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Structure and dynamics of pollination networks: the role of alien plants

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Research on ecological communities, and plant–pollinator mutualistic networks in particular, has increasingly benefited from the theory and tools of complexity science. Nevertheless, up to now there have been few attempts to investigate the interplay between the structure of real pollination networks and their dynamics. This study is one of the first contributions to explore this issue. Biological invasions, of major concern for conservation, are also poorly understood from the perspective of complex ecological networks. In this paper we assess the role that established alien species play within a host community by analyzing the temporal changes in structural network properties driven by the removal of non-native plants. Three topological measures have been used to represent the most relevant structural properties for the stability of ecological networks: degree distribution, nestedness, and modularity. Therefore, we investigate for a detailed pollination network, 1) how its dynamics, represented as changes in species abundances, affect the evolution of its structure, 2) how topology relates to dynamics focusing on long-term species persistence; and 3) how both structure and dynamics are affected by the removal of alien plant species. Network dynamics were simulated by means of a stochastic metacommunity model. Our results showed that established alien plants are important for the persistence of the pollination network and for the maintenance of its structure. Removal of alien plants decreased the likelihood of species persistence. On the other hand, both the full network and the subset native network tended to lose their structure through time. Nevertheless, the structure of the full network was better preserved than the structure of the network without alien plants. Temporal topological shifts were evident in terms of degree distribution, nestedness, and modularity. However the effects of removing alien plants were more pronounced for degree distribution and modularity of the network. Therefore, elimination of alien plants affected the evolution of the architecture of the interaction web, which was closely related to the higher species loss found in the network where alien plants were removed.

The introduction of alien species into native ecosystems, together with habitat deterioration and climatic change, constitute the major anthropogenic threats for the persistence and integrity of pollination systems (Memmott and Waser 2002). The effects of alien plant invasions on native pollination systems may be competitive, neutral, or facilitative (Bjerknes et al. 2007, Sargent and Ackerly 2008). Alien plants may compete with native ones either through reducing visitation rates of pollinators or through increasing heterospecific pollen transfer on native flowers (Chittka and Schürkens 2001). However, an alien's effects may be neutral if native plants are not pollen limited, or if they compensate for the loss of pollinators (Totland et al. 2006). At the landscape level, whenever alien plants represent valuable food resources for many pollinators, their effect on native biota could be more facilitative than competitive by means of increasing pollinator densities (Bjerknes et al. 2007).

Recently, the study of anthropogenic impacts on pollination systems has switched from a 'single species' approach, which focuses on one or a few plant–animal species interactions, to the 'pollination web' approach, which focuses on entire communities (Memmott and Waser 2002, Olesen et al. 2002, Morales and Aizen 2006, Memmot et al. 2007, Aizen et al. 2008). Here we use the pollination web approach to evaluate the roles played by established alien plants in the preservation of the structure and the persistence of the member species in a real plant–pollinator network.

The dynamics of pollination networks, here represented as changes in species abundances, may be affected by the availability of mutualistic partners and by the pattern of interactions between plants and animals. That is, the dynamics within the network depends on its topology. Conversely, the evolution of the topology of a network is influenced by the dynamics of its member species, given that species and interactions are removed when populations go extinct following severe decreases in their abundances. Such systems of interconnected parts in which there is a causal and bidirectional relationship between their structure and dynamics have been referred to as adaptive networks (Gross and Blasius 2008).

Until now, pollination web studies have not explicitly adopted the adaptive network approach. Studies of anthropogenic impacts on pollination webs (Memmott and Waser 2002, Morales and Aizen 2002, 2006) and analyses of network robustness to species removal (Memmott et al. 2004) are based on a purely network topology perspective that ignores the dynamics of constituent species and disregards the evolution of the topology. On the other hand, Olesen et al. (2008) investigate the mechanisms underlying the topology of a pollination web by following daily pollination dynamics over successive flowering seasons. These previous approaches provide the backdrop for this project which focuses on the bidirectional causality between topology and dynamics in pollination network and how this interplay could be affected by forcing variables such as biological invasions or habitat loss.

A theoretical way of incorporating dynamics into complex mutualistic networks was introduced by Fortuna and Bascompte (2006), who presented a stochastic metacommunity model in which the pattern of species interactions follows exactly that of an empirical pollination network. In this paper we make use of their model, which merges the tradition of dynamical systems research with that of complex networks based on graph theory, to reveal how the removal of an established set of alien plants could affect the interplay between topology and dynamics in a well-resolved pollination network. Specifically, for both the full network and the sub-network without alien plants we explore: 1) how network dynamics, represented as changes in species abundances, affects the evolution of network topology through changes in several structural properties (degree distribution, nestedness, and modularity); and 2) how topology relates to dynamics, with a focus on long-term species persistence.

Material and methods

Database and adjacency matrices

Our analyses were made on a plant–pollinator community of the subandean zone of central Chile, at 33°S latitude and 1800 m a.s.l. This zone correspond to a Mediterranean-type climate with precipitation concentrated in the winter months, followed by progressive drying in the summer and autumn (Arroyo et al. 1981). The vegetation is mainly composed by herbs and shrubs, and around 83% are biotically pollinated. Important characteristics of the Andean zone in central Chile, in contrast to many other temperate mountain areas, are the richness of the bee fauna and the high occurrence of bee-pollinated plants (Arroyo et al. 1982). Effective visits of insects on flowers were recorded during the flowering season from November 2006 until March 2007. Effective visitors were defined as insects that make contact with reproductive structures of flowers, with a cessation of flying.We used two sampling procedures: (1) recording the number of effective visits per insect species on each of the plant species, by means of repeated 15-min observation periods, and (2) recording the occurrence of effective visits by each insect species on each plant, through slow walks along random transects. Plants and insects were identified to species or morphospecies with the help of taxonomists. The pollination network was composed of 77 plant species and 110 insect species with a total of 362 pollination interactions. Among the plant species, 14 were alien plants.

From collected data, we constructed two different adjacency matrices corresponding to: 1) the complete observed network (hereafter the 'full network'), and 2) the observed full network without alien plants species and their interactions (hereafter the 'native network'). Elements of the adjacency matrices m_{ij} were ones or zeros, representing respectively observed and unobserved effective visits of insect j on plant i. A comparison of the two matrices allowed us to characterize the role of alien plants within the observed community in terms of their contribution to species persistence, network structure, and evolution of network topology. We do not know what the network structure was before alien species entered the community. Here we explore the role of the established alien species through simulating the fate of the system after the complete removal of aliens, assuming that if these species disappear the network cannot reorganize by establishing new links or redistributing existing links.

Network dynamics and persistence

In order to study the dynamics of the network we used the metacommunity model presented by Fortuna and Bascompte (2006). Their model considers mutualists inhabiting a landscape consisting of an infinite number of identical, well-mixed patches. The interaction is obligate for the animals, while plants are able to survive in the absence of animals but cannot reproduce without them. Fortuna and Bascompte (2006) introduced a set of differential equations describing the fraction of the total available patches occupied by plant i, p_i, and animal j, a_j. The general model is represented by:

$$\frac{dp_i}{dt} = \sum_{j=1}^{n} \left(c_{ij} \frac{p_i a_j}{\Omega_j} \right) (1 - d - p_i) - e_i p_i$$

$$\frac{da_j}{dt} = c_j a_j (\Omega_j - a_j) - e_j a_j$$

where c_{ij} is the per capita colonization rate of plant i when pollinated or dispersed by animal j, and c_j is the per capita colonization rate of animal j (which may only colonize patches occupied by the plants it interacts with). Per capita extinction rates for plant i and animal j are given respectively by e_i and e_j. It is assumed that the extinction of plants from a patch causes the secondary extinction of animals exclusively dependent on that plant. Parameter d represents the fraction of patches permanently lost through habitat destruction, and ω_j is the union of the patches occupied by n plant species interacting with the same j animal species (i.e. the total available patches for the jth animal, see Fortuna and Bascompte 2006 for model details).

Following Fortuna and Bascompte (2006), we randomly sampled the value of e/c from a uniform distribution centered in chosen values of $k_p = e_i/c_i$ for plants and $k_a = e_j/c_j$ for animals, with an interval size of 0.1. We used $k = 0.25$, $k = 0.5$, and $k = 0.75$, with $k = k_p = k_a$. Initial conditions for each species in the network were also randomly sampled from a uniform distribution on the unit interval. A species was considered extinct when its fraction of occupied patches fell below a threshold value of 0.001. We performed simulations at three levels of habitat loss: $d = 0.25$, $d = 0.5$ and $d = 0.75$. The metacommunity model was implemented with MATLAB codes. Each adjacency matrix was run for 2000 iterations, a time at which the fraction of occupied patches remained constant for all species.

For each combination of parameter values, 1000 model realizations were run for each adjacency matrix. To evaluate if the differences in persistence between the full and native networks could be attributed to the removal of the alien species and not to reduction in matrix size, in each realization we selected and removed a random sample of 14 plant species. We thus created an empirical distribution for what to expect of the dynamics of networks with the same species richness as the native networks. We refer to these null matrices as 'random-species networks'.

Network topology and its evolution

Topological properties feature specific patterns of organization of the components (i.e. species) within the network and are used to characterize the architecture of interactions. Such properties provide a static description of the network connectivity, i.e. the degree to which species are connected to one another through the network. Throughout the sequence of changes in species persistence resulting from runs of the dynamic model, three main topological properties were monitored: degree distribution, nestedness, and modularity. These network metrics allow characterizing the organization of the constituent species in terms of their interactions and according to their degree of specialization. The specific structure of a pollination network, represented through these topological metrics, informs us about the ability of the community to respond to different kinds of environmental perturbations.

The degree of a species consists of the number of its interacting species. The function which describes the histogram of all species degrees in a network is called a degree distribution. In mutualistic networks, as in other real networks, degree distributions are very heterogeneous (Jordano et al. 2003), with many specialist species and few super-generalist species. We calculated the cumulative degree distribution $P(k)$ (Newman 2003) of animals and plants for each network. This distribution shows the fraction of plant (or animal) species in the network that interact with k or more animals (or plants). For each observed distribution we fitted three alternative models: exponential ($P(k) \sim e^{-\alpha k}$), power law ($P(k) \sim e^{-\gamma}$) and truncated power law ($P(k) \sim k^{-\gamma} e^{-k/k_c}$) where α and γ are fitted constants and k_c is the truncation value that defines the exponential cut-off. The truncated power law is the most general of these three models. If γ is zero, the truncated power law model will be equivalent to the exponential model, and if k_c is higher than the maximum observed degree, the truncated power law will approach the power law model in the positive quadrant. Akaike's approach was used to select the best model describing the observed degree distribution (Burnham and Anderson 2004). To avoid overparameterization, we used the corrected AIC (AICc), which converges to AIC as the sample size gets large. The individual AICc values were rescaled to $\Delta i = AICc_i - AICc_{min}$, where $AICc_{min}$ is the minimum among the $AICc_i$ values calculated for the different models. This transformation forces the best model to have $\Delta i = 0$, with the rest having positive values. Models with $\Delta i \leq 2$ are considered to have substantial support (Burnham and Anderson 2004). When more than one model had $\Delta i \leq 2$, the highest percentage of explained variance was used to discriminate between the models supported by AICc. In order to compare the degree distribution among the studied networks, we standardized the value of the exponent γ of the fitted truncated power-law model by means of standard normal deviates (z-scores) from the mean of 1000 random matrices generated by the null model II of Bascompte et al. (2003). This null model assumes that each plant–animal pair interacts with a probability proportional to the observed number of interactions of both species (Bascompte et al. 2003, Guimarães and Guimarães 2006). This null model lacks nestedness but preserves the heterogeneity of the adjacency matrix. This procedure allows us to eliminate the effect of changing matrix size and connectance (i.e. the fraction of all possible links that are realized in the network) on the assessment of this topological property.

A nested network implies that the more specialist species tend to interact with species that are proper subsets of those species interacting with the more generalist ones (Bascompte et al. 2003). We measured the degree of nestedness through the matrix temperature T, with values ranging from 0 for perfectly nested networks to 100 for completely non-nested networks (Atmar and Patterson 1993). In order to evaluate the statistical significance of observed nestedness and to compare the degree of nestedness among the studied networks, we standardized the index T by means of standard normal deviates (z-scores) of each matrix with respect to the distribution of T obtained from 1000 matrices generated from null model II of Bascompte et al. (2003). This allows elimination of the effect of changing matrix size and connectance on the nestedness measure. Calculation of matrix temperatures were performed with the software ANINHADO (Guimarães and Guimarães 2006).

A network is said to be modular when its member species are organized into compartments (modules) in which plant and animal species have more interactions among them than with species that belong to other modules. Modules may reflect the specificity of interactions, convergence toward pollination syndromes, and phylogenetic clustering of closely related species (Olesen et al. 2007). Therefore a network exhibiting many little modules represents a community composed of several groups of a few coevolving species. The extinction of a species in such a network will mostly affect species within its module. On the other hand, the deleterious effect of species extinction could spread widely over a network structured into a few large modules. The degree of network compartmentalization into modules was measured through the modularity index M of Guimerà and Amaral (2005a, 2005b). This algorithm identifies modular structure that leads to many within-module links and as few as possible between-module links. From that structure, we obtained the number and size of modules, as well as the fraction of network interactions that occurr both within-modules and among-modules. Statistical significance of modularity was assessed through estimating M on 100 random networks with the same degree distribution as the full network (Guimerà et al. 2004). From the obtained empirical distribution of M we expressed network modularity as z-scores to control for matrix size and connectance. Two additional indices were used in the modularity analysis to associate a role to each of the interacting species (Guimerà and Amaral 2005a, 2005b). Within-module standardized connectivity of species i, z_i, is given by $z_i = \frac{k_{is} - \overline{k_s}}{\sigma_{ks}}$ where k_{is} is number of interactions of i with other species in its own module s. Parameters $\overline{k_s}$ and σ_{ks} are the average and standard deviation of within-module k of all species in s. Among-module connectivity of species i, c_i, is given by $c_i = 1 - \Sigma_{t=1}^{N_M} \left(\frac{k_{it}}{k_i}\right)^2$ where k_{it} is number of interactions of i with species in module t, and k_i is the number of interactions (i.e. degree) of species i. Roles for each species were assigned following Olesen et al. (2007): (1) network hubs, $z > 2.5$ and $c > 0.62$; (2) module hubs, $z > 2.5$ and $c \leq 0.62$; (3) peripherals, $z \leq 2.5$ and $c \leq 0.62$; and (4) connectors, $z \leq 2.5$ and $c > 0.62$. Network hubs are species that act as a 'glue' within an ecological network since they monopolize most of species interactions. Therefore, these species are very important for preserving the network structure (Olesen et al. 2007). A module hub is a species that interacts mostly with species within its module and has few interactions outside of it. Peripheral species have very few interactions with other species. Connector species interact more with species outside their module than with species in their own module (Olesen et al. 2007).

To evaluate the evolution of the topology of both the full and native network, we identified the adjacency matrices at time 100, 200, 400, 800 and 2000 from each of 100 realizations of the model. For the 1000 matrices so obtained plus the two initial matrices, we analyzed the three topological properties described previously. For each time step, we computed the mean and 95% CI of the z-scores of the (size-controlled) topological measures, in order to test for differences between networks as well as across time.

Results

Network dynamics and species persistence

The fraction of alien species increased through time (Table 1), revealing that the persistence of alien plants was higher than the persistence of the native species. These differences in species persistence also imply that the fraction of alien links increased with time (Table 1). Furthermore, global extinction (the number of networks in which >90% initial species went extinct) occurred more frequently in the native network than in the full network (Table 1). To assess the role of alien plants in shaping the observed differences between the full and native networks we contrasted the dynamic outcomes with that obtained from a set of random-species networks.

The fraction of species that went extinct in the native network was significantly higher than in the full network and in the random-species networks (Kruskal–Wallis test, multiple comparisons of mean ranks, $p < 0.05$, Fig. 1). Exceptions to this trend were found where extinctions were rather high as a consequence of a large value of the parameter k. Therefore, for low and moderate ratios of the extinction/colonization rate, the removal of alien plants decreased species persistence. For an extinction/colonization value of $k = 0.75$ combined with habitat loss rates of $d = 0.25$ and 0.5, the fraction of extinct species was so large that the effect of initial deletions of nodes was unimportant. The largest differences in persistence between the full and the native network were found at $d = 0.5$ and $k = 0.5$.

Network topology and its evolution

Alien plant species were visited by more pollinator species and are therefore more generalist than their native counterparts (Mann–Whitney test, $p < 0.05$). However, none of the aliens was the most connected species in the network. The range of generalism for the native flora is 1–31 pollinators and for alien flora is 1–10 pollinators. Therefore, most alien plants fall in the upper middle position within the range of generalism exhibited by all plants in the network. Similarly, most alien plants fell in the upper

Table 1. Basic properties (average of 100 realizations ± 95% CI) of the full and native pollination networks through time. Parameters values were $k = 0.5$ and $d = 0.5$. Global extinction refers to the number of networks in which >90% of initial species went extinct.

Time	0	100	200	400	800	2000
Full network						
Plants	77	54.5 ± 0.8	47.7 ± 1.1	42.4 ± 1.4	38.8 ± 1.7	35.7 ± 2.1
Animals	110	66.4 ± 1.7	51.9 ± 1.6	43.7 ± 1.4	38.8 ± 1.3	34.8 ± 1.6
Fraction of alien species	0.182	0.218 ± 0.003	0.236 ± 0.005	0.258 ± 0.007	0.278 ± 0.010	0.293 ± 0.012
Fraction of alien links	0.229	0.236 ± 0.002	0.245 ± 0.003	0.257 ± 0.004	0.270 ± 0.006	0.278 ± 0.007
Connectance	0.043	0.080 ± 0.002	0.105 ± 0.003	0.130 ± 0.005	0.150 ± 0.007	0.170 ± 0.009
Global extinction		0	0	0	0	2
Native network						
Plants	63	40.0 ± 0.9	30.0 ± 1.3	22.3 ± 1.7	15.7 ± 2.0	10.0 ± 2.0
Animals	97	56.1 ± 1.4	43.4 ± 1.6	32.5 ± 2.4	23.9 ± 2.8	15.1 ± 3.0
Connectance	0.046	0.092 ± 0.003	0.134 ± 0.007	0.187 ± 0.014	0.227 ± 0.030	0.226 ± 0.034
Global extinction		0	0	8	23	52

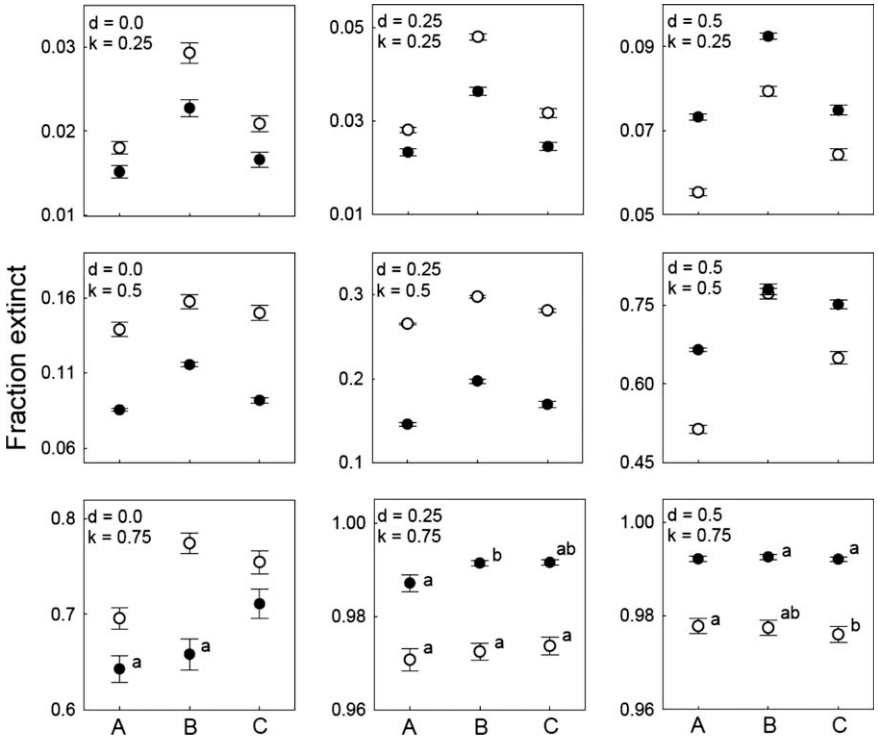

Figure 1. Fraction of extinct species averaged over 1000 model realizations for the full network (A), the native network (B), and the random-species networks (C). Different parameter values were used to represent habitat loss (d) and extinction/colonization ratio (k). Open and closed circles represent plants and animals respectively. Error bars are 95% CI. Equal letters indicate non-significant differences (Kruskal–Wallis, multiple comparisons of mean ranks, $p < 0.05$).

middle position of the nested matrix. Thus, although aliens should not be considered the core of the pollination network, they monopolize an important fraction of mutualistic interactions.

Next we tested how the removal of alien plants compares to equivalent levels of random plant removal. Table 2 shows that the effects of the experimental removal of aliens did not differ from those of random removals, in terms of secondary extinctions, number of interactions, or connectance. This is a key result because it demonstrates that the cause of differences in persistence between the full and native networks does not rest on trivial topological divergences. This suggests that the differences in dynamic outcomes between the tested networks lie on more complex topological properties associated with alien species. The examination of degree distribution, nestedness and modularity of both the full and native networks may help to disentangle the causes of their differences in persistence.

The exponential model best described the plants' degree distributions for both networks prior to running the dynamic model. Initial degree distributions of animals for both networks were best described by a truncated power law. The evolution of the degree distributions of animals in the networks was similar: they changed from a truncated power law to a power law distribution. However, the full and native networks differed in the evolution of plants' degree distributions. For both networks, degree distributions of plants initially changed from exponential to truncated power law. However, plants in the full network retained a truncated power law distribution until the end of simulations, while plants in the native network shifted to a power law distribution. The evolution of the degree distributions for plants in the two networks is graphically shown in Appendix 1. In order to describe the evolution of degree distribution in the full and native networks, we fitted a truncated power law model to the observed cumulative degree distributions at each time step. The value of the degree distribution exponent of the fitted model increased asymptotically with time (results not shown), but its deviations from the null models (z-scores) decreased with time for both plants and animals (Fig. 2). In the long term, the degree distributions of both networks became similar to that of random networks of equal size and similar connectance, although this structural decay was faster and more pronounced in the native network. Therefore, the structure of degree distribution was more conserved in the full network than in the native network, after controlling for network size and connectance.

Both the full network and the native network were significantly nested before running the dynamic model. However, controlling for size and connectance, both networks lost their nested structure over the course of the

Table 2. Comparison between basic topological features of the native network and random-species networks. For random-species networks, mean of 1000 runs and 95% CI are given.

	Native network	Random-species networks	p-value
Number of animals	97.0	99.57 ± 0.28	0.572
Number of links	279.0	295.63 ± 1.01	0.306
Connectance	0.046	0.047 ± 0.0001	0.449

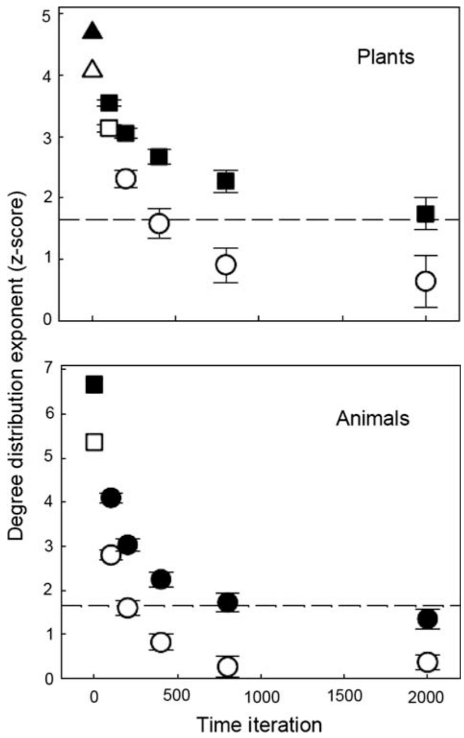

Figure 2. Temporal shifts of cumulative degree distributions for plants and animals in the full network (closed symbols) and the native network (open symbols). Triangles, squares and circles represent networks in which the best fitted model was exponential, truncated power law, and power law respectively. The values on the ordinate are z-scores of the exponents of the fitted truncated power law model. Average of 100 model realizations and 95% CI are shown, with parameters d = 0.5 and k = 0.5. Values above the horizontal reference line are significantly different ($p < 0.05$, one-tailed test) from those of null networks of equal size and similar connectance.

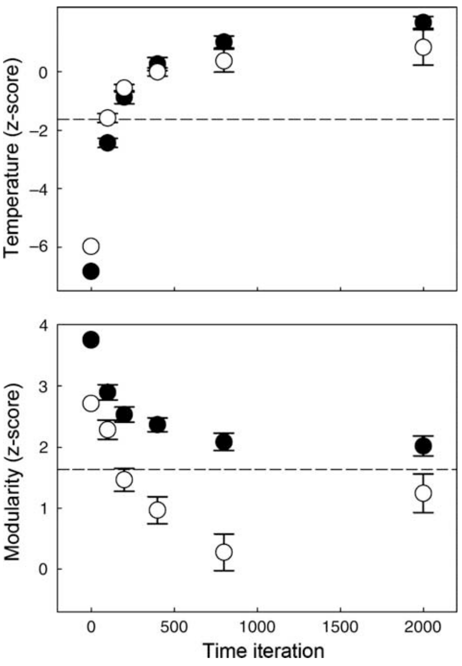

Figure 3. Standard normal deviates (z-scores) of temperature (upper plot) and modularity (lower plot) indices through time, with parameters d = 0.5 and k = 0.5. Average of 100 model realizations and 95% CI are shown for the full network (closed circles) and the native network (open circles). Values below (for temperature) and above (for modularity) the horizontal reference line are significantly different ($p < 0.05$, one-tailed test) from those of null networks of equal size and similar connectance.

model simulations. Thus, although the native network lost its nested structure sooner than the full network, the presence of alien plants does not appear to be a determining factor for the conservation of the nested structure (Fig. 3).

In their initial states, both the full and native networks were significantly modular and exhibited the same number of modules, but had different module sizes (Table 3). At the outset of the dynamic simulations, the number of modules remained homogeneous between the two networks until time 200 (Table 3). After that point, the native network had significantly fewer modules than the full network. This divergence in the number of modules occurred simultaneously with the lost of modularity of the native network. Although the modularity of both networks decayed through time, only the full network retained its modular structure in the long term (Fig. 3) Species identified as network hubs or module hubs constituted a minor fraction of the nodes of both networks, as compared to peripheral and connector species (Fig. 4). The fractions of hubs and peripherals (i.e. the number of nodes belonging to each role over the total number of nodes) decreased through time in both networks while the fraction of connectors increased. The processes behind these role shifts are summarized in Table 4. The decrease in the relative abundance of peripheral nodes is driven by their extinction, while hub species decreased because their role shifted to peripheral or connector species. Connectors increased their representation in the networks due to their low extinctions together with the conversion of some hubs into connectors. Across the entire time interval used in the simulations, the network in which alien plants were removed presented more extinctions in all roles as compared to the full network and the full network presented more role shifts than the native network. Only

Table 3. Basic description (average of 100 realizations ± 95% CI) of the modular structure of the full and native pollination networks throughout time.

Time	0	100	200	400	800	2000
Full network						
Number of modules	12.0	7.3 ± 0.2	6.6 ± 0.2	6.1 ± 0.2	5.8 ± 0.1	5.6 ± 0.1
Modules' median size	18.5	16.7 ± 0.4	15.4 ± 0.5	14.2 ± 0.4	13.4 ± 0.4	12.7 ± 0.4
Native network						
Number of modules	12.0	7.3 ± 0.2	6.3 ± 0.2	5.4 ± 0.2	4.5 ± 0.4	5.0 ± 0.3
Modules' median size	15.0	13.3 ± 0.4	11.7 ± 0.4	10.3 ± 0.6	8.6 ± 0.8	10.4 ± 0.9

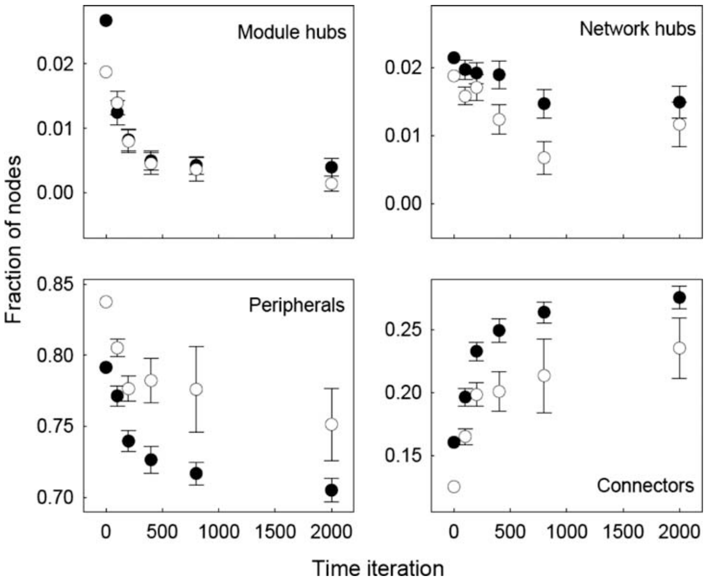

Figure 4. Temporal shifts of the fraction of nodes belonging to the classes of network hubs, module hubs, peripherals, and connectors. Average of 100 model realizations and 95% CI are shown for the full network (closed circles) and the native network (open circles). Parameter values were d = 0.5 and k = 0.5.

the relative number of module hubs remained similar between the two networks over time.

Through time, species richness decreased while connectance increased. The negative relationship between species richness and connectance displays similar slopes in both networks ($p = 0.107$, GLM test for homogeneity of slopes) but a lower elevation for the native community ($p < 0.05$, ANCOVA, Fig. 5). This means that, controlling for network size, the removal of alien plants decreased connectance. Note also from Fig. 5 that only the native network exhibits richness < 34 species, indicating that the persistence of the community members is sensitive to alien removal.

Discussion

The few available studies that evaluated the network consequences of alien species in plant–pollinator webs concluded that invasive species become well integrated into the existing network (Memmott and Waser 2002, Olesen et al. 2002, Morales and Aizen 2002, 2006, Aizen et al. 2008). These studies focused on how the patterns of connections between plants and pollinators differ between native and alien complexes. However, these studies did not evaluate the dynamic implications of the alien species within the network. In this project we assessed how the simulated experimental removal of established alien plants is likely to modify the long-term dynamics of the network, and at the same time we tracked the evolution of network topology behind the projected dynamics.

Our results on long-term network dynamics suggest that alien plants are important for the persistence of the studied pollination network. The removal of alien plants decreased the likelihood of species persistence over a large fraction of the sampled parameter space. Our results corroborate previous work which suggests that alien species, once established, do not form an isolated set of species and interaction, but are intimately integrated into the host network (Memmott and Waser 2002, Olesen et al. 2002, Morales and Aizen 2002, 2006, Aizen et al. 2008). Therefore, their eventual removal from the community could cause profound effects. Furthermore, we found that those effects were more severe than expected from the removal of any other set of plants. Since our methods did not consider idiosyncratic properties of species other than

Table 4. Dynamic processes behind temporal shifts of species' modularity roles (average of 100 realizations ± 95% CI) in the full and native pollination networks with parameter values of k = 0.5 and d = 0.5.

Time	0–100	100–200	200–400	400–800	800–2000
Full network					
Extinctions of peripheral nodes	65.60 ± 2.21	21.02 ± 0.86	13.32 ± 0.72	8.19 ± 0.65	6.14 ± 0.63
Extinctions of hub or connector nodes	0.53 ± 0.15	0.25 ± 0.11	0.24 ± 0.11	0.25 ± 0.10	0.18 ± 0.08
Nodes converting to peripherals	16.90 ± 0.70	8.55 ± 0.72	8.11 ± 0.73	7.01 ± 0.76	6.27 ± 0.72
Nodes converting to hubs or connectors	6.05 ± 0.43	6.98 ± 0.68	5.93 ± 0.69	5.73 ± 0.65	5.53 ± 0.60
Native network					
Extinctions of peripheral nodes	63.49 ± 2.11	22.27 ± 0.99	16.57 ± 1.38	14.64 ± 1.75	16.58 ± 3.13
Extinctions of hub or connector nodes	0.39 ± 0.11	0.55 ± 0.19	1.39 ± 0.52	1.76 ± 0.73	3.63 ± 0.92
Nodes converting to peripherals	11.87 ± 0.45	6.97 ± 0.59	5.81 ± 0.63	4.69 ± 0.77	4.25 ± 0.82
Nodes converting to hubs or connectors	4.89 ± 0.39	5.12 ± 0.50	3.60 ± 0.52	3.47 ± 0.67	3.94 ± 0.76

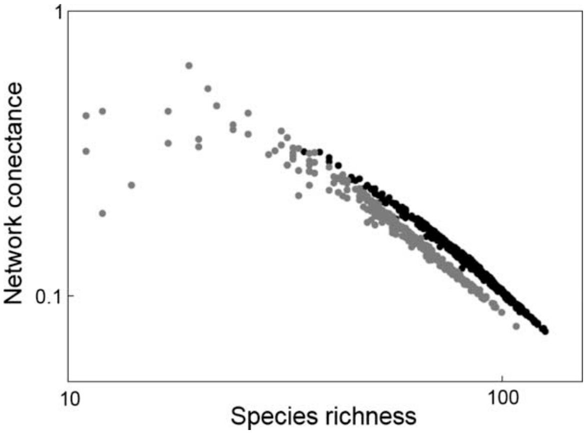

Figure 5. Relationship between network connectance and species richness for the analyzed networks. At each of the times 100, 200, 400, 800 and 2000, one hundred matrices were obtained from both the full and the native network. At time 0 there is a single initial matrix for each of the two networks. Black points represent 501 full networks and gray points represent 501 native networks.

their connectivity, we searched for possible mechanisms behind the projected dynamic, given the influence that alien species exerted on the topology of the observed full network. Although both the full and native networks tended to lose their initial structure over time, the structure of the full network was better preserved than the structure of the native one. Removing the alien plants allowed better understanding of their connectivity properties that might explain their topological role in the network. Their exclusion from the community produced a gap in the central region of the degree distribution of the network. As a consequence, the structure of the native network became more sensitive to extinctions driven by dynamics. Although the initial topology of the native network did not differ from that of the full network, extinctions that took place after the initiation of dynamics resulted in the increasing divergence of the topology of the two networks over time.

Regarding degree distribution, the native network lost its structure more dramatically than the full network, becoming indistinguishable from a random network after a relatively short time. Degree distributions of full, native, and random networks increased in steepness across time, revealing that increasing representation of specialists. This can be explained by the primary extinction of specialists generated by the dynamics (Fortuna and Bascompte 2006), which leads to decreasing connectivity of generalists, and is supported by demographic processes underlying temporal shifts in the distribution of species across the four primary modularity roles. Dynamics promoted the extinction of peripheral nodes, leading to decreased connectivity of the hubs and their shift to peripheral or connector roles. For the overall degree distributions, dynamics mainly resulted in a switch from a truncated power law to a power law degree distribution, with the exception of plants in the full network which conserved the truncated power law distribution. Networks with truncated power law distributions are less fragile to the loss of the most-connected nodes than networks with power law distributions, while both kinds of networks have shown to be robust to random deletion of nodes (Albert et al. 2000, Jordano et al. 2003). Therefore, the pollination network studied may be comparatively more fragile to perturbations affecting the most-connected species if alien plants are removed.

Two results deserve special attention in relation to changes in nestedness over time. First, pollination networks lost their nested structure with time, as a consequence of species extinctions. Second, although both networks were initially strongly nested as compared to corresponding null models, the native network exhibited a lesser degree of nestedness as compared to the full network. This asymmetry could induce slight differences in initial conditions between both networks that could explain the subsequent differences in dynamic outcomes. We also found, in agreement with previous work (Bascompte et al. 2003, Memmott et al. 2004, Fortuna and Bascompte 2006), that both native and full networks exhibited a higher long-term species persistence that a null network lacking nestedness (results not shown). This suggests that the loss of nested structure through time is both a consequence of previous extinctions and a driver of subsequent species loss.

Modularity was also conserved in the full network but not in the native one. A relationship between modularity and species richness could help to explain this trend. Olesen and coworkers (2007) tested modularity in 51 pollination systems and found that networks with more than 150 species were always modular, but networks with less than 50 species did not exhibit significant modularity. Consequently, differences in modularity between the two networks analyzed here could be explained by the higher rate of species extinction – and consequently decreased richness – in the native network. According to Olesen et al. (2007), possible reasons for the lack of modularity in smaller networks are: 1) a lack of module-detecting power of the algorithm at small network sizes, and 2) the increase of connectance in pollination networks with network size decreases, which leads to an increase in the links between generalist species, which may reduce the level of modularity. This reasoning remains valid in our study since we used the same algorithm, and we also verified an inverse relationship between network size and connectance (Fig. 5). On the other hand, disturbances are expected to spread more slowly through a modular structure than through a non-modular one (Olesen et al. 2007). Furthermore, modularity is able to confer stability by dampening deviations from equilibrium in the transients of nonlinear systems (Ruiz-Moreno et al. 2006). Conversely, the network consequences of deleting a species depends on its modularity role, e.g. an extinction of a module hub may cause its module to fragment with minor impact on other modules (Prado and Lewinsohn 2004), whereas the extinction of connector species may cause the entire network to fragment into isolated units, probably with a negligible impact on the internal structure of each module (Olesen et al. 2007). Regarding connectivity roles derived from our modularity analysis, 16% of species in the initial native network were structurally important (i.e. they were assigned to the roles of hubs or connectors), in contrast to 21% in the full network. This difference was approximately conserved with the addition of dynamics. Olesen et al. (2007) found that on average 15% of species were structurally important in mutualistic networks, with their loss potentially leading to extinction cascades. Therefore, the highest proportion of structurally important species in the full pollination network relative to the native network agrees with the observed differences in their persistence.

In the pollination network studied here, alien plants enhanced connectance for all levels of species richness. Dunne et al. (2002) studied the effect of connectance on the robustness of real food networks to the removal of species, and their results suggested that higher connectance confers robustness. This suggests that in our study system, alien plants may increase the robustness of the pollination network by increasing its connectance. Memmott and Waser (2002) explored the contribution of alien plants to the connectance of a well resolved pollination network from the central USA. They found that the connectance of the sub-network of alien plants was lower than the connectance of sub-networks of equal size with only native plants. Nevertheless they did not test the contribution of aliens to the connectance of the whole network. In our study network, the sub-network of alien plants also showed a lower connectance than native networks of equal size, but we showed that the effect of removing the set of alien plants was to increase overall network connectance. However, in contrast to our system, the alien plants studied by Memmott and Waser (2002) were more specialist than their native counterparts. Therefore we hypothesize that the removal of alien plants from such a community would be less deleterious than in the community we studied.

In this research we were not able to fully address the effects of biological invasions on native pollination communities. To investigate this effect properly it is necessary to know the interaction network before the arrival of the invasive species, after their establishment and ideally after the invasive species have been removed experimentally in the field. Our aim in this project was to evaluate how the simulated removal of an established set of alien plants is likely to affect the temporal evolution of a pollination network in terms of changes in topology and the consequences of such removals at the level of species persistence. In this way we approached the question about the likely roles played by the established alien flora through the interplay between structure and dynamics of pollination networks. As in any theoretical study, ours suffers from limitations imposed by implicit and explicit model assumptions. We explored the role of alien plant species by assuming that if these species disappear, the network would not be able to reorganize by creating new interactions or distributing some of the existing ones. The model used here assumes that the mutualistic interactions markedly affect the abundances of species, and does not consider explicit spatial structure or climatic forcing. Therefore our results must be interpreted with caution, considering that the model does not take into account several important components of natural biological complexity. Nevertheless, these limitations also open new avenues for further research, in which our results could be used as a template to be compared with the outcomes of more realistic and sophisticated models. The main message arising from our analyses is that the removal of alien plant species from a community could erode the structure of the pollination network leading to an increase in species extinctions. Therefore, management plans for eradication of alien species should consider investigating the long-term community consequences, with particular attention paid to the complex network structure and dynamics of the community and its constituent native and alien species.

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Appendix 1

Temporal shift of the cumulative degree distribution of plants for a single model realization with parameters d = 0.5 and k = 0.5. Solid circles represent the observed distribution. Dotted, solid, and dashed lines represent fitted power law, truncated power law, and exponential functions respectively. Plants in the full network (A) present an initial degree distribution that was best fitted by the exponential function. From iteration 100, a truncated power law model best fitted the distribution. In the native network (B), degree distribution began as a truncated power law, but from time iteration 400 it changed into a power law.

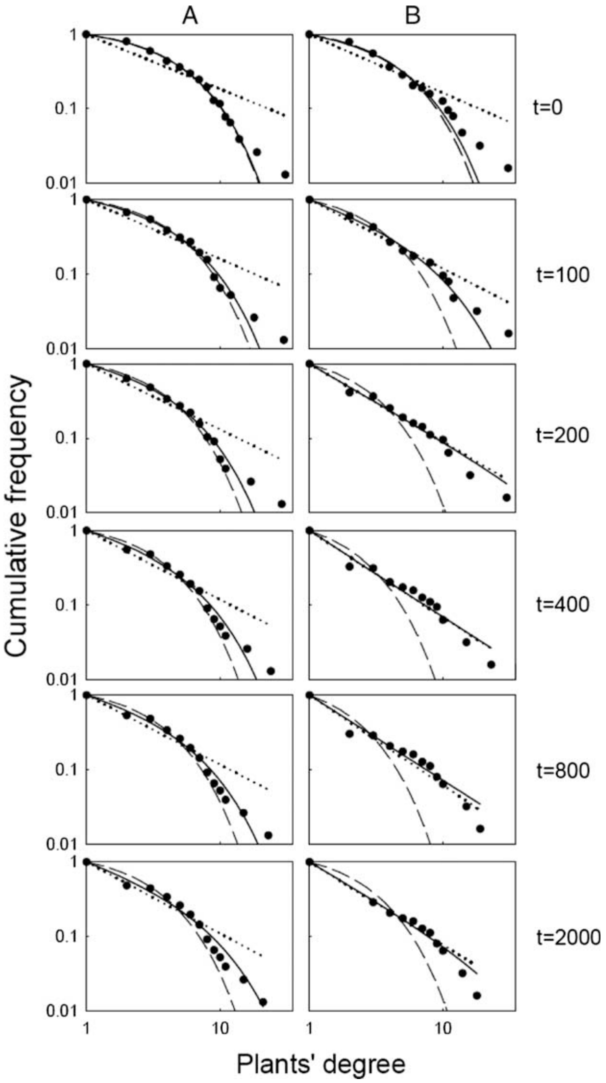

Figure A1.