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Mutualistic Networks: Moving closer to a predictive theory

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Abstract

Plant-animal mutualistic networks sustain terrestrial biodiversity and human food-security. Global environmental changes threaten these networks, underscoring the urgency for developing a predictive theory on how networks respond to perturbations. Here I synthesize theoretical advances towards predicting network structure, dynamics, interaction strengths, and responses to perturbations. I find that mathematical models incorporating biological mechanisms of mutualistic interactions provide better predictions of network dynamics. Those mechanisms include trait matching, adaptive foraging, and the dynamic consumption and production of both resources and services provided by mutualisms. Models incorporating species traits better predict the potential structure of networks (fundamental niche), while theory based on the dynamics of species abundances, rewards, foraging preferences, and reproductive services can predict the extremely dynamic realized structures of networks, and may successfully predict network responses to perturbations. From a theoretician's standpoint, model development must more realistically represent empirical data on interaction strengths, population dynamics, and how these vary with perturbations from global change. From an empiricist's standpoint, theory needs to make specific predictions that can be tested by observation or experiments. Developing models using short-term empirical data allows models to make longer-term predictions of community dynamics. As more longer-term data become available, rigorous tests of model predictions will improve.

Introduction

Mutualistic interactions between animal and plant species sustain terrestrial biodiversity (Thompson 1994) and human food-security (Potts et al. 2016, Ollerton 2017). Unfortunately, global environmental changes threaten these diverse systems with species extinctions, climate

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change, habitat loss, and species invasions (Goulson et al. 2015, Ollerton 2017). This global environmental crisis underscores the urgency for developing theory capable of understanding and predicting the structure and dynamics of mutualistic systems. Predicting the structure of mutualistic systems is critical for understanding and predicting their dynamics, and the dynamics of these systems underlie their important ecosystem functions and will determine their response to anthropogenic perturbations (Memmott et al. 2004, Bascompte & Jordano 2014, Valdovinos et al. 2016, 2018). Understanding how these mutualistic systems operate today, and predicting their dynamics as environments change, is critical for developing plans and policies to manage these systems with the objective of preserving their key ecosystem functions and services. In this review, I synthesize 20 years of scientific advances towards predicting the structure, dynamics, and response of mutualistic networks to global change.

Qualitative predictions produced by mathematical models and tested by empirical research have been key to the progress of Ecology as a science. Starting with Gause (1932), who experimentally tested the prediction of competitive exclusion produced by the Lotka-Volterra model of competition, research producing (e.g., Rosenzweig & MacArthur 1963, May 1973, Holt 1977) and testing (e.g., Vandermeer 1963, Murdoch & Oaten 1975, Stearns 1977, Wooton 1997, Schmitz 1997, Morin 1999) model predictions on ecological systems have shaped our discipline. Recent research on complex food webs has successfully predicted interaction strengths (Berlow et al. 2009) and relative biomasses of species (Boit et al. 2012) in aquatic systems. Notoriously, however, most of such research has been conducted on antagonistic interactions, leaving our understanding of mutualistic interactions far behind. Fortunately, the last decade has seen a blooming of ecological research on mutualistic interactions promoted by the study of mutualistic networks (Bascompte & Jordano 2014). Here, I organize the abundant literature focusing on the qualitative predictions made by theoretical research and discuss how those predictions have been or need to be tested with empirical data (see Table 1).

Networks have helped ecologists to identify patterns in the structure of species interactions in highly complex multi-species systems (i.e., several tens to hundreds of species, Martinez 1991, Bascompte et al. 2003, Thèbault & Fontaine 2010). There are almost infinite ways in which hundreds of species can possibly interact based only on all possible combinations of species interactions. This high complexity precluded for long time the detailed study of

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complex multi-species systems. That is, the seeming intractability of those complex systems caused ecologists to only study the dynamics of a few interacting species even when communities are composed by hundreds of interacting species. Contributions of network studies (and computers) to ecology made the complexity of communities more tractable by identifying clear patterns in the structure of interactions among tens to hundreds of species (Martinez 1991, Bascompte et al. 2003, Thèbault & Fontaine 2010) and showing that such structure strongly influences the dynamics of ecological systems (Brose et al. 2004, Bascompte & Jordano 2014, Valdovinos et al. 2016)

Initially, research on ecological networks was all about descriptive metrics of the structure of food webs (Martinez 1991, Dunne 2006) and mutualistic networks (Jordano 1987, Bascompte et al. 2003). More recent research, however, takes a dynamic path (e.g., Brose et al. 2004, Bascompte et al. 2006, Valdovinos et al. 2013) by using the type of mathematical modelling that ecologists have used for decades to study the dynamics of interacting species (e.g., Rosenzweig & MacArthur 1963, Holt 1977, Yodzis & Innes 1992). The main point of this review is to show that research on ecological networks has recently taken another step forward by producing more testable predictions. This step forward has moved ecological studies closer to predicting the structure (first section), dynamics (second section), and responses (third section) of ecological systems to global change, via better integrating theoretical and empirical research of ecological networks. Further developing and solidifying such predictive theory (e.g., theory that can be empirically tested with data) will be critical in future years to manage and preserve ecological systems in the era of global change.

I. Towards predicting the structure of mutualistic networks

This review considers network structure consisting of both the **binary structure** (i.e., who interacts with whom, Box 1) and the **strength** of those interactions. The first subsection synthesizes the state of the art on proposed mechanisms predicting the binary structure including species traits and abundances, and incomplete sampling. The second subsection conceptualizes interaction strengths and synthesizes the few works predicting them in mutualistic networks.

A. Predicting the binary structure

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Most of the research on mutualistic networks has been devoted to characterizing, explaining, and more recently, predicting their binary structure (Box 1; Jordano 1987, 2016, Bascompte & Jordano 2007, 2014, Ramos-Jiliberto et al. 2010, Chacoff et al. 2012, Bartomeous et al. 2016). This subsection organizes the scope and results of such research within three main questions, which constitute sequential steps towards predicting the binary structure. Those questions are: 1) What is the common structure to all mutualistic networks? 2) What are the mechanisms producing such structure? 3) Can we predict interactions among species based on species traits and abundances?

1) What is the common structure to all mutualistic networks?

If a new mutualistic network was sampled in the field, it would likely exhibit: 1) more animal than plant species, 2) moderate connectance, 3) highly heterogeneous degree distribution, 4) high nestedness, and 5) moderate modularity (see Box 1 for definitions; Jordano 1987, 2016, Bascompte & Jordano 2007, 2014, Ramos-Jiliberto et al. 2010, Chacoff et al. 2012, Bartomeous et al. 2016). These properties characterize the binary structure of most of the empirical networks reported worldwide.

2) What are the mechanisms producing such structure?

Much research has been devoted to explain the prevalence of the above-mentioned properties (reviewed in Vázquez et al. 2009 and Bascompte & Jordano 2014). One of the key mechanisms proposed to explain those properties are the **barriers or constraints on interaction formation** (Table 1; also called forbidden links, Jordano 1987, 2016, Vázquez et al. 2009a). Mechanisms constraining species interactions include temporal or spatial uncoupling (i.e., species do not co-occur in either time or space), constraints to the accessibility of the resources due to trait mismatches (e.g., proboscis size very different from corolla size), and physiological-biochemical constraints that prevent the interactions (e.g., chemical barriers). Empirical (reviewed in Vázquez et al. 2009a and Jordano 2016) and theoretical (Santamaría & Rodríguez-Gironés 2007) research has shown that those constraining mechanisms predict the absence of interactions among specialist species (characteristic of nestedness), the existence of numerous specialist species and a few highly generalist species (characteristic of heterogeneous degree distributions), and the observed low connectance of networks.

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Other work, however, has shown that properties of the binary structure observed in mutualistic networks can emerge as a **sampling artefact** (Table 1; Blüthgen et al. 2008, Blüthgen 2010). Blüthgen et al. developed a neutral model assuming incomplete sampling of species interactions, skewed species abundances, and fully generalized systems (i.e., all plant species interact with all animal species). Such a model predicts that the often-missing interactions between rare species (characteristic of nestedness and heterogeneous degree distributions) result from low sampling efforts failing to record the interactions of rare species. This prediction raised the question of whether the observed structure of mutualistic networks represents the 'true' architecture of interactions (produced by evolutionary and ecological mechanisms), or merely an artefact of **incomplete sampling**. This question promoted many studies investigating sampling effects on network structure by varying sampling effort both in the field (Nielsen & Bascompte 2007, Petanidou et al. 2008, Hegland et al. 2010, Chacoff et al. 2012, Rivera-Hutinel et al. 2012) and in models generating network structures (Blüthgen et al. 2008, Vázquez et al. 2007, Bartomeous 2013, Fründ et al. 2016). Those studies showed that incomplete sampling strongly underestimates the number of interactions and overestimates the degree of specialization.

Fortunately, recent niche-based models (e.g., Fründ et al. 2016) help disentangle the effect of incomplete sampling from the effect of species' abundances and traits in structuring mutualistic networks. Moreover, complementary data sources can reduce the incidence of missing links caused by incomplete sampling and, therefore, reduce the impacts of sampling effort on network data (Olesen et al. 2010, Jordano 2016). For example, pollen-transport data effectively complement pollinators' visitation data to show the structure of plant-pollinator network (Bosch et al. 2009, Olesen et al. 2010, Coux et al. 2016). Overall, studies evaluating the impacts of missing links and sampling effort on network structure show that low sampling effort strongly underestimates the number of links and degree of generalization but does not necessarily affect higher-order network properties such as nestedness. This results mostly because the averaging of processes for higher-order function minimizes the effects of outliers. Consequently, a robust characterization of higher-order properties of networks is still possible even when true interactions are under-sampled (Morales-Castilla et al. 2015, Jordano 2016).

3) Can we predict interactions among species based on species traits and abundances?

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Building on the knowledge generated by studies analyzing properties of the binary structure, recent models are predicting the occurrence of interactions based on species traits and abundances (Vázquez et al. 2009b, Eklöf et al. 2013, Gravel et al. 2013, Morales-Castilla et al. 2015, Bartomeus et al. 2016, Crea et al. 2016, Fründ et al. 2016). For example, Bartomeus et al. (2016) use a Bayesian block-model approach (Clauset et al. 2008) in which the probability of an interaction between co-occurring species depends on their traits. Such models can also account for species abundances by making the trait distribution dependent on abundances. Using maximum likelihood, the authors fit the model parameters to three empirical datasets ranging from predator-prey to mutualistic interactions, and use the parameterized models to predict species interactions and estimate unobserved traits for each dataset. As another example, Morales-Castilla et al. (2015) sequentially remove species interactions based on constraining mechanisms (e.g., spatial or temporal decoupling) and estimate the interaction probabilities for the residual links. These types of models advance the discipline of ecological networks by producing predictions of specific interactions that can be tested against empirical data, which can further describe the relative effects of different mechanisms (i.e., species traits constraining interaction formation, species abundances, and incomplete sampling) on the structure of mutualistic networks.

Finally, related to predicting interactions based on species traits, **phylogenetic signal** has been detected in the structure of mutualistic networks (Rezende et al. 2007, Peralta 2016). This suggests that the evolutionary history encoded in species phylogenies may have influenced the assembly of mutualistic networks. In a seminal paper detecting phylogenetic signal in mutualistic networks, Rezende et al. (2007) find that phylogenetically related species tend to interact with a similar set of species and exhibit similar numbers of interactions. Explanatory mechanisms for this ‘conservatism of interactions’ (Peralta 2016) still need to be evaluated, but one plausible mechanism is that species may have inherited their traits involved in mutualistic interactions from common ancestors. Thus, related species exhibit similar traits and, therefore, a similar set of mutualistic partners (Eklöf et al. 2013). Other research detecting phylogenetic signal in mutualistic networks (reviewed by Peralta 2016) shows that modularity might depend on the clustering of phylogenetically related species in a network (Dupont & Olesen 2009) and on trait convergence such as pollination syndromes (Corbet 2000). However, more research is required to evaluate causation in the correlations reported between network structure and phylogenetic

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trees. For example, network assembly models show that nested or modular structures fail to emerge when simulating phylogenetic relatedness (Perazzo et al. 2014, Ponisio & M'Gonigle 2017). Without such key cause-effect connections, much of the phylogenetic signal of networks remains speculative (but see Raimundo et al. 2018). Moreover, most studies investigating phylogenetic signal in networks use taxonomic instead of phylogenetic trees, which represent important challenges including underestimating evolutionary differences and arbitrarily assigning branch lengths (Peralta 2016).

In summary, research on mutualistic networks has provided answers to the three questions examined in this subsection. First, general properties including high nestedness, moderate connectance, and heterogeneous degree distribution are common to most observed networks. Second, biological mechanisms including trait (miss)matching and phenological (de)coupling together with incomplete sampling have proven to determine those properties. In particular, incomplete sampling strongly diminish detection of specific interactions but less strongly affects network-wide measures of structure. Third, the theoretical (*a priori*) predictions of network structure are improving, mainly due to iterative comparisons with empirical datasets, but understanding the causal relationships between empirical properties (e.g., phylogenetic similarity) and network structure (e.g., modularity) remain a challenge.

B. Predicting interaction strengths

The distribution of interaction strengths among species strongly influences the dynamics of communities (McCann et al. 1998, Wootton & Emmerson 2005, Bascompte et al. 2006, Okuyama & Holland 2008). Therefore, predicting the distribution of interaction strengths in mutualistic networks provides important information for predicting their dynamics. This sub-section emphasizes the need to distinguish per-capita effects from interaction frequencies when defining interaction strengths (e.g., standardizing by species abundances). This is to avoid predicting (e.g., Bascompte et al. 2006) that abundant species (usually generalists) provide higher per-capita benefits to their mutualistic partners than do rare species (usually specialists), which contradicts empirical (Vázquez et al. 2005, Gómez & Zamora 2006) and theoretical (Valdovinos et al. 2016, Benadi & Gegear 2018) evidence showing that specialists tend to provide higher per-capita benefits than generalists.

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One of the most used definitions of interaction strength is **per-capita effect**, defined as the direct effect of an average individual of one species on the average individual of another species (Wootton & Emmerson 2005, Vázquez et al. 2015). Bascompte et al. (2006) proposed to estimate per-capita effects in mutualistic networks (α_{ij}^A and α_{ji}^P in Eqs. 2-3 of Box 2) by using the frequency of interaction between plant and animal species (i.e., frequency of contact or visits). More specifically, the authors proposed to estimate those per-capita effects as the **dependence** of a species on their mutualistic partners (Box 1), which effectively measures the relative frequency of interaction between species. However, this approach potentially confounds per-capita effects with species abundances. The metric of dependence results in species depending more strongly on species with whom they interact more often, which is highly correlated with species abundance (see above, Vázquez et al. 2007). That is, Bascompte et al. (2006) predict that a visit by an average individual of an abundant species provides higher benefits to their mutualistic partners than a visit by an average individual of a rare species, which contradicts empirical data (Vázquez et al. 2005, Morris et al. 2010, Aizen et al. 2014). The meta-analysis conducted by Vázquez et al. (2005) 'confirms findings of previous studies suggesting that the most abundant animal mutualists are not necessarily the most effective ones on a per visit basis'. Paradoxically, Bascompte et al. (2006) based their prediction on Vázquez et al. (2005), which is reiterated in Bascompte & Jordano (2014) as: 'Once again, we assume that dependence is a good surrogate for per-capita effect, which is justified both in mathematical terms and as observed in empirical studies (Vázquez, Morris, et al. 2005a; see Chap. 4)'. Unfortunately, such justification cannot be found in the cited reference. Vázquez et al. (2005) found the frequency of interactions as good surrogate for **total effects** on populations but not for **per-capita** effects.

To my knowledge, the only way to use the frequency of interaction to predict **per-capita effects** is to know the relationship among frequency of interaction, species abundance, fitness components (e.g., seed production, survival of different stages), and per-capita growth rates (Vázquez et al. 2015). Moreover, the frequency of mutualistic interactions does not always estimate well the **total effects** of mutualisms on populations. An increase in such frequency can also negatively affect the interacting populations when the costs of the mutualisms exceed their benefits (see below; Morris et al. 2010). For example, alien pollinators may increase the reproduction success of native plants when moderately abundant but decrease the plant

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reproduction when highly abundant (Aizen et al. 2014, Valdovinos et al. 2018). In addition, saturating functional responses (Eq. 4 in Box 2) and adaptive foraging (Benadi & Gegear 2018) can make the net effects of mutualisms independent of the interaction frequency.

Another approach to conceptualizing the strength of mutualistic interactions is to calculate **net effects** resulting from the **benefits** minus **costs** incurred by the interacting organisms (Bronstein 1994, 2001, 2006). As defined by Holland et al. 2002, 'benefits are goods and services that organisms cannot obtain affordably, or at all, in the absence of their partner(s)'. Benefits obtained through mutualistic interactions include food, transportation, and protection. Costs 'include investments in structures to attract mutualists, substances to reward them, and the energy and time spent obtaining those rewards' (Holland et al. 2002). Importantly, benefits and costs of mutualisms vary depending on the abundance of the mutualistic partners as well as through time and across space (Bronstein 1994, 2006), which ultimately determines the net effects of a mutualism in a particular time and location. Holland et al. (2002) build on this conceptualization of mutualisms to develop ecological theory that incorporates the density-dependent nature of benefits and costs. More specifically, the authors develop functional responses of mutualisms (i.e., per-capita benefit as a function of the abundance of the mutualistic partner) as net effects resulting from different density-dependent functions (linear, unimodal, saturating) of benefits and costs. Using the resultant functional responses, the authors evaluate the effects of the different density-dependent functions of benefits and costs on the dynamics of mutualistic systems composed by two interacting species.

In summary, predicting interaction strengths needs to distinguish per-capita effects adjusted for species abundance from the total effects of mutualisms on populations. In addition, better estimations of benefits and costs are one approach to a more clear understanding of interaction strengths.

II. Towards predicting the dynamics of mutualistic networks

Research reviewed in the past section shows that species traits and abundances influence the structure of mutualistic networks. This section reviews models predicting the dynamics of those abundances and the effect of network structure on network dynamics. The first subsection

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describes the assumptions and predictions of the two general frameworks used for modeling population dynamics in mutualistic networks. The second subsection reviews research modeling the plasticity of species interactions determined by the ability of animals to change their interactions in response to changes in their resource availability.

A. Population dynamics models and their predictions

This subsection synthesizes the assumptions of **Lotka-Volterra type** (Fig. 1A, Box 2) and **consumer-resource** (Fig. 1B, Box 3) models and explains how different assumptions produce contrasting predictions on the effect of network structure on network stability (Table 1).

Because of their simplicity and mathematical convenience, Lotka-Volterra type models have been the most commonly used models of population dynamics to study mutualistic networks (Fig. 1A, Box 2). These comprise the Lotka-Volterra model of mutualism and all its extensions (Boucher 1985), including replacing the linear positive effects of mutualisms (Type I functional response) by saturating positive effects (Type II functional response, see Box 2). Those models represent mutualistic relationships as net positive effects between species using a positive term in the growth equation of each mutualist that depends on the population size of the partner. However, by phenomenologically assuming net positive effects between mutualistic partners, those models (a) disregard important biological processes associated with plant-animal interactions that can result in negative net effects on the interacting populations (Bronstein 1994, Holland et al. 2002), and (b) produce very different dynamic outputs for populations and communities compared to models where the net effects are described mechanistically (Holland & DeAngelis 2010, Valdovinos et al. 2016). Key processes ignored by these models include visitation, feeding, and reproductive mechanisms that determine how direct interactions between mutualistic partners vary through time and across densities or total abundances of the interacting species (Abrams 1987, Holland & DeAngelis 2010, Valdovinos et al. 2013, Box 3).

Lotka-Volterra type models predict that structural properties including species richness, connectance, nestedness, the asymmetry of interaction frequencies, and modularity (Box 1) affect the stability of mutualistic networks. However, studies analyzing the effects of those properties on network stability show contrasting results on the direction of the effects (Box 4), especially for nestedness and connectance. Extensive analyses performed by Pascual-Garcia & Bastolla (2017) explained the contrasting results by demonstrating that connectance always

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increases network stability for saturating mutualisms, while the effect of nestedness depends on the level of inter-specific competition among plants and animals (hereafter **intra-guild competition**), and whether mutualisms are facultative or obligate (i.e., species persist or go extinct when their partners are absent). The authors demonstrate that: 1) saturating mutualisms (Eq. 4) are necessary for the system to be stable (i.e., **feasible**, Box 1), 2) *without* intra-guild competition, saturating mutualisms are always stable and their **feasibility** only requires mutualisms to be facultative (i.e., $r_i > 0$ in Eqs. 2-3 with Eq. 4), and 3) *with* intra-guild competition, the feasibility of saturating mutualisms requires that the intrinsic growth rates (r_i in Eqs. 5-6) negatively correlate with the species' number of mutualistic interactions and that the ratio between plant and animal abundances (density, biomass) is higher than $2 \cdot 10^5$. In summary, under the assumptions of Lotka-Volterra type models, highly connected networks of saturating and facultative mutualisms exhibiting the lowest intra-guild competition are the most stable.

The extensive analysis conducted by Pascual-Garcia & Bastolla (2017, see above) shows that nestedness is a weaker predictor for network stability than connectance, intra-guild competition, and whether mutualisms are facultative or obligate, which resolves discrepancies among previous studies using Lotka-Volterra type models. For example, Bastolla et al. (2009) and Rohr et al. (2014) find that nestedness increases **structural stability** (Box 1) of networks with saturating mutualisms and intra-guild competition because the authors assumed fully connected networks and low intra-guild competition (both stabilizing), respectively. In contrast, James et al. (2012) find that nestedness decreases species persistence because the authors adopt similar intrinsic growth rates for all species, which is destabilizing for networks with intra-guild competition (see point 3 above).

A more mechanistic alternative to the Lotka-Volterra type models is the consumer-resource approach to mutualisms (Holland & DeAngelis 2010, Holland et al. 2005, Valdovinos et al. 2013, 2016, 2018). This approach decomposes net effects assumed always positive by Lotka-Volterra models (Fig. 1A) into the biological mechanisms producing those effects (Fig. 1B). While this approach has been applied to study pairwise interactions (Holland et al. 2005, Holland & DeAngelis 2010) to my knowledge only Valdovinos et al. (2013, 2016, 2018) have developed a consumer-resource model for mutualistic networks. The key advance of Valdovinos et al.'s model is separating the dynamics of the plant vegetative biomass from the dynamics of

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the plant rewards (Fig. 1B, Box 3). This separation allows: i) tracking the depletion of plant rewards, ii) evaluating exploitative competition among animal species visiting the same plant species, and iii) incorporating adaptive foraging (i.e., behavioral responses to resource availability). Another advance of this model is incorporating the dilution of conspecific pollen carried by animals, which tracks the competition among plants for the animals' pollination services. That is, pollinator species assigned visits to many different plant species carry more diluted conspecific pollen, which also works as a proxy for quality of visits (σ_{ij} of Eq. 8 in Box 3, Fig. 1D). This model predicts that highly nested but moderately connected networks will exhibit the highest **species persistence** when animals are adaptive foragers (Valdovinos et al. 2016). Without adaptive foraging, however, nestedness decreases and connectance increases species persistence. This is because increasing nestedness increases niche overlap among animal (Fig. 1C) and plant (Fig. 1D) species, and increasing connectance increases the number of food sources for animals. Introducing adaptive foraging (Eq. 11 in Box 3) allows generalist pollinators to partition most of their foraging effort to specialist plants (with high availability of rewards, compare Figs. 2B and 2A). This partitioning stabilizes the highly nested and moderately connected networks by releasing the rewards of generalist plants to specialist pollinators, and increasing the quantity and quality of visits received by the specialist plants. The results and equations of this model can be extended to other plant-animal mutualisms (e.g., frugivory) by assuming that plant rewards represent fruits instead of floral rewards and by assuming dilution of seed-dispersal services instead of dilution of pollination services.

In summary, Lotka-Volterra type models predict that highly connected networks of saturating and facultative mutualisms exhibiting the lowest intra-guild competition are the most stable, while a consumer-resource model predicts that highly nested but moderately connected networks will exhibit the highest stability when animals are adaptive foragers.

B. Predicting the plasticity of interactions

The previous subsection synthesized two frameworks to model population dynamics, one assuming static interactions (i.e., Lotka-Volterra type models) while the other allowing plastic interactions (i.e., consumer-resource model by Valdovinos et al. type). This subsection synthesizes studies that provide further understanding of the highly plastic nature of mutualistic interactions (CaraDonna et al. 2017, Ponisio et al. 2017).

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The plasticity of mutualistic interactions was first modeled topologically as ‘interaction rewiring’, that is, by algorithmically defining which, when, and how species interactions were rewired to new species (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012). This modeling was first developed to evaluate the network responses to species extinctions (see next section). Kaiser-Bunbury et al. (2010) simulated interaction rewiring based on all the potential interactions observed for pollinator species during a flowering season in two representative sites on Mauritius Island. The authors analyzed the **robustness** to species removals (Box 1) and the subsequent topological co-extinctions of 12 consecutive snapshots (2-week periods) that depicted the plant-pollinator interactions recorded bi-weekly over the flowering season. The whole-season network (i.e., 12 snapshots combined) was assumed to record all the potential interactions of each pollinator species. That is, if a pollinator species interacted with a particular plant species in the whole-season network, but was not observed visiting such species within a particular snapshot, the pollinator species was assumed able to rewire any of its observed interactions to that plant species. The interaction rewiring was then simulated within each of the 12 snapshots as the response of pollinators to the extinction of their plant partners by reassigning those interactions to the persistent plant species with which they can potentially interact (determined by the whole-season network). As expected, the authors find that this rewiring algorithm increases the robustness of the networks to species extinctions.

Ramos-Jiliberto et al. (2012) take a step forward towards predicting the plasticity of mutualistic interactions by incorporating both interaction rewiring and population dynamics into the analysis of the network responses to extinctions. To model population dynamics, a meta-community model developed by Fortuna & Bascompte (2006, Eqs. 13-14) was used to evaluate the effects of different rewiring algorithms (which and how interactions rewire) on network **robustness** to species removals (Box 1). They found that interaction rewiring increases the network robustness to species extinctions especially when specialist pollinators are more likely to rewire their interactions, and when the rewired interactions are more likely to be connected to plant species with the highest proportion of patches occupied per animal interaction. Valdovinos et al. (2013) take another step forward towards predicting the plasticity of mutualistic interactions by not only combining population dynamics with interaction plasticity but also more explicitly modeling adaptive foraging (see previous section, Eq. 11 in Box 3). Moreover, in

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Valdovinos et al.'s model, the plasticity of foraging efforts not only determines the presence or absence of interactions but also their strength.

Zhang et al. (2011) also combined population dynamics and interaction rewiring but to evaluate the emergence of nestedness as a consequence of adaptive foraging. The authors used a Lotka-Volterra type model of saturating mutualisms without intra-guild competition (Eqs. 2-4), assuming facultative mutualists (specifically with r_i between 0 and 1). Interaction rewiring was implemented in each time step by randomly choosing a pollinator species that will rewire its interaction with the lowest per-capita positive effect to a randomly chosen species. This model starts with random networks having the species richness and connectance of empirical networks as initial conditions, and converges to stable nested networks that successfully predict the nestedness levels found in empirical networks. This model also predicts the asymmetry of interaction frequencies, the heterogeneous degree distribution, and the positive relationship between species' degree and total impacts commonly found in empirical networks (Box 1). Note that these results are a reflection of previous results of Lotka-Volterra type models assuming saturating facultative mutualisms without intra-guild competition (see section 3, Box 4). When those types of mutualisms are assumed, nested, heterogeneous, and asymmetric networks are expected to emerge with adaptive foraging because those structures are the ones providing the highest benefits per species. Suweis et al. (2013) confirm this result using an optimization principle that maximizes species abundance. The authors demonstrate analytically and numerically that because of the assumed positive net effects between mutualistic species, increasing the abundance of a particular species increases both the networks' nestedness and the total species abundance. In fact, their optimization algorithm also predicts the emergence of nested networks.

In summary, research modeling interaction plasticity as responses to resource availability shows that plastic interactions stabilize mutualistic networks and may predict their structure.

III. Towards predicting the responses of networks to global change

Global environmental changes threatening mutualistic networks include species extinctions, climate change, habitat loss, and species invasions (Goulson et al. 2015, Ollerton

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2017). This final section synthesizes recent research that uses knowledge of the network structure and dynamics reviewed in the last two sections for predicting the response of networks to global environmental changes.

A. Species extinctions and topological co-extinctions

Memmott et al. (2004) simulated species extinctions by removing the respective nodes from networks and evaluated the subsequent co-extinctions caused by those extinctions based only on the binary structure of the networks, but ignoring species abundances, population dynamics, and interaction plasticity. The authors used this approach to evaluate the effect of the structure of two empirical plant-pollinator networks on their **robustness** against species extinctions (Box 1). The authors simulated pollinator extinctions by removing the corresponding nodes from the network, with the consequent loss of plant species that only interacted with the removed pollinator species. Such models assume that species completely depend on their mutualistic partners to persist and that organisms of those species do not respond to the extinction of their mutualistic partners by rewiring their mutualistic interactions to other species.

This topologically-determined approach to co-extinctions inevitably shows that increasing **connectance** increases the robustness of mutualistic networks to species extinctions due to an increased redundancy of interactions. In addition, increasing **nestedness** consistently increases network robustness to random extinctions and the extinction of the most specialist (i.e., least connected) species. The former is explained by the latter because random extinctions will more likely draw on specialist than on generalist species given that specialists are more frequent than generalists in the nested networks observed for empirical systems (Bascompte & Jordano 2007, 2014). Nested networks are robust to the extinction of specialist species because in those networks specialist species tend to interact with the most generalist (i.e., most connected) species that usually will not go extinct after the extinction of one of their specialist partners. Nested networks, however, are very fragile to the extinction of the most connected species, which usually produces the co-extinction of many specialist species.

B. Species extinctions and stochastic co-extinctions

An alternative approach to the one used by Memmott et al. relaxes the assumption that co-extinctions require the loss of all mutualistic partners (Vieiria et al. 2013). Vieira and

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coworkers proposed a stochastic model for determining the probability of species *i* going extinct following the extinction of species *j*, $P_{ij} = R_i d_{ij}$, as the product between the intrinsic dependence of species *i* on mutualisms to persist, R_i, and the realized **dependence** of species *i* on species *j*, d_{ij} (Box 1). Under this model, species can go extinct even when still connected with persistent species. As a result, increasing connectance decreases network robustness to extinctions by increasing the pathways for the effects of primary extinctions to propagate (Vieiria et al. 2013, Vieiria & Almeida-Neto 2015).

C. Species extinctions and population dynamics

A more mechanistic approach considers population dynamics to evaluate the co-extinctions caused by species removals. For example, Ramos-Jiliberto et al. (2009) simulated the extinction of different plant and animal species of an empirical plant-pollinator network by removing the respective nodes and evaluated the impact of those extinctions on the dynamics of the remaining species. In another example, Valdovinos et al. (2009) simulated the removal of all alien plant species from an empirical network, finding that such a restoration practice could actually harm the native species when alien species are well integrated in the network. In those two examples, as in the 'stochastic co-extinctions' (see previous sub-section), the co-extinctions caused by the species removals could occur even when all the mutualistic partners of a species did not go extinct. When simulating population dynamics, co-extinctions can also happen when the benefits of the mutualisms do not compensate for the mortality rates of the interacting populations.

D. Species extinctions and plastic interactions

Overall, studies modeling the plasticity of interactions (see previous section) predict that such plasticity increases the robustness of networks to species extinctions in comparison to the case of fixed interactions (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012, Valdovinos et al. 2013). Those studies reached the same conclusion even when their approaches were very different. Kaiser-Bunbury et al. (2010) simulated interaction rewiring based on all the potential interactions observed for pollinator species during a flowering season, but disregarded species abundances and population dynamics. Therefore, co-extinctions only occurred when all the mutualistic partners of a species went extinct, which overestimates network robustness. Ramos-Jiliberto et al. (2012) incorporated both interaction rewiring and population dynamics into the

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analysis of the network responses to extinctions, which makes co-extinctions more realistic. Finally, Valdovinos et al. (2013) also incorporated population dynamics, but took a consumer-resource approach (Box 3) in which the plasticity of foraging efforts determined the weights of the links (i.e., interaction strengths), as opposed to the binary approach taken in modeling the rewiring of interactions.

E. Climate change

Memmott et al. (2007) evaluated the potential effect of phenological shifts caused by climate change on mutualistic networks by simulating early first flowering and onset of the flight season of plant and pollinator species, respectively, predicted as responses to increased temperatures. The authors evaluated the effect of those phenological shifts on the availability of flowers and pollinator activity for a highly resolved empirical network, predicting that 17-50% of pollinator species would exhibit temporal gaps in their food supply because of the increased temperatures. The authors proposed that this reduction in temporal overlap between flowers and active pollinators will increase the extinction risk of the species in the network, particularly for the more specialized pollinators with small diet breadths. It would be interesting to re-evaluate those predictions assuming interaction plasticity.

F. Habitat loss

Fortuna & Bascompte (2006) evaluated the response of mutualistic networks to habitat loss by developing a metacommunity model that simulates habitat loss as the destruction rate of available patches (parameter d in Eq. 13 of Box 3). The authors calculated the fraction of extinct species caused by increasing levels of such destruction rate on nested and random networks. Their model predicts that nested networks would be less resistant to habitat loss (i.e., exhibit higher fractions of extinct species) than random networks at lower rates of patch destruction, but more resistant than the random networks at higher rates of patch destruction.

G. Species invasions

Valdovinos et al. (2018) use the consumer-resource model (Box 3) to develop a mechanistic framework to predict the invasion success of pollinator introductions and the networks' responses to pollinator invasions. We introduced pollinator species with different foraging traits (i.e., level of generality, foraging efficiency, and fixed vs adaptive foragers) into

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networks with different levels of species richness, connectance, and nestedness. Among 31 factors tested for the 43200 simulated introductions, we found that aliens with high foraging efficiency were the most successful invaders, while networks with higher diet overlap between alien and native pollinators were more impacted by invaders. In terms of the response of the native pollinators exhibiting adaptive foraging, we predict that those pollinators will persist in lower abundances by reassigning their visits to plants that are not visited by the invader, while native pollinators without alternative resources will go extinct (Fig. 3).

H. Perturbations altering interaction strengths

The studies described above explicitly modeled the type of perturbation affecting networks. For example, node removals and introductions modeled species extinctions and invasions, respectively. Phenological shifts simulated the effect of climate change, while patch destruction simulated habitat loss. In contrast, Saavedra et al. (2013) evaluated the general response of mutualistic networks to any type of perturbation that alters the interaction strength of mutualisms. Specifically, they simulated changes in interaction strengths by systematically varying the values of the parameters defining those strengths (i.e., b_{ij}^{A} and b_{ji}^{P} of Eq 5-6 in Box 2) in the Lotka-Volterra type model with direct intra-guild competition and saturating mutualisms. The networks' response to such perturbation was quantified as the amount of change in interaction strength that each species was able to sustain before going extinct. The authors also evaluated whether the tolerance of species to such change correlated with species degree and contribution to nestedness (Box 1), without finding any significant relation. Species' tolerance was very sensitive to the sign of the change in interaction strength and to the trade-offs between the number of partners and the strength of the interactions (Eq. 7 in Box 2).

Discussion

Qualitative predictions made by mathematical models have shaped much of our understanding in Ecology. This started with predictions made by the simple Lotka-Volterra model on competitive exclusion (Gause 1932) and predator-prey cycles (Solomon 1949), followed by the paradoxes of enrichment (Rosenzweig 1971) and biological control (Luck 1990, Arditi & Berryman 1991) predicted by the Rosenzweig-MacArthur (1963) model. Later

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predictions included indirect effects in trophic interactions such as apparent competition (Holt 1977) and the stabilizing effect of weak interactions in food webs (McCann et al. 1998). Finally, more recent predictions are made by the Allometric Trophic Network model on predator-prey body size ratios (Brose et al. 2006), interaction strengths (Berlow et al. 2009), and the relative biomasses of species in a lake (Boit et al. 2012). These predictions have guided much empirical research and provided general understanding that ecologists use to explain how ecological systems behave and would respond to perturbations including global change. Notoriously, most of those predictions concern antagonistic interactions, leaving mutualistic interactions understudied, which is unfortunate given the relevance of mutualisms for terrestrial biodiversity (Thompson 1994) and human food security (Potts et al. 2016, Ollerton 2017). In this work, I describe predictions in the ecological literature of mutualistic interactions with a particular focus on mutualistic networks.

Table 1 summarizes the qualitative predictions reviewed in this work together with the type of empirical data already used (or to be collected) to test those predictions. I find that models incorporating biological mechanisms that empirical research has shown to determine mutualistic interactions produce predictions that can be better tested against empirical data, compared to the more phenomenological models (e.g., Lotka-Voletrra type). Those mechanisms include trait matching (Jordano 2016, Bartomeus et al. 2016), the consumption of resources provided by the mutualisms (Holland & DeAngelis 2010, Valdovinos et al. 2013, 2016), adaptive foraging, and the dynamics of reproductive services (Valdovinos et al. 2013, 2016, Benadi & Gegear 2018). For example, trait matching can predict who interacts with whom given species co-occurrence (Bartomeus et al. 2016), while adaptive foraging can predict the effort that an average individual of a population partitions to each of those interactions (Valdovinos et al. 2016). Moreover, modeling benefits and costs of mutualisms can predict the functional responses of mutualistic interactions (Holland et al. 2002, Morris et al. 2010). I also find that several modeled mechanisms or potential biases (i.e., incomplete sampling, species abundances and traits, Table 1) successfully predict the observed **structure** of mutualistic networks. Therefore, further empirical research (including manipulative experiments) is needed to disentangle the actual mechanisms versus the artefacts producing those structures. For example, measurements of species abundances independent of visitation data (e.g., Brosi & Briggs 2013, Valdovinos et al. 2016) can distinguish the relative effects of incomplete sampling, individuals' foraging

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preferences, and species traits. In addition, measuring species traits more systematically and analyzing their effects on species interactions (number and identity) can distinguish between the effects of species traits and incomplete sampling in structuring mutualistic networks (Fründ et al. 2016).

Producing empirical data to test model predictions on network **dynamics**, however, is more challenging. In particular, testing model predictions on the effect of network structure on the stability of ecological systems (e.g., species persistence, local stability, resilience, see Box 1) seems difficult unless working with very long-term data-sets or systems with very fast generation times (Table 1). In fact, this difficulty of collecting empirical data to answer questions on long-term dynamics is one of the main reasons for using mathematical models in ecology because models can provide those answers where most empirical data cannot. Nevertheless, there is a way to connect short-term (hours/days/months) empirical data with long-term (decades/centuries) model predictions. More mechanistic models (e.g., Valdovinos et al. 2016, Benadi & Gegear 2018) not only make predictions of long-term processes such as stability but also of short-term processes that can be assessed empirically. Then, the specifics of those processes empirically tested can be linked back to network stability using the mathematical model. For example, Valdovinos et al. (2016) predict that generalist pollinators (per-capita) behaviorally prefer specialist plants, which was empirically corroborated with a plant-pollinator system in the Colorado Rockies. Then, such preferences were shown to determine the long-term stability of networks via partitioning niches between generalists and specialists for both animal and plant species.

A key to this research is the use of networks to study ecological systems. Networks provided tractability to the study of complex, multi-species systems of several tens to hundreds of interacting species. That is, the early descriptive metrics on network structure (reviewed in Dunne 2006, Bascompte & Jordano 2007) provided a general picture of how species interactions are organized in complex communities. From that picture, we can model the population dynamics of each species dependent on the interactions described by the network structure and further ask about the dynamic consequences of such structure. This earned tractably in the study of complex multi-species systems substantially advances our ability to predict ecological dynamics. Ecology has learned much from studying modules of a few interacting species in

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isolation from their entangled bank, but we also need to understand the dynamics of the entangled bank itself, especially if we want to predict the response of ecological systems to global change.

One of the main limitations of ecological networks, however, is a need for large amounts of empirical data to parameterize models and test their predictions. Nevertheless, there are some ways around this limitation. For example, Brose et al. (2004) used the bioenergetic model of Yodzis & Innes (1992) and its parameterization based on allometric scaling to successfully parametrize complex food webs of several tens of species. Then, Boit et al. (2012) used such model and parameterization to successfully predict the relative biomasses of 25 trophic groups in Lake Constance, leveraging 20 years of empirical data on abiotic and biotic factors including species biomasses. In mutualistic networks, much needs to be done to parameterize models based on empirical data. We still need to find those empirical patters like the allometric scaling in aquatic food webs to parameterize our models. As discussed above, more mechanistic models can also help in this endeavor by connecting short-term processes that can be measured in the field with long-term processes that can be investigated using models. In addition, our discipline requires more centralized, systematic empirical data across long-enough temporal series, allowing for cross-model comparison.

Based on 20 years of theoretical advances reviewed here, I think the most promising path to develop theory capable of predicting (Houlahan et al.2017) how networks respond to global change is incorporating the key biological mechanisms determining mutualistic interactions. In particular, I propose that theory based on species traits can predict the potential structure of the networks (fundamental niche) while theory based on the dynamics of species abundances, rewards, foraging preferences and reproductive services can predict the extremely dynamic realized structures of networks and may successfully predict their responses to perturbations. Recent work proposes a similar approach for the study of restoration ecology (Raimundo et al. 2018), where ‘adaptive network models’ combined with ‘phylogenetically-structured network data’ could play an important role in predicting the outcome of restoration practices based on the interplay among rapid trait evolution, species abundances, and species interactions. Key to the development of such predictive theory is a deep integration between empirical and theoretical research. Theoretically-oriented empirical work should provide biological mechanisms and

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parameter values to inform mathematical models, while the predictions of empirically-informed mathematical models should be tested with new empirical data.

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Table 1. Summary of modeling approaches and predictions reviewed in this study. Includes empirical data needed or already used to test the models' predictions. The abbreviations **long-time/short-gen*** and **already-tested*** stands for "requires data at very long time scales or system with very short generational time" and "already tested against empirical data", respectively.

Modeling approach	**Prediction**	**Empirical data needed**	**References**
		First section: Predicting network structure	
Interaction constraint models	Network structure is the product of various interaction constraints, e.g., temporal/spatial uncoupling, trait mismatches, physiological/ biochemical barriers.	**Already-tested*:** interaction constraints predict absence of interactions between specialists, heterogeneous degree distribution, and moderate network connectance. Still research is needed to more systematically relate species traits with network structure.	Santamaría & Rodríguez-Gironés 2007. e.g., Bartomeus et al. 2016.
Neutral (sampling artefact): incomplete sampling of interactions, skewed abundances, and fully generalized systems	Network structure results from incomplete sampling effort failing to record the interactions of rare species. Network structure is independent of species differences in traits.	**Already-tested*:** incomplete sampling of interactions, skewed species abundances, and fully generalized systems produce observed structure. Still needs to be tested with **independent measures of plant and animal abundances** (i.e., not estimated from interaction frequencies).	Blüthgen et al. 2007, 2008 e.g., Brosi & Briggs 2014, Valdovinos et al. 2016.

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Niche-based: disentangles species' abundances and generality level (i.e., number of interactions)	Sampling bias overestimates specialization in generalized networks but not necessarily in more specialized networks.	**Already-tested*:** model distinguishes the relative effects of species abundances and trait differences on predicting network structure. <u>Still</u> needs to be tested with independent measures of abundances and systematic analysis of species traits.	Fründ et al. 2016
	Second section: Predicting network dynamics		
Lotka-Volterra type models	Highly **connected** networks of **facultative** mutualisms exhibiting the lowest **within-guild competition** will be the most stable networks. Effect of **nestedness** on stability depends on the parameter values assumed.	**Long-time/short-gen***. Might be tested with time-series of plant and animal population across decades. Their assumptions (e.g., functional responses, Box 2) <u>still</u> need to be tested with empirical data.	Pascual-Garcia & Bastolla 2017
Consumer-resource: floral rewards dynamics, adaptive foraging, conspecific pollen dilution.	**Adaptive foraging** reverses the destabilizing effect of nestedness on **species persistence** and the stabilizing effect of connectance by partitioning niches among plant species (pollination	<u>Species persistence:</u> **long-time/short-gen***. <u>Niche partitioning</u> (short-term): **already** tested with data on foraging efforts. <u>Still</u> needs to be tested with data on pollination	Valdovinos et al. 2013, 2016, 2018.

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	services) and among animal species (floral rewards).	success, floral rewards, functional responses and benefit accruals.	
	On a per-capita (plant and animal) basis, generalist pollinator species prefer specialist plant species.	**Already-tested*** with empirical foraging efforts standardized by abundance of plants and animals	Valdovinos et al. 2016
Interaction plasticity based on adaptive foraging	Interaction plasticity increases network robustness against species extinctions in comparison to the case of fixed interactions	Behavioral responses at short time scales. Can be tested using manipulative experiments in the field.	Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012, Valdovinos et al. 2013.
	Nestedness emerges as a result of adaptive foraging	**Long-time/short-gen***	Zhang et al. 2011, Suweis et al. 2013.
Functional responses as **net effects:** benefits minus costs experienced by the interacting organisms	How benefits/costs of mutualisms vary with species density will affect their stability. Net effects likely follow a saturating or unimodal function with species density.	**Already fitted** net-benefit curves to measures of plant reproductive success. Still need curves to be fitted to measures of animal reproductive success.	Holland et al. 2002, Morris et al. 2010, Vázquez et al. 2012

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Individual based model: adaptive foraging, pollen transfer and floral rewards	Adaptive foraging favors pollination of the least-abundant plant species at high flower abundances. Least-abundant plant species will benefit more from offering higher levels of floral rewards than the most-abundant plant species.	Still needs to be tested with independent measures of population abundances, reproductive success, and floral rewards offered by an average plant of each population.	Benadi & Gegear 2018
	Third section: Predicting network responses to global change		
Species extinctions and **topological** co-extinctions	**Nested** networks are robust to specialists' but fragile to generalists' extinctions. Increasing **connectance** increases network robustness to extinctions.	**Long-time/short-gen***	Memmott et al. 2004
Species extinctions and **stochastic** co-extinctions	Increasing **connectance** decreases network robustness to extinctions.	**Long-time/short-gen***. To be tested with independent measures of **total impacts** of mutualisms.	Vieiria et al. 2013, Vieiria & Almeida-Neto 2015.
Species extinctions and **dynamic** co-extinctions	Extinction of trees or hymenopterans will make the studied pollination network collapse.	**Long-time/short-gen***	Ramos-Jiliberto et al. 2009

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	Removal of all alien plants harm native species when the alien plants are well integrated into the network.	Still needs to be tested by cutting the flowers of alien plants and evaluating the response of native pollinators	Valdovinos et al. 2009
Phenological shifts driven by **climate change**	17-50% of pollinator species would exhibit temporal gaps in their food supply due to increased temperatures	Still needs to be tested with phenological data of plants and pollinators across several years in a particular system.	Memmott et al. (2007)
Habitat loss as **patch destruction**	**Nestedness** decreases network resistance to habitat loss at low patch destruction but increases it at high patch destruction rates.	**Long-time/short-gen***	Fortuna & Bascompte (2006)
Species invasions as **node introduction**	Highly efficient foragers will likely invade networks, while networks with higher diet overlap between aliens and natives will be highly impacted by invaders.	The impact on natives still needs to be tested by measuring the distribution of floral rewards and visits in systems with and without invasive pollinators.	Valdovinos et al. (2018)
Altering interaction strengths in **Lotka-Volterra type model** with direct intra-guild competition, saturating	Species' tolerance to changing in interaction strengths not determined by species' degree or contribution to nestedness. Species' tolerance very sensitive to the sign of the change in	Highly phenomenological. Difficult to infer what to measure in the field to test predictions of this type of modeling.	Saavedra et al. (2013)

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mutualisms, and trade-offs (Eq. 7 in Box 2)	interaction strength and to the trade-offs between the number of partners and the strength of the interactions.

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Figure legends

Figure 1. Illustration of Lotka-Volterra type (A) and Valdovinos et al.'s consumer-resource (B) models. **A** illustrates the key assumption of Lotka-Volterra type models (Box 2), i.e., mutualist partners always positively affect each other (indicated by a circled 1, in a linear Eqs. 2-3 or saturating Eq. 4 way), which results in species of the same guild benefiting each other indirectly via sharing the same mutualistic partners (indicated by 2). Some models also incorporate direct competition (independent of mutualistic interactions) among all species of the same guild (i.e., intra-guild competition in plants or animals indicated by 3, Eqs. 5-6). **B** illustrates how Valdovinos et al. model (Box 3) decomposes net effects of mutualisms into two key mechanisms: consumption of floral rewards (indicated by 'Consumption', Eqs. 9 and 10) and pollination services (indicated by 'Pollination', Eq. 8). The model separates the dynamics of the plant vegetative biomass (Eq. 8) from the dynamics of floral rewards (red rectangles, Eq. 9), connecting them by the plant production of rewards (indicated by 'Production', parameter β of Eq. 9). Adaptive foraging (Eq. 11) allows pollinators to assign higher foraging effort (thicker arrow) to plant species with higher floral rewards (larger rectangle). **C** illustrates the high niche overlap among pollinator species that share floral rewards (follow thicker lines) of the most-generalist plant species (indicated by the red arrow) in a nested network. **D** illustrates the high niche overlap among plant species that share pollination services (follow thicker lines) of the most-generalist pollinator species (indicated by the red arrow) in a nested network. This model also assumes that the conspecific pollen is diluted in the body of generalist pollinators (see function σ_{ij} in Eq. 8).

Figure 2. Results of Valdovinos et al. consumer-resource model for nested networks. **A** without adaptive foraging, pollinator species partition the same foraging effort to each of their plant species (follow the width of the lines for each pollinator species, see Eq. 12 in Box 3), which results in generalist plant species (top right) receiving more visits than specialists (bottom right). This results in generalist plants having lower floral rewards than specialists do (red bars). In this scenario, specialist plant and animal species can go extinct because specialist plants receive very few and low quality visits while specialist pollinators have access to very low floral rewards and starve. **B** with adaptive foraging, generalist pollinator species (top left) partition higher foraging effort on specialist plant species (bottom right, follow thick line) which releases

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the rewards of generalist plant species now consumed by the specialist pollinators. In this scenario, specialist species persist because specialist plants receive more and higher quality of visits by generalist pollinators and specialist pollinators have enough food to persist.

Figure 3. Predicting the response of mutualistic networks to species invasions (results of Valdovinos et al. 2018). On the left panel, an alien pollinator species invades a plant-pollinator network and forages on the most generalist (top right) and most specialist (bottom right) plant species. This invasion drives extinct the native pollinator species (bottom left) that only forages on resources shared with the invasive pollinator, in this case, the most-generalist plant species. On the right panel, native pollinator species that have alternative resources (blue flower in the middle, not shared with the alien) can persist by shifting their foraging efforts to the plant species not visited by the alien. These native pollinators, however, decrease in abundance (smaller animal size) because they are obligated to forage on a less preferred resource (i.e., less profitable).

Figure 1

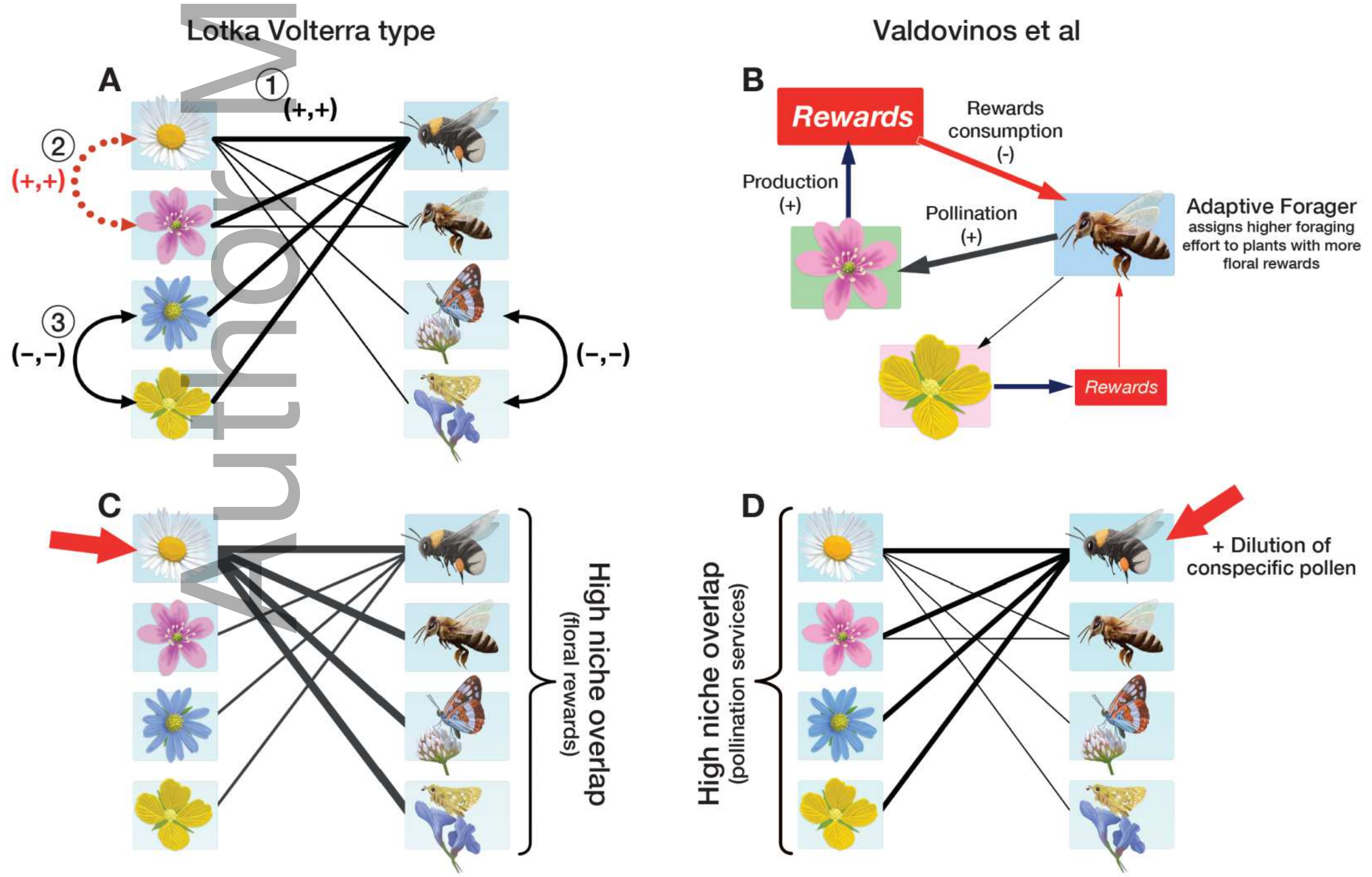

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Figure 2.

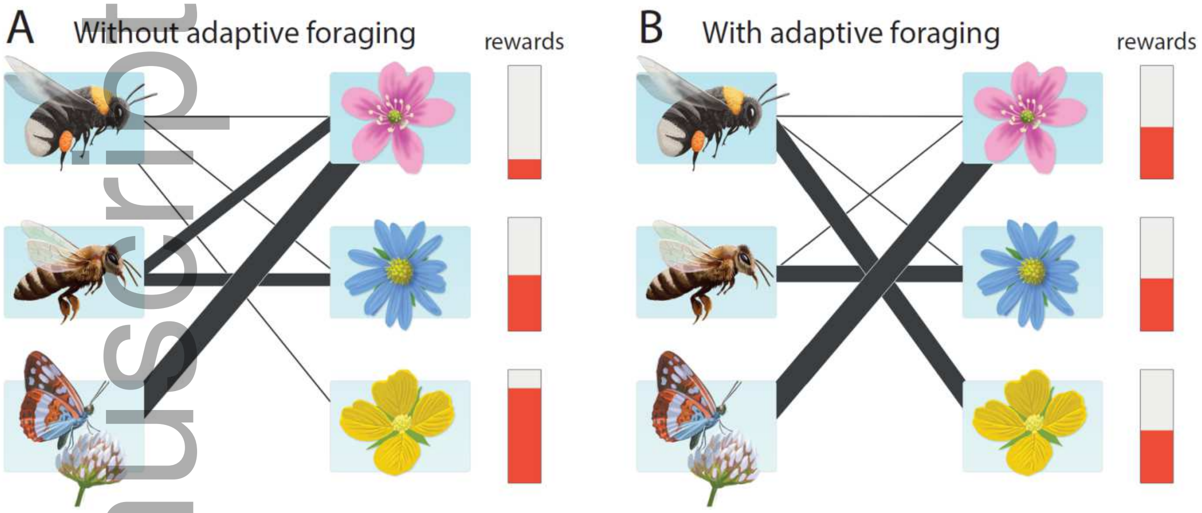
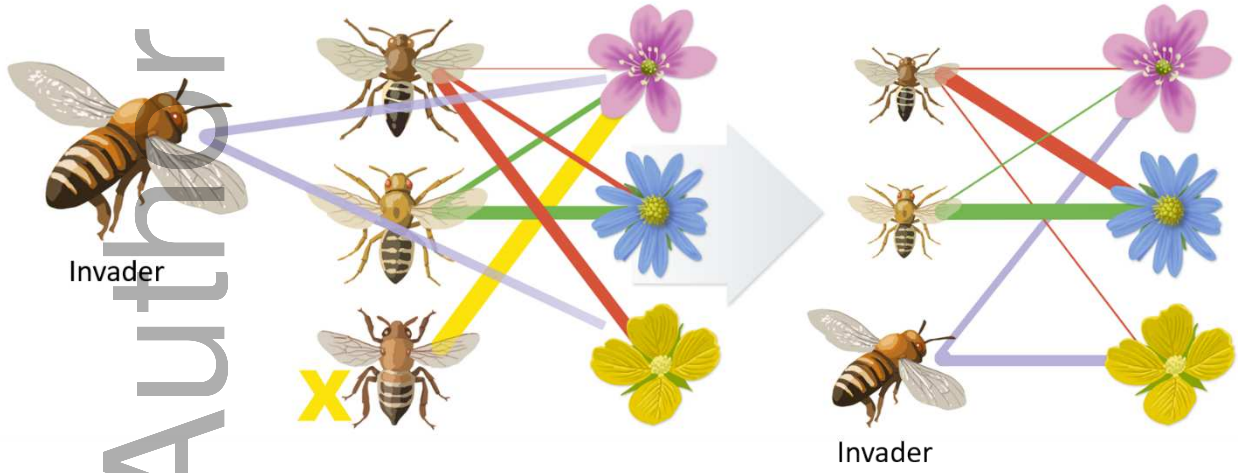


Figure 3.



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Box 1: Glossary of terms commonly used in the study of mutualistic networks

Mutualistic network: Ecological network in which one class of nodes represents one type of species (e.g., plants) and the other class represents another type of species (e.g., pollinators),

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while links connecting nodes of the two different classes represent the mutualistic interactions (e.g., pollination, Fig. 1A).

Binary structure (also called **network topology**): Set of species (represented by nodes) and the architecture of species interactions (represented by links connecting the interacting species).

Species richness (*S*): Total number of species in the network, $S = P + A$, where P and A are total number of plant and animal species, respectively.

Connectance (*C*): Fraction of potential interactions that are realized, $C = L / (P*A)$ where L is the number of realized interactions (links connecting species).

Degree: The total number of interactions for a single species

Heterogeneous degree distribution: Most species have one or a few interactions (specialists) and a few species have most of the interactions in the network (hyper-generalists).

Nestedness: Tendency of the interactions of the most specialist species to be subsets of the interactions of the most generalist species. Also defined as the tendency of species with fewer interactions (specialists) to interact with subsets of the mutualistic partners of species with more interactions (generalists).

Interaction asymmetry: Tendency of the interaction pairs between species 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.

Dependence: Measure of the relative dependence of one species (i) on another (j) calculated as the fraction of *i's* total interactions with species j. For example, if a pollinator species only visits one plant species, the pollinator’s dependence on that plant species is 1 (complete), but the plant species depends less on that pollinator species if the plant species is also visited by other pollinator species.

Feasibility: All species exhibit stationary abundances that are non-zero and positive, i.e., none of the species in the network go extinct (complete species persistence).

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Local equilibrium: State at which all abundances stay the same unless perturbed. Mathematically, species abundances at which all the dynamic equations are 0 (no change in abundance).

Local stability: Measures the tendency of a system to return to equilibrium after small perturbations. Mathematically, an equilibrium point is stable if all the eigenvalues of the corresponding Jacobian matrix evaluated at the equilibrium point have negative real parts.

Structural stability: Local stability with respect to modifications in the parameters of a dynamic model. A system is more structurally stable if it can endure larger changes in parameter values without exhibiting species extinctions. Usually represented as the volume in parameter space compatible with positive abundances at the equilibrium point.

Resilience: Return rates to an equilibrium point following a perturbation.

Robustness: Network resistance to the loss of species caused by species extinctions.

Species persistence: Fraction of initial species that persist until the end of a simulation. In systems exhibiting equilibrium, persistence is the fraction of initial species surviving after the system has reached its equilibrium.

Box 2. Lotka-Volterra-type models of mutualistic networks

The Lotka-Volterra type models of mutualistic networks can be organized along a continuum of complexity. The first type of model in ascending order of complexity does not simulate population dynamics but uses a 'community matrix' $\boldsymbol{A}$ (the Jacobian matrix evaluated at an equilibrium point) to describe and analyze a system of n interacting species. The n x n elements of $\boldsymbol{A}$, α_{ij}, characterize the effect of species j on species i near an equilibrium. This approach analyzes the stability of such an equilibrium using the Taylor series in its neighborhood (May 1973), characterized by the equation:

$$\frac{d\boldsymbol{N}}{dt} = \boldsymbol{A}\boldsymbol{N} \qquad (1)$$

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where $\boldsymbol{N}$ is the n x 1 vector of species populations. The system (Eq. 1) is locally stable if all the eigenvalues of $\boldsymbol{A}$ have negative real parts. In locally unstable systems, even infinitesimal perturbations cause the system to move away from equilibrium, potentially leading to the loss of species (May 1973). Allesina & Tang (2012) extended the stability criterion proposed by May through constructing community matrices that represent more defined interactions (e.g., predator-prey, mutualistic, or competitive; in contrast to interaction signs drawn completely at random) and more realistic network structures (i.e., reflecting some of the properties observed in empirical networks).

The community matrix (Eq. 1) is also a linearization of the Lotka-Volterra model at an equilibrium point (Kot 2001), such as the model used by Bascompte et al. (2006):

$$\frac{\overbrace{dN_i^P}^{per-capita\ growth\ of\ plant\ sp\ i}}{N_i^P dt} = \overbrace{r_i^P - s_i^P N_i^P}^{intrinsic\ asymptotic\ growth} + \overbrace{\textstyle\sum_{j=1}^{n} \alpha_{ij}^A N_j^A}^{gain\ from\ mutualistic\ interactions}$$

(2)

$$\frac{\overbrace{dN_j^A}^{per-capita\ growth\ of\ animal\ sp\ j}}{N_j^A dt} = \overbrace{r_j^A - s_j^A N_j^A}^{intrinsic\ asymptotic\ growth} + \overbrace{\textstyle\sum_{i=1}^{m} \alpha_{ji}^P N_i^P}^{gain\ from\ mutualistic\ interactions}$$

(3)

which defines the per-capita population growth rate of each plant (P) species i and animal (A) species j as function of their intrinsic growth rate, $r^P{}_i$ and $r^A{}_j$, intraspecific competition, $s^P{}_i$ and $s^A{}_j$, and gain from each mutualistic interaction, respectively. This model assumes that the average individual of one mutualistic partner always benefits an average individual of the other mutualistic partner (indicated by 1 in Fig. 1A) at the same magnitude, $\alpha^A{}_{ij}$ or $\alpha^P{}_{ji}$, regardless of the abundance of the interacting populations. In other words, mutualistic species linearly increase their abundance with the increase in abundance of their mutualistic partners (i.e., Type I functional response).

Next in model complexity, Holland et al. (2005) and Okuyama & Holland (2008) incorporated nonlinear functional responses to the model used by Bascompte et al. (2006), in which the beneficial effects of one species on another (i.e., $\alpha^A{}_{ij}$ and $\alpha^P{}_{ji}$ in Eqs. 2 and 3, respectively) saturate with increasing population size of the mutualistic partners as:

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$$\alpha_{ij}^{A} = \frac{b_{ij}}{1 + h_{ij} b_{ij} N_j^{A}}, \qquad \alpha_{ji}^{P} = \frac{b_{ji}}{1 + h_{ij} b_{ji} N_i^{P}} \tag{4}$$

where h_{ij} is the handling time of the Type II functional response. Modeling saturating benefits of mutualistic interactions (as opposed to linear benefits) constitutes an advance in biological realism of the model (Holland et al. 2005, Morris et al. 2010). Bastolla et al. (2009) added intra-guild competition to the saturated mutualisms model (indicated by 3 in Fig. 1A), where each species competes with all other species in its guild (plants or animals), as follows:

$$\overbrace{\frac{dN_i^P}{N_i^P dt}}^{per-capita\ growth\ of\ plant\ sp\ i} = \overbrace{r_i^P - \sum_{k=1}^{m} s_{ik}^P N_k^P}^{asymptotic\ growth\ -\ intra.guild.competition} + \overbrace{\sum_{j=1}^{n} \frac{b_{ij}^A N_j^A}{1 + h_{ij} b_{ij} N_j^A}}^{gain\ from\ mutualism} \tag{5}$$

$$\overbrace{\frac{dN_j^A}{N_j^A dt}}^{per-capita\ growth\ of\ animal\ sp\ j} = \overbrace{r_j^A - \sum_{k=1}^{n} s_{jk}^A N_k^A}^{asymptotic\ growth\ -\ intra.guild.competition} + \overbrace{\sum_{i=1}^{m} \frac{b_{ji}^P N_i^P}{1 + h_{ij} b_{ji} N_i^P}}^{gain\ from\ mutualism} \tag{6}$$

where s^P_{ik} (s^A_{jk}) is the interspecific competition coefficient that defines the negative effect of species k on species i (j) which also defines the intraspecific competition when $k = i$ ($k = j$). The last variation to this Lotka-Volterra type model was made by Rohr et al. (2014) who modified the parameters b^A_{ij} and b^P_{ji} in Eqs. 5-6 to:

$$b_{ij}^A = b_{ji}^P = \frac{b_0 y_{ij}}{k_i^{\delta}} \tag{7}$$

where $y_{ij} = 1$ if species i and j interact and zero otherwise, k_i is the number of interactions of species i, b_0 represents the level of mutualistic strength, and δ corresponds to the mutualistic trade-off. The mutualistic trade-off modulates the extent to which a species that interacts with few other species does it strongly, whereas a species that interacts with many partners does it weakly.

Box 3. Valdovinos et al.'s consumer-resource model and Fortuna & Bascompte's metacommunity model.

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The Valdovinos et al. (2013) model recognizes a common characteristic of all mutualisms: the gathering of resources by organisms of one species through the interaction with organisms of another species that benefit from the interaction. The key advance of this model is separating the dynamics of the plants' vegetative biomass from the dynamics of the plants' rewards (Fig. 1B). This separation allows tracking the rewards depletion by animal consumption (indicated by 'Consumption' in Fig. 1B) separately from the animal contribution to plants' population via reproductive services (indicated by 'Pollination' in Fig. 1B). Focusing on plant-pollinator networks, this model tracks plant population growth separate from floral-rewards dynamics as:

$$\overbrace{\frac{dp_i}{dt}}^{\textit{population growth of plant sp i}} = \overbrace{\gamma_i \sum_{j=1}^{n} e_{ij}\sigma_{ij}V_{ij}}^{\textit{reproduction reduced by plants' competition}} - \overbrace{\mu_i^P p_i}^{\textit{mortality loss}} \tag{8}$$

$$\overbrace{\frac{dR_i}{dt}}^{\textit{floral} - \textit{rewards dynamics of plant sp i}} = \overbrace{\beta_i p_i - \varphi_i R_i}^{\textit{saturated production of rewards}} - \overbrace{\sum_{j=1}^{n} V_{ij} b_{ij} \frac{R_i}{p_i}}^{\textit{consumption by pollinators}} \tag{9}$$

where $V_{ij} = \alpha_{ij}\tau_{ij}a_j p_i$ defines the frequency of visits by animal species *j* to plant species *i*, which increases the population growth of plant *i* (Eq. 8., 'Pollination' in Fig. 1B) but decreases its floral rewards (Eq. 9, 'Consumption' in Fig. 1B). Those visits are determined by the adaptive preference (thickness of pollinator's arrows in Fig. 1B) of animal *j* for rewards of plant *i* (α_{ij}, see below), the pollinator's visitation efficiency on plant *i* (τ_{ij}), and the population densities of animal *j* (a_j) and plant *i* (p_i).

In Eq. 8, only a fraction $\sigma_{ij} = \frac{\varepsilon_i V_{ij}}{\sum_{k \in P} \varepsilon_k V_{kj}}$ of *j*'s visits successfully pollinates plant *i*, which accounts for dilution of plant *i*'s pollen when *j* visits other plant species (indicated by the red arrow in Fig. 1D). A fraction e_{ij} of those pollination events produces seeds. Among those seeds, a fraction $\gamma_i = g_i\left(1 - \sum_{l \neq i \in P} u_l p_l - w_i p_i\right)$ recruit to adults, where g_i is the maximum fraction of *i*-recruits subjected to both inter-specific (u_l) and intra-specific (w_i) competition. The population dynamics of animal species *j* is defined as:

$$\overbrace{\frac{da_j}{dt}}^{\textit{population growth of animal sp j}} = \overbrace{\sum_{i=1}^{m} c_{ij} V_{ij} b_{ij} \frac{R_i}{p_i}}^{\textit{recruit to adults from rewards consumption}} - \overbrace{\mu_j^A a_j}^{\textit{mortality loss}} \tag{10}$$

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where c_{ij} represents the per-capita efficiency of j converting plant i's floral resources into j's births. b_{ij} is the efficiency of j extracting plant i's floral resources (R_i, Eq. 9).

Another key advance of this model accounts for the widely observed adaptive foraging of pollinators (Fig. 1B) by modeling the adaptation of animal species j's foraging preference on i as:

$$\frac{d\alpha_{ij}}{dt} = G_j\alpha_{ij}\left(\overbrace{c_{ij}\tau_{ij}b_{ij}R_i}^{R\ consumption\ from\ plant\ i} - \overbrace{\sum_{k=1}^{m}\alpha_{kj}c_{kj}\tau_{kj}b_{kj}R_k}^{average\ R\ consumption\ from\ all\ j's\ plants}\right) \tag{11}$$

with $\sum_{i=1}^{m}\alpha_{ij} = 1$ (i.e., animal j's total preferences sum 1 over all plant species it visits). The preference α_{ij} increases when the resources obtained from i exceed the resources obtained from the other plants in j's diet (defined by the network), and decreases when resources obtained from i are lower than the resources obtained from the other plants (follow thicker pollinator's arrow in Fig. 1B). When adaptive foraging is not considered, pollinator foraging efforts are fixed to:

$$\alpha_{ij} = 1/m_j \tag{12}$$

where m_j is the number of plant species visited by pollinator species j.

Fortuna & Bascompte (2006) recognizes that populations are not homogenously distributed but structured in space. The authors developed a metacommunity model for mutualistic networks following the patch dynamics model for two species generated by Amarasekare (2004). In this model, p_i^P and p_j^A represent the fraction of patches occupied by plant and animal species i and j, modeled as functions of colonization and extinction rates for plants (c_{ij}^P and e_i^P) and animals (c_{ji}^A and e_j^A), the fraction of patches lost by the habitat destruction rate, d, and the total number of available patches for animals Ω_j, as follows:

$$\frac{dp_i^P}{dt} = \sum_{j=1}^{n}\left(c_{ij}^P\frac{p_i^P p_j^A}{\Omega_j}\right)\left(1-d-p_i^P\right) - e_i^P p_i^P \tag{13}$$

$$\frac{dp_j^A}{dt} = c_{ji}^A p_j^A\left(\Omega_j - p_j^A\right) - e_j^A p_j^A \tag{14}$$

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Box 4. Stability analysis of Lotka-Volterra type models of mutualistic networks.

Studies using the simplest model with linear mutualisms differ in how they analyze **local stability**. Bascompte et al. (Eqs. 2-3) assume a fully connected network in which all plants interact with all animals and all species are equivalent. By this assumption, the authors simplify the model to find four equilibrium points (i.e., species abundances at which $dN^P/dt = 0$ and $dN^A/dt = 0$), among which one is **feasible**. This procedure shows that weak or asymmetric per-capita effects between plant and animal species increase the **local stability** of the **feasible equilibrium**. By contrast, Allesina & Tang (2012) assume the existence of a feasible equilibrium without finding it. This strong assumption allows the authors to evaluate the local stability of different community matrices (Eq. 1) representing distinct interaction types (i.e., mutualistic, trophic, competitive) and network structures (e.g., nestedness, modularity) without restricting their exploration to a feasible equilibrium nor to a 'fully connected network'.

Okuyama & Holland (2008) used computer simulations to show that a model with nonlinear functional responses (Eq. 4) does not require weak or asymmetric interaction strengths for species coexistence. The authors find that strong symmetric interactions stabilize network dynamics in terms of resilience. Additionally, contrary to Allesina & Tang (2012), Okuyama & Holland find that mutualisms are very stable and that increasing levels of species richness, nestedness, and connectance increase resilience of the networks. Moreover, the authors used resilience as their only measure of stability because all networks they simulated (order of thousands) were locally stable and fully **persistent**. Thèbault & Fontaine (2010) computationally analyzed Okuyama & Holland's model to evaluate the effects of species richness, connectance, nestedness, and modularity on species persistence and resilience of mutualistic and trophic networks. In accordance with Okuyama & Holland, Thèbault & Fontaine found for mutualistic networks that: i) nestedness increases resilience, ii) species richness strongly increases both resilience and species persistence, and iii) connectance slightly increases species persistence. But contrary to Okuyama & Holland, Thèbault & Fontaine found that nestedness slightly decreases species persistence and connectance decreases the resilience of mutualistic networks (all results depicted in Thèbault & Fontaine's Fig. 2A, C). Thèbault & Fontaine did not emphasize their result of nestedness slightly decreasing species persistence of mutualistic networks because that

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result strongly depended on parameter values (E. Thèbault personal communication). The differences between the results of Okuyama & Holland and Thèbault & Fontaine can be explained by the parameter values of the intrinsic growth rate, $r^{P}{}_{i}$ and $r^{A}{}_{j}$ (Eqs. 2-3). Okuyama & Holland assumed positive values while Thèbault & Fontaine assumed negative values for intrinsic growth rates, which can be interpreted as facultative and obligate mutualism, respectively. Thus, with saturated benefits, facultative mutualisms are more stable than obligate mutualisms.

Bastolla et al. (2009) added competition among all species in the same guild to the model of saturated mutualisms (Eqs. 5-6). By using **structural stability** analysis (Box 1), the authors showed that nestedness stabilizes mutualistic networks by reducing effective interspecific competition (see main text). James et al. (2012) used computer simulations to contradict Bastolla et al.'s results by showing that nestedness does not stabilize the networks in terms of **species persistence.** As mentioned above, Thèbault & Fontaine (2010) also found that nestedness decreases species persistence but that result strongly depended on parameter values. However, Saavedra & Stouffer (2013) argue that species persistence in the James et al. (2012) study was a result of changes in degree distribution and not in nestedness. James et al. (2013) responded to such criticism arguing that nested networks exhibit higher species persistence only in comparison to random networks of the same size, connectance, and degree distribution. Therefore, to the question of which network structures explain species persistence in the Bastolla et al. (2009) model, James et al. (2013) affirms that nestedness is less important than network size, connectance, degree distribution, intrinsic growth rates, competition coefficients, and the strength of the mutualistic interaction. Rohr et al. (2014) corroborates Bastolla et al.'s result that nestedness maximized the network **structural stability**, and proposed that the contradictory results on the effect of nestedness in different studies arise if the necessary conditions for a **feasible equilibrium** are not met (e.g., Allesina & Tang 2012), or because of sensitivity to model parameterization in computer simulations (e.g., James et al. 2012). However, Pascual-Garcia & Bastolla (2017) demonstrate how the discrepancies among results are better explained by the different ways in which each study incorporated competition among species of the same guild (main text).

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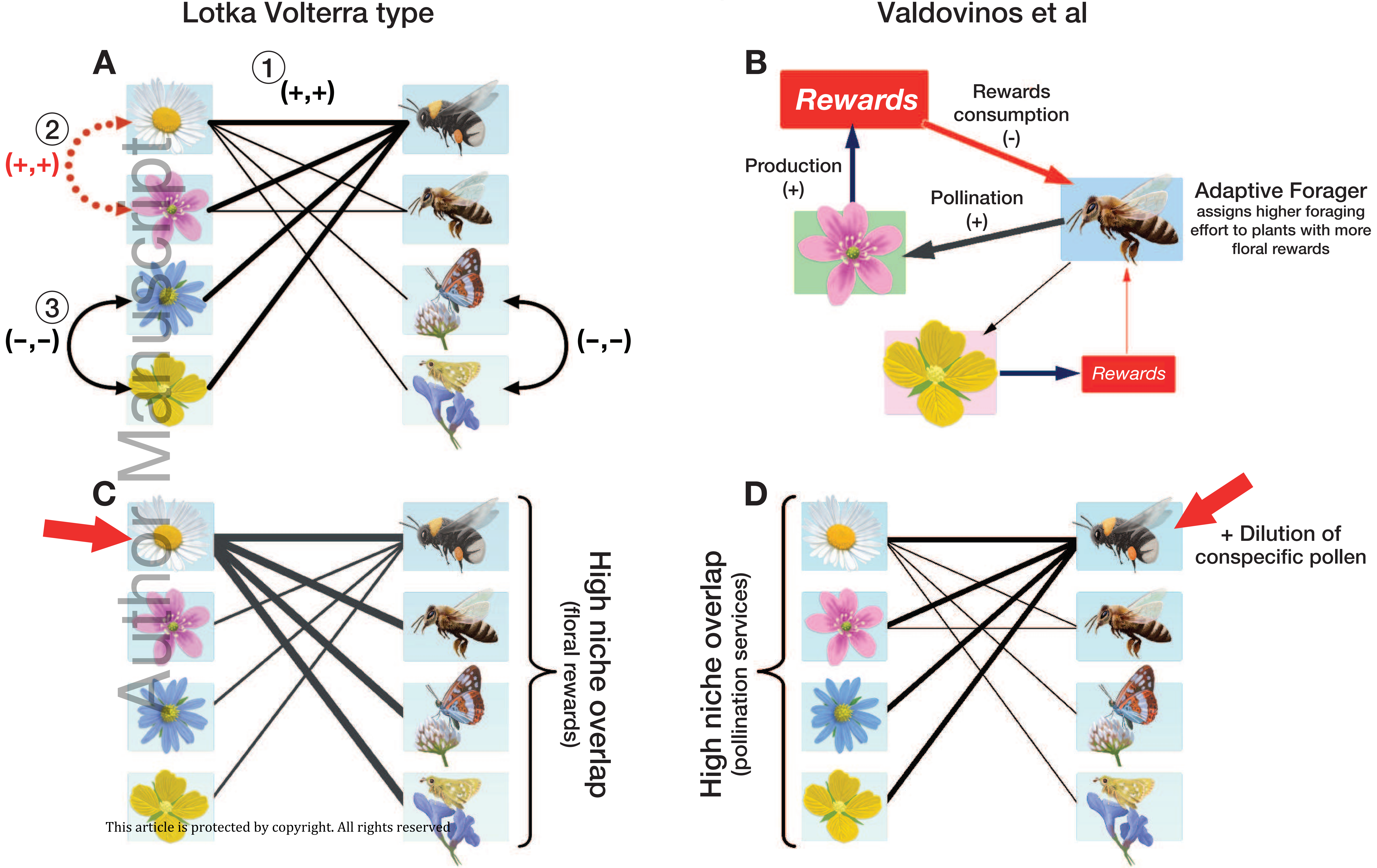

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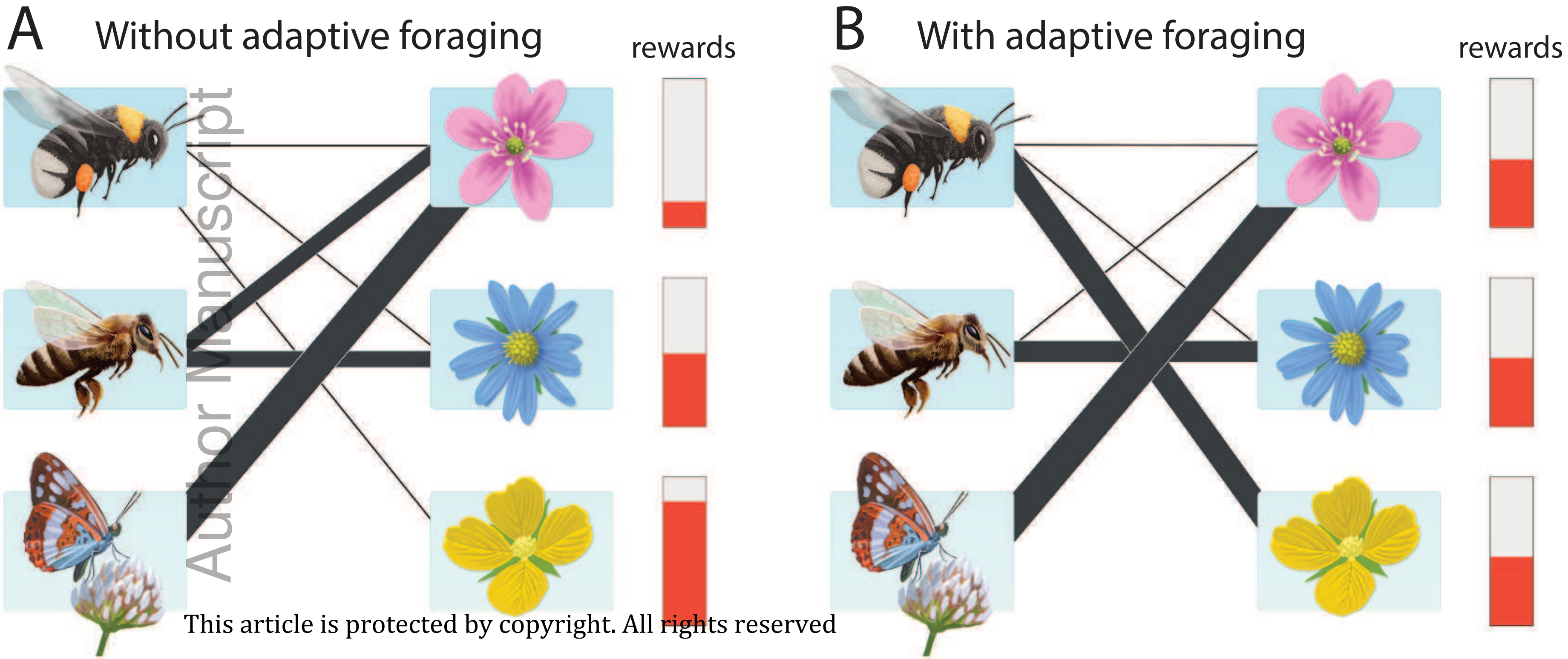

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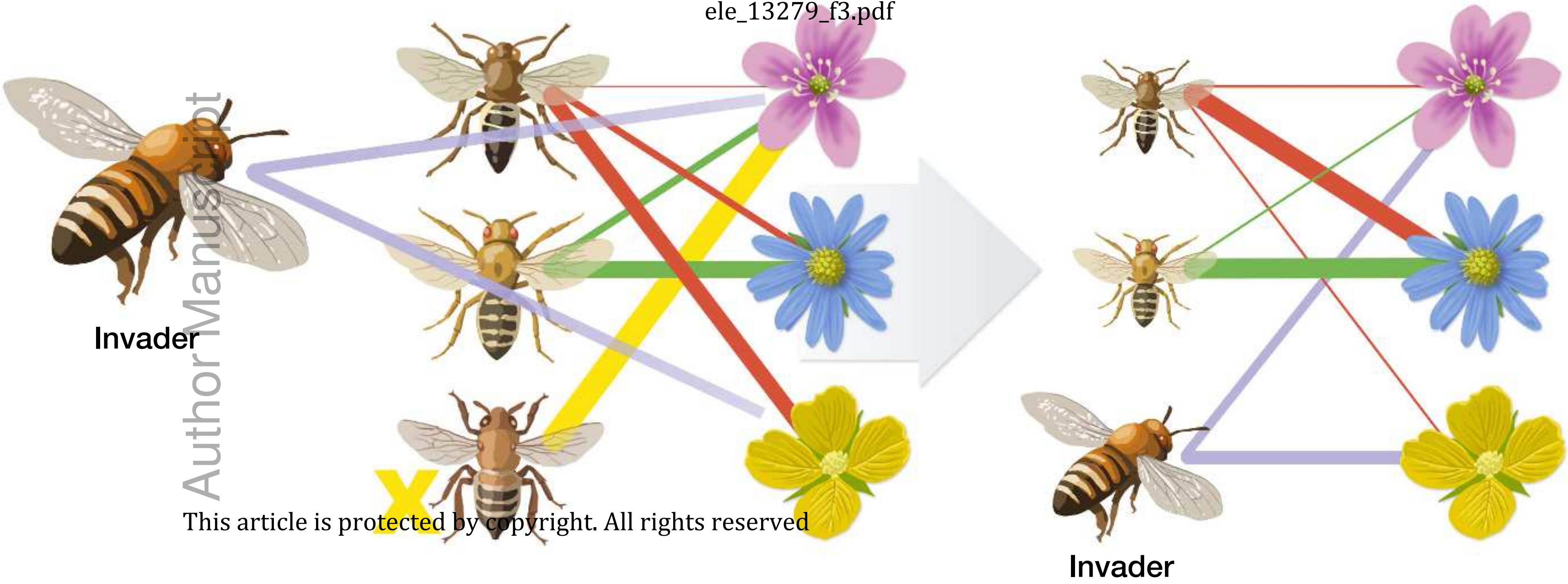

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