PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

A network analysis of plant–pollinator interactions in temperate rain forests of Chiloé Island, Chile

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Abstract This study characterizes the structure of a plant–pollinator network in a temperate rain forest of Chiloé Island, southern Chile, where woody species are strongly dependent on biotic pollinators, and analyzes its robustness to the loss of participating species. Degree distribution, nestedness, and expected species persistence were evaluated. In addition, we assessed the roles of predefined subsets of plants (classified by life forms) and pollinators (grouped by taxonomic orders) in the network's structure and dynamics. For this, we simulated the complete removal of each plant and pollinator subset and analyzed the resultant connectivity patterns, as well as the expected long-term species losses by running a stochastic model. Finally, we evaluated the sensitivity of the network structure to the loss of single species in order to identify potential targets for conservation. Our results show that the plant–pollinator network of this Chilean temperate rain forest exhibits a nested structure of interactions, with a degree distribution best described by a power law model. Model simulations revealed the importance of trees and hymenopterans as pivotal groups that maintain the core structure of the pollination network and guarantee overall species persistence. The hymenopterans *Bombus dahlbomii* and *Diphaglossa gayi*, the shrubs *Tepualia stipularis* and *Ugni molinae*, the vines *Mitraria coccinea* and *Asteranthera ovata*, and the entire set of tree species exerted a disproportionately large influence on the preservation of network structure and should be considered as focal species for conservation programs given current threats from selective logging and habitat loss.

Keywords Mutualistic networks · Pollination web · Degree distribution · Nestedness · Network dynamics

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Introduction

Underlying the functioning of biological systems is a complex network of interactions and exchange of energy, materials and information. Thus, analysis of the network structure of ecological systems has emerged as a fundamental approach to gain better insights into community

function, and as a simple way of dealing with complex, many-species systems (see Pascual and Dunne 2006). Recently, network theory has been applied to the analysis of complex ecological interaction networks, both as a testing ground for topological relationships found in other complex networks and as a tool to gain understanding on their structure and functioning. These applications have dealt primarily with the analysis of food webs (Martinez 1992; Williams and Martinez 2000; Montoya and Solé 2003; Pascual and Dunne 2006) and plant–pollinator systems (Jordano 1987; Memmott 1999; Bascompte et al. 2003; Jordano et al. 2003; Bascompte and Jordano 2007).

The structure of species-rich pollination webs is typically represented as bipartite graphs whose nodes represent one out of two categories (animals or plants). The fragility of plant–pollinator networks has been shown to be dependent on their topology, i.e. the specific pattern of connections among nodes (Memmott et al. 2004). Consequently, both structure and dynamics of pollination networks ought to be considered in order to evaluate the community robustness to current or future environmental perturbations (Bascompte and Jordano 2007).

In this work we characterize and analyze a well-defined pollination network from temperate rain forests of northern Chiloé Island, southern Chile. In this ecosystem most woody species are strongly dependent upon biotic pollination for reproduction (Armesto et al. 1996; Smith-Ramírez et al. 2005). We first characterize the structure of the pollination network through the evaluation of two basic topological properties: degree distribution and nestedness. Then, we discern the potential importance of selected groups of species, as well as of individual species, on maintaining the structure and diversity of the studied network.

"Degree distribution" is the frequency of species with a given number of links, and for pollination networks it follows a skewed distribution best described by functions such as power law or truncated power law with exponential decay (Jordano et al. 2003; Vázquez 2005). Networks exhibiting skewed degree distributions tend to be robust to random node loss and susceptible to loss of high-degree nodes (Albert et al. 2000; Dunne et al. 2002b). This pattern will be more pronounced in networks with greater skew. The second topological property analyzed here is "nestedness". In a perfectly nested network the more specialized species interact with species that are proper subsets of those species interacting with the more generalist ones (Bascompte et al. 2003). Thus, a small number of generalists form the core of interactions in the network. Nestedness is also related to robustness of mutualistic networks to random species extinctions (Memmott et al. 2004).

In order to discern the importance of predefined subsets of plants and pollinators in maintaining the network structure and species diversity, we deconstruct the pollination network (Marquet et al. 2004) by simulating the loss of different subsets of plants (according to their life form) and pollinators (according to their taxonomic order). For each of the remnant subwebs we analyze their topological properties and project, by means of a dynamic model, the expected amount of long-term species extinctions. Finally, and given that members of each removed species group can differ markedly in their connectivity attributes, we evaluate the sensitivity of the network structure to the loss of individual species. This allows the identification of key network components for the maintenance of community integrity, which may be sensible targets for local conservation efforts.

Materials and methods

Study site and network sampling

Records of flower visitors were obtained during three consecutive reproductive seasons, October 1999–January 2000, October 2000–March 2001, and October 2001–February 2002, in a mosaic of old-growth and second-growth forest patches, within a rural landscape in northern Chiloé Island, southern Chile (42°S, 73°35′W, 30 m above sea level). Floristic composition of forest fragments is typical of the highly endemic Valdivian and North Patagonian rain forests (Heywood 1995; Aravena et al. 2002), some of the richest forest associations in southern South America. The forests are dominated by evergreen broad-leaved tree species, with a profuse cover of vines and epiphytes, and receive about 2,050 mm of rain per year under a cool-temperate climate moderated by oceanic influence. Additional climatic, geographic and biological information on the study system has been provided elsewhere (Smith-Ramírez et al. 2005)

To assess the identity, number, and frequency of animal pollinators visiting the flowers, field observations were concentrated during the period (approximately 1 week) of maximum flowering of each plant species, anticipated from previous phenological records in the same study area (Smith-Ramírez and Armesto 1994). Floral visitors to each plant species that contacted the anthers and/or stigmas of the flowers were recorded during several 20-min observation periods (sample unit). Observations were made on flowers from ground level up to 3.5 m above ground (in the case of trees). Observation periods were uniformly distributed between 10 a.m. and 6 p.m. each day. During each 20-min period, a single plant species was observed from a fixed point by one observer and each pollinator visit to a previously defined number of visible (exposed) open flowers was recorded. With the exception of one hummingbird species, all flower visitors were insects. Additional methods, as well as the complete plant and pollinator

species list and network, can be found in Smith-Ramírez et al. (2005).

Pollinator network statistics

Degree distribution describes the frequency with which species with different numbers of links occur in any given network (Newman 2005). To assess the form of this distribution, it is customary to use the cumulative probability of the number of links (Amaral et al. 2000; Strogatz 2001) to avoid the problem of the arbitrary exclusion of null bins, thus improving the estimation for small and noisy datasets (Dunne et al. 2002a).

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 the 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 models. If γ is zero, the truncated power law model is equivalent to the exponential model, and if K_c is higher than the maximum observed degree, the truncated power law approaches the power law model in the positive quadrant (Valdovinos et al. 2009). The Akaike information criterion (AIC) was used to select the best model describing the observed degree distribution (Burnham and Anderson 2004). To avoid over fitting, we used the corrected AIC, which converges to AIC as sample size increases.

Nestedness was measured through the matrix temperature (T), with values ranging from 0 for perfectly nested networks to 100 for perfectly non-nested networks (Atmar and 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 the statistical significance of observed nestedness, we compared the T value of each network matrix against the distribution of T obtained from 1,000 networks with equal numbers of animals and plants, 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). Nestedness was estimated using the program BINMATNEST (Rodríguez-Gironés and Santamaría 2006). For comparison of nestedness between the full network and the subwebs produced by the removal of species we used a batch version of BINMATNEST, specially developed to perform rapid analysis of many matrices. This version of the software is available upon request from its author M. A. Rodríguez-Gironés.

The probability of "species persistence" was assessed by connecting the observed qualitative pattern of mutualistic interactions to a stochastic dynamic model (Fortuna and Bascompte 2006). The model considers mutualists inhabiting a landscape consisting of an infinite number of identical, well-mixed patches. The interaction is obligate for the animals, while the plants are able to survive in the absence of animals, but cannot reproduce without them. The temporal dynamics of the fractions of total available patches occupied by plant i, p_i, and animal j, a_j, are described by:

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

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

where c_{ij} is the per capita colonization rate of plant i when pollinated by animal j, and c_j is the per capita colonization rate of animal j. 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 those plants. Parameter Ω_j (see Fortuna and Bascompte 2006 for details) is the union of patches occupied by n plant species interacting with the same j animal species (i.e. the total available patches for the j animal).

Following Fortuna and Bascompte (2006), we randomly sampled the value of e/c from a uniform distribution centered on $k_p = e_i/c_i$ for plants and $k_a = e_j/c_j$ for animals, with an interval size of 0.1. Initial conditions for each species in the network were also randomly sampled from a uniform distribution in the unit interval. A species was considered extinct when the proportion of occupied patches fell below a threshold value of 0.001. Each pollination network was run for 2,000 iterations and then the fraction of extinct species was recorded. Parameter values used were $k = 0.25$, $k = 0.5$ and $k = 0.75$.

For each combination of parameter values, 1,000 model realizations were run for each analyzed network. These were: the complete observed network P, and the networks in which we removed the species of vines (V), shrubs (S), trees (T), hymenopterans (H), dipterans (D), and coleopterans (C). In order to control for changes in network size, we also ran the model (1,000 realizations each) for networks in which an equal number of randomly chosen species were removed. These null networks were labeled, accordingly, as V_0, S_0, T_0, H_0, D_0, and C_0.

The effects of individual species loss on the network topology were assessed through measuring network temperature and the value of the fitted exponent of the degree distribution, after deleting with replacement each of the participant species. These manipulations include the secondary loss of those specialists directly linked only with the deleted species, together with the subtraction of one degree from all other species directly linked with the deleted one.

Results

The pollination network involved 128 pollinator and 26 plant species displaying 313 mutualistic interactions (Table 1). Among the plants there were 11 shrub species, nine tree species, and five vines; insect species were dominated by 21 hymenopterans, 52 dipterans, and 47 coleopterans.

Degree distribution and nestedness

The power law model best described the degree distribution of both the whole network and the animal subweb, while the exponential model best described the degree distribution of plants (Fig. 1). Nevertheless, rigorously discerning the form of a degree distribution by means of standard fitting procedures is problematic due to the limited range of degree values inherent to ecological networks. Therefore, the shape of degree distributions found should be taken as indicative of general trends. On the other hand the network presented a significantly nested structure, when compared to the null model (Table 2). A visual representation of the nested network (Fig. 2) was obtained with the software PAJEK (http://vlado.fmf.uni-lj.si/pub/networks/pajek/default.htm).

We assessed the role that different plant life forms and orders of insects play on the network structure by evaluating both degree distribution and nestedness of the plant–pollinator network after removal of each target group (see Tables 2, 3, 4). No qualitative changes in the degree distributions were observed after the removal of vines, trees, or coleopterans. On the other hand, degree distribution of the whole network changed from power law to truncated power law when dipteran pollinators were removed. Degree distribution for forest plants changed from exponential to power law after removing flower-visiting hymenopterans. Finally, animals' degree distribution changed from power law to exponential when excluding either shrubs or hymenopterans. Values of fitted parameters are shown in Table 3.
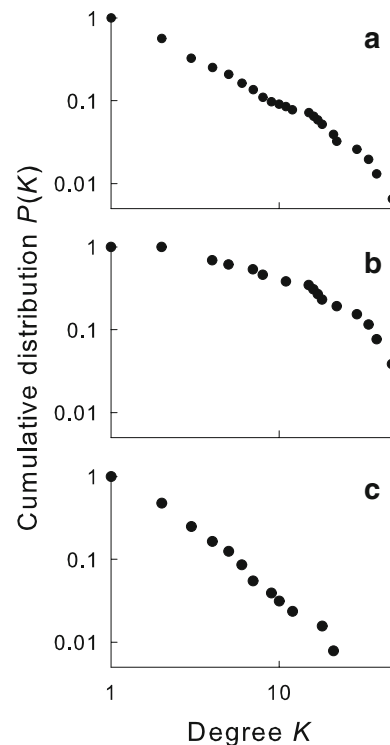

Fig. 1 Cumulative degree distribution of the Chiloé rain forest pollination network. **a** Whole network **b** plants and **c** animals. See Table 3 for model fitting

Removing any of the target plant or insect pollinator groups did not eliminate the nestedness of the remaining network (Table 2). Nevertheless quantitative effects on nestedness were detected when shrubs or hymenopterans were removed. T of the network without shrubs was significantly higher than the temperature of matrices where equal numbers of plants were removed at random. Likewise, T of the hymenopterans-free network was significantly higher than that of their corresponding null matrices (Table 4). We obtained the same qualitative results using the software ANINHADO (Guimarães and Guimarães 2006) for calculating T, suggesting that our results are robust.

Table 1 Basic statistics of the number of interactions (degree) within each species subset

	Number of species in system	Mean number of interactions	Median	Minimum	Maximum
Flowering plants					
Vines	5	3	2	2	7
Shrubs	11	8.55	4	2	47
Trees	9	21.89	18	8	38
Insect pollinators					
Hymenopterans	21	4.48	2	1	21
Dipterans	52	2.12	1	1	12
Coleopterans	47	1.87	1	1	6

Table 2 Basic features of the Chiloé pollination network and the subwebs obtained after removal of a given subset of species

| | Analyzed network | | | | | | |
	Whole	V	S	T	H	D	C
Plant species	26	21	15	17	22	24	26
Animal species	128	128	105	66	107	76	81
Connectivity	0.093	0.110	0.138	0.102	0.092	0.109	0.104
Interactions	311	296	217	114	217	199	220
Nestedness[a]	2.80**	4.10**	6.99**	1.54**	3.38**	3.05**	3.50**

V Vines, *S* shrubs, *T* trees, *H* hymenopterans, *D* dipterans, *C* coleopterans

** $P < 0.001$

[a] Significance of nestedness was tested against a null model where the probability of occurrence of an interaction was proportional to the mean connectivity of each plant-animal pair
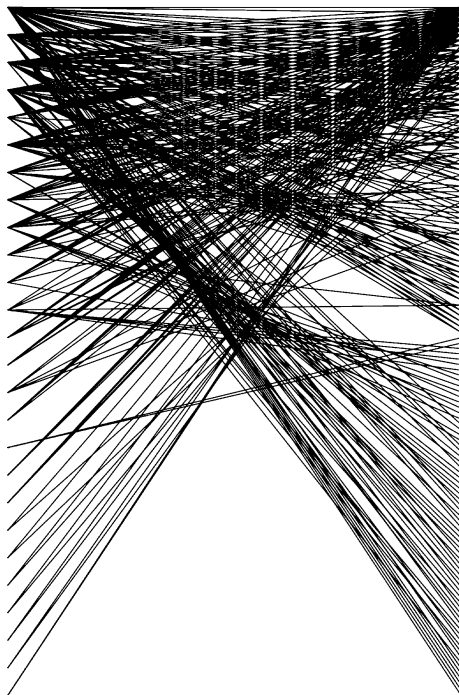

Fig. 2 Bipartite graph of the Chiloé rain forest pollination network *P*, arranged to display its nested structure. Plant and animal species are presented in the *left* and *right columns*, respectively

We then evaluated the role of the plant life form and insect order on network persistence by projecting the meta-community dynamics of the network and assessing dynamic extinction of species following the removal of each target group.

The model predicted that the removal of trees would increase the fraction of plant and animal extinctions relative to both the unmanipulated network and the null model, with the exception of plant extinctions at an extinction/colonization ratio $k = 0.25$ (Fig. 3). On the other hand, the removal of shrubs was predicted to lead to a decrease in species extinctions compared to the corresponding null model, with the only exception of pollinator extinctions at

$k = 0.25$. Note that for $k = 0.75$, the fraction of species predicted to go extinct following removal of shrubs was not smaller than that in the unmanipulated network. The effect of vine removal was less clear. At $k = 0.75$ species extinctions were lower than in the null model, although the reverse effect resulted (only for plants) at $k = 0.5$. No differences were observed at $k = 0.25$.

Model results after removal of insect groups are shown in Fig. 4. Removal of hymenopterans largely increased species extinctions when compared to both the unmanipulated network and to random insect removal, except for pollinators at $k = 0.25$. The removal of coleopterans enhanced plant persistence as compared to random removals, and showed no effect on insect species persistence. Deleting dipterans from the network exerted no effect, relative to random deletion, for $k = 0.75$. On the other hand, for $k = 0.25$ and $k = 0.5$ the effect was inverse between plants and animals (see details in Fig. 4).

To identify species of rain forest mutualists that may be of conservation concern, we evaluated the contribution of each species to the topological shifts driven by experimental removals. We measured nestedness (network temperature) and the exponent of the power law model fitted to the degree distribution of the network after single species deletions (Fig. 5). Among plants, the removal of the vines *Mitraria coccinea* and *Asteranthera ovata* (Gesneriaceae) markedly decreased network nestedness. On the other hand, the decrease in nestedness caused by the removal of shrubs (Table 4) was largely explained by the removal of the supergeneralist *Tepualia stipularis* (Myrtaceae), followed by *Ugni molinae* (Myrtaceae) (Fig. 5, left). Conversely, the removal of the tree species *Myrceugenia planipes, Myrceugenia ovata,* and *Amomyrtus meli* (all Myrtaceae) exerted the largest effect towards decreasing *T*. Among insects, the decrease in network nestedness caused by the removal of hymenopterans seems to be a group effect, not fully explained by the loss of individual species, although the removal of *Diphaglossa gayi* exerted

Table 3 Model selection for degree distribution $P(K)$ of the whole web of interactions, and those of the plants and animal pollinators separately

	Best model[a]	Parameter values (±95% CI)	Explained variance
Observed network			
Whole	PL	$\gamma = 0.999\ (0.033)$	0.990
Plants	EX	$\alpha = 0.088\ (0.010)$	0.952
Animals	PL	$\gamma = 1.275\ (0.090)$	0.993
Vines removed			
Whole	PL	$\gamma = 1.015\ (0.032)$	0.996
Plants	EX	$\alpha = 0.069\ (0.005)$	0.983
Animals	PL	$\gamma = 1.310\ (0.108)$	0.991
Shrubs removed			
Whole	PL	$\gamma = 1.081\ (0.055)$	0.992
Plants	EX	$\alpha = 0.059\ (0.006)$	0.966
Animals	EX	$\alpha = 0.714\ (0.054)$	0.997
Trees removed			
Whole	PL	$\gamma = 1.330\ (0.057)$	0.997
Plants	EX	$\alpha = 0.207\ (0.056)$	0.932
Animals	PL	$\gamma = 1.937\ (0.194)$	0.996
Hymenopterans removed			
Whole	PL	$\gamma = 1.137\ (0.036)$	0.998
Plants	PL	$\gamma = 0.559\ (0.052)$	0.967
Animals	EX	$\alpha = 0.739\ (0.092)$	0.992
Dipterans removed			
Whole	TPL	$\gamma = 0.733\ (0.047)$	0.999
		$K_c = 15.665\ (3.880)$	
Plants	EX	$\alpha = 0.135\ (0.010)$	0.987
Animals	PL	$\gamma = 1.198\ (0.081)$	0.994
Coleopterans removed			
Whole	PL	$\gamma = 0.907\ (0.046)$	0.987
Plants	EX	$\alpha = 0.122\ (0.011)$	0.971
Animals	PL	$\gamma = 1.190\ (0.053)$	0.997

CI Confidence interval, *EX* exponential model $P(K) \sim e^{-\alpha K}$, *PL* power law model $P(K) \sim K^{-\gamma}$, *TPL* truncated power law model $P(K) \sim K^{-\gamma} e^{-K/K_c}$, α fitted constant, γ fitted constant

[a] The best model was selected according to the corrected Akaike's information criterion

Table 4 Nestedness analyses for networks structured following removal of different species subsets. Values of temperature (T) for the observed subwebs and the mean and SD of T for 1,000 realizations of the corresponding null models

Species group removed	T	Mean T	SD T	P-value
Vines	4.10	3.14	0.65	0.140
Shrubs	6.99	3.78	1.29	**<0.05**
Trees	1.54	3.55	1.08	0.063
Hymenopterans	3.38	2.78	0.30	**<0.05**
Dipterans	3.05	3.06	0.69	0.988
Coleopterans	3.50	3.01	0.61	0.422

Significant P-values are in *bold*

the most pronounced relative effect. It can also be observed that dipterans and coleopterans exert a relatively minor effect on network structure.

Regarding changes in degree distribution caused by deletion of single species (Fig. 5, right), it can be noted that the effect of removing shrubs rested mainly on the loss of

Tepualia stipularis, whereas every tree species appeared to have a strong impact on network degree distribution. Among insects, hymenopterans were the most important group contributing to the preservation of the shape of degree distribution, where *Bombus dahlbomii*, followed by *Apis mellifera*, exerted the largest impact.

Discussion

The temperate rain forests of Chiloé Island in southern Chile are characterized by a high degree of endemicity, with nearly 34% of woody plant genera being endemic to the region (Heywood 1995). Among temperate ecosystems, this flora exhibits the highest incidence of biotic pollination and dispersal, with up to 85% of woody species being pollinated or dispersed by animals (Armesto and Rozzi 1989; Armesto et al. 1996; Aizen and Ezcurra 1998). Specifically, 75% of woody plants in Chiloé forests present insect pollination syndromes (Smith-Ramírez and Armesto 1994).
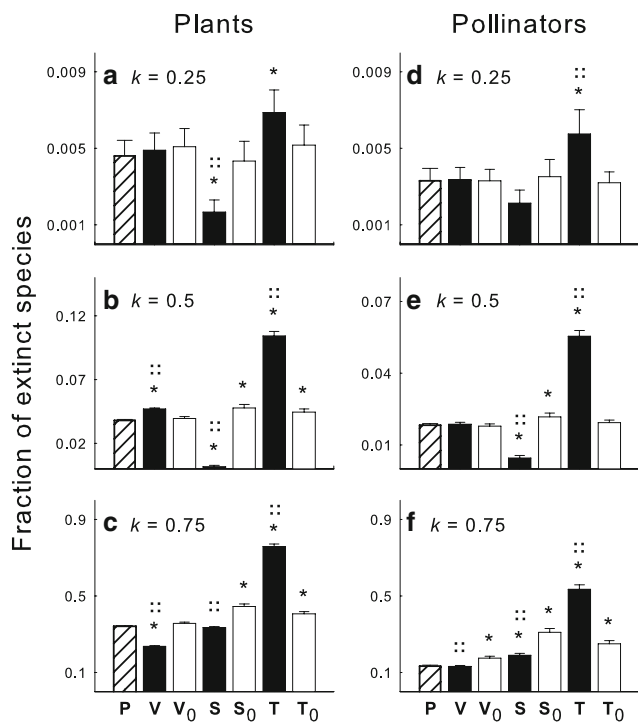
Fig. 3 Outcome of model simulations after removing vines (*V*), shrubs (*S*) or trees (*T*) from the pollination web of Chiloé rain forest. *Bars* show the fraction of extinct species for plants (**a–c**) and pollinators (**d–f**) for varying levels of k after 3,000 time iterations (mean of 1,000 realizations ±95% confidence interval). *Hatched bar* Whole network, *black bars* networks after species removal, *white bars* null models. **a–f** Results for different values of extinction/colonization ratio k. *Significant differences with respect to the unmanipulated network *P*, ::significant differences with respect to the corresponding null model

Fig. 4 Outcome of model simulations after removing hymenopterans (*H*), dipterans (*D*) and coleopterans (*C*). *Bars* show the fraction of extinct species for plants (**a–c**) and pollinators (**d–f**) for varying levels of k after 3,000 time iterations (mean of 1,000 realizations ±95% confidence interval). *Hatched bar* Whole network, *black bars* networks after species removal, *white bars* null models. *Significant differences with respect to the unmanipulated network *P*, ::significant differences with respect to the corresponding null model. **a–f** Results for different values of extinction/colonization ratio k

The conservation of austral South American temperate forests constitutes a global priority (Dinerstein et al. 1995; Arroyo and Hoffman 1997; Armesto et al. 1998; Myers et al. 2000). Despite their importance, the biological diversity of Chiloé rain forests continues to be threatened by anthropogenic disturbances such as fire, logging, cattle grazing, forest fragmentation and land conversion for agriculture (Figueroa et al. 1996; Newton 2007). Because the maintenance and recovery of these forests largely depend on animal pollination and seed dispersal services, the understanding of animal–plant mutualistic interaction is a must for acquiring a comprehensive knowledge about the structure and functioning of these ecosystems, as well as for developing management and conservation guidelines (Armesto et al. 1996). Unfortunately, few studies in these austral temperate rain forests have examined insect–plant interactions, including pollination (Aizen et al. 2002). The works of Riveros et al. (1991), Aizen et al. (2002), and Smith-Ramírez et al. (2005) on austral rain forests, revealed that insect pollinators are far more diverse than previously thought, and that the pattern of mutualistic
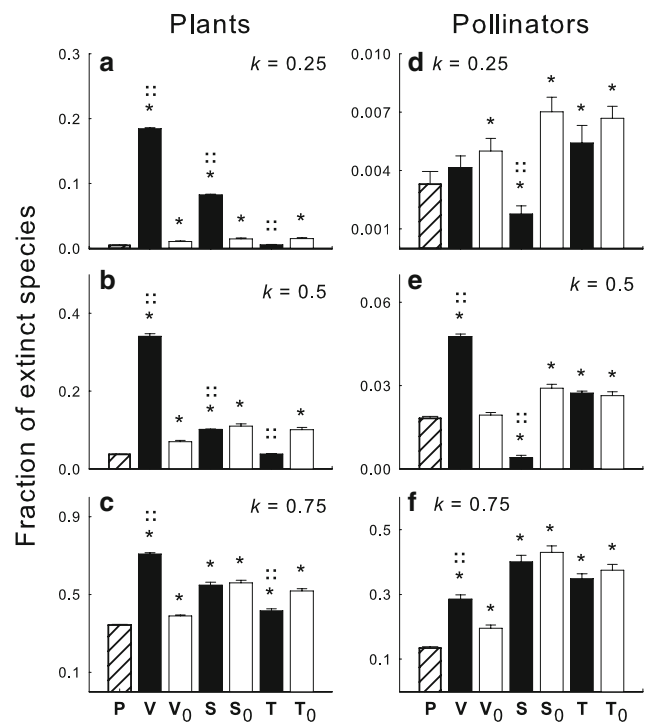
interactions is highly asymmetric, with a few species of plants monopolizing a large fraction of pollinators and a few generalist insect pollinators visiting a large fraction of flowering plant species.

The temperate rain forest pollination network exhibited a nested structure of plant–animal interactions, which means that interactions of the less connected species comprise a subset of the interactions of the more connected ones. On the other hand, while generalist species are linked with both specialists and generalist species, specialists are predominantly linked with generalists. The underlying biological processes behind the structure of mutualistic networks are still poorly understood, but recent advances suggest that nestedness is a pattern that may arise as a consequence of the simultaneous development of phenotypic complementarity between plants and pollinators and floral traits acting as barriers against parasites (Santamaría and Rodríguez-Gironés 2007; see also its ensuing discussion). A nested pattern implies the existence of asymmetric specialization (Vázquez and Aizen 2004) and it is related to asymmetries in dependence levels between plants and their pollinators (Bascompte et al. 2006). The nested pattern of
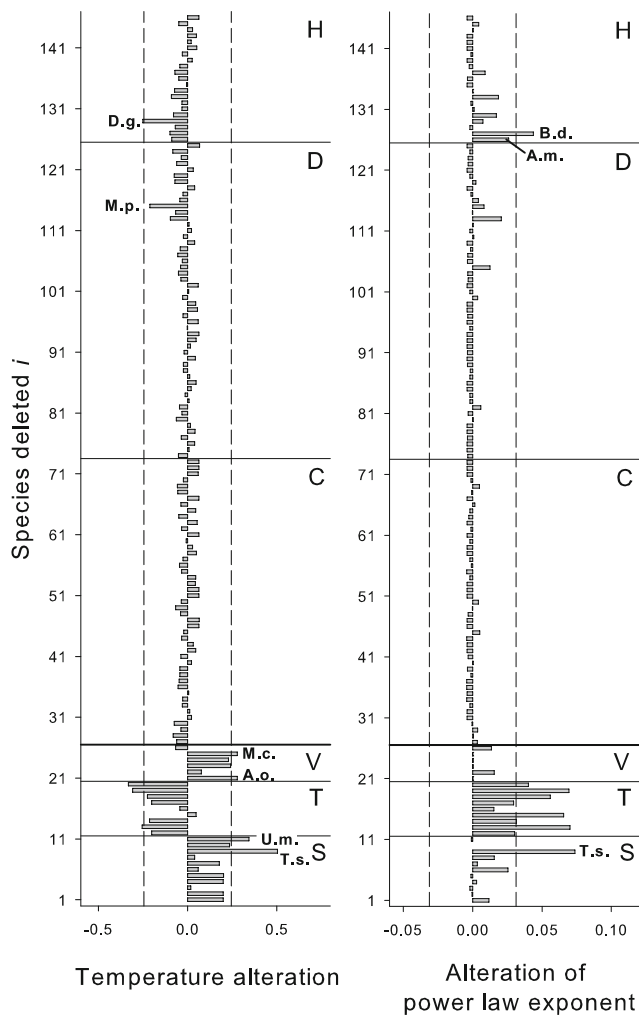
Fig. 5 Species contribution to topological shifts driven by selective removals. *Left-hand panel* Change in network temperature after deleting species *i* (ordered in the ordinate). *Right-hand panel* Change in the value of the fitted exponent of the power law degree distribution. *Dashed vertical lines* ±95th percentile of the absolute value of deviations from the whole network. Tree species are (from bottom to top) *Amomyrtus luna, Amomyrtus meli, Caldcluvia paniculata, Eucryphia cordifolia, Embothrium coccineum, Gevuina avellana, Luma apiculata, Myrceugenia ovata, Myrceugenia planipes. D.g. Diphaglossa gayi, B.d. Bombus dahlbomii, A.m. Apis mellifera, M.p. Mesograpta philippi, M.c. Mitraria coccinea, A.o. Asteranthera ovata, U.m. Ugni molinae, T.s. Tepualia stipularis*; for other abbreviations, see Figs. 3 and 4

the Chiloé rain forest network is consistent with many well-resolved pollination and seed dispersal bipartite networks (Bascompte et al. 2003; Vázquez and Aizen 2004) and gives quantitative support to earlier community characterizations (Smith-Ramírez et al. 2005). On the other hand, the Chiloé rain forest network exhibited a connectivity pattern best described by a power law (scale-free) cumulative degree distribution. This pattern is widespread across many complex networks including ecological interaction webs, as well as protein, metabolic, social and

information networks (Albert and Barabási 2002; Newman 2003; but see Dunne et al. 2002a). Scale-free degree distributions and nestedness are associated with network robustness against random loss of species, but also with high sensitivity to deletion of hub species (Albert et al. 2000). This indicates that the studied community exhibits a structure of interactions well suited for facing unselective extinctions.

What is the relative importance of defined groups of plant and insect species for the maintenance of the Chiloé rain forest network? There were numerous shrubs species and they were more specialized than trees in terms of pollinator visits, although they were in turn more generalist than the fewer vine species. Consequently, their removal was predicted to decrease the steepness of the degree distribution of plants, although it would not change its exponential shape. As a result, the network without shrubs retained the core generalist tree species and increased their persistence. Nevertheless, the loss of the more specialized shrubs, together with the supergeneralist *Tepualia stipularis* (degree = 47), would cause a decrease in the level of nestedness of the network because most of the remnant species were weakly nested generalists. Because in nested networks specialist pollinators are mostly linked to generalist plants (Bascompte et al. 2003), the loss of shrubs would cause a decrease in the degree of generalist pollinators. The loss of shrubs, therefore, changed the power law distribution of the animals' degree distribution in the original network to exponential. On the other hand, because trees were more generalist in their pollinators, their removal made the exponential degree distribution of plants steeper, and increased the extinction probability of both plants and pollinators.

Hymenopterans were the most generalist group of species among pollinators visiting large numbers of plants and, unlike trees, they included the supergeneralist bumblebee *Bombus dahlbomii* (degree = 21). This caused the animals' degree distribution to shift from power law to exponential when hymenopterans were deleted from the system. On the other hand, this also caused the loss of specialist plants, shifting the plants' degree distribution from exponential to long-tailed power law. Both the removal of generalist animals and the loss of specialist plants explain the decrease in network nestedness. Associated with these topological changes, we found that the probability of extinction largely increased after loss of hymenopterans from the system.

The removal of dipterans had an appreciable quantitative effect on the degree distribution of rain forest plants in the system, which became steeper due to a decrease in the degree of generalist forest plants. This shift also caused the degree distribution of the whole network to shift from power to a truncated power. Although nestedness remained

unchanged after deleting flies, the dynamic output did change. At high extinction/colonization rates, removing dipterans did not differ from random pollinator species deletion. At low and moderate k, species extinctions were lower after removing dipterans compared to random removal, which is explained by the strong effect of hymenopterans. Hence, random hymenopteran removal would constitute a more severe perturbation than dipteran removal. The exception was found for plants at $k = 0.25$, where deletion of dipterans predicted the extinction of two plant species (*Gaultheria mucronata* and *Myrteola nummularia*) that depend exclusively on them.

Removing coleopterans from the web exerted only a marginal effect on network persistence, because extinction of pollinators was entirely explained by decreased animal species richness. Plant extinction probability was lower when removing beetles relative to random species loss, and not different from the dynamics of the unmanipulated network (except at $k = 0.75$). Removal of coleopterans did not change the shape of the degree distributions, either for the whole network or for plants and animals separately. The same occurred when vines, mostly related to specialized visitors, were removed from the mutualistic web.

The effect of vine removal on extinction probability can be considered negligible at low and moderate k because of the low number of extinct species (mean $= 0.99$ plant species, range 0–3). At $k = 0.75$, random removal exerted a more severe effect on species persistence than removal of vines due to the greater relative weight of trees.

Overall, this work highlights the importance of flowering canopy trees and hymenopterans as the core groups that maintain the species richness, structure and dynamics of the Chiloé rain forest pollination network. This was revealed by the changes detected in topological and dynamic features of the rain forest network after modeling the removal of each group of species. Furthermore, discerning which species are mostly responsible for the effects observed after removal of multi-species groups can be of great value from a conservation perspective, because research, conservation and management efforts can be directed to few pivotal species in cases where protecting the entire community is not possible. By assessing the sensitivity of degree distribution and nestedness to the removal of individual nodes we obtained a measure of the relative contribution of each species to the maintenance of community structure and diversity. In this way, we identified a number of species that deserve special attention for the conservation of the entire species assemblage. The hymenopterans *Bombus dahlbomii* and *Diphaglossa gayi*, the shrubs *Tepualia stipularis* and *Ugni molinae*, the vines *Mitraria coccinea* and *Asteranthera ovata*, and the whole set of trees were predicted to exert a disproportionately large influence on the preservation of the structure of the

network under study. Their extinction would seriously harm the reproductive success of plants in this temperate rain forest. Some tree species with the richest sets of pollinators, such as the emergent *Eucryphia cordilfolia*, are currently under severe and rapid decline due to selective logging and land clearing, and their loss may promote cascade extinctions of network participants (Armesto et al. 1996). In particular, the woody species *Tepualia stipularis* and *Eucryphia cordifolia* were shown in this study to play an important structural role within the Chiloé network and they are also relevant for habitat provision (Díaz et al. 2005). Unfortunately, they both are highly threatened species in Chiloé Island, representing respectively 55 and 11% of the total commercialized firewood (unpublished data).

It is accepted that the stability and robustness of pollination networks to species loss are sensitive to structural attributes of the network. More specifically, nestedness and long-tailed degree distribution have been postulated as key topological properties that prevent species loss (Memmott et al. 2004; Fortuna and Bascompte 2006; Bascompte and Jordano 2007). Here we explored the possible interplay between structure and dynamics of a pollination system that supports a highly valued and remarkably endangered forest ecosystem. A better understanding of the functioning and evolution of target ecological systems would be gained if further efforts were made to ensure that most of the participant species were recorded. In addition, it is necessary to identify them at the best level of taxonomic resolution, recording their temporal and spatial variation, and to develop better analytical tools to manage, organize and take advantage of the data.

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