) order in the animal’s abundance. In these expansions are \( \kappa_n \)'s with \( n = 2, 3, 4 \), which are characteristic structural factors mediating the direct or indirect interspecific interaction and defined as

\[
\kappa_2^{(P)} = \frac{1}{N} \sum_{pp'} (AA^\top)_{pp'}, \quad \kappa_2^{(A)} = \frac{1}{N} \sum_{aa'} (A^\top A)_{aa'},
\]

\[
\kappa_3 = \frac{1}{N} \sum_{pa} (AA^\top A)_{pa} = \frac{1}{N} \sum_{a,p} (A^\top AA^\top)_{ap},
\]

\[
\kappa_4^{(A)} = \frac{1}{N} \sum_{a,a'} (A^\top AA^\top A)_{aa'},
\] (22)

with examples in figure 6(a). The \( \kappa_n^{(P,A)} \) indicates the total number of length-\( n \) paths connecting two nodes of given type. Notice that \( \kappa_2^{(A)} \) is the average overlap between animals \( \kappa_2^{(A)} = N^{-1} \sum_{aa'} k_{aa'} \) with \( k_{aa'} \) in equation (8). Also \( \kappa_2 \) is directly related to the

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standard deviation of degree, i.e. \( \kappa_{2}^{(P)} = \left( \sigma_{k}^{(A)} \right)^{2} + \langle k \rangle^{2} \) and \( \kappa_{2}^{(A)} = \left( \sigma_{k}^{(P)} \right)^{2} + \langle k \rangle^{2} \), and similar to the nestedness [6] except that the overlap is summed only over the pairs of nodes having different degrees for the nestedness.

The \( \kappa_{n} \)'s measured in simulation data are shown in figure 6(b). In the range \( 0 < \rho \lesssim 0.1, \) \( \kappa_{2}^{(P)} \) and \( \kappa_{3} \) increase while \( \kappa_{2}^{(A)} \) and \( \kappa_{4}^{(A)} \) decrease. For \( \rho \gtrsim 0.1 \), those factors do not change or decrease with \( \rho \). Inserting those measured values of \( \kappa_{n} \)'s into equations (20) and (21), we obtain the species abundance in good qualitative agreement with those of the directly measured abundance for \( \rho \) small, less than 0.1, as shown in figure 6(c). In particular, the increasing abundance of plants with \( \rho \) is reproduced also by equation (20) despite significant deviation for \( \rho \gtrsim 0.1 \).

If there is no exploitative competition \( (\rho = 0) \), the larger the average overlap \( \kappa_{2} \) is, the larger the abundance of plants and animals is according to equations (20) and (21). The \( \kappa_{2}^{(P)}(\kappa_{2}^{(A)}) \) term appears in the second order of \( \sigma \), as it represents an indirect interaction between plants (animals) arising from their respective mutualistic interactions with common pollinators (plants). This distance-2 mutualistic interaction obviously makes a positive contribution to the species abundance, underlying the well-known positive correlation between the nestedness and the species abundance [7, 10]. If \( \rho > 0 \), \( \kappa_{2}^{(A)} \) is utilized also for the exploitative competition between animals which reduces directly the animal abundance in the first order of \( \sigma \) in equation (21). \( \kappa_{2}^{(A)} \) should be therefore made small to reduce the decrease of the animal abundance. Animals' stronger preference of plant partners with small degrees during evolution, as shown in equation (16), can bring smaller \( \kappa_{2}^{(A)} \) and smaller \( \sigma_{k}^{(P)} \) in the stationary stage for larger \( \rho \). Nevertheless the abundance of animals cannot help but decrease with \( \rho \) (figure 6(c)).

The exploitative competition affects the plant abundance only indirectly; the \( \kappa_{3} \) term in equation (20) represents the indirect interaction between a plant \( p \) and an animal species \( a \), having another animal species \( a' \) interacting mutualistically with \( p \) and competing exploitatively with \( a \). The abundance of \( a \) is thus detrimental to \( p \) in this example. As long as \( \rho \lesssim 0.1 \), such negative effect of the next-nearest neighbors on the plant abundance in the \( \sigma^{2} \) order is not so strong as the positive effect of the distance-2 mutualistic interaction mediated by \( \kappa_{2}^{(P)} \), which enables the anomalous increase of \( x^{(P)}(\infty) \) with \( \rho \). While \( \rho \) increases to 0.1, \( \kappa_{2}^{(P)} \) of the evolved networks increases significantly overcoming the increasing negative effect \( -\rho \kappa_{3} \) given in equation (20). See figure 6(b). As the networks with many hub nodes tend to have high nestedness [23], plants' preferential partnering with animals of large degrees, indicated by equation (14), is expected to be the mechanism used to increase \( \kappa_{2}^{(P)} \) and equivalently \( \sigma_{k}^{(A)} \) during evolution.

These results suggest that \( \kappa_{2}^{(P)} \) and \( \kappa_{2}^{(A)} \) are the key driver of the structural evolution, controlling the distance-2 indirect mutualistic interaction benefit and the direct exploitative competition cost. For \( 0 < \rho \lesssim 0.1 \), \( \kappa_{2}^{(A)} \) is made small whereas \( \kappa_{2}^{(P)} \) is made large during evolution, which is the evolution strategy to maximize the species abundance. Moreover, the increase of \( \kappa_{2}^{(P)} \) with \( \rho \) underlies the counterintuitive increase of the plant abundance.
When $\rho$ is sufficiently large ($\rho \gtrsim 0.1$), the increasing effect of the indirect interaction $-\rho \kappa_3$ on the plant’s abundance is significant, which can be a reason for the decrease of $\kappa_3$ with $\rho$. As $\kappa_n$’s are just different powers of the same adjacency matrix, the decrease of $\kappa_2^{(P)}$ with $\rho$ may be related to the decrease of $\kappa_3$. $\kappa_2^{(A)}$ remains almost the same while $\kappa_4^{(A)}$ decreases with $\rho$. It should be noted that $\kappa_3$ and $\kappa_4$ can contribute to the species abundance in the $\sigma^3$ and $\sigma^4$ order, beyond the scope of equation (20) or (21). Moreover,
the abundance of plants for large $\rho$ remains much larger than the prediction by equation (20), implying the non-negligible roles of higher-order structural features.

5. Summary and discussion

In this work, we investigated how the plant-pollinator mutualistic partnership is organized to increase the species abundance given the exploitative competition between the pollinators sharing the same plant partners. The relevance of such exploitative competition to the structure of mutualistic networks has been implied previously but its effects on the network evolution coupled with the species abundance have been first investigated here. The most interesting finding is that the exploitative competition between pollinators results in an anomalous increase of the plant abundance while the animal abundance is decreased. The evolutionary pressure is imposed in the direction of making the connectivity of plants homogeneous and that of animals heterogeneous. Expanding the inverse of the interaction matrix in the weak-interaction limit uncovers the first few leading direct and indirect interactions affecting the species abundance, which allows us to find that the average overlaps between plants and between animals are instrumental for the structural optimization to achieve the maximum possible species abundance in the presence of both mutualism and the exploitative competition.

Our study demonstrates that a structural factor can be enhanced or suppressed during evolution depending on the interplay between different types of interspecific interactions, emphasizing its importance in understanding the structure and function of an ecological community. Given that the indirect mutualistic interaction and the exploitative competition drive the overlap or the nestedness in the opposite directions, it is desirable to develop a method to infer the relative strength of the exploitative competition of real-world mutualistic networks from the empirical data. Also, asymmetry in the overlap or nestedness between plants and pollinators can be measured empirically and its comparison across different mutualistic communities may inform us of different strengths of exploitative competition across communities. When the empirical data of the overlap and the species abundance of plants and pollinators are available, their relation can be checked against the theoretical prediction presented in this work.

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