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Adaptive foraging allows the maintenance of biodiversity of pollination networks

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Pollination systems are recognized as critical for the maintenance of biodiversity in terrestrial ecosystems. Therefore, the understanding of mechanisms that promote the integrity of those mutualistic assemblages is an important issue for the conservation of biodiversity and ecosystem function. In this study we present a new population dynamics model for plant–pollinator interactions that is based on the consumer–resource approach and incorporates a few essential features of pollination ecology. The model was used to project the temporal dynamics of three empirical pollination network, in order to analyze how adaptive foraging of pollinators (AF) shapes the outcome of community dynamics in terms of biodiversity and network robustness to species loss. We found that the incorporation of AF into the dynamics of the pollination networks increased the persistence and diversity of its constituent species, and reduced secondary extinctions of both plants and animals. These findings were best explained by the following underlying processes: 1) AF increased the amount of floral resources extracted by specialist pollinators, and 2) AF raised the visitation rates received by specialist plants. We propose that the main mechanism by which AF enhanced those processes is (trophic) niche partitioning among animals, which in turn generates (pollen vector) niche partitioning among plants. Our results suggest that pollination networks can maintain their stability and diversity by the adaptive foraging of generalist pollinators.

Since the early days of ecology, population and community ecologists have made significant progress in understanding the mechanisms underlying competitive and resource-consumer interactions and in determining the consequences of these antagonistic interactions for the structure and dynamics of biological communities (Gause 1934, Connell 1961, Pimm 1982). But species within communities are not only trophically or competitively related. Mutualistic relationships among species, despite the scant attention that community ecologists have traditionally devoted to their study, have played a critical role in the maintenance of terrestrial biodiversity (Thompson 1994). However, the causal relationships between the processes that build up and modulate mutualistic interactions among species and the structural and dynamic patterns emerging at the community level are still not well understood.

Recent research on mutualistic networks (Bascompte et al. 2003, Jordano et al. 2003, Fortuna and Bascompte 2006, Okuyama and Holland 2008, Bastolla et al. 2009, Ramos-Jiliberto et al. 2009, 2010, 2012, Valdovinos et al. 2009, Holland and DeAngelis 2010, Benadi et al. 2012) has expanded our knowledge about the structure and dynamics of large mutualistic assemblages composed of flowering plants and their pollinators or seed dispersers. This research has focused mainly on revealing structural patterns of empirical networks (Bascompte et al. 2003, Jordano et al. 2003), although more recent studies have used simple population dynamics models to simulate the evolution of the abundances of mutualistic species (Bascompte et al. 2006, Fortuna and Bascompte 2006, Okuyama and Holland 2008, Bastolla et al. 2009, Holland and DeAngelis 2010, Benadi et al. 2012). While these models have provided an initial picture of the dynamics of complex mutualistic systems, they disregard important biological processes associated with plant–animal interactions. This may lead to an inadequate representation of net effects among species, which could distort the dynamics of the whole system. These processes include: 1) the production and animal consumption rates of plant rewards (Duffy and Stout 2008), 2) the competition and/or facilitation among plants via shared pollen/seed animal vectors (Hegland et al. 2009, Mitchell et al. 2009), and 3) the competition among animals for plant rewards (Zimmerman and Pleasants 1982). The omission in previous models of these important biological processes arose because they represented mutualistic relationships as simple phenomenological positive effects among species (but see Holland and DeAngelis 2010, Benadi et al. 2012), by a positive term in the growth equation of each mutualist that depends on the population size of the partner (Bascompte et al. 2006, Fortuna and

Bascompte 2006, Okuyama and Holland 2008, Bastolla et al. 2009). A mechanistic alternative to this phenomenological representation is the consumer–resource approach to mutualistic relationships (Holland and DeAngelis 2010), in which the effects among mutualists are defined as consumer–resource interactions. This approach recognizes a common characteristic of all mutualisms, which is the gathering of resources by organisms of one species through the interaction with organisms of another species that also takes benefit from the interaction (Holland et al. 2005). This approach represents an important step towards building a mature theory of mutualisms, and positions predation, competition and mutualism under a common ecological framework (Holland and DeAngelis 2009, 2010).

Within the consumer–resource approach to mutualistic networks, foraging preferences of animals determine which plant–animal interactions are realized, and govern the interaction strength among species, the reproductive rate of plants, and the food intake of animals. Consequently, the foraging behavior of animals in relation to plant rewards lies at the core of mutualistic relationships, presumably affecting network structure and dynamics, as has been shown to occur in networks in which species interact only via consumer–resource relationships (Valdovinos et al. 2010).

Adaptive foraging (AF), defined as fitness-enhancing changes in the foraging efforts of individuals due to variation in the availability of their resources, has been shown to be a key stabilizing mechanism for the dynamics of complex food webs (Valdovinos et al. 2010). However, to our knowledge no studies have addressed explicitly the influence of AF on the dynamics of pollination networks (but see Kaiser-Bunbury et al. 2010 for a static model), despite empirical evidence indicating that certain pollinator species do exhibit this behavior in nature (Ginsberg 1983, Keasar et al. 2002). The consumer–resource approach to mutualistic interactions offers a direct avenue for including the adaptive dynamics of foraging efforts into models of community dynamics of mutualistic networks. In this study we evaluate the effects of adaptive foraging exhibited by pollinators on the collective dynamics of pollination networks. For this purpose, we present a new population dynamics model for plant–pollinator interactions based on the consumer–resource approach, and use this model to simulate the temporal dynamics of an empirical and highly resolved pollination network, considering both population dynamics and adaptive dynamics of foraging efforts. Specifically we address how AF shapes the outcome of community dynamics in terms of biodiversity and network robustness to species loss.

Methods

Database

To evaluate the effect of AF on the dynamics of pollination networks, we simulated the time evolution of a network from an oceanic island published by Kaiser-Bunbury et al. (2009), which to our knowledge is the network built with field data of the highest resolution. The network data cover a full flowering season from September 2003 to March 2004, recorded in each two-week period. Specifically, the dataset of Kaiser-Bunbury et al. (2009) consists of two fully quantitative pollination networks from two natural heathland sites, in one of which the exotic plants were removed. In the present study, we utilized the qualitative structure (i.e. who visits whom) of the network that was not subjected to plant removal. The network exhibits a highly significant nested structure, which we tested with the software Aninhado (Guimarães and Guimarães 2006) using the algorithm NODF (Almeida-Neto et al. 2008) as the nestedness index. The NODF value of this network is 16.23. It contains 64 plant species, 100 pollinator species and 534 mutualistic interactions. As in other pollination networks (Jordano et al. 2003), most of species are specialists and very few are super-generalists. Most pollinators (51 species) only visited one plant species, while the three most-connected pollinators visited 34, 30 and 28 plant species. 53% of the plant species were visited by five or less pollinators, while the two most connected plants were visited by 38 and 33 pollinator species. For a detailed description of site characteristics and the plant–pollinator community see Kaiser-Bunbury et al. (2009).

In addition to the network of Kaiser-Bunbury et al. (2009), we included the analysis of other two networks to support our main conclusions. One is from Bristol, UK, described by Memmott (1999), which contains 25 plant and 79 animal species. The other network is from the Andes of Mendoza, Argentina, described by Medan et al. (2002), which contains 23 plant and 72 animal species. These two networks exhibit highly significant nested structures with NODF values of 23.11 and 12.81, respectively.

The dynamic model

The model assumes that plant species and their flowers are uniformly distributed over a homogeneous landscape. The pollination interaction between a plant population (i) and an animal population (j) is based on the number of visits that the individuals of population j make to flowers of plant i per unit time:

$$V_{ij} = \alpha_{ij}\tau_{ij}a_j p_i \tag{1}$$

State-variables (p_i) and (a_j) represent the density of flowers of plant population i (individuals/area) and the density of animals (individuals/area) of population j. We further assume that each individual plant has a single flower at a time and that each flower can produce a unique seed. This simplifying assumption is necessary for the demographic equation of plants. The function (α_{ij}) (dimensionless) is the foraging effort displayed by pollinator j on plant i, which takes values between 0 and 1. It holds that the sum of α_{ij} over all plants visited by pollinator j is equal to one. The parameter (τ_{ij}) is the visitation efficiency of animal j to plant i (see Table A1 in the Supplementary material Appendix A1 for a list of parameters and their meanings).

Let A be the set of all pollinator (i.e. animal) species and P the set of all plant species. The population dynamics of plants and pollinators are governed by:

$$\frac{dp_i}{dt} = \gamma_i \sum_{j\in A} e_{ij}\sigma_{ij}V_{ij} - \mu_i^P p_i \tag{2}$$

$$\frac{da_j}{dt} = \sum_{i \in P} c_{ij} V_{ij} f_{ij}\left(R_i, p_i\right) - \mu_j^A a_j \quad (3)$$

where $V_{ij} = 0$ if plant i and animal j do not interact. Function (σ_{ij}) is the fraction of visit that ends in a pollination event, parameter (e_{ij}) is the expected number of seeds produced by a pollination event, and (γ_i) is the fraction of seeds that recruit to adulthood, assuming that recruitment is limited by competition among plants (Tilman 1997). Parameters (μ_i^P) and (μ_j^A) describe the density-independent per capita mortality rates of plants and animals respectively. In Eq. 3, the 'functional response' $f_{ij}(R_i, p_i)$ represents the amount of floral resources that population j extracts in each visit to plant i. Variable (R_i) is the amount of floral resources per unit area that the population of plant i has available for the feeding of its pollinators. Parameter (c_{ij}) represents the conversion efficiency of floral resources obtained from plant i to births of pollinator j. We define exact formulations for f_{ij} in subsection 4.

Key functions in Eq. 2 are the pollination and recruitment probabilities σ_{ij} and γ_i. Function σ_{ij} is assumed to be directly related to the probability that an individual j carries pollen of species i at the time of visiting one of its flowers, taking into consideration the loss of conspecific pollen produced by the transfer of heterospecific pollen made by pollinators that visit more than one plant species (Morales and Traveset 2008). Assuming that the amount of pollen extracted in a visit and pollen lost between visits of animal j is homogeneous over plant species, then σ_{ij} is equivalent to the fraction of total visits that pollinators of species j are making to plants of species i, that is:

$$\sigma_{ij} = \frac{V_{ij}}{\sum_{k \in P_j} V_{kj}} \quad (4)$$

Limitation of seed recruitment by competition among plants (Tilman 1997) is represented by

$$\gamma_i = g_i \left(1 - \sum_{l \neq i \in P} u_l p_l - w_i p_i \right) \quad (5)$$

where g_i is the background recruitment fraction from seeds to plants of species i, and u_l and w_i are the inter- and intra-specific competition coefficients, respectively.

Finally, the amount of floral resources R_i in Eq. 3 and the foraging effort α_{ij} in Eq. 1 are also state-variables of the model, whose dynamical equations are:

$$\frac{dR_i}{dt} = \beta_i p_i - \phi_i R_i - \sum_{j \in A} V_{ij} f_{ij}\left(R_i, p_i\right) \quad (6)$$

$$\frac{d\alpha_{ij}}{dt} = G_j \alpha_{ij} \left(c_{ij} \tau_{ij} p_i f_{ij}\left(R_i, p_i\right) - \sum_{k \in P} \alpha_{kj} c_{kj} \tau_{ij} p_i f_{kj}\left(R_k, p_k\right) \right) \quad (7)$$

where β_i is the per individual production rate of resources of species i, and ϕ_i is a self-limitation parameter. In Eq. 7, parameter G_j is the basal adaptation rate of foraging efforts α_{ij} of animal j on its plant resources, i.e. the speed of change in α_{ij} when the term within parenthesis in Eq. 7 is nonzero. Equation 7 is known as the replicator equation, and is used to describe the adaptive change of a trait (Valdovinos et al. 2010). The foraging effort that pollinators j allocate to plant i increases through time whenever this decision enhances their food intake as compared to increasing the allocating effort to any other plant.

Model implementation and sensitivity analysis

The topology of the Mauritian pollination network (Kaiser-Bunbury et al. 2009) was used to define the number of plant and animal species, and the pair-wise mutualistic interactions of the network, i.e. which animal species j visits each plant species i. Each plant species was represented by two state variables in the model (Eq. 2 and 6), and each animal species was represented by one state variable (Eq. 3). Each pairwise interaction between animal and plant species (i.e. each 1 of the adjacency matrix) associates to Eq. 1 and 7. The model was run 6000 time steps for every simulation, and all parameter values and initial conditions of plants, animals and floral resources were drawn from uniform random distributions with mean equal to 0.5 and variances to 10% of the means. Initial foraging efforts were set as $\alpha_{ij} = 1/k_{aj}$, where k_{aj} is the number of interactions of pollinator species j. The means of the parameter values are shown in Table A1 (Supplementary material Appendix A1), while their variances were 10% and 0.01% of means for plant and animal parameters, respectively. The variances for animal parameters were selected to be small because the model without AF required a little divergence among their parameters to allow coexistence. Following Thébault and Fontaine (2010) we used Latin hypercube sampling to evaluate how robust were the model outputs to different combinations of parameter means. Methods and results of this sensitivity analysis are shown in the Supplementary material Appendix A1.

The effect of AF on the dynamics of pollination networks

To evaluate the influence exerted by adaptive foraging (AF) on the dynamics of pollination networks, we analyzed its effect on the stability of the Mauritian network and on some structural attributes of its plant–pollinator community. As stability measures, we used species persistence and network robustness against species extinctions. For species persistence we used the definition reviewed by Pascual and Dunne (2006) as the fraction of initial species of the community that survived until the end of a simulation. As robustness we defined the resistance of the network to losing species as result of primary species removal (Dunne et al. 2002). We considered a species to be extinct when its density fell below 0.02 for plants and 0.001 for animals, since below these extinction thresholds species densities continue decreasing to 0. As structural attributes of the plant–pollinator community, at the end of the simulations, we measured species diversity (determined by the Shannon index $H' = -N_i \sum_{i \in A_i} \log N_i$, where N_i is the relative density of species i), and population densities. To give more support to the results obtained by this methodology we performed the same analyses on the plant–pollinator networks published by Memmott (1999) and Medan et al. (2002).

To test the effect of AF on species persistence and network robustness against primary extinctions, we ran an in-silico experiment that consisted of a two-way factorial design. The first factor was percentage of pollinators exhibiting adaptive foraging (AF), with levels 0 and 100. The second factor was percentage of species removed from the network, with levels 0 and 40. A pollinator exhibits AF if its foraging efforts change as defined in Eq. 7, otherwise it allocates the same fixed effort to all its plant resources with value of $\alpha_{ij} = 1/k_{aj}$. Regarding factor 2, the extinction of a species was simulated by removing the column or row of the adjacency matrix that represents that species. In each treatment the model was run 100 times, each time with different parameters and initial conditions. Species removals (separated into deletions of plants and animals for recording consequences on animals and plants, respectively) were performed at time step 3000, at which the system was in a steady state.

The procedure above described was replicated under four scenarios of density-independent mortality rates: 1) mu1: high mortality rates of animals (mean of $\mu^{A}_{j} = 0.01$) and low mortality rates of plants (mean of $\mu^{P}_{i} = 0.002$), 2) mu2: low mortality rates of animals (mean of $\mu^{A}_{j} = 0.004$) and high mortality rates of plants (mean of $\mu^{P}_{i} = 0.008$), 3) mu3: low mortality rates of animals (mean of $\mu^{A}_{j} = 0.004$) and plants (mean of $\mu^{P}_{i} = 0.002$), 4) mu4: high mortality rates of animals (mean of $\mu^{A}_{j} = 0.01$) and plants (mean of $\mu^{P}_{i} = 0.008$). All the other parameters were obtained from uniform random distributions whose mean values are defined in Supplementary material Appendix A1 Table A1. The complete procedure (i.e. two levels of AF × 2 levels of species removals × 4 scenarios of mortality rate) was replicated for three alternative versions of the model, which represent different rules for the population dynamics of pollinators (Eq. 3). The three tested versions of the model that modify Eq. 6 and 7, were: 1) LFR model: linear functional response for pollinators $f_{ij} = b_{ij} \times R_i/p_i$, where b_{ij} is the efficiency of pollinator i for extracting floral resources of plant j, 2) NFR model: nonlinear functional response for pollinators $f_{ij} = b_{ij}^{max} \times R_i/(\kappa_{ij} \times p_i + R_i)$, where b_{ij}^{max} is the maximum extraction efficiency of floral resources of plant i by pollinator j and κ_{ij} is the half saturation parameter, and 3) self-limited-LFR model: linear functional response for pollinators with self-limitation control of their population growth rates. In this version the sum of Eq. 3 is multiplied by the term $s_j = 1 - a_j/K_j$, where s_j is the self-limitation factor of animal j due to density-dependence and K_j is its carrying capacity. Note that we do not use a functional response with interfering competition as Fishman and Hadany (2010) did, because competition among pollinators is already present in our model by the shared exploitation of plants rewards.

For a deeper analysis of the effect of AF on the robustness of pollination networks against species extinctions, we sequentially removed the species of the network and recorded the number of secondary extinctions after removing species and then running the dynamic model. For this procedure we chose the simplest version of the model (i.e. LFR model), because the results of the two-way factorial experiment described above showed that the effects of AF on network dynamics were qualitatively the same among the different versions of the model. We defined five levels of AF: 0, 25, 50, 75 and 100% of pollinators in the network that were adaptive foragers. The animal species exhibiting AF were selected at random in each model run. After the first 3000 time steps, we removed 0, 1, 2, …, $S - 1$ species following one of three different sequences: 1) randomly (rand sequence), 2) from the least to the most connected species (least sequence), and 3) from the most to the least connected species (most sequence). For each removal set we recorded the number of extinctions at the final time step. Each sequence was run 100 times, with different parameters and initial conditions, for each of the four mortality rate scenarios defined above.

Finally, to find plausible mechanisms that could explain the results of the experiments, for each species in the network we recorded: 1) its persistence (fraction of the 100 simulations in which the species persisted at the final time), 2) population density, 3) total visits received by each individual plant and 4) total floral resources extracted by each individual animal. We plotted these four variables of each species against its degree and the minimum degree of all its interacting species. We also recorded the foraging effort α_{ij} that each animal j assigns to each of its interacting plants, and plotted it against the degree of its host plant species. We measured all these variables for the LFR model, parameterized by the mortality scenario mu1, for systems with 0 and 100% of pollinators exhibiting AF. The results of the first two experiments showed that there were no qualitative differences among the four mortality scenarios in terms of the effect of AF on species persistence.

Results

Adaptive foraging (AF) enhanced the diversity (measured by the Shannon index), stability (measured as species persistence and network robustness against species extinctions), and total population densities of the Mauritian network. These results held for the three versions of the model, for the four mortality rate scenarios, and for both plant and animal species (see Fig. 1 for LFR model; in Supplementary material Appendix A1 Fig. A2 and A3 for NFR and self-limited-LFR models, respectively). Conversely, the variability of population densities decreased when pollinators exhibited AF. The above was true when no species were removed as well as when 40% of plant or animal species were removed from the network. In addition, the same trends were found for the networks of Memmott (1999) (Supplementary material Appendix A1 Fig. A4), and Medan et al. (2002) (Supplementary material Appendix A1 Fig. A5) for the LFR version of our model, which give support to our main conclusion.

The sensitivity analysis (Supplementary material Appendix A1 Fig. A1) demonstrated that AF increased species persistence of the Mauritian network when parameter values were varied in the range of one quarter to four times the baseline values. Moreover, for the model with 100% of pollinators exhibiting AF, the persistence of both plant and animal species was quite robust to changes in the set of parameter values, since about 60% of the tested

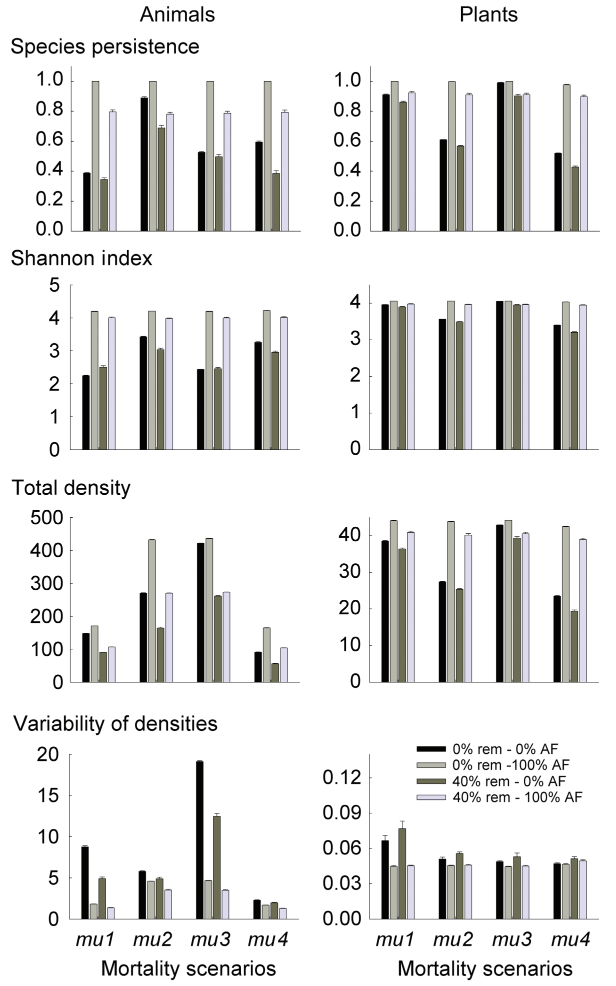

Figure 1. The effect of AF on the stability and diversity of pollination networks. Model output of four variables characterizing animal and plant species at the end of simulations of the LFR model (see Fig. A2 and A3 for the other two versions of the model) parameterized with the four mortality rate scenarios used in the study: 1) mu1: high mortality rate for animals and low for plants, 2) mu2: low mortality rates for animals and high for plants, 3) mu3: low mortality rates for animals and plants, and 4) mu4: high mortality rates for animals and plants. Results are shown in which no removals (0% rem) and removal of 40% of plant and animal species (for animals' and plants' response variables, respectively; 40% rem) were performed, and where no pollinator (0% AF) and all pollinators (100% AF) exhibited AF. 'Total density' refers to the sum of densities over all species. Error bars are 95% confidence intervals.

combinations of parameter values allowed the persistence of all species at the end of simulations, while in about 30% of them they led all species toward extinction. Thus 93% of the parameter values that allowed the persistence of at least one species at the end of simulations resulted in all species coexisting through time.

The robustness of the Mauritian network against species extinctions increased with AF, as shown in Fig. 2 for mortality scenario mu1 and in the Supplementary material Appendix A1 Fig. A6, A7 and A8 for mortality scenarios mu2, mu3 and mu4 respectively. These figures illustrate the extinction patterns of plant and animal species for the three removal sequences defined in the Methods section, and for the four mortality scenarios used in this study. Figure 2 shows the results for the mortality scenario mu1, while the Supplementary material Appendix A1 Fig. A6, A7 and A8 present the results for mu2, mu3 and mu4, respectively. The resulting extinction patterns were different for plant and animal species, and they exhibited large divergences among removal sequences and between treatments of plant and animal removals. But the common result is that in all cases, except for the extinction patterns of plants in the low mortality scenario mu3 (Supplementary material Appendix A1 Fig. A7), AF decreased the number of species extinctions. Note that the effect of AF on the robustness of both plant and animal species was stronger when mortality rates were higher (i.e. mu1 and mu4 for animals; mu2 and mu4 for plants), since the extinction driven by species removal was very little under low mortality scenarios.

In the search for explanatory mechanisms for the observed patterns of species persistence, our results showed that the visits received by each individual plant (compare Fig. 3E and 3F) and the floral resources extracted by each individual animal (compare Fig. 4E and 4F) were both increased for specialist species when pollinators exhibited AF. These increments were particularly strong in pollinators that were specialists on generalist plants, and for plants that were specialists on generalist animals, which remarkably resulted in very similar visitation rates received by all individual plants and also very similar amounts of floral resources extracted by all individual animals. Moreover, the population densities of plants became very even across all species (compare Fig. 3C and 3D) and those of animals increased their evenness in relation to the system without AF (compare Fig. 4C and 4D). Without AF, the network resulted to be composed of a few super-generalist pollinator species exhibiting high densities and many specialist pollinator species displaying very low densities (Fig. 4C). Therefore specialist plant and animal species were less prone to extinction in the system with AF (Fig. 3B, 4B) as compared to the system without AF (Fig. 3A, 4A). Finally, Fig. 5 shows that pollinators exhibiting AF and interacting with two or more plant species allocated higher foraging efforts to their most specialist plant species.

Discussion

Pollination systems are recognized as critical for the maintenance of biodiversity in terrestrial ecosystems (Thompson 1994). Therefore, the understanding of mechanisms that promote integrity of those mutualistic assemblages is an important issue for the conservation of biodiversity and associated ecosystem function. In this study we found that the incorporation of AF into the dynamics of a pollination network increased the persistence and diversity of its constituent species (Fig. 1, Supplementary material Appendix A1 Fig. A2–A5), and reduced secondary extinctions of both plant and animal species driven by primary species loss (Fig. 2 and Supplementary material Appendix A1 Fig. A6–A8). These central findings were best explained by the following underlying processes: 1) AF increased

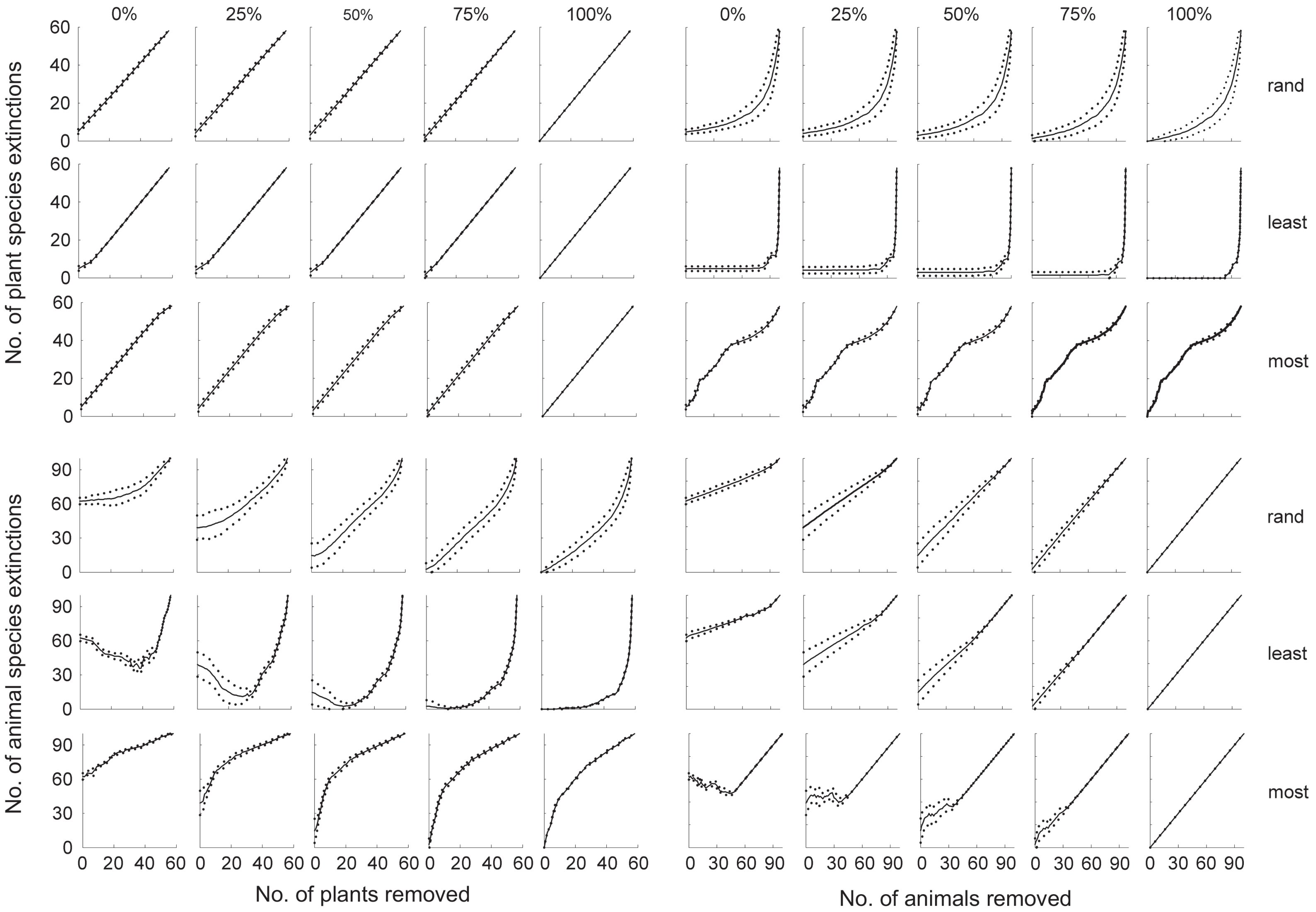

Figure 2. The effect of AF on the robustness of Mauritian pollination network. Extinction patterns of plants and animals after the sequential removal of plant and animal species. This and the following figures show the results for the LFR model parameterized with mortality scenario mu1 (see Fig. A6–A8 for the other mortality rates scenarios). In each quadrant, sequential removals were organized in rows (from top to bottom: random, least to most connected and most to least connected species), while in the columns are plotted 0, 25, 50, 75 and 100% pollinators exhibiting AF. Solid lines show the mean of 100 model runs, and dashed lines show 95% confidence intervals.

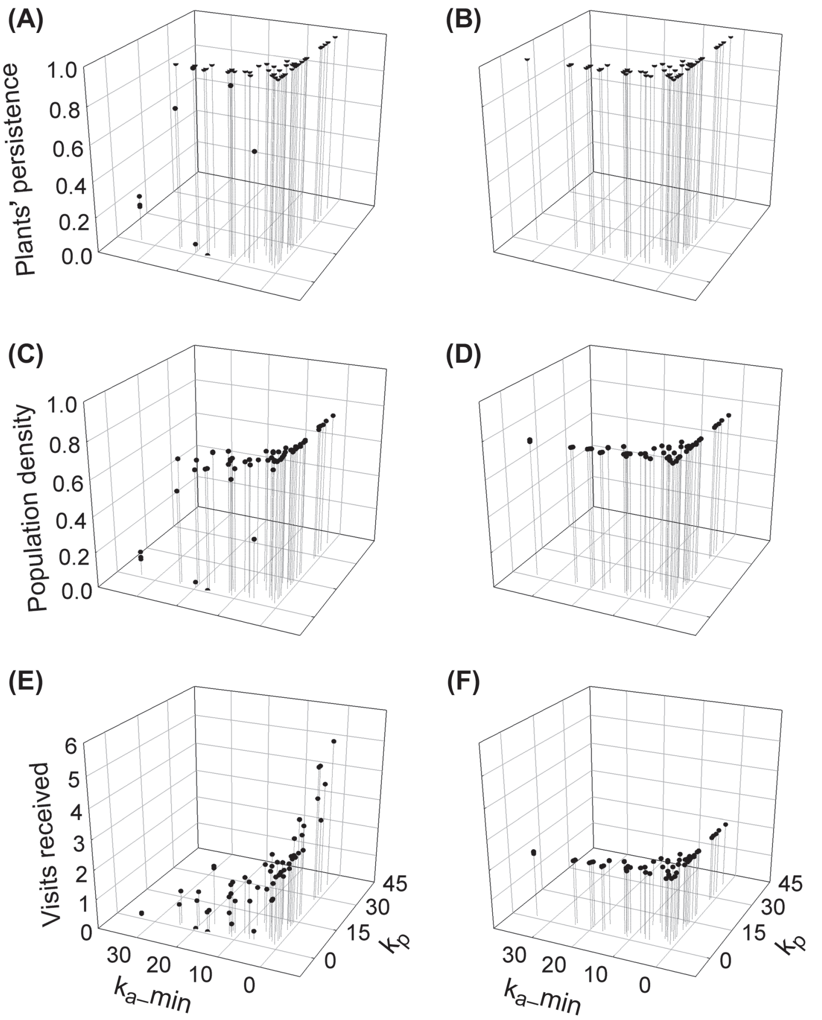

Figure 3. Explanatory mechanisms for plants. Persistence (fraction of the 100 simulations that a species persisted at the end), population density and visits received (averaged over 100 simulations) of each plant species, against its own degree (k_p) and the minimum degree of its visitor species (k_a_min), for systems whose pollinators did not (A, C and E) and did (B, D and F) exhibit AF.

the amount of floral resource extracted by specialist pollinators (Fig. 3), and 2) AF raised the visitation rates received by specialist plants (Fig. 4). Here, we propose that the main mechanism by which AF enhanced those processes is (trophic) niche partitioning among animals, which in turn generates (pollen vector) niche partitioning among plants.

AF and niches partitioning in nested pollination networks

There is ample evidence that interactions in natural pollination networks exhibit a nested structure (Bascompte et al. 2003, Thébault and Fontaine 2010). In a nested web, the interactions of specialist species are subsets of the interactions of the more generalist species. Accordingly, generalists interact with both generalists and specialists, while specialists tend to interact only with generalists. Thus, nestedness in pollination networks results in most pollinators sharing the rewards offered by the most-connected plants, and in most plants sharing the pollination service given by the most-connected animals. In this setting, specialist pollinators might be at a disadvantage compared to generalist species in terms of available resources, since generalists usually exhibit elevated visitation rates that tend to monopolize the rewards offered by their interacting plants (Vázquez et al. 2005). Likewise, specialist plants might be at a disadvantage compared to generalists in terms of the frequency of visits received (Mitchell et al. 2009).

Our results showed that, because of the high number of pollinators sharing and depleting the floral resources of the most-generalist plants, pollinators exhibiting AF assign higher foraging efforts to their specialist plants (Fig. 5). Previous studies have found that when two nectarivorous species compete for the rewards of two plant species, AF promotes resource partitioning (Rosenzweig 1981, Pyke 1982, Harder 1985, Possingham 1992, Rodríguez-Gironés and Santamaría 2005). In agreement with our results, this competition for floral resources favors the exploitation of specialist plants by generalist pollinators and of generalist plants by specialist pollinators (Rodríguez-Gironés and Santamaría 2005). Consequently, floral resources of generalist plants were released for their specialist pollinators, which enhanced their floral resource extraction (Fig. 4F), increased their population densities (Fig. 4D) and increased their persistence probabilities

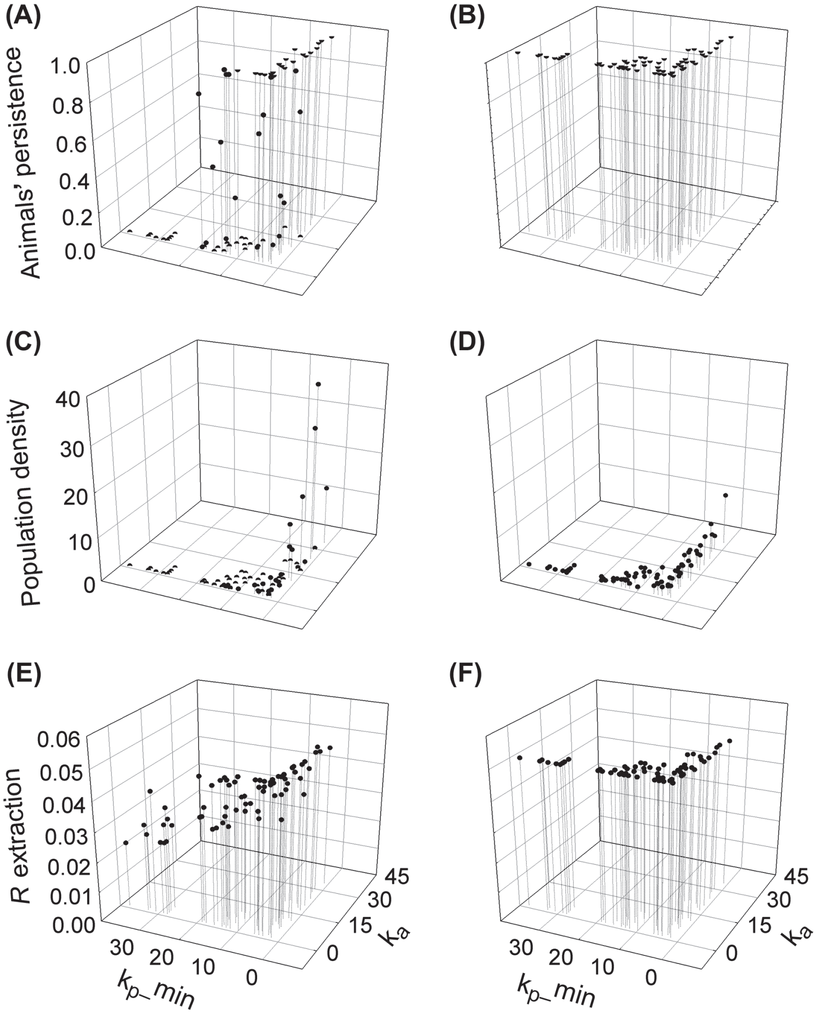

Figure 4. Explanatory mechanisms for animals. Persistence (fraction of the 100 simulations that a species persisted at the end), population density and resource extraction (averaged over 100 simulations) of each animal species, against its own degree (k_a) and the minimum degree of its plant species (k_p_min), for systems whose pollinators did not (panels A, C and E) and did (panels B, D and F) exhibit AF.

(Fig. 4B). Note that the increase in population density of these pollinator species was small but statistically significant (data not shown). Likewise, this specialization process of generalist pollinators to specialist plants raised the visitation rate received by the specialist plants, generating a homogeneously distributed frequency of visits among the individuals of all plant species (Fig. 3F). In this way, the pollination niche of plants was partitioned into generalist pollinators that mostly visit specialist plants and specialist pollinators that mostly visit generalist plants. This niche partitioning among plants and among animals explain the general increase of the population densities and persistence of the species of the network (Fig. 1, Supplementary material Appendix A1 Fig. A2–A3), in addition to the general increment of evenness observed among species abundances (Fig. 3, 4).

AF and the competition among species for shared partners in nested networks

The hypothesis of competition among pollinators for floral resources is supported by the non-monotonic curves of the extinction patterns of animals for mortality scenarios mu1 (i.e. low mortality rates for plants and high mortality rates for animals, Fig. 2) and mu3 (i.e. low mortality rates for both plant and animal species, Supplementary material Appendix A1 Fig. A7), when plants were removed from least to most connected species, and when pollinators were removed from most to least connected species. These graphs indicate that when pollinators did not exhibit AF, the removals of super-generalist pollinators or specialist plants increased the persistence of animal species. These results suggest that when super-generalist pollinators were removed, floral resources were released in favor of specialist pollinators, increasing their ability to persist. Likewise, when specialist plants were removed total floral resources for super-generalist pollinators decreased, slowing down their positive population growth rates and suppressing their monopolization of the resources shared with specialist pollinators. To test these hypotheses, we measured the amount of floral resources extracted by the pollinator species that are specialist to super-generalist plants (SPSGP, i.e. pollinator species with only one interaction that visit plants with more than 27 interactions).

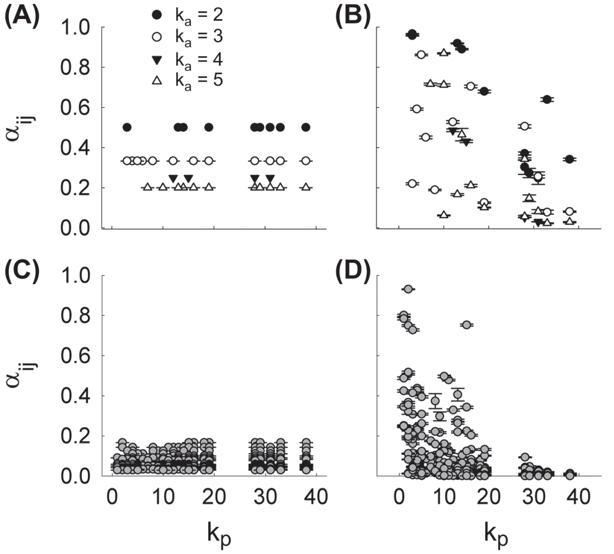

Figure 5. The effect of AF on the distribution of foraging efforts. Foraging effort (α_{ij}) that each animal of the network allocated to each of its interacting plants, against the number of interactions of the same plants (k_p). Graphs A and B show the foraging efforts of non-generalist animals, whose number of interactions k_a were 2, 3, 4 and 5. Graphs C and D show the foraging efforts of generalist and super-generalist animals, whose number of interactions were above 6. The 51 animal species with only one interaction are not shown, since their unique α_{ij} had a fixed value of 1.

This was measured when plants were removed from least to most connected species, and when pollinators were removed from most to least connected species (Supplementary material Appendix A1 Fig. A9). For the case of pollinators without AF, Supplementary material Appendix A1 Fig. A9 shows that floral resource extraction by SPSGP species increased when 30 to 50 species of specialist plants were removed; while the opposite occurred when pollinators exhibited AF. On the other hand, resource extraction by SPSGP species always increased with the number of generalist animals that were removed. Similar arguments explain why these monotonic curves did not appear for removal sequences in high mortality scenarios of plants (i.e. mu2 and mu4), since there were not enough floral resources for strong competitive exclusion.

Regarding competition among plant species for the pollination service, Fig. 3 suggests that AF relaxed its quantitative component (i.e. competition for pollination based on frequency of visits, Mitchell et al. 2009). The initially heterogeneous distribution of visits received by each individual plant of all network species (Fig. 3E) was converted into a homogeneous one (Fig. 3F), where every individual plant received a similar frequency of visits. Conversely, little effect was exerted by AF on the qualitative component of competition for pollination (based on purity of pollen loads, Mitchell et al. 2009), since the fraction of visits that ends in a pollination event for each individual plant (the variable σ_{ij}/p_i in the model) maintained a heterogeneous distribution when pollinators exhibited AF (Supplementary material Appendix A1 Fig. A10), with generalist plants obtaining the higher pollination quality from the visits. However, in agreement with Benadi et al. (2012), our results showed that the competition among plants for recruitment was more important in controlling plant densities than competition for pollination (data not shown). This hierarchy of competition processes explains the asymmetry between the effects that AF exerted on animal and plant species (Fig. 1–4, Supplementary material Appendix A1 Fig. A2–A8).

AF and the diversity of pollination networks

Despite the vast progress in our understanding of the structure and dynamics of pollination networks (Bascompte et al. 2003, Jordano et al. 2003, Fortuna and Bascompte 2006, Okuyama and Holland 2008, Ramos-Jiliberto et al. 2009, 2012, Valdovinos et al. 2009, Holland and DeAngelis 2010, Benadi et al. 2012), how biodiversity is shaped in these systems is still an open question. Recently, Bastolla et al. (2009) demonstrated analytically that nestedness reduced interspecific competition among plants and among animals, enhancing the number of coexisting species. They found that nestedness increases the number of shared partners, also due the indirect positive effects among species outweighing the negative effects, which arise from direct inter-specific competition and are independent of nestedness. As a consequence, the coexistence of species is enhanced by nestedness. However, these results may be attributed to certain unrealistic assumptions of their model. In particular, the competition among species is simply defined as phenomenological negative effects among competing populations, the dynamics of floral resources is disregarded, and the interactions among plant and animal species are not defined by the visits that animals make to plants. Therefore, indirect competition among species mediated by shared partners (i.e. competition among animals for floral resources and among plants for animal visits) is overlooked. Conversely, the assumptions of our model allow the emergence of indirect competition among species. Therefore as nestedness increases the number of shared partners the indirect competition among plants is greater for shared pollinators, and vice versa. Nevertheless, we found that this competition is relaxed by niche partitioning generated by the ability of pollinators to adaptively prefer plants with a lower load of pollinator visits. Thus, for pollination systems in which indirect competition occurs among plant species for shared pollinators (Hegland et al. 2009, Mitchell et al. 2009) and among animal species for shared plants (Zimmerman and Pleasants 1982), AF could be regarded as an important mechanism that allows the maintenance of species diversity.

Conclusions

Our study presents a new model for the population dynamics of plants and their interacting pollinators embedded in complex networks. The model represents an advance in relation to previous ones (Bascompte et al. 2006, Fortuna and Bascompte 2006, Okuyama and Holland 2008, Bastolla et al. 2009, Holland and DeAngelis 2010, Benadi et al. 2012) by incorporating a few essential ingredients of pollination biology. In particular, the model incorporates the dynamics of floral resources, which allowed us to address competition among animals for floral resources. The model also includes the dynamics of the visits that animal species allocate to each of their host plants, which allowed us to analyze competition among plants for pollinator visits. This model can be used to address a wide spectrum of questions related to pollination ecology. The incorporation of AF into the dynamic model drove niche partitioning and specialization, which enhanced population growth of both plant and pollinator species. This promoted species diversity and network robustness to species loss. Our results suggest that nested pollination networks may maintain their stability and diversity by the adaptive foraging of generalist pollinators.

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Supplementary material (available as Appendix O20830 at <www.oikosoffice.lu.se/appendix>). Appendix A1: Table A1, Fig. A1–A10.