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Topological plasticity increases robustness of mutualistic networks

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Summary

1. Earlier studies used static models to evaluate the responses of mutualistic networks to external perturbations. Two classes of dynamics can be distinguished in ecological networks; population dynamics, represented mainly by changes in species abundances, and topological dynamics, represented by changes in the architecture of the web.

2. In this study, we model the temporal evolution of three empirical plant–pollination networks incorporating both population and topological dynamics. We test the hypothesis that topological plasticity, realized through the ability of animals to rewire their connections after depletion of host abundances, enhances tolerance of mutualistic networks to species loss. We also compared the performance of various rewiring rules in affecting robustness.

3. The results show that topological plasticity markedly increased the robustness of mutualistic networks. Our analyses also revealed that network robustness reached maximum levels when animals with less host plant availability were more likely to rewire. Also, preferential attachment to richer host plants, that is, to plants exhibiting higher abundance and few exploiters, enhances robustness more than other rewiring alternatives.

4. Our results highlight the potential role of topological plasticity in the robustness of mutualistic networks to species extinctions and suggest some plausible mechanisms by which the decisions of foragers may shape the collective dynamics of plant–pollinator systems.

Key-words: complexity, dynamics, optimal foraging, plant–animal interaction, pollination, rewiring, stability

Introduction

Since the beginnings of ecology as a scientific discipline, it has been recognized that the persistence of a species is strongly linked to the dynamics of the other species in the community (see Pascual & Dunne 2006). Nevertheless only recently, with the advent of network theory into ecology, has it been possible to build upon those early ideas, so as to deepen our understanding of the responses of large assemblages of interacting species to environmental perturbations and unravel the underlying mechanisms of biodiversity maintenance and loss.

Pioneering studies addressing the community responses to perturbations utilized static models of species interaction networks (Dunne, Williams & Martinez 2002). Static models are simple, as they require only empirical topological information and have proved to be useful tools for identifying structural properties associated with the robustness (in the face of species loss) of both trophic (Dunne, Williams & Martinez 2002) and mutualistic (Memmott, Waser & Price 2004) networks. However, a major effort is currently underway to incorporate realistic dynamics into ecological network models (Borrvall, Ebenman & Jonsson 2000; Drossel, Higgs & McKane 2001; Williams & Martinez 2004; Ebenman & Jonsson 2005; Fortuna & Bascompte 2006; Ives & Carpenter 2007). This approach may allow us to obtain more accurate projections of community dynamics and a better assessment of the risk of species extinctions in the light of current threats to biodiversity.

The temporal evolution of networks can be studied as two different processes: local dynamics and topological dynamics (Gross & Blasius 2008). Local dynamics refers to temporal changes in the values associated with network components (nodes and links); in the case of ecological networks, they normally represent changes in population abundance (either in numbers or biomass) over time, as well as changes in the strength of interactions. On the other hand, topological dynamics refers to the temporal variation in node composition

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and changes in the distribution of connections among nodes. In topological dynamics, the network architecture itself is regarded as a dynamical system whose temporal evolution is governed by specific rules. For ecological networks, topological dynamics consists of changes in species composition and the rewiring of interactions among species. Importantly, in ecological systems, both topological and local dynamics are interdependent processes. Local dynamics may promote topological dynamics through generating extinctions of both species and interactions, and by triggering interaction rewiring when organisms adjust their behaviour in response to changes in their trophic environment. Conversely, topological dynamics may influence local dynamics because the variation of species composition and shifts in the pattern of interactions among species may produce changes in population sizes and interaction strengths.

Recent studies have greatly improved our understanding of the functioning of complex ecological networks through incorporating local dynamics, in the form of population dynamics (Williams & Martinez 2004) and interaction strength flexibility based on adaptive behaviour (Kondoh 2003, 2007). This body of research has revealed that adaptive local dynamics increase the stability of ecological networks and their robustness to primary extinctions (Valdovinos *et al.* 2010). Conversely, little is known about the effects of topological dynamics on the stability and robustness of ecological networks, although it is well known that species composition and their interactions change through time in response to temporal variation in resources, and the conditions or spatial structure of their environment. In pollination systems, this translates to shifts in opportunities and preferences of pollinators for visiting plants (Kaiser-Bunbury *et al.* 2010).

Only a single study has considered topological dynamics in mutualistic networks to date, that of Kaiser-Bunbury *et al.* (2010) (see Staniczenko *et al.*(2010) and Thierry *et al.* (2011) for ones on food webs). Kaiser-Bunbury *et al.* (2010) found that behavioural shifts in the connections between plants and pollinators increased the tolerance of networks to species loss. Nevertheless, this work did not include population dynamics, while topological dynamics was implicitly incorporated based on the analysis of series of static snapshots of the networks. Without considering population dynamics, secondary extinctions will not occur unless all resources of a species become extinct, a condition quite restrictive and unrealistic, which may tend to overestimate network robustness. In contrast, in this investigation, we adopt an approach that explicitly incorporates both population and topological dynamics into the empirical structure of plant–pollination networks, to analyse their temporal evolution and resulting patterns of species persistence. Specifically, we test the hypothesis that topological plasticity, defined as the ability of networks to reorganize their connections among nodes in response to changes in the internal or external environment, enhances tolerance of mutualistic networks to primary species loss. In addition, we comparatively evaluate the effect of alternative simple rewiring rules on the robustness of mutualistic networks to uncover plausible mechanisms of stability in these systems.

Materials and methods

EMPIRICAL MUTUALISTIC NETWORKS

We used the topology of three empirical plant–pollinator networks reported in the literature (see Fig. S1, Supporting information): (i) the Llao-Llao network (Llao), containing 11 plant species, 29 pollinators and 52 pollination interactions, which was recorded in a temperate forest of southern Argentina (Aizen, Morales & Morales 2008), (ii) the palm-swamp network (Palm), containing 28 plants, 53 pollinators and 109 interactions, from the Venezuelan central plains (Ramírez & Brito 1992) and (iii) the Chiloé network (Chil), containing 26 plant species, 128 pollinator species and 311 interactions, which was recorded in the austral rainforests in Chiloé Island, Chile (Smith-Ramírez *et al.* 2005; see also Ramos-Jiliberto *et al.* 2009). From the statistics of the set of pollination networks reviewed in Olesen *et al.* (2007), our selected networks (Llao, Palm and Chil respectively) lie in the percentiles 80, 26 and 50 for connectance (number of interactions/number of plants × number of pollinators); 38, 24 and 76 for the ratio of pollinator to plant species; and 10, 35 and 67 for total species richness. Thus, the selected webs can be considered to be a good minimal sample within the variety of reported empirical networks. From each of these empirical networks, we assembled a dynamic network model keeping the number of plant and animal species, and the exact structure of interactions among each plant and each animal in the network.

POPULATION DYNAMICS

The population dynamics of the species in the mutualistic networks was modelled following Fortuna & Bascompte (2006). This model considers *m* plant species and *n* pollinator species inhabiting a landscape consisting of an infinite number of identical, well-mixed patches. The general equations are:

$$\begin{aligned}\frac{\mathrm{d}p_i}{\mathrm{d}t} &= \sum_{j=1}^{n} c_{ij}^{p} \frac{p_i a_j}{\Omega_j}(1-p_i) - e_i^p p_i \\ \frac{\mathrm{d}a_j}{\mathrm{d}t} &= c_j^a a_j(\Omega_j - a_j) - e_j^a a_j\end{aligned} \qquad \text{eqn 1}$$

where p and a represent proportion of patches occupied by plants and animals, $c_{ij}^p$is the colonization rate (per unit occupied patch) of plant i when pollinated or dispersed by animal j, and c_j^a is the colonization rate of animal j. Plant species i become extinct in patches at a rate e_i^p (e_j^a for animal species j). It is assumed that the extinction of plants from a patch causes the secondary extinction of the animal depending exclusively on that plant. Function Ω_j is the union of the patches occupied by plant species interacting with the same animal species j (i.e. the total available patches for animal j). Note that in this model, it is assumed that colonization rate of a given plant species (the first term in the plant equation) increases linearly with the abundance and species richness of their interacting pollinators. Also, eqn (1) assumes that there is no competition among insect species for floral resources. For a more detailed explanation of the model, see Fortuna & Bascompte (2006).

Following Fortuna & Bascompte (2006) and our own previous work (Ramos-Jiliberto *et al.* 2009; Valdovinos *et al.* 2009), we randomly sampled the value of e/c from a uniform distribution centred on chosen values of $k_p = e_i^p / c_{ij}^p$ for plants and $k_a = e_j^a / c_j^a$ for animals, with intervals defined as $\pm 0{\cdot}1\ k_p$ and $\pm 0{\cdot}1\ k_a$, respectively. Then, we randomly chose the parameters c_{ij}^p and c_j^a within the interval [0, 1], and finally the mortality parameters as $e_i^p = k_p * e_i^p$ and $e_j^a = k_a * c_j^a$. We examined $k = 0{\cdot}2$, $k = 0{\cdot}4$ and $k = 0{\cdot}6$, with $k = k_p = k_a$. Initial conditions for each species in the network were also randomly sampled from a uniform distribution in the interval [0, 1]. A species was considered extinct when its fraction of occupied patches fell below a threshold value of 10^{-4}.

INCORPORATING TOPOLOGICAL PLASTICITY

Here, we consider topological plasticity of pollination networks emerging from the ability of pollinators to change the plant species with which they interact. The rules governing the topological dynamics considered in this study comprise a two-step decision process. The first step is to determine whether a pollinator will rewire, the second is to determine which new host plant they will rewire to, if the first step is fulfilled. These steps are explained below.

Step 1

As the abundance p_i of a plant species i falls below a threshold U, the link l_{ij} between each animal j that interacts with plant i will be reallocated to other plant species in the network with probability R and held in its original position with probability $1-R$. Reallocating a link of animal j from plant i towards plant k means that animal species j ceases to interact with plant i. This implies that (a) c_{ij}^p falls to zero, (b) Ω_j loses the patches occupied by plant i, and (c) c_{kj}^p achieves a positive value. This leads to decrease the colonization rate of plant i and increase that of plant k. When the link is deleted, only (a) and (b) hold. If the abundance of plant i rises again to above U, it recovers its original links. Three values of U were tested: 10^{-1}, 10^{-2} and 10^{-3}. The probability R will be a function of the connectivity properties of the animal species connected to the plant whose abundance was reduced. Six alternative assumptions (hereafter 'options') for the dependence of R on the connectivity of vertices were considered: (i) 'ALL', $R = 1$, that is the animal always rewires to another plant in the network; (ii) 'RND', $R = 0{\cdot}5$, that is rewire and not rewire are equally probable; (iii) 'GEN', R increases linearly with the number of plants with which insect j interacts, that is the degree of insect j. This option gives more generalist animals a better chance to establish a new interaction with another plant, replacing its depleted resource. Specifically, R increases from 0 for pollinators interacting only with a single plant to $R = 1$ for the most generalist pollinator species in the network. Specialist insects are assumed to have little chance to be plastic because their phenotypes only match the ones of a few plants in the network; (iv) 'SPE', R decreases linearly with insect degree. Here R decreases from 1 for pollinators interacting only with a single plant to $R = 0$ for the most generalist pollinator species in the network. This assumes that more generalist animals will continue exploiting their many remaining resources if one of them goes extinct, while specialists are pressured to exploit a new resource if their current ones are depleted; (v) 'HMP', a convex (humped) relationship between R and insect degree. Combining the rationale behind (iii) and (iv), here it is assumed that super-generalists and strict specialists have reduced probability to rewire, that is R is a parabolic function of insect degree with $R = 0$ for pollinators interacting only with a single plant and also for the most generalist pollinator species in the network, with a maximum of $R = 0{\cdot}5$; (vi) 'LRA', R decreases linearly with resource availability for the animal species. This assumes that pollinator species with scarce resources will be more prone to replace those host plants that are becoming scarce. Resource availability for animal j is measured as

$$F_j = \sum_{i \in \{P_j\}} f_i \qquad \text{eqn 2}$$

with

$$f_i = \frac{p_i}{\sum\limits_{k \in \{A_i\}} \frac{a_k}{\Omega_k}} \qquad \text{eqn 3}$$

where $\{P_j\}$ and $\{A_i\}$ represent the set of plants interacting with animal j and the set of animals interacting with plant i, respectively. Thus, f_i represents the total amount of resources that plant i offers to all their exploiter animals, considering the level of exploitation that all these animals exert on the plant i. The denominator of eqn (3) weights the abundance of plant i by the level of exploitation that all animals k exert on i, the latter being represented by abundance of pollinators k of plant i divided by the availability of plant patches they exploit. For comparison, a control (C) treatment was considered with $R = 0$, where pollinators never rewire.

Step 2

If link l_{ij} is to be rewired, then it will be connected to a plant $k \neq i$ according to one of the four following options: (i) 'RND', random rewiring, that is all remaining plants in the network have equal probability to be attached to animal j; (ii) 'GEN' preferential attachment to the more connected plant, which assumes that generalist plants have more chance to receive new pollinators; (iii) 'SIM', preferential attachment to the plant most similar to the depleted plant i, according to the Sorensen index (Chao *et al.* 2005). Sorensen similarity index between a pair of plants is proportional to the number of sharing pollinators over the sum of the pollinator species of both plants. This assumes that topological similarity is associated with phenotypic similarity; (iv) 'RES', preferential attachment to the plants offering more resources to insect j, that is plants with higher values of r_i according to eqn (3).

In our analyses, we varied all options of both step 1 and step 2 in a factorial fashion.

NETWORK ROBUSTNESS

Network robustness to species loss was based on the number of extinct species in the network after removing 0, 1, 2, ... $s-1$ species at the start of the simulations, being s the number of plant or animal species. The model was run after each step in the removal sequence, and the number of extinct species was recorded after 1000 time units, where the system had reached a steady state. We removed the species using three sequences: at random, from the most connected to the least connected species, and from the least connected to the most connected species (Dunne, Williams & Martinez 2002; Memmott, Waser & Price 2004). In the cases of species with equal degree, the removed one was chosen at random. Each removal sequence was replicated 300 times. Thus, for each empirical pollination network, we run the model 900*s times, including population dynamics as well as topological dynamics. We calculated the R50 index as a measure of robustness (Dunne, Williams & Martinez 2002). This index represents the number of primary extinctions (species removals) that causes the extinction of 50% of the species in the network. Given that plant–pollinator webs are represented as bipartite networks, we then analysed separately the extinction responses of plants and animals to removals of plants and animals (Kaiser-Bunbury *et al.* 2010). Thus, we calculated the indices R50A and R50P that indicate the fraction of species (either plants or animals) leading to the extinction of 50% of animals and plants, respectively. The larger the R50A and R50P values, the higher the robustness of the animal and plant assemblages to primary extinctions, respectively. The values of R50A and R50P were calculated by fitting a sigmoid curve to each obtained data set of cumulative extinctions vs. number of removed plants. Then to compare the performance of the different rewiring options, we recorded the fraction of extinct plants and animals that resulted from primary extinction of 25% of plant or animal species in each network. This measure allows evaluating the performance of each option of step 1 averaging their outcome over all options of step 2, and vice versa. In the main text, we focus on the consequences of topological plasticity in networks subjected to experimental removal of plants. In the Supporting information, we show the equivalent results after removal of animals.

Results

The robustness of plant–pollinator networks to primary species loss markedly increased with the incorporation of topological plasticity. In Fig. 1, we show the robustness results, expressed as R50 values, for all rewiring alternatives and for the three analysed networks subjected to random removal of plant species. Persistence of both plants and animals was enhanced with all forms of network rewiring when the communities were exposed to primary plant extinctions, as compared to the control (C), which does not include topological dynamics. The same was obtained when animals were removed (Fig. S2, Supporting information).

Changes in parameter values did not alter qualitatively the results shown in Fig. 1 (data not shown). However, quantitative changes were noticed expressed as differences in R50 among rewiring alternatives. On the other hand, the enhancement in species persistence driven by topological plasticity was more pronounced with larger values of both U (higher responsiveness of animals to the decrease in plant abundance) and k (higher extinction rates or lower colonization rates). This enhancement was more pronounced under these conditions because of lower R50 values exhibited by the control. Likewise, the differences in R50 among rewiring options increased, compared to random removal, when the sequence of primary extinctions occurred from the most to the least connected plants, and decreased when removing from the least to the most connected plant, because the networks were quite robust to this extinction sequence. However, almost any form of rewiring produced significantly higher species persistence as compared to static topologies.

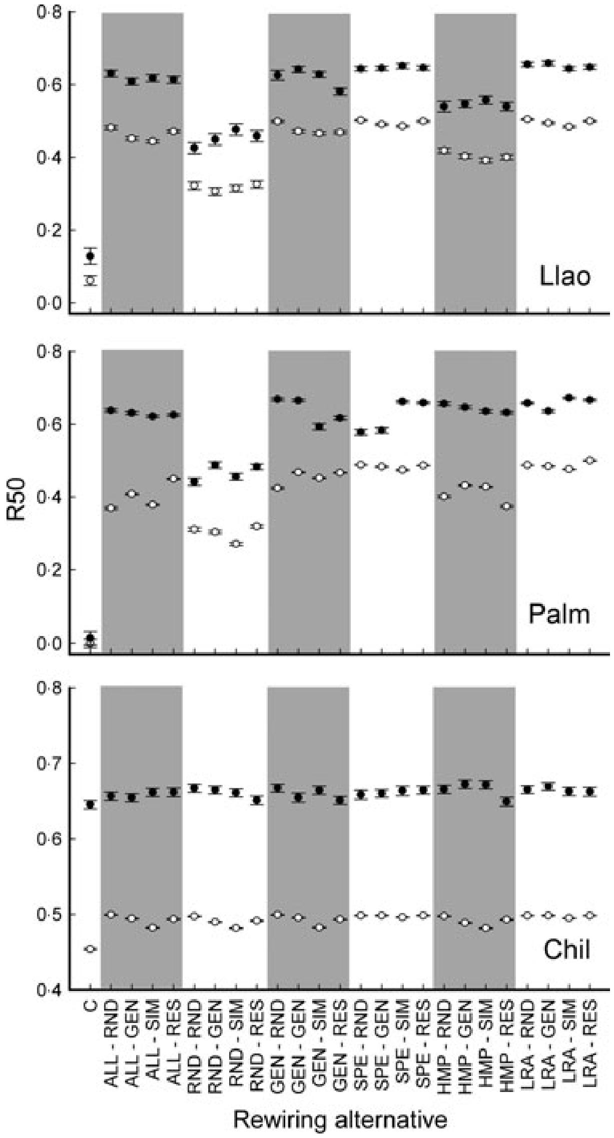

Fig. 1. Robustness of three empirical plant–pollinator networks to plant removal. R50 indicates the fraction of plants in the network needed to be removed to drive the extinction of 50% of animals (closed circles) or plants (open circles). Means and 95% confidence intervals are shown. Primary plant extinctions were chosen at random. Parameter values were $k = 0{\cdot}6$ and $U = 10^{-2}$. Alternative C is the control, where no rewiring was allowed. The six rewiring options of step one (ALL, RND, GEN, SPE, HMP and LRA) are separated by shading. Inside each option of step 1, the four options of step 2 (RND, GEN, SIM and RES) are shown. Note that the maximum possible R50 value for plants is 0·5, while it approaches 1 for animals. The minimum possible R50 value is 0 for both plants and animals.

The relative performance of the different rewiring algorithms is more clearly depicted in Figs 2 and 3, where species extinctions are shown after experimentally removing 25% of plants in each network. Regarding the first rewiring decision adopted by pollinators after primary extinctions of plants, the persistence of both plants and pollinators was particularly enhanced by options SPE and LRA, across all networks and sequences of primary extinctions analysed (Fig. 2). That is to say, species persistence was most enhanced when rewiring probability was higher for either specialists or more starved pollinators. Note that when rewiring was random (RND), species persistence fell to minimum values. In addition, when rewiring was activated in all cases (ALL), there was a higher fraction of extinct species. Very similar results were obtained when animals were experimentally removed (Fig. S3, Supporting information). These

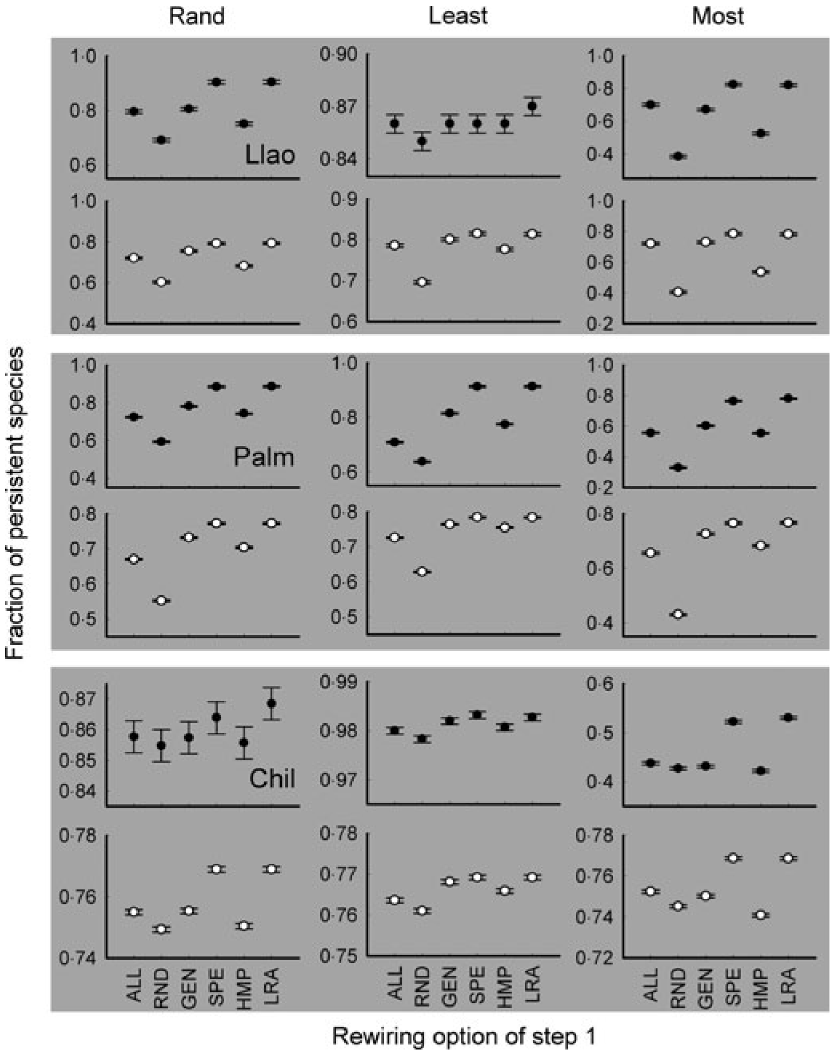

Fig. 2. Fraction of persistent animals (closed circles) and plants (open circles) after removal of 25% of plants in each network. Sequences of primary extinctions were random (rand), from the least connected plant (least) and from the most connected plant (most). In the *x*-axis are shown the six rewiring options of decision step 1. Marginal means are shown, over the four rewiring rules of the step 2, together with 95% confidence intervals. Model parameter values as in Fig. 1.

results demonstrate that considering which properties determine a pollinator's ability to adapt the interactions it takes part in is highly relevant for the stability of mutualistic networks.

The second rewiring decision, that is to which plant a lost interaction is reallocated, was also important for the maintenance of species richness in the pollinator networks, although differences were less clear as compared to step 1. In this case, responses of pollinators to plant removals diverged from those of plants (Fig. 3). Random rewiring (RND) favoured persistence of plants but drove the highest extinction rates of pollinators, for the three extinction sequences. Conversely, preferential attachment to the plant most similar topologically to the removed one (option SIM of step 2) performed best for pollinators when plant removal was carried out from the most connected plant, but it drove the highest extinction rates of plants with both random removal and removing from the most connected plant. Preferential attachment to the plants offering higher level of resources (option RES of step 2) was favourable for persistence of both plant and animal species in many cases. The results of the experimental removal of animals (Fig. S4, Supporting information) showed that option RES was slightly more favourable for persistence of animals but less favourable for plants.

Discussion

Ecological systems have been recognized as inherently dynamical entities for a long time. Their dynamics include not only temporal changes in species abundance, but also the evolution of community-level properties related to the number, identity and organization of their constituent species and interactions (Schoenly & Cohen 1991). Nevertheless, only recently have ecologists started to analyse the collective behaviour of large ensembles of populations with explicit dynamic models governing the temporal evolution of species abundances. Dynamic modelling of ecological networks, including both local as well as topological evolution, is just emerging in recent years as a necessary step towards developing a quantitative theory of functioning and responsiveness of natural systems to current biodiversity threats (Sala *et al.* 2000; Pereira *et al.* 2010). This is particularly true for mutualistic networks, whose understanding has been delayed in comparison to other complex ecological structures (e.g. food

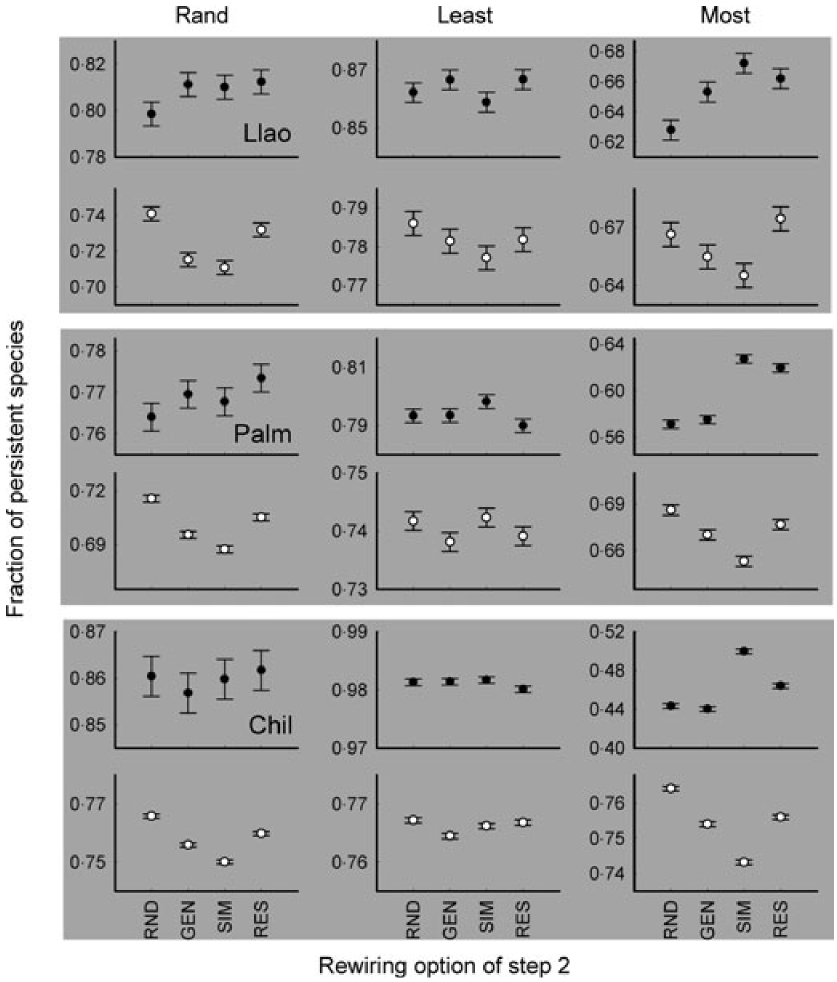

Fig. 3. Fraction of persistent animals (closed circles) and plants (open circles) after removal of 25% of plants in each network. Sequences of primary extinctions were random (rand), from the least connected plant (least) and from the most connected plant (most). In the *x*-axis are shown the four rewiring options of decision step 2. Marginal means are shown, over the six rewiring rules of step 1, together with 95% confidence intervals. Model parameter values as in Fig. 1.

webs, see Bascompte & Jordano 2007). In this study, we advance our knowledge of the properties of mutualistic networks that promote their stability, particularly their tolerance to species loss.

The first analyses of mutualistic networks visualizing them as complex systems revealed that their dynamics are strongly associated with exhibited structural patterns that deviate from randomness. Nestedness (Bascompte *et al.* 2003; Bastolla *et al.* 2009), asymmetry in interaction strength (Bascompte, Jordano & Olesen 2006; Vázquez *et al.* 2007) and more controversially modularity (Olesen *et al.* 2007; but see Thébault & Fontaine 2010) are structural properties that pervade mutualistic networks and have been suggested to enhance their robustness against environmental perturbations. Our results highlight the role that topological dynamics, in interplay with local dynamics, play in determining the robustness of plant–pollinator networks to species loss.

It is well known that interaction partnerships change markedly over time in plant–pollinator networks (Olesen *et al.* 2008; Petanidou *et al.* 2008), although high-level structural properties of the network such as nestedness and connectance may remain relatively unchanged (Petanidou *et al.* 2008). Thus, empirical evidence supports the wide occurrence of topological plasticity, but its underlying mechanisms as well as its consequences on the dynamics and robustness of mutualistic networks had remained scarcely addressed up to now. In this study, we showed that topological plasticity confers robustness to mutualistic ecological networks to species removals. This main result held for any tested form of rewiring, for three empirical networks with different structure and for a wide range of parameter values. Network Chil exhibited high species persistence without topological plasticity, and consequently, the effect of rewiring was less marked as compared to Llao and Palm networks. According to previous results, this could be attributed to the larger network size, higher ratio of animal/plant species richness and higher nestedness ($N = 0{\cdot}94$), relative to the two other studied networks (0·7 and 0·83, respectively) (Memmott, Waser & Price 2004; Okuyama & Holland 2008). For consistency with previous literature (Bascompte *et al.* 2003; Okuyama & Holland 2008), $N = (100-T)/100$, where T = matrix temperature. Equivalent results were obtained by the use of other nestedness metrics (NODF) and null model analysis (Almeida-Neto *et al.* 2008).

Our analyses also revealed that when animals with lesser host availability (i.e. being more of a specialist or having less available resources) were more likely to rewire their interactions, network robustness increased at maximum levels, even when compared with the option in which rewiring is assured for all animals at risk of losing a host. An explanation for this pattern can be found considering previous results for static mutualistic networks, where specialist species are the more fragile components in the community because they are more prone to secondary extinctions driven by loss of their partners (Memmott, Waser & Price 2004). Because of the heterogeneous distribution of mutualistic interactions, this effect is most pronounced when primary extinctions act preferentially on the most connected nodes. Therefore, the incorporation of topological plasticity based on the rewiring ability of specialist animals prevents their secondary extinction, thus increasing network robustness. The same rationale extends to the analysis of preferential rewiring by animals whose resource may be less available because they have few host species, or because their hosts either have low abundances or are being exploited by many animals. Why network robustness is not maximum when rewiring is assured ($R = 1$, option ALL of step 1) can be explained because host switching inhibits the recovery of depleted plants. Conversely, if some animals do not rewire when a host is depleted, they can maintain plant reproduction and promote its recovery.

The algorithms governing the second rewiring decision (i.e. which plant to switch to) had differing consequences for plants and animals. Persistence of plants tends to be favoured when animals rewire with equal probability over all available hosts (option RND of step 2). Animal richness tends to be enhanced when they choose most similar plants (SIM) when plants were removed, and when they choose richer hosts (RES) when animals were removed. However, in most of the cases studied, the rewiring option of step 2 that gave the best combination of animal and plant persistence was preferential attachment to richer hosts, that is to those plants exhibiting higher abundances and few exploiters. A plausible hypothesis to explain this result is that animals exploiting richer hosts will tend to increase their growth rates, leading to increasing animal as well as plant abundances via mutualistic relationships.

Therefore, our results suggest that greater increases in robustness of plant–pollinator networks are expected to occur whenever animals make their rewiring decisions (steps 1 and 2) based on reliable information about the amount of resources each plant offers in the network. The preferential rewiring of specialists in step 1 also renders a good performance, but it is likely that specialists will be more limited in their ability to switch among hosts. Instead, optimal foraging is known to be exhibited by some pollinators whose behaviour has been well studied (Ginsberg 1983; Keasar *et al.* 2002) and shares the fundamental aspects of with our algorithm based on resource availability. Consequently, optimal foraging of pollinators could be a mechanism leading to robustness enhancement in mutualistic networks by driving topological dynamics. A future development could be to use a more mechanistic approach when modelling topological plasticity based for example on optimal diet theory (Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008).

It is remarkable that some of our results mimic those of Kaiser-Bunbury *et al.* (2010). In particular, both studies concluded that behaviourally driven topological plasticity of mutualistic networks enhances robustness to species extinctions, and that this effect is stronger when highly connected species are removed first, while little difference is observed when specialists are removed first, random removal being a middle scenario. Interestingly, our analytic procedures differ substantially from those of Kaiser-Bunbury *et al.* (2010) (hereafter K-B) who did not use a dynamic model and thus topological dynamics were included implicitly. On the other hand, the K-B model strongly relies on highly resolved field information. Instead, our approach only uses qualitative field information, which can be gathered more quickly and easily. K-B model uses aggregated field data for establishing 'potential links'. Instead, we used a probabilistic approach in which all plants are potential partners but the likelihood of constituting a new interaction is a function of their connectivity properties. From this scheme, we were able to test different alternative scenarios for rewiring and compare their performance in terms of their ability to enhance network robustness. While the K-B approach is strongly empirically based, the one presented here is essentially dynamically based. We believe that both approaches represent complementary research strategies, whose application would improve our understanding of the functioning of natural systems as well as our ability to provide projection-based management guidelines. However, both research tactics have their own limitations. The information needed for building quantitative networks is hardly to obtain from fieldwork, and it is subjected to a considerable amount of sampling error. This adds an uncertainty whose consequences for the projection of community functioning need to be systematically evaluated. Besides this, the lack of dynamic modelling does not allow to considerate several processes leading to species decline, extinction and recovery. Conversely, qualitative networks merged with dynamic models exhibit a behaviour that is dependent on the set of assumptions defined in the network topology as well as functional relationships and values of parameters and initial conditions that feed the algorithms, which is partially solved by means of randomly sampling a wide range of values and testing different topologies. Combining empirically based quantitative networks with parameterization of dynamics models is not an easy task. Field information is not readily transferable to models that have indeed a minimum of realism. However, models may be improved by means of respecting field quantitative patterns, such as heterogeneity of population abundances and interaction strength, and phenological dynamics. This may constitute the next step in modelling dynamic mutualistic webs.

Our results highlight the potential role of topological plasticity in the robustness of mutualistic networks to species extinctions and suggest some plausible mechanisms by which foragers' decisions may shape the collective dynamics of plant–pollinator systems. Modelling ecological networks as adaptively evolving systems should be the basic framework of the next generation of models whenever realistic behaviour is to be favoured. Nevertheless, a higher amount of high-quality field information will be required to support local and global dynamic rules included in network formulation and to assess the predictive power of model outcomes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Structure of the three empirical networks used in this study.

Fig. S2. Robustness of two empirical plant-pollinator networks to animal removal.

Fig. S3. Fraction of persistent animals (closed circles) and plants (open circles) after removal of 25% of animals in each network. Sequences of primary extinctions were random (rand), from the least connected plant (least) and from the most connected plant (most). In the *x*-axis are shown the six rewiring options of decision step 1. Marginal means are shown, over the four rewiring rules of the step 2, together with 95% confidence intervals. Model parameter values as in Fig. 1.

Fig. S4. Fraction of persistent animals (closed circles) and plants (open circles) after removal of 25% of animals in each network. Sequences of primary extinctions were random (rand), from the least connected plant (least) and from the most connected plant (most). In the *x*-axis are shown the four rewiring options of decision step 2. Marginal means are shown, over the six rewiring rules of step 1, together with 95% confidence intervals. Model parameter values as in Fig. 1.