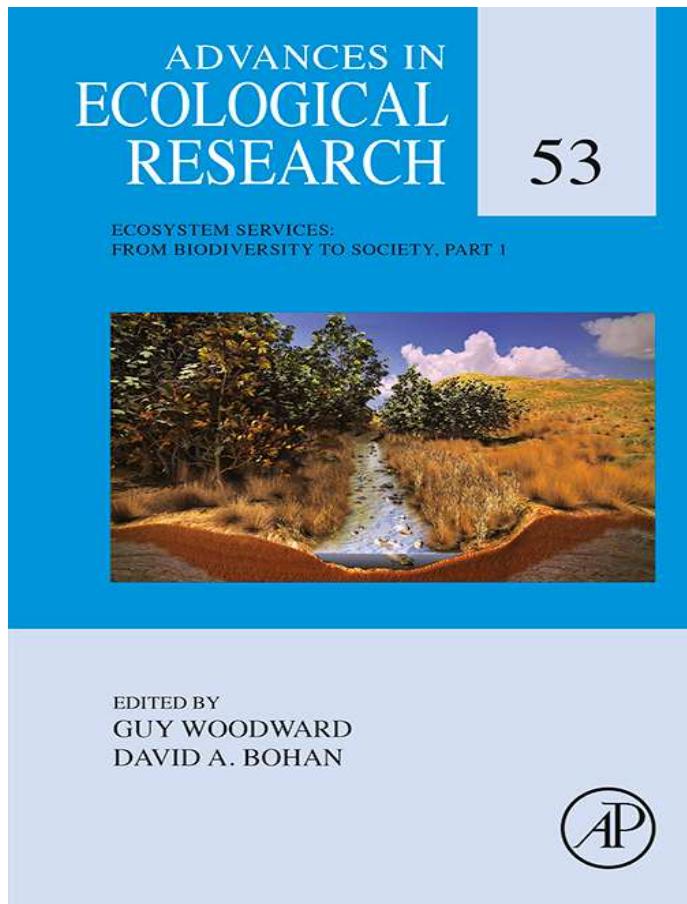


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Persistence of Plants and Pollinators in the Face of Habitat Loss: Insights from Trait-Based Metacommunity Models

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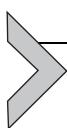
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Abstract

The loss of natural habitats is one of the main causes of the global decline of biodiversity. Understanding how increasing habitat loss affects ecological processes is critical for mitigating the effects of environmental changes on biodiversity and thus on the supply of ecosystem services by natural habitats. Habitat loss negatively affects pollinator diversity and the pollination service provided by insects, a key ecosystem service supporting the quantity, quality and diversity of crops directly consumed by humans and the sexual reproduction of most flowering plants. By integrating evolutionary relationships among traits that may modulate plant response to habitat loss, the structure of plant–pollinator interaction networks and metacommunity models, we examine how plant–pollinator metacommunities might respond to habitat loss. The main predictions of our trait-based metacommunity model are that (1) variation on dispersal ability among plant species may prevent full metacommunity collapse under pollinator loss associated with increasing habitat loss; (2) habitat loss may select for plants with higher dispersal ability and higher autogamous self-pollination, and will typically decrease the incidence of pollination generalist plants; (3) metacommunities that comprise plants with high autonomous self-pollination ability may harbour higher richness of rare plant species when pollinator diversity declines with increased habitat loss. We discuss the implications of our results for the vulnerability of pollination services for biotically pollinated wild plants and crops co-occurring in human-dominated landscapes.



1. INTRODUCTION

1.1 Habitat Loss and Fragmentation Effects on Pollinator Diversity, Pollination Service and Plant Reproduction

It is expected that anthropogenic land-use change will have the largest impact on global biodiversity for the foreseeable future (Haddad et al.,

2015; Krauss et al., 2010; Sala et al., 2000). Habitat loss and habitat fragmentation *per se* are among the main consequences of land-use change (Fahrig, 2003; Fisher and Lindemayer, 2007). These two consequences of anthropogenic land-use change have not only detrimental effects on biodiversity but also on the supply of multiple ecosystem services (e.g. pollination and flood and pest regulation) by remnant fragments of natural habitat to the surrounding human-dominated landscapes (Mitchell et al., 2015a).

Conceptually, habitat loss implies the removal of natural habitat from a landscape, while habitat fragmentation *per se* implies the “breaking apart” of continuous habitat (Fahrig, 2003). Although habitat loss has greater negative effect on biodiversity than habitat fragmentation (Fahrig, 2003), few empirical studies have evaluated separately the effects of these two different consequences of land-use change (Fahrig, 2003; Hadley and Betts, 2012; Tscharntke et al., 2012) mainly because habitat loss and fragmentation typically occur together in human-dominated landscapes (Fahrig, 2003). Thus, even most of the available empirical studies are presented as evaluations of the effects of habitat fragmentation they generally should reflect the confounding effects of both processes (Fahrig, 2003).

Habitat loss and fragmentation have negative effects on the population size of plants and animals and on the ecological interactions between them (Biesmeijer et al., 2006; Fahrig, 2003). These negative effects seem to be more consistent for mutualistic (pollination and seed dispersal) than for antagonistic interactions (predation and herbivory; Magrach et al. 2014) and are considered one of the chief causes of the decline of pollinator richness and abundance (Potts et al., 2010; Steffan-Dewenter et al., 2005; Winfree et al., 2009). Interestingly, pollinator diversity seems to be rather resilient to intermediate levels of habitat loss, with noticeable negative effects on diversity only at high levels of habitat loss (Ekroos et al., 2010; Winfree et al., 2009). However, even without species extinctions, important reductions in population size may decrease species encounter probability and thus can lead to the loss of ecological interactions well before species disappearance in human-dominated landscapes (Aizen et al., 2012; Sabatino, et al. 2010; Valiente-Banuet et al., 2015).

Plant–pollinator interactions are essential for generating and maintaining biodiversity and ecosystem services and functions (Bascompte et al., 2006; Fontaine et al., 2006; MEA, 2005; Potts et al., 2010; van der Niet and Johnson, 2012). Most flowering plants (87.5%) and most crops directly consumed by humans depend to some degree on the pollination service provided by animals to produce fruits and seeds (Klein et al., 2007; Ollerton et al., 2011). Thus, animal pollination contributes not only to the

productivity of crops but also to the sexual reproduction of wild plants that either provide other services (e.g. medicinal plants) or serve as food sources for other organisms that provide other ecosystems services (e.g. natural enemies; Kremen et al., 2007). The amount and the performance of the seeds produced by wild plants and crops are important demographic and agricultural yield components. Seed quantity and quality determine the maximum population recruitment potential for the next generation (Ashworth et al., 2015a; González-Varo et al., 2010; Mathiasen et al., 2007; Wilcock and Neiland, 2002) and the productivity and nutritional quality of crops (Ashworth et al., 2009; Eliers et al., 2011). Changes induced by habitat loss and fragmentation on pollinator diversity and behaviour may therefore affect directly plant species diversity (Aguilar et al., 2008; Anderson et al., 2011; Fontaine et al., 2006; Potts et al., 2010) and crop yield, quality and the diversity of production (Ashworth et al., 2009; Eliers et al., 2011; Garibaldi et al., 2013, 2015; Klein et al., 2007).

The proximate and ultimate causes of wild plant diversity loss due to habitat fragmentation have been recently reviewed. A quantitative global synthesis showed negative effects of fragmentation on the pollination of wild animal-pollinated plants with concomitant reductions in plant reproductive success (Aguilar et al., 2006). Moreover, wild plant progeny generated in fragmented habitats can have lower performance, e.g., lower capacity of seed germination and seedling growth (e.g. Aguilar et al., 2012; Breed et al., 2012; González-Varo et al., 2010) as they had higher inbreeding coefficients compared to progeny from continuous habitats (Aguilar et al., 2008; Eckert et al., 2010). Thus, wild plant species in fragmented habitats produce not only a lower quantity but also a lower quality of progeny compared to those in continuous habitats (Aguilar et al., 2006, 2008).

However, we expect that plant species persistence in fragmented landscapes may depend on biological traits associated with plant sensitivity to pollinator loss such as breeding system (i.e. plant reproductive dependence on pollinators), pollination generalization and plant dispersal ability (Aguilar et al., 2006; Eckert et al., 2010; Hagen et al., 2012; Magrach et al., 2014). Here, we review evidence supporting the idea that these biological traits may determine differential responses of plants to habitat fragmentation.

1.2 Traits Modulating Wild Plant Response to Habitat Fragmentation

To produce seeds sexually, flowering plants range from complete dependence on animal pollination up to complete autonomy from pollinators

either via spontaneous self-pollination (Lloyd, 1992; Richards, 1997; Vogler and Kalisz, 2001) or via wind pollination (Faegri and van der Pijl, 1979; Mulder et al., 2005). Dioecious, monoecious and hermaphrodite self-incompatible plant species are obligate outbreeders that completely depend on pollinator agents to exchange pollen among plants and to sexually reproduce with success. Conversely, self-compatible plant species may be considered facultative outbreeders that partially depended on animal pollination. Although animal pollinators are needed to transport pollen, a single visit of a pollinator to each individual flower may allow seed production. Moreover, some self-compatible species may have the ability to reproduce sexually via autonomous self-pollination, without the intervention of pollinators (Richards, 1997). As expected, results from a meta-analysis on the effects of habitat fragmentation on plant pollination and reproduction show that the reproductive success of plant species with higher dependence on animal pollination (i.e. self-incompatible plants) was more negatively and strongly affected than that of less dependent ones (i.e. self-compatible species; Aguilar et al., 2006). Moreover, habitat fragmentation can decrease the incidence of species highly dependent on animal pollination, as reported for tropical trees of a fragmented landscape of the Brazilian Atlantic Forest (Girão et al., 2007).

The sensitivity of plants to habitat fragmentation may also be determined by their degree of pollination generalization (Bond, 1994; Johnson and Steiner, 2000; Renner, 1998). Plant species range from “super-generalists” that interact with hundreds of pollinator species to “extreme specialists” interacting with just a single pollinator species (Faegri and van der Pijl, 1979; Waser et al., 1996). Conventionally, the expectation has been that the sexual reproduction of specialist plants should be more affected by habitat fragmentation than that of generalists because losing a few pollinator species locally is more likely than losing all the pollinators associated with a generalist plant species. This prediction was grounded in the idea that any change imposed by fragmentation in pollinator assemblages is more likely to cause reproductive failure in plants interacting with pollinator assemblages of lower richness (Aizen et al., 2002; Bond, 1994; Waser et al., 1996). Conversely, generalist plants are expected to be more resilient to the changes imposed by fragmentation on their pollinator assemblages because of the functional redundancy among their pollinators (Faegri and van der Pijl, 1979; Morris, 2003). For both self-compatible and self-incompatible species, however, the negative effect of habitat fragmentation on plant reproductive success seems to be independent of plant pollination generalization (Aguilar et al., 2006).

The number of seeds produced by plants and their dispersal mode are the main traits determining species dispersal success (Willson and Traveset, 2000). Habitat fragmentation may modify seed dispersal success by affecting seed size and quantity (e.g. Aguilar et al., 2006; Fakheran et al., 2010; Galetti et al., 2013), plant and inflorescence height (Fakheran et al., 2010; Lobo et al., 2011) and the diversity and behaviour of dispersal vectors (Cordeiro et al., 2009; Galetti et al., 2013). Overall, increased dispersal ability would appear to be favoured in fragmented landscapes (Hagen et al., 2012; but see Cheptou et al., 2008). It has been reported, for instance, that habitat fragmentation affects more negatively the proportion of seeds of plant species with larger seeds and of animal-dispersed plants arriving in habitat fragments (Magrach et al., 2014; McEuen and Curran, 2004). The negative relationship between seed size and fragment occupancy (Ehrlén and Eriksson, 2000) and the lower diversity of animal-dispersed plant species in forest fragments (Tabarelli et al., 1999) also suggest that fragmentation may select for smaller seed size and abiotically dispersed species (Fakheran et al., 2010; Galetti et al., 2013; Lobo et al., 2011; Magrach et al., 2014; Melo et al., 2010). Moreover, as seed production may be positively related to the probability of plant species occurrence in isolated habitat fragments (Eyju et al., 2015), more fecund plant species will have higher probabilities of persistence in fragmented landscapes (McEuen and Curran, 2004). Finally, it has been recently suggested that when a landscape becomes more fragmented over evolutionary relevant time scales, increased (mean and long-distance) dispersal rates will be selected (Aparicio et al., 2008; Koh et al., 2015; but see Cheptou et al., 2008). This prediction seems to be supported by empirical evidence showing that increased isolation among patches leads to increased richness of species with long-distance dispersal and to decreased richness of species with short-distance dispersal (Aparicio et al., 2008; Koh et al., 2015).

1.3 Linking Plant Breeding System, Dispersal Ability and Pollination Generalization

As species are characterized by sets of traits, associations among these plant traits may ultimately determine plant response to fragmentation. The question of how breeding systems and dispersal traits interact in plants has been discussed widely in the literature. As sexual reproduction typically requires more than one partner, it is expected a link between the traits of movement (dispersal) and those associated with the breeding system. Moreover, seeds are mostly the product of sexual reproduction across plant species, which

suggests *a priori* that breeding and dispersal may be functionally constrained. In this regard, a very influential line of argument has been inspired by island studies in the 1960s. [Baker \(1955\)](#) hypothesized that uniparental reproduction should be advantageous in recently colonized areas where pollinators or mating partners are scarce (this hypothesis is often referred to as "Baker's Law"). The ability of species to frequently colonize new areas is expected to be correlated with high dispersal ability. As a consequence, outbreeding strategies such as full outcrossers or dioecious species are expected to be associated with low colonization (dispersal) ability, while selfers are expected to be associated with higher colonization (dispersal) ability. The data for associations between these traits are, however, inconclusive ([Auld and de Casas, 2013](#); [Martén-Rodríguez et al., 2015](#)) and equivocal (see [Cheptou, 2012](#) for a review).

Historically, the high proportion of dioecious plants on islands was considered a problem for Baker's law ([Carlquist, 1966](#)). Remote island floras are, however, difficult to interpret because post-colonization evolution may obscure effects consistent with Baker's expectations. Using historical data on forest colonization, [Réjou-Méchain and Cheptou \(2015\)](#) were able to show unambiguously that recently colonized areas exhibit a higher proportion of dioecious species than the mature forests close by. Thus, in contrast to the expectations of Baker's law, [Réjou-Méchain and Cheptou \(2015\)](#) data suggest a positive association between outcrossing levels and plant dispersal ability that is also predicted by some theoretical models.

In agreement with this last empirical finding, a recent metapopulation model examining the joint evolution of self-fertilization and seed dispersal with locally variable pollination environment over time showed that outcrossing and dispersal jointly evolve ([Cheptou and Massol, 2009](#)). The outcrossing-disperser syndrome emerges because the temporal variability in the deposition of outcross pollen into stigmas creates fitness heterogeneity for outcrossers but not for self-pollinated plants. This temporal heterogeneity encountered by outcrossers selects for good dispersal, as already demonstrated in evolutionary models of dispersal ([Comins et al., 1980](#); see also [Massol and Débarre, 2015](#)). As fluctuations in pollinator service may limit the deposition of outcross pollen on stigmas, [Cheptou and Massol's \(2009\)](#) model highlights the importance of these fluctuations for the evolution of plant dispersal ability. As a consequence of buffering fluctuations in pollination service, plant pollination generalization may reduce selection for good dispersal, and it can be hypothesized that low dispersing plants with high dependence on pollinators to reproduce should be generalists

(Astegiano et al., 2015). A positive association between plant dependence on pollinators and generalization was recently reported for a dune marshland plant community in the Balearic Islands (Tur et al., 2013). However, a study comparing plant species with different dependence on pollinators and dispersal ability in 10 plant–pollinator communities around the world found that plants highly dependent on pollinators or with low dispersal ability may not be more generalist (Astegiano et al., 2015).

The detailed study of interactions between individuals of co-occurring plant and pollinator species shows that these interactions are immersed in complex networks, with highly regular patterns of organization (Bascompte et al., 2003; Jordano, 1987; Jordano et al., 2003; Olesen et al., 2007). The topological properties of networks have different consequences for the ecology and the evolution of species (Bascompte and Jordano, 2007; Bascompte et al., 2006; Guimarães et al., 2011). Thus, our understanding of the way metacommunities of plants and pollinators may persist in fragmented landscapes may be improved by studies integrating not only relationships among plant traits determining plant sensitivity to pollinator loss but also the topological properties of plant–pollinator interaction networks.

1.4 Plant–Pollinator Networks Organization and Its Role in Promoting Species Persistence in Fragmented Landscapes

In plant–pollinator networks, most species interact with a small proportion of possible partners, whereas few species are “super-generalists” (Jordano et al., 2003; Vázquez, 2005). Indeed, interactions are mainly organized in a nested way (Bascompte et al., 2003; but see Blüthgen, 2010; Dorman et al., 2009), which means that specialist plants interact with subsets of pollinators interacting with more generalist plants. Moreover, there is a high incidence of asymmetric plant–pollinator interactions, with specialist plants and pollinators interacting, respectively, with generalist pollinators and plants (Vázquez and Aizen, 2004). These network features imply that a high proportion of plants and pollinators may persist, while generalist species persist and that plant–pollinator networks may be highly stable (Astegiano et al., 2015; Bastolla et al., 2009; Kaiser-Bunbury et al., 2010; Memmott et al., 2004; Okuyama and Holland, 2008; Rezende et al., 2007; Rohr et al., 2014; Suweis et al., 2013; Thébaud and Fontaine, 2010; but see Allesina and Tang, 2012; James et al., 2012; Vieira and Almeida-Neto, 2015).

Consequently, it has been proposed that the nested and asymmetric nature of the interactions among plants and pollinators could explain the fact

that pollination generalist and specialist plants show similar decrease in their reproductive success in fragmented landscapes (Aizen et al., 2002; Ashworth et al., 2004). While specialist pollinators are typically those most affected by habitat fragmentation (Bommarco et al., 2010), their decline should only affect generalist plant species (Ashworth et al., 2004). Generalist plants should maintain their pollination service by interacting with generalist (redundant) pollinators and specialist plants may interact mostly with generalist pollinators, thus generalist and specialist plants should have their reproduction equally affected by fragmentation (Ashworth et al., 2004). In support of this hypothesis, recent theoretical work predicts that specialist species may have lower probability of extinction in networks with a higher incidence of asymmetric interactions (Abramson et al., 2011). However, differences in the probability of specialist species dying out among these differentially structured networks decline progressively with increasing levels of habitat loss (Abramson et al., 2011). In the same vein, a theoretical study explicitly evaluating plant–pollinator network robustness to habitat loss suggested that the nested organization of interactions may increase the persistence of mutualistic species in the face of habitat loss (Fortuna and Bascompte, 2006). In this study, mutualistic networks with nested structures persisted at higher levels of habitat loss than randomly structured networks (Fortuna and Bascompte, 2006). Nestedness implies both a redundancy of mutualistic partners and an indirect facilitation effect among species sharing interaction partners (Lever et al., 2014), which may increase species persistence in the face of species loss.

Although we can identify some general patterns for the consequences of habitat fragmentation on species persistence (see Sections 1.1. and 1.2), our understanding of how the organization of ecological networks of mutualistic species at local and regional scales is affected by habitat fragmentation is still in its infancy (Gonzalez et al., 2011; Hagen et al., 2012). As the disruption of mutualistic interactions may predict future species extinctions and network collapse (Aizen et al., 2012; Fortuna et al., 2013; Valiente-Banuet et al., 2015), interactions, and not species, should be the focus of studies aiming to understand plant and pollinator species persistence in fragmented landscapes. Theoretical work suggests that plant–pollinator interactions are highly sensitive to habitat loss and that the structure of networks can change abruptly once a critical fraction of interactions have been lost this critical fraction being positively associated with the number of interactions of the network and to the number of possible interactions that are actually realized (network connectance; Fortuna et al., 2013). Moreover, the distribution of the number

of interactions in each fragment may change from homogeneous when the habitat is continuous to a very skewed distribution when habitat loss reaches levels close to the global extinction of interactions (Fortuna et al., 2013).

To our knowledge, only three empirical studies have explicitly evaluated the effects of habitat fragmentation on plant–pollinator network structure. Sabatino et al. (2010) studied plant pollination webs of 12 isolated hills immersed in an agricultural matrix in the Argentinean pampas. They showed that both species and interaction richness decreased with decreasing habitat area but interactions were lost faster than species (Sabatino et al., 2010). Although it was only a marginal effect, isolation (a fragment metric directly related to habitat loss levels) also diminished interaction richness (Sabatino et al., 2010). In the same study system, Aizen et al. (2012) showed that interactions involving high specialization between interacting partners and occurring at low frequency were more likely to be lost with decreases in habitat area, potentially reflecting lower probability of encounter among specialist species with extremely low abundances in smaller fragments. Finally, Spiesman and Inouye (2013) explicitly studied the effects of sandhill habitat loss on 15 plant–pollinator local webs in North Florida, USA. They found that regional habitat loss contributes directly to species loss and indirectly to the reorganization of plant–pollinator interactions in local communities. Local networks became more connected and modular, and less nested with increasing habitat loss.

Therefore, to bridge the existing gap between theoretical models of habitat loss impact on plant–pollinator networks (Fortuna and Bascompte, 2006) and empirical observations of the impacts of habitat loss on real plant–pollinator communities (Sabatino et al., 2010; Spiesman and Inouye, 2013), the next step is to integrate links between plant species traits and their level of generalization on pollinators (Section 1.3) within a metacommunity model incorporating the effects of habitat loss on species occupancy.

1.5 Predicting Species Persistence in the Face of Habitat Loss Using Trait-Based Metacommunity Models

Predictions on the effects of habitat fragmentation on local species persistence may be substantially altered when the dispersal of individuals among fragments is explicitly considered, as proposed by metacommunity theory (Leibold et al., 2004). Landscapes can be viewed as a set of patches inhabited by communities and connected by the dispersal of individuals (Leibold et al., 2004; Urban et al., 2008). The explicit modelling of dispersal and of other traits associated with the movement of individuals across the landscape can

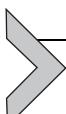
substantially change predictions of the effects of habitat fragmentation on biodiversity and therefore on the supply of ecosystem services from remnants fragments to the surrounding matrix (Keitt, 2009; Mitchell et al., 2015a). The existence of trade-offs between colonization and competitive ability may lead to superior competitors being either more negatively affected by habitat loss due to their low dispersal ability (Nee and May, 1992; Tilman et al., 1994) or positively affected by habitat destruction in metacommunities with source–sink spatial structures (Mouquet et al., 2011), for example. In spatially structured food chains, the association of predator presence with different rates of colonization or extinction, through top-down control, leads to different outcomes on the average food chain length at the metacommunity level (Calcagno et al., 2011). Results from metacommunity models also predict that the positive effects of high dispersal ability on metacommunity persistence might depend on the costs associated with the dispersal of individuals throughout the matrix surrounding fragments. In small food webs, high dispersal ability can increase metacommunity persistence by reducing, via rescue effects, the risk of bottom-up extinction cascades (Eklöf et al., 2012). However, when surrounding matrices decrease the probability of survival of species dispersing among fragments, high dispersal decreases metacommunity persistence (Eklöf et al., 2012).

The few metacommunity models that have studied the persistence of mutualistic species in fragmented landscapes have focused on the effects of network structure rather than the influence of dispersal (Fortuna and Bascompte, 2006; Fortuna et al., 2013). An interesting result is that, even when there is no habitat loss and plants are allowed to persist without pollinators (i.e. plants only depend on pollinators to colonize new fragments), metacommunity collapse occurs when the pollinator extinction rates approach colonization rates (Fortuna and Bascompte, 2006). Thus, habitat loss may lead to the collapse of plant–pollinator metacommunities because of a reduction of both the habitat available to persist and the species colonization ability via decreasing the availability of mutualistic partners. Moreover, a metacommunity model that explicitly considered the interaction of pollinators with animal-pollinated crops (but not network structure) showed that allowing pollinators to use crops as food sources might prevent the total collapse of pollinators but not the extinction of wild plants depending on pollinators to reproduce, if habitat loss is high (>50%; Keitt, 2009).

Results from recent studies provide some indication of the importance of modelling, explicitly, dispersal and other biological traits in metacommunity

models in order to understand the persistence of mutualistic assemblages in fragmented landscapes. The analysis of the association between species interaction patterns and species sensitivity to partner loss in empirical plant–pollinator networks suggests that the persistence of plants with both low dispersal ability (e.g. dispersed by gravity) and high reproductive dependence on pollinators (e.g. dioecious species) may be highly compromised if their pollinators disappear (Astegiano et al., 2015). These plants share a low proportion of their interaction partners with other plants of the community (Astegiano et al., 2015), and thus their pollinators may only be maintained by the persistence of other less sensitive plants (Lever et al., 2014). Moreover, in communities where plants show a lower mean ability to self-pollinate, a higher number of co-extinctions per extinction event may occur, which may increase network fragility to the loss of generalists (Vieira and Almeida-Neto, 2015).

Although dispersal ability and breeding systems may be key traits determining plant persistence in fragmented landscapes (see Sections 1.1 and 1.2), we still poorly understand how these biological traits may influence the robustness of plant–pollinator networks to habitat loss and thus species persistence. By unifying the available theory on how breeding system, dispersal ability and the structure of complex networks may modulate the response of species assemblages to species loss, the present study aims at improving our understanding of how plant–pollinator webs may persist in the face of habitat loss. We propose a trait-based metacommunity model to investigate the persistence of plant–pollinator networks under different levels of habitat loss. We hypothesize different scenarios of evolutionary associations between biological traits formerly associated to species response to habitat fragmentation (i.e. plant dispersal ability, breeding system and pollination generalization) to understand (i) how plant and pollinator species and interactions between them persist in the landscape, (ii) how regional network structure changes and (iii) how biological traits in the metacommunity vary, with increasing levels of habitat loss.



2. A TRAIT-BASED METACOMMUNITY MODEL TO UNDERSTAND PLANT AND POLLINATOR PERSISTENCE IN THE FACE OF HABITAT LOSS

2.1 Constructing Theoretical Plant–Pollinator Networks

We constructed 800 interaction networks between 60 plant species and 120 pollinator species, in which 20% of the possible interactions among plants

and pollinators were actually realized (i.e. connectance = 0.2). These 800 networks represented a subsample of the possible network configurations that can be achieved by considering that the degree distribution of plants and pollinators follows a power law function with an exponent ranging from 2.2 to 2.9, as described in [Appendix A](#). By varying the exponent of the power law degree distributions (i.e. varying the heterogeneity in degrees among species of the same trophic level), we were able to generate a gradient of nestedness ([Almeida-Neto et al., 2008](#); [Podani and Schemera, 2012](#); see [Box A1 in Appendix A](#)). We decided to use different power law exponents for network construction because of the small range of nestedness that can be achieved by using the same power law exponent to generate a given number of networks (see [Appendix B](#)). Thus, in agreement with results reported by [Dorman et al. \(2009\)](#), we found that variation in nestedness among networks is highly explained by variation in degree distribution, with lower nestedness being associated with higher power law exponents (see [Appendix B](#)).

2.2 Constructing the Trait-Based Metacommunity Model

We modified the metacommunity model proposed by [Fortuna and Bascompte \(2006\)](#) to study the persistence of mutualistic species in fragmented landscapes, in order to evaluate how different associations among plant traits (i.e. autonomous self-pollination, dispersal ability and plant pollination generalization) may influence plant–pollinator network persistence under different levels of habitat loss. The original model considers plants and pollinators inhabiting a landscape consisting of an infinite number of identical, well-mixed fragments ([Fortuna and Bascompte, 2006](#)). Thus, it represents an n -species version of the classic metapopulation model proposed by [Levins \(1969\)](#). In [Fortuna and Bascompte's \(2006\)](#) model, the interaction is obligate for animals, but plant species are able to survive in the absence of pollinators. However, plants cannot colonize new fragments without the presence of pollinators ([Fortuna and Bascompte, 2006](#)). Thus, the fractions of patches occupied by plants (Eq. 1) and pollinators (Eq. 2) in species-rich mutualistic metacommunities are described by the following differential equations:

$$\frac{dp_i}{dt} = \sum_{j=1}^A \left(s_{ij} \frac{p_i a_j}{M_j} \right) (1 - d - p_i) - e_i p_i \quad (1)$$

$$\frac{da_j}{dt} = c_j a_j (M_j - a_j) - e_j a_j \quad (2)$$

where A is the number of pollinator species, p_i and a_j are the fractions of fragments that plant i and animal j inhabit, respectively, s_{ij} is the colonization rate of new fragments by plant i through seeds produced by the pollination service performed by animal j , c_j is the colonization rate of new fragments by animal j , M_j is the fraction of fragments inhabited by plants used by animal j , d is the fraction of habitat fragments that is lost due to human activity and e_i and e_j are the local extinction rates of plant species i and animal species j , respectively. The colonization rate of a given plant encompasses both reproduction and subsequent establishment of new populations via random dispersal. The extinction rate summarizes all forms of extinction sources for plants and animals (Fortuna and Bascompte, 2006). Finally, we assumed in this model that plant extinction causes the subsequent extinction of animals depending exclusively on that plant, i.e., there is no rewiring (Fortuna and Bascompte, 2006).

In the model proposed here, we have assumed that plants can colonize new sites without pollinators by producing seeds through autonomous self-pollination. Moreover, colonization rate also depends on plant dispersal ability, which is explicitly considered in the model. Thus, in our modified version of the model, the dynamics of the fraction of patches occupied by plant species i , p_i , is described by the following differential equation:

$$\frac{dp_i}{dt} = \alpha_i \left[(1 - \delta)b_i + (1 - b_i) \sum_{j=1}^A s_{ij} \frac{a_j}{M_j} \right] p_i (1 - d - p_i) - e_i p_i \quad (3)$$

where α_i is the dispersal rate of plant i , b_i is the proportion of seeds produced by autonomous self-pollination by plant i , δ is the inbreeding depression rate endured by seeds produced by autogamy, $(1 - b_i)$ represents the fraction of the progeny produced by pollination due to pollinators visits to plant i and s_{ij} measures the effects of pollination by a given pollinator on total seed production. All other parameters and variables are the same as described previously for the original model (Fortuna and Bascompte, 2006). For simplicity, we assumed that δ and s_{ij} are equal for all species in all the scenarios. In the following, all pollinator extinction rates were set at e_A , all plant extinction rates were set at e_P and all pollinator colonization rates were set at c_A .

2.3 Constructing Theoretical Scenarios Linking Plant Traits

In order to evaluate how different associations among plant traits may modulate plant–pollinator metacommunity persistence, we constructed metacommunity models with different covariance structures among

autonomous self-pollination and dispersal rates, and plant degree, i.e., the number of pollinator species interacting with a given plant species. Autonomous selfing and dispersal rates of each plant species were sampled from a multinormal distribution, which linked normalized versions of these plant traits. Dispersal rate, α , took values between zero and ∞ . Thus, we set the normalized linearized version of this variable as $\beta = \log \alpha$. The proportion of seeds produced by autonomous self-pollination, b , took values between zero and one. Thus, we set the normalized linearized version of this variable as $\xi = \log \frac{b}{1-b}$.

We tested metacommunity persistence under the following eight scenarios, summarized below (Fig. 1):

- (a) *Neutral*, in which all species received the same value of β and ξ ;
- (b) *Random*, in which β and ξ were randomly assigned to plant species following two independent normal distributions (with variances set at 0.1);
- (c) *AGnegDrdm*, in which ξ was negatively correlated with species degree (i.e. its mean was determined by species degree), and β was randomly assigned, following two independent normal distributions (with variances set at 0.1);
- (d) *AGnegDneutral*, in which ξ was negatively correlated with species degree (i.e. its mean was determined by species degree) and assigned following a normal distribution (with variance set at 0.1), and all species received the same value of β ;
- (e) *DGnegArdm*, in which β was negatively correlated with species degree (i.e. its mean was determined by species degree), and ξ was randomly assigned, following two independent normal distributions (with variances set at 0.1);
- (f) *DGnegAneutral*, in which β was negatively correlated with species degree (i.e. its mean was determined by species degree) and assigned following a normal distribution (with variance set at 0.1), and all species received the same value of ξ ;
- (g) *DAnegGrdm*, in which β was negatively correlated with ξ , and the values of these traits were randomly assigned to plants independently of their degree, following a correlated multinormal distribution (with variances set at 0.1 and correlation set at -0.5);
- (h) *DAposGrdm*, where β was positively correlated with ξ , and the values of these traits were randomly assigned to plants independently of their degree, following a correlated multinormal distribution (with variances set at 0.1 and correlation set at 0.5).

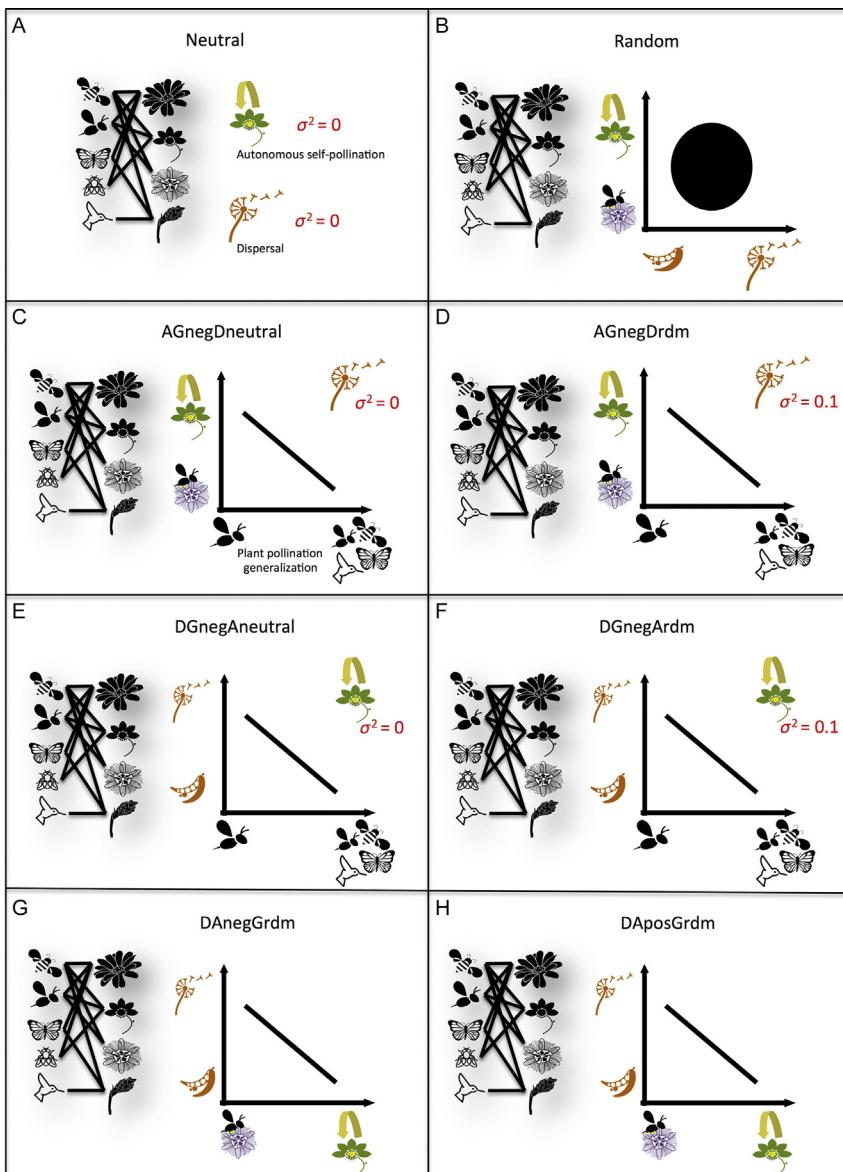


Figure 1 Constructing theoretical scenarios linking plant traits. Schematic representation of the eight scenarios in which metacommunity persistence was explored, as described in Section 2.3. Scenarios represent different associations between plant pollination generalization, autonomous self-pollination and dispersal rates that have been theoretically and empirically explored in previous studies. Designs created by Peter Silk, Galo Chiriboga, Cassie McKnown, Cherish Watson, Tom Ingebretsen, Alec Dhuse, Gabi McKensie, Lane F. Kinkade, Matt Brooks, Ambilera Adaleru and Karen Ardila Olmos for the Noun Project (<https://thenounproject.com>).

We explored how changing the mean proportion of seeds produced by autonomous self-pollination ($b_i=0.25, 0.5, 0.9$), the ratio between plant extinction and mean dispersal rate ($e_P/d_P=0.25, 0.5, 0.75$ and 0.95) and the ratio between pollinator extinction and colonization rates ($e_A/c_A=0.25, 0.5, 0.75$ and 0.95), affected the persistence of metacommunities under the eight scenarios when all species can colonize all fragments ($d=0$; Fig. 2). We simulated the dynamics of 96 metacommunities sampled from the initial 800 networks. These 96 metacommunities were obtained by taking 12 networks that encompass the range of nestedness observed in 100 networks from a given power law distribution. Species were considered to have maximum occupancy (100% of fragments of natural habitat) at the beginning of each simulation. Once we identified the combinations of mean autonomous self-pollination rate, plant extinction/dispersal and pollinator extinction/colonization ratios that allowed full plant and pollinator species persistence under the eight scenarios of association among plant traits, we explored how these different scenarios influenced metacommunity persistence under different levels of habitat loss ($d=0.3$ and 0.6 ; Fig. 2).

We obtained the final proportion of plant and pollinator species and plant–pollinator interactions that persisted under different levels of habitat loss at the end of each simulation (Fig. 2). We also explored how the distribution of occupancies of (1) plants species, (2) pollinators species and (3) plant–pollinator interactions varied among scenarios, in the absence of habitat loss and 30% and 60% of habitat loss, for all initial combinations of model parameters. We first described the distribution of occupancies in each metacommunity at the end of each simulation and then we obtained the proportion of networks leading to a given distribution per scenario/habitat loss level/initial combination of parameters. To describe the distribution of occupancies of plant and pollinator species within each metacommunity, we constructed rank-occupancy curves, following the method proposed by Jenkins (2011) for species occupancy. We built the rank-occupancy curve of plants or pollinator species within each metacommunity, by plotting species in order of decreasing occupancy. The shape of the decaying curve of this rank-occupancy relationship describes the degree of variation of occupancy among species within metacommunities and the degree of dominance of species with the highest occupancies.

To describe the shape of the rank-occupancy curve within a given metacommunity, we used linear and non-linear regression models. Among the non-linear regressions, we chose two equations of the exponential family—the same used by Jenkins (2011) to fit empirical rank-occupancy

distributions. The first equation describes a convex exponential curve, i.e., high dominance of a few species. The second equation describes a concave exponential curve, i.e., low species dominance with species having similar proportions of occupancies. We also decided to fit the linear model because it allowed us to describe an intermediate curve between the convex and concave exponential curves, i.e., an intermediate case of dominance. For all the regression models, we assumed normal errors and homogeneity of variance. We fitted the models only for the data sets (metacommunities) with a minimum variation of species occupancy. When the difference in occupancy between the most and the least frequent species was smaller than 0.1, we considered the variation among species to be low and thus dominance to be null, i.e., that the curve for this distribution was approximately constant. This lack of dominance with a constant curve includes metacommunity dynamics leading to either full species extinction or to species (interactions) with similar frequencies of occupancy. We divided the null dominance into two categories: (i) null dominance associated with full species extinction and (ii) null dominance associated with either all species or some species persisted. Thus, we had five possible descriptions of curves, i.e., (i) constant with total extinction of species (complete collapse), (ii) constant with persistence of all or some species (no dominance with persistence of species), (iii) concave (low dominance), (iv) linear (intermediate dominance) and (v) convex (high dominance). All models were fitted to the data by using maximum likelihood, with the values of maximum likelihood also used to select the best model through a selection procedure that did not penalize by the number of parameters. The highest value of likelihood, then, indicated the best model. We obtained the percentage of occupancy distributions that were better described by each rank-occupancy model for each initial combination of parameters, scenario and level of habitat loss (i.e. absence of habitat loss, 30% and 60% of habitat loss).

To describe the distribution of occupancy of plant–pollinator interactions within metacommunities, we followed the same procedure as for species. The occupancy of each plant–pollinator interaction (I_{ij}) was obtained as described in Eq. (3) in Section 2.2:

$$I_{ij} = \frac{p_i a_j}{M_j} \quad (4)$$

where p_i and a_j are the fractions of fragments that plant i and animal j inhabit, respectively, and M_j is the fraction of fragments inhabited by plants used by animal j .

We also measured the relative change in nestedness ($\text{NODF}_{\text{max}_{\text{final}}} - \text{NODF}_{\text{max}_{\text{initial}}})/\text{NODF}_{\text{max}_{\text{initial}}}$ and in connectance ($\text{connectance}_{\text{final}} - \text{connectance}_{\text{initial}}$) after each simulation (Fig. 2). Nestedness was measured as NODF_{max} and PRSN (Podani and Schemera, 2012; Appendix A, Box A1). As both measures showed similar behaviours, we only show results from NODF_{max}.

Finally, in order to evaluate if particular sets of traits favoured the persistence of plants under the different scenarios and at different levels of habitat loss, we compared the relative change in the mean and the coefficient of variation of plant dispersal, autonomous self-pollination and degree (i.e. plant pollination generalization), among scenarios within combinations of parameters that led to the extinction of at least 10% of the plant species and to the persistence of at least one plant species (Fig. 1). Comparisons were performed within those combinations of parameters that met these criteria in most scenarios. The relative changes in the mean and the coefficient of variation of the three plant traits were measured as (final value – initial value)/initial value.

2.4 Statistical Analyses

We compared the parameter range of plant and pollinator species persistence among all scenarios, in the absence of habitat loss and with 30% and 60% of habitat loss. These two levels of habitat loss were chose arbitrarily, but they reflect mean and maximum estimations of the percentage of natural habitats that have been converted across different biomes (Hoekstra et al., 2005). We also evaluated the statistical significance of differences in the final proportion of plants and pollinators species, and in the relative change in nestedness and connectance, among *a priori* planned pair-wise comparisons between the different scenarios, within situations of absence of habitat loss and 30% and 60% of habitat loss within combinations of parameters. The *Random* and *Neutral* scenarios were compared with all scenarios. We also performed pair-wise comparisons within scenarios describing negative associations between species degree and autonomous self-pollination or dispersal rates, by contrasting the results obtained when values of dispersal rates or autonomous self-pollination, respectively, were randomly assigned or were the same for all species. Finally, the two scenarios describing negative and positive associations between plant autonomous self-pollination and dispersal rates were also compared. Differences between means among pairs of scenarios were considered significant when the 95% confidence interval of the difference did not breach zero. All simulations were performed in Matlab, 2011.

We evaluated if the mean relative change in the mean and the coefficient of variation of the dispersal rate, autonomous self-pollination and degree of species within metacommunities, within habitat loss level, scenarios and parameter combinations, were significantly different from zero, by calculating the 95% confidence interval of each mean. Then we evaluated the statistical significance of differences among *a priori* pair-wise comparisons between the different scenarios, within situations of no habitat loss and 30% and 60% of habitat loss within combinations of parameters as described before.



3. RESULTS

3.1 Plant–Pollinator Metacommunity Persistence

We first evaluated the dynamics of the 96 metacommunities in the absence of habitat loss, for different initial combinations of three parameters: autonomous self-pollination rate, plant extinction-to-dispersal ratio and animal extinction-to-dispersal ratio (Fig. 2). For most combinations of these parameters, full metacommunity persistence (i.e. no species went extinct) occurred (Fig. 3). However, the prevalence of full metacommunity persistence varies among scenarios (Fig. 3). Full metacommunity persistence was observed for a wider combination of parameters under the assumption of neutrality in both dispersal ability and in autonomous self-pollination rate, and of neutrality in dispersal ability and a negative association between plant pollination generalization and autonomous self-pollination (Neutral and AGnegDneutral scenarios, respectively; Fig. 3A and C). Lower plant and pollinator diversity and high plant dominance were observed in simulations with the highest levels of plant autonomous self-pollination, plant extinction-to-dispersal ratios (e_P/d_P) and animal extinction-to-colonization ratios (e_A/c_A) for most scenarios, while under all other initial combinations of these parameters, the most prevalent pattern was the absence of dominance, in all scenarios (Fig. 3 and Table S1 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Under the assumption of neutrality in dispersal ability and autonomous self-pollination (Neutral scenario), metacommunities always showed no plant dominance, with mean plant occupancy decreasing with increases of plant extinction-to-dispersal ratios and of animal extinction-to-colonization ratios (Table S1 and Fig. S2A (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Metacommunities showed no dominance of pollinator species under all scenarios and combinations of parameter values, with mean pollinator occupancy decreasing with increases in the

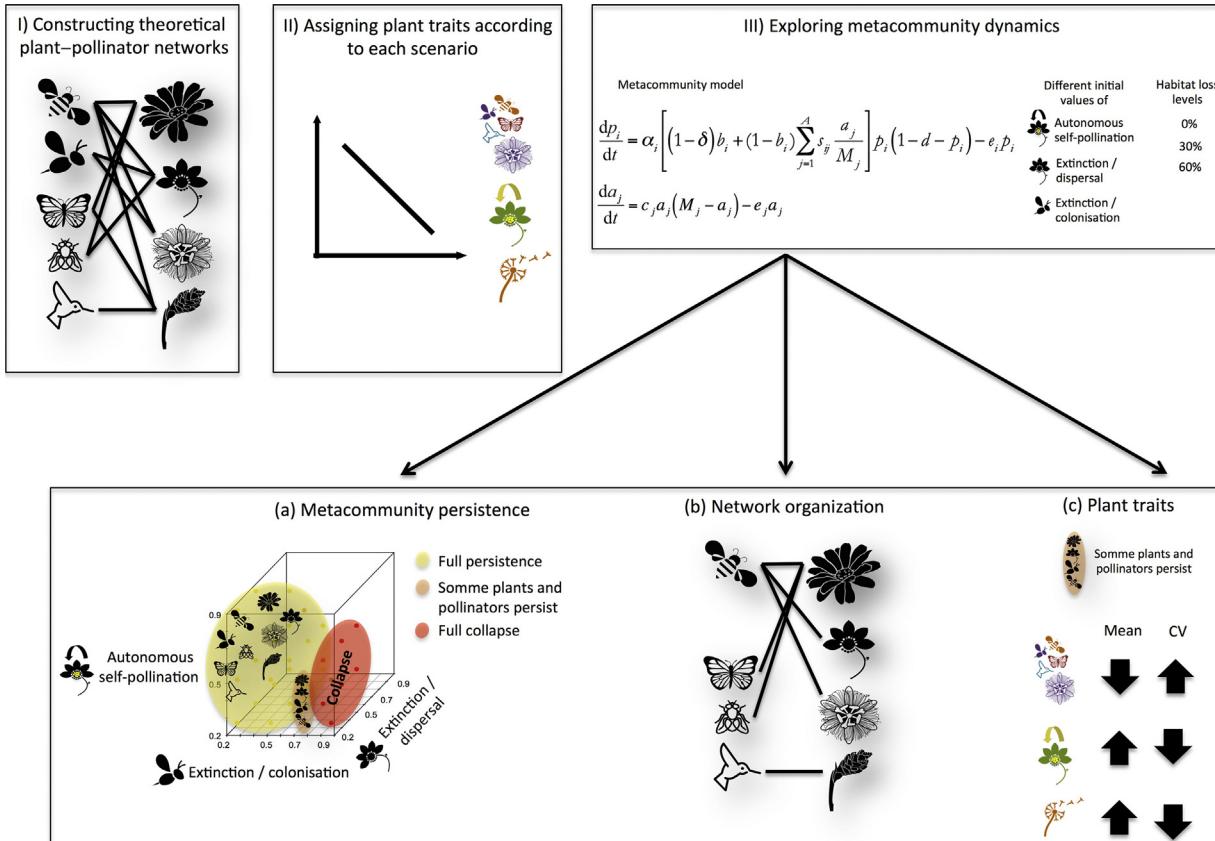


Figure 2 Schematic summary of the general theoretical and methodological framework used in this study. Each box summarizes the main steps described in [Section 2](#). References: CV, coefficient of variation. Designs are as in [Fig. 1](#).

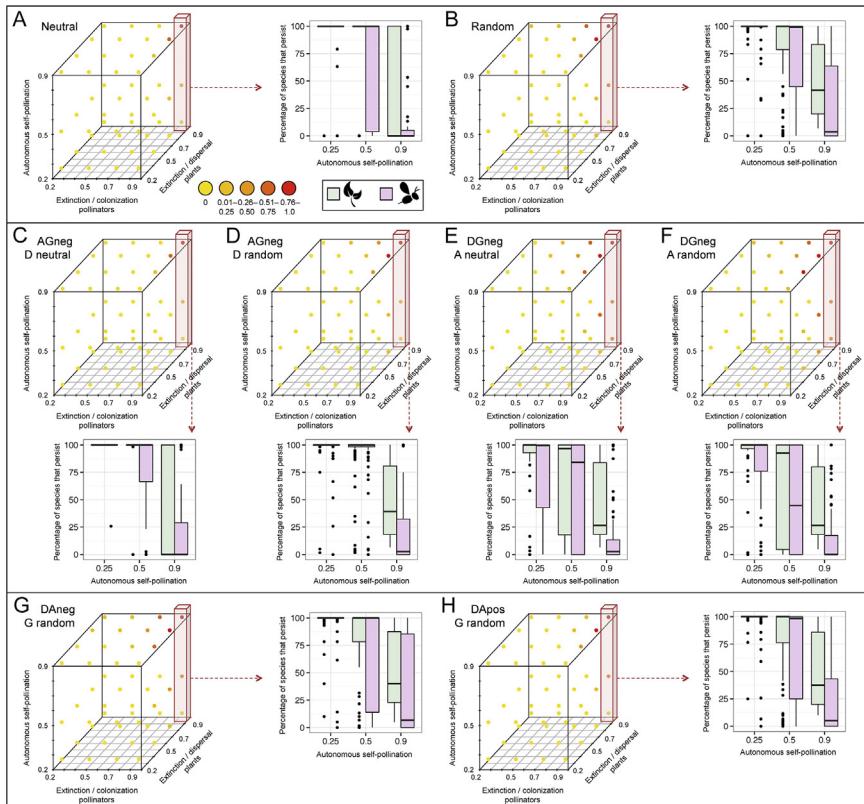


Figure 3 Metacommunity persistence in non-fragmented landscapes. The percentage of network replicates ($n=96$) leading to at least one species extinction for each combination of parameter values (initial values of pollinator extinction/colonization ratios, mean plant extinction/dispersal ratios and mean autonomous self-pollination rates) are shown inside each cube, under each scenario. This percentage ranges from 0% of network replicates leading to species extinction (yellow (light grey in the print version) dots) to most or all network replicates leading to species extinction (75–100%, red (dark grey in the print version) dots). Box-plots show final plant and pollinator richness for initial conditions set at the maximum e_A/c_A and e_p/d_p considered in this study (0.95), at different initial values of mean autonomous self-pollination rate (abscissas). Green (light grey in the print version) and purple (grey in the print version) boxes represent plant and pollinator species richness, respectively. Black lines within boxes represent median values. Upper and lower limits of boxes represent first and third quartiles, respectively. Black dots represent outliers. Scenarios are those described in Section 2.3 and Fig. 1. Plant and pollinator designs created by Guillaume Bahri and Peter Silk for the Noun Project (<https://thenounproject.com>).

extinction-to-colonization ratio of animal species (Table S1; Fig. S5 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Likewise, metacommunities showed no dominance of plant–pollinator interactions when full metacommunities persisted, under all scenarios, with interactions occurring in a decreasing fraction of the landscape with increasing animal extinction-to-colonization ratios and plant extinction-to-dispersal ratios (Table S1; Fig. S8 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). In the absence of habitat loss, extinction was limited to the combination of the highest values of autonomous self-pollination (0.9), the highest extinction-to-colonization ratio for animals (0.95) and the two highest extinction-to-dispersal ratios considered for plants (0.75 and 0.95; **Fig. 3**). For this combination of parameters, total neutrality in dispersal ability and autonomous self-pollination rate (Neutral scenario), and neutrality in dispersal associated with a negative relationship between autonomous self-pollination and plant pollination generalization (AGnegDneutral scenario) led to the extinction of all plant and pollinator species (i.e. complete metacommunity collapse occurred), whereas some plants and pollinators persisted in a small fraction of the landscape under the other scenarios (**Figs. 3, S2 and S5** (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)).

We now describe the effects of habitat loss. No matter the scenario, the complete collapse of the metacommunities—or at least of all pollinator species—occurred when 30% of the original natural habitat was removed, for some of the initial combinations of parameters that allowed full metacommunity persistence in absence of habitat loss (**Fig. 4**). These collapses occurred when animal extinction-to-colonization ratio was high (0.75 or 0.95), for all values of extinction-to-dispersal ratio for plants (**Fig. 4**). As occurred in the absence of habitat loss, the collapse of metacommunities was the most prevalent catastrophic outcome under both the scenario assuming neutrality in plant dispersal ability and autonomous self-pollination rate, and that assuming neutrality in plant dispersal ability and a negative relationship between autonomous self-pollination and plant pollination generalization (Neutral and AGnegDneutral scenarios; **Fig. 4A and C**). Pollinator collapse prevailed as the most likely catastrophic outcome under the other scenarios (**Fig. 4B, D–H**). The percentage of plant and pollinator species surviving with extinction-to-colonization ratio = 0.75 varied with mean autonomous self-pollination rate and among scenarios (**Fig. 4**). For instance, when the mean autonomous self-pollination rate varied from 0.5 to 0.9 and plant extinction-to-dispersal ratio was set to 0.25, the percentage of plant species surviving increased with autonomous self-pollination rate in five

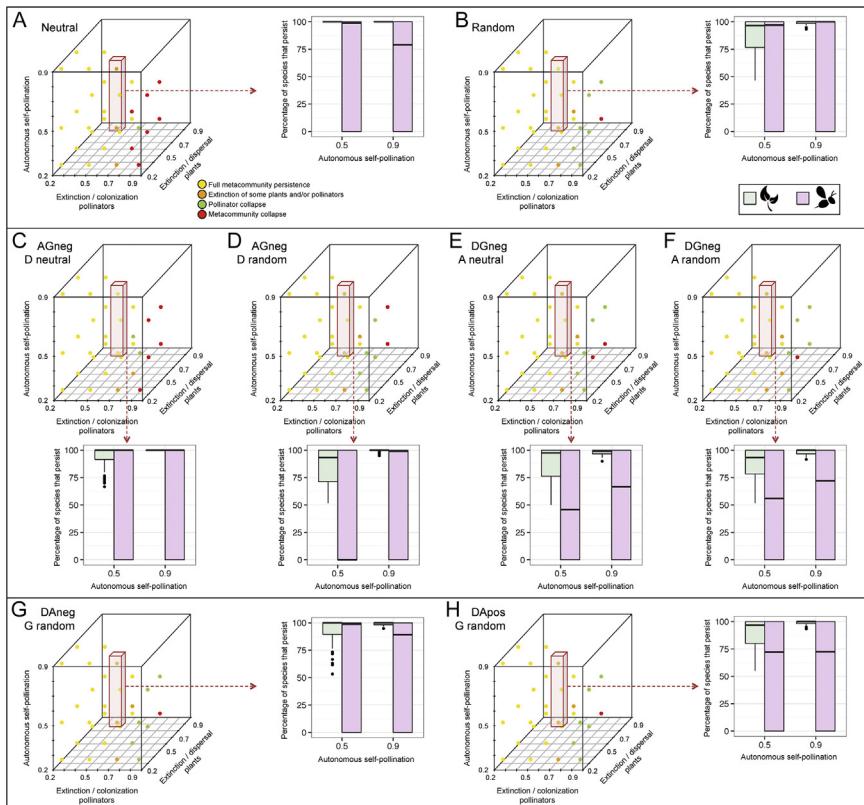


Figure 4 Metacommunity persistence with 30% of habitat loss. Combination of initial values for three parameters (pollinator extinction/colonization ratios, mean plant extinction/dispersal ratios and mean autonomous self-pollination rates) leading to full metacommunity persistence (yellow (light grey in the print version) dots), the extinction of some plants and/or some pollinators (orange (grey in the print version) dots), complete pollinator collapse (i.e. only plant species persist; green (grey in the print version) dots) and complete metacommunity collapse (red (dark grey in the print version) dots), is shown inside each cube for each scenario. Box-plots show variation in final plant and pollinator richness for initial conditions set at $e_A/c_A = 0.75$ and $e_P/d_P = 0.25$, at different initial values of mean autonomous self-pollination rate (abscissas). Green (light grey in the print version) and purple (grey in the print version) boxes represent plant and pollinator species richness, respectively. Box-plot interpretation is as in Fig. 3. Scenarios are those described in Section 2.3 and Fig. 1. Plant and pollinator designs are as in Fig. 3.

scenarios (Fig. 4B, D–F, H), whereas the percentage of pollinators surviving increased in four scenarios (Fig. 4B, D–F) and decreased in two (Fig. 4A and G).

With the loss of 30% of the original natural habitat, a combination of high frequency of autonomous self-pollination (0.9), low extinction-to-dispersal

ratios for plants ($e_P/d_P=0.25$) and high extinction-to-colonization ratios for animals ($e_A/c_A=0.75$) led to metacommunities highly dominated by some plant species under most scenarios (Table S1 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Lower levels of selfing (0.5) lead to metacommunities showing no dominance or intermediate dominance of plants (Table S1 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Metacommunities showed no dominance of pollinator species under all combinations of parameters (Table S1 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Nevertheless, the mean occupancy of pollinators decreased with increased extinction-to-colonization ratios (Table S1; Fig. S6 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Accordingly, the patterns of interaction occupancy showed no dominance under most parameter combinations, with decreasing interaction occupancy with both increasing animal extinction-to-colonization ratio and plant extinction-to-dispersal ratio (Table S1; Fig. S9 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>))).

With the loss of 60% of the original natural habitat, no matter the combination of parameters or the scenario, complete metacommunity collapse was the prevalent outcome of metacommunity dynamics (Fig. 5). Full metacommunity persistence only occurred when pollinators had the lowest extinction-to-colonization ratio (0.25, Fig. 5). All plant species showed maximum occupancy when the complete metacommunity persisted, under most scenarios (Table S1; Fig. S4 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). With full metacommunity persistence, pollinators showed similar occupancies (i.e. no dominance), occurring in less than 20% of the landscape under all scenarios (Table S1; Fig. S7 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Interactions among plants and pollinators also occurred at a similar proportion of fragments, which was lower than 0.1 under all scenarios, when there was full metacommunity persistence (Table S1; Fig. S10 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). When the initial ratio of extinction-to-colonization for animals was higher than 0.25, the whole set of pollinator species died out, under all scenarios (Fig. 5). Assuming neutrality in plant dispersal and autonomous self-pollination (Neutral scenario), initial values of extinction-to-colonization ratio for animals higher than 0.25 also led to the extinction of the whole set of plant species in almost all combinations of extinction-to-dispersal ratio for plants (Fig. 5A). Plant persistence without pollinators was observed for a similar range of parameters under most of the other scenarios, except in the scenario assuming neutrality in plant dispersal and a negative association between autonomous self-pollination and plant pollination generalization (AGnegDneutral scenario)

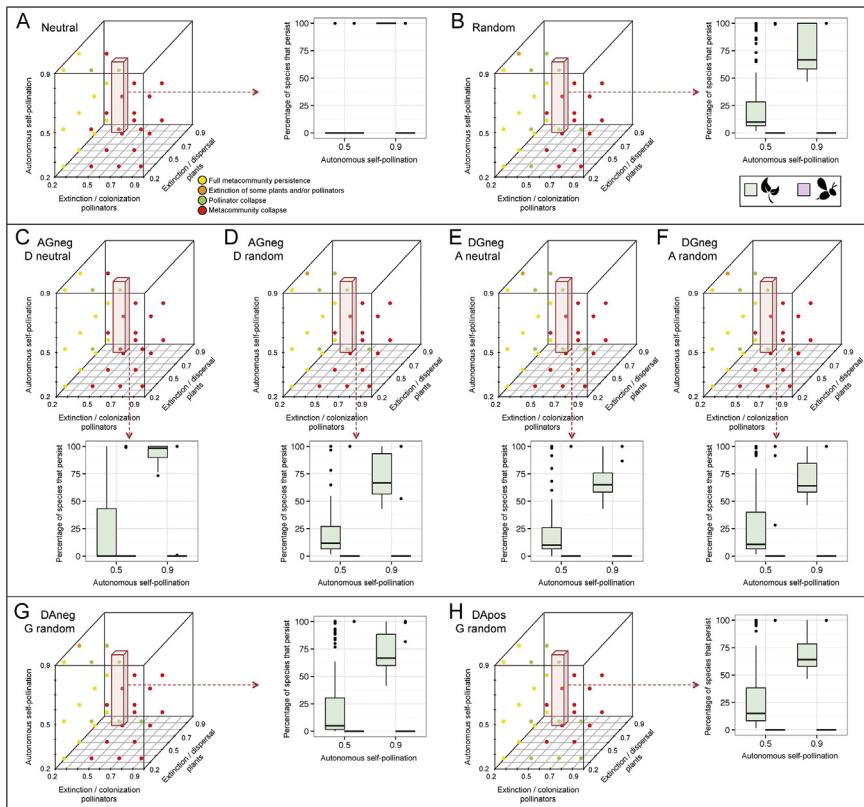


Figure 5 Metacommunity persistence with 60% of habitat loss. Combination of initial values for three parameters (pollinator extinction/colonization ratios, mean plant extinction/dispersal ratios and mean autonomous self-pollination rates) leading to full metacommunity persistence (yellow (light grey in the print version) dots), the extinction of some plants and/or some pollinators (orange (grey in the print version) dots), complete pollinator collapse (i.e. only plant species persist; green (grey in the print version) dots) and complete metacommunity collapse (red (dark grey in the print version) dots), is shown inside each cube for each scenario. Box-plots show variation in final plant and pollinator richness for initial conditions set at $e_A/c_A = 0.75$ and $e_p/d_p = 0.25$, at different initial values of mean autonomous self-pollination rate (abscissas). Green (light grey in the print version) and purple (grey in the print version) boxes represent plant and pollinator species richness, respectively. Box-plot interpretation is as in Fig. 3. Scenarios are those described in Section 2.3 and Fig. 1. Plant and pollinator designs are as in Fig. 3.

for which this outcome was observed under a narrower combination of parameter values (Fig. 5C). Increases from intermediate (0.5) to high (0.9) values of autonomous self-pollination rate increased the percentage of plant species surviving and led to the prevalence of high plant dominance when there was complete pollinator collapse, but only at intermediate values

of plant extinction-to-dispersal ratios ($e_P/d_P=0.5$) (Table S1 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>); Fig. 5).

3.2 Plant–Pollinator Network Organization

Relative changes in network connectance and nestedness were only analyzed for 30% of habitat loss. With 60% of habitat loss, most metacommunities either fully persisted or completely collapsed, or only plants persisted, and thus in all cases, there was either no change in connectance and nestedness or both dropped to zero. When 30% of the habitat was lost, most scenarios showed either no change in connectance or nestedness, or these metrics dropped to zero (relative change = −1; Figs. S11 and S12 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). When there was a change, both connectance (i.e. the proportion of realized interactions) and the overlap of interactions among species of the same trophic level (i.e. nestedness) barely decreased (e.g. Figs. S11E and F, and S12E and F (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>))).

3.3 Plant Traits

Mean dispersal rate increased and its variation decreased, across all habitat loss levels, initial parameter combinations and under most scenarios (Fig. 6; Table S2 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). In contrast, the mean autonomous self-pollination rate and its variation showed no or small variation after some plant species were lost (Fig. 7; Table S3 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Among the different combinations of parameters, the highest increases in mean autonomous self-pollination rates were observed in the scenario assuming neutrality in dispersal rates and a negative association between autonomous self-pollination ability and plant pollination generalization (AGnegDneutral), and the scenario assuming a positive association between dispersal and autonomous self-pollination rate (DAposGrdm scenario), under both habitat loss levels (Fig. 7B and D; Table S3 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). These two scenarios also showed the highest relative decreases in the coefficient of variation of autonomous self-pollination with 60% of habitat loss (Fig. 7D–F; Table S3 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>))).

Mean plant pollination generalization (i.e. plant degree) decreased and its variation increased, significantly, with 30% and 60% of habitat loss, across most scenarios and initial parameter combinations (Fig. 8; Table S4 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)). Under the Random

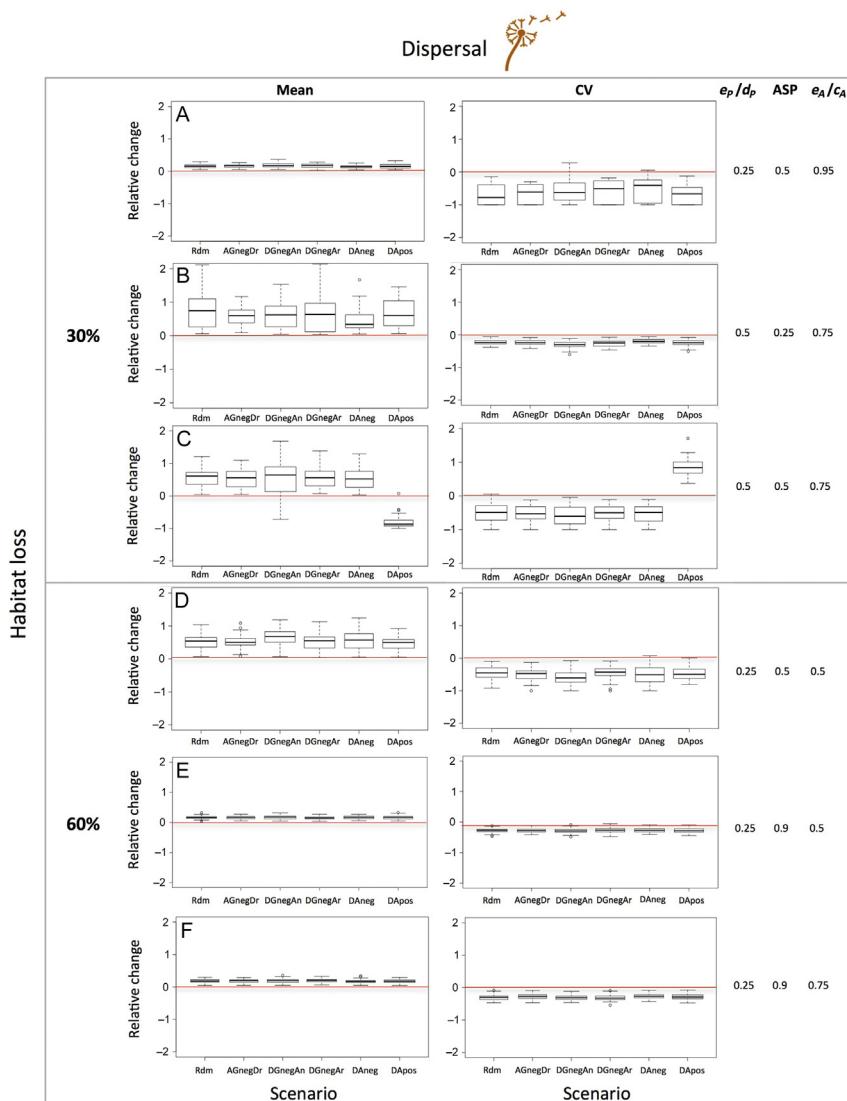


Figure 6 Relative change of the mean and the coefficient of variation (CV) of plant dispersal within metacommunities when >10% of plant species went extinct. Results for initial combinations of parameters allowing the persistence of plants in most scenarios at each habitat loss level are shown (A–C for $d=0.3$; D–F for $d=0.6$). Scenarios in which species had the same value of dispersal (Neutral and AGnegDneutral) are not shown. Relative change was obtained as (final value – initial value)/initial value, as described in *Methods*. Initial values for each parameter are shown on the right side of the figure: ASP, initial mean autonomous self-pollination rate; e_A/c_A , initial ratio between the extinction and the colonization rate of pollinators; e_p/d_p , initial ratio between the extinction and dispersal rate of plants. Box-plot interpretation is as in Fig. 3. Boxes were drawn with widths proportional to the number of networks in which the extinction of >10% of plant species occurred. Scenarios are those described in Section 2.3 and Fig. 1. References: d , proportion of habitat that was lost. Designs are as in Fig. 1.

Autonomous self-pollination

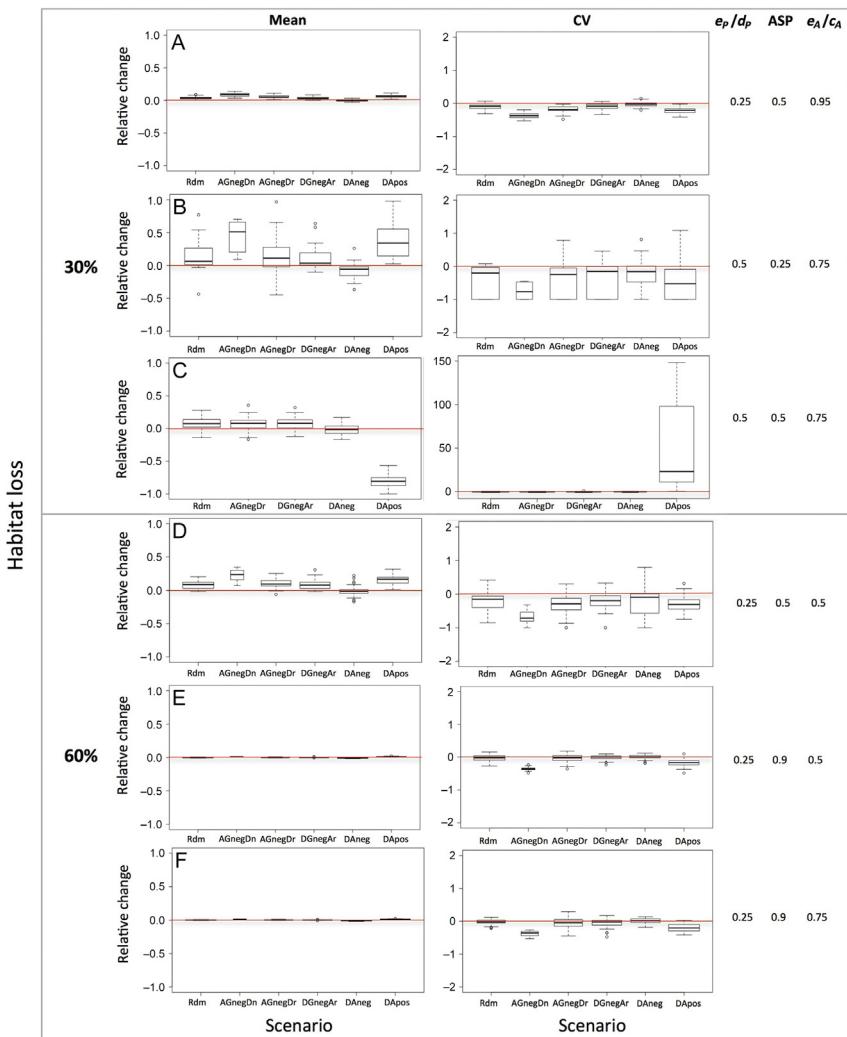


Figure 7 Relative change of the mean and the coefficient of variation (CV) of autonomous self-pollination rate within metacommunities when >10% of plant species went extinct. Results for initial combinations of parameters allowing the persistence of plants in most scenarios at each habitat loss level are shown (A–C for $d = 0.3$; D–F for $d = 0.6$). Scenarios in which species had the same value of autonomous self-pollination rate (Neutral and DGnegAneutral) are not shown. Relative change was obtained as (final value – initial value)/initial value, as described in Section 2.3. Initial values for each parameter are shown on the right side of the figure: ASP, initial mean autonomous self-pollination rate; e_A/c_A , initial ratio between the extinction and the colonization rate of pollinators; e_p/d_p , initial ratio between the extinction and dispersal rate of plants. Box-plot interpretation is as in Fig. 3. Boxes were drawn with widths proportional to the number of networks in which the extinction of >10% of plant species occurred. Scenarios are those described in Section 2.3 and Fig. 1. References: d , proportion of habitat that was lost. Designs are as in Fig. 1.

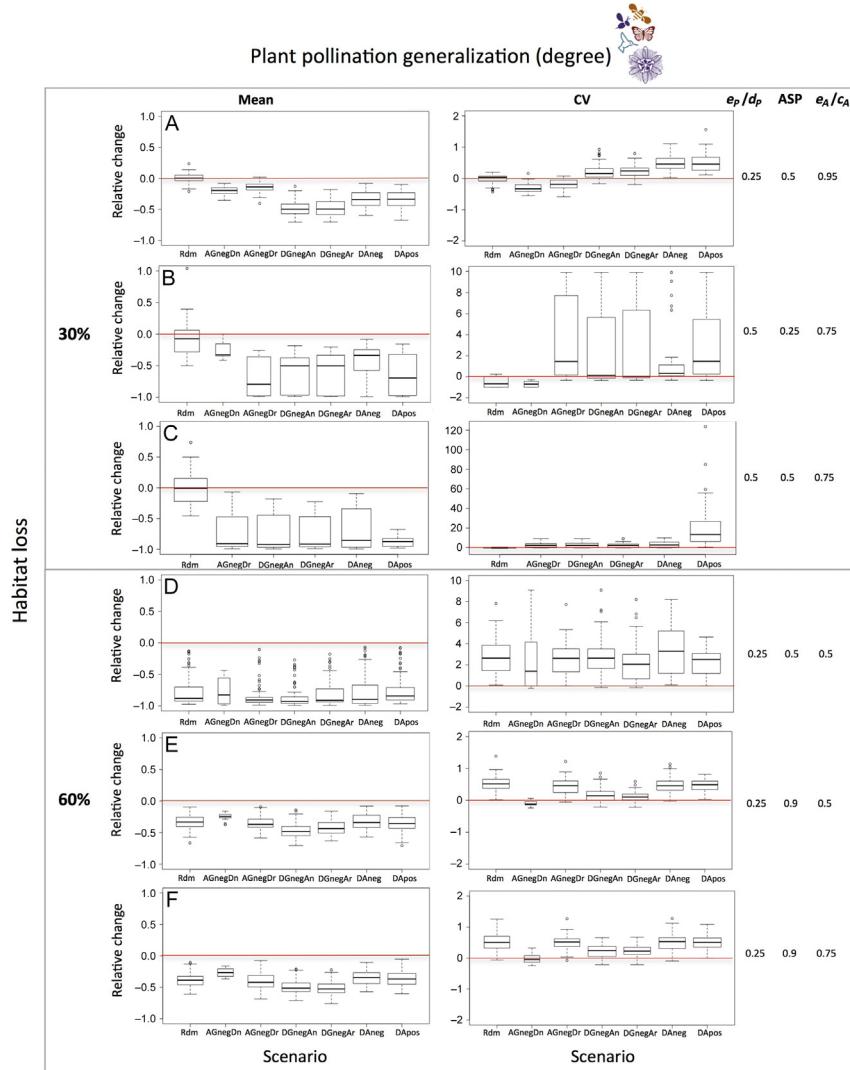


Figure 8 Relative change of the mean and the coefficient of variation (CV) of plant pollination generalization (degree) within metacommunities when >10% of plant species went extinct. Results for initial combinations of parameters allowing the persistence of plants in most scenarios at each habitat loss level are shown (A–C for $d=0.3$; D–F for $d=0.6$). Relative change was obtained as (final value – initial value)/initial value, as described in *Methods*. Initial values for each parameter are shown on the right side of the figure: ASP, initial mean autonomous self-pollination rate; e_A/c_A , initial ratio between the extinction and the colonization rate of pollinators; e_p/d_p , initial ratio between the extinction and dispersal rate of plants. Box-plot interpretation is as in Fig. 3. Boxes were drawn with widths proportional to the number of networks in which the extinction of >10% of plant species occurred. Scenarios are those described in Section 2.3 and Fig. 1. References: d , proportion of habitat that was lost. Designs are as in Fig. 1.

scenario, mean plant pollination generalization did not change with 30% of habitat loss, but significantly diminished with 60% of habitat loss (Fig. 8A–C; Table S4 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>)).



4. DISCUSSION

The destruction of natural habitats is one of the main causes of decline in global biodiversity (Haddad et al., 2015). Understanding how increasing habitat loss affects biodiversity patterns and ecological processes is critical for mitigating the effects of global environmental change (Tscharntke et al., 2012). In this sense, there is wide evidence that high habitat loss decreases pollinator diversity (Winfree et al., 2009) and that habitat fragmentation negatively affects the pollination processes (e.g. Aguilar et al., 2006; Hadley and Betts, 2012), i.e., a key ecological process that participates in supporting the diversity of wild plants and the production of crop species (Garibaldi et al., 2013; Kleijn et al., 2015; Klein et al., 2007; Ollerton et al., 2011). In the present work, by integrating evolutionary relationships among traits modulating plant response to habitat fragmentation, the structure of plant–pollinator interaction networks and metacommunity models, we have shed some light on how plant–pollinator metacommunities might respond to the progressively destruction of their natural habitats. The main predictions of our trait-based metacommunity model are that (1) variation on dispersal ability among plant species may prevent full metacommunity collapse under pollinator loss associated with increasing habitat loss; (2) habitat loss may select for plants with higher dispersal ability and higher autogamous selfing, and will typically decrease the incidence of pollination generalist plants; (3) metacommunities that comprise plants with high autonomous self-pollination ability may harbour higher richness of rare plant species when pollinator diversity declines with increased habitat loss but can lead to metacommunity collapse in non-fragmented landscapes.

4.1 Harbouring Plant Species with Different Dispersal Ability Matters for Metacommunity Persistence

Habitat loss may have more detrimental effects on plant and pollinator densities than habitat fragmentation *per se*, although their effects have rarely been separated in empirical studies (Hadley and Betts, 2012). Declines in pollinator density should trigger a negative feedback in which plants fail to produce seeds, decrease in density and become less attractive to pollinators, which in turn may decrease even more pollinator density (Hadley and Betts, 2012;

([Scheper et al., 2014](#)). However, it has been proposed that the nested structure of networks should confer high robustness to plant–pollinator meta-communities to the negative effects of habitat loss ([Fortuna and Bascompte, 2006](#)). Moreover, other traits associated with species sensitivity to partner loss may increase or decrease the robustness of networks to species extinction ([Astegiano et al., 2015](#); [Kaiser-Bunbury et al., 2010](#); [Tur et al., 2013](#); [Vieira and Almeida-Neto, 2015](#)). Our model predicts that when pollinator availability decreases metacommunities originally harbouring plants with different dispersal ability (10% of variance) may persist longer than those with plants showing similar dispersal abilities. With 30% of habitat loss and the extinction rate of pollinators being high (i.e. more than 75% of their colonization rate), metacommunities originally showing variation in dispersal ability among plants tended to support higher plant and pollinator richness. With 60% of habitat loss, although variation in plant dispersal ability did not prevent pollinator collapse, it allowed the persistence of some plant species, while the lack of variation in dispersal among plants likely led to full metacommunity collapse. Variation in dispersal ability among plants may increase metacommunity persistence by maintaining the fraction of fragments colonized by some plant species higher than the fraction in which these species went extinct. Instead, when dispersal rates are similar among all plant species and the occupancy of pollinators decline, even when specialist plants may produce seeds by having high autonomous self-pollination rates metacommunities may lose species or completely collapse because plant colonization ability may be highly limited by seed production. Thus, as showed for other interspecific interactions ([Calcagno et al., 2011](#); [Mouquet et al., 2011](#)), we found that the effects of the dispersal of individuals among communities can substantially alter predictions on the effects of habitat loss on plant–pollinator persistence, even those predictions obtained from models explicitly considering the structure of interaction networks ([Fortuna and Bascompte, 2006](#)).

Marked decreases in pollinator diversity have been empirically observed only with high levels of habitat loss ([Ekroos et al., 2010](#); [Winfrey et al., 2009](#)). Our model predicts that with 30% of habitat loss and when pollinators are going extinct from a fraction of fragments barely smaller than that of colonized fragments, full pollinator collapse will be prevalent even in meta-communities in which most plant species (food resources) persist. This result implies that, although food resources may barely be diminished by habitat loss (70% of natural habitat remaining), complete pollinator collapse might still occur with time. Our model assumes that all pollinators had the

same extinction rate, i.e., are negatively and equally affected by other factors decreasing pollinator occupancy besides food resources. Therefore, the collapse of pollinators with 30% of habitat loss may reflect situations in which pollinator diversity strongly decreases across different functional groups due to factors associated with increasing habitat loss different from the decrease in food sources. For instance, habitat loss may act synergistically with other drivers such as agricultural intensification or pathogen spread, negatively affecting pollinator diversity (González-Varo et al., 2013; Potts et al., 2010). Agricultural intensification may imply increases of pesticides inputs, while the spread of pathogens may occur from managed to wild pollinators, both processes directly affecting the fitness of pollinators and leading to pollinator declines (González-Varo et al., 2013). With 60% of habitat loss, pollinators are predicted to persist only when all animal-pollinated plant species persist, thus the joint negative effects of decreases in food resource density and of the increasing isolation of natural habitats may result in the complete collapse of pollinators. Previous theoretical studies have also predicted the existence of a critical threshold for plant–pollinator metacommunity persistence at 60% of habitat loss (Fortuna et al., 2013; Keitt, 2009). After high natural habitat destruction, the negative effects of certain landscape configurations (e.g. several small fragments) and the synergistic effects between habitat loss and other drivers of pollinator decline should become more evident (Hadley and Betts, 2012; González-Varo et al., 2013). However, how surrounding fields with temporally available pollen- or nectar-rewarded crops may alter the predictions of our model under high agricultural intensification, e.g., by temporally increasing pollinator occupancy (Scheper et al., 2014) remains to be tested (but see Keitt, 2009).

Although our model predicts that full metacommunities may persist with 60% of habitat loss (with low plant and pollinator extinction rates), species may co-occur and interact in a very small fraction of the landscape. This is because, in our model, it was assumed that if interaction partners persist in the landscape, the interaction does occur with certainty. Recent empirical studies have showed that in fragmented landscapes, interactions can be lost before species have disappeared (Aizen et al., 2012; Sabatino et al., 2010). Interaction loss may be associated with higher specificity between partners and lower interaction frequency (Aizen et al., 2012). Thus, our model may overestimate metacommunity persistence with high habitat loss. Moreover, our model may underestimate the existence of an “extinction debt” (Tilman et al., 1994) if many species are almost at the threshold capacity of the landscape that ensures meta-population persistence (Hanski and Ovaskainen, 2000).

4.2 Habitat Loss May Select for Higher Dispersal and Autonomous Self-Pollination but Not Pollination Generalization

Differences in plant species responses to the negative effects of the destruction of habitats have been associated with different biological traits determining plant sensitivity to pollinator loss (Aguilar et al., 2006; Ashworth et al., 2004; Eckert et al., 2010; Girão et al., 2007). However, which plant trait or set of traits may favour plant persistence after habitat fragmentation also depends on the limitations imposed by the characteristics of the surrounding matrix (Hadley and Betts, 2012). Landscape composition and configuration can impose different filters on species and ultimately determine metacommunity composition, an effect known as “the landscape moderation of functional trait selection” hypothesis (Tscharntke et al., 2012). Our model predicts that habitat loss may select for plants with higher dispersal ability. Good dispersers may be selected under either low or high habitat loss and independently of the original association between dispersal and other biological traits determining plant response to habitat loss (i.e. autonomous self-pollination and pollination generalization). Mean dispersal rate was always higher, and variation among plants in dispersal ability was generally lower in surviving plants than in the original set of plants present in landscapes without habitat loss. The increased survival of plants with higher dispersal ability is in agreement with the higher incidence of good dispersal plants in fragmented landscapes reported in recent empirical studies (Aparicio et al., 2008; Koh et al., 2015). When isolation among patches increases (a by-product of higher habitat loss), the richness of species with long-distance dispersal increases while that of species with short-distance dispersal decreases (Aparicio et al., 2008; Koh et al., 2015).

As we did not consider dispersal costs, it was expected that species with higher dispersal rates would be favoured by habitat loss. When the surrounding matrix imposes a high cost to dispersal (i.e. individuals dispersing to the matrix have higher extinction probability), low dispersal may be locally selected (Cheptou et al., 2008). Then, populations of low dispersal species will lack the *rescue effect* allowed by dispersal of conspecifics from other populations and high dispersal species will be affected by the costs imposed by high-risk matrices (Tscharntke et al., 2012). Thus, the ability of meta-communities to respond to future disturbances (e.g. conversion of low-risk matrices to high-risk ones under agricultural intensification) might decline following habitat loss due to decreases in response traits variability (i.e.

dispersal ability), ultimately reducing the resilience of ecosystem functions (Elmqvist et al., 2003; Laliberte et al., 2010).

“Landscape-moderated” filtering (*sensu* Tscharntke et al., 2012) of biotically pollinated plant species with low dependence on pollinators can be expected under habitat loss (Aguilar et al., 2006; Eckert et al., 2010). Unlike dispersal, our model predicts that the relative incidence of species with higher autonomous self-pollination may barely increase with habitat loss, as relative changes in mean autogamous selfing and its variation are comparatively small to those observed for dispersal. It is important to point out that, with 30% of habitat loss, our model predicts that several pollinator species may persist even when some plants went extinct. Thus, with low habitat loss, plants with high reproductive dependence on pollinators may persist by being generalists (Astegiano et al., 2015; but see Aguilar et al., 2006; Aizen et al., 2002). However, since complete pollinator collapse is predicted to occur with both 30% and 60% of habitat loss, high dispersal ability seems to be crucial for the persistence of plant species with low autonomous self-pollination ability.

Surprisingly, the relative incidence of generalist plants was not favoured by habitat loss compared with the original set of plant species. The subset of surviving species had lower mean and higher variation in pollination generalization than plant species in non-fragmented landscapes. Thus, under most scenarios, generalist plant species were relatively more affected by habitat loss than specialist species. These results contrasted with predictions based on the pervasiveness of asymmetric interactions in mutualistic networks (Ashworth et al., 2004; Vázquez and Aizen, 2004). It has been proposed that specialist and generalist plants may be equally affected by habitat fragmentation because the higher decline of specialist pollinators (Bommarco et al., 2010; Steffan-Dewenter and Tscharntke, 2002) may mainly affect generalist plants (Ashworth et al., 2004). Specialist plants may decrease their extinction probability with increasing habitat loss by interacting with generalist pollinators (Abramson et al., 2011). In our model, persistence ability may differ among pollinator species interacting with different number of plant species. However, we assumed that pollinator colonization and extinction rates did not differ among pollinator species. The pollinator extinction-to-colonization ratio seems to govern the dynamics of the occupancy of pollinators, which may lead to specialist and generalist pollinators being similarly affected by habitat loss when extinction is approximately equal to colonization, even if the feed on a different number of resources. Given that generalist plants had lower autonomous self-pollination or dispersal rate

under most scenarios, pollinator extinction may negatively affect more the occupancy of generalist plants than that of specialist ones. In this regard, when pollination generalization was not negatively associated with dispersal or autogamous selfing (i.e. under the *Random* scenario) and habitat loss was low (30%), surviving plants were as generalists as the initial set of plants in non-fragmented landscapes.

4.3 Integrating the Network Approach to the Management of Pollination Services in Human-Dominated Landscapes

Understanding how landscape fragmentation may affect ecological interactions has largely been improved by network approaches (Aizen et al., 2012; Cagnolo et al. 2009; Ebeling et al., 2011; Fabian et al., 2013; Fortuna and Bascompte, 2006; Hagen et al., 2012; Massol and Petit, 2013; Melián and Bascompte, 2002; Sabatino et al., 2010; Spiesman and Inouye, 2013; Tylianakis et al. 2010; Valiente-Banuet et al., 2014). In this regard, it has been proposed that conservation of interaction networks should involve the monitoring of network structural characteristics, such as connectance or nestedness (Tylianakis et al., 2010; but see Kaiser-Bunbury and Blüthgen, 2015). In principle, changes in connectance and nestedness should alert about changes in functional redundancy of species within networks and thus may be good indicators of the fragility of ecological networks in the face of species loss (Tylianakis et al., 2010; Vieira and Almeida-Neto, 2015). However, for plant–pollinator webs with nested structures, our model predicts that network connectance and nestedness may either barely change or drop to zero with increased habitat loss. This lack of change in network connectance and nestedness when some plant and pollinator species went extinct indeed show the lack of sensitivity of these structural network measures to the loss of a few species (Kaiser-Bunbury and Blüthgen, 2015; Nielsen and Bascompte, 2007).

Scale-free networks, such as the ones modelled here, are intrinsically robust (i.e. connectance does not change, and the general shape of the distribution of degrees does not change either) to random removals of nodes (i.e. species in our networks) but are particularly fragile in the face of removals targeted at hubs (i.e. the “super-generalists” in our networks; Barabási and Albert, 1999; Cohen et al., 2000, 2001). This robustness to random extinction of species has been showed for several plant–pollinator networks in studies simulating the random removal of either plants or pollinators (Astegiano et al., 2015; Kaiser-Bunbury et al., 2010; Memmott et al., 2004; but see Vieira and Almeida-Neto, 2015). Secondary

extinctions are generally low until the core of the network (symmetric generalist–generalist interactions) has been highly eroded. However, as discussed in the previous sections, generalist plant species seem to be more affected than specialist plants by habitat loss when pollination generalization is negatively associated with either dispersal or autonomous self-pollination rate. Thus, the small change on network connectance even when some species are lost suggests that habitat loss is a perturbation that might not be intensively targeting high-degree species, but rather more random. As far as nestedness is concerned, the same reasoning can apply since we have shown ([Appendix B](#)) that there is a strong association between the degree of nestedness of a network (NODF_{max} scores) and the shape parameter of the power law distribution determining the distribution of degree. If habitat loss does not select against “super-generalist” species (hubs) and maintains the shape of the degree distribution, the robustness of nestedness to habitat loss may be expected. In this sense, changes in connectance and nestedness should occur when networks are near to global collapse, i.e., when the distribution of interactions becomes very skewed as showed recently by [Fortuna et al. \(2013\)](#).

It has been proposed that integrating the network approach in studies aiming to conserve or restore natural biodiversity and to manage ecosystem services in agricultural landscapes should improve management results and also advance ecological network theory ([Bohan et al., 2013; Kaiser-Bunbury and Blüthgen, 2015; Tylianakis et al., 2010](#)). In the face of our results, which metrics will be useful to track in human-dominated? As stated by [Kaiser-Bunbury and Blüthgen \(2015\)](#), the first step will be to establish monitoring goals. For example, as natural areas are usually converted to expand cultivable lands, monitoring goals may be associated with the preservation of the pollination service of both wild plants providing several ecosystem services and insect-pollinated crops. This double goal may impose conflicting interests to landscape design ([Keitt, 2009; Kremen and Tscharntke, 2007; Mitchell et al. 2015a](#)) because the provision of pollination services to wild plants and the supply of pollinators to crop pollination may be maximized by different configurations of landscapes ([Mitchell et al., 2015a](#)). In this sense, the provision of pollination services generally is focused on maximizing crop production ([Garibaldi et al., 2014; Kremen et al., 2004; Schepers et al., 2013](#); but see [Gill et al., 2016; Kennedy et al., 2013](#)). However, if the goal is to maximize crop pollination services but also assure the reproduction of wild plants in natural areas to maintain the provision of the pollination service in the long term, monitoring the size and the functional

redundancy of the core of plant–pollinator networks in natural areas might represent a more simplified strategy than monitoring the structure of the network. Detecting decreases in the interaction diversity and evenness (Kaiser-Bunbury and Blüthgen, 2015) of species representing the core of plant–pollinator networks (those “super-generalists” symmetrically interacting among them) should alert about the capacity of natural areas to supply these services and to support natural metacommunities. The seed production of insect-pollinated crops and wild plants is increased by interacting with richer pollinator assemblages (Fontaine et al., 2006; Garibaldi et al., 2013; Hoehn et al., 2008). On the other hand, maintaining the preferred host plants for generalist pollinators should be a key strategy to assure pollination services (Scheper et al., 2014). Indeed, by maintaining generalist pollinators, we should promote the persistence of high pollinator-dependent and low dispersal wild plants (Astegiano et al., 2015; Tur et al., 2013). Moreover, monitoring not only pollinator richness but also evenness matters for crop production (Garibaldi et al., 2015). However, the morphological matching between crop flowers and different pollinator features affect crop production, thus different crops should benefit from the maintenance of different functional groups of pollinators (Garibaldi et al., 2015). Therefore, as recently proposed, a hierarchical network approach to the conservation of interactions should advance adaptive management in human-dominated landscapes (Kaiser-Bunbury and Blüthgen, 2015).

4.4 Evidencing the Contrasting Effects of Lower Dependence on Pollinators on Species Persistence

Recently, it has been proposed that plant–pollinator networks harbouring plants with high dependence on pollinator service may be less robust to extinctions (Vieira and Almeida-Neto, 2015). Our model predicts that increasing the autonomous self-pollination rate of plants within metacommunities may lead to contrasting results depending on both the level of habitat loss and the association between plant biological traits. In non-fragmented landscapes, when pollinator extinction/colonization ratios and plant extinction/dispersal ratios approached one, increasing plant autogamous selfing led to decreases in plant and pollinator richness under all scenarios of associations among plant traits. Moreover, under scenarios in which only species generalization varied among plants and pollinators (i.e. the *Neutral* scenario) or when autonomous self-pollination was negatively associated with plant pollination generalization, increasing autonomous self-pollination led to full metacommunity collapse. Decreases in

species richness or even complete metacommunity collapse may be explained by increasing autogamous selfing decoupling plant and pollinator dynamics. In our model, increasing seed production by autonomous self-pollination decreased the contribution of pollinators to plant reproduction, i.e., pollinator dynamics may affect less plant dynamics. Moreover, if plant and pollinator dynamics are decoupled, the facilitation effect among species that may arise because of high partner overlap in plant–pollinator webs may be less important (Lever et al., 2014). Thus, contrary to common expectations, increasing autonomous selfing may decrease the robustness provided by high interaction overlap in plant–pollinator assemblages, ultimately decreasing metacommunity persistence. This is a surprising result that may shed light on likely effects of climate change. For instance, it has been predicted that climate change may alter species phenology, increasing the mismatch between plants and their pollinators (Hegland et al., 2009; Memmott et al., 2007; Miller-Rushing and Inouye, 2009; but see Bartomeus et al., 2011). This phenological mismatch might trigger a cycle in which higher autogamy may be selected in plants, decreasing floral attraction and reward, and thus also pollinator visitation (Eckert et al., 2010).

Another prediction of our model is that metacommunities originally comprising plants with higher autonomous self-pollination ability may harbour higher plant richness with increased habitat loss than metacommunities with lower autogamous selfing levels. However, pollinator richness may either not change or barely increase with increased mean plant autogamous selfing. These results may be explained by metacommunities originally comprising plants with lower reproductive dependence on pollinators harbouring more rare plants, even with high levels of habitat loss. The higher plant dominance found in these metacommunities may support this last idea. Rare plants occupying remnants of natural habitat may suffer from pollen limitation if pollinators preferentially feed on mass co-flowering crops (the “dilution hypothesis”; Holzschuh et al., 2011; Tscharntke et al., 2012). Interactions between wild plant species and generalist pollinators are more prone to be temporally lost, since these pollinators are the most likely to be attracted by these crops as reported in recent empirical studies (Holzschuh et al., 2010; Kleijn et al., 2015).

4.5 Caveats of the Trait-Based Metacommunity Model

In our model, it was assumed equal inbreeding depression for all plant species. Inbreeding depression can reduce the performance of the progeny with

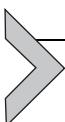
consequences for populations and species persistence. Higher probability of inbreeding depression is expected when mating system shift from out-crossing or mixed mating to mainly selfing (Goodwillie et al., 2005). Indeed, it has been reported that habitat fragmentation and disturbance can modify mating systems by decreasing outcrossing rates (Aguilar et al., 2008; Eckert et al., 2010). Such change in mating system is expected to differentially affect species seed production, dispersal and survival in fragmented landscapes.

Lower outcrossing rates in strictly self-incompatible species should decrease seed production (Aguilar et al., 2006). How such changes in the mating system of self-compatible species may affect plant reproduction is less predictable (Eckert et al., 2010). Historically selfing species may suffer slight or no inbreeding depression, but outcrossing and mixed mating species may show a reduction in seed production and in progeny performance (Goodwillie et al., 2005). Moreover, the effects of inbreeding depression can be stronger in stressful habitats (Armbruster and Reed, 2005). Thus, habitat fragmentation may select for the persistence of historically selfing species.

Our model also assumes that pollinator colonization and extinction rates do not differ among pollinator species. Differences in occupancy among pollinator species can only arise as a result of generalist species being temporally favoured by interacting with more plant species, in accordance with empirical data showing lower negative impacts of habitat fragmentation in species with wider foraging diets (Bommarco et al., 2010; Öckinger et al., 2010; but see Williams et al., 2010). The sensitivity of animal pollinators to habitat loss and fragmentation also seems to be related to other biological traits. Higher sensitivity has been associated with smaller body size, lower dispersal ability, lower reproductive capacity, species that nest above ground and solitary species (Ferreira et al., 2015; Jauker et al., 2013; Klein et al., 2008; Kotiaho et al., 2005; Öckinger et al., 2010; Williams et al., 2010). Moreover, like plants, pollinator response to fragmentation may be conditioned by relationships among biological traits (Bommarco et al., 2010; Williams et al., 2010). By being able to use food resources and nest sites from different patches and even from the surrounding matrix, generalist species may have higher dispersal ability and may be less affected by habitat loss. However, as showed by Fahrig (2007), whether dispersal is favourable or increases, the extinction probability of pollinators will depend on the suitability of the surrounding matrix. Moreover, identifying links between suites of traits that may determine pollinator sensitivity to habitat loss and the importance of these pollinators to wild plants by characterizing pollinator centrality in interaction networks seems to be crucial (Hagen et al., 2012). For instance, it has

recently been proposed that, by interacting with generalist pollinators, low dispersal plants may persist in local communities (Astegiano et al., 2015). Thus, future trait-based models including associations between plant and pollinator traits may certainly improve our understanding of plant–pollinator persistence in the face of habitat loss.

Functional redundancy among pollinator species was assumed in our model. Functional redundancy implies that for a given plant species, different pollinator species are similarly efficient, such that if one pollinator species goes extinct, another pollinator may fulfil its function (see Valiente-Banuet et al., 2014). Although functional redundancy among pollinators has been reported for several plant species (Fleming et al., 2001; Fumero-Cabán and Meléndez-Ackerman, 2007; Larsen et al., 2005), it seems not to be a general feature not for wild plants (Ashworth et al., 2015b) neither for crop species (Garibaldi et al., 2015). For instance, plant species with bat- or fly-syndrome flowers have higher probabilities of having redundant pollinators from different functional groups than bird- and bee-syndrome flowers (Ashworth et al., 2015b). Moreover, bees and butterflies are redundant pollinators in bat-syndrome flowers (Ashworth et al., 2015b). Given that species richness within Hymenoptera and Lepidoptera can be more strongly diminished by habitat loss than other insect groups (Spiesman and Inouye, 2013), habitat loss might decrease both pollination levels of bee- and butterfly-syndrome flowers and the likelihood of having redundant pollinators in bat-syndrome flowers. Therefore, understanding how pollinator functional redundancy is related to pollinator response to habitat loss may also improve our ability to predict the persistence of species and interactions in fragmented landscapes.



5. FUTURE DIRECTIONS: POLLINATION SERVICES IN HUMAN-DOMINATED LANDSCAPES

Changes induced by habitat loss and fragmentation will modify the taxonomic, genetic and functional diversity of ecosystems in fragmented landscapes over the long term (e.g. Aguilar et al., 2008; Cagnolo et al., 2006; Laurance et al., 2006; Spiesman and Inouye, 2013), decreasing ecosystems resilience and the supply of ecosystem services (Diaz et al., 2006; Haddad et al., 2015; Valiente-Banuet et al., 2014). Impoverished ecosystems will provide low-quality services such as reduced productivity, pollination, pest control and carbon retention (Haddad et al., 2015; Mitchell et al., 2015b). Moreover, natural habitats in fragmented landscapes retain lower

diversity of pollinators (e.g. Öckinger et al., 2010; Spiesman and Inouye, 2013; Winfree et al., 2009), which in turn can negatively affect the amount, quality and stability of crop pollination and harvests (Garibaldi et al., 2013; Ricketts et al., 2008). In addition, crop yield is better explained by the trait matching between crop flowers and pollinators and by pollinator evenness, than only by pollinator richness (Garibaldi et al., 2015). Thus, a key question for predicting the vulnerability of ecosystem services faced with changing environmental drivers is how traits determining species' ecosystem-level effects and species responsiveness to drivers also determine species interaction patterns within ecological networks (Díaz et al., 2013; Gill et al., 2016; Lavorel et al., 2013; Mulder et al., 2012). For instance, generalist pollinators form the core of the structure of plant–pollinator networks (Bascompte et al., 2003), providing functional redundancy and complementarity (Blüthgen and Klein, 2011; Tscharntke et al., 2012) and interacting with plants more sensitive to pollinator loss, i.e., specialist, highly pollinator-dependent and low dispersal plants (Astegiano et al., 2015; Tur et al., 2013; Vázquez and Aizen, 2004). Generalist pollinators are also among the main pollinators of several mass-flowering crops (Holzschuh et al., 2011; Kleijn et al., 2015). Thus, it will be crucial to evaluate how functional redundancy among generalist pollinators or pollinator guilds is related to the diversity in the response of pollinators to likely disturbances in human-dominated landscapes (Elmqvist et al., 2003; Kaiser-Bunbury and Blüthgen, 2015; Tylianakis et al., 2010). Pollination service resilience may depend on pollinators response diversity, i.e., how functionally similar pollinators respond differently to disturbance. Generalist pollinators may respond to habitat loss in very different ways (Bommarco et al., 2010; Williams et al., 2010), which may increase the resilience of pollination services to habitat loss. However, how redundancy is distributed in plant–pollinator networks and how it changes with pollinator loss, for instance because of the rewiring process (Kaiser-Bunbury et al., 2010), remain to be understood.

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APPENDIX A. GENERATING BIPARTITE INCIDENCE MATRICES WITH DETERMINED DEGREE SEQUENCES

To generate bipartite incidence matrices (i.e. binary matrices in which rows represented animal species, columns, plant species, and 1's indicated realized interactions), we resorted to the following procedure based on an algorithm proposed by [Chung et al. \(2003\)](#), adapted to the problem of generating incidence matrices with a known number of connections.

Following Chung et al. (2003), a non-increasing sequence of degrees (summing to C) can represent a sample from a power law distribution of parameter γ if the degree of the i th element in the sequence is roughly proportional to $i^{-1/(\gamma-1)}$. In practice, we used sequences of degrees k_i defined by:

$$k_i = \max \left[1, \min \left\{ \left\lfloor xi^{-1/(\gamma-1)} \right\rfloor, n \right\} \right] \quad (\text{A.1})$$

where n is the maximal degree (given by the number of species in the other trophic level), $\lfloor \cdot \rfloor$ is the integer part symbol and x is a constant obtained by numerically solving:

$$C = \sum_i k_i \quad (\text{A.2})$$

The following code can generate these sequences of degrees in R:

```
## function alpha: computes parameter necessary for adjusting the power
# law degree sequences
## parameters: s = number of species in the focal group, beta = power law
# parameter, c = total number of connections, d = number of species in the
# other group
alpha<-function(s,beta,c,d){
  locfun<-function(x){
    ((rep(1,s)%*%sapply(sapply(floor(x*(1:s)^(-(1/
    (beta-1)))),function(z) min(z,d)),function(y) max(y,1)))-c)
  }
  uniroot(f=locfun,interval = c(0,2*c))$root
}
```

```
## function powerlawdegreeeseq: yields a sequence of non-increasing
degrees such that the ensuing distribution follows a power law of parameter beta,
following Chung et al. 2003
powerlawdegreeeseq<-function(s,beta,c,d){
  a <- alpha(s,beta,c,d)
  sapply(sapply(floor(a*(1:s)^(-(1/(beta-1)))),function
(z) min(z,d)),function(y) max(y,1))
}
```

Once degree sequences are obtained, the rest of the procedure consists in generating random incidence matrices such that summing by row or column generates sequences identical to the desired degree sequences. To do so, we first check that the degree sequences used for animals and plants can effectively generate a bipartite incidence matrix (i.e. are graphical sequences in the mathematical sense). The Gale–Ryser theorem (see [Brualdi and Ryser, 1991](#)) manages to check this by recursively comparing sums of degrees to a minimal constraint. This test can be implemented in R as:

```
galerysertest <- function(rowtotal,columntotal){
  row <- length(rowtotal)
  column <- length(columntotal)
  total <- sum(rowtotal)
  test0<-(sum(columntotal)==total)
  delta <- sort(rowtotal, decreasing = T)
  d <- sort(columntotal, decreasing = T)
  left <- cumsum(d)
  right <- sapply(1:column, FUN = function(x) (1/2)*(total +
row*x - sum(abs(rowtotal-x))))
  test1 <- ((right-left)>=0)
  test0 && all(test1)
}
```

If the degree sequences are indeed graphical, we first generate a quantitative incidence matrix (i.e. with integer entries instead of binary entries) that keep row and column sums equal to the matching degree sequences, and then resort to the quasi-swap/sum of squares algorithm of [Miklós and Podani \(2004\)](#) to generate a binary incidence matrix through random swapping of checkerboard patterns that decreased the sum of squares of elements in the matrix. The following R code implements this procedure.

```
library(vegan)
library(igraph)
sumofsquare<-function(rowtotal,columntotal){
  row <- length(rowtotal)
```

```

column <- length(columntotal)
m <- r2dtable(1, rowtotal, columntotal)[[1]]
ssmin <- sum(rowtotal)
ss <- sum(m*m)
while(ss>ssmin){
  ik <- igraph.sample(1, row, 2)
  jl <- igraph.sample(1, column, 2)
  if((m[ik[1],jl[1]]>0)&&(m[ik[2],jl[2]]>0)&&(m[ik[1],jl[1]]+m[ik[2],jl[2]]-m[ik[1],jl[2]]-m[ik[2],jl[1]]>=2)){
    ss <- ss-2*(m[ik[1],jl[1]]+m[ik[2],jl[2]]-m[ik[1],jl[2]]-m[ik[2],jl[1]]-2)
    m[ik[1],jl[1]] <- m[ik[1],jl[1]] - 1
    m[ik[2],jl[2]] <- m[ik[2],jl[2]] - 1
    m[ik[1],jl[2]] <- m[ik[1],jl[2]] + 1
    m[ik[2],jl[1]] <- m[ik[2],jl[1]] + 1
  }
  else {
    if((m[ik[1],jl[2]]>0)&&(m[ik[2],jl[1]]>0)&&(m[ik[1],jl[2]]+m[ik[2],jl[1]]-m[ik[1],jl[1]]-m[ik[2],jl[2]]>=2)){
      ss <- ss-2*(m[ik[1],jl[2]]+m[ik[2],jl[1]]-m[ik[1],jl[1]]-m[ik[2],jl[2]]-2)
      m[ik[1],jl[2]] <- m[ik[1],jl[2]] - 1
      m[ik[2],jl[1]] <- m[ik[2],jl[1]] - 1
      m[ik[1],jl[1]] <- m[ik[1],jl[1]] + 1
      m[ik[2],jl[2]] <- m[ik[2],jl[2]] + 1
    }
  }
}
m
}

```

Finally, once a single incidence matrix corresponding to the desired degree sequences is generated through the quasi-swap method, we can generate other such matrices by swapping entries in the matrix following the trial swap procedure of [Miklós and Podani \(2004\)](#) and implement in the R package “vegan”. The following R code exemplifies how we can use this procedure to generate 100 random bipartite matrices following degree sequences mimicking power laws of parameter 2.5.

```

## function generateZ sums up the various functions defined above
generateZ <- function(sa,sp,betaa,betap,c){
  delta <- powerlawdegreeseq(sa,betaa,c,sp)

```

```

d <- powerlawdegreeseq(sp,betap,c,sa)
sumofsquare(delta,d)
}
galerysertest(powerlawdegreeseq(60,2.5,1440,120),
powerlawdegreeseq(120,2.5,1440,60))
initmat <- generateZ(120,60,2.5,2.5,1440)
setofmat<-simulate(nullmodel(initmat,"tswap"),nsim=100,burnin      =
1000000, thin = 1000000)

```

BOX A1 Measures of Nestedness

To measure nestedness in a given bipartite network linking plants and pollinators, we used two different measures of nestedness, NODF_{max} and PRSN ([Podani and Schmera, 2012](#)). Considering the incidence matrix **M** with element m_{ij} being equal to 1 if pollinator i interacts with plant j , and writing $\delta_i = \sum_j m_{ij}$

the degree of pollinators, $d_j = \sum_i m_{ij}$ the degree of plants, A the number of pollinators and P the number of plants, the formula for NODF_{max} given by [Podani and Schmera \(2012\)](#), averaged over its column-wise and row-wise definitions, can be expanded as:

$$\text{NODF}_{\max} = \frac{\text{NODF}_{\max}^{\text{pollinators}} + \text{NODF}_{\max}^{\text{plants}}}{2} \quad (\text{A.3})$$

$$\text{NODF}_{\max}^{\text{pollinators}} = \frac{100}{\binom{A}{2}} \sum_{k < l} (1 - 0^{|d_k - d_l|}) \frac{\sum_j m_{kj} m_{lj}}{\min(d_k, d_l)} \quad (\text{A.4})$$

$$\text{NODF}_{\max}^{\text{plants}} = \frac{100}{\binom{P}{2}} \sum_{k < l} (1 - 0^{|d_k - d_l|}) \frac{\sum_i m_{ik} m_{il}}{\min(d_k, d_l)} \quad (\text{A.5})$$

Essentially, what NODF_{max}^{plants} measures is the percentage of overlap of interacting partners among all pairs of plants, the denominator being given by the plant with the lowest degree. The $1 - 0^{|d_k - d_l|}$ factor indicates that, in case of ties (i.e. when both plant species have the same degree), the comparison always results in the addition of zero to the sum of overlaps. NODF_{max}^{pollinators} measures the same quantity, but from the viewpoint of pairs of pollinator species sharing a more or less high proportion of the interacting plant partners.

The second measure of nestedness used is PRSN (for percentage relativized strict nestedness) can be computed in the same way:

$$\text{PRSN} = \frac{\text{PRSN}_{\text{pollinators}} + \text{PRSN}_{\text{plants}}}{2} \quad (\text{A.6})$$

BOX A1 Measures of Nestedness—cont'd

$$\text{PRSN}^{\text{pollinators}} = \frac{100}{\binom{A}{2}} \sum_{k < l} (1 - 0^{|\delta_k - \delta_l|}) \left(1 - 0^{\sum_j m_{kj}m_{lj}} \right) \frac{\sum_j m_{kj}m_{lj} + |\delta_k - \delta_l|}{\delta_k + \delta_l - \sum_j m_{kj}m_{lj}} \quad (\text{A.7})$$

$$\text{PRSN}^{\text{plants}} = \frac{100}{\binom{P}{2}} \sum_{k < l} (1 - 0^{|d_k - d_l|}) \left(1 - 0^{\sum_i m_{ik}m_{il}} \right) \frac{\sum_i m_{ik}m_{il} + |d_k - d_l|}{d_k + d_l - \sum_i m_{ik}m_{il}} \quad (\text{A.8})$$

**APPENDIX B. NESTEDNESS DEPENDS ON THE DISTRIBUTION OF DEGREES**

Here, we show that one can cover a rather wide span of nestedness values for a given bipartite network with a given number of connections by simply adjusting the distribution of degrees among the nodes. Or, in other words, that there exists a very strong dependence of the expected values of nestedness indices on the distribution of node degree.

A first observation simply comes from rewriting the elements of Eq. (A.4), which gives $\text{NODF}_{\max}^{\text{pollinators}}$ for a given bipartite network of incidence matrix \mathbf{M} . In addition to the degrees of the pollinator species, this quantity depends on the elements of $\mathbf{M} \cdot \mathbf{M}^T$ through the sums $\sum_j m_{kj}m_{lj}$.

One can naturally rewrite elements $(\mathbf{M} \cdot \mathbf{M}^T)_{kl}$ as an expectation of random binary interaction variables ($m_{k\bullet}$ and $m_{l\bullet}$):

$$(\mathbf{M} \cdot \mathbf{M}^T)_{kl} = \sum_j m_{kj}m_{lj} = P \times \mathbb{E}[m_{k\bullet}m_{l\bullet}] \quad (\text{A.9})$$

where P is the number of plant species in the network. If we note $\rho[m_{k\bullet}, m_{l\bullet}]$ the correlation between the random binary variables $m_{k\bullet}$ and $m_{l\bullet}$, the following expression links $\rho[m_{k\bullet}, m_{l\bullet}]$ with $(\mathbf{M} \cdot \mathbf{M}^T)_{kl}$:

$$(\mathbf{M} \cdot \mathbf{M}^T)_{kl} = P\rho[m_{k\bullet}, m_{l\bullet}] \sqrt{\delta_k\delta_l \left(1 - \frac{\delta_k}{P} \right) \left(1 - \frac{\delta_l}{P} \right)} + \frac{\delta_k\delta_l}{P} \quad (\text{A.10})$$

Thus, in the absence of an explicit correlation between $m_{k\bullet}$ and $m_{l\bullet}$, we still expect $(\mathbf{M}_k \mathbf{M}_l^T)_{kl}$ to take values of $\delta_k \delta_l / P$.

Now, assuming that rows (i.e. pollinators) are sorted in decreasing order of degrees (i.e. $\delta_1 \geq \delta_2 \geq \dots \geq \delta_A$) and ignoring the $1 - 0^{|\delta_k - \delta_l|}$ factors in Eq. (A.4), we have the following expectation for $\text{NODF}_{\max}^{\text{pollinators}}$ under the assumption of no correlations between the $m_{k\bullet}$ and $m_{l\bullet}$ of any pair of pollinators:

$$\text{NODF}_{\max}^{\text{pollinators}} \approx \frac{100}{\binom{A}{2}} \sum_{k=1}^{A-1} \sum_{l=k+1}^A \frac{\delta_k}{P} = \frac{100}{P \binom{A}{2}} \sum_{k=1}^{A-1} (A-k) \delta_k \quad (\text{A.11})$$

The expression (A.11) clearly depends on the degree distribution as the quantity $\sum_{k=1}^{A-1} k \delta_k$ will vary depending on the realized sequence of (δ_k) .

A practical example of the dependence of NODF_{\max} on the degree distribution can be found in Fig. S1 (<http://dx.doi.org/10.1016/bs.aecr.2015.09.005>). For the same connectance and species richness values, the shape of the degree distribution determines the value of NODF_{\max} unequivocally, with low-power degree distributions leading to higher NODF_{\max} values than high-power degree distributions (from >70 to <40 NODF_{\max} values between powers of 2.2 and 2.9).

REFERENCES

- Abramson, G., Trejo Soto, C.A., Oña, L., 2011. The role of asymmetric interactions on the effect of habitat destruction in mutualistic networks. *PLoS One* 6, e21028.
- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Determinants of plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* 9, 968–980.
- Aguilar, R., Quesada, M., Ashworth, L., Herreras-Diego, Y., Lobo, J., 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. *Mol. Ecol.* 17, 5177–5188.
- Aguilar, R., Ashworth, L., Calviño, A., Quesada, M., 2012. What is left after sex in fragmented forests: assessing the quantity and quality of progeny of *Prosopis caldenia* (Fabaceae) an endemic tree from central Argentina. *Biol. Conserv.* 152, 81–89.
- Aizen, M.A., Ashworth, L., Galetto, L., 2002. Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *J. Veg. Sci.* 13, 885–892.
- Aizen, M.A., Sabatino, M., Tylianakis, J.M., 2012. Specialization and rarity predict non-random loss of interactions from mutualist networks. *Science* 335, 1486–1489.
- Allesina, S., Tang, S., 2012. Stability criteria for complex ecosystems. *Nature* 483, 205–208.
- Almeida-Neto, M., Guimaraes, P., Guimaraes, P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1227–1239.

- Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., Terry, J., 2011. Cascading effects of bird functional extinction reduce pollination and plant density. *Science* 331, 1068–1070.
- Aparicio, A., Albaladejo, R.G., Olalla-Tárraga, M.A., Carrillo, L.F., Rodríguez, M.Á., 2008. Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. *For. Ecol. Manag.* 255, 2894–2906.
- Armbruster, P., Reed, D.H., 2005. Inbreeding depression in benign and stressful environments. *Heredity* 95, 235–242.
- Ashworth, L., Aguilar, R., Galletto, L., Aizen, M.A., 2004. Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *J. Ecol.* 92, 717–719.
- Ashworth, L., Quesada, M., Casas, A., Aguilar, R., Oyama, K., 2009. Pollinator-dependent food production in Mexico. *Biol. Conserv.* 142, 1050–1057.
- Ashworth, L., Calviño, A., Martí, L., Aguilar, R., 2015a. Offspring performance and recruitment of the pioneer tree *Acacia caven* (Fabaceae) in a fragmented subtropical dry forest. *Austral Ecol.* 40, 634–641.
- Ashworth, L., Aguilar, R., Martén-Rodríguez, S., Lopezaraiza-Mikel, M., Avila-Sakar, G., Rosas-Guerrero, V., Quesada, M., 2015b. Pollination syndromes: a global pattern of convergent evolution driven by the most effective pollinator. In: Pontarotti, P. (Ed.), *Evolutionary Biology: Biodiversification from Genotype to Phenotype*. Springer International Publishing, Switzerland, pp. 203–224.
- Astegiano, J., Massol, F., Vidal, M.M., Cheptou, P.O., Guimarães Jr., P.R., 2015. The robustness of plant-pollinator assemblages: linking plant interaction patterns and sensitivity to pollinator loss. *PLoS One* 10, e0117243.
- Auld, J.R., de Casas, R.R., 2013. The correlated evolution of dispersal and mating-system traits. *Evol. Biol.* 40, 185–193.
- Baker, H.G., 1955. Self-compatibility and establishment after “long-distance” dispersal. *Evolution* 9, 347–349.
- Barabási, A.L., Albert, R., 1999. Emergence of scaling in random networks. *Science* 286, 509–512.
- Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S., Winfree, R., 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci. U.S.A.* 108, 20645–20649.
- Bascompte, J., Jordano, P., 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38, 567–593.
- Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. U.S.A.* 100, 9383–9387.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.T., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354.
- Blüthgen, N., 2010. Why network analysis is often disconnected from community ecology: a critique and an ecologist’s guide. *Basic Appl. Ecol.* 11, 185–195.
- Blüthgen, N., Klein, A.M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant-pollinator interactions. *Basic Appl. Ecol.* 12, 282–291.
- Bohan, D.A., Raybould, A., Mulder, C., Woodward, G., Tamaddoni-Nezhad, A., Blüthgen, N., Pocock, M.J.O., Muggleton, S., Evans, D.M., Astegiano, J.,

- Massol, F., Loeuille, N., Petit, S., Macfadyen, S., 2013. Networking agroecology: integrating the diversity of agroecosystem interactions. *Adv. Ecol. Res.* 49, 1–67. Chapter one.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I., Öckinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. Lond. B* 277, 2075–2082.
- Bond, W.J., 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philos. Trans. R. Soc. Lond. B* 344, 83–90.
- Breed, M.F., Gardner, M.G., Ottewell, K.M., Navarro, C.M., Lowe, A.J., 2012. Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany. *Ecol. Lett.* 15, 444–452.
- Brualdì, R.A., Ryser, H.J., 1991. Combinatorial Matrix Theory. Cambridge University Press, Cambridge, UK.
- Cagnolo, L., Cabido, M., Valladares, G., 2006. Plant species richness in the Chaco Serrano woodland from central Argentina: ecological traits and habitat fragmentation effects. *Biol. Conserv.* 132, 510–519.
- Cagnolo, L., Valladares, G., Salvo, A., Cabido, M., Zak, M., 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conserv. Biol.* 23, 1167–1175.
- Calcagno, V., Massol, F., Mouquet, N., Jarne, P., David, P., 2011. Constraints on food chain length arising from regional metacommunity dynamics. *Proc. R. Soc. Lond. B* 278, 3042–3049.
- Carlquist, S., 1966. The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. *Evolution* 20, 30–48.
- Cheptou, P.-O., 2012. Clarifying Baker's Law. *Ann. Bot.* 109, 633–641.
- Cheptou, P.-O., Massol, F., 2009. Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *Am. Nat.* 174, 46–55.
- Cheptou, P.-O., Carrue, O., Rouifed, S., Cantarel, A., 2008. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proc. Natl. Acad. Sci. U.S.A.* 105, 3796–3799.
- Chung, F., Lu, L., Vu, V., 2003. Spectra of random graphs with given expected degrees. *Proc. Natl. Acad. Sci.* 100, 6313–6318.
- Cohen, R., Erez, K., ben-Avraham, D., Havlin, S., 2000. Resilience of the internet to random breakdowns. *Phys. Rev. Lett.* 85, 4626–4628.
- Cohen, R., Erez, K., ben-Avraham, D., Havlin, S., 2001. Breakdown of the internet under intentional attack. *Phys. Rev. Lett.* 86, 3682–3685.
- Comins, H.N., Hamilton, W.D., May, R.M., 1980. Evolutionarily stable dispersal strategies. *J. Theor. Biol.* 82, 205–230.
- Cordeiro, N.J., Dangalasi, H.J., McEntee, J.P., Howe, H.F., 2009. Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90, 1030–1041.
- Diaz, S., Fargione, J., Chapin III, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. *PLoS Biol.* 4, e277.
- Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P., Pearse, W.D., 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* 3, 2958–2975.
- Dorman, C.F., Fründ, J., Blüthgen, N., Gruber, B., 2009. Indices, graphs and null models: analysing bipartite ecological networks. *Open Ecol. J.* 2, 7–24.
- Ebeling, A., Klein, A.M., Tscharntke, T., 2011. Plant–flower visitor interaction webs: temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic Appl. Ecol.* 12, 300–309.

- Eckert, C.G., Kalisz, S., Geber, M.A., Sargent, R., Elle, E., Cheptou, P.-O., Goodwillie, C., Johnston, M.O., Kelly, J.K., Moeller, D.A., Porcher, E., Ree, R., Vallejo-Marín, M., Winn, A.A., 2010. Plant mating systems in a changing world. *Trends Ecol. Evol.* 25, 35–43.
- Ehrlén, J., Eriksson, O., 2000. Dispersal limitations and patch occupancy in forest herbs. *Ecology* 81, 1667–1674.
- Eilers, E.J., Kremen, C., Greenleaf, S.S., Garber, A.K., Klein, A.M., 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS One* 6, e21363.
- Eklöf, A., Kaneryd, L., Münger, P., 2012. Climate change in metacommunities: dispersal gives double-sided effects on persistence. *Proc. R. Soc. Lond. B* 367, 2945–2954.
- Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *J. Appl. Ecol.* 47, 459–467.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* 1, 488–494.
- Evju, M., Blumentrath, S., Skarpaas, O., Stabbetorp, O.E., Sverdrup-Thygeson, A., 2015. Plant species occurrence in a fragmented grassland landscape: the importance of species traits. *Biodivers. Conserv.* 24, 547–561.
- Fabian, Y., Sandau, N., Bruggisser, O.T., Aebi, A., Kehrli, P., Rohr, R.P., Naisbit, R.E., Bersier, L.-F., 2013. The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem. *J. Anim. Ecol.* 82, 1203–1214.
- Fægri, K., van der Pijl, L., 1979. *The Principles of Pollination Ecology*, third rev. ed. Pergamon Press, Oxford.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* 34, 487–515.
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015.
- Fakheran, S., Paul-Victor, C., Heichinger, C., Schmid, B., Grossniklaus, U., Turnbull, L.A., 2010. Adaptation and extinction in experimentally fragmented landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 107, 19120–19125.
- Ferreira, P.A., Boscolo, D., Carvalheiro, L.G., Biesmeijer, J.C., Rocha, P.L., Viana, B.F., 2015. Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest. *Landsc. Ecol.* 30, 1–12.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280.
- Fleming, T.H., Sahley, C.T., Holland, J.N., Nason, J.D., Hamrick, J.L., 2001. Sonoran Desert columnar cacti and the evolution of generalized pollination systems. *Ecol. Monogr.* 71, 511–530.
- Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol.* 4, e1. <http://dx.doi.org/10.1371/journal.pbio.0040001>.
- Fortuna, M.A., Bascompte, J., 2006. Habitat loss and the structure of plant-animal mutualistic networks. *Ecol. Lett.* 9, 281–286.
- Fortuna, M.A., Krishna, A., Bascompte, J., 2013. Habitat loss and the disassembly of mutualistic networks. *Oikos* 122, 938–942.
- Fumero-Cabán, J.J., Meléndez-Ackerman, E.J., 2007. Relative pollination effectiveness of floral visitors of *Pitcairnia angustifolia* (Bromeliaceae). *Amer. J. Bot.* 94, 419–424.
- Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.S., Pires, M.M., Guimarães Jr., P.R., Brancalion, P.H., Ribeiro, M.C., Jordano, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340, 1086–1089.

- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.
- Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Kremen, C., Morandin, L., Scheper, J., Winfree, R., 2014. From research to action: enhancing crop yield through wild pollinators. *Front. Ecol. Environ.* 12, 439–447.
- Garibaldi, L.A., Bartomeus, I., Bommarco, R., Klein, A.M., Cunningham, S.A., Aizen, M.A., Boreux, V., Garratt, M.P.D., Carvalheiro, L.G., Kremen, C., Morales, C.L., Schüepp, C., Chacoff, N.P., Freitas, B.M., Gagic, V., Holzschuh, A., Klatt, B.K., Krewenka, K.M., Krishnan, S., Mayfield, M.M., Motzke, I., Otieno, M., Petersen, J., Potts, S.G., Ricketts, T.H., Rundlöf, M., Sciligo, A., Sinu, P.A., Steffan-Dewenter, I., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2015. Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *J. App. Ecol.* in press.
- Gill, R.J., Baldock, K.C.R., Brown, M.J.F., Cresswell, J.E., Dicks, L.V., Fountain, T., Garratt, M.P.D., Gough, L.A., Heard, M.S., Holland, J.M., Ollerton, J., Stone, G.N., Tang, C.Q., Vanbergen, A.J., Vogler, A.P., Woodward, G., Arce, A.N., Boatman, N.D., Brand-Hardy, R., Breeze, T.D., Green, M., Hartfield, C.M., O'Connor, R.S., Osborne, J.L., Phillips, J., Sutton, P.B., Potts, S.G., 2016. Protecting an ecosystem service: Approaches to understanding and mitigating threats to wild insect pollinators. *Adv. Ecol. Res.* 54, in press.
- Girão, L.C., Lopes, A.V., Tabarelli, M., Bruna, E.M., 2007. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. *PLoS One* 2, e908.
- Gonzalez, A., Rayfield, B., Lindo, Z., 2011. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. *Am. J. Bot.* 98, 503–516.
- González-Varo, J.P., González-Albaladejo, R., Aparicio-Martínez, A., Arroyo-Marin, J., 2010. Linking genetic diversity, mating patterns and progeny performance in fragmented populations of a mediterranean shrub. *J. Appl. Ecol.* 47, 1242–1252.
- González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H.G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M., Vilà, M., 2013. Combined effects of global change pressures on animal-mediated pollination. *Trends Ecol. Evol.* 28, 524–530.
- Goodwillie, C., Kalisz, S., Eckert, C.G., 2005. The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. *Annu. Rev. Ecol. Syst.* 36, 47–79.
- Guimarães Jr., P.R., Jordano, P., Thompson, J.N., 2011. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14, 877–885.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.E., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C., King, A., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D., Townsend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science* 1, e1500052.

- Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biol. Rev.* 87, 526–544.
- Hagen, M., Kissling, D.W., Rasmussen, C., Carstensen, D.W., Dupont, Y.L., Kaiser-Bunbury, C.N., O'Gorman, E.J., Olesen, J.M., De Aguiar, M.A.M., Brown, L.E., Alves-Dos-Santos, I., Guimarães Jr., P.R., Maia, K.P., Marquitti, F.M.D., Vidal, M.M., Edwards, F.K., Genini, J., Jenkins, G.B., Trøjelsgaard, K., Woodward, G., Jordano, P., Ledger, M.E., McLaughlin, T., Morellato, L.P.C., Tylianakis, J.M., 2012. Biodiversity, species interactions and ecological networks in a fragmented world. *Adv. Ecol. Res.* 46, 89–120.
- Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404, 755–758.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* 12, 184–195.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* 8, 23–29.
- Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 2283–2291.
- Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. Lond. B* 278, 3444–3451.
- Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids?. *J. Anim. Ecol.* 79, 491–500.
- James, A., Pitchford, J.W., Plank, M.J., 2012. Disentangling nestedness from models of ecological complexity. *Nature* 487, 227–230.
- Jauker, B., Krauss, J., Jauker, F., Steffan-Dewenter, I., 2013. Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landsc. Ecol.* 28, 107–120.
- Jenkins, D.G., 2011. Ranked species occupancy curves reveal common patterns among diverse metacommunities. *Glob. Ecol. Biogeogr.* 20, 486–497.
- Johnson, S.D., Steiner, K.E., 2000. Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* 15, 140–143.
- Jordano, P., 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *Am. Nat.* 129, 657–677.
- Jordano, P., Bascompte, J., Olesen, J.M., 2003. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* 6, 69–81.
- Kaiser-Bunbury, C.N., Blüthgen, N., 2015. Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants* 7, plv076.
- Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B., Caflisch, A., 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* 13, 442–452.
- Keitt, T.H., 2009. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol. Appl.* 19, 1561–1573.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundløf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee, A.N.,

- Ascher, J.S., Baldi, A., Batary, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Feon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlof, M., Sardinas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissiere, B.E., Veldtman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6, 7414. <http://dx.doi.org/10.1038/ncomms8414>.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci.* 274 (1608), 303–313.
- Klein, A.M., Cunningham, S.A., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. *Ecology* 89, 935–943.
- Koh, I., Reineking, B., Park, C.R., Lee, D., 2015. Dispersal potential mediates effects of local and landscape factors on plant species richness in maeulsoop forests of Korea. *J. Veg. Sci.* 26, 631–642.
- Kotiaho, J.S., Kaitala, V., Komonen, A., Päivinen, J., 2005. Predicting the risk of extinction from shared ecological characteristics. *Proc. Natl. Acad. Sci. U.S.A.* 102, 1963–1967.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkilä, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* 13, 597–605.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change.. *Ecol. Lett.* 10, 299–314.
- Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. Lond. B* 274, 303–313.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* 7, 1109–1119.
- Laliberte, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Sánchez Merlos, D., Vesk, D.A., Mayfield, M.M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.* 13, 76–86.
- Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* 8, 538–547.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L., Capretz, R.L., 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87, 469–482.
- Lavorel, S., Storkey, J., Bardgett, R.D., Bello, F., Berg, M.P., Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S., Harrington, R., 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.* 24, 942–948.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004.

- The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613.
- Lever, J.J., Nes, E.H., Scheffer, M., Bascompte, J., 2014. The sudden collapse of pollinator communities. *Ecol. Lett.* 17, 350–359.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240.
- Lloyd, D.G., 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *Int. J. Plant Sci.* 153, 370–380.
- Lobo, D., Leao, T., Melo, F.P.L., Santos, A.M.M., Tabarelli, M., 2011. Forest fragmentation drives Atlantic forest of north-eastern Brazil to biotic homogenization. *Divers. Distrib.* 17, 287–296.
- Magrach, A., Laurance, W.F., Larrinaga, A.R., Santamaria, L., 2014. Meta-analysis of the effects of forest fragmentation on interspecific interactions. *Conserv. Biol.* 28, 1342–1348.
- Martén Rodríguez, S.M., Quesada, M., Castro, A.A., Lopezaraiza-Mikel, M., Fenster, C.B., 2015. A comparison of reproductive strategies between island and mainland Caribbean Gesneriaceae. *J. Ecol.* 103, 1190–1204.
- Massol, F., Débarre, F., 2015. Evolution of dispersal in spatially and temporally variable environments: the importance of life cycles. *Evolution* 69 (7), 1925–1937.
- Massol, F., Petit, S., 2013. Interaction networks in agricultural landscape mosaics. *Adv. Ecol. Res.* 49, 291–338.
- Mathiasen, P., Rovere, A.E., Premoli, A.C., 2007. Genetic structure and early effects of inbreeding in fragmented temperate forests of a self-incompatible tree, *Embothrium coccineum*. *Conserv. Biol.* 21, 232–240.
- Matlab, 2011. The MathWorks, Inc., Natick, MA, United States.
- McEuen, A.B., Curran, L.M., 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. *Ecology* 85, 507–518.
- MEA (Millennium Ecosystem Assessment), 2005. *Ecosystems and Human Well-Being: A Framework for Assessment*. Island Press, Washington, DC.
- Melián, C.J., Bascompte, J., 2002. Food web structure and habitat loss. *Ecol. Lett.* 5, 37–46.
- Melo, F.P.L., Martínez-Salas, E., Benítez-Malvido, J., Ceballos, G., 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. *J. Trop. Ecol.* 26, 35–43.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B* 271, 2605–2611.
- Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.* 10, 710–717.
- Miklós, I., Podani, J., 2004. Randomization of presence-absence matrices: comments and new algorithms. *Ecology* 85, 86–92.
- Miller-Rushing, A.J., Inouye, D.W., 2009. Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wild-flower species. *Am. Nat.* 96, 1821–1829.
- Mitchell, M.G.E., Bennett, E.M., Gonzalez, A., 2015a. Strong and nonlinear effects of fragmentation on ecosystem service provision at multiple scales. *Environ. Res. Lett.* 10, 094014.
- Mitchell, M.G.E., Suarez-Castro, A.F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K.J., Johansen, K., Rhodes, J.R., 2015b. Reframing landscape fragmentation's effects on ecosystem services. *Trends Ecol. Evol.* 30, 190–198.
- Morris, W.F., 2003. Which mutualists are most essential? Buffering of plant reproduction against the extinction of pollinators. In: Kareiva, P., Levin, S.A. (Eds.), *The Importance of Species: Perspectives on Expendability and Triage*. Princeton University Press, Princeton, pp. 260–280.

- Mouquet, N., Matthiessen, B., Miller, T., Gonzalez, A., 2011. Extinction debt in source-sink metacommunities. *PLoS One* 6, e17567.
- Mulder, C., Aldenberg, T., De Zwart, D., Van Wijnen, H.J., Breure, A.M., 2005. Evaluating the impact of pollution on plant-Lepidoptera relationships. *Environmetrics* 16, 357–373.
- Mulder, C., Boit, A., Mori, S., Vonk, J.A., Dyer, S.D., Faggiano, L., Geisen, S., González, A.L., Kaspari, M., Lavorel, S., Marquet, P.A., Rossberg, A.G., Sterner, R.W., Voigt, W., Wall, D.H., 2012. Distributional (in)congruence of biodiversity–ecosystem functioning. *Adv. Ecol. Res.* 46, 1–88.
- Nee, S., May, R.M., 1992. Dynamics of metapopulation: habitat destruction and competitive coexistence. *J. Anim. Ecol.* 61, 37–40.
- Nielsen, A., Bascompte, J., 2007. Ecological networks, nestedness and sampling effort. *J. Ecol.* 95, 1134–1141.
- Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Poiry, J., Settele, J., Summerville, K.S., Bommarco, R., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol. Lett.* 13, 969–979.
- Okuyama, T., Holland, J.N., 2008. Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.* 11, 208–216.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *Proc. Natl. Acad. Sci. U.S.A.* 104, 19891–19896.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Podani, J., Schmera, D., 2012. A comparative evaluation of pairwise nestedness measures. *Ecography* 35, 889–900.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.
- Réjou-Méchain, M., Cheptou, P.-O., 2015. High incidence of dioecy in young successional tropical forests. *J. Ecol.* 103, 725–732.
- Renner, S.S., 1998. Effects of habitat fragmentation on plant-pollination interactions in the tropics. In: Newbery, D.M., Prins, H.H.T., Brown, N.D. (Eds.), *Dynamics of Tropical Communities*. Blackwell Science, London, pp. 339–360.
- Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P., Bascompte, J., 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448, 925–928.
- Richards, A.J., 1997. *Plant Breeding Systems*, second ed. Chapman & Hall, London.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A., Mayfield, M.M., Morandin, L.A., Ochieng, A., Viana, V.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11, 499–515.
- Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. *Science* 345, 1253497.
- Sabatino, M., Maceira, N., Aizen, M.A., 2010. Direct effects of habitat area on interaction diversity in pollination webs. *Ecol. Appl.* 20, 1491–1497.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., et al., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. *Ecol. Lett.* 16, 912–920.
- Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T., Schaminée, J.H., Spiepel, H., Kleijn, D., 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proc. Natl. Acad. Sci. U.S.A.* 111, 17552–17557.

- Spiesman, B.J., Inouye, B.D., 2013. Habitat loss alters the architecture of plant–pollinator interaction networks. *Ecology* 94, 2688–2696.
- Steffan-Dewenter, I., Tscharntke, T., 2002. Insect communities and biotic interactions on fragmented calcareous grasslands—a mini review. *Biol. Conserv.* 104, 275–284.
- Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* 20, 651–652.
- Suweis, S., Simini, F., Banavar, J.R., Maritan, A., 2013. Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature* 500, 449–452.
- Tabarelli, M., Mantovani, W., Peres, C.A., 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biol. Conserv.* 91, 119–127.
- Thébaud, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 351, 65–66.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., et al., 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biol. Rev.* 87, 661–685.
- Tur, C., Castro-Urgal, R., Traveset, A., 2013. Linking plant specialization to dependence in interactions for seed set in pollination networks. *PLoS One* 8, e78294.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Conserv.* 143, 2270–2279.
- Urban, M.C., Leibold, M.A., Amarasekare, P., De Meester, L., Gomulkiewicz, R., Hochberg, M.E., et al., 2008. The evolutionary ecology of metacommunities. *Trends Ecol. Evol.* 23, 311–317.
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307.
- van der Niet, T.A., Johnson, S.D., 2012. Phylogenetic evidence for pollinator-driven diversification of angiosperms. *Trends Ecol. Evol.* 27, 353–361.
- Vázquez, D.P., 2005. Degree distribution in plant–animal mutualistic networks: forbidden links or random interactions? *Oikos* 108, 421–426.
- Vázquez, D.P., Aizen, M.A., 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. *Ecology* 85, 1251–1257.
- Vieira, M.C., Almeida-Neto, M., 2015. A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. *Ecol. Lett.* 18, 144–152.
- Vogler, D.W., Kalisz, S., 2001. Sex among the flowers: the distribution of plant mating systems. *Evolution* 55, 202–204.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems, and why it matters. *Ecology* 77, 1043–1060.
- Wilcock, C., Neiland, R., 2002. Pollination failure in plants: why it happens and when it matters. *Trends Plant Sci.* 7, 270–277.
- Williams, N.M., Crone, E.E., Tai, H.R., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143, 2280–2291.
- Willson, M., Traveset, A., 2000. The ecology of seed dispersal. In: Fenner, M. (Ed.), *The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 85–110.
- Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076.