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Estructura y dinámica de las redes de polinización: el rol de las plantas introducidas.

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A mis padres y hermanas



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Índice de Contenidos

Prefacio	1
Abstract	6
Resumen	7
Introduction	8
Materials and Methods	10
Database and adjacency matrices	10
Network dynamics and persistence	11
Network topology and its evolution	13
Results	16
Network dynamics and persistence	16
Network topology and its evolution	19
Discussion	30
Literature Cited	35
Discusión General	39
Conclusiones Generales	41
Anexo	44

Índice de Tablas

Table 1. Networks' basic information	17
Table 2. Topological features of alien plants	21
Table 3. Description of the modular structures	23
Table 4. Processes behind the evolution of modularity roles	26

Índice de Figuras

Figure 1. An adaptive network	9
Figure 2. Networks' persistence	19
Figure 3. Evolution of networks' persistence	20
Figure 4. Evolution of the nested and modular structures 1	22
Figure 5. Evolution of nested and modular structure 2	23
Figure 6. Evolution of modularity roles	25
Figure 7. Evolution of degree distributions 1	28
Figure 8. Evolution of degree distributions 2	29
Figure 9. Network connectance vs. species richness	30

Prefacio

Por donde miremos, nos encontramos con redes. La Internet, los grupos familiares, las interacciones ecológicas que vemos en nuestros jardines o las conexiones entre neuronas que existen en nuestros cerebros. Todos estos sistemas se pueden distinguir como un conjunto de elementos interactuando, es decir, como nodos interconectados.

Recientemente, digamos la última década, se ha constituido una nueva disciplina que se ha dedicado a estudiar estos sistemas representables como nodos interactuando. Esta nueva disciplina es la Teoría de Redes, la cual busca, describe y analiza las propiedades dinámicas y estructurales comunes a toda red, sea esta teórica o del mundo real. Esta disciplina ha sido principalmente impulsada por físicos, aunque sus aplicaciones las han desarrollado científicos de diversas áreas como la economía, sociología y de la biología. En cuanto a los estudios teóricos en redes, estos se basan en la Teoría matemática de Grafos, cuyos comienzos datan de 1736, cuando un gran matemático llamado Leonard Euler utilizó por primera vez un grafo (objeto matemático

consistente en puntos o nodos conectados por líneas o aristas).

En ecología, la aproximación de redes ha dado un gran impulso al estudio de las comunidades. Esta aproximación permite ir más allá de las interacciones de a pares de especies, debido a que toma el conjunto de especies y sus interacciones como un todo. Así, las preguntas que se pueden responder son a nivel del ensamble comunitario completo. Por ejemplo, qué le ocurre a una red ecológica cuando se extingue una especie, ¿se extinguen las especies con las cuáles ésta interactuaba? O por el contrario ¿estas especies son capaces de interactuar con otras y seguir persistiendo? Otro caso es, qué ocurre cuando una especie nueva se introduce a una comunidad, ¿su introducción modifica el patrón de interacciones de las nativas? ¿Qué tipo de estructura de interacción hace a las redes más permeables a las invasiones biológicas? ¿Qué características permiten a una especie introducida invadir una red? Por otro lado, cómo responden estos sistemas a los cambios ambientales o a las perturbaciones antrópicas, ¿cambia el patrón de interacción? ¿Se extinguen especies? ¿Qué hace a algunas redes más

robustas que otras a las alteraciones ambientales producidas por el Hombre?

El presente trabajo, es un estudio teórico, basado en datos de terreno, específicamente de un ensamble de plantas y sus polinizadores del sector de Lagunillas, ubicado en la comuna El Cajón del Maipo, Región Metropolitana. A partir del registro de presencia o ausencia de visitas de todos los polinizadores a todas las plantas, se definió una red de polinización, en que los nodos fueron las especies y sus conexiones, las interacciones de polinización. De esta red se estudiaron sus propiedades estructurales y también se le acopló un modelo metacomunitario, a fin de estudiar su dinámica. Todo esto con el objetivo último de estudiar la relación entre la estructura y dinámica de una red de polinización, es decir, determinar los efectos que ejerce el patrón de interacción de la red sobre su dinámica y, a su vez, determinar cómo esta estructura cambia dada la dinámica del sistema. Por otro lado, dentro del ensamble, se registraron plantas introducidas, por lo que surgió la pregunta acerca de los posibles efectos que éstas producen sobre la estructura y dinámica de la red de polinización.

Entré a Biología Ambiental con el objetivo de contribuir en las políticas ambientales de nuestro país, muy sensibilizada por la destrucción de los ecosistemas, la extinción masiva de especies y los problemas ambientales que como sociedad estamos viviendo. Pero a poco andar de mi primer año en la Facultad de Ciencias, me di cuenta que quería dedicar mi vida profesional a la investigación. A pesar de este giro, me quedaron las preguntas y objetivos ambientales que entrega mi carrera, con los cuales quiero dirigir mi incipiente quehacer como científico.

Como siempre me preocuparon los problemas de conservación biológica, en primer año me dirigí al laboratorio de Javier Simonetti, a quien insistí, hasta que me aceptó trabajar con él. Igualmente desde mi primer año en la carrera, me apasionaron las matemáticas. Aproveché lo que más pude los cursos matemáticos que existen en la malla de Biología Ambiental, pero también recurrí a profesores del Departamento de Matemáticas de la Facultad de Ciencias, quienes, mediante varios cursos tutoriales, se volvieron mis maestros en esta maravillosa forma de concebir mundos.

A medida que iba aprendiendo de mis maestros en matemáticas y en ecología, quise unir ambas disciplinas, por lo que me acerqué a Rodrigo Ramos. Con él empecé a trabajar en ecuaciones de depredador-presa, pero terminamos trabajando en redes complejas. Es así como nació el trabajo que hoy presento como mi Seminario de Título. Este trabajo reúne todos los aspectos que me motivan seguir en la vida de la investigación, pues se encuentra en la interfase de la ecología, de las matemáticas y las ciencias de la computación, pero enfocándose en un problema ambiental.

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Abstract

In this study, a complex network approach is used to evaluate the influence of alien plants on a real pollination network subjected to habitat loss. More specifically, we focus on how state dynamics affects the topology evolution in terms of degree distribution, modularity, and nested structure of the network, and how topology evolution relates to state dynamics in terms of species persistence. Network topology was evaluated using tools from complex systems theory, and network dynamics was simulated by means of a stochastic metacommunity model. Our results showed that alien plants are important for the persistence of the pollination web and for the maintenance of its structure. Removal of alien plants decreased the likelihood of species persistence, and both the whole and the alien-free network tended to lose their structure along iterations. Nevertheless, the structure of the whole 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; although removal of alien plants mainly affected degree distribution and modularity of the web. Therefore, alien plants affected the evolution of the architecture of the interaction web, which was closely related to the higher species loss found in the alien-free network.

Resumen

En este estudio, se usó la aproximación de red compleja para evaluar la influencia de las plantas introducidas sobre una red de polinización real sujeta a pérdida de hábitat. Más específicamente, nos enfocamos en cómo la dinámica de estado afecta la evolución de la topología en términos de distribución de grado, modularidad y estructura anidada de la red; y cómo la evolución topológica se relaciona, a su vez, con la dinámica de estado en términos de persistencia. La topología de la red fue evaluada usando herramientas provenientes de la Teoría de Sistemas Complejos, mientras que la dinámica de la red fue simulada mediante un modelo metacomunitario estocástico. Nuestros resultados mostraron que las plantas introducidas son importantes para la persistencia de la red de polinización y para la conservación de su estructura. La remoción de las plantas introducidas, disminuyó la probabilidad de persistencia de las especies y tanto la red completa como la red sin las plantas introducidas tendieron a perder su estructura a lo largo de las iteraciones del modelo. No obstante, la estructura de la red completa se conservó más que la estructura de la red sin las plantas introducidas. Los cambios topológicos temporales fueron evidentes en términos de distribución de grado y modularidad de la red. Concluimos que las plantas introducidas afectan la evolución de la arquitectura de interacción de la red en estudio, la cual se relaciona cercanamente a la mayor pérdida de especies encontrada en la red sin las plantas introducidas.

Introduction

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 (Memmot & Waser 2002). Nonetheless, the effects of alien plant invasions on native pollination systems may be competitive, neutral, or facilitative (Bjerknes et al. 2007; Sargent & 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 & Schürkens 2001). However, 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).

During the last years, the study of these anthropogenic impacts on pollination systems has switched from a 'single species' approach, which focus on one or a few plant-animal species interactions, to the 'pollination web' approach, which focus on entire communities (e.g. Memmot and Waser 2002, Olesen 2002, Morales and Aizen 2006, Memmot et al. 2007, Aizen et al. 2008). Here we use the pollination web approach in order to evaluate the influence of alien plants on a real plant-pollinator network.

In a pollination network the abundance of a species, i.e. the dynamic state of a node, depends on the availability of mutualistic partners and the specific pattern of connections between plants and animals. That is, the network state dynamics depends on

its topology. Conversely, the topology evolution of the network is influenced by its state dynamics, since nodes are removed from the network when populations go extinct following severe decreases in their abundances. Therefore, pollination webs can be properly analyzed as adaptive networks, whose topology evolution depends on their node dynamics and vice versa (Fig. 1, modified from Gross and Blasius 2008).

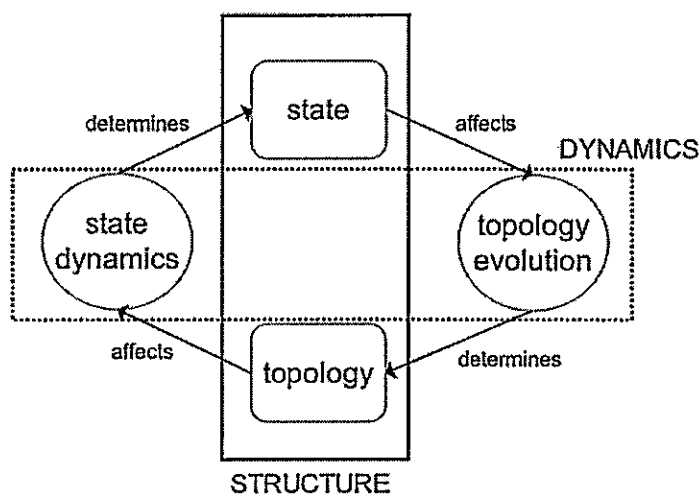


Figure 1. An adaptive network: The evolution of an adaptive network is based on the interdependence of its structure and its dynamics. Modified from Gross and Blasius (2008).

As far as we know, until now pollination web studies have not explicitly adopted the adaptive network approach. Studies of anthropogenic impacts over pollination webs (Memmott & Waser 2002; Morales & Aizen 2002, 2006) and analyses of network robustness to species removal (Memmott et al. 2004) are based on a purely network-topological perspective that ignores state dynamics and disregards topology evolution. On the other hand, Olesen et al. (2008) discern the mechanisms driving the topology structuring through following the daily dynamics of a real pollination web over

successive flowering seasons. These works, therefore, leave open the research avenue on the bidirectional causality between topology and dynamics, and more specifically on how this interplay could be affected by forcing variables such as biological invasions or habitat loss.

A direct theoretical way of incorporating state 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 work we make use of their model, which merges the tradition of dynamical systems with that of complex networks based on graph theory, in order 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 web. Specifically, we focus on how state dynamics affects the topology evolution in terms of degree distribution, modularity and nested structure of the network, and how topology evolution relates to state dynamics in terms of long-term species persistence.

Materials 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. of altitude. 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 take contact with reproductive structures of flowers while cease flying. Two sampling procedures were adopted. The one was recording the number of effective visits per insect species on each of the detected plant species, by means of repeated 15-min observation periods. The second procedure was recording the occurrence of effective visits by each insect species on each plant, through slow walks along many random transects. Plants and insects were identified to species or morphospecies with the help of taxonomists. The pollination network was composed by 77 plant species and 110 insect species with a total of 362 pollination interactions. Among the plant species, 14 were alien plants.

From obtained field information, two different adjacency matrices were constructed corresponding to: i) the complete unmanipulated network, and ii) the observed network without alien plants species and their interactions. 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 topology evolution.

Network dynamics and persistence

In order to project the states of the network through time we used the metacommunity model developed by Fortuna and Bascompte (2006). Their model considers mutualists inhabiting a landscape consisting of a large 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 the animal depending exclusively 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 j th animal).

Following Fortuna and Bascompte (2006), we randomly sampled the value of e/c from a uniform distribution centered in chosen values of $k_p = e_p/c_i$ 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 falls 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 in MATLAB codes. Each adjacency matrix was run for 2000 iterations, 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. In order to evaluate if the differences in persistence between the complete network and the network without the 14 alien plants could be attributed to the removal of the alien species and not to the reduction in matrix size, a third matrix from which 14 randomly chosen species were removed was also run with 1000 realizations.

Network topology and its evolution

Throughout the sequence of network states resulting from the runs of the dynamic model, three main topological properties were monitored: nestedness, modularity, and degree distribution.

Nestedness was measured through the matrix temperature T , with values ranging from 0 for perfectly nested networks to 100 for completely non-nested networks (Atmar & Patterson 1993). A perfectly nested network implies that the more specialist species interact with species that are proper subsets of those species interacting with the more generalist ones (Bascompte et al. 2003). In order to evaluate statistical significance of observed nestedness, we compared the value T of each adjacency matrix against the distribution of T obtained from 1000 matrices generated from a null model which 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 et al. 2006). This null model lacks nestedness but preserves the heterogeneity of the adjacency matrix. These calculations were performed with the software ANINHADO (Guimarães & Guimarães 2006). Finally, we standardized the nestedness index T by means of standard normal deviates (z-scores) in order to compare the degree of nested structure among the studied networks.

The degree of organization of the plant-animal interactions into interconnected modules was measured through the modularity index M of Guimerà & Amaral (2005a,b).

The simulated annealing algorithm (Guimerà and Amaral 2005a,b) was used to find the network partition that maximizes M , i.e. this algorithm identify the modular structure that lead to many within-module links and as few as possible between-module links. From that partition, we obtained the number and size of modules, as well as the fraction of network interactions that occurred both within-modules and among-modules. Statistical significance of modularity was assessed through estimating M on 100 random networks with the same degree distribution than the real network (Guimerà et al. 2004). Two additional indices were used in the modularity analysis, which permit associating a role to each of the interacting species (Guimerà & Amaral 2005a,b). Within-module standardized connectivity of species i , z_i , is given by $z_i = \frac{k_{is} - \bar{k}_s}{\sigma_{ks}}$ where k_{is} is number of interactions of i with other species in its own module s . Parameters \bar{k}_s and σ_{ks} are average and standard deviation of within-module k of all species in s . Among-module

connectivity of species i , c_i , is given by $c_i = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i} \right)^2$ 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): (i) network hubs, $z > 2.5$ and $c > 0.62$; (ii) module hubs, $z > 2.5$ and $c \leq 0.62$; (iii) peripherals, $z \leq 2.5$ and $c \leq 0.62$; and (iv) connectors, $z \leq 2.5$ and $c > 0.62$.

The degree of a species consists of the number of its interacting species. Here 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 interacts 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 ($P(k) \sim k^{-\gamma}$) 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. 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 & 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 $\Delta i = \text{AICc}_i - \text{AICc}_{\min}$, where AICc_{\min} is the minimum among the AICc_i values calculated for the different models. This transformation forces the best model to have $\Delta i = 0$, and the rest having positive values.

Models with $\Delta i \leq 2$ are considered to have substantial support (Burnham & 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.

To evaluate the topology evolution of both the unmanipulated network and the network without alien plants, from each of 100 realizations of the stochastic metacommunity model we captured the evolving adjacency matrices at iterations 100, 200, 400, 800 and 2000. For the 1002 matrices so obtained, we analyzed the three topological properties described above. The 100 realizations allowed us to construct 95% confidence intervals and test for differences in the metrics between networks and among iterations.

Results

Network dynamics and species persistence

The original, unmanipulated network that includes alien plants (our control) was more robust to habitat loss and density-independent extinction/colonization ratio k , as compared to the network where the alien plants were removed (Table 1; Fig. 2). The number of collapsed networks (i.e. networks in which species extinction surpassed 90% of the initial species) was notably higher for simulations where alien plants were removed (Table 1). It can be seen from Table 1 that the fraction of alien species and alien links increased through the model iterations, revealing that the persistence of alien

plants was higher than the persistence of the other species, and that their importance for network connectivity increased with community relaxation.

Time iteration	0	100	200	400	800	2000
With alien plants						
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
Collapsed networks		0	0	0	0	2
Without alien plants						
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
Collapsed networks		0	0	8	23	52

Table 1. Networks' basic information: Basic information (average of 100 realizations ± 95% confidence intervals) of both the unmanipulated network and the network without alien plants along time iterations. Parameters values were $k=0.5$ and $d=0.5$. Collapsed networks refer to number of networks out of 100 realizations with species persistence below 10% of the initial richness.

The long-term dynamic responses of the networks, using model simulations were evaluated at a time horizon of 2000 iterations. Overall, the fraction of extinct species in the control network was significantly lower than in the network with the 14 alien plants

removed, and it was also lower than extinctions in the null matrices where 14 species were deleted at random in each realization (Fig. 2). 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 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 $d=0.5$, 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 control and the alien-free network were found at $d=0.5$ and $k=0.5$. The evolution of the fraction of species extinctions with these parameter values is shown in Fig. 3, for the 2000 model iterations of the control and alien-free networks. The fraction of extinct species in the control network was significantly lower as compared to the alien-free network after ≈ 120 model iterations for plants and after ≈ 300 model iterations for animals.

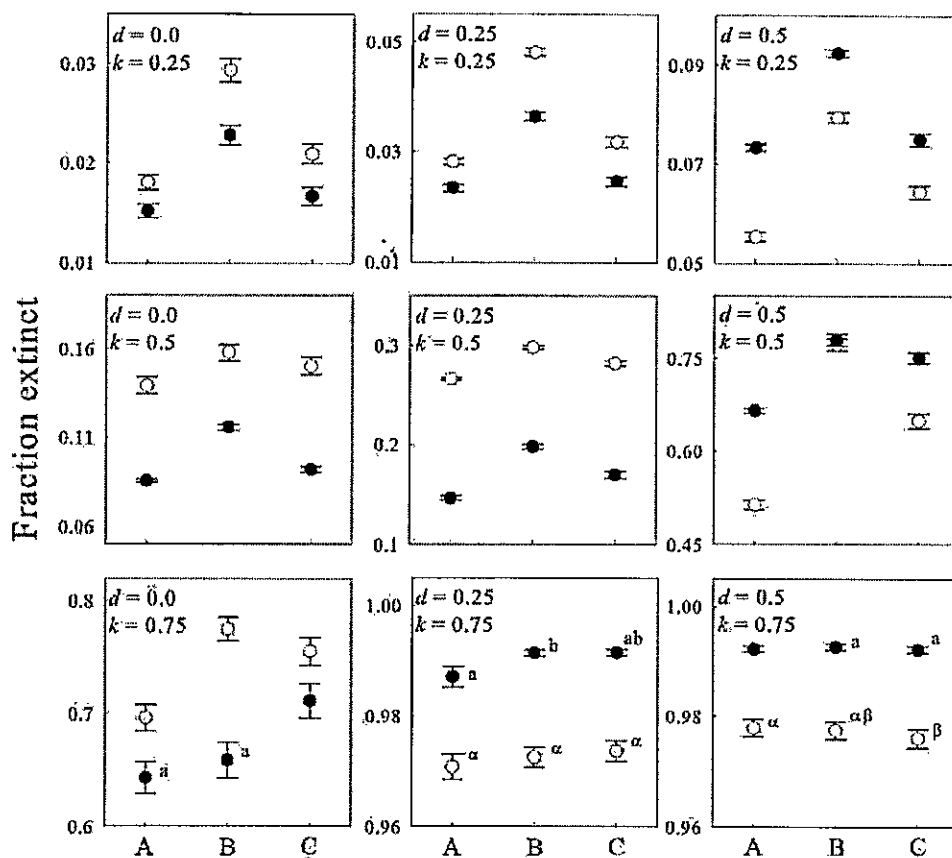


Figure 2. Networks' persistence: Fraction of extinct species averaged over 1000 model realizations for the unmanipulated network (A), the network without alien plants (B), and networks without randomly selected sets of 14 species (C). There were used different parameter values representing habitat loss (d) and extinction/colonization ratio (k). Open and closed circles represent plants and animals respectively. Error bars are 95% confidence intervals. Equal letters indicate non-significant differences ($P > 0.05$).

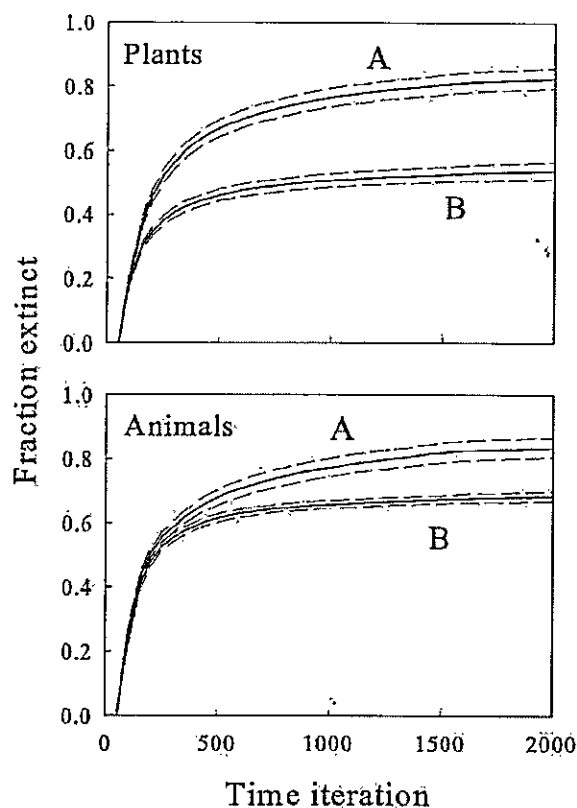


Figure 3. Evolution of networks' persistence: Fraction of extinct species through 2000 model iterations for the unmanipulated network (A), and the network without alien plants (B). Solid lines indicate the average of 1000 realizations, and dashed lines are 95% confidence intervals. Parameter values were $d=0.5$ and $k=0.5$.

Network topology and its evolution

What characterizes alien plants in this network? First, their degree is less heterogeneous as compared to native flora (mean, median, and range of degree are respectively 5.97, 6.5, 1-10 for aliens; and 5.67, 3.0, 1-31 for native plants). Degree of generalism of alien plants can be considered to fall midway within the entire range exhibited by the network, although Mann-Whitney test indicated that aliens have a higher degree than their native counterparts ($P<0.05$). Next, we tested how the removal of alien plants compares to the

random removal of plants in equal numbers. Table 2 shows that the effects of the experimental removal of aliens did not differ from those of random removal of 14 plant species, in terms of secondary extinctions, number of interactions, and connectance. This suggests that differences in dynamic outcomes between the tested networks rest on more complex topological properties associated to alien species. Therefore, we examined nestedness, modularity, and degree distribution of the webs.

Table 2. Topological features of alien plants: Comparison between basic topological features of the network after removing of alien plants versus removing 14 randomly chosen plants. For null networks, mean of 1000 runs and 95% confidence intervals are given.

	Alien-free network	Null 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

Both the control network and the network without alien plants showed to be significantly nested and modular before running the dynamic model (Fig. 4). They had the same number of modules but different module sizes (Table 3). In the course of the model simulations both networks lost their nested structure, specifically between iterations 100-200 for the control network and 0-100 for the network with alien plants removed (Fig. 4). On the other hand, although the modularity of both networks decayed through the iterations, the network with alien plants retained its modular structure over

all iterations. Conversely, the network without alien plants lost its modular structure at the time iteration interval 100-200 (Fig. 4). The evolution of the nested and modular structures of both networks can be graphically seen for one model run in Fig. 5.

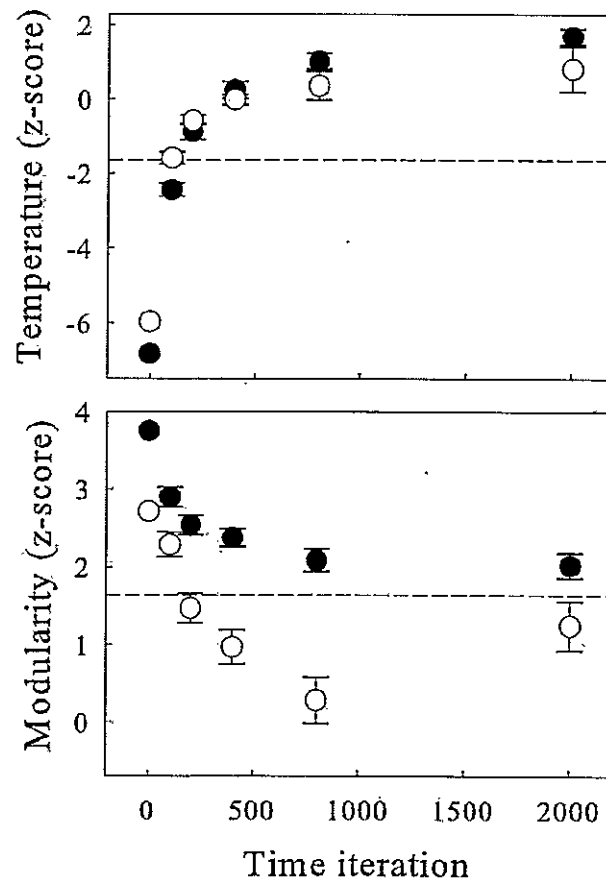


Figure 4. Evolution of the nested and modular structures 1: Standard normal deviates of temperature (upper plot) and modularity (lower plot) indices through 2000 model iterations with $d=0.5$ and $k=0.5$. Average of 100 model realizations and 95% confidence intervals are shown for the unmanipulated network (closed circles) and the network without alien plants (open circles). Below (for temperature) and above (for modularity) the horizontal reference line the indices are significantly different ($P<0.05$) from a null model.

Table 3. Description of the modular structures: Basic description (average of 100 realizations \pm 95% confidence intervals) of the modular structure of the networks at different model iterations.

Time iteration	0	100	200	400	800	2000
With alien plants						
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
Without alien plants						
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

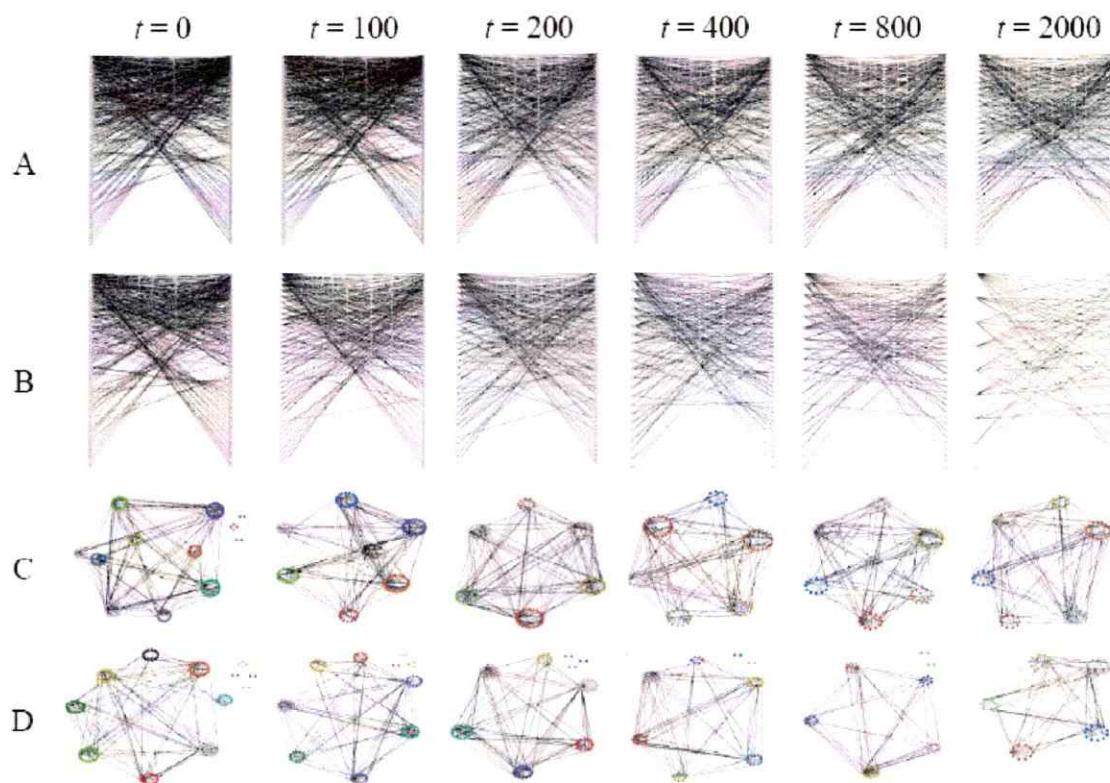


Figure 5. Evolution of nested and modular structure 2: Graph representation of the topological evolution of the unmanipulated network (A, C) and for the network without alien

plants (B, D), for a single model realization with parameters $d=0.5$ and $k=0.5$. Nested structure is more easily captured as bipartite graphs packed for minimal temperature (A, B), where plants are represented by nodes at the left and insect species at the right column of the graph. Modularity is shown in C and D, where each module is composed by plants and animals densely linked within that module and weakly linked to species in other modules. Note that each set of graphs represent an instant of a continuously changing topology along 2000 time iterations.

When dynamics is incorporated through the model simulations, the number of modules remained homogeneous between the two networks until iteration 200 (Table 3). After that point, the alien-free network had significantly fewer modules than the control network. This divergence in number of modules occurs simultaneously with the lost of modularity of the alien-free network. Regarding the distribution of nodes among the four predefined connectivity roles, Fig. 6 shows that network hubs together with module hubs constituted a minor fraction of the nodes of both networks, as compared to peripherals and connectors. 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 relative abundance of peripheral nodes is driven by their extinctions, while hub species decreased because their role changed toward peripherals or connectors. On the other hand, connectors increased their representation in the networks due to their low extinction number along realizations together with the conversion of some hubs into connectors. Considering the entire time interval used in the simulations, the network in which alien plants were removed presented more extinction in all roles as compared to the control network; and the

control network presented more role shifts than the alien-free network. Only the relative number of module hubs remained similar between the two networks over the time iterations.

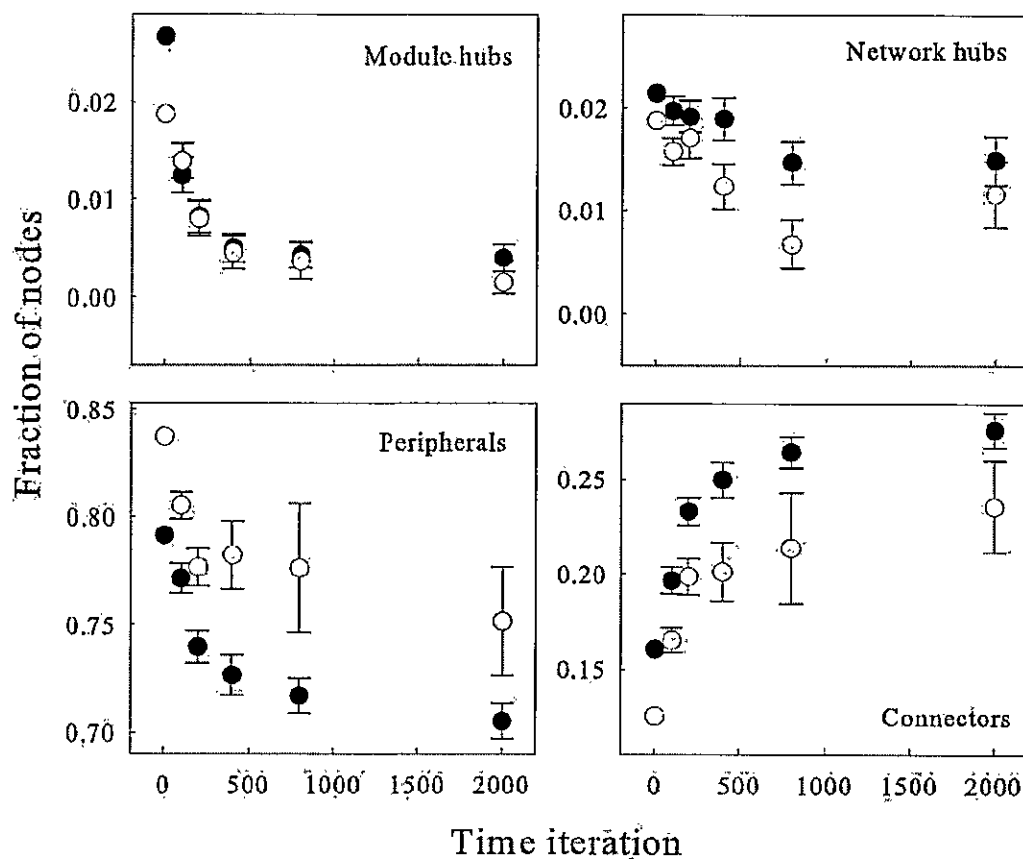


Figure 6. Evolution of modularity roles: Temporal shifts of the fraction of nodes belonging to the classes of network hubs, module hubs, peripherals, and connectors. Average of 100 model realizations and 95% confidence intervals are shown for the unmanipulated network (closed circles) and the observed network without alien plants (open circles). Parameter values were $d=0.5$ and $k=0.5$.

Table 4. Processes behind the evolution of modularity roles: Dynamic processes behind temporal shifts of species' modularity roles (average of 100 realizations \pm 95% confidence intervals) with parameter values of $k=0.5$ and $d=0.5$.

Time iteration interval	0-100	100-200	200-400	400-800	800-2000
With alien plants					
Extinctions of peripheral nodes	65.60 \pm 2.21	21.02 \pm 0.86	13.32 \pm 0.72	8.19 \pm 0.65	6.14 \pm 0.63
Extinctions of hub or connector nodes	0.53 \pm 0.15	0.25 \pm 0.11	0.24 \pm 0.11	0.25 \pm 0.10	0.18 \pm 0.08
Nodes converting to peripherals	16.90 \pm 0.70	8.55 \pm 0.72	8.11 \pm 0.73	7.01 \pm 0.76	6.27 \pm 0.72
Nodes converting to hubs or connectors	6.05 \pm 0.43	6.98 \pm 0.68	5.93 \pm 0.69	5.73 \pm 0.65	5.53 \pm 0.60
Without alien plants					
Extinctions of peripheral nodes	63.49 \pm 2.11	22.27 \pm 0.99	16.57 \pm 1.38	14.64 \pm 1.75	16.58 \pm 3.13
Extinctions of hub or connector nodes	0.39 \pm 0.11	0.55 \pm 0.19	1.39 \pm 0.52	1.76 \pm 0.73	3.63 \pm 0.92
Nodes converting to peripherals	11.87 \pm 0.45	6.97 \pm 0.59	5.81 \pm 0.63	4.69 \pm 0.77	4.25 \pm 0.82
Nodes converting to hubs or connectors	4.89 \pm 0.39	5.12 \pm 0.50	3.60 \pm 0.52	3.47 \pm 0.67	3.94 \pm 0.76

The exponential model best described the plants' degree distributions for both networks before running the dynamic model. Initial conditions of animals' degree distributions for both networks were best described by a truncated power law. The evolution of animals' degree distributions in networks was similar: they changed from a truncated power law to a power law distribution at the time iteration interval 0-100. However, both networks differed in the evolution of plants' degree distribution. For both networks, degree distribution of plants changed from being exponential towards truncated power law at the time iteration interval 0-100. Afterwards, the control network kept a truncated power law distribution until the end of simulations, while plants in the alien-free network shifted to a power law distribution at time iteration interval 100-200.

The evolution of the degree distribution for plants in both networks is graphically shown in Fig. 7. The value of the degree distribution exponent of the corresponding model (either truncated or power law) increased asymptotically with time (Fig. 8), which means that the degree distributions became steeper as the network lost nodes. The connectance of both networks increased as they disintegrate through time (Table 1). Along the iterations, species richness decreased while connectance increased. The negative relationship between species richness and connectance presented similar slopes in both networks ($P=0.107$, GLM test for homogeneity of slopes) but a lower elevation for the alien-free community ($P<0.05$, ANCOVA, see Fig. 9). This means that, controlling network size, the removal of alien plants decreased connectance. Note also from Fig. 9 that only the alien-free network exhibits richness < 34 species, indicating that the persistence of the community members is sensitive to alien removal.

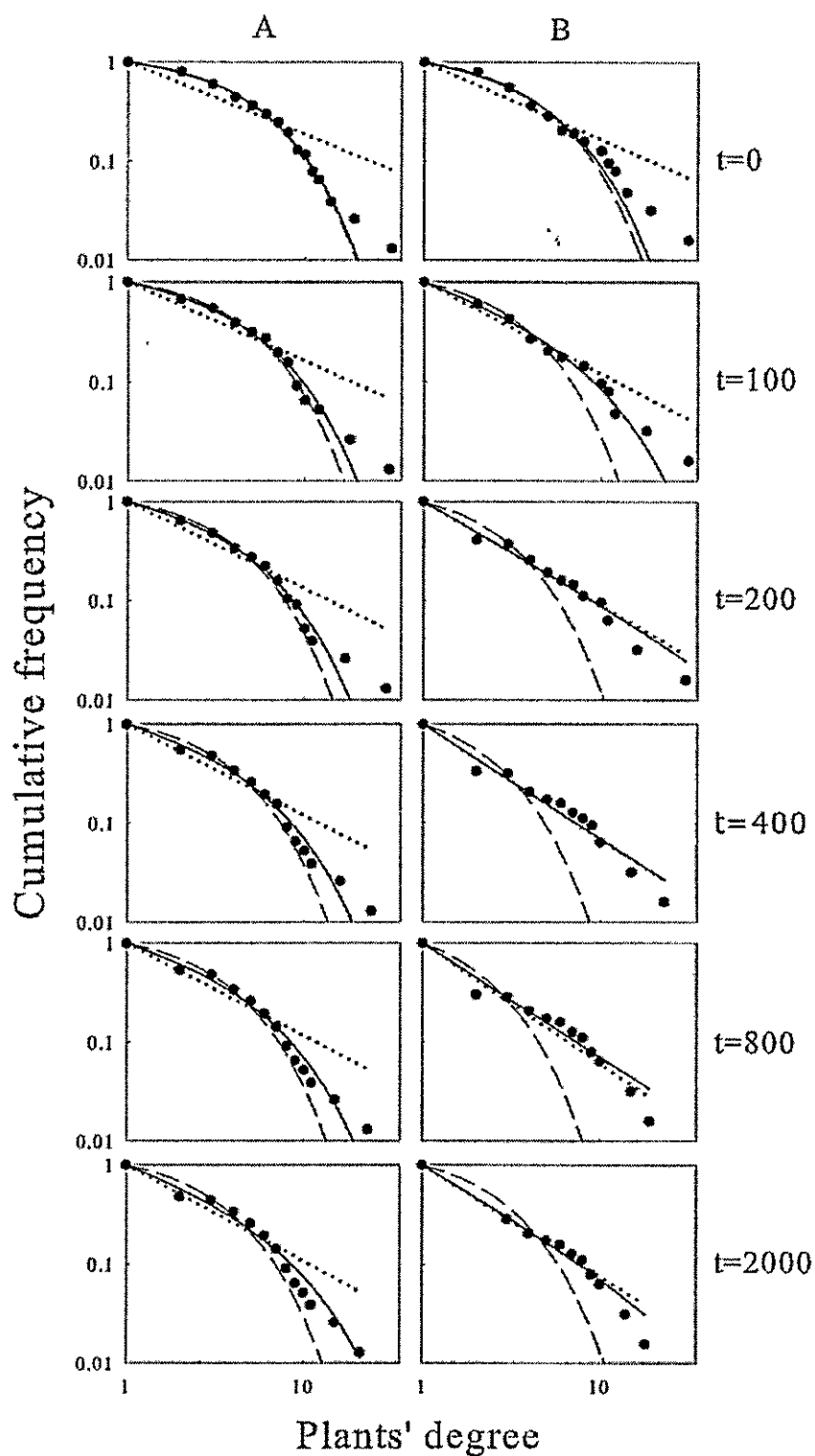


Figure 7. Evolution of the degree distributions 1: Temporal shift of the cumulative degree distribution of plants for a single model realization with parameters $d=0.5$ and $k=0.5$. Solid

circles represent the observed distribution. Dotted, solid, and dashed lines represent fitted power law, truncated power law, and exponential functions respectively. Plants in the unmanipulated network (A) present an initial degree distribution that was best fitted by the exponential function. From iteration 100, the truncated power law model best fitted the distribution. In the alien-free network (B), degree distribution began as truncated power law, but from time iteration 400 it changed into power law.

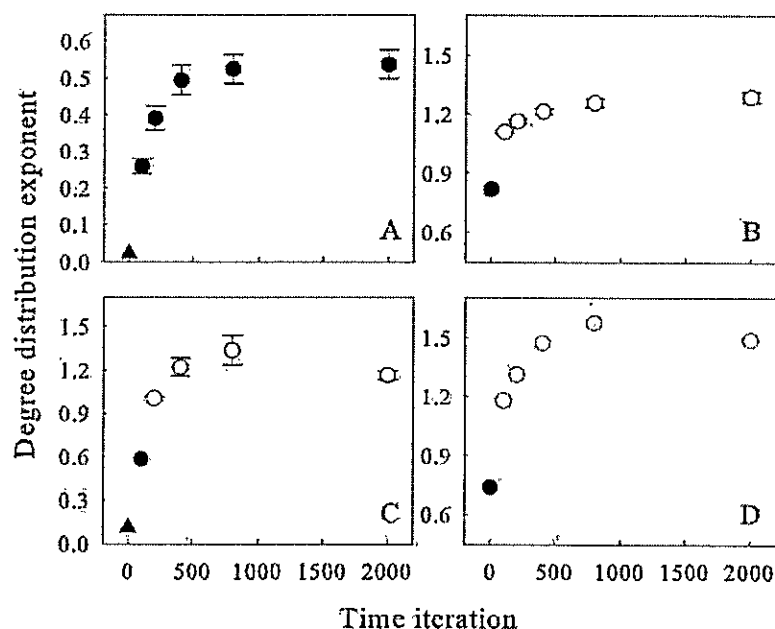


Figure 8. Evolution of degree distributions 2: Temporal shifts of cumulative degree distributions for plants (A, C) and animals (B, D) in the unmanipulated network (A, B) and the network without alien plants (C, D). The values on the ordinate are the exponents of the fitted truncated power law model. Average of 100 model realizations and 95% confidence intervals are shown, with parameters $d=0.5$ and $k=0.5$. Triangles, closed circles, and open circles indicates that $>50\%$ of the realizations resulted in best fit of exponential, truncated power law, and power law models respectively. Note that both exponential and power law functions are nested into the truncated power law. Therefore, the values of the exponents of the truncated power law and the power law models are very close when the latter best describe the data. Exponential distributions were only observed as initial conditions of plants.

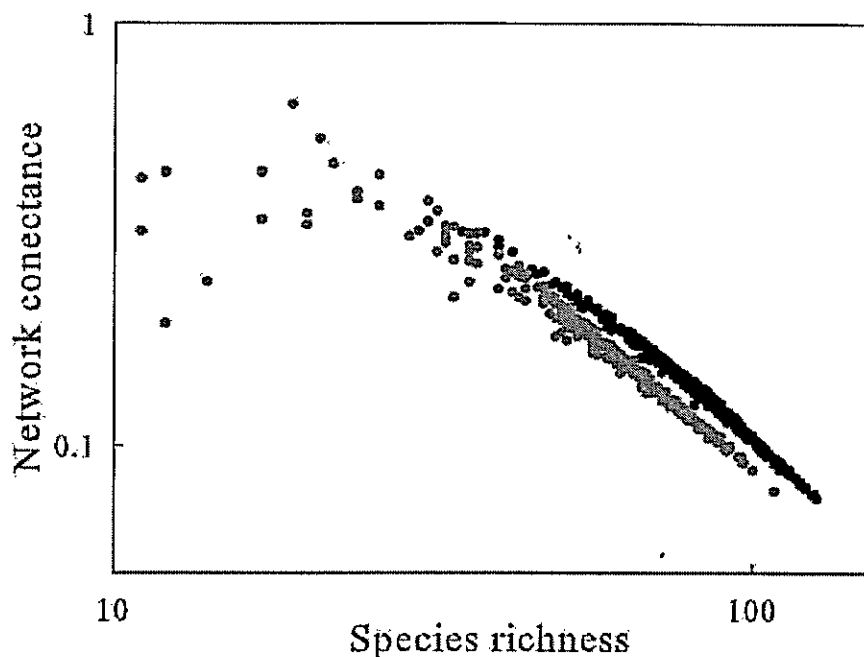


Figure 9. Network connectance vs. species richness: Network connectance versus species richness of the 1002 networks analyzed in this study. Black points represent networks with alien plants included and gray points represent networks without alien plants.

Discussion

The few available studies aimed to evaluate the network consequences of alien species in plant-pollinator webs concluded that invasive species become well integrated into the existing network (Memmott & Waser 2002, Olesen et al. 2002, Morales & Aizen 2002, 2006, Aizen et al. 2008). These studies focused on how the pattern of connections between plants and pollinators differs between native and alien complexes. Nevertheless, they did not test the dynamic disruption that alien species introduce into the web. In this work we assess, by means of a dynamic model that preserves the observed pattern of interactions, how the experimental removal of alien plants modifies

the long term dynamics of the network, and at the same time we track the topological evolution of the web behind the projected dynamics.

Alien plants turned out to be important for the persistence of the studied pollination network as much as for the preservation of its structure. Our results indicated that removing alien plants decrease the likelihood of species persistence over a large fraction of the sampled parameter space. Indeed, removing the complex of alien plants exerted a more deleterious effect on the network than did the random removal of the same number of plant species. More than paradoxical, our results confirm the previous suggestions that alien species become well integrated within the interaction network. Since our methods did not consider idiosyncratic properties of species apart from their connectivity, we searched for possible mechanisms behind the projected dynamics in the bounds of the influence that alien species exert on the topology of the observed network.

In general terms, both the whole and the alien-free network tended to loss their structure along time. Nevertheless the structure of the unmanipulated network was better preserved than the structure of the network without alien plants. The connectivity features of alien plants that might explain their topological role in the network are revealed when those species are removed. Their exclusion from the community produced a gap in the central region of the degree distributions of both plants and the whole network. As a consequence of this gap, the structure of the network without alien plants became more sensitive to extinctions driven by the state dynamics.

Both networks had similar initial topologies. When state dynamics was incorporated through the model simulations, extinctions took place and the topology of both networks diverged with time. Although both webs lost their nestedness, only the

control conserved its modular structure throughout the time iterations. A relationship between modularity and species richness could explain this trend. Olesen and coworkers (2007) tested for modularity in 51 pollination webs and found that networks with more than 150 species were always modular, but all 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 highest rate of species extinction -and consequently decreased richness- in the alien-free network. According to Olesen et al. (2007), possible reasons for the lack of modularity in smaller networks are: i) a lack of module-detecting power of the algorithm at small network sizes, and ii) the increment of connectance in pollination networks when the network size decreases, which leads to an increment of 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. 7).

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 through dampening deviations from equilibrium in the transients of nonlinear systems (Ruiz-Moreno et al. 2006). On the other hand, the network consequences of deleting a species depend 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 & Lewinsohn 2004), whereas the extinction of connectors 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 initial species in the alien-free network were structurally important (i.e. they were assigned to the roles of hubs or connectors), in contrast to 21% in the control network. This difference in the proportion of structurally important species was roughly conserved through the temporal state dynamics. Olesen et al. (2007) found that in average only 15% of species were structurally important in mutualistic networks, underlining that their deletion could lead to extinction cascades. Therefore, the highest proportion of structurally important species in the control network relative to the alien-free web agrees with the observed differences in their persistence.

Degree distributions of plants and animals of both alien-free and control networks increased in steepness along model iterations. That is, specialists increased their representation in both webs. This can be explained by the extinction of specialists generated by the model (Fortuna & Bascompte 2006), which leads to decreasing the connectivity of generalists. We support the above explanation on the base of the demographic processes behind the temporal shifts of the modularity roles. The state dynamics promoted the extinction of peripheral nodes, leading to a decreased connectivity of the hubs and the shift of their roles to peripherals or connectors.

Except for plants in the control web, the state dynamics resulted in a switching from a truncated power law degree distribution into a power law one. Networks with truncated power law distributions are less heterogeneous than power law networks (Bascompte & Jordano 2007). Therefore, 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). On the other hand, plants in the unmanipulated web conserved their truncated power law degree distribution. Therefore, the alien-free network may be comparatively more fragile to perturbations affecting the most-connected species.

Alien plants also enhanced network connectivity for any level of species richness. Dunne et al. (2002) studied the effect of connectance on the robustness of real food webs to the removal of species, and found that higher connectance confer robustness. This supports the fact that, in our study system, alien plants could increase robustness of the pollination network by increasing its connectance.

Two issues related to the evolution of nestedness deserve special attention. First, pollination webs lost their nested structure with time, associated to species losses. Second, although both networks are initially strongly nested, the alien-free network exhibits a higher temperature as compared to the control web. This asymmetry could induce slight differences in initial conditions between both networks that could explain the subsequent differences in dynamic outcome. We also found, in agreement with previous works (Bascompte et al. 2003; Memmott et al. 2004; Fortuna & Bascompte 2006), that both alien-free and control webs exhibited a higher long-term species persistence than a null network lacking nestedness (results not shown).

The aim of this work was twofold. First, to reveal the temporal evolution of a pollination network in terms of changes in topology and its consequences at the level of species persistence. Second, to evaluate the role of alien plants in the interplay between network topology and state dynamics. This was done by means of deconstructing the plant assemblage into its native set, and comparing the outcomes with those obtained for

the whole network. We observed that differences in topological evolution between the pollination systems with and without the alien plants rested mainly on degree distribution and modularity. Therefore, the effect of alien removal was apparent at a level of the evolution of the architecture of the interaction web, which was closely related to the higher species loss found in the alien-free network.

Our understanding of the interplay between structure and dynamics of ecological networks is still very limited. More high-quality data on temporal dynamics (Olesen et al. 2008) together with further advances in coevolutionary network modeling will certainly improve our ability to explain complex ecosystem interactions in nature.

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Discusión general

El resultado más importante del presente trabajo es que la remoción de las plantas introducidas de una red polinización disminuye su persistencia de especies, siendo su retiro más dañino para la red que el retiro de cualquier otro conjunto de igual número de especies. Para la obtención de este resultado se construyeron 1000 redes nulas retirando para cada una 14 especies de plantas al azar (Figura 2). Así se pudo contrastar la persistencia promedio de 1000 realizaciones del modelo para la red sin introducidas con el promedio de las persistencias de las 1000 redes nulas. El objetivo de utilizar estas redes nulas fue descartar la posibilidad de que la menor persistencia de la red sin plantas introducidas se debiera sólo a una disminución en número de especies. Otra posibilidad habría sido construir redes nulas retirando 14 especies de plantas nativas al azar, con lo que se acotaría la pregunta a una comparación entre nativas e introducidas. Sin embargo, dado que son más las plantas nativas que las introducidas (63 y 14, respectivamente) es más probable que se escojan al azar plantas nativas. Por lo tanto, debiéramos tener el mismo resultado de mayor daño al retirar las plantas introducidas que 14 plantas nativas al azar.

Los alcances y limitaciones de este estudio tienen que ver con los supuestos del modelo utilizado. Este modelo describe la dinámica de interacciones mutualistas dentro de una localidad, manteniendo el patrón de

interacción observado. Se asume que los polinizadores no pueden vivir sin sus plantas interactuantes, mientras que las plantas pueden vivir sin sus polinizadores, pero no reproducirse. La colonización de parches vacíos por plantas y la colonización de nuevos parches de plantas por polinizadores, son denso-dependientes, es decir, disminuyen en velocidad con el aumento de parches ocupados, respectivamente. Además, la red no es capaz de reorganizarse creando nuevas interacciones o re-distribuyendo las existentes. Los resultados presentados debieran ser robustos a cualquier cambio en el sistema de ecuaciones que conserve su estructura denso-dependiente en cuanto a ocupación de nuevos parches y manteniendo el supuesto de no reorganización de la red tras pérdida de especies. Queda abierta la pregunta de lo que ocurriría si se permite que nuevas interacciones se establezcan tras la extinción de ciertas especies.

El mensaje que entrega este estudio a la Biología de la Conservación es de considerar la estructura de la comunidad antes de llevar a cabo un plan de erradicación de las especies introducidas. Específicamente, llama a evaluar los potenciales efectos de eliminar las especies introducidas de un ensamble planta-polinizador, antes de considerar erradicarlas. Los resultados de este trabajo pueden ayudar a orientar investigaciones de campo que tengan como objetivo evaluar los impactos de erradicar las especies de plantas introducidas de una comunidad. Por ejemplo, se puede diseñar un estudio que consista en estudiar por largo tiempo distintas áreas

de similares características en que a algunas se le extraigan todas las plantas introducidas. Además, en ambos tipos de área se debieran retirar aleatoriamente plantas, simulando pérdida de hábitat. De cada sitio se debieran construir matrices de incidencia (ver sección métodos de este trabajo) a distintos tiempos como también la abundancia de las plantas nativas. La hipótesis puesta a prueba sería que las redes de polinización provenientes de las áreas sin plantas introducidas, sujetas a pérdida de hábitat, irían perdiendo su estructura de manera más pronunciada que las redes provenientes de áreas en que estas especies estén presentes, afectando la abundancia de las especies de plantas nativas.

Conclusiones generales

1. La aproximación de redes permitió estudiar el ensamble de plantas y sus polinizadores, como un todo integrado. Tanto las propiedades topológicas analizadas, como la persistencia de las especies, son variables respuesta que refieren al ensamble completo y no pueden extraerse de la suma de interacciones entre pares de especies.
2. Se encontró un efecto directo de la dinámica de estado (cambio en abundancia de las especies) sobre la topología de la red de polinización. La dinámica de estado, definida por el modelo

metacomunitario, determinó la evolución topológica mediante bajas en abundancia de ciertas especies que derivaron en extinciones. Junto con estas extinciones, también se perdieron las conexiones de las especies extintas, lo cual modificó el patrón de interacción de la red completa.

3. Se encontró evidencia del efecto que la evolución topológica tendría sobre la dinámica de estado. Se obtuvo que la red que conservó más su estructura inicial fue la de mayor persistencia de especies en el tiempo.

4. Las plantas introducidas presentes en la red de polinización, cumplen un rol en la evolución topológica de ésta, lo que afecta directamente en la persistencia de las especies que la conforman. Este resultado es consistente con lo que otros autores han señalado, las plantas introducidas se encuentran muy bien integradas a la red de especies nativas. Como corolario de esta conclusión surge la indicación de no eliminar las especies introducidas de los sistemas naturales en los que ya están integradas. Sin embargo queda abierta la pregunta de cuáles fueron sus efectos sobre la red de polinización nativa al momento de producirse su llegada.

5. Como proyecciones futuras se encuentra la incorporación de supuestos más realistas al modelo. Por ejemplo, puede que los resultados aquí obtenidos cambien si se incorpora plasticidad de interacción, es decir, que las especies cuyas interactuantes se extingan sean capaces de interactuar con otras de las que antes no lo hacían. Incorporando plasticidad de interacción, las conexiones que antes se perdían por extinción de especies, se reasignarían a las especies remanentes. También queda abierta la pregunta acerca de la evolución de la red desde el momento en que son reclutadas las plantas introducidas.

Anexo

Definiciones básicas en teoría de redes complejas

Concepto	Definición
Red (<i>network</i>)	descripción informal de un conjunto de elementos con conexiones (o interacciones) entre ellos
Grafo (<i>graph</i>)	objeto matemático compuesto por vértices (nodos) y aristas, que representan respectivamente elementos y conexiones de una red
Grafo bipartita (<i>bipartite graph</i>)	representación matemática de una red consistente de dos conjuntos de nodos con interacciones entre (pero no dentro) cada conjunto
Grado (<i>degree</i>)	número de conexiones por nodo
Topología de una red (<i>network topology</i>)	patrón de conexiones (interacciones) específico entre los nodos de una red
Distribución de grado (<i>degree distribution</i>)	distribución de frecuencias del número de conexiones por nodo
Anidamiento (<i>nestedness</i>)	patrón de conexión en que las conexiones de los nodos de menor grado son subconjuntos de las conexiones de los nodos de mayor grado