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Effects of Network Structure and Adaptive Foraging on Pollination Systems

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Fernanda Sofía Valdovinos Urrutia

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Director de Tesis Dr: Rodrigo Ramos
Dr: Diego Vázquez

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Fernanda Sofía Valdovinos Urrutia

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Director de Tesis:
Dr. Rodrigo Ramos.

Co-Director de Tesis
Dr. Diego Vázquez

Comisión de Evaluación de la Tesis

Dr. Ramiro Bustamante

Dr. Rodrigo Vázquez

Dr. Sergio Navarrete

Dr. Fernando Córdova


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A mi familia

Biography



Fernanda Valdovinos got her undergraduate degree in Environmental Biology in 2008 at the Faculty of Science of the University of Chile. She began her PhD at 2009 in science, mention in Ecology and Evolutionary Biology also at University of Chile with the support of a CONICYT grant. During the last period of her PhD program (2012-2013), Fernanda won Chilean government grants to visit labs that are pioneers and world leaders in the study of complex systems in ecology. Specifically, one 2-month visit to the Integrative Ecology Group of CSIC in Sevilla to work with Dr. Jordi Bascompte and a 1-month and another 3-month visit to the Pacific Ecoinformatics and Computational Ecology (PEaCE) Lab in Berkeley to work with Dr. Neo Martinez. Since April 2013, Fernanda has been working as a Research Intern in PEaCE Lab to finish her PhD thesis in collaboration with Dr. Neo Martinez.

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Effects of Network Structure and Adaptive Foraging on Pollination Systems

Fernanda S. Valdovinos

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Effects of Network Structure and Adaptive Foraging on Pollination Systems

Summary

Our human existence depends on the function and stability of ecological systems. Better understanding of these properties of ecosystems is needed to stop or at least reduce the degradation of ecosystems by human activities. This dissertation embraces the architecture of interactions among the species in a community and the adaptive behavior of organisms responding to environmental changes as primary determinants of the function and stability of ecosystems. I did this by more explicitly modeling networks of feeding and reproductive interactions among plants and animals to better understand how the structure and function of these networks affect the stability of ecological communities facing two major anthropogenic challenges; species extinctions and biological invasions. By computationally exploring our model, I discovered that adaptive foraging of pollinators appears to interact with the structure of pollination networks to stabilize pollination systems against species extinctions by apparent altruism. Apparent altruism occurs in these systems when adaptive pollinators decrease their own abundance while increasing that of specialists by effectively ceding resources to those fixed foragers, which ultimately stabilizes the networks against the extinction of highly specialized pollinators. This counterintuitive finding suggests that classically selfish interactions may be effectively altruistic not only in plant-pollinator networks but also in other types of complex networks. I also found that more complex plant-pollinator communities are more resistant to species invasions, and that adaptive

foraging increases community resilience to species invasions. A more holistic consideration of these systems by including more trophic levels such as herbivores and other consumers is still needed to generate more complete understanding of the functioning and stability of ecosystems.

Resumen

Nuestra existencia humana depende de la función y estabilidad de los sistemas ecológicos. Se necesita desesperadamente una mejor comprensión de estas propiedades de los ecosistemas para detener o al menos reducir la degradación de los ecosistemas producida por las actividades humanas. Esta tesis abarca la arquitectura de las interacciones entre las especies de una comunidad y la conducta adaptativa de los organismos (que responden a los cambios ambientales), como determinantes primarios de la función y la estabilidad de los ecosistemas. Esto se realizó mediante modelar más explícitamente redes de interacciones tróficas y reproductivas entre plantas y animales, para comprender mejor cómo la estructura y función de estas redes influyen en la estabilidad de las comunidades ecológicas enfrentando dos grandes amenazas antropogénicas: extinción de especies e invasiones biológicas. Mediante explorar computacionalmente nuestro modelo, descubrí que el forrajeo adaptativo de los polinizadores parece interactuar con la estructura de las redes de polinización para estabilizar estos sistemas contra la extinción de especies, mediante altruismo aparente. Altruismo aparente se produce en estos sistemas cuando polinizadores adaptativos disminuyen su propia abundancia, aumentando la abundancia y persistencia de los especialistas, mediante ceder efectivamente los recursos a aquellos forrajeadores fijos; lo que en última instancia estabiliza las redes contra la extinción de los polinizadores

altamente especializados. Este hallazgo contra-intuitivo sugiere que las interacciones clásicamente egoístas pueden ser efectivamente altruistas, no sólo en redes de plantas y polinizadores, sino también en otros tipos de redes complejas. También encontré que las comunidades de plantas-polinizadores más complejas son más resistentes a las invasiones de especies, y que el forrajeo adaptativo aumenta la resistencia comunitaria a la invasión de especies. Una consideración más integral de estos sistemas mediante la inclusión de los niveles tróficos como herbívoros y otros consumidores sigue siendo necesaria para generar una comprensión más completa del funcionamiento y la estabilidad de los ecosistemas.

General Introduction

Our human existence depends on the function and stability of ecological systems. Better understanding of these properties of ecosystems is needed to stop or at least reduce the degradation of ecosystems by human activities. This dissertation embraces two factors as primary determinants of the function and stability of ecosystems. These factors include the architecture of interactions among the species in a community and the adaptive behavior of organisms responding to environmental changes. Ecologists have highlighted the importance of these factors applied to ecological stability and consumer-resource interactions for decades. Here, I add more explicit consideration of reproductive interactions to classically studied networks of consumer-resource interactions known as food webs. To pollination biologists, it may seem just the opposite: that I am adding more explicit consideration of feeding interactions to networks of animals that enable plant reproduction by visiting and transporting the gametes of plants among their sexual organs. From both perspectives, my dissertation applies an integrative approach to complex plant-pollinator systems to understand how the network structure of feeding and reproductive interactions combined with the foraging behavior of consumers affects both the general stability of biological communities and the stability of these systems facing two major anthropogenic impacts, species extinctions and biological invasions. I did this by building with collaborators, a sophisticated mathematical model of network structure and dynamics that models trophic and reproductive interactions between plant and pollinator species more explicitly and synthetically than previous models from which ours is derived. By

computationally exploring the model, I discovered novel answers to traditional questions about mutualistic networks. Perhaps my most important finding is that adaptive foraging of pollinators appears to interact with the structure of pollination networks to stabilize pollination systems against species extinctions by apparent altruism. This is an ecological mechanism by which adaptive pollinators decrease their own abundance while increasing that of specialists by effectively ceding resources to those fixed foragers, which ultimately stabilizes the networks against the extinction of highly specialized pollinators. This counterintuitive finding suggests that classically selfish interactions may be effectively altruistic not only in plants-pollinators networks but also in other types of mutualistic networks and, even more generally, in other types of complex networks. Additionally, I found that as complexity of the plants-pollinators community increases, so does its resistance against species invasions, and that adaptive foraging by native pollinators increased the resilience of the communities to species invasions. This dissertation contributes significant new understanding of the factors that stabilize plant-pollinator assemblages. This is especially important because these systems are key promoters of terrestrial biodiversity and ecosystem functions. Still, more holistic consideration of ecological systems by including more trophic levels such as herbivores and other consumers would be a critical advance needed to generate more complete understanding of the functioning and stability of ecosystems.

Background and structure of this thesis

Back in 2008, as I was finishing my undergraduate thesis entitled “Structure and dynamics of pollination networks: the role of alien plants” (published in *Oikos* as

Valdovinos *et al.* 2009), the motivation of my doctoral research popped up. That study assessed the role of established alien species within a host community by analyzing the temporal changes in structural network properties driven by the removal of non-native plants, using a meta-population dynamics model (Fortuna & Bascompte 2006). By simulating the removal of alien plant species, I realized the importance of including the response of native pollinators to such removal to more realistically address the evolution of networks after species extinctions. Therefore, adaptive behavior of consumers started appealing my curiosity.

In addition, before and during my undergraduate thesis I worked on the topological property of nestedness applied to different types of networks (from biogeographic to species-interactions networks). Through the understanding on nestedness that I obtained with all this work plus the knowledge on pollination biology that I learnt during my undergrad studies, I was not convinced by the claim of previous works that nestedness stabilizes pollination systems (Fortuna & Bascompte 2006, Okuyama & Holland 2008). A perfectly nested structure in pollination networks means that specialist plants only depend on the visits of generalist pollinators, and specialist pollinators only depend on the floral resources of generalist plants. Consequently, specialist plants are pollinated only by pollinators carrying pollen of many other plant species and specialist pollinators forage on resources shared with many other animal species, which may cause extinction of specialists because of the high heterospecific pollen transference suffered by specialist plants and high resource competition suffered by specialist animals. Previous studies did not consider these costs of specialist species interacting with generalist species in nested networks since they only addressed the positive effects among mutualistic partners (Fortuna & Bascompte 2006, Okuyama & Holland 2008), which may explain their results supporting the stabilizing effect of

nestedness. All these thoughts encouraged me to pursue my doctoral research by generating, in conjunction with collaborators, a new population dynamics model that includes the negative effects of diluted pollen and depleted rewards as well as animals' adaptation to such dynamics, by more explicitly exploring trophic dynamics in pollination networks; which also allowed us to incorporate another essential element of consumers-resources systems, the widely observed preference of consumers for more available resources called adaptive foraging (Stephens & Krebs 1986). I used this model to address the effects of network structure and adaptive dynamics of pollinators on the stability of pollination systems in terms of species persistence, robustness against species extinctions, and resistance and resilience against species invasions.

In the first chapter of this thesis, I reviewed the studies that addressed the effects of adaptive trophic behavior on the structure and dynamics of complex food webs. By reviewing and synthesizing those studies, I developed my understanding on how to model adaptive foraging in population models of complex ecological networks and how to analyze its effects on their structure and dynamics. Specifically, I found that the best way to model adaptive foraging for my questions was by the replicator equation, which was included in our new model (see Valdovinos *et al.* 2010).

In the second chapter, we developed a novel population dynamics model that includes the adaptive dynamics of pollinators, the negative effect of pollinators' consumption on the dynamics of the floral rewards, and the pollen dilution on the body of pollinators visiting more than one plant species. The model was used to project the temporal dynamics of three empirical pollination network, in order to analyze how adaptive foraging of pollinators shapes the outcome of community dynamics in terms of biodiversity and network robustness to species loss (see Valdovinos *et al.* 2013).

In the third chapter, I assessed the interplay between the network structure and adaptive dynamics of pollinators that stabilizes pollination networks. By using 1200 stochastically generated network topologies to parameterize the model's equations of chapter 2 varying species richness, connectance and nestedness. I found that nestedness maximizes the stabilizing effect of adaptive foraging of pollinators by "Apparent Altruism", i.e. generalist pollinators decrease their own abundance while increasing that of specialists, which ultimately stabilizes the networks against the extinction of specialists. Interestingly, the predicted novel distribution of preferences among pollinators closely matches the observed empirical preferences.

In the fourth chapter, I evaluated the relative influence of adaptive foraging, network structure and the species' traits on the resistance and resilience of pollination networks to simulated species introductions. My specific questions were: 1) which network structures confer more resistance to biological invasions?, 2) which characteristics allow species to successfully invade new communities?, 3) how do traits of both native and alien pollinators affect invasion success and impacts of invasions?. I used the dynamics model of chapter 2 and simulated networks of chapter 3 to answer these questions.

CHAPTER 1

Consequences of adaptive behavior for the structure and dynamics of food webs

Abstract

Species coexistence within ecosystems and the stability of patterns of temporal changes in population sizes are central topics in ecological theory. In the last decade, adaptive behavior has been proposed as a mechanism of population stabilization. In particular, widely distributed "adaptive trophic behavior" (ATB), the set of individuals' responses to changes in their trophic environment leading to fitness enhancement, may play a key role in modulating the dynamics of feeding relationships within natural communities. In this article, we review and synthesize models and results from theoretical research dealing with the consequences of ATB on the structure and dynamics of complex food webs. We discuss current approaches, point out limitations, and consider questions ripe for future research. In spite of some differences in the modeling and analytic approaches, there are points of convergence: i) ATB promotes the complex structure of ecological networks, ii) ATB increases the stability of their dynamics, iii) ATB reverses May's negative complexity-stability relationship, iv) ATB provides resilience and resistance of networks against perturbations. Current knowledge supports ATB as an essential ingredient for models of community dynamics, and future research that incorporates ATB will be well-positioned to address questions important for basic ecological research and its applications.

I. Introduction

The coexistence of species in natural ecosystems and the stability of patterns of temporal changes in population sizes is a central topic in contemporary ecological theory (McCann 2000). Since the transformative work of May (1972), the earlier conventional wisdom that more diverse communities are more stable than simple communities (McArthur 1955; Hutchinson 1959) lost its hegemony. May (1972), using a mathematical approach to modeling dynamical systems and local stability as the stability criterion, demonstrated that the greater the number of interacting populations in a community, the more unstable the population dynamics tend to be. However, this result rests on simplifying assumptions that there are no constraints on the architecture of species interactions or in the magnitude of the interaction strengths (May 1972), whereas most natural populations appear to display dampened dynamics (Kendall *et al.* 1998), despite being embedded in complex communities (Pascual & Dunne 2006a). May (1972) encouraged scientists to find the biological mechanisms, the “devious strategies,” that promote the stability of real multispecies systems which, regarded simply as randomly interacting physical entities, would exhibit unstable dynamics. Since then, various stability concepts have been used in relation to food web organization and dynamics, including local stability of population densities, persistence of species in the community, and robustness of food webs to species loss (McCann 2000, Pascual & Dunne 2006b). Recently proposed mechanisms that appear to promote various aspects of stability of interacting species in complex systems include high incidence of omnivory (Fagan 1997), particular predator-prey body size ratios (Brose *et al.* 2006), and type III functional responses of predators (Williams 2008).

One mechanism of population stabilization that has received considerable attention among ecologists and evolutionary biologists is adaptive behavior exhibited by the individuals that compose populations (Abrams 2000; Bolker *et al.* 2003). For example, early predator-prey models for plankton systems included adaptive prey switching, which tends to stabilize dynamics (e.g. Fasham *et al.* 1990). Among the different types of adaptive traits suggested to have important implications for the dynamics and stability of populations are the adaptive behavior of prey in response to predation risk (Abrams 2000), the choice of optimal time for ontogenetic niche transition (Takimoto 2003), decisions related to microhabitat occupation (Ramos-Jiliberto & González-Olivares 2000), and optimal diet choice (Krivan & Sikder 1999). A few recent modeling studies of food web dynamics have begun to explore the implications of adaptive behaviors for the stability of complex ecological networks (e.g. Drossel *et al.* 2001; Kondoh 2003a; but see Matsuda & Namba 1989 for an earlier study). This area of theoretical research has developed quickly through work by a diverse group of researchers from different academic backgrounds using a variety of techniques, concepts and vocabularies (e.g. Drossel *et al.* 2001, 2004; Kondoh 2003a, 2006, 2007; Brose *et al.* 2003; Beckerman *et al.* 2006; Uchida *et al.* 2007; Uchida & Drossel 2008; Guill & Drossel 2008; Staniczenko *et al.* 2010). Given the major influence that adaptive behavior likely has on the functioning, stability, and persistence of natural communities, we undertake a review and synthesis of theoretical work dealing with the consequences of individuals' adaptive behavior on the structure and dynamics of complex food webs, discussing current approaches, their strengths and limitations, and questions ripe for future research.

Adaptive foraging (AF) exhibited by top predators has recently been proposed as an important driver of community persistence, through consumers' coupling of fast and slow

trophic pathways in the community as related to the abundances of their resources (Rooney *et al.* 2006, 2008). However, not only top consumers behave as adaptive foragers (Stephens & Krebs 1986). There are numerous empirical studies giving evidence that grazers and secondary consumers engage in AF; for example planktonic micro-crustaceans (DeMott 1989) and benthic invertebrates (Taghon 1982) in aquatic ecosystems, as well as birds (Shochat *et al.* 2004), small mammals (Giraldeau & Kramer 1982) and insects (Scheirs *et al.* 2002) in terrestrial ecosystems. Given the likely importance of top predator AF for community dynamics and the apparently widespread occurrence of AF across trophic levels and ecosystems, it may be a key aspect of how consumers interact with their resources within food webs, and a major ecological process that enhances stability and persistence of complex natural communities.

In addition to AF by consumers, organisms can respond adaptively to their consumers, both at ecological time scales in terms of the presence and abundance of consumers (Lima & Dill 1990; Harvell 1990), and at evolutionary time scales in terms of the strong selection pressure that consumers can exert on their resources (Lind & Cresswell 2005). We refer to changes in resource behavior in response to consumers as “adaptive resource responses” (ARR). Many types of ARR have been reported in the ecological literature. For example, organisms make behavioral decisions that take into account the current level of predation risk, affecting where and when they feed, reproduce, hide, and flee (Lima & Dill 1990). Environmental cues associated with changing levels of predation risk can trigger phenotypic changes in resource organisms (e.g., inducible defenses; Harvell 1990). Effective ARRs can significantly decrease the strength and rate of consumption (Lind & Cresswell 2005) and therefore are likely to alter dynamics of trophically



interacting populations (McCann *et al.* 1998), with impacts on community stability and persistence.

Thus, within any food web, in which most taxa play both consumer and resource roles, particular organisms will act both as adaptive foragers and as resources that avoid their consumers through adaptive responses. This widely distributed "adaptive trophic behavior" (ATB), the set of an individual's responses to changes in its trophic environment leading to fitness enhancement, may play a key role in modulating the structure and dynamics of feeding relationships among populations within natural communities. In what follows, we show that addressing the consequences of ATB for food web structure and dynamics gives insights into at least four core topics in community ecology, with important implications for conservation biology: 1) the incorporation of individuals' traits into understanding the features of food webs (DeAngelis & Mooij 2005; Woodward *et al.* 2005), 2) the potential mechanisms underlying the structure of empirical food webs (Pimm 1982; Williams & Martinez 2000), 3) the classic debate about complexity-stability relationships within communities (McArthur 1955; May 1972; McCann 2000), and 4) the biotic properties that support resilience and resistance of ecosystems to anthropogenic and other perturbations (Westman 1978; Levin & Lubchenco 2008). In the next section, we present a unified framework for assessing the most prominent approaches to including ATB in complex food web models, providing insight into topic 1. Then, we synthesize the theoretical results concerning the role of ATB in food webs in terms of its consequences on the structure and dynamics of those ecological networks, providing a way to link ATB with topics 2, 3, and 4. We finish by offering some perspectives on how the incorporation of ATB into food web structural and dynamical analysis and modeling opens new directions

for research that will advance ecological theory and its applications for conservation biology.

II. Modeling ATB within food webs: The interplay between adaptive traits dynamics and population dynamics

Food webs are ecological networks which denote who eats whom within communities (Pimm *et al.* 1991). Form and function of food webs can be characterized respectively by their topology and dynamics. The topology of food webs consists of the set of species that belong to the community, together with the architecture of trophic interactions linking them (Dunne 2006). Food web dynamics can refer to either the temporal changes in abundance or biomass of their constituent populations (i.e., population dynamics), or sequential changes in the topology of the network as nodes and/or links appear or disappear (i.e., structural dynamics, e.g., Stanizcenko *et al.* 2010).

When researchers mathematically model population dynamics of food webs, their equations usually take the form:

$$\frac{dN_j}{dt} = r_j N_j + \sum_{i \in R_j} e_{ij} g_{ij} N_j - \sum_{k \in C_j} g_{jk} N_k \quad (1)$$

where N_j is the population size of species j , in units of individuals number, biomass or density. Functions r_j , g_{ij} and e_{ij} are the intrinsic growth rate, functional response, and conversion efficiency of species j consuming species i , respectively. Function r_j is generally

set to zero for non-basal species. The biomass intake of species j that is converted into units of its population size is the sum of the intake from all of its food resources, $\{R_j\}$. Conversely, the population outflow is the sum of losses due to predation by all of its consumers, $\{C_j\}$.

Many implementations of this type of dynamical model treat species' traits as static. There are a number of dynamical food web modeling studies that allow for consumers to switch among resource species according to their relative biomasses, for example through the implementation of a Type III multispecies functional response (e.g., Brose *et al.* 2006; Williams 2008; Berlow *et al.* 2009; Brose & Dunne 2009). However, this is a form of passive resource switching that does not reflect explicit adaptive dynamics. As discussed previously, the traits and behaviors of organisms in the context of complex trophic interactions often change adaptively in response to their interactions with (or even the presence of) other organisms. Such adaptive trophic behavior (ATB) can result in a full array of organismal changes from behavioral change, through developmental plasticity, to changes in gene frequency (Abrams 2005). Despite the scant attention that it has received historically by community ecologists (Abrams 2001, 2005), adaptive trait dynamics may influence population dynamics of interacting species by affecting interaction strengths (Houston & McNamara 1999; Abrams 2001, 2005) and therefore community structure and stability (McCann 2000). Like other adaptive traits, ATB may influence food web dynamics on both ecological and evolutionary timescales (McCann *et al.* 1998; Abrams 2005). At the same time, ecological and evolutionary dynamics can influence the evolution of traits. Most foraging and anti-predator adaptations are frequency-dependent processes (Abrams 2005) as they depend on the relative frequencies of the interacting phenotypes. As a result, changes in population densities cause the fitness optima for trait values to vary,

thus promoting trait evolution (Abrams 2005). Therefore, traits and population dynamics shape each other at multiple time scales (Houston & McNamara 1999; Abrams 2001, 2005).

One of the first approaches to modeling adaptive trait dynamics was developed by Lande (1976). He generated phenotypically-based quantitative genetics models consisting of simple recursive relationships of the form $Z=h^2S$, where Z is the population mean trait value, h^2 is the heritability of the trait, and S is the differential of selection for the trait in the population. However, the incorporation of frequency-dependence in these models makes their analysis complicated (Day & Taylor 1996). Fortunately, there exists an approximation to this recursion that has a simple form and allows for frequency-dependence. This function defines the rate of change of Z varying at a rate proportional to the slope of fitness W with respect to the value of an individual's trait z (i.e., the fitness gradient or marginal fitness; Abrams 2005):

$$\frac{dZ}{dt} = c \frac{\partial W_j}{\partial z} \quad (2)$$

Although the choice of which specific trait z is considered will depend on the questions at hand and the modeling strategy, a recurring candidate in studies that include ATB is the amount of energy or time that individuals allocate to consuming resources (i.e., foraging efforts; e.g., Drossel *et al.* 2001; Kondoh 2003a) or avoiding consumers (i.e., anti-predator efforts; e.g., Matsuda *et al.* 1996; Uchida *et al.* 2007). Both effort types affect the consumers' capture efficiency of resource (Stephens & Krebs 1986; Harvell 1990; Lind & Cresswell 2005). The higher the foraging effort invested in a particular resource, the larger

the capture efficiency is of that resource (Stephens & Krebs 1986). Conversely, the higher the anti-predator effort of a resource against a consumer, the lower the capture efficiency of that consumer (Harvell 1990; Lind & Cresswell 2005). Hence, these efforts modulate the functional responses of consumers within a community. This modulation may be incorporated into a type I or a type II functional response as

$$g_{ij} = a_{ij}f_{ij}(1-v_{ji})N_i \quad (3a)$$

$$g_{ij} = \frac{a_{ij}f_{ij}(1-v_{ji})N_i}{1 + \sum_{i \in R_i} h_{ij}a_{ij}f_{ij}(1-v_{ji})N_i} \quad (3b)$$

respectively, where the capture efficiency $a_{ij}f_{ij}(1-v_{ji})$ is composed of the potential encounter rate a_{ij} , the foraging effort of species j on their resource i f_{ij} , and the anti-predator effort of i against j v_{ji} (Uchida & Drossel 2007).

Combining equations (1), (2), and (3a) or (3b) to model the interplay between ATB and population dynamics makes it possible to address the temporal changes of foraging and anti-predator efforts as a function proportional to the fitness gradient, taking the per capita population growth rate $G_j = dN_j/N_j dt$ as a measure of fitness W , that is

$$\frac{df_{ij}}{f_{ij} dt} = \kappa_j \frac{\partial G_j}{\partial f_{ij}} \quad (4a)$$

$$\frac{dv_{kj}}{v_{kj} dt} = \kappa_j \frac{\partial G_j}{\partial v_{kj}} \quad (4b)$$

where κ_j and κ'_j are the adaptation rates of foraging and avoidance efforts of species j , respectively. If $\kappa_j < 1$ or $\kappa'_j < 1$, adaptation is slower than population dynamics and the shift of strategies reflects changes in the gene frequencies within the population j , while $\kappa_j > 1$ or $\kappa'_j > 1$ represents faster adaptive trait changes acquired through behavioral responses (Guill & Drossel 2008).

However, system (4) is incomplete because it ignores constraints on natural selection (sensu Lloyd & Venable 1992). A fundamental constraint is represented by allocation costs (Futuyma 2001), derived from the impossibility of individuals infinitely and simultaneously assigning energy and/or time to every task, since they have a finite available total effort to allocate across their activities. This constraint can be expressed as

$$\sum_{i \in R_j} f_{ij} + \sum_{k \in C_j} v_{jk} = 1 \quad (5)$$

The combined system (4) and (5) represents rules of evolution for adaptive foraging and anti-predator efforts. Obtaining the optimal set of these efforts represents a constrained optimization problem, which consists of finding the set of foraging $\{f_{ij}^*\}$ and anti-predator $\{v_{kj}^*\}$ efforts that maximize the corresponding fitness gradient in (4) restricted to (5), and following population dynamics rules of equation (1) with functional responses (3a) or (3b) (Matsuda *et al.* 1996; Uchida *et al.* 2007). The available mathematical technique for solving this problem is the Lagrange Multipliers, which results in a system of replicator equations (Lloyd & Venable 1992; Matsuda *et al.* 1996; Uchida *et al.* 2007)

$$\frac{df_{ij}}{dt} = \kappa_j f_{ij} \left(\frac{\partial G_j}{\partial f_{ij}} - \gamma \right) \quad (6a)$$

and

$$\frac{dv_{kj}}{dt} = \kappa_j v_{kj} \left(\frac{\partial G_j}{\partial v_{kj}} - \gamma \right) \quad (6b)$$

with $i = 1, 2, \dots, \#R_j$ and

$$\gamma = \sum_{i \in R_j} f_{ij} \frac{\partial G_j}{\partial f_{ij}} + \sum_{k \in C_j} v_{kj} \frac{\partial G_j}{\partial v_{kj}} \quad (6c)$$

System (6) is an optimal strategy, which defines that each f_{ij} and v_{kj} grows whenever its fitness gradient is higher than the fitness gradient averaged over all of j 's efforts, γ , and decreases when it is lower than γ . In that context, individuals of population j will increase their foraging efforts on i or their anti-predator efforts against k if their payoffs are higher than increasing their efforts on any other resource or against any other consumer. These adaptive dynamics will reach an equilibrium (i.e. $df_{ij}/dt = dv_{kj}/dt = 0$ for every i and k) when the marginal fitness of all efforts become equal; that is when there are not potential changes in any effort that will enhance the per capita growth rate of the population. In this way, the equilibrium solution $\{f_{ij}^*\}$ and $\{v_{kj}^*\}$ of system (6) is both the solution of the constrained optimization problem and an evolutionary stable strategy (ESS) (Hines 1987; Lloyd & Venable 1992; Matsuda *et al.* 1996; Uchida *et al.* 2007).

Note, however, that the population dynamics described by (1) and (3a) incorporating both AF (adaptive foraging) and ARR (adaptive resource responses) determine that all $\{v_{kj}\}$ go to zero since the per capita population growth rate G_j is always negative unless no effort

is being allocated to consumer avoidance (Uchida *et al.* 2007). Thus, under the framework of (1) with linear functional responses (3a) we can only model AF or ARR, but not both simultaneously. Nevertheless, positive values of $\{v_{kj}^*\}$ are ensured, even in presence of AF, when assuming that foraging contributes to the growth rate in a nonlinear way, that is

$$\frac{dN_j}{dt} = B \left(\sum_{i \in R_j} a_{ij} f_{ij} (1 - v_{ji}) N_i \right) N_j - \sum_{k \in C_j} g_{jk} N_k \quad (7)$$

with $B(z) > z$ (Uchida *et al.* 2007). This condition is achieved by $B(z) = \beta z / (1 + \beta z)$ (i.e. type II functional response) or $B(z) = \sqrt{z}$, whenever $0 < z < 1$ (e.g. Matsuda *et al.* 1994, 1996), which reflects the fact that the use of food becomes inefficient when large quantities are consumed. Another way to ensure positive values of $\{v_{kj}^*\}$ is to assume non-linear constrains in the allocation cost of (5), that is

$$\sum_{i \in R_j} f_{ij}^x + \sum_{k \in C_j} v_{jk}^x = 1 \quad (8)$$

where $x > 1$ represents that consumers have access to other resource while they are searching for a specific one, and that specific anti-predator responses may also allow avoidance of attacks by other consumer species (Table 1).

Table 1. Different combinations of adaptive and population dynamics modeling approaches used to include ATB (adaptive trophic behavior) within complex food webs. In bold are the

few works that have modeled ARR (adaptive resource responses). x represents both effort types f_{ij} and v_{kj} .

Adaptive dynamics	ATB equations	Functional response	Constraints	References
Replicator-based	$\frac{dx_{ij}}{dt} = kx_{ij} \left(\frac{\partial G_j}{\partial x_{ij}} - \gamma \right)$	type I	linear allocation costs	Kodoh 2003a, 2007
		type II or similar	linear allocation costs	Matsuda <i>et al.</i> 1996; Kodoh 2003b, 2005, 2006; Brose <i>et al.</i> 2003; Uchida & Drossel 2007; Uchida <i>et al.</i> 2007; García-Domingo & Saldaña 2007, 2008
			non-linear allocation costs	Uchida & Drossel 2007; Uchida <i>et al.</i> 2007
			trade-off with intrinsic growth rate	Matsuda <i>et al.</i> 1996
Game Theory-based	$f_{ij} = \frac{g_{ij}}{\sum_k f_{kj}}$	ratio-dependent	linear allocation costs	Drossel <i>et al.</i> 2001, 2004; McKane 2004; Quince <i>et al.</i> 2005a,b; Powell & McKane 2008; Powell & Boland 2009
			predator-dependent	linear allocation costs
Solitary optimal-based	$\frac{\sum_{i=1}^k \lambda_{ij} E_i}{1 + \sum_{i=1}^k \lambda_{ij} H_{ij}}$	type II	animal and mathematical assumptions	Beckerman <i>et al.</i> 2006; Petchey <i>et al.</i> 2008

Besides the optimal strategy based on the replicator equation described in (6a), other ways have been developed for incorporating AF into the dynamics of complex food webs

(Table 1). For example, Drossel *et al.* (2001) assume that the total foraging effort of any species j is allocated so that the gain per unit effort g_{ij}/f_{ij} is equal for all $\{R_j\}$. This is satisfied by the expression

$$f_{ij} = \frac{g_{ij}}{\sum_{i \in \{R_j\}} f_{ij}} \quad (9)$$

Note that Drossel *et al.* (2001) *a priori* assume that consumers exhibit an ideal free distribution across resources (Fretwell & Lucas 1970), which requires a continuous updating of the efforts values in (9) that depends recursively on the functional response g_{ij} (Drossel *et al.* 2001; Quince *et al.* 2005b). In this way, equation (9) also leads to an ESS (Drossel *et al.* 2001), an important feature of the ideal free distribution (Fretwell & Lucas 1970). Since the derivation of equation (9) uses principles from game theory combined with ratio-dependent functional responses (see Appendix in Drossel *et al.* 2001), we refer to this type of adaptive dynamics modeling as a game theory-based approach (Table 1).

Another approach used to include AF in complex food web dynamics relies on optimal foraging theory (Stephens & Krebs 1986). Beckerman *et al.* (2006) employed the optimal diet breadth model (Stephens & Krebs 1986) for projecting the instantaneous number of links that each species is expected to have within an empirical food web. This model defines how many resources should be optimally included in the diet of an individual of the species j K_j , considering the net energy E_i , encounter rate λ_{ij} , and handling time H_{ij} that it experiences by consuming an individual of species i (Stephens & Krebs 1986; Beckerman *et al.* 2006). By sorting resources in a decreasing order of profitability (i.e. E_i/H_{ij}), the

model projects the optimal value of diet breadth K_j that maximizes the per-capita total rate of food intake of j , G'_j

$$G'_j = \frac{\sum_{i=1}^{K_j} \lambda_{ij} E_i}{1 + \sum_{i=1}^{K_j} \lambda_{ij} H_{ij}} \quad (10)$$

where λ_{ij} is defined as the product between the attack A_{ij} and the resource density N_i . In this way, population density of resources but not that of consumers determines λ_{ij} (Stephens & Krebs 1986; Beckerman *et al* 2006), and hence this model assumes that there is not frequency-dependence. This point constitutes the biggest difference between game theory and optimality theory approaches (Giraldeau 2008), since that optimal value does not necessarily constitute an evolutionarily stable strategy (ESS).

In summary, three major approaches have been used to model AF within complex food webs (Table 1). The game theory approach, replicator approach, and optimality theory approach form a frequency dependence gradient. The replicator approach is the most general of the three approaches, as it converges to the same behavior as the game theory approach (i.e., a long-term foraging effort allocation leading to an ideal free distribution across resources) when the foraging effort is frequency dependent. The replicator approach converges to the same behavior as the optimality theory approach (i.e., consumers feeding on the most profitable resource) when the foraging effort does not depend on the dynamics of the entire food web (Uchida *et al.* 2007). Since the replicator equation is based on fitness

gradients, it is useful for modeling a broad array of traits (e.g., anti-predator effort), a property that is not shared by the other two approaches.

Extensions to the theory presented above include the incorporation of other costs of ATB, such as a trade-off between anti-predator efforts and intrinsic growth rate of resources (Matsuda *et al.* 1996; Table 1), the consideration of different functional responses (Table 1), and the modeling of ARR that are effective against many consumer species, for example

$$\frac{dv_j}{dt} = \kappa_j (1 - v_j) v_j \frac{\partial G_j}{\partial v_j} \quad (11)$$

which assumes that the defense v_j is effective against all of j 's consumers (e.g. Matsuda *et al.* 1994, 1996; Kondoh 2007).

III. Consequences of ATB on the structure and dynamics of food webs

Based on an analysis of the dynamical properties of the models presented above, there are a number of theoretical studies that have addressed the consequences of ATB for the structure and dynamics of complex food webs. In spite of some differences in the modeling and analytic approaches adopted by different researchers, that are some central points of convergence in their findings about the results of ATB. These points are: i) ATB promotes the complex structure of those networks, ii) ATB increases the stability of their dynamics, iii) ATB inverts May's negative complexity-stability relationship, and iv) ATB provides resilience and resistance to ecological networks against external perturbations that generate

changes in species composition or species abundances (Table 2). In this section we synthesize the main results of studies addressing these issues.

Table 2. Structural and dynamical consequences of ATB in complex food webs. In bold are the studies that have modeled ARR. Stability includes both persistence and robustness.

Consequences	Non-Adaptive	Adaptive	References
<i>Structural</i>			
Number of species	Poorer	Richer	Guill & Drossel 2008
Realized connectance	Equal to the potential one	Lower than the potential one	Kondoh 2003a,b; 2005, 2006, 2007; Beckerman <i>et al.</i> 2006; Guill & Drossel 2008; Uchida <i>et al.</i> 2007; Uchida & Drossel 2007; Matsuda & Namba 1991
	Equal to the potential one	Equal to the potential one (with non-linear constraints on efforts) Higher when defenses are specific rather than general	Uchida <i>et al.</i> 2007; Uchida & Drossel 2007 Matsuda <i>et al.</i> 1994, 1996
Number of trophic levels	Fewer than field food webs	Closer to field food webs	Drossel <i>et al.</i> 2004; Guill & Drossel 2008; Uchida & Drossel 2007
Effect of enrichment	None	Increase the number of species	Guill & Drossel 2008
Effect of body size	None	Increase the number of trophic levels	Guill & Drossel 2008
<i>Dynamical</i>			
Stability	Less permanent	More permanent	Uchida <i>et al.</i> 2007; Matsuda <i>et al.</i> 1996
	Less persistent	More persistent	Kondoh 2003a, 2005, 2006, 2007; Brose <i>et al.</i> 2003; Uchida & Drossel 2007 Matsuda <i>et al.</i> 1996
		Persistence is higher when resource's defenses are specific rather than general	Matsuda <i>et al.</i> 1996
Response to external perturbations	Fragile to species removal	Robust to species removal	Uchida & Drossel 2007; Quince <i>et al.</i>

	Fragile to species invasion or speciation	Robust to species invasion or speciation	2005b Drossel <i>et al.</i> 2001; Guill & Drossel 2008 Kondoh 2003a, 2006; Uchida & Drossel 2007
Stability-potential connectance relationship	Negative	Positive	
	Negative	Negative	Brose <i>et al.</i> 2003
	Negative	Unimodal (specific defenses), negative (general defenses)	Kondoh 2007
Persistence-richness relationship	Negative	Negative	Uchida & Drossel 2007
Robustness-richness relationship	None	Positive	Uchida & Drossel 2007

i) Structural consequences

Since the beginning of ecology as a scientific discipline, the characterization and analysis of food web structure has occupied a central place (e.g. Elton 1927, 1958; MacArthur 1955; Watt 1964), and has provided a basis for assessing the relationship between community structure and community stability and function (Odum 1953; MacArthur 1955; Elton 1958; Watt 1964; Pimm 1982, 1991; Dunne 2006; Stouffer & Bascompte 2010). Nevertheless, only recently have appropriate tools and enough computational power for dealing with complex communities been available to ecologists. In the search for simple rules of community structure that generate complex food webs with properties resembling those of natural ones, several simple, one-dimensional network models have been proposed (Cohen *et al.* 1990; Williams & Martinez 2000; Cattin *et al.* 2004; Stouffer *et al.* 2005). The niche model (Williams & Martinez 2000) and its variants (Cattin *et al.* 2004; Stouffer *et al.* 2005; Allesina *et al.* 2008) predict many aspects of food web structure reasonably well (Stouffer *et al.* 2005, 2007; Williams & Martinez 2008; Allesina *et al.* 2008), but they are

phenomenological and do not give a mechanistic basis for explaining structure (Loeuille & Loreau 2005). Other studies which we subsequently describe suggest that AF may be an explanatory mechanism underlying the structure of complex natural food webs. However, the comparison between predicted and observed structural properties has been confined to a small number of network properties, more limited than those analyzed from networks assembled using the niche model and its variants.

Petchey *et al.* (2008) proposed an “allometric diet breadth model” (ADBM) for food web structure based on solitary optimal theory (Table 1). The ADBM contains parameters representing species richness S , encounter rates, handling times, and energetic values of resources. That model uses equation (10) to construct the network of interactions by assuming that every species in the network is a potential resource for every other species. Species richness S is obtained from the empirical food web, while the remaining parameters are calculated from body masses of consumers and resources through empirical relationships. This model, which incorporates AF, predicts 5% to 65% of the links in 15 empirical food webs. In addition, the model produces mean standardized errors (MSE) for a set of 12 network structure properties (e.g., mean trophic level, mean path length, proportion of species that are omnivores, etc.) that fall within the range of MSE for the niche model for 12 of the 15 webs. While not as simple as the prior structural models, the ADBM predicts specific links, reproduces the phenomenological rules used in those models, and provides a mechanistic basis for suggesting that AF may underlie the generation of complex food web structure observed natural systems.

Beckerman *et al.* (2006) introduced the use of the solitary optimal model, but with a parameterization based on published type II functional responses spanning a wide range of taxa, instead of allometric equations. This earlier “diet breadth model” (DBM) predicts

species diet breadths that are similar to those observed in empirical food webs. In both the DBM and ADBM, the network of feeding interactions is created by successively applying equation (10) to each species as a consumer, assuming that all individuals of each species are identical and that all food web species can be preyed upon (Beckerman *et al.* 2006; Petchey *et al.* 2008). Therefore, the maximal potential diet breadth of each species is $S-1$. However, equation (10) restricts the resources that each species consumes to those that are the most profitable for the consumer. As a result, highly constrained values of food web connectance ($C=L/S^2$) emerge as a consequence of individual optimal foraging behavior (Beckerman *et al.* 2006). In this way, the DBM predicted well both the level of connectance and the relationship between connectance and species richness of empirical food webs. Note, however, that Allesina (2010) questioned the utility of ADBM and DBM as predictors of trophic relationships, demonstrating a strong similarity between the results of the ADBM and those of the niche model and its variants, which include fewer parameters. This analysis favors simpler models which may represent simpler mechanisms of community structuring (Allesina 2010). Nevertheless, it is plausible that adaptive foraging might be the biological mechanism underlying the rules of simple models, which have been criticized as lacking of mechanistic basis for explaining structure.

The restricted connectance predicted by Beckerman *et al.* (2006) is a key outcome of most models that include AF in complex food webs, independent of the specific model in use (e.g. Kondoh 2003a, 2005, 2006; Uchida *et al.* 2007; Guill & Drossel 2008; Table 2). Generalist foragers are morphologically and physiologically able to consume various types of food items, but they are also able to choose a subset of them as a function of their profitabilities and abundances (Stephens & Krebs 1986). Therefore, AF constrains the diet breadth of consumers (Stephens & Krebs 1986), a constraint that scales up to the whole

network, restricting the possible values of food web connectance. It is possible to distinguish between potential and realized connectance (Kondoh 2003a, 2005, 2006), where potential connectance C_P considers those links representing the feeding interactions that each species is morphologically and physiologically capable engage in, while the realized connectance C_R only considers those links representing the interactions that actually occur (Kondoh 2003a, 2005, 2006; Table 2). When both population and adaptive dynamics are explicitly modeled, which is the case for the replicator and game theory modeling approaches (Table 1), the potential number of links L_P are defined by a non-zero encounter rate a_{ij} in equations (3a) and (3b), while the realized links L_R are defined by a non-zero effort f_{ij} in those equations. This allows expressing C_R as L_R/S^2 and C_P as L_P/S^2 .

Another important result regarding restricted C_R is what Matsuda and Namba (1991) found analytically. They demonstrated that L_R in a food web with Lotka-Volterra dynamics defined by (3a) and linear constraints on foraging effort as in (5) is always smaller than $2S$ (Matsuda & Namba 1991). However, when relaxing the allocation cost of equation (5) by the incorporation of non-linear constraints on foraging efforts as in equation (8) with $x > 1$, foraging efforts always increase when they become too small (Uchida *et al* 2007; Uchida & Drossel 2007). In this way, at a fixed point all efforts are nonzero, and therefore C_R becomes equal to C_P .

Another key consequence of AF on food web structure is the emergence of the heterogeneous distribution of link strengths, consisting of many weak interactions and few strong interactions. However the studies which suggest a relationship between weak links and stability have relied on fairly low-dimensional systems (McCann *et al.* 1998; but see Wilmers *et al.* 2002), or on local stability results that suggest the importance of weak links in long cycles (Neutel *et al.* 2002). This has been shown to be negligible compared to

shorter cycles and the sign of interactions (Allesina & Pascual 2008). Nonetheless, this distribution has been observed in experimental field food web studies (Paine 1992; Goldwasser & Roughgarden 1993; Wootton 1997), and has been suggested as an important driver of the stability of complex food webs in nature (McCann *et al.* 1998; Neutel *et al.* 2002). Kondoh (2003) and Quince *et al.* (2005a), respectively using a replicator approach and a game theory approach, (Table 1), suggest that AF is an explanatory mechanism for that interaction strength distribution. This result was achieved using foraging effort dynamics described in equations (6a) and (8), which resulted in most of $\{f_{ij}\}$ reaching low values and few of them reaching large values. Hence, the same foraging effort dynamics produced both a constrained C_R^{\dagger} and a heterogeneous interaction strength distribution, which are key properties of empirical food webs. More results dealing with structural consequences of AF in complex food webs are given in Table 2.

With respect to ARR (adaptive resource responses), there are few studies addressing its consequences on food web structure (bold references in Table 2). Matsuda *et al.* (1994, 1996) studied the different structural consequences that specific (6b) and non-specific (11) anti-predator defenses exert on food webs when they are modeled with species' population dynamics also incorporating AF (adaptive foraging). When ARR is modeled as non-specific defenses, L_R is restricted to be lower than $2S$, but when it is modeled as specific defenses L_R does not have such a constraint (Matsuda *et al.* 1994). Furthermore, non-specific defenses allow higher richness, diversity, and total abundance of consumer species, higher connectance, fewer isolated sub-webs, and lower total abundance of resources, as compared with non-specific defenses (Matsuda *et al.* 1996). Thus, consumer-specific defenses may promote more complex food webs than non-specific counterparts.

ii) Dynamical consequences

The stability and persistence of ecosystems in response to perturbations has been a central concern for ecologists and conservation biologists for a long time (Pimm 1991; McCann 2000; Pascual & Dunne 2006a). Identifying the intrinsic factors that promote or enhance stability and persistence of populations and communities is both a fascinating scientific challenge and a key issue for making management decisions in a rapidly changing world. Regarding food web ecology, there is a long-standing and still active debate over what stabilizes complex communities (McCann 2000). In this section we present results of studies that propose ATB as an intrinsic factor that stabilizes food web dynamics, a process which can invert the negative complexity-stability relationship proposed by May (1972), and that can increase food web resilience and resistance against environmentally-driven changes in species composition or abundances.

Despite their central position in the ecological knowledge, the concepts of complexity and stability are used in a variety of ways in the ecological literature (Pascual & Dunne 2006b), which can lead to apparently contradictory conclusions when analyzing the results of research that addresses their relationship (Pimm 1982, 1991). Below we summarize the different concepts of food web complexity and stability used in research that studies the consequences of ATB, and then present the main related results and conclusions.

The measures of complexity mainly used in those works are connectance (e.g. Kondoh 2003a, 2005; Brose *et al.* 2003; Drossel *et al.* 2004) and species richness (e.g. Kondoh 2006 2007; Uchida & Drossel 2007). The stability definitions these studies employ

can be grouped into three concepts: permanence, persistence, and robustness. None of them rest on the existence of a locally stable equilibrium for the entire food web, but instead consider whether species will remain in the system over a given time horizon. Permanence is often used when the dynamics of a system are analytically studied, and is defined by the existence of a positive boundary for population densities that repel them far from zero. Thus a system is said to be permanent when there is some mechanism in the system of equations that ensure that species never go extinct (Krivan & Sikder 1999). On the other hand, persistence is assessed when using numerical simulations for studying model dynamics, and it is defined as the number or proportion of initial species that remain in the system after a finite number of model iterations (e.g., Brose *et al.* 2003, 2006; Ramos-Jiliberto *et al.* 2009; Valdovinos *et al.* 2009). Finally, robustness is also used for numerical simulations and it focuses on the response of some feature of a system to a perturbation, particularly perturbations not common in its development or history (Jen 2003). For example, structural robustness of food webs has been characterized as the amount of secondary extinctions that result from sequential species loss of different types (e.g. Dunne *et al.* 2002; Srinivasan *et al.* 2007; Dunne & Williams 2009; Staniszenko *et al.* 2010). ATB has been shown to promote all three types of stability in dynamical food webs that incorporate AF (Table 2).

AF stabilizes food web dynamics, in terms of increasing permanence and persistence, by allowing resources to recover their abundances when they become rare (Uchida *et al.* 2007; Uchida & Drossel 2007). This stabilizing mechanism is possible because adaptive consumers decrease foraging efforts against rare resources, provided that other resources are sufficiently abundant (Uchida *et al.* 2007; Uchida & Drossel 2007). This is a similar effect to what is achieved by using a Type III multispecies functional response, where

passive switching based on relative abundances of resources can result in reduced pressure on low abundance resources (e.g., Williams & Martinez 2004; Williams 2008; Berlow *et al.* 2009; Brose & Dunne 2009). Conversely, specific ARR increases persistence and may set permanence in food web dynamics by enabling the recovery of rare consumers whose resources decrease their avoidance efforts against them (Matsuda *et al.* 1994, 1996; Kondoh 2007). In this way, foraging efficiency of rare consumers is increased until their abundances are recovered. Conversely, if defenses are general (11) resources continue to defend against all their consumers whenever at least one of them is sufficiently abundant; therefore rare consumers are unable to recover their densities when competitors are abundant (Matsuda *et al.* 1994, 1996; Kondoh 2007). Those recovering mechanisms for both ARR (Matsuda *et al.* 1994, 1996; Kondoh 2007) and AF (Uchida *et al.* 2007; Uchida & Drossel 2007) can be seen as apparent mutualisms that emerge due to the inherent frequency dependence of ATB, as reported by studies that use replicator approaches to modeling (Table 1).

Another ATB mechanism that has been proposed as stabilizing food web dynamics, in terms of persistence and robustness is what we call fitness-enhancing decisions, i.e., the optimal allocation of effort, defined by their adaptive dynamics, which the organisms of a species distribute among their resources and consumers. Those fitness-enhancing decisions might ensure the necessary food intake and a sufficient reduction of consumption risk for a non-negative population growth rate, even in a changing environment. This mechanism is the most widely proposed explanation for the enhancement of food web persistence (Drossel *et al.*, 2001, 2004; Kondoh 2003a, 2005, 2006; Uchida & Drossel 2007) and robustness (Quince *et al.* 2005b; Uchida & Drossel 2007; Guill & Drossel 2008) due to AF (Table 1).

Both stabilizing mechanisms mentioned above can be encompassed by the more general concept of flexibility of food web structure (Kondoh 2003a, 2007). This flexibility concept considers a background architecture of interactions composed by the potential links which are activated or inactivated as the respective f_{ij} and v_{kj} become positive or zero. This results in a stabilizing effect on food web dynamics which can be attributed to both the emergence of apparent mutualisms and fitness-enhancing decisions, keeping the realized connectance at low values (Kondoh 2003a, 2007). Note, however, that flexibility requires an adaptation speed sufficiently high to be effective in conferring stability to food webs, since it should induce food web restructuring soon after the environmental changes occur (Kondoh 2003a). When modeling AF by means of the replicator equation (6a), adaptation speed of forager j is defined by the constant κ_j (see section II). The values of κ_j that have been studied are 0.0025, 0.025, 0.25 (Brose *et al.* 2003; Kondoh 2003a) and $\kappa_j = 2$ (Uchida & Drossel 2007; Guill & Drossel 2008), and it has been shown that the faster the foraging adaptation, the more persistent the food web (Kondoh 2003a). Conversely, the same analysis can be done when modeling ARR by means of the replicator equation (6b), where κ_j' determines the speed of species j for reallocating its defense efforts against its consumers. However, no study has addressed its consequences for food web stability.

The flexibility of food web structure due to AF may lead to a positive complexity-stability relationship whenever higher complexity implies an increase in potential resource species per consumer (Kondoh 2003a, 2006; Uchida & Drossel 2007). As more potential resources are available for a given species, it has more possibilities to optimally reallocate its foraging efforts after a perturbation. In this way, the higher the potential connectance of a food web, the higher is its flexibility and, consequently, the more persistent and robust it

will be (Kondoh 2003a, 2006; Uchida & Drossel 2007). But this conclusion has been questioned. Brose *et al.* (2003) show that stability decreases with potential connectance if more realistic population dynamics are used, for example a type II instead of type I functional response, and the more realistic niche model is used to generate the initial food web structure instead of random or cascade (Cohen *et al.* 1990) models. Kondoh (2006) countered this objection by suggesting that the niche model increases potential connectance and decreases the fraction of basal species, which in turn destabilizes the system. He demonstrated that if this confounding effect is removed, a population is more prone to persist in a more complex food web independent of the assembly and functional response models in use (Kondoh 2006). However, as noted above, the definitions of complexity and stability are crucial for understanding their relationship. When complexity is measured as species richness and stability is measured as persistence, their relationship is always negative regardless of whether AF is included or not in the food web dynamics (Kondoh 2006; Uchida & Drossel 2007; Table 2). Nevertheless, the effect of species richness on stability is reversed when the stability is defined as community robustness (Uchida & Drossel 2007; Table 2). In short, the sign of the complexity-stability relationship arising from food web dynamics including AF is dependent on the definitions used for these two properties. The relationship will tend to be positive either if complexity is defined as potential connectance, regardless the definition of stability, or if stability is defined as robustness, independent of the measure of complexity.

Regarding food web flexibility due to ARR, generalized defenses lead to a negative complexity-persistence relationship even when complexity is defined as potential connectance (Kondoh 2007; Table 2). However, specific defenses lead to a unimodal relationship where the positive region can be explained by the increased extinction risk of

consumers that depend on few resource species that likely allocate all their available defense effort against it. The incorporation of another consumer may result in the emergence of apparent mutualisms, allowing the recovery of the focal consumer. However, a high number of consumer species increases the likelihood that resource competition overcomes apparent mutualism, which explains the negative part of the unimodal relationship (Kondoh 2007).

Food web flexibility is also a key mechanism supporting resilience and resistance of communities to external perturbations that generate changes in species composition or abundances. Among the several types of perturbation that could fall into this class, three of them have been studied for their consequences for food web dynamics with AF: 1) species deletions (Quince *et al.* 2005b; Uchida & Drossel 2007; Guill & Drossel 2008), 2) species introductions (Drossel *et al.* 2001; Guill & Drossel 2008), and 3) random changes in vital rates, represented as parameter values into the models of population dynamics (Kondoh 2003a). The issue of resistance of food webs against species deletion was discussed previously, under the label of robustness. With regard to resistance of food webs to species introductions, the incorporation of AF into food web dynamics enhances robustness against species introductions via speciation or invasions (i.e., introductions of species drive fewer extinctions of native species; Drossel *et al.* 2001; Guill & Drossel 2008; Table 2). Less has been studied about the role of ATB in relation to resilience of food webs facing environmental perturbations, with one study demonstrating that higher values of adaptive rate κ_j of equation (6a) confer resilience to food webs subjected to random changes in populations' vital rates (Kondoh 2003a).

IV. Synthesis and perspectives

In a world experiencing profound changes at a fast rate due to anthropogenic impacts, a deep understanding of ecosystem complexity—what it means, how it emerges and evolves, and what intrinsic factors allow its maintenance—constitutes a critical and deeply challenging task (Pimm 1991). Throughout this review, we synthesized evidence demonstrating that adaptive trophic behavior (ATB) is a fundamental driver of key aspects of complexity in food web structure, in particular constrained realized connectance (Kondoh 2003a, 2005, 2006; Beckerman *et al.* 2006; Guill & Drossel 2008; Uchida *et al.* 2007) and heterogeneous distributions of link strengths (Kondoh 2003a; Quince *et al.* 2005a). We described how these two structural properties lead to the emergence of stabilizing mechanisms for food web dynamics. Although the stabilizing role played by heterogeneous link strength distribution for food web dynamics has been reported elsewhere (McCann *et al.* 1998; McCann 2000; Neutel *et al.* 2002), the significance of constrained realized connectance has not been fully appreciated. Constrained realized connectance promotes flexibility of food web structure (Kondoh 2003a; Guill & Drossel 2008), ensuring the emergence of at least two stabilizing mechanisms, apparent mutualisms (Matsuda *et al.* 1994, 1996; Kondoh 2007; Uchida *et al.* 2007) and fitness-enhancing decisions (Drossel *et al.* 2001, 2004; Kondoh 2003a, 2005, 2006; Uchida & Drossel 2007). Since at least some structural features that ATB promotes in model food webs match those observed in field food webs (Beckerman *et al.* 2006; Petchey *et al.* 2008), and since ATB is ubiquitous across organisms belonging to nearly every taxon and ecosystem type (Stephens & Krebs 1986; Lima & Dill 1990), its incorporation into models of food web dynamics

appears important for future model-based research. The incorporation of ATB into food web dynamics highlights the interplay between adaptive and population dynamics, which can help advance more unified ecological theory.

The study of the consequences of ATB on community structure and dynamics has developed quickly in the last decade. However, the technical terminology and implementation of many of the relevant papers has unnecessarily limited their impact on important lines of research in ecology and conservation biology. We have attempted to present, using accessible language, the main insights thus far emerging from this type of mathematical, model-based research, as a means of increasing its utility for the development of both basic theory and better applied research related to complex ecological systems. The latter depends crucially on the former. It will take robust theories of the structure and dynamics of species interactions in ecosystems to forecast responses at multiple scales to changes in the environmental context with enough understanding of both the main drivers and the uncertainties to make appropriate decisions about conservation and management.

While the explicit consideration of ATB in models of community dynamics offers important new insights on complex ecological structure and dynamics, it comes at the cost of additional model complexity, often driving the models into very high dimensional space where thorough sensitivity analyses are difficult to implement. Another key challenge will be how to validate aspects of the dynamical models against empirical data. Such validation of complex models is challenging, but not impossible, as demonstrated for dynamical models without explicit ATB (Brose *et al.* 2006; Otto *et al.* 2007, Berlow *et al.* 2009). In addition, there are aspects of ATB that have not yet been addressed in current models that could be included in next generation models. For example, current models do not consider

evolutionary or structural constraints that impede organisms from reaching optimal states with respect to their interactions with every trophic resource or natural enemy. Organisms are unlikely to respond optimally in all circumstances. This issue may fundamentally alter the dynamics of ecological networks, and could change our understanding of the effects of species turnover driven by dispersal, anthropogenic perturbations, and other factors.

Complex dynamical models such as those described here that include ATB can generate qualitative predictions that are relatively robust to changes in parameter values, allowing use of field data to evaluate contrasting predictions without the need to assume a fixed set of parameter values. The benefits of such models include the large array of important questions they open up to quantitative, computational analysis and more robust theory development and implementation. For example, which structural properties of communities composed of adaptive organisms confer more resistance or tolerance to species invasion? How does the decrease in the proportion of species exhibiting ATB, as expected from extinction of large-bodied predators driven by habitat fragmentation, impact the dynamics of communities and their robustness to environmental perturbations? How does the ATB of pollinators and seed dispersers shape the structure and dynamics of bipartite networks? These are just a few of the many open and important questions that can be addressed by the next generation of dynamical models that include adaptive trophic behavior.

CHAPTER 2

Adaptive foraging allows the maintenance of biodiversity of pollination networks

Abstract

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 networks, 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: i) AF increased the amount of floral resources extracted by specialist pollinators, and ii) 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.

INTRODUCTION

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 (e.g. 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 (e.g. 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: i) the production and animal consumption rates of plant rewards (Duffy and Stout 2008), ii) the competition and/or facilitation among plants via shared pollen/seed animal vectors (Hegland et al. 2009, Mitchell et al. 2009), and iii) 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 (e.g. 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

1. 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 2-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 5 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 et al. (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.

2. 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:

$$V_{ij} = \alpha_{ij} \tau_{ij} a_j p_i. \quad (1)$$

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 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:

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

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

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 (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 (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

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

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 (3) and the foraging effort α_{ij} in (1) are also state-variables of the model, whose dynamical equations are:

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

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

where β_i is the per individual production rate of resources of species i , and ϕ_i is a self-limitation parameter. In (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 (7) is nonzero. Eq. 7 is known as the replicator equation, and is used to describe the adaptive change of a trait (see 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.

3. 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 (Eqs. 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 Eq. 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), 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 Appendix 1.

4. 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 $H' = -\sum_{i \in A_i} N_i \log N_i$, 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 et al. (1999) and Medan et al. (2002), described in subsection 1.

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 equation (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 as defined in subsection 3. 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: i) mu1: high mortality rates of animals (mean of $\mu^A_j = 0.01$) and low mortality rates of plants (mean of $\mu^P_i = 0.002$), ii) mu2: low mortality rates of animals (mean of $\mu^A_j = 0.004$) and high mortality rates of plants (mean of $\mu^P_i = 0.008$), iii) mu3: low mortality rates of animals (mean of $\mu^A_j = 0.004$) and plants (mean of $\mu^P_i = 0.002$), iv) 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 Table A1 (Supplementary material), as explained in subsection 3. The complete procedure (i.e. 2 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 Eqs. 6 and 7, were: i) LFR model: linear functional response for pollinators $f_{ij} = b_{ij} * R_i / p_i$, where b_{ij} is the efficiency of pollinator i for extracting floral resources of plant j, ii) NFR model: nonlinear functional response for pollinators $f_{ij} = b_{ij}^{max} * R_i / (\kappa_{ij} * p_i + R_i)$, 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 iii) 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 (see results). 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: i) randomly (rand sequence), ii) from the least to the most connected species (least sequence), and iii) 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 as defined in subsection 3, 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: i) its persistence (fraction of the 100 simulations in which the species persisted at the final time), ii) population density, iii) total visits received by each individual plant and iv) 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 μ_1 , 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, as defined in Methods), 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 Fig. A2 and Fig. 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 et al. (1999) (see Fig. A4), and Medan et al. (2002) (see Fig. A5) for the LFR version of our model, which give support to our main conclusion.

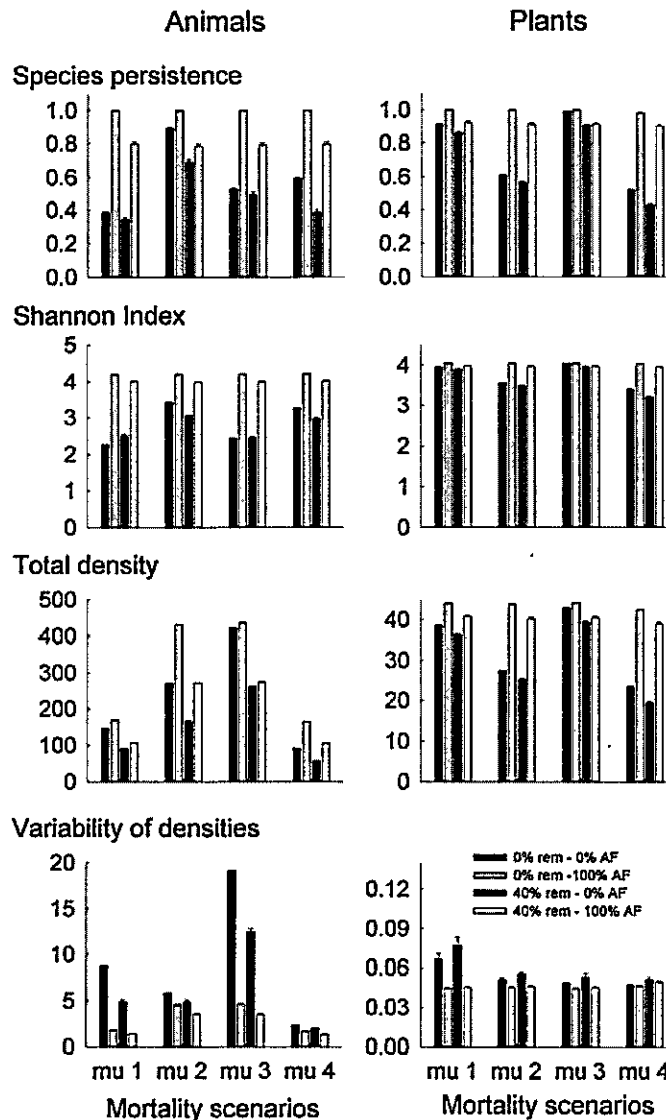


Fig. 1. The effect of AF on the stability and diversity of pollination networks. Model output of four variables characterizing animal and plant species at the end of simulations of the LFR model (see Figs. A2 and A3 for the other two versions of the model) parameterized with the four mortality rate scenarios used in the study: i) mu1: high mortality rate for animals and low for plants, ii) mu2: low mortality rates for animals and high for plants, iii) mu3: low mortality rates for animals and plants, and iv) 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.

The sensitivity analysis (Appendix1, 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 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 μ_1 and in Figs. A6, A7 and A8 (Supplementary material) for mortality scenarios μ_2 , μ_3 and μ_4 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. Fig. 2 shows the results for the mortality scenario μ_1 , while Figs. A6, A7 and A8 present the results for μ_2 , μ_3 and μ_4 (see Methods), 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 μ_3 (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. μ_1 and μ_4 for animals; μ_2 and μ_4 for plants), since the extinction driven by species removal was very little under low mortality scenarios.

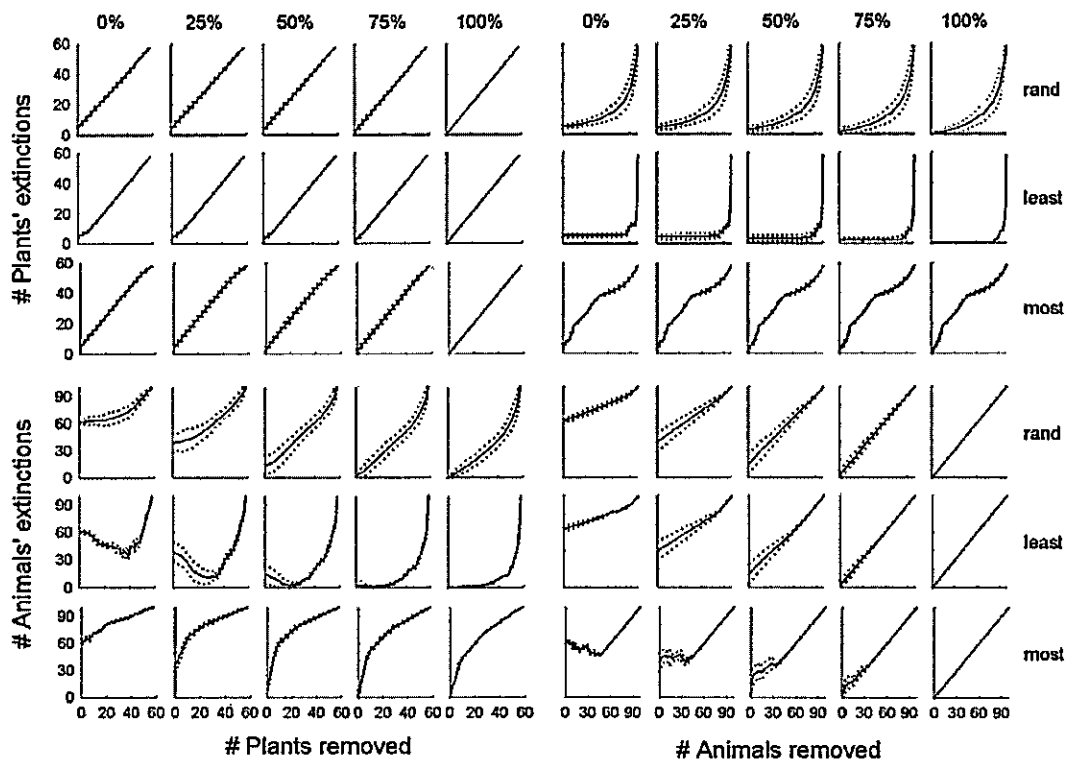


Fig. 2. The effect of AF on the robustness of Mauritian pollination network. Extinction patterns of plants and animals after the sequential removal of plant and animal species. This and the following figures show the results for the LFR model parameterized with mortality scenario mu1 (see Figs. A6-A8 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.

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 Fig. 3F) and the floral resources extracted by each individual animal (compare Fig. 4E and Fig. 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 Fig. 3D) and those of animals increased their evenness in relation to the system without AF (compare Fig. 4C and Fig. 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 and Fig. 4B) as compared to the system without AF (Fig. 3A and Fig. 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.

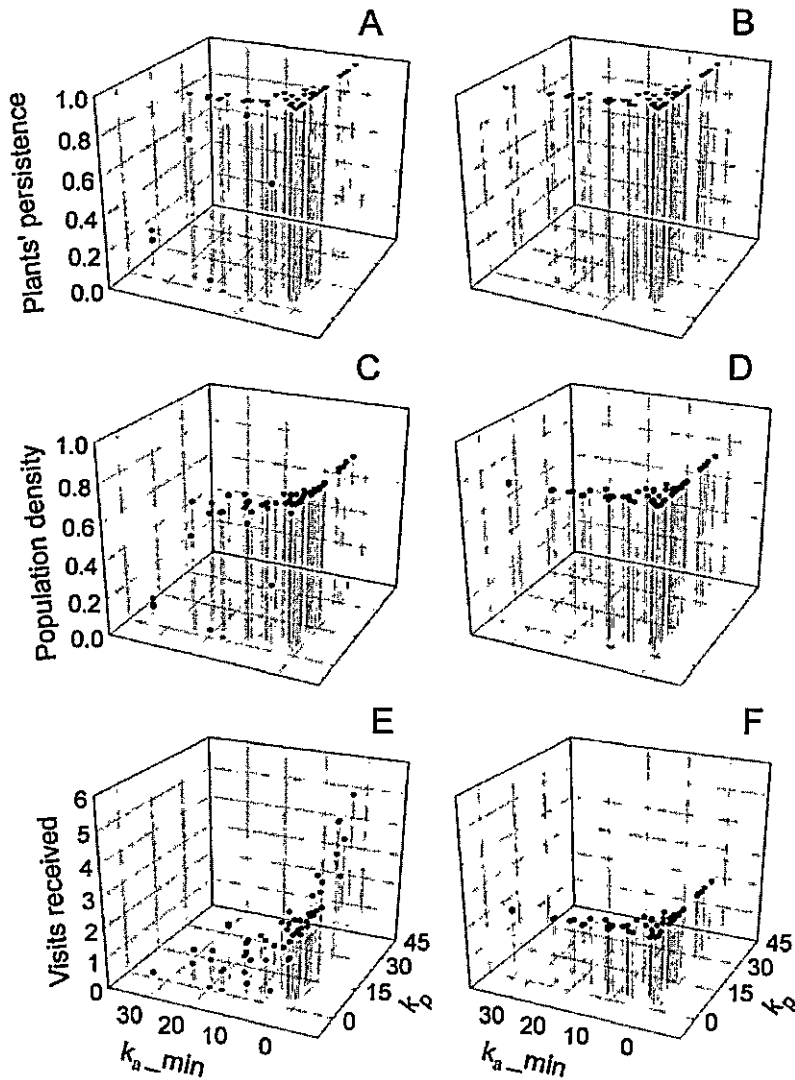


Fig. 3. Explanatory mechanisms for plants. Persistence (fraction of the 100 simulations that a species persisted at the end), population density and visits received (averaged over 100 simulations) of each plant species, against its own degree (k_p) and the minimum degree of its visitor species (k_{a_min}),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

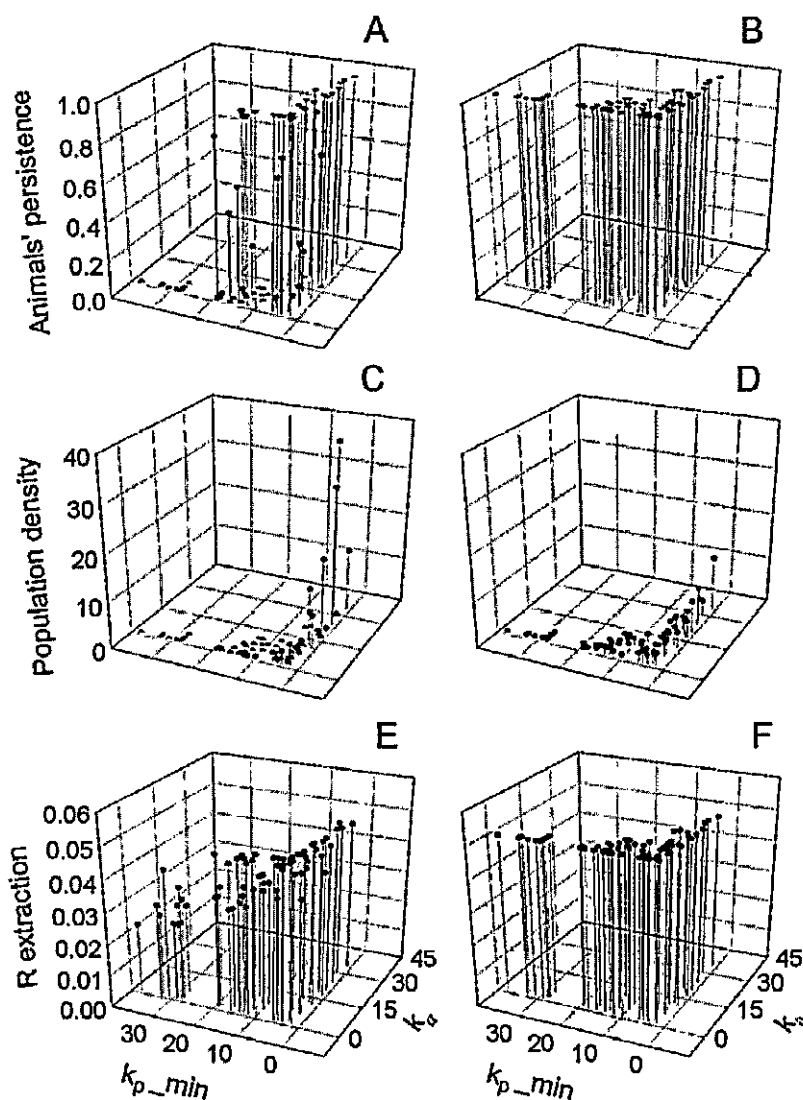


Fig. 4: Explanatory mechanisms for animals. Persistence (fraction of the 100 simulations that a species persisted at the end), population density and resource extraction (averaged over 100 simulations) of each animal species, against its own degree (k_a) and the minimum degree of its plant species (k_{p_min}),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

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 and Fig A2, A3, A4, A5), and reduced secondary extinctions of both plant and animal species driven by primary species loss (Fig. 2 and Fig. A6, A7, A8). These central findings were best explained by the following underlying processes: i) AF increased the amount of floral resource extracted by specialist pollinators (Fig. 3), and ii) 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.

1. 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 (Pyke 1982, Harder 1985, Rosenzweig 1986, 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 (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, and Figs. A2, A3 of the Supplementary material), in addition to the general increment of evenness observed among species abundances (Figs. 3 and 4).

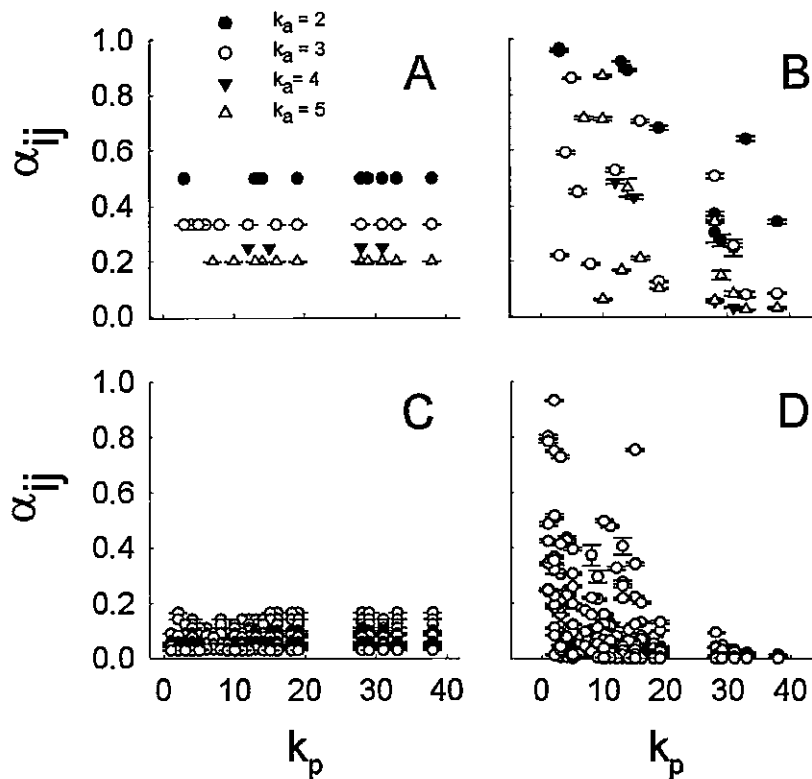


Fig. 5: The effect of AF on the distribution of foraging efforts. Foraging effort (α_{ij}) that each animal of the network allocated to each of its interacting plants, against the number of interactions of the same plants (k_p). Graphs A and B show the foraging efforts of non-generalist animals, whose 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.

2. 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 μ_1 (i.e. low mortality rates for plants and high mortality rates for animals, Fig. 2) and μ_3 (i.e. low mortality rates for both plant and animal species, 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). This was measured when plants were removed from least to most connected species, and when pollinators were removed from most to least connected species (Fig. A9). For the case of pollinators without AF, 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. μ_2 and μ_4), 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 (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 (Figs. 1, 2, 3, 4 and Figs. A2, A3, A4, A5, A6, A7, A8).

3. 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 (e.g. Hegland et al. 2009, Mitchell et al. 2009) and among animal species for shared plants (e.g. Zimmerman and Pleasants 1982), AF could be regarded as an important mechanism that allows the maintenance of species diversity.

4. 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.

CHAPTER 3

Adaptive foraging stabilizes pollination networks via apparent altruism

Researchers are increasingly recognizing that the stability of complex networks often depends on different types of interactions (Bastolla *et al.* 2009, Szell *et al.* 2010) e.g., mutualistic and competitive, and how network nodes dynamically adapt to the variable quality of their interactions (Valdovinos *et al.* 2010, Gross & Blasius 2008). However, scientists studying the iconic mutualistic networks of plants and their pollinators (Bastolla *et al.* 2009, Okuyama & Holland 2008, Thébault & Fontaine 2010, James *et al.* 2012, Allesina & Tang 2012) have typically focused on positive effects of plants trading food for sex work by animals while ignoring animals' adaptation to depleted floral rewards. Here, we incorporate these neglected processes by more explicitly exploring trophic dynamics in pollination networks and their implications for plant reproduction. Our analyses show that by selfishly preferring plants with the most profitable trophic resources, generalists evenly allocate both food resources among pollinator species and also reproductive vectors among plant species. This leads to the counterintuitive result that adaptive foraging by generalist pollinators decreases their own abundance while increasing that of specialists, which ultimately stabilizes the networks against the extinction of specialists. This mechanism is apparently altruistic because adaptive foragers effectively cede resources to other species that would otherwise go extinct. The predicted novel distribution of preferences among pollinators

closely matches the observed empirical preferences. These surprising findings suggest that classically selfish interactions may be effectively altruistic in complex networks.

Networks of mutualistic interactions between plants and pollinating animals are one of the most important mechanisms generating and maintaining vast amounts of terrestrial biodiversity (Thompson 1994). Threats to these mechanisms including pollinator loss and disease make it critically important to understand what stabilizes and destabilizes these systems. Research on mutualistic networks has shown that some structural properties such as species richness, connectance and nestedness significantly affect the stability of plant-animal mutualistic systems (Bastolla *et al.* 2009, Okuyama & Holland 2008, Thèbault & Fontaine 2010, James *et al.* 2012, Allesina & Tang 2012). However, there is little agreement on the actual effects of each structural property on the stability of those systems (see Supplementary Information for a brief review). For example, consider nestedness (Bascompte *et al.* 2003), the tendency of specialists---species with few interactions---to interact with subsets of the mutualistic partners of generalists---species with many interactions. Different studies suggest nestedness stabilizes (Bastolla *et al.* 2009, Okuyama & Holland 2008, Thèbault & Fontaine 2010) or destabilizes (James *et al.* 2012, Allesina & Tang 2012) mutualistic networks. Not only are such debates unsettled, but also the theory underlying the debate excludes fundamental aspects of the interactions within these networks. For example, the network models used in these debates almost exclusively focus on the positive effects between mutualistic partners and neglect the negative effect on floral rewards by pollinating consumers of those rewards (Stephens & Krebs 1986). Here, we analyze the stability of plant-pollinator networks by explicitly exploring the trophic dynamics of floral rewards and adaptive foraging---the widely observed preference of consumers for more available

resources (Valdovinos *et al.* 2010, Stephens & Krebs 1986).

Adaptive foraging (AF) can be defined as the fitness-enhancing changes in the feeding efforts of individuals due to variation in the availability of their resources (Valdovinos *et al.* 2010) AF has been shown to be a key stabilizing mechanism for the dynamics of complex food webs (Valdovinos *et al.* 2010) and, more recently, mutualistic networks (Kaiser-Bunbury *et al.* 2010, Ramos-Jiliberto *et al.* 2012, Valdovinos *et al.* 2013). However, the interplay between structural properties of ecological networks and AF is poorly understood (Brose *et al.* 2003). We address this interplay here by exploring how network structure affects the stability and dynamics of pollination networks when trophic and reproductive interactions are explicitly considered.

We used a mechanistic consumer-resource model (Valdovinos *et al.* 2013) consisting of coupled ordinary differential equations describing the population dynamics of plant and animal species within pollination networks. The model is mechanistic in that, instead of assuming positive interactions between pollinators and plants, the effect of interactions are calculated based on the dynamics of floral rewards, AF, pollen loads and resultant rates of feeding and pollination. The model was run for 1200 stochastically generated network topologies (Thébault & Fontaine 2010) with levels of species richness, connectance and nestedness commonly found in empirical networks (Methods). We simulated these networks both with and without AF. Foragers in networks without AF exert equal effort to visiting all individual plants that the forager pollinates. Foragers in networks with AF put more effort into visiting plant individuals that possess higher rewards. Note that specialist animals cannot forage adaptively because they are specialized on one plant species and cannot switch resources, thus specialist and fixed pollinators are interchangeably in networks with AF,

as well as adaptive and generalized foragers. We measured 21 structural properties of each network (Methods) to associate the properties to species persistence using Regression Tree Analysis (CART).

In realistically complex systems, we found that AF increased stability measured as species persistence i.e., the fraction of initially present species that maintain their abundance for 3,000 time steps (Fig. 1A). AF also increased the abundance of specialists and decreased that of generalist animals (Fig. 1B). In unrealistically highly complex systems, AF can decrease species persistence (Supplementary Material). The result in more realistic systems is surprising because adaptive behavior is not expected to decrease the abundance of those engaged in the behavior nor is it expected to increase the abundance of species such as specialists which cannot change their foraging preferences.

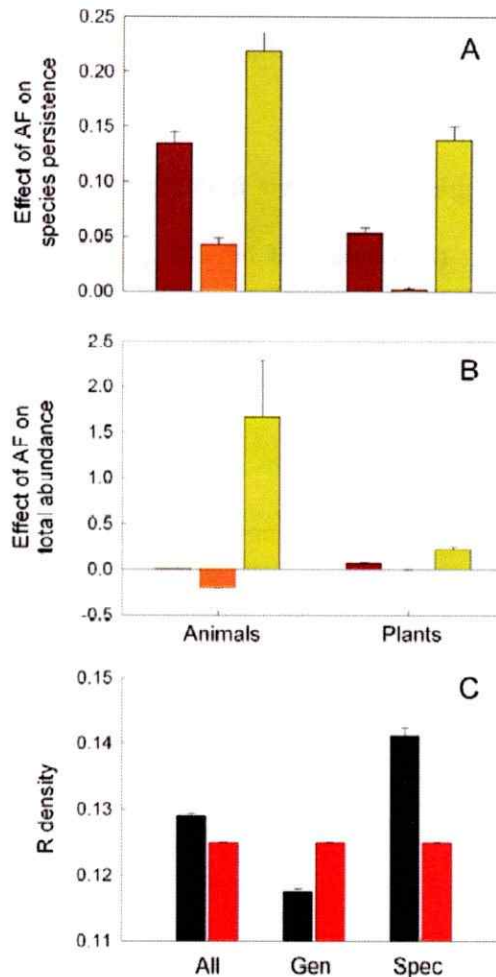


Fig 1. Results of the simulations and apparent altruism. Panels A and B show the effect of AF on species persistence and total abundances for animal and plant species. First column (dark red) of each group (either Animals or Plants) represents all species, second column (orange) represents generalist species, and third (light green) represents specialist species. Panel C shows the total amount of floral resources (R density) offered by all (All), generalist (Gen), and specialist (Spec) plants. Black columns represent networks without AF and red columns represent networks with AF.

Variation in nestedness is key to understanding the variation in this counter-intuitive result. By CART analysis, we found that the main structural driver of the stability of the networks was for far nestedness. In networks without AF, CART analyses found that nestedness measured as *NODF_{st}* (Methods) best explained species

persistence (training data: $r^2=0.80$, 84% explained by nestedness, test data: $r^2=0.76$, 84% explained by nestedness). Nestedness strongly reduced the persistence of both animal (linear regression: $y= 1-0.34*NODFst$, $r^2=0.75$, $p < 0.00001$) and plant (linear regression: $y= 1-0.15*NODFst$, $r^2=0.51$, $p < 0.0001$) species. AF eliminated this effect on animal species all of which always persisted in networks with AF irrespective of nestedness. AF also greatly reduced the negative effect of nestedness on plant persistence (linear regression: $y= 1-0.04*NODFst$, $r^2=0.14$, $p = 0.0001$). Thus, in comparison to networks without AF, nestedness maximized the stabilizing effect of AF (training data: $r^2=0.79$, 84% explained by nestedness, test data: $r^2=0.83$, 95% explained by nestedness), especially for animal specialists (Fig. 2A). Nestedness also increased AF's stabilizing effect on plant specialists and explained 44% of the variability in these plants persistence (Fig. 2C). However, the maximum similarity between plants of their sets of pollinators (maximum topological niche overlap) explains even more of the variance (88%) of specialized plant persistence (Methods). Interestingly, nestedness also reinforced the negative effect of AF on the abundance per species of generalist animals (Fig. 2B).

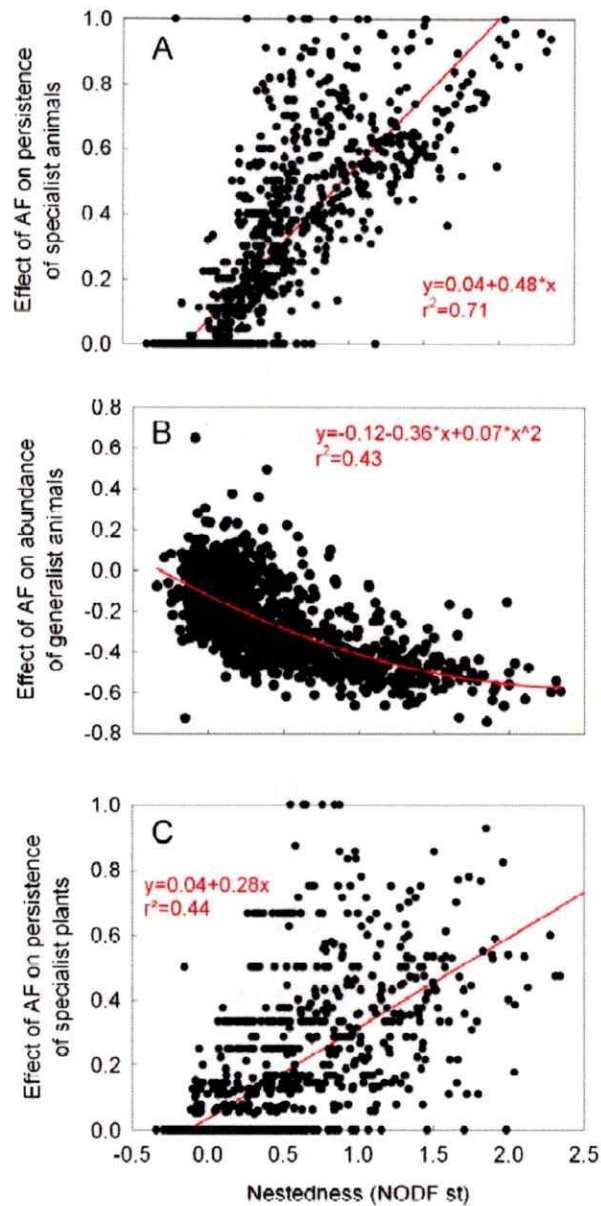


Fig 2. Influence of nestedness on the effect of adaptive foraging (AF) on persistence of specialist animals (A), abundance per species of generalist animals (B), and persistence of specialist plants (C).

The counter-intuitive result of AF decreasing the abundance of adaptive foragers while increasing the abundance and persistence of fixed foragers, and the strong effect of AF on the stability of nested networks, can both be explained by pollinators' preferring more specialized plant species' in nested networks (Fig. S4). Pollinator

species are most connected to generalist plants in nested networks. This depletes the rewards of generalized plants (Fig. 1C, networks without AF). Adaptive pollinators respond by assigning more effort to foraging on specialized plants. This cedes subsequent rewards produced by generalized plants to the many specialized pollinators that depend most on generalist plants in nested networks (Fig. 1C, rewards of generalist plants increased with AF). This allows specialized animals to increase their abundance and persistence, which decreases the total amount of floral rewards in the community (Fig. 1C, total rewards are lower with than without AF). This decrease in rewards reduces the abundance of adaptive animals. Therefore, although adaptive animals are by definition selfish since they are simply choosing for themselves to forage on plants with the most rewards, they are effectively altruistic at the network level. Altruism defined by Oxford dictionary is “behaviour of an animal that benefits another at its own expense”. Here AF harms the organism conducting the behavior while benefitting organisms not exhibiting AF. This apparent altruism also increases the persistence of specialized plants due to the increased pollination (data not shown) they receive from generalized pollinators who focus their foraging efforts on specialist plants (Fig. S4).

We tested whether the apparent altruism predicted by our model operates in nature by comparing our model's central prediction that pollinators' foraging effort decreases with increasing plant generality with preferences observed in the field. Indeed, the negative trend ($p = 0.003$, $r^2=0.09$, linear regression) between the empirical pollinators' preferences among different bee species in a plant-pollinator community (Brosi & Briggs 2013), and the generality of plant species both qualitatively and quantitatively corroborates our theory of apparent altruism (Fig. 3). That is, both our model (Fig. S4) and high quality empirical data show that generalist pollinators may often invest orders of magnitude more effort foraging on specialist than on generalist

plant species. Although the negative trend explains low variance of the empirical preferences---not surprisingly there is high natural variation---the trend is highly significant and quantitatively important. Specifically, both our model and the field data show effort decreasing 100 fold with plant generality increasing from 1 to 7 pollinator species. While previous work (Bascompte et al 2006, Vázquez *et al.* 2007) finds that more connected plants are visited more frequently, assertions that this pattern reflects patterns in preference are confounded by effects of abundance on visitation. Our model and empirical analysis avoids this problem by normalizing for variation in abundance. Although recently other theoretical work (Valdovinos *et al.* 2013, Staniczenko *et al.* 2013) has also suggested a negative relation between per-capita pollinators' preferences and plants' generality, ours appears to be the first study to demonstrate a qualitative and quantitative match between such theory and empirical data. This match suggests that, in addition to apparent altruism, the average abundance of rewards within plant populations and the variability of these populations connectivity are key properties driving the dynamics of plant-pollinator networks.

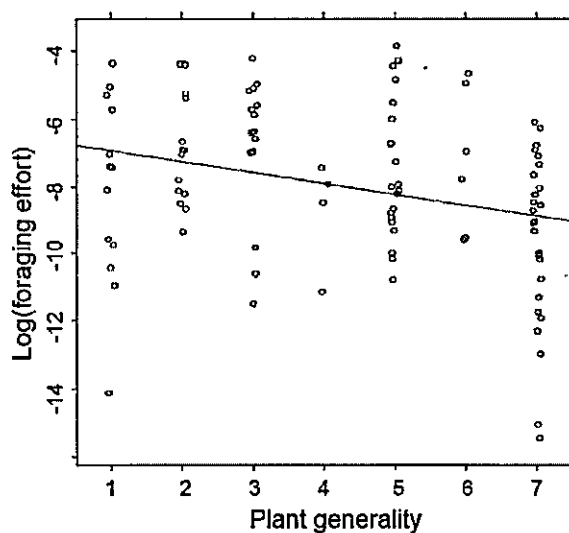


Fig 3. Effect of plant generality on pollinator preference. Plant generality is measured as the

number of species that pollinate a species of plant. Foraging effort is measured as relative foraging effort normalized by the abundance of each plant species, calculated as the fraction of an individual pollinator's visits to plant j divided by plant j 's floral abundance as a fraction of the floral abundance of all plants of all plant species that the pollinator species visits within a plot. Each data point represents the average of the normalized preferences among all observed individuals of a pollinator species that visited a particular plant species within the plot. The slope of the regression is -0.32 which standard error is 0.11, and $r^2 = 0.09$.

Our results suggest an empirically supported mechanism by which selfish individuals may be effectively altruistic in complex networks. We achieve our results by breaking down assumed properties of interactions such as mutualism into measurable mechanisms responsible for whether and how much mutualistic partners actually help each other. Such work supports a more general trend in network analysis to focus on mechanisms of interactions as opposed to phenomenological classifications of interactions. We suggest that research that continues this trend will further help scientists discover surprising and profoundly counter-intuitive behaviors of complex ecological and other networks.

METHODS SUMMARY

Simulations

We used an integrative model of adaptive and nonlinear population dynamics (Valdovinos *et al.* 2013), parameterized by 1200 stochastically generated networks (Thébault & Fontaine 2010) varying species richness (S), connectance (C), and nestedness, distributed around: S=40 and C=0.25, S=90 and C=0.15, S=200 and C=0.06, which are the values most commonly found in empirical networks (Fig. S1). The ratio between number of animal and plant species was centered at 2.5 among all simulated networks matching the empirical distribution. We measured 21 structural properties of each network to associate these properties with species persistence by training the

CART analysis on 600 networks and then testing it against 600 different networks (Berlow *et al.* 2009). The 21 structural properties were species richness, connectance, ratio between the number of plant and animal species, 3 measures of link density (links per number of species, per number of plant species, and per number of animal species), 4 measures of degree heterogeneity (the power law coefficients for the plant and animal degree distributions, standard deviations of generality and vulnerability, Williams & Martinez 2000), 10 measures of interaction overlap (5 for plants and 5 for animals including maxima and means of asymmetric and symmetric Jaccardian indexes), and nestedness. Nestedness was measured as *NODF* (Almeida-Neto *et al.* 2008) calculated by the software ANINHADO (Guimarães & Guimarães 2006) using its most conservative null model. To compare nestedness among networks, we used standardized *NODF*: $NODF_{st} = (NODF_{obs} - NODF_{null}^m) / NODF_{null}^m$, where $NODF_{obs}$ is the observed *NODF* value and $NODF_{null}^m$ is the mean over 1,000 null networks. CART results for the variance of specialized plant persistence were: training data: $r^2=0.52$, 88% explained by maxJP, and 13% by nestedness; test data: $r^2=0.63$, 88% explained by maxJP, and 12% by nestedness, where maxJP is the maximum asymmetric Jaccardian index.

Empirical data

The abundance normalized visitation rate of generalist pollinator individuals used to compare the empirical data with our model simulations, was measured as (fraction of an individual pollinator's visits to plant *j*) / (floral abundance of plant *j* / sum of floral abundance of all plant species that the pollinator species visits within a plot), and averaged for each bee species on each plant species.

CHAPTER 4

Resistance and resilience of pollination networks to simulated invasions depend on adaptive foraging, network structure and the invaders' traits

Abstract

The invasion of native ecosystems by alien species constitutes one of the major anthropogenic threats to the function and integrity of pollination systems. However, ecologists lack a clear understanding of factors driving invasion success and subsequent effects on the invaded ecosystems. Here, we use an integrative model of adaptive and nonlinear population dynamics to search for characteristics of alien species and network structures of native communities that drive invasion success and effects on native ecosystems. We simulated the introduction of plant and animal species with different traits into 1,200 networks with different levels of richness (15-238 species), connectance (0.04-0.34) and nestedness (NODFst 0.036-4.8). We then determined which among 21 structural properties of the networks best explained our results. Overall, larger networks with more links per animal better resisted invasions and adaptive foraging helped native pollinators resist the impacts of animal invasions. However, invaders with increased visitation efficiency more strongly decreased the abundance of native pollinators. Additionally, alien plant species with high floral rewards were very successful invaders and more productive pollen producers more strongly decreased native plants' pollination events and abundances. Our findings

demonstrate how the traits of invaders, the network structure of native communities, and the adaptive behavior of native pollinators may drive the resistance, resilience, and sensitivity of pollination systems to invasions.

INTRODUCTION

Mutualistic networks of plants and their pollinators are key promoters of terrestrial biodiversity (Thompson 1994). The introduction of alien species into native ecosystems, together with habitat deterioration and climatic change severely threaten the persistence and integrity of pollination systems (Memmott and Waser 2002). However, the factors driving invasion success (Sakai et al. 2001, Ghazoul 2002) and subsequent effects on native ecosystems (Traveset and Richardson 2006, Vilà et al. 2011) are poorly understood.

Better understanding of invasion processes has been inhibited by the complexity of the ecological interaction networks at the community level (Traveset and Richardson 2006) which may determine whether the effects of alien plant invasions on native plants are competitive, neutral or facilitative (Bjerknes et al. 2007, Sargent and Ackerly 2008). Alien plants may harm native plants by reducing visitation by pollinators and increasing heterospecific pollen deposition (Chittka and Schurkens 2001). However, pollination networks may be robust to invasion if native plants are not pollen limited or if native plants effectively compensate for loss of pollinators (Totland et al. 2006). When alien plants provide valuable food resources for many pollinators, their invasion may facilitate the native biota by increasing pollinator densities (Bjerknes et al. 2007). Alternatively, when alien animals consume limited floral resources or even monopolize the floral resources as do *Apis mellifera* and *Bombus terrestris* invaders (Goulson 2003),

alien pollinators may extirpate native pollinators. While such outcomes are possible, few general rules have been discovered that successfully predict which or which combination of the many potential outcomes are realized. Given that network structure (Bascompte *et al.* 2003, Okuyama & Holland 2008), adaptive foraging (Kaiser-Bunbury *et al.* 2010, Ramos-Jiliberto *et al.* 2012, Valdovinos *et al.* 2013) and other species' traits may affect the overall stability and function of pollination systems, we suspect general rules may emerge from searching for systematic effects of these factors on invasion success and impacts on native ecosystems.

The few available studies that evaluated the impacts of alien species on the structure of pollination networks concluded that invasive species become well integrated into the existing network (Memmott and Waser 2002, Olesen *et al.* 2002, Morales and Aizen 2002, 2006, Lopezaraiza-Mikel *et al.* 2007, Aizen *et al.* 2008, Valdovinos *et al.* 2009). These studies focused on how the patterns of connections between plants and pollinators differ between un-invaded and invaded plant-pollinator networks. These studies did not, however, evaluate the dynamics of alien species within the networks. To help address this shortcoming, Valdovinos *et al.* (2009) studied how simulated experimental removals of established alien plants modify the long-term dynamics of species in networks thus paving the way for simulating the introduction of new species to the network (e.g. Romanuk *et al.* 2010); a much more direct and appropriate method of investigating the success and impacts of biological invasions. This approach differs, conceptually, from the approach used by the above empirical studies in knowing the state of the system before and after the introduction of the alien species, which allows us to analyze the invasion process and its effect on the native system before the alien species is completely integrated in the network.

A key component of mutualistic dynamics is the adaptive foraging of pollinators on preferred sources of food (Valdovinos et al. 2010, 2013). Native pollinators clearly change their foraging behavior when including alien plants in their diets (Ghazoul 2002) and altered foraging preferences can affect both the quantity (e.g. visits to flowers) and quality (e.g. pollen deposition on stigmas) of pollinator visits to native plants (Brosi and Briggs 2013). Here, we investigate the combined effects of the network structure of plant-pollinator interactions, the characteristics of the introduced species and the adaptive foraging of pollinators, on the invasion success and its effects on the long term dynamics of native species in pollination systems. To achieve this, we simulated the introduction of species with different characteristics to networks with different levels of richness, connectance and nestedness, using a model that integrates population and adaptive dynamics. We ask: 1) which network structures are more resistant to biological invasions, 2) which characteristics allow species to successfully invade new communities, 3) how do traits of both native and alien pollinators affect invasion success and impacts of invasions.

METHODS

We used Valdovinos et al.'s (2013) mechanistic consumer-resource model that calculates the change of the density (p_i) of plant individuals, each with a single flower, of species i over time as;

$$\frac{dp_i}{dt} = \gamma_i \sum_{j \in A} e_{ij} \sigma_{ij} V_{ij} - \mu_i^p p_i \quad (1)$$

where the first and second terms on the right represent population gains and losses, respectively. γ_i is plant recruitment from seeds to adults;

$$\gamma_i = g_i \left(1 - \sum_{l \neq i \in P} u_l p_l - w_i p_i \right) \quad (2)$$

where g_i is the fraction of seeds that intrinsically recruit to adulthood. g_i is subjected to intra-specific (w_i) and inter-specific (u_l) competition with $w_i > u_l$ (Tilman 1997). e_{ij} in eq. (1) is the constant expected number of seeds produced by a pollination event. The fraction of visits by animal j to plant i that successfully pollinate plant i (σ_{ij}) is the amount of j 's pollen load of i 's pollen divided by j 's load of all plants' pollen;

$$\sigma_{ij} = \frac{\varepsilon_i V_{ij}}{\sum_{k \in P_j} \varepsilon_k V_{kj}} \quad (3)$$

where ε_i is the pollen production of the plant i and V_{ij} is the frequency of visits by animal species j to plant species i ;

$$V_{ij} = \alpha_{ij} \tau_{ij} a_j p_i \quad (4)$$

The dimensionless function discussed below, $0 \leq \alpha_{ij} \leq 1$, is the foraging effort of pollinator j on a plant i . τ_{ij} is the pollinator's visitation efficiency on plant i . μ_i^P in eq. (1) is the constant density-independent per capita mortality rate of plant i .

The change of the density (a_j) of animal individuals of species j over time is;

$$\frac{da_j}{dt} = \sum_{i \in P} c_{ij} V_{ij} b_{ij} \frac{R_i}{p_i} - \mu_j^A a_j \quad (5)$$

where c_{ij} represents the constant per-capita conversion efficiency of pollinator j converting plant i 's floral resources into j 's births. b_{ij} is the constant efficiency of pollinator j extracting plant i 's floral resources (R_i) whose change over time is;

$$\frac{dR_i}{dt} = \beta_i p_i - \phi_i R_i - \sum_{j \in A_i} V_{ij} b_{ij} \frac{R_i}{p_i} \quad (6)$$

where β_i is plant i 's per capita resource production rate and ϕ_i is a constant self-limitation parameter. μ_j^A in eq. (5) is animal j 's constant density-independent per capita mortality rates.

Adaptation of pollinator j 's foraging effort on plant i (α_{ij} in eq.4) is:

$$\frac{d\alpha_{ij}}{dt} = G_j \alpha_{ij} \left(c_{ij} \tau_{ij} b_{ij} R_i - \sum_{k \in P_j} \alpha_{kj} c_{kj} \tau_{kj} b_{kj} R_i \right) \quad (7)$$

where G_j is the basal adaptation rate of foraging effort and $\sum \alpha_{ij} = 1$ for all plants that each j pollinates. Pollinator j allocates more foraging effort to plant i whenever such reallocation enhances j 's food intake.

Initial p_i , a_j , and R_i were drawn from uniform random distributions with a mean of 0.5 and a variance of 0.05. $\alpha_{ij} = 1/k_{aj}$ in networks without AF where k_{aj} is the number of plant individuals pollinated by j . α_{ij} in networks with AF were allowed to vary from those initial values. w_i linearly decreased with increasing number plant i 's pollinator species at a rate that depends on the degree distribution of plants within each network (Thébault and Fontain 2010). Constants in eq. 1 differed with a 10% variance among all plant species within each network. Constant in eq. 5 were fixed for all animal species. These rules and values enabled all species to persist throughout all simulations (see Table A1 in Supplementary material, see Valdovinos et al. 2013 for sensitivity analyses) which facilitated our focus on effects of network structure and adaptive foraging. If, for example, animal species' constants (eq. 5) varied, multiple subsequent extinctions would increase the variation in results and obscure the effects on which we focus.

The dynamic model above was further parameterized based on stochastic model of network structure developed by Thébault and Fontaine (2010) which we used to generate 1,200 networks distributed around the parameter values: $S=40$ and $C=0.25$, $S=90$ and $C=0.15$, $S=200$ and $C=0.06$. These parameter values are those most commonly found in empirical networks (see Fig. S1). Before introducing alien species, we run the model for 10,000 time steps (t) for each of the 1200 networks both with and without AF for 2400 initial simulations. Most networks achieve stable equilibrium at $t \leq 3,000$ which minimizes effects of initial transition dynamics (Hastings 2010).

One 'alien' plant or animal species is added into the network at $t = 10,001$ with an initial abundance of a factor 0.1 of the average abundance of plant or animal species. A successful plant species introduction requires a switch of preferences of native animals to be included to the network and to better address this switch. One of 8 different types of plant species was only added each of the 1200 initial simulations without AF. One of 6 types of animal species was added to each one of the 2400 initially simulated networks with and without AF. This means that a total of 24,000 ($8 \cdot 1200 + 6 \cdot 2400$) different simulations of species introductions into 1200 different systems occurred. Alien species' parameters were assigned as the average of natives, unless otherwise stated. Alien species' interactions were stochastically assigned to native species. Native animal species assigned as in introduced plant's pollinators had a small amount (10^{-4}) of its foraging effort assigned to its preferred plant (typically $\approx 5 \cdot 10^{-1}$) subtracted and reallocated to the alien species. Effort of introduced animal species j (α_{ij}) foraging on plant species i is $1/k_{aj}$.

The 8 different kinds of alien plant species were full factorial combinations of two levels of 3 different properties ($8 = 2^3$): generality, pollen production, and reward production. Those 8 kinds are: 1) specialists, 2) high pollen producing specialists, 3)

high reward producing specialists, 4) high reward and pollen producing specialists, 5) generalists, 6) high pollen producing generalists, 7) high reward producing generalists, and 8) high pollen and reward producing generalists. Specialists only had one interaction within native networks, while generalists had the mean interaction number of the 30% most general native species. High pollen and reward production was set by assigning the aliens' ε_i and β_i (eq. 3 and 5, respectively) to be four times the natives' mean ε_i and β_i . We used this criteria based on previous sensitivity analysis (see Valdovinos et al. 2013)

The 6 types of alien animal species were combinations of two levels of 3 different properties: generality, visitation efficiency, and adaptive foraging with the exception of specialists which do not adaptively forage. Those 6 types are: 1) specialists, 2) efficiently visiting specialists, 3) generalists, 4) efficiently visiting generalists, 5) adaptively foraging generalists, 6) non-adaptively foraging and efficiently visiting generalists. Efficient visitors' τ_{ij} (eq. 4) was assigned to be twice the natives' mean τ_{ij} . Introduced adaptive foragers' α_{ij} were assigned by eq. 6 with initial condition $1/k_{aj}$. Non-adaptive foragers' $\alpha_{ij} = 1/k_{aj}$.

We measured 21 structural properties of each network at $t = 10,000$ and $20,000$ including species richness (S), connectance (C), ratio between plant and animal species (A/P), 3 measures of links density (links per number of species, links per number of plant species, and links per number of animal species), 4 measures of degree heterogeneity (the power law coefficients for the plant and animal degree distributions, standard deviations of generality and vulnerability sensu Williams and Martinez 2000), 10 measures of interaction overlap (5 for plants and 5 for animals including maxima and means of asymmetric and symmetric Jaccardian indexes), and nestedness. Nestedness was measured as NODF (Almeida-Neto *et al.* 2008) calculated by the software

ANINHADO (Guimarães & Guimarães 2006) using its most conservative null model. To compare nestedness among networks, we used standardized NODF which formula is: $NODF_{st} = (NODF_{obs} - NODF_{null}^m) / NODF_{null}^m$, where $NODF_{obs}$ is the observed NODF value and $NODF_{null}^m$ is the mean over 1,000 null networks. We use Classification and Regression Tree (CART) analysis to associate these properties with invasion success and other dynamical variables by training the CART analysis on 600 networks and then testing it against 600 different networks (Berlow *et al.* 2009).

RESULTS

Invasion success for plants typically depends both on the traits of the invader (Fig. 1) and the structure of the network (Fig 2). In contrast, animal invasions were invariably successful (Fig. 1). Plant invasion success was increased most with increasing floral rewards and less so by increased pollen production and specialization (Fig. 1). Network resistance to all types of plant invaders increased most with increasing species richness and less so with increasing density of links per animal (Fig. S2). These general results are best illustrated by the factors that best explain the highly variable success of invading generalist plants that produce high rewards (Gen high R in Fig. 1). Overall, CART analysis explained 82% of this variability in the training data and 79% in the test data; where 82% and 83% of the variance was explained by richness, 14% and 12% by the average links per animals, and 4% and 5% by the ratio between animal and plant species (Fig. 2).

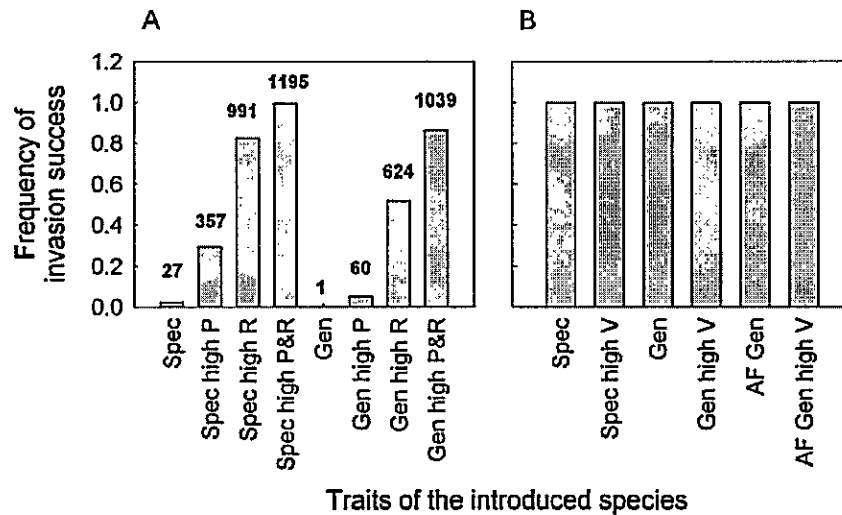


Fig. 1. Frequencies that different kinds of plant and animal alien species successfully invaded 1,200 different pollination networks with adaptive foraging. **A:** plant invaders include: specialists (Spec), high pollen producing specialists (Spec high P), high reward producing specialists (Spec high R), high reward and pollen producing specialists (Spec high P&R), generalists (Gen), high pollen producing generalists (Gen high P), high reward producing generalists (Gen high R), and high pollen and reward producing generalists (Gen high P&R). Numbers above the bars indicate the number of networks successfully invaded by each species kind which also indicate the sample size of statistical analyses each type of invasion. **B:** animal invaders include: specialists (Spec), efficiently visiting specialists (Spec high V), generalists (Gen), efficiently visiting generalists (Gen high V), adaptively foraging generalists (AF Gen), efficiently visiting and adaptively foraging generalists (AF Gen high V).

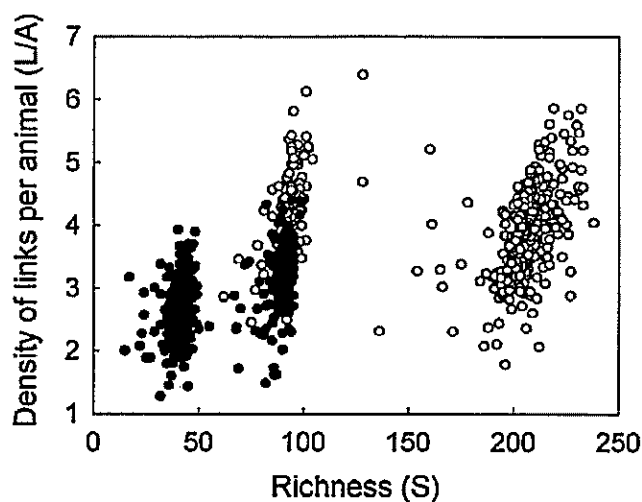


Fig. 2. Invasions success for high reward producing generalist plants (Gen high R in Fig. 1) as a function of the species richness and the density of links per animal within the invaded network. Filled circles indicate invasion success and unfilled circles indicate failure.

Invasions had significant effects on the abundances of plant and pollinator species, the densities of floral resources, and the pollination events experienced by each plant species as indicated by the per-species and total differences between those variables at equilibrium before and after the successful introductions. Overall, plant species invasion increased total pollination events and total plant abundances but decreased the average number of pollination events and plant abundances for native plants (Fig. 3 and S3). Interestingly, generalist alien plants and high pollen producers affected native plants most strongly and negatively even though those invaders succeeded less frequently than specialists and more prolific reward producers. Networks with AF were more resilient to animal invasions than networks without AF (Fig. 4) because adaptive foraging allowed native pollinators to resist better the impacts of animal invasions. Similarly, invading pollinators facilitated native plants less in networks with AF than in those without AF. In networks with AF, only more efficient visitors, especially the more general of these, decreased the abundance of native pollinators. Invading pollinators that were generalist adaptive foragers and efficient

visitors (AF Gen high V, in Fig. 4) are the only invaders that increased pollination of native generalists over specialists.

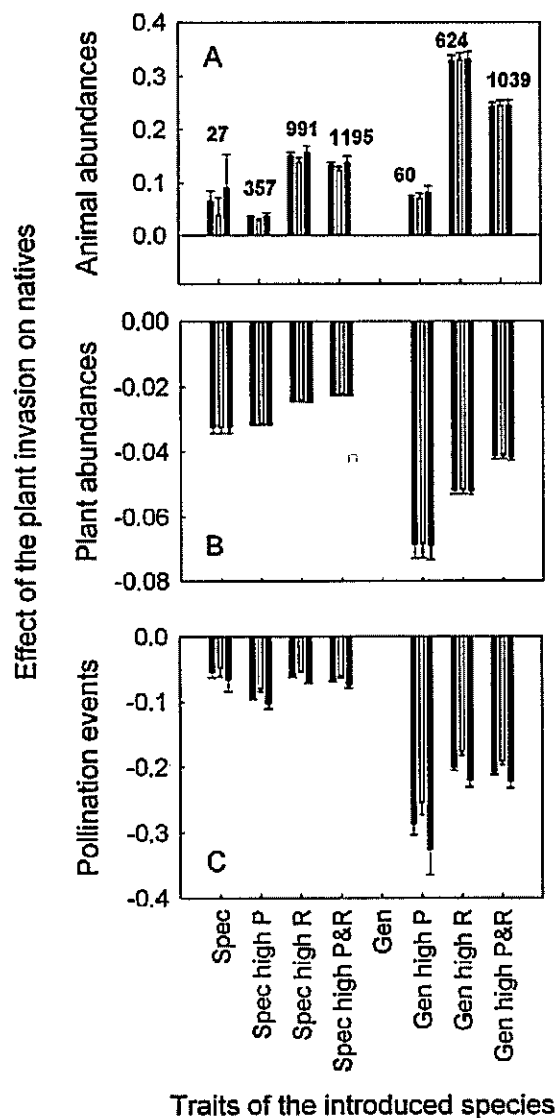


Fig. 3. Means and 95% confidence intervals for effects of successfully invading plants on native populations in networks with adaptive foraging. We normalized these differences by dividing the differences between the variables after invasion and those before invasion by the variables before invasion. Numbers in A indicate the number of networks that were successfully invaded by each type of species. Black, light grey and dark grey bars indicate all, generalized and specialized species. Types of invaders are the same as in Fig. 1.

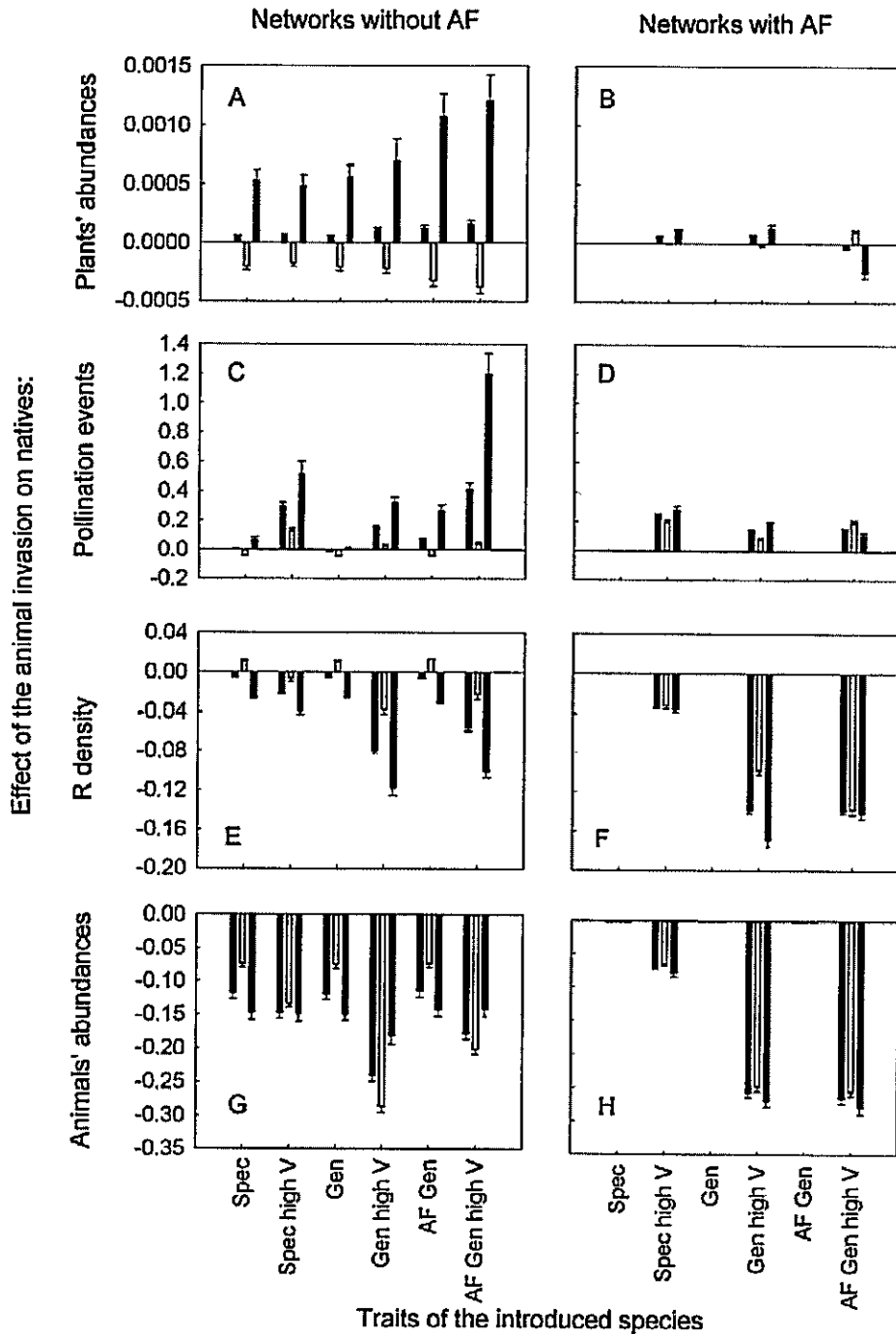


Figure 4. Effects (mean and 95% confidence intervals) of plant invasions of 1200 different networks on native species in networks without (left panels) and with (right panels) adaptive foraging (AF). Black, light grey and dark grey bars indicate all, generalist and specialist species, respectively. Types of invaders are the same as in Fig. 1.

DISCUSSION

While the introduction of alien species into native ecosystems constitutes a major anthropogenic threat for the persistence and integrity of pollination systems (Memmott and Waser 2002), we inadequately understand the factors driving alien invasions (Sakai et al. 2001, Ghazoul 2002) or effects of successful invasions on native species in plant-pollinator communities (Traveset and Richardson 2006, Vilà et al. 2011). To address this gap in our understanding, we simulated here, for the first time to our knowledge, species' introductions into dynamic pollination networks exhibiting the key behavioral trait of adaptive dynamics. Our findings show how alien's characteristics, the network structure of native communities, and adaptive behavior of native pollinators may drive the success and impacts of invasions in pollination systems. Such success and impacts may challenge system resistance and resilience to invasions, two central aspects of ecological stability (Holling 1973).

Ecologists have debated the relationship between complexity and stability of ecological systems for decades (McCann 2000). Our key finding that larger networks with higher density of links per animal species are most resistant to species invasions supports the classically asserted (MacArthur 1955) yet mathematically highly improbable (May 1973) positive complexity-stability relationship in plant-pollinator communities. This support emerges from the specific form of stability i.e., invasion resistance, asserted by one of the earliest and best known proponents of complexity enhancing stability (Elton 1958). However, the early and eminent (May 1973) mathematical improbability of this relationship in complex networks has continued to be broadly supported (Allesina & Tang 2012, Martinez et al. 2006) with some exceptions showing that complexity enhances stability (e.g., Brose et al. 2006, Okuyama & Holland 2008, Thébault & Fontaine). Our study adds yet another

exception by helping to explain mechanistically how more complex ecological networks increase their mathematically improbable, yet empirically manifest, stability.

Beyond resistance, we also show how complex ecological networks may achieve resilience which is probably the most discussed aspect of stability besides resistance. Adaptive foraging does this by allowing to native pollinators better maintain their abundances by reallocating their foraging efforts when new consumers are introduced. Such adaptation strongly dampens the impacts of animal introductions. Only when the invader's trait of foraging efficiency was enhanced over that of natives could alien invaders reduce the abundance of native pollinators that exhibit adaptive foraging.

Adaptive foraging was also key to plant invasions which were only successful when native pollinators switched their foraging preferences to alien plant species as previously suggested (Ghazoul 2002) and necessary when introduced plants require pollination by native animals for reproduction. Alien plant species producing the highest levels of floral rewards were especially successful invaders due to their provision of more food for native pollinators over that provided by native plants. Interestingly, we found that specialist plants were more successful invaders than generalist plants because nested network structure enhances pollinator competition and depletes rewards available from generalist plants species (Valdovinos et al. 2013). While relatively unsuccessful at invasion, generalist alien plants most strongly reduce pollination events and abundances of native plants when they are successful. High pollen production adds lower invasion success to the plants than does high reward production, but when high pollen producers are successful, they greatly impact native plants by decreasing their pollination events and thus plant abundances. This higher negative impact was due to alien plants' ability to decrease the native pollen loads that native pollinators carried by increasing the alien pollen loads.

Whether or not adaptive foraging occurred, alien animal invaders were always successful due to the low mortality rates in our model which allowed the persistence of all animal species introduced into the networks. We did this to focus on invasion processes free from animal extinction processes. Our results highlight the importance of adaptively foraging and efficiently visiting generalist invaders which is similar to the reported behavior of *Apis Mellifera* and *Bombus terrestris* (Goulson 2003). In our simulations, these aliens' characteristics produced the highest negative impacts on native animals, and were the only ones increasing the pollination events of native generalist plants over specialist ones in networks whose native pollinators were adaptive foragers. Introduced animals were connected preferentially to specialist plants because most native plants species are specialists and introduced animals were randomly linked to native plant species. This appears to be why animal introductions facilitate specialist over generalist plants.

Our results suggest a new approach to analyze the complexity of biological invasions, by integrating the traits of invaders, the network structure of native communities, and the adaptive behavior of native pollinators to evaluate their combined effects on the resistance, resilience, and sensitivity of pollination systems to invasions. We achieve our results by breaking down assumed properties of interactions such as mutualism into measureable mechanisms responsible for whether and how much mutualistic partners actually help each other. Such work supports a more general trend in network analysis to focus on mechanisms of interactions as opposed to phenomenological classifications of interactions. We suggest that research that continues this trend will further help scientists discover surprising and profoundly counter-intuitive behaviors of complex ecological networks.

General Discussion

Understanding the function and stability of ecological systems is key to ensure the sustainability of human activities in the planet. This dissertation tried to make a small but valuable contribution in our understanding of how ecological systems function and respond to perturbations such as species extinctions and biological invasions. I focused on plants-pollinators systems to illustrate that analyzing ecological interactions using a more mechanistically approach can elucidate ecological phenomena not predicted or observed before. Elucidating unexpected phenomena in ecological systems is especially important when those phenomena may contribute to stabilize ecological systems, which was the case of the present dissertation.

Research on community ecology typically analyzes interactions among species by using a phenomenological approach, i.e. by defining the effects that species exert on each other as a result of their interaction. By this approach, species affect each other positively (+), negatively (-) or neutrally (0). Consequently, all pair-wise interactions between species can be classified by the signs of the two involved effects, as mutualistic (+,+), competitive (-,-), predatory or parasitic (+,-), comensalistic (+,0), and ammensalistic (-,0). However, the effects between species are not fixed but vary regarding the environmental context. Usually, mutualistic interactions turn to parasitic and vice versa, competitive interactions switch to mutualistic, mutualistic interactions can be also comensalistic, etc. This dissertation pursue to replace the phenomenological approach of defining a priori fixed effects between species by addressing the mechanisms (i.e. biological processes) that are behind ecological interactions. By more explicitly model the biological processes behind interactions, the effects between species emerge from the dynamics of the system and vary regarding the environmental

context. To achieve this goal, I explicitly analyzed plants-pollinators systems considering them composed by two types of consumer-resource interactions. One is the classic interaction established by animals consuming plant biomass, in this case floral rewards. The other one is less conventional; the resource that plants ultimately consume is the intra-specific pollen transferred by animals. By this more mechanistically approach, I found that adaptive foraging stabilizes pollination networks against species extinctions via a mechanism that we called apparent altruism. We chose that name knowing that altruism is typically applied to related organisms. However, I think that the best science changes how we see the world. That instead of flat, it is round. That instead of absolute, it is relative. Unconventional use of language can be key to achieving that end. Apparent competition opened peoples' eyes to competition being mediated by other species rather than more direct interactions between competing species. While terms like altruism typically is applied to more related organisms, this study attempts to open people's eyes to the idea that altruism can happen between organisms of different species as well as between e.g., siblings within a family. The definition is clear. Altruism is a behavior that harms the organism choosing to conduct the behavior (e.g., calling out when a predator is present) and benefits a different organism. Adaptive foraging harms the organism conducting the behavior while benefitting organisms not exhibiting adaptive foraging. Key to this thesis is that the mechanism of Apparent Altruism functions in situations other than biologists typically recognize.

A mechanistic approach also allows us to create a bridge between empirical and theoretical research. The assumptions and results of models generated based on biological processes have more chances to be validated with empirical data than those of phenomenological models. Chapter 3 exemplifies how this validation is possible, by

testing the predictions derived from a mathematical model that is based on biological processes with empirical data. Besides, the incorporation of biological processes in the analysis of pollination networks allowed me to simulate the introduction of species with plausible characteristics and to measure the effect of species introductions on the natives, regarding those processes. There is much work to do concerning species invasions that this mechanistic approach can help through addressing the biological processes by which alien species may invade the host system and affect the natives. Elucidating these processes would help us to manage species invasions in diverse ecological systems.

One limitation of this dissertation is to neglect the rest of the community to which plants and pollinators belong. For instance, pollinators are predated and parasitized by other animals, and plants are consumed by other herbivores. Therefore, the dynamics of the abundance of plants and pollinators addressed by this study might be biased to the processes of reproduction and food intake, disregarding the lost of abundances produced by the consumption of herbivores and predators. As further steps in my scientific career I want to continue with the mechanistically approach for studying the function and stability of ecological networks, but considering the whole biological community.

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Supplementary Material (CHAPTER 2)

Table A1: Model parameters and state-variables: short definition, units and mean values of parameters and initial conditions used in the simulations. Values were drawn from a uniform random distribution with the specified mean, and variances of 10% and 0.01% of means for plants' and animals' parameters, respectively. Asterisks indicate initial conditions and k_{aj} is the number of interactions of animal j .

Definition	Symbol	Dimension	Mean value
Density of plant population i	p_i	individuals /area	0,5*
Density of animal population j	a_j	individuals /area	0,5*
Total density of floral resources of plant population i	R_i	mass/ area	0,5*
Foraging effort	α_{ij}	None	$1 / k_{ij}$ *
Visitation efficiency	τ_{ij}	(visits *area) / (time*individuals*individuals)	1
Expected number of seeds produced by a pollination event	e_{ij}	Individuals / visits	0.8
Per capita mortality rate of plants	μ_i^P	1 / time	0.002
Conversion efficiency of floral resources to pollinator births	c_{ij}	individuals/ mass	0.2
Per capita mortality rate of pollinators	μ_j^A	1 / time	0.01
Pollinator extraction efficiency of resource in each visit (linear model)	b_{ij}	individuals / visits	0.4
Maximum pollinator extraction efficiency of resource in each visit (nonlinear model)	b_{ij}^{max}	mass / visits	0.4
Half saturation parameter (nonlinear model)	κ_{ij}	mass / individuals	0.4
Maximum fraction of total seeds that recruit to plants	g_i	None	0.4
Inter-specific competition coefficient of plants	u_i	area / individuals	0.002
Intra-specific competition coefficient of plants	w_i	area / individuals	1.2
Production rate of floral resources	β_i	mass / (individuals * time)	0.2
Self-limitation parameter of resource production	φ_{ij}	1 / time	0.04
Adaptation rate of foraging efforts of pollinators	G_j	None	2
Carrying capacity of pollinators (self-limitation model)	K_j	Individuals / area	20

Appendix A1. Sensitivity analysis

The results presented in the main text were obtained from model simulations run with parameter values drawn from uniform random distributions, whose means are shown in **Table A1**. Our sensitivity analysis of the model consisted of evaluating how robust are the model outputs to different combinations of parameter means, varying all of them simultaneously. Following Thébault and Fontaine (2010), we used Latin hypercube sampling to select different parameter combinations. This sampling technique allows examining wide areas of the parameter space from a relatively small number of simulations (McKay et al. 1979; Downing et al. 1985). The range of means for each parameter was defined as between one fourth and four times the baseline values shown in **Table A1**. Each range was then equally divided into 100 intervals. Secondly, we randomly generated a Latin hypercube sample of size 100. In such sampling each one of the 100 intervals is sampled once and only once. With this sampling procedure, we obtained 100 different combinations of selected intervals for the 12 parameters of the LFR model (see subsection 4 of Methods in main text), corresponding to 100 sets of simulations. We applied this procedure to the model with and without adaptive foragers. For each simulation we recorded the following response variables: 1. the fraction of persistent plants, 2. the fraction of persistent animals, 3. the mean abundance of plant species, 4. the mean abundance of animal species, 5. the variance of plant abundances, and 6. the variance of animal abundances. Values of these response variables were obtained after 6000 iterations of the model. The results of this part of the sensitivity analysis are shown in **Fig. A1**.

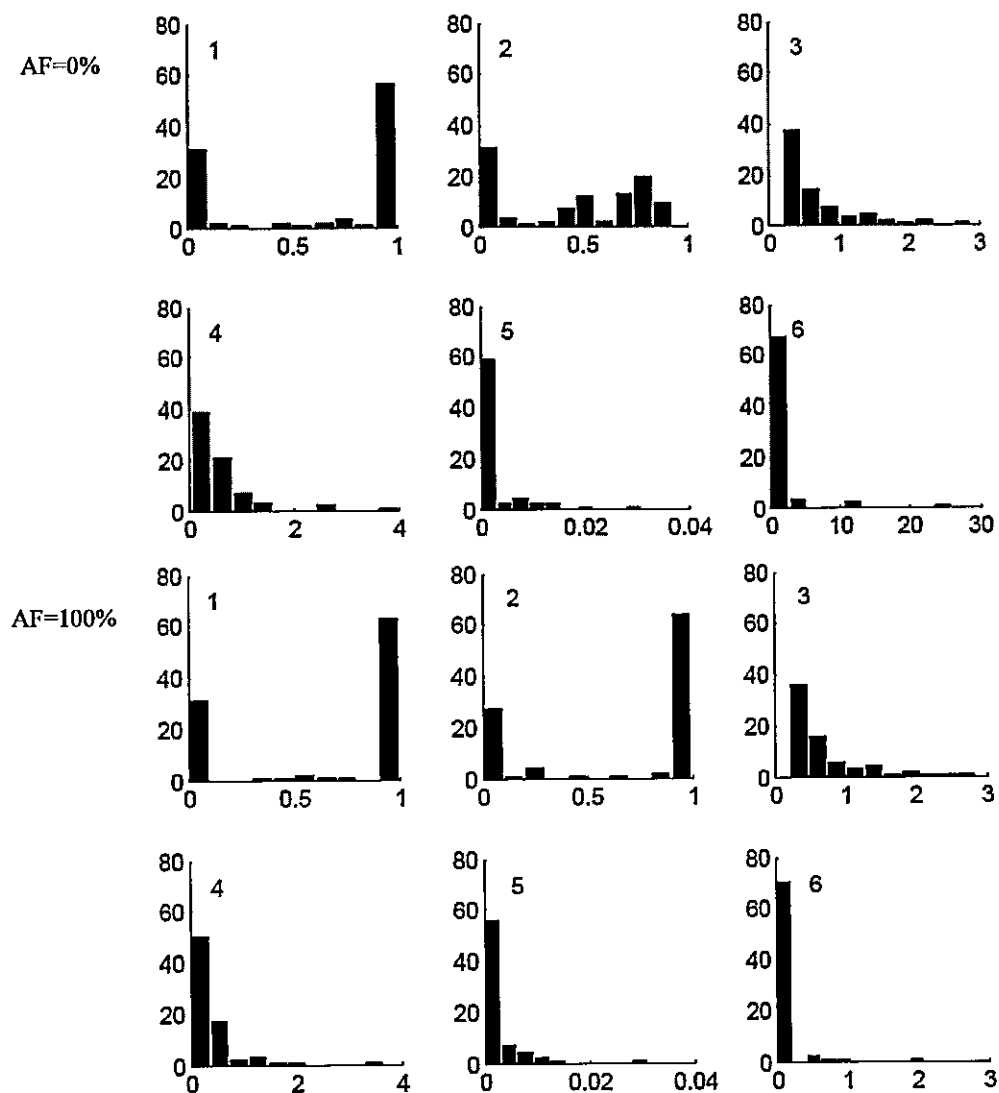


Figure A1: Results of the sensitivity analysis. By mean of Latin hypercube sampling, 100 parameter combinations were drawn. Here it is shown the frequency histograms of the corresponding 100 simulations for the six response variables, whose labels are: 1= fraction of persistent plants, 2= fraction of persistent animals, 3= mean abundance of plant, 4= mean abundance of animal, 5= variance of plant abundances, and 6= variance of animal abundances. AF refers to the percentage of pollinators that were adaptive foragers

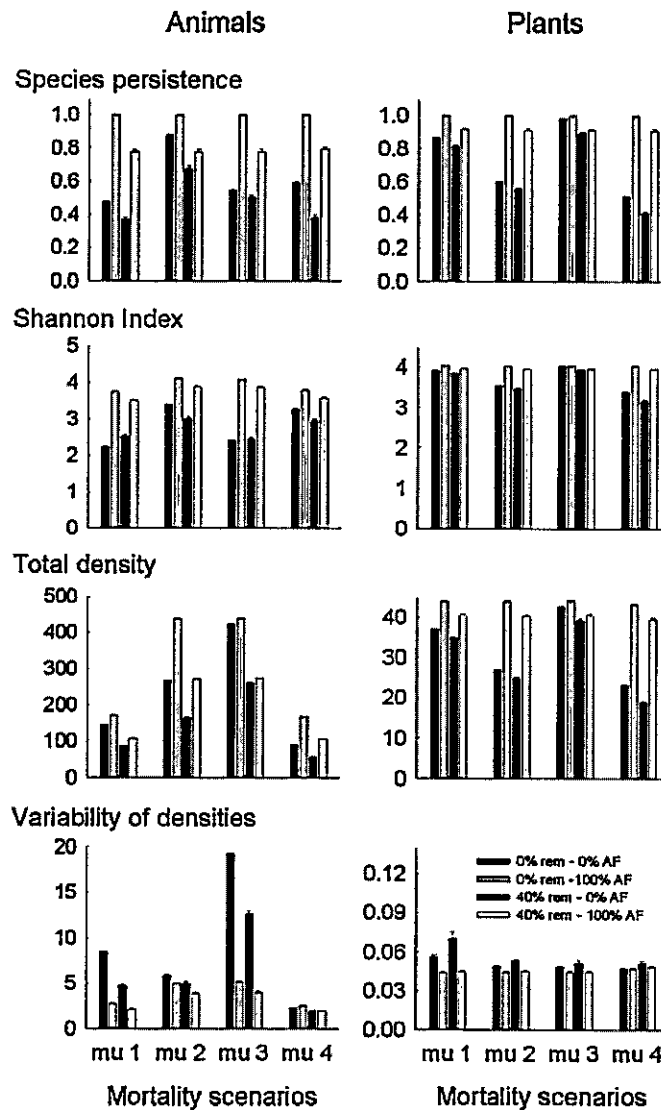


Figure A2: The effect of AF on the stability and diversity of pollination networks using the NFR model. This figure illustrates four variables characterizing animal and plant species at the end of simulations of the NFR model (see Figs. A2 and A3 for the other two versions of the model), parameterized with the four mortality rate scenarios used in this study: i) mu1: high mortality rate for animals and low for plants, ii) mu2: low mortality rates for animals and high for plants, iii) mu3: low mortality rates for animals and plants, and iv) mu4: high mortality rates for animals and plants; in which no removals (0% rem) and the removal of 40% of plant and animal species (for animal and plant response variables, respectively; 40% rem) were performed, 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.

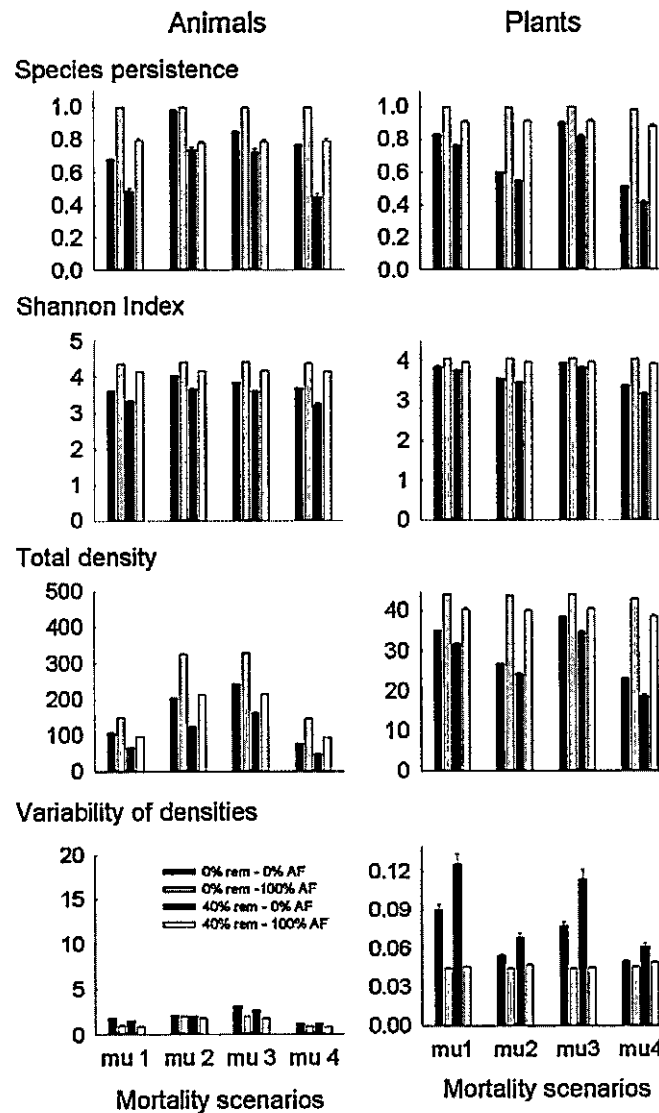


Figure A3: The effect of AF on the stability and diversity of pollination networks using the self-limited-LFR model. This figure illustrates four variables characterizing animal and plant species at the end of simulations of the self-limited-LFR model (see Figs. A2 and A3 for the other two versions of the model), parameterized with the four mortality rate scenarios used in this study: i) mu1: high mortality rate for animals and low for plants, ii) mu2: low mortality rates for animals and high for plants, iii) mu3: low mortality rates for animals and plants, and iv) mu4: high mortality rates for animals and plants; in which no removals (0% rem) and the removal of 40% of plant and animal species (for animal and plant response variables, respectively; 40% rem) were performed, 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.

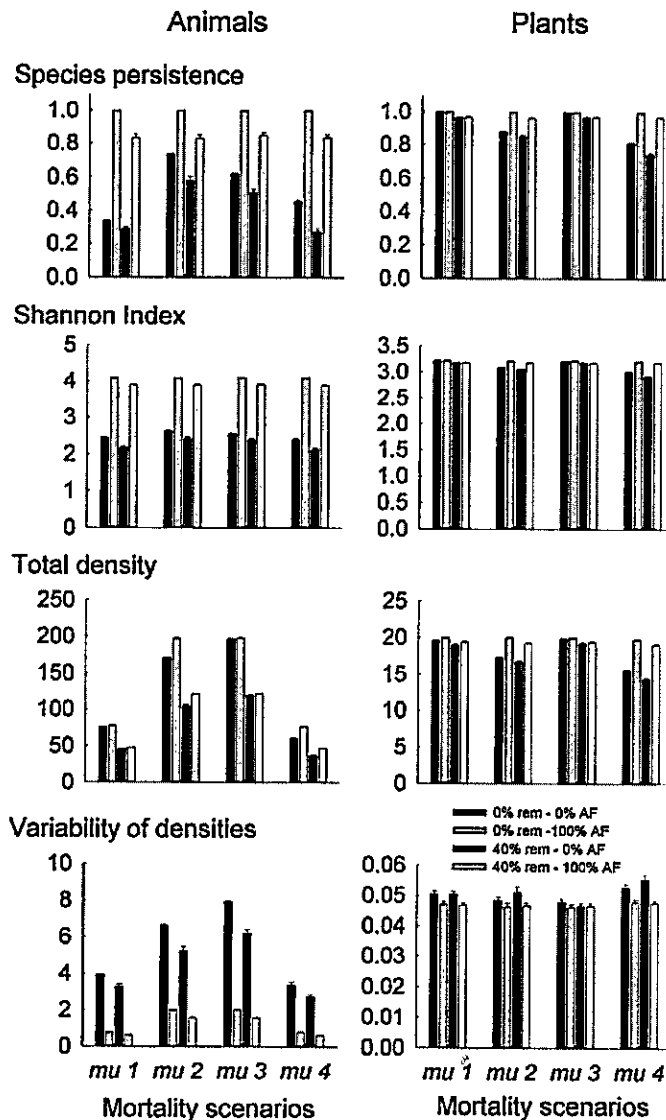


Figure A4: The effect of AF on the stability and diversity of pollination network described by Memmott et al. (1999) using the LFR model. This figure illustrates four variables characterizing animal and plant species at the end of simulations of the LFR model, parameterized with the four mortality rate scenarios used in this study: i) mu1: high mortality rate for animals and low for plants, ii) mu2: low mortality rates for animals and high for plants, iii) mu3: low mortality rates for animals and plants, and iv) mu4: high mortality rates for animals and plants; in which no removals (0% rem) and the removal of 40% of plant and animal species (for animal and plant response variables, respectively; 40% rem) were performed, 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.

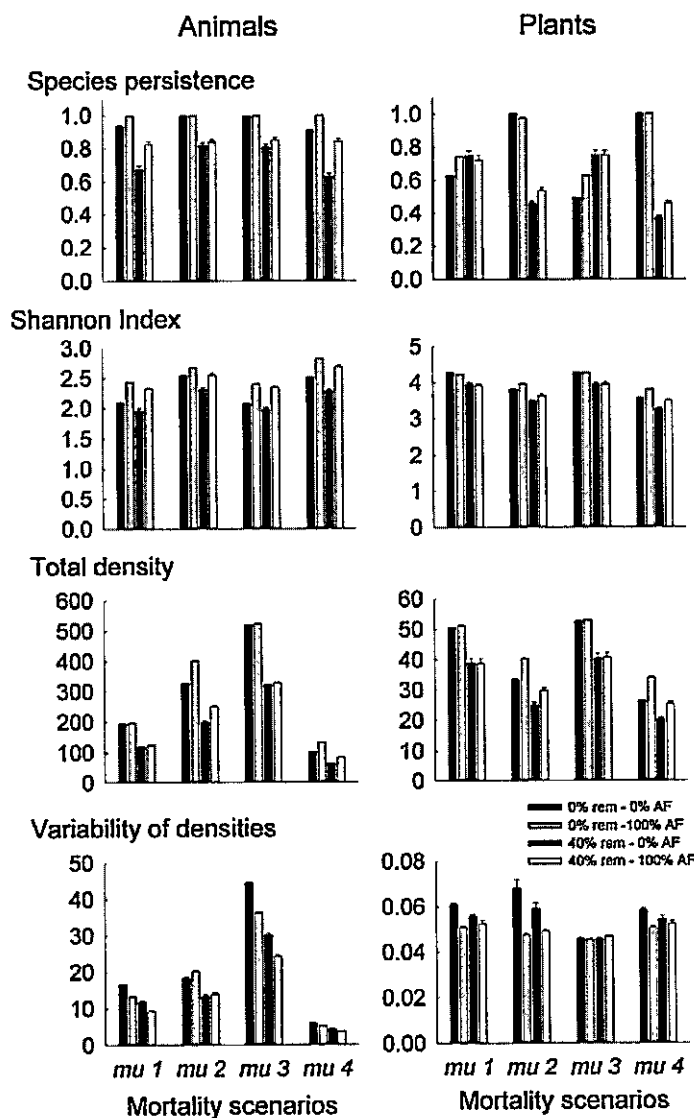


Figure A5: The effect of AF on the stability and diversity of pollination network described by Medan et al. (2002) using the LFR model. This figure illustrates four variables characterizing animal and plant species at the end of simulations of the LFR model (see Figs. A2 and A3 for the other two versions of the model), parameterized with the four mortality rate scenarios used in this study: i) mu1: high mortality rate for animals and low for plants, ii) mu2: low mortality rates for animals and high for plants, iii) mu3: low mortality rates for animals and plants, and iv) mu4: high mortality rates for animals and plants; in which no removals (0% rem) and the removal of 40% of plant and animal species (for animal and plant response variables, respectively; 40% rem) were performed, 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.

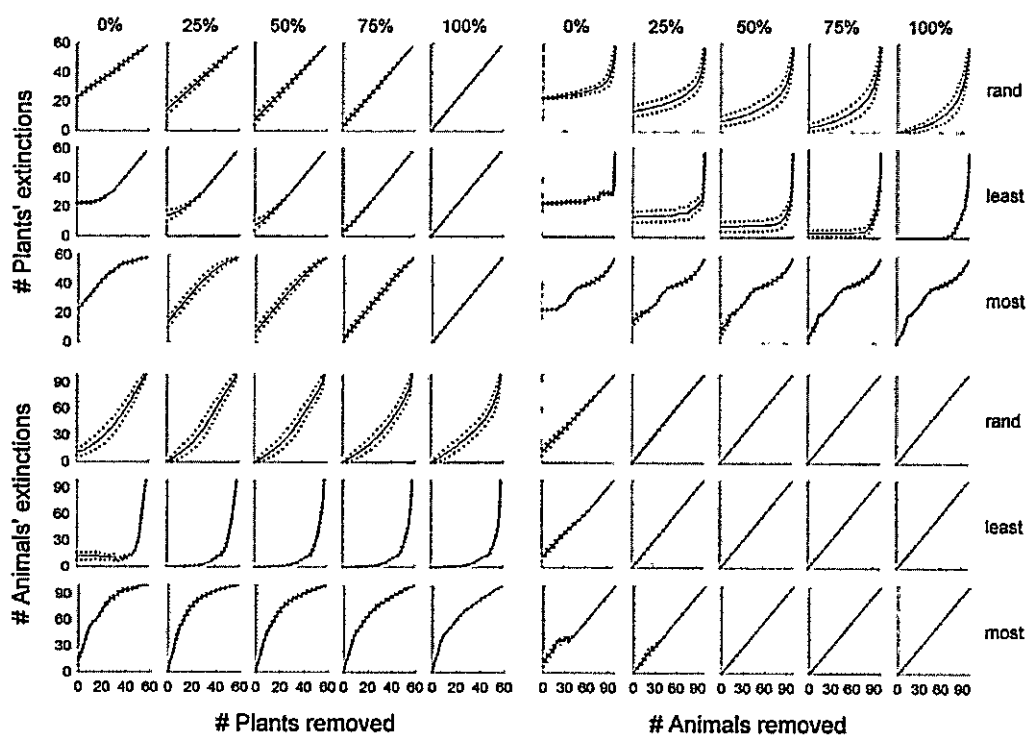


Figure A6: Extinction patterns for the LFR model parameterized with mortality scenario μ_2 . In each of the quadrants, sequential removals were organized in rows (from top to bottom: random, least to most connected and most to least connected species), while in columns are plotted 0, 25, 50, 75 and 100% of pollinators exhibiting AF. Solid lines show the mean of 100 model runs and dashed lines show 95% confidence intervals.

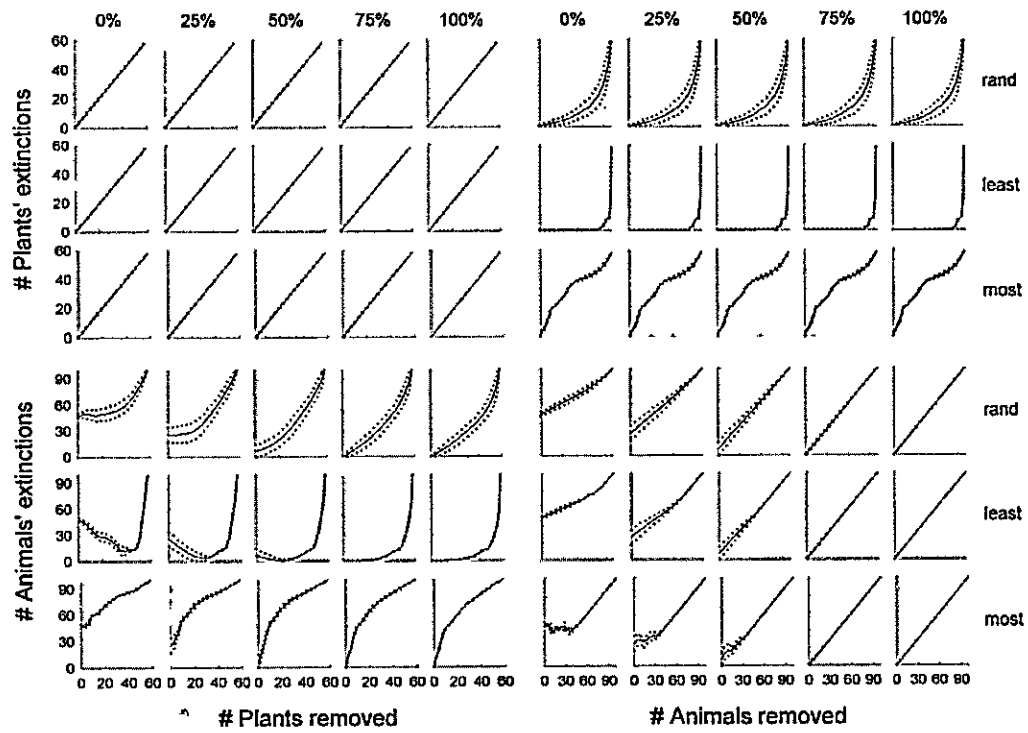


Figure A7: Extinction patterns for the LFR model parameterized with mortality scenario μ_3 . In each of the quadrants, sequential removals were organized in rows (from top to bottom: random, least to most connected and most to least connected species), while in columns are plotted 0, 25, 50, 75 and 100% of pollinators exhibiting AF. Solid lines show the mean of 100 model runs and dashed lines show 95% confidence intervals.

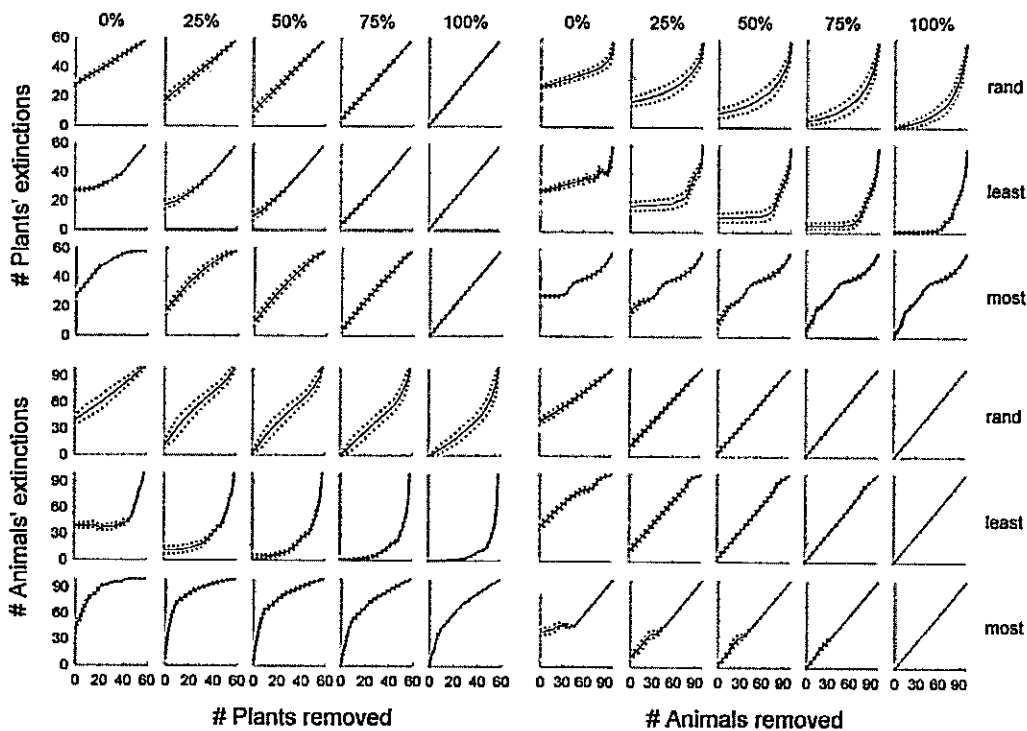


Figure A8: Extinction patterns for the LFR model parameterized with mortality scenario μ_4 . In each of the quadrants, sequential removals were organized in rows (from top to bottom: random, least to most connected and most to least connected species), while in columns are plotted 0, 25, 50, 75 and 100% of pollinators exhibiting AF. Solid lines show the mean of 100 model runs and dashed lines show 95% confidence intervals.

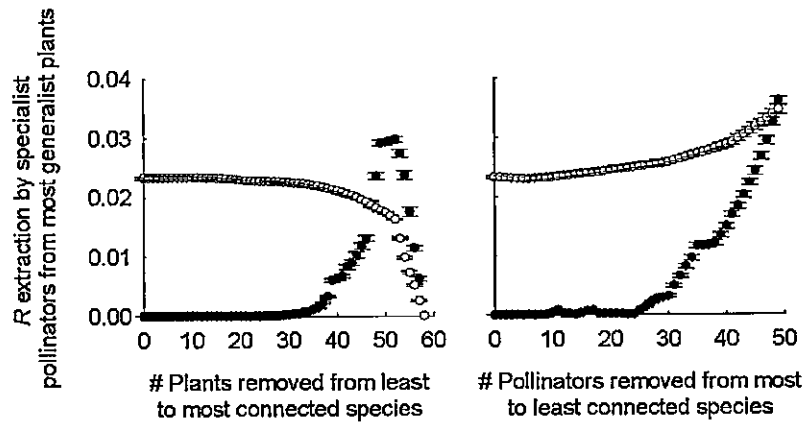


Fig. A9: Floral resource (R) extraction by specialist pollinators from super-generalist plants. Open and solid circles represent systems whose pollinators were and were not adaptive foragers, respectively.

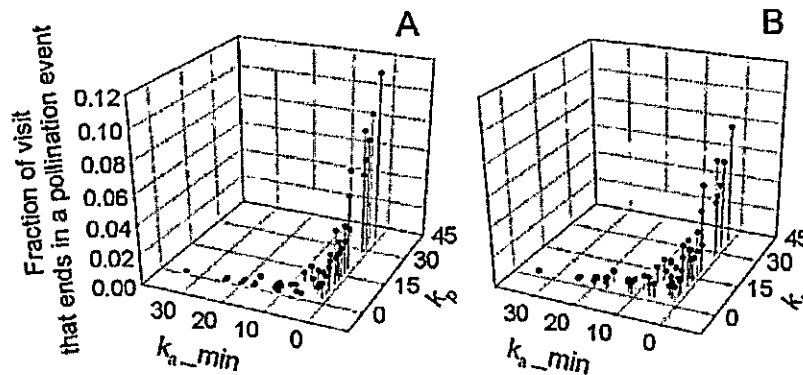


Fig. A10: Fraction of visits that ends in a pollination event of each individual plant. This figure shows average (over 100 simulations) of the model variable σ_{ij}/p_i at the end of simulations for each plant species, against its own degree (k_p) and the minimum degree of its visitor species (k_{a_min}), for systems whose pollinators did not (panel A) and did (panel B) exhibit AF.

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Supplementary Material (CHAPTER 3)

Section 1: Effect of network structure on the stability of mutualistic systems in previous works

Research on mutualistic networks has shown that some structural properties as species richness, connectance, nestedness, interaction strengths and distribution significantly affect the stability of plant-animal mutualistic systems (see Table S1 for the definition of all structural properties reviewed here). However, there is still not an agreement on what is the effect of each structural property on the stability of those systems (Table S2). The main reason for the inconsistency among results is that different studies used different models for population dynamics, definitions of stability (see Table S1 for stability definitions), network generating algorithms and structural measurements to respond the same question. In this section, we present a brief review on the studies that evaluate the effect of structure on the stability of mutualistic networks, describing the main differences among their methods and results (see Table S2).

Table S1. Structural properties and stability definitions for ecological networks.

Concepts, definitions and descriptions.

Concept	Definition/ description
Structural Properties	
Species richness (S)	Number of species in a network.
Conectance (C)	Proportion of possible links between species that are realized (links/animals*plants).
Nestedness	Tendency of species with fewer interactions to interact with subsets of the mutualistic partners of the species with more interactions.
Degree (k)	Number of links (interactions) species have with other species.
Degree distribution coefficient (γ)	The frequency distribution of k for a community of interacting species often follows a power distribution, $P(k) \propto k^\gamma$, where γ is the degree exponent and is typically a negative value. As γ increases (i.e. less negative values), the number of links per species and C increase.
Interaction strength	An estimate of the magnitude of the effect of one species on another. There are numerous quantitative estimates of it in ecological systems, e.g. per-capita interaction strength (direct effect of an individual of one species on an individual of another species), and the elements of Jacobian matrix (direct effects of an individual of one species on the whole population of another species at equilibrium). In mutualistic networks, it has been used the frequency (or relative frequency) of interaction, measured as visits.
Interactions asymmetry	Tendency of the interaction pairs that contain one strong interaction strength to be accompanied by a weak interaction strength.
Modularity	Network compartmentalization into modules, whose species interact more among them than with species belonging to other modules.
Stability definitions	
Robustness	Network resistance to loss species as a consequence of species extinctions.

Local stability	Measures the tendency of the system to return to equilibrium after small perturbations. Local equilibrium is defined by setting all equations to 0, i.e. the abundances of all populations in the system are in a stationary state. Mathematically, an equilibrium point is stable if all the eigenvalues of the corresponding Jacobian matrix have negative real part.
May's criterion	Local stability analysis using random Jacobian matrices that represent any set of first-order differential equations (i.e. linear direct effects among species), by which he demonstrated that the probability of a random structured community to be stable is close to 0 whenever the "network complexity" $K = \sigma \sqrt{SC} > 1$, where σ represents interaction strength.
Structural stability	Local stability with respect to modifications in the parameters of the dynamical system. In this section, structural stability is meant as the volume in parameter space compatible with positive densities at the fixed point.
Resilience	Return rates to the equilibrium following a perturbation.
Persistence	Fraction of initial species that persist until the end of a simulation. In systems exhibiting equilibrium, is the fraction of initial species surviving after the system has reached it.

The first big separation among studies is the presence or not of population dynamics in the network model. Memmott *et al.* (2004) and Burgos *et al.* (2007) studied the effect on network robustness against species extinctions statically, that is, without considering the dynamics of populations that are constituent of the network. Memmott *et al.* (2004) removed pollinators at random, systematically from least-linked to most-linked, and from most- to least-linked with the consequent loss of plants that only depend on them for reproduction. On the other hand, Burgos *et al.* 2007 simulated the assembly process of mutualistic networks, which produced extinctions. Both studies

found that mutualistic networks are robust to the extinction of least connected species because of network redundancy or nestedness (see Table S2).

Among studies that include population dynamics into their analysis they can be classified by the complexity/realism of the dynamical model and by the definition of stability used. Bascompte *et al.* (2006) and Allesina & Tang (2012) utilized Lotka-Volterra type models, consisting on linear positive interactions among species (see Table S2). On one hand, Bascompte *et al.* (2006) used local stability approach to show that a complex mutualistic network would be stable if its constituent pair-wise interactions are weak; or if one of the interactions is strong, the accompanying interaction is very weak, which they called asymmetry on interactions. On the other hand, Allesina and Tang (2012) extended the stability criterion proposed by May (1972) by constructing Jacobian matrices that represent more defined interactions (e.g. predator-prey, mutualistic or competitive; in opposition to interaction signs drawn at random) and more realistic network structures. They found predator-prey interactions increased stability of communities, while mutualistic and competitive destabilized them. Besides, they found that stability was negatively impacted by nestedness in bipartite mutualistic networks.

Holland *et al.* (2006) and Okuyama & Holland (2008) produced the next complexity level model for population dynamics of mutualisms by incorporating nonlinear functional responses to the positive effects among mutualist partners, i.e. beneficial effects of one species on another tend to saturate with increasing population size of the mutualistic partner. In contrast to Bascompte *et al.* (2006), they showed that a model with nonlinear functional responses does not require weak or asymmetric interaction strengths for community coexistence; and contrary to Allesina & Tang (2012), they demonstrated that mutualisms are very stable.

Bastolla *et al.* (2009) added interspecific competition to the saturated mutualisms modeled by Holland *et al.* (2006) and Okuyama & Holland (2008). Each species competes with all other species in its own class (plant or pollinator) and interacts mutualistically with a subset of species, determined by the empirical network, from the opposite class. They showed that a nested network will naturally emerge if new species are more likely to enter the community “where they have minimal competitive load” (Bastolla *et al.* 2009). On the contrary, James *et al.* (2012) using the same model than Bastolla *et al.* (2009) showed that nestedness does not have significant effect on persistence and suggested that the number of mutualistic partners and connectance are enough to explain species persistence in mutualistic networks. Saavedra & Stouffer (2013) argued that James *et al.* (2012) overlooked the critical link between connectance, degree distribution, and species’ survival when comparing empirically-observed networks to random networks, which result in specialists became less specialist and generalists less generalist in their random networks. The random networks were observed to be more persistent than nested empirical ones, because persistence was a result of the changes in the degree distribution. Saavedra & Stouffer (2013) showed that nestedness increased species persistence, using a more conservative randomization scheme that explicitly maintains the observed degree distribution and another definition of nestedness- one that considers both the competitive and facilitative implications of each mutualistic interaction developed by Bastolla *et al.* (2009). However, James *et al.* (2012) argued that the “small but critical step” needed to see a positive relationship with nestedness is to group the data by network, which effectively confines the analysis to individual networks. For a given network, nestedness is positively correlated with persistence provided that network size, connectance and degree distribution are held constant for random networks, with which the nested

empirical network is being compared. To the question if is nestedness important for predicting persistence in these models, James *et al.* (2012) claimed that it is less important than: network size, connectance, degree distribution, intrinsic growth rates, competition coefficients, and the strength of the mutualistic interactions.

Table S2. Synthesis of methods and results for studies that evaluate the effect of structure on the stability of mutualistic networks.

Reference	Methods	Results
Memmott et al. 2004	No population dynamics. Simulation of species extinctions by species removals from two empirical networks. Stability as robustness against species extinctions.	Nestedness (called redundancy) increased network robustness against removals of least connected species.
Bascompte et al. 2006	Population dynamics consisted on intrinsic growth rate plus unsaturated positive interactions defined by the network. Local stability.	Weak and asymmetric interactions enhanced local stability, while S decreased it.
Holland et al. 2006	Same model of Bascompte et al. 2006, excepting by positive interactions that are defined as saturated.	Weak or asymmetric interaction strengths not required for community coexistence.
Burgos et al. 2007	No population dynamics. Networks assembly process. Stability as robustness against species extinctions	Nestedness increased robustness against species extinctions but only when the least linked species have the greater probability of becoming extinct.
Okuyama & Holland 2008	Same model than Holland et al. 2006. Stability measured as resilience of the model's equilibrium obtained by simulations. Networks were randomly generated, controlling S, C, nestedness and degree distribution.	S, C and interaction strength increased resilience. Asymmetry and nestedness reduced and increased the stability of networks, respectively, but only for very heterogeneous networks (i.e. $\gamma = -2.5$). For $\gamma = -0.5$ and -1.5 , they have no effect. The average of their empirical data was -1.4 ± 0.15 .
Bastolla et al. 2009	Population dynamics model consisted on intrinsic growth rate plus competition coefficients and saturated positive interactions defined by the network. Stability was measured as the maximum S	Nestedness enhanced the number of coexistent species by reducing effective interspecific competition.

	achievable for a given network, obtained by structural stability approach. The effect of nestedness was evaluated by inspection of the effective competition matrix obtained analitically from the population model	
Thèbault & Fontaine 2010	Same population dynamics model than Bastolla et al. 2009. Stability measured as persistence and resilience from model simulations. Networks were randomly generated, controlling S, C, nestedness and modularity. Networks were randomly generated, controlling S, C, nestedness, degree distribution and interaction strength.	Resilience was decreased by C and modularity but was increased by S and nestedness. Persistence was increased by C (slightly) and S but was decreased by modularity and by nestedness (slightly).
Allesina & Tang 2012	Lotka-Voltera type model for population dynamics. Local stability approach by extending May's criterion of community matrices.	S, C and nestedness decreased stability.
James et al. 2012	Same dynamical model than Bastolla al. 2009. Stability as persistence. Combination of direct numerical integration and a root-finding algorithm to determine the community equilibrium. Networks were randomly generated, controlling S, C and nestedness.	Persistence highly correlated with the number of mutualistic partners and C, which increased with mutualism strength. Nestedness did not have significative effect on persistence.

Section 2: Description of the dynamical model

We used Valdovinos *et al.*'s (2013) mechanistic consumer-resource model that calculates the change of the density (p_i) of plant individuals, each with a single flower, of species i over time as;

$$\frac{dp_i}{dt} = \gamma_i \sum_{j \in A} e_{ij} \sigma_{ij} V_{ij} - \mu_i^P p_i \quad (1)$$

where the first and second terms on the right represent population gains and losses, respectively. γ_i is plant recruitment from seeds to adults;

$$\gamma_i = g_i \left(1 - \sum_{l \in P} u_l p_l - w_i p_i \right) \quad (2)$$

where g_i is the fraction of seeds that intrinsically recruit to adulthood. g_i is subjected to intra-specific (w_i) and inter-specific (u_i) competition with $w_i > u_i$ (Tilman 1997). e_{ij} in eq. (1) is the constant expected number of seeds produced by a pollination event. The fraction of visits by animal j to plant i that successfully pollinate plant i (σ_{ij}) is the amount of j 's pollen load of i 's pollen divided by j 's load of all plants' pollen;

$$\sigma_{ij} = \frac{\varepsilon_i V_{ij}}{\sum_{k \in P_j} \varepsilon_k V_{kj}} \quad (3)$$

where ε_i is the pollen production of the plant i and V_{ij} is the frequency of visits by animal species j to plant species i ;

$$V_{ij} = \alpha_{ij} \tau_{ij} a_j p_i \quad (4)$$

The dimensionless function discussed below, $0 \leq \alpha_{ij} \leq 1$, is the foraging effort of pollinator j on a plant i . τ_{ij} is the pollinator's visitation efficiency on plant i . μ_i^P in eq. (1) is the constant density-independent per capita mortality rate of plant i .

The change of the density (a_j) of animal individuals of species j over time is;

$$\frac{da_j}{dt} = \sum_{i \in P} c_{ij} V_{ij} b_{ij} \frac{R_i}{P_i} - \mu_j^A a_j \quad (5)$$

where c_{ij} represents the constant per-capita conversion efficiency of pollinator j converting plant i 's floral resources into j 's births. b_{ij} is the constant efficiency of pollinator j extracting plant i 's floral resources (R_i) whose change over time is;

$$\frac{dR_i}{dt} = \beta_i P_i - \phi_i R_i - \sum_{j \in A} V_{ij} b_{ij} \frac{R_i}{P_i} \quad (5)$$

where β_i is plant i 's per capita resource production rate and ϕ_i is a constant self-limitation parameter. μ_j^A in eq. (5) is animal j 's constant density-independent per capita mortality rates.

Adaptation of pollinator j 's foraging effort on plant i (α_{ij} in eq.4) is:

$$\frac{d\alpha_{ij}}{dt} = G_j \alpha_{ij} \left(c_{ij} \tau_{ij} b_{ij} R_i - \sum_{k \in P_j} \alpha_{kj} c_{kj} \tau_{kj} b_{kj} R_k \right) \quad (6)$$

where G_j is the basal adaptation rate of foraging effort and $\sum \alpha_{ij} = 1$ for all plants that each j pollinates. Pollinator j allocates more foraging effort to plant i whenever such reallocation enhances j 's food intake.

Initial conditions of plant and animal abundances 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 (α_{ij}) equal $1/k_{aj}$, where k_{aj} is the number of interactions of pollinator species j . The selection of parameter space is shown in Table S3. Two adaptive foraging (AF) treatments are applied to each network. Networks without AF fix the foraging effort of pollinators to $\alpha_{ij} = 1/k_{aj}$ among all individual plants that the forager pollinates. Networks with AF contain foragers that put more effort into visiting plant individuals that possess higher rewards, ruled by Eq. 6. As outputs we computed abundances of plant and pollinator species, the densities of floral resources and the pollination events experienced by each plant species.

Table S3: Model parameters and state-variables: short definition, units and mean values of parameters and initial conditions used in the simulations. Values were drawn from a uniform random distribution with the specified mean, and variances of 10% and 0.01% of means for plants' and animals' parameters, respectively. Asterisks indicate initial conditions and k_{aj} is the number of interactions of animal j .

Definition	Symbol	Dimension	Mean value
Density of plant population i	p_i	individuals /area	0,5*
Density of animal population j	a_j	individuals /area	0,5*
Total density of floral resources of plant population i	R_i	mass/ area	0,5*
Foraging effort	α_{ij}	None	$1 / k_{aj}$ *
Visitation efficiency	τ_{ij}	(visits *area) / (time*individuals*individuals)	1
Expected number of seeds produced by a pollination event	e_{ij}	Individuals / visits	0.8
Per capita mortality rate of plants	μ_i^p	1 / time	0.002
Conversion efficiency of floral resources to pollinator births	c_{ij}	individuals/ mass	0.2
Per capita mortality rate of pollinators	μ_j^A	1 / time	0.01
Pollinator extraction efficiency of resource in each visit (linear model)	b_{ij}	individuals / visits	0.4
Maximum fraction of total seeds that recruit to plants	g_i	None	0.4
Inter-specific competition coefficient of plants	u_i	area / individuals	0.002
Intra-specific competition coefficient of plants	w_i	area / individuals	1.2
Production rate of floral resources	β_i	mass / (individuals * time)	0.2
Self-limitation parameter of resource production	\square_{ij}	1 / time	0.04
Adaptation rate of foraging efforts of pollinators	G_j	None	2

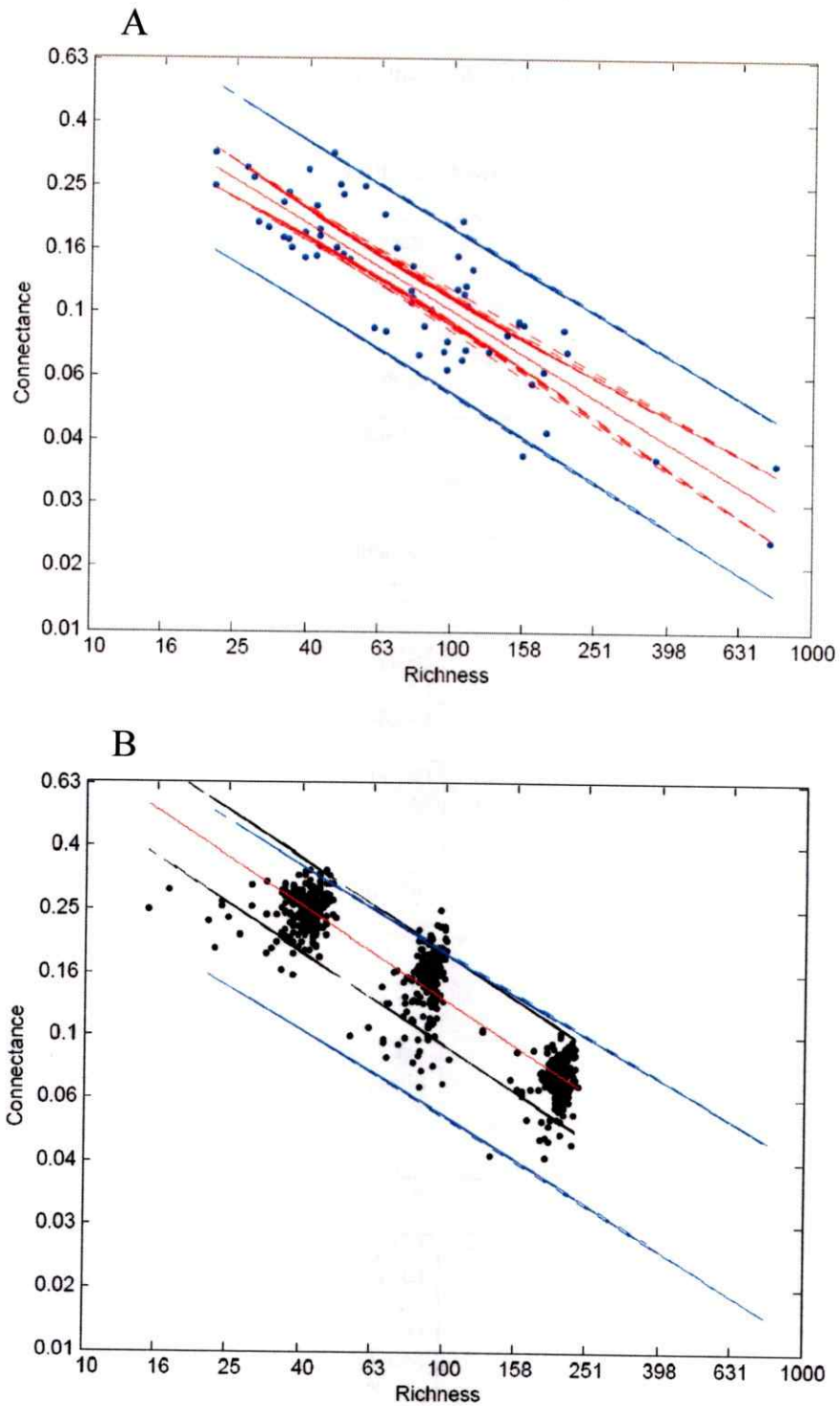


Fig S1. A: Prediction (blue) and confidence intervals (red) for the regression of the logarithm of connectance to the logarithm of richness of 57 empirical networks (blue filled circles) listed in Table S4. **B:** The 1200 simulated networks (black filled circles). Prediction (blue) and confidence intervals (red) are kept from A.

Table S4: Description of the 57 empirical plant-pollinator networks used for Fig. S1.

Main source:

http://www.nceas.ucsb.edu/interactionweb/resources.html#plant_pollinator

	Dataset	Habitat type	Location	Data type	# plants	# pollin
1	Arroyo <i>et al.</i> (1982) (3 webs)	Andean scrub	Chile	binary	87	98
2					43	62
3					41	28
4	Barrett and Helenurm (1987)	Boreal forest	Canada	individuals caught	12	102
5	Bartomeus <i>et al.</i> (2008) (3webs)	Mediterranean shrublands	Catalonia, Spain	no. visits	31	77
6					31	79
7					29	75
8	Bezerra <i>et al.</i> (2009)	Caatinga (semi-arid vegetation)	Pernambuco State, Brazil	no. visits	13	13
9	Clements and Long (1923)	Montane forest and grassland	USA	binary	96	276
10	Dupont <i>et al.</i> (2003)	High-altitude desert	Tenerife, Canary Islands	binary	11	38
11	Elberling and Olesen (1999)	Alpine subarctic community	Sweden	no. visits	23	118
12	Hocking (1968)	Arctic community	Canada	binary	29	86
13	Kaiser-Bunbury <i>et al.</i> (2009)	Heathland habitat heavily invaded by introduced plants	Mauritius	rates	135	74
14		Heathland habitat from which introduced plants were removed	Mauritius	rates	100	64
15	Kato <i>et al.</i> (1990)	Beech forest	Japan	individuals caught	93	679
16	Kevan (1970)	High Arctic	Lake Hazen, Ellesmere Island, Northern Territory, Canada	no. visits	32	115
17	Inouye and Pyke (1988)	Montane forest	Australia	individuals caught	42	91
18	McMullen (1993)	Multiple communities	Galápagos Islands	binary	106	54
19	Medan <i>et al.</i> (2002)	Xeric scrub	Laguna Diamante, Mendoza, Argentina	binary	21	45
20		Woody riverine vegetation and xeric scrub	Río Blanco, Mendoza, Argentina	binary	23	72
21	Memmott (1999)	Medow	Bristol, U.K.	frequency of visits	25	79
22	Mosquin and Martin (1967)	Arctic community	Canada	individuals caught	11	18
23	Motten (1982)	Deciduous forest	USA	no. visits	13	44
24	Olesen <i>et al.</i> (2002) (2)	Coastal forest	Mauritius Island	no. visits	14	13

	webs)					
25		Rocky cliff and open herb community	Azores Islands	no. visits	10	12
26	Ollerton <i>et al.</i> (2003)	Upland grassland	KwaZulu-Natal region, South Africa	individuals caught	9	56
27	Ramírez and Brito (1992)	Palm swamp community	Venezuela	binary	33	53
28	Robertson (1929)	Agricultural area dominated by crops, with some natural forest and pasture	USA	binary	456	1429
29	Santos <i>et al.</i> (2010)	Caatinga (semi-arid vegetation)	Bahia State, Brazil	binary	51	25
30	Schemske <i>et al.</i> (1978)	Maple-oak woodland	USA	no. visits	7	32
31	Small (1976)	Peat bog	Canada	individuals caught	13	34
32	Vázquez and Simberloff (2002)(8 webs)	Evergreen montane forest	Argentina	no. visits	10	29
33					9	33
34					9	27
35					10	29
36					8	35
37					8	26
38					7	24
39					8	27
40	Smith <i>et al.</i> (2005)	Temperate rain forest	Chiloe island, Chile	binary	26	128
41	Valdovinos <i>et al.</i> (2009)	Andean scrub	Chile	binary	77	110
42	Aizen <i>et al.</i> (2008) (8 webs)	South-Andean Temperate Forest	Argentina	binary	4	17
43					7	28
44					12	34
45					17	51
46					11	29
47					17	52
48					14	36
49					16	37
50	Montero <i>et al.</i> (unpublished) (8 webs)		Menorca, Spain		7	24
51					11	36
52					11	33
53					9	26
54					9	35
55					10	43
56					7	16
57					10	19

Section 3: Effect of AF on the stability of unrealistically complex networks

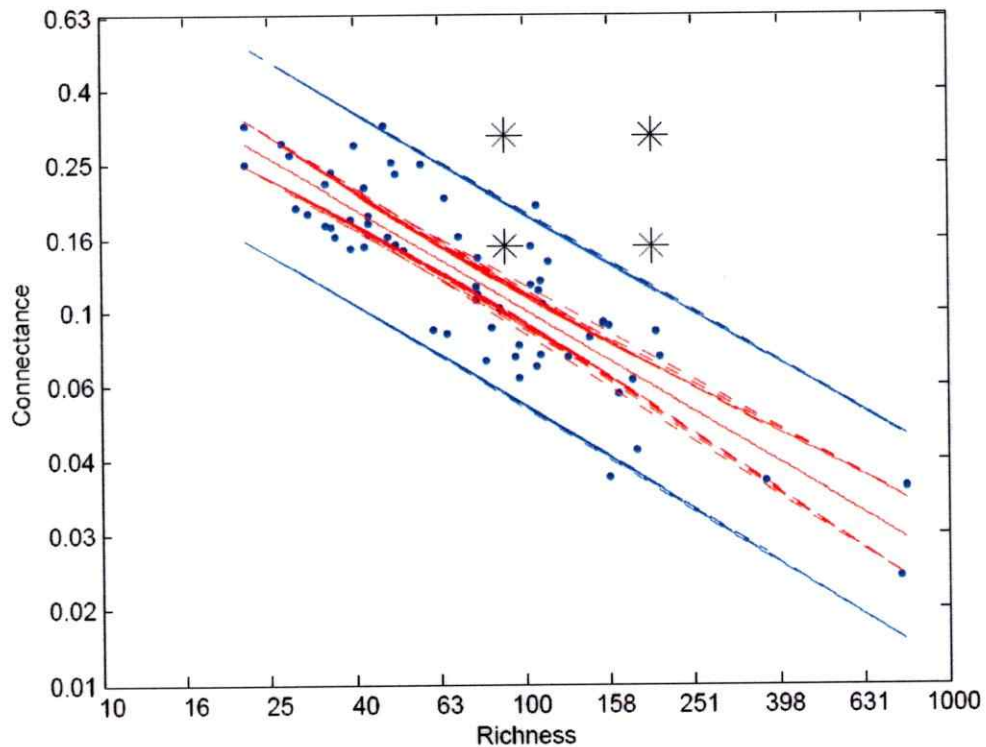


Fig S2. Prediction (blue) and confidence intervals (red) for the regression of the logarithm of connectance (C) to the logarithm of richness (S) of 57 empirical networks (blue filled circles) listed in Table S4. The four asterisks indicate $S=90$ $C=0.15$, $S=90$ $C=0.3$, $S=200$ $C=0.15$, and $S=200$ $C=0.3$, which were the average parameter values for the 800 simulated networks (200 networks for each S and C combination) used to run the dynamical model (Section 2) for the results shown in Fig. S3. The goal of these simulations was to compare the effect of adaptive foraging (AF) on species persistence of unrealistically complex networks ($S=90$ $C=0.3$, $S=200$ $C=0.15$, and $S=200$ $C=0.3$) to realistically complex networks ($S=90$ $C=0.15$).

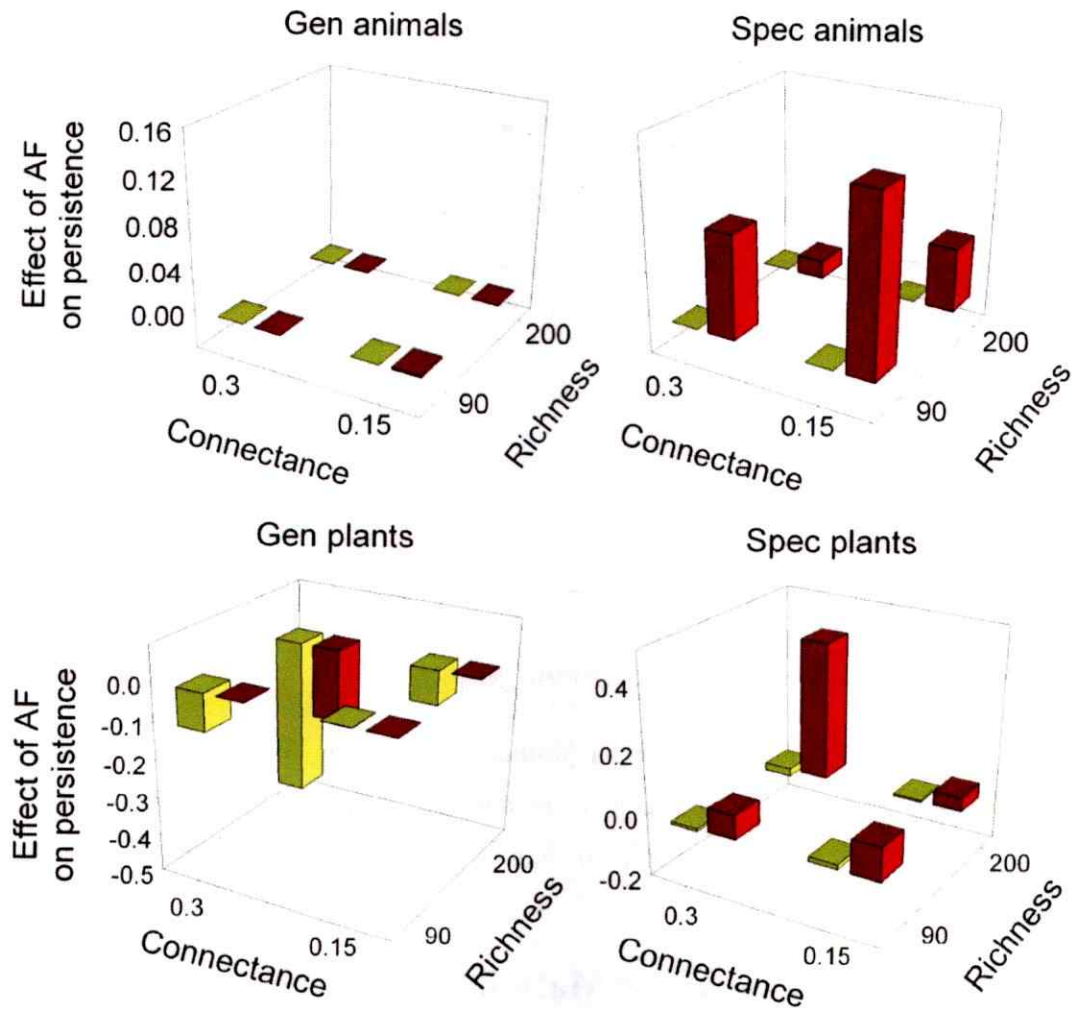


Fig S3. Effect of adaptive foraging (AF) on the persistence of generalized animal (Gen animals) and plant (Gen plants) species and of specialized animal (Spec animals) and plant (Spec plants) species. Bars represent average over 100 nested (red) and 100 non-nested (yellow) networks. The goal of these simulations was to compare the effect of adaptive foraging (AF) on species persistence of unrealistically complex networks ($S=90$ $C=0.3$, $S=200$ $C=0.15$, and $S=200$ $C=0.3$) to realistically complex networks ($S=90$ $C=0.15$). In unrealistically complex networks, AF exerted a negative effect on generalist plants.

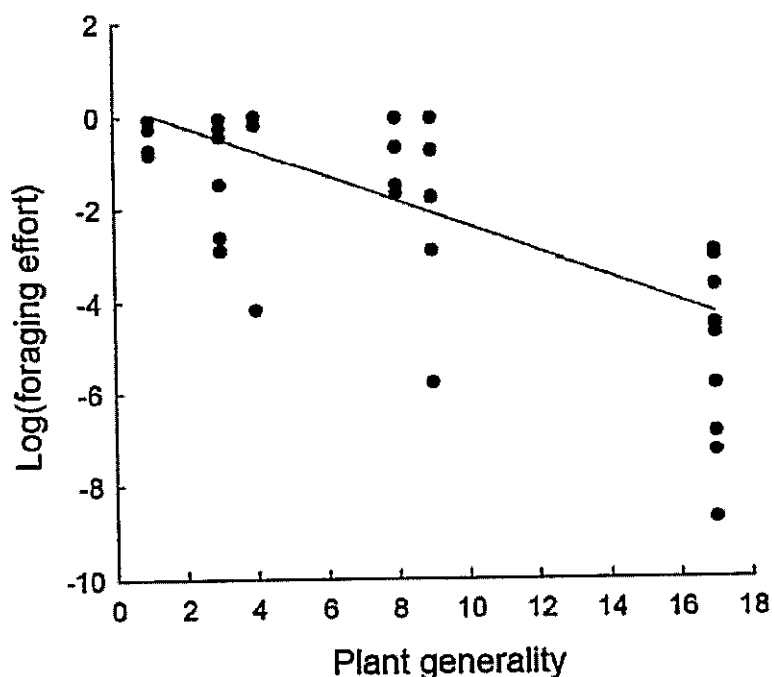


Fig S4. Effect of plant generality on pollinator preference for a typical simulated network. Plant generality is measured as the number of species that pollinate a species of plant. The slope of the regression is -0.27 , with a standard error of 0.04 .

Supplementary Material (CHAPTER 4)

Table S1: Model parameters and state-variables: short definition, units and mean values of parameters and initial conditions used in the simulations. Values were drawn from a uniform random distribution with the specified mean, and variances of 10% and 0% of means for plants' and animals' parameters, respectively. Asterisks indicate initial conditions and k_{aj} is the number of interactions of animal j .

Definition	Symbol	Dimension	Mean value
Density of plant population i	p_i	individuals / area	0,5*
Density of animal population j	a_j	individuals / area	0,5*
Total density of floral resources of plant population i	R_i	mass/ area	0,5*
Foraging effort	α_{ij}	None	$1/k_{aj}$ *
Visitation efficiency	τ_{ij}	(visits *area) / (time*individuals*individuals)	1
Expected number of seeds produced by a	e_{ij}	Individuals / visits	0.8

pollination event			
Per capita mortality rate of plants	μ_i^P	1 / time	0.001
Conversion efficiency of floral resources to pollinator births	c_{ij}	individuals/ mass	0.2
Per capita mortality rate of pollinators	μ_j^A	1 / time	0.001
Pollinator extraction efficiency of resource in each visit (linear model)	b_{ij}	individuals / visits	0.4
Maximum fraction of total seeds that recruit to plants	g_i	None	0.4
Inter-specific competition coefficient of plants	u_i	area / individuals	0.06
Intra-specific competition coefficient of plants	w_i	area / individuals	$f(k_{pi})^{\S}$
Production rate of floral resources	β_i	mass / (individuals * time)	0.2
Self-limitation parameter of resource production	ϕ_{ij}	1 / time	0.04
Adaptation rate of foraging efforts of pollinators	G_j	None	2

$\S f(w_i) = [-0.7/(k_{p_max} - k_{p_min})] * k_{pi} + [0.7/(k_{p_max} - k_{p_min}) * k_{p_min}] + 1$. Where k_{pi} , k_{p_max} and k_{p_min} are the degree of the plant i , and the maximum and minimum plant degrees of the network. $f(w_i)$ is a simple linear function with a slope and an intercept that depends on the plants' degree distribution of each network that is always power law with coefficient of 2 (as in Thébault and Fontaine 2010).

Figure Captions

Fig S1. Prediction and Confidence Intervals in Regression. Plot regression curve on a scatter plot, plus the ci 95% range of the regression line and the ci 95% of the data range. Hystogram of 63 empirical networks, classified by richness and connectance. The values of richness and connectance are just labels for intervals of those structural properties.

Fig S2. Invasions success for plant invaders: specialists (Spec), high pollen producing specialists (Spec high P), high reward producing specialists (Spec high R), high reward and pollen producing specialists (Spec high P&R), generalists (Gen), high pollen producing generalists (Gen high P), high reward producing generalists (Gen high R), and high pollen and reward producing generalists (Gen high P&R); as a function of the

structural properties that better explained the variance of invasions success regarding CART analysis. Red crosses indicate invasion success and black circles indicate failure.

Figure S3. The effect of alien plants invasions on total pollination events and total abundances of pollination networks. We normalized these differences by dividing the differences between the variables after invasion and those before invasion by the variables before invasion. Labels mean: specialists (Spec), specialist high pollen producers (Spec high P), specialist high rewards producers (Spec high R), specialist high rewards and pollen producers (Spec high P&R), generalists (Gen), generalist high pollen producers (Gen high P), generalist high rewards producers (Gen high R), and generalist high pollen and rewards producers (Gen high P&R). Bars are the mean over 1,200 networks and error bars are their 95% confidence intervals. Black, light grey and dark grey bars indicate all, generalist and specialist species, respectively.

Fig S1

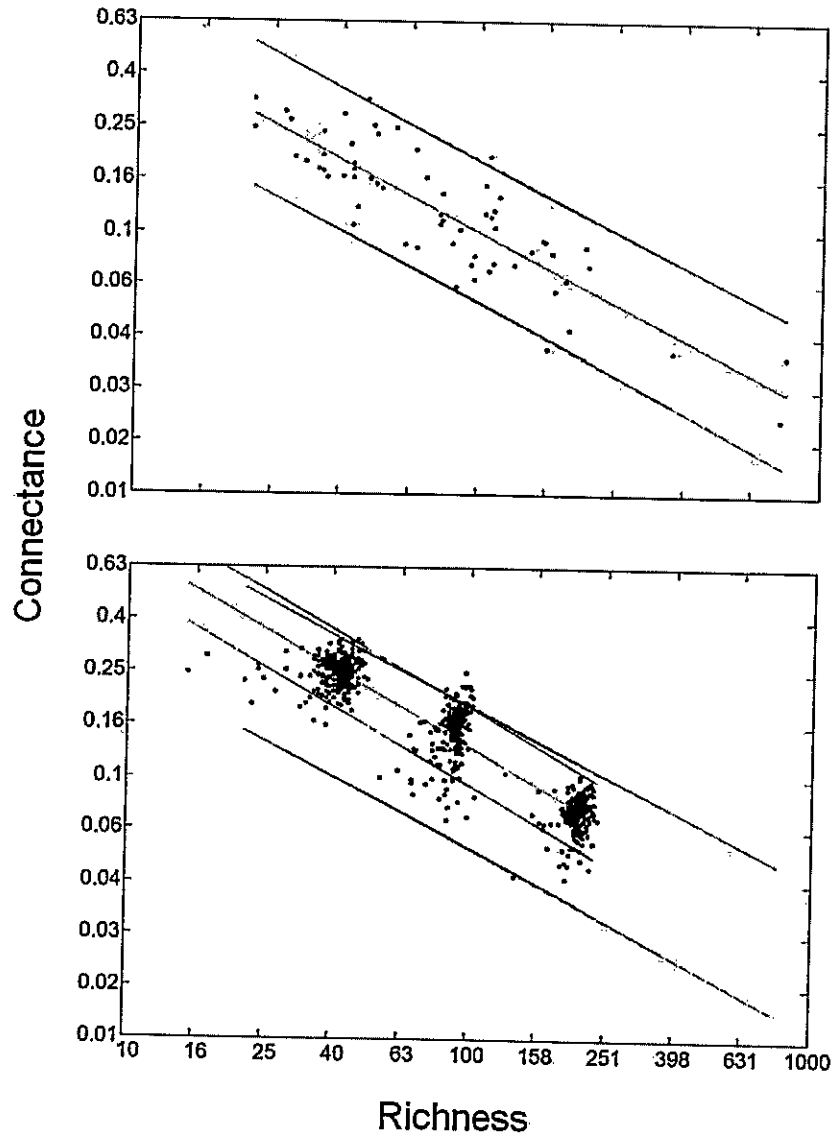


Fig S2

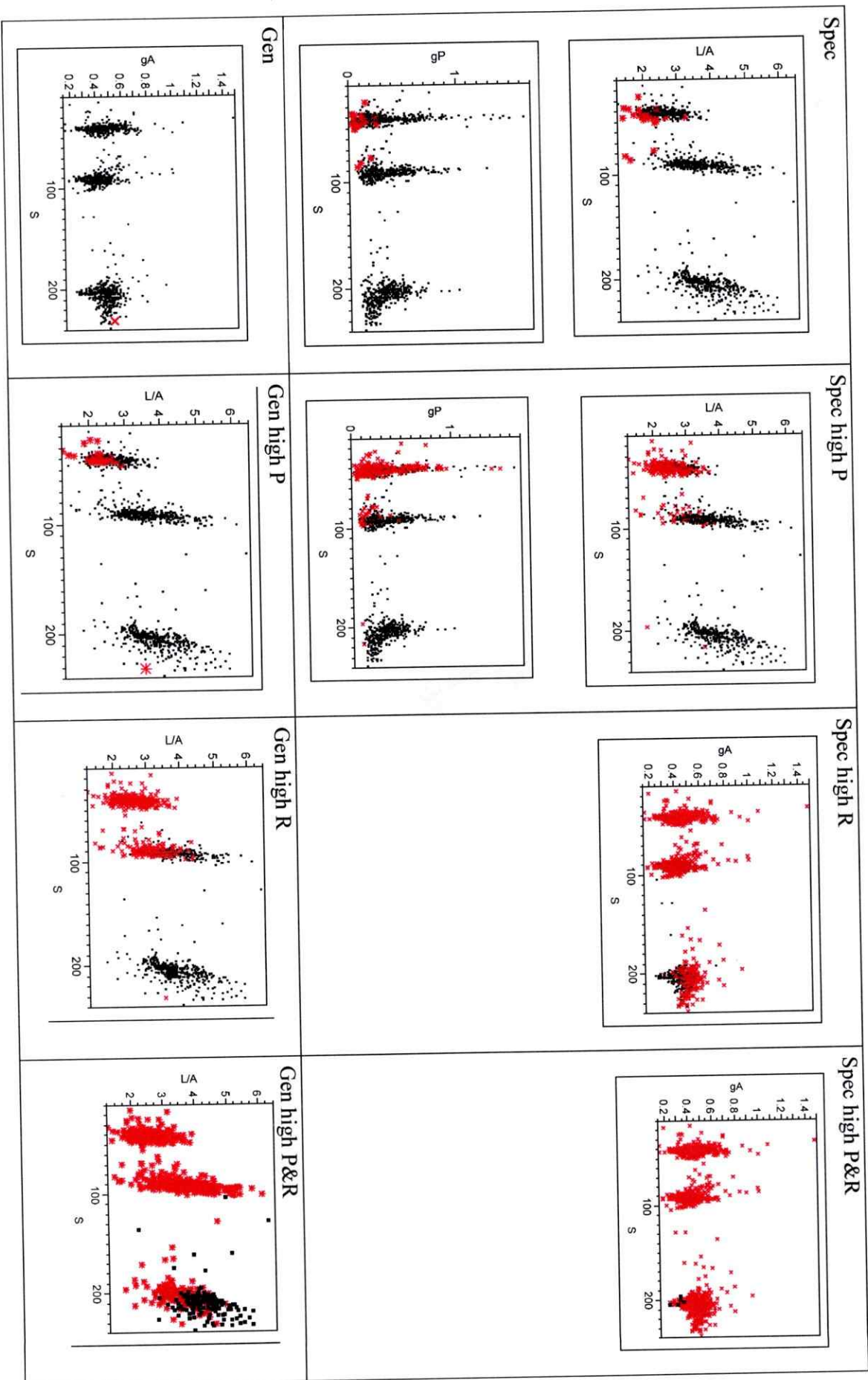


Fig S3

