Drivers of variability in plant-pollinatorand host-parasitoid communities: effects on interaction network structure and ecosystem function

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Drivers of variability in plant-pollinator and host-parasitoid communities: effects on interaction network structure and ecosystem function

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A Alba,

el mayor descubrimiento de mi tesis doctoral.

“Quiero decir unas palabras a favor de la Naturaleza,

de la libertad absoluta y del estado salvaje”

H.D. Thoreau, Caminar, 1851

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Empiezo esta sección con una definición de la disciplina que se trata: la Ecología es historia natural científica (Wheelwright y Heinrich, 2017). Adentrarse humildemente en el entorno y vestirse de paciente observación, aprender y generar conocimiento así. Para mí, la belleza y la nobleza de la ciencia, así como la virtud del científico, reside en hacer las cosas con este rigor.

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10 años de formación y profesión en la universidad dan para generar identidad y valores. Creo que después de suplir nuestras necesidades básicas lo único que puede elevar el espíritu humano es el conocimiento, y el oficio de estudiante e investigador no puede ser mejor para tal fin. La libertad absoluta y la felicidad extrema pasan por comprender el mundo.

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Cerdanyola, 1.VI.20

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General Abstract

Ecological communities are dynamic entities whose structure and composition are shaped by ecological processes and environmental variability. Because species interact with one another, changes in community structure and composition are likely to alter interaction networks and ecosystem functioning. In this thesis I study how an ecological process (the colonization of a habitat by a new species) and an important component of spatial variability (habitat area) affect pollinator and bee-wasp communities and their mutualistic and antagonistic interactions. I also investigate whether these changes affect interaction network structure and the potential consequences on ecosystem function (pollination, plant reproduction, and parasitism).

Changes in plant community composition are becoming increasingly frequent in the current context of pervasive biological invasions. However, plant invasions usually represent extreme scenarios of ecological dominance and their effects have been relatively well studied. By contrast, the effects of habitat colonization by native species (for example, as a result of changes in geographical distribution mediated by climate change) have received much less attention.

In Chapter 1 we analyze the effects of the arrival of a new native plant into a scrubland community, including changes in pollinator community composition, plant–pollinator interaction patterns and network structure, and the consequences for pollination and reproductive success of resident plant species. To do so, we experimentally manipulated patches of scrubland by introducing a native plant (henceforth colonizing plant), adjusting the number of flowers introduced to the amount of floral resources locally available. The colonizing plant attracted bumblebees, facilitating interactions to resident

plants. Colonized communities exhibited higher network generalization, nestedness, and modifications in the composition of network modules. All these changes resulted in higher heterospecific (but not conspecific) pollen deposition and had contrasting effects on the reproductive success of resident plants (neutral, positive, or negative depending on the species). Our study shows that plant-pollinator interactions are rapidly rearranged in response to novel situations (even when the new plant is not overly dominant), with important functional consequences on pollination and plant reproduction.

The species-area relationship (increasing species richness with area) is one of the oldest and most fundamental laws in Ecology and, in recent years, has extended to interaction richness (link-area relationship) and network structure (network-area relationship). However, although the species- and link-area relationships have received ample support from empirical studies, the relationship between network structure and area remains largely unexplored. Understanding this relationship is important because anthropogenic habitat fragmentation is having a profound impact on habitat configuration and effectively reducing the size of natural habitats.

In Chapter 2 we test several hypothesis related to the species-area, link-area and network-area relationships using cavity-nesting bee-wasp communities and their nest associates (henceforth hosts and parasitoids, respectively), as a study system. To obtain bee-wasp nests we set up nest-trapping stations in patches of (favorable) open habitat - surrounded by dense forest (unfavorable habitat)- of three size categories (small, ~0.1 ha; medium, ~5 ha; and large, continuous open habitat). The nests obtained in each patch were dissected and their contents analyzed by noting the identity and abundance of each host and parasitoid species. Host, parasitoid, and interaction richness increase from small to medium patches, but not from medium to large patches. Links per species

increased with patch size, but parasitism rate did not follow any patch-size-mediated trend. Network specialization decreased from small to medium patches, but large patches showed similar specialization to that of small and medium patches. Modularity decreased from small to medium patches but there were no differences between medium and large patches. The number of modules increased with patch size. Our results are mostly in partial agreement with the species-area and the link-area relationships. The lack of differences between medium and large patches indicates the existence of a threshold above which local species/link richness are no longer limited by habitat size, with important implications for conservation. On the other hand, our results are mostly in disagreement with the predictions of the network-area relationship. We suggest that community impoverishment in small patches results in limited host choice by generalist parasitoids, leading to high levels of ecological specialization and modularity.

Changes in plant composition are expected to affect plant-pollinator communities in multiple ways depending on the flower context, the relative abundance of the colonizing plant, its degree of generalization, and its pollination syndrome. Facilitation or competition for pollinators may result in predictable responses in network structure and pollination, but the effects on plant reproduction are expected to be highly contingent on each species. Habitat size is expected to affect species and interactions following the species-area and the link-area relationships. Merging empirical evidence with theoretical predictions, we developed a framework for the network-area relationship. Mutualistic and antagonistic network responses to changes are predictable. However, consequences on ecosystem function remain highly contingent.

Resumen General

Las comunidades ecológicas son entidades dinámicas cuya estructura y composición está conformada por procesos ecológicos y por variabilidad ambiental. Debido a que las especies interaccionan entre ellas, los cambios en la estructura y composición de las comunidades pueden alterar las redes de interacción y el funcionamiento de los ecosistemas. En esta tesis estudio cómo un proceso ecológico (la colonización de un hábitat por una nueva especie) y un componente importante de la variabilidad espacial (el tamaño del hábitat) afecta a las comunidades de polinizadores, de abejas y avispas, así como a sus interacciones mutualistas y antagonistas. También investigo si estos cambios afectan a la estructura de la red de interacciones y las consecuencias potenciales sobre la función ecosistémica (polinización, reproducción de las plantas, y parasitismo).

Los cambios en la composición de las comunidades de plantas son cada vez más frecuentes en el contexto actual de las invasiones biológicas. Sin embargo, las invasiones de plantas normalmente representan escenarios extremos de dominancia ecológica y sus efectos han sido estudiados relativamente bien. Por el contrario, los efectos de la colonización de los hábitats por especies autóctonas (por ejemplo, como resultado de los cambios en la distribución geográfica mediados por el cambio climático) han recibido mucha menos atención.

En el Capítulo 1 analizamos los efectos de la llegada de una nueva especie de planta autóctona en un matorral, incluyendo los cambios en la composición de la comunidad de polinizadores, los patrones de interacción y la estructura de la red planta-polinizador, y las consecuencias para la polinización y para el éxito reproductivo de las especies de

plantas residentes. Para ello manipulamos experimentalmente parches de matorral introduciendo una planta autóctona (planta colonizadora de ahora en adelante), ajustando el número de flores introducidas a la cantidad de recursos florales localmente disponibles. La planta colonizadora atrajo a abejorros, facilitando las interacciones a las plantas residentes. Las comunidades colonizadas exhibieron una mayor generalización de la red, un mayor anidamiento, y modificaciones en la composición de los módulos de la red. Todos estos cambios resultaron en una mayor deposición de polen heteroespecífico (pero no conespecífico) y tuvo efectos contrastados en el éxito reproductivo de las plantas residentes (neutral, positivo, o negativo dependiendo de la especie). Nuestro estudio muestra que las interacciones planta-polinizador se reorganizan rápidamente en respuesta a nuevas situaciones (incluso cuando la nueva planta no es excesivamente dominante), con consecuencias funcionales importantes en la polinización y en la reproducción de las plantas.

La relación especies-área (incremento de la riqueza de especies con el área) es una de las leyes de la Ecología más antiguas y fundamentales y, recientemente, ha sido extendida a la riqueza de interacciones (relación enlaces-área) y a la estructura de la red (relación red-área). Sin embargo, a pesar que las relaciones especies- y enlaces- área han recibido un soporte amplio de estudios empíricos, la relación entre la estructura de la red y el área permanece en gran parte inexplorada. Entender esta relación es importante porque la fragmentación antropogénica de los hábitats está teniendo impactos profundos en la configuración de los hábitats y está reduciendo el tamaño de los mismos.

En el Capítulo 2 testamos varias hipótesis relacionadas con las relaciones especies-área, enlaces-área y red-área utilizando comunidades de abejas y avispas nidificantes en cavidades preestablecidas así como la fauna asociada a sus nidos (huéspedes y parasitoides de ahora en adelante, respectivamente) como sistema de estudio. Para obtener nidos de abejas y avispas instalamos estaciones de nidales en parches de hábitat abierto (favorable) –rodeados por bosque denso (hábitat desfavorable)- de tres categorías de tamaño (pequeños, ~0.1 ha; medianos, ~5 ha; y grandes, hábitat abierto continuo). Los nidos obtenidos en cada parche fueron diseccionados y sus contenidos fueron analizados anotando la identidad y la abundancia de cada especie de huésped y parasitoide. La riqueza de huéspedes, parasitoides, e interacciones incrementó de los parches pequeños a los medianos, pero no de los parches medianos a los grandes. Los enlaces por especie incrementaron con el tamaño del parche, pero la tasa de parasitismo no siguió ninguna tendencia relacionada con el tamaño del hábitat. La especialización de la red disminuyó de los parches pequeños a los medianos, pero los parches grandes mostraron una especialización similar a la de los parches pequeños y medianos. La modularidad disminuyó de los parches pequeños a los medianos, pero no hubo diferencias entre los parches medianos y los grandes. El número de módulos incrementó con el tamaño del parche. Nuestros resultados están, en su mayor parte, parcialmente de acuerdo con las relaciones especies-área y enlaces-área. La ausencia de diferencias entre los parches medianos y grandes indica la existencia de un umbral por encima del cual la riqueza de especies y de interacciones ya no está limitada por el tamaño del hábitat, con implicaciones importantes para la conservación. Por otro lado, nuestros resultados están mayoritariamente en desacuerdo con las predicciones de la relación red-área. Sugerimos que el empobrecimiento de las comunidades en los parches pequeños resulta en una limitación en la elección de los huéspedes por parte de los parasitoides generalistas, dando lugar a altos niveles de especialización ecológica y de modularidad.

Se espera que los cambios en la composición de plantas afecten a las comunidades planta-polinizador de múltiples maneras dependiendo del contexto floral, de la abundancia relativa de la planta colonizadora, de su grado de generalización, y de su síndrome floral. La facilitación o la competencia por los polinizadores pueden resultar en cambios predecibles en la estructura de la red y en la polinización, pero se espera que los efectos sobre la reproducción de las plantas sean altamente contingentes en cada especie. Se espera que el tamaño del hábitat afecte a las especies y a las interacciones siguiendo las relaciones especies-área y enlaces-área. Uniendo las evidencias empíricas con las predicciones teóricas, desarrollamos un marco de referencia para la relación red-área. Las respuestas de las redes mutualistas y antagonistas a los cambios son predecibles. Sin embargo, las consecuencias sobre la función ecosistémica siguen siendo altamente contingentes.

GENERAL INTRODUCTION

Variability in ecological communities

Ecological communities are not static, but dynamic entities which show high levels of variation in space and time. At the global scale, evolution and climate are the main determinants of biogeographical species distribution patterns (Pianka 1982). At finer scales, *e.g.* regional or local, ecological processes and environmental variation are at play, originating important changes in community structure and composition over relatively small distances and short periods of time (Levin 1992).

On the one hand, ecological processes may induce changes in community composition. Communities are open to the arrival of new species (colonization), as a result of foraging and dispersal events (*e.g.* Stefanescu et al. 2017). At the same time, some species may become locally extinct, as a result of migration or mortality (Hanski 1999). Human-induced processes may also originate changes in community composition. These include biological invasions, which represent extreme cases of community structure modification (Shea and Chesson 2002), but also more gradual, long-term changes such as those mediated by shifts in the geographical distribution of species as a response to climate change (Chen et al. 2011).

On the other hand, environmental variation may determine community variability across space and time. The amount of resources and the quality and diversity of habitats determine how many individuals and species may inhabit a given area (Lawton 1999). However, physical barriers such as water bodies and geographical accidents may limit species dispersal and therefore species occurrence (Post et al. 2007). For these reasons, landscape composition and landscape structure are good predictors of community assemblage (*e.g.* Holzschuh et al. 2007). In addition, ecological communities also show variation within uniform habitats and across the year as a consequence of variability in microhabitat conditions and phenology (Herrera 1988, Bosch et al. 1997, Reverté et al. 2019). Again, human-induced environmental variation may also influence community variability. Habitat fragmentation and habitat loss usually lead to community simplification (Fahrig 2003, Tscharntke et al. 2012), whereas other long-term processes such as deforestation-aforestation dynamics (*e.g.* Cervera et al. 2019) may negatively affect some species while favoring others.

Related changes in ecological interactions and ecosystem function

Because species are not isolated but interact among themselves, changes in community composition may affect species interactions. In turn, because species interactions determine community dynamics (*e.g.* predator-prey dynamics), changes in species interactions may have cascading effects on community structure and composition, ultimately altering ecosystem function (Chapin et al. 1997).

Colonization – extinction dynamics produce new combinations of species that may lead to changes in species interactions, promoting competitive exclusion or changes in mutualistic or predatory relationships, modifying species abundances (Paine 1966, Laverty 1992). For instance, the frequent colonization of ecological communities by preys as a result of windborne transport and life-history movements usually fuels local food webs (Polis et al. 1997). This may originate top-down effects, in which an increase in predator abundance strengthens predator-prey interactions, leading to the extinction of local preys (Polis et al. 1997). Similarly, introduction or extirpation of predators in ecological communities may have dramatic consequences on ecological communities, altering food web structure and changing ecosystem function (Carpenter et al. 1987, Witte et al. 1992, Bergstrom et al. 2009). Sudden extinction of a species may originate secondary extinctions of specialist partners as well as negative effects on opportunistic ones (Harrison 2000). Species extirpation may also promote generalized changes in interaction patterns, a situation that may result in profound changes in ecosystem function (Brosi and Briggs 2013, Biella et al. 2019).

Variation in species assemblages across space as a consequence of environmental variation drives differences in species interactions between contrasting habitats (*e.g.* Kruess 2003), but also across a region and even at small spatial scales (Trøjelsgaard et al. 2015, Torné-Noguera et al. 2020). In turn, different interactions may generate different ecological outputs (*e.g.* reproductive success) across space (Gómez et al. 2010), with important consequences on evolutionary dynamics (Thompson 1982, Gómez et al. 2009).

Habitat size is a major component of spatial variability, that not only affects ecological communities through the number of individuals and species that can inhabit a given area. Due to energetic constraints, food webs are shortened in small habitats (Schoener 1989). For example, no large predators are found in small habitats. This important effect of environmental variation on food web structure has direct consequences on species interactions and derived ecosystem functions. Because higher trophic levels are more affected by habitat size than lower trophic levels (Holt et al. 1999), not only communities but also interactions are impoverished in small habitats (Brose et al. 2004), resulting in lower levels of ecosystem functionality (Aizen and Feinsinger 1994, Kruess and Tscharntke 1994).

Ecological networks: disentangling Darwin's entangled bank

Traditionally, ecologists have studied ecological interactions between pairs of species in relatively simple multi-species systems. In the last decades, though, ecological research has moved to study the organization and the interdependencies of all interactions involving all species present in ecological communities, *i.e.*, ecological networks (Proulx et al. 2005, Montoya et al. 2006, Bascompte et al. 2009).

An ecological network is a set of nodes (one for each species in the community) connected by edges (each interaction between species of the community). To characterize and study ecological networks several network metrics have been developed. These include metrics analogous to those used in the study of community structure, such as interaction richness and interaction diversity, but also other metrics that only apply to networks. These second group includes statistics that examine the properties of individual nodes (*e.g.*, species closeness, a measure of species centrality in the network), as well as statistics that examine the aggregate properties of all nodes (*e.g.*, network specialization, a measure of resource use at the community level) (Dormann et al. 2008). These new methods have been extensively used to characterize and study multiple types of networks, including mutualistic (*e.g.* plant-pollinator) and antagonistic (*e.g.* host-parasitoid) networks (Ings et al. 2009).

Network analysis has allowed ecologists to unveil generalized, recursive patterns in the topology of ecological networks (*i.e.*, network structure, or how interactions of ecological communities are organized), deciphering what has been called "the architecture of biodiversity" (Bascompte and Jordano 2007). The basic architecture of ecological networks can be summarized as follows: 1) networks are heterogeneous, *i.e.*, most species have few links and few species are highly connected (Jordano et al. 2003). In other words, the bulk of species are (or behave as) specialists, and there is a low proportion of generalist species; 2) Networks are asymmetric, *i.e.*, species A may strongly depend on species B, but species B does not necessarily depend strongly on species A (Bascompte et al. 2006); 3) Networks are nested, *i.e.*, specialist species interact with subsets of species with which generalist species interact (Bascompte et al. 2003). In other words, ecological networks are organized around a central core of supergeneralists species which interact with almost all the species in the community. Then, as the number of interaction partners decreases along the generalist-specialist continuum, the most specialist species only interact with supergeneralist species; 4) Networks are modular, *i.e.*, there are groups of species that interact frequently among them but rarely with the rest of species (Olesen et al. 2007). This produces a compartmentalized network structure of more or less independent groups of interacting partners. Some species may act as connectors, linking species from different compartments.

The ecological and evolutionary mechanisms that underlie these patterns include preferential attachment (new species tend to interact with most-connected ones), neutrality (abundant species interact with more species simply because they are abundant), and forbidden links (interaction constraints imposed by differences in spatial distribution, phenology and phenotype) (Barabasi and Albert 1999, Vázquez et al. 2009).

Several theoretical studies have demonstrated that network structure is essential for the stability of ecological communities. Generalist species usually act as keystone species in ecological communities. As a result, the extinction of highly connected species results in secondary extinctions and network collapse (Solé and Montoya 2001, Memmot et al. 2004). A similar pattern occurs when interactions between specialist species disappear (Santamaría et al. 2015). In a situation of system disassembly, species and overall network persistence may be enhanced if species are able to switch partners (rewiring) (Kaiser-Bunbury et al. 2010). Similarly, the existence of asymmetric dependencies between species favors species coexistence and prevents secondary extinctions and trophic cascades (Bascompte et al. 2005). Network nestedness promotes facilitation (sharing of interaction partners) between species in mutualistic networks, enhancing species richness and stability. Finally, network modularity (degree of compartmentalization) diminishes apparent competition between species in antagonistic networks, enhancing the stability of these communities (Bastolla et al. 2009, Thébault and Fontaine 2010).

Network analysis has also strengthened our understanding of the relationship between network structure and ecosystem function. Empirical studies suggest that individual and species centrality, as well as network connectivity and nestedness, are related to increased plant fitness in mutualistic networks (Gómez et al. 2011, Gómez and Perfectti 2012, Lázaro et al. 2020). Even then, examples of community-wide effects caused by changes in network structure remain scarce. The exclusion of native supergeneralist pollinators by a managed species reduced network nestedness, increased network modularity, and had negative effects on the reproduction of several plant species (Valido et al. 2019).

Thesis overview: general context, study system and background information

This thesis addresses how ecological processes (changes in species composition) and environmental variation (habitat size) shape ecological communities and the structure of their interaction networks, as well as related ecosystem functions. These aspects are of increasing interest in the current scenario of global change, because they are intimately related to climate change and habitat loss (Vitousek 1994). These two components of global change act both separately and synergistically, eroding biodiversity and affecting ecosystem functioning and services (Ehrlich and Wilson 1991, Brook et al. 2008, Cardinale et al. 2012).

We use pollinators in general and solitary bees and wasps in particular, as well as their mutualistic (plants) and antagonistic (parasitoids) partners, as a study models.

In Chapter 1 we address the effect of changes in plant species composition on pollinator communities, plant-pollinator interaction networks, pollination, and plant reproductive success.

Changes in species composition (both locally and regionally) are becoming more frequent in the context of climate change. Through its multiple manifestations (increased temperature and precipitation variability) climate change affects biodiversity from population genetics to biome integrity. Although species may respond in multiple manners (phenotypic plasticity, migration and adaptation), models suggest that climate change will result in a massive species extinction event (Bellard et al. 2012). A potential response of species facing climate change is to change their current geographical distribution to more bioclimatically suitable areas (Araújo and Rahbek 2006). Eventually, the arrival of a new species into an existing ecological community may change community structure and the ecological “theater” in which all species are embedded. Under this novel scenario, interacting species and the organization of these interactions may change (Lurgi et al. 2012), disturbing short-term ecological function and long-term coevolutionaty dynamics.

Pollinators include a wide range of animals, most of them insects (bees, butterflies, beetles, flies, etc.), but also vertebrates (mostly birds and bats) (Proctor et al. 1996, Ollerton 2017). Pollinators play a central role in ecosystem functioning, providing essential ecosystem services. They are responsible of the reproduction of the 87.5% of flowering plants world-wide (Ollerton et al. 2011). Pollinators engage in mutualistic interactions with plants, which are determined both by ecological factors and evolution (Waser and Ollerton 2006), generating complex interaction networks (Bascompte and Jordano et al. 2007).

How do changes in plant community composition affect pollinator communities, plant-pollinator interaction networks, and pollination? The vast literature addressing invasions of exotic plants provide a scenario of colonization of ecological networks (*see* Vanbergen et al. 2018). Invasive plants are usually pollinator-generalist species that are incorporated into ecological networks by native generalist pollinators (Traveset and Richardson 2006). They can attract pollinators to local communities, facilitating visitation to native plants, but can also compete for pollinators with resident species (Brown et al. 2002, Bartomeus et al. 2008, Molina-Montenegro et al. 2008). This scenario may lead pollinators to change their foraging decisions, altering interaction patterns and network structure (Ghazoul 2004, Aizen et al. 2008). In turn, these changes may alter pollen transfer patterns, with potential consequences on pollination and reproductive success of native plants (Lopezaraiza-Mikel 2007, Morales and Traveset

2009). However, plant invasions represent extreme cases of community dominance by a single species that often produces large amounts of floral resources in comparison to the native species (Chittka and Schürkens 2001, Vanbergen et al. 2018), making it difficult to discern between changes in community composition and changes in floral resources.

In this chapter we are interested in changes in plant community composition *per se* involving native species. Thus, our experiment is based on the manipulation of natural scrubland communities by introducing a native plant, while controlling for the amount of floral resources introduced.

In Chapter 2 we address the effect of variation in habitat size on host-parasitoid communities, host-parasitoid interaction networks, and parasitism.

The amount of habitat favorable to ecological communities is decreasing as a consequence of habitat loss. Habitat loss has caused the disappearance of ~70% of the area occupied by biodiversity hotspots, causing local extinctions and threatening species of all kinds (Brooks et al. 2002, Prugh et al. 2008). The main mechanism behind these extinctions is that small habitat areas cannot sustain viable populations due to inbreeding and demographic stochasticity (Hanski 2011). However, because species traits differ (for example in terms of mobility and reproduction rate), not all species are equally affected by habitat area reduction (*e.g.* Öckinger et al. 2010). Consequently, communities resulting from processes of habitat loss are not random subsets of the original communities. In addition to species, habitat loss may also differentially affect interactions between species, making some interactions more prone to extinction than others (*e.g.* Aizen et al. 2012). The extinction of species and interactions caused by the selective filtering of habitat area reduction may have far-reaching consequences in the structure of ecological communities and the resulting interaction networks, affecting ecosystem function and promoting evolutionary changes (Valiente-Banuet et al. 2015).

Bees are a diversified group of pollinators comprising around 20.000 species worldwide (Michener 2000). Bees are ecologically diverse, comprising social, solitary, and cleptoparasitic species. Solitary species comprise around 75% of the species of bees worldwide, and are the most abundant and efficient group of pollinators (Proctor et al. 1996). Solitary bees are also ecologically diverse, showing a range of nesting habits (O'Toole and Raw 1991, Benton 2017). Some of them nest in pre-existing cavities, a behavior that is also shared with some solitary wasps that, besides acting as pollinators, play an important role in the regulation of arthropod populations by acting as predators (O'Neill 2001). Besides the above-mentioned mutualistic interactions, solitary bees and wasps also engage in antagonistic interactions with their natural enemies (Hawkins 1994). Natural enemies include a diversity of taxonomic groups (Hymenoptera, Diptera, Coleoptera, etc.) with a wide range of lifestyles (parasitoids, cleptoparasites, predators and scavengers; henceforth parasitoids), and are the main factor of mortality of their hosts (Hawkins 1994, Pennachio and Strand 2006).

How do changes in the amount of habitat affect solitary bee/wasp and parasitoid communities, host-parasitoid interaction networks and rates of parasitism? The species-area relationship, one of the most fundamental laws in ecology (Lawton 1999), can shed light into this question. This theory, which predicts greater species abundance and richness in larger areas, has been tested empirically in communities of solitary bees / wasps and their associated parasitoids (Steffan-Dewenter et al. 2003). In addition, the species-area relationship has been extended to species interactions, showing that the number of links increases linearly with area (Brose et al. 2004). Most of the studies relating host-parasitoid interactions and area are related to habitat fragmentation and habitat loss. At any rate, resulting small habitat patches contain fewer specialist species of parasitoids (Rand and Tscharntke 2007). In addition, because parasitoids are more affected by patch size reduction than hosts, small patches harbor lower rates of parasitism (Kruess and Tcharntke 1994, Thies and Tscharntke 1999). More recently and from a theoretical perspective, Galiana and collaborators (2018) explored the relationship between network structure and area, suggesting that, because specialist species are gradually gained with patch size, networks should be more specialized and modular as area increases. The few available empirical studies than can be related to this issue reached contrasting results (Aizen et al. 2012, Spiesman and Inouye 2013, Traveset et al. 2018).

In this chapter we are interested in the relationship between patch size (habitat amount *per se*) and community and network structure. Thus, our experiment consists in patches of open habitat (favorable to solitary bee-wasp communities; Osorio et al. 2015) of varying size surrounded by dense forest matrix (not favorable).

Objectives

The general objective of this thesis is to study the role of community and habitat variability in shaping ecological communities, interaction patterns and network structure, and the resulting consequences on ecosystem function.

In **Chapter 1**, we study how changes in plant community composition affect plant-pollinator networks (Fig. 1, Chapter 1). To simulating a colonization process, we experimentally manipulate patches of a natural scrubland community by introducing a native plant, adjusting the number of flowers introduced to the amount of local resources in each patch. We have two objectives: 1) to analyze the effects of the arrival of a new species in the pollinator community, plant-pollinator interaction patterns, and the structure of the plant-pollinator networks; 2) to evaluate the consequences of these changes on pollination and plant reproductive success (Fig. 1, Chapter 1).

In **Chapter 2**, we study the relationship between patch size and host-parasitoid networks (Fig. 1, Chapter 2). In an area of 270 km^2, we set up nesting traps for cavity-nesting bees and wasps (Krombein 1967, Tscharntke 1998) in patches of varying size of favorable habitat within a matrix of unfavorable habitat. We aim to analyze the relationship between patch size and the structure of the host and parasitoid communities as well as the structure of their interaction networks.

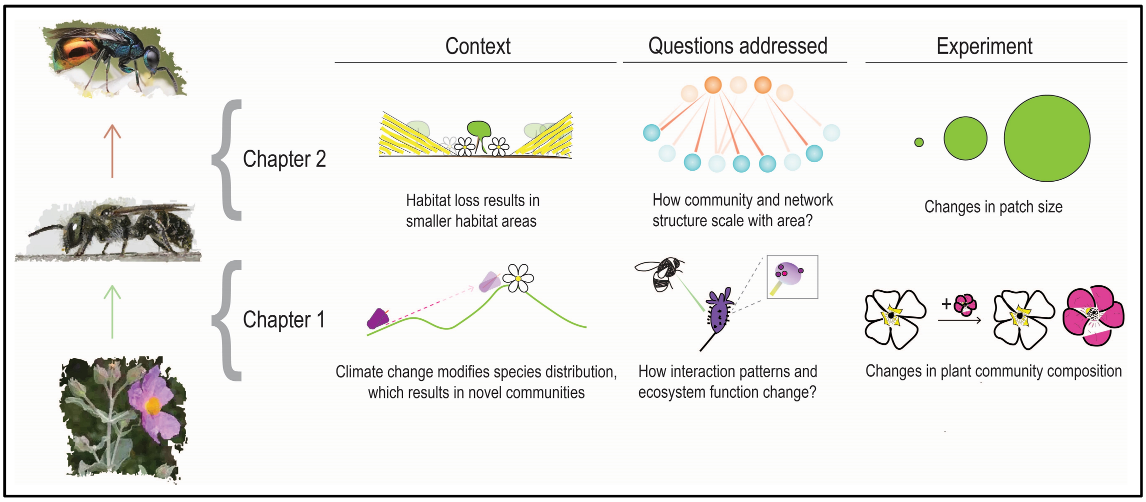

Fig. 1 Graphic representation of this PhD Thesis. Plant-pollinator networks (green arrow) and host-parasitoid networks (red arrow) are the study system of Chapter 1 and Chapter 2, respectively. For each chapter, an overview of the ecological context in which each study is embedded, the questions addressed and the experimental setting and is shown.

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CHAPTER 1

A new native plant in the neighborhood: effects on plant-pollinator networks, pollination, and plant reproductive success

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Abstract

Ecological communities are dynamic entities subjected to extinction/colonization events. Because species are connected through complex interaction networks, the arrival of a new species is likely to affect various species across the community, as observed in plant biological invasions. However, plant invasions usually represent extreme scenarios in which the community is strongly dominated by the alien species, confounding the effects of a change in species composition with a massive increase in floral resource availability. Our study addresses changes in plant community composition involving native species, a common phenomenon under the current climate change scenario in which plants are modifying their distribution ranges. We experimentally manipulated patches of a natural scrubland community by introducing a native plant (henceforth colonizing plant). To avoid introducing a disproportionate amount of floral resources we adjusted the number of flowers of the colonizing plant to the amount of floral resources locally available in each patch. We had two objectives: 1) to analyse the effects of the arrival of a new plant on the pollinator community, the rearrangement of plant–pollinator interactions and the structure of the plant–pollinator network; 2) to evaluate potential consequences for pollination and the reproductive success of resident plant species. The colonizing plant acted as a magnet species, attracting bumblebees and facilitating interactions to other plants through spill-over. The introduction of the colonizing plant also affected the structure of plant–pollinator networks (colonized networks were more generalized and more nested than control networks) and modified the arrangement of plant and pollinator species into modules. Ultimately, these changes resulted in higher heterospecific (but not conspecific) pollen deposition and had contrasting effects on the reproductive success of two resident plant species (higher fruit set and lower seed set, respectively). Our study shows that relationships between plants and pollinators are rapidly rearranged in response to novel situations (even when the new plant is not overly dominant), with important functional consequences on pollination and plant reproductive success. Our study establishes a link between network structure and pollination and plant reproductive success, which may be mediated by differences among pollinator species in foraging behavior.

Keywords: *Cistus albidus, Cistus salviifolius*, field experiment, *Lavandula stoechas,* plant colonization, plant community, plant–pollinator interactions, *Thymus vulgaris*

1.1. Introduction

Ecological communities are dynamic entities subjected to changes in species composition through extinction and colonization events. These changes may occur more or less gradually over long periods of time, due to ecological processes such as competition/facilitation (Tilman 2004) and shifts in environmental conditions (*e.g.* climate change; Chen et al. 2011), or more rapidly as a result of ecological disturbances and human-induced biological introductions (Paine 1966, Shea and Chesson 2002).

The species of a community interact among themselves generating complex interaction networks. Thus, the extinction/colonization of a given species will not only affect the interactions involving this species but may also have cascading effects on other species interactions, either by causing a redistribution of interactions (rewiring) or by modifying the strength of interactions (Poisot et al. 2015, Tylianakis and Morris 2017). In turn, these changes may have important consequences on the reproduction of certain species and ultimately on community structure and ecosystem functioning (Bergstrom et al. 2009). Network analysis has been intensively used in the last decade to study interactions among plants and pollinators at the community level. In general, plant–pollinator networks are heterogeneous, asymmetric, nested and modular (Jordano et al. 2003, Bascompte et al. 2003, Bascompte et al. 2006, Olesen et al. 2007). Network topology and network stability are intimately related (*e.g.* Tylianakis et al. 2010), and theoretical approaches suggest that the loss of keystone species/interactions may result in secondary extinctions and network fragmentation (Memmot et al. 2004, Santamaría et al. 2015, Traveset et al. 2017).

Human-induced translocations of exotic plants provide scenarios of relatively rapid incorporation of new species into ecological networks. Invasive plants are usually pollinator-generalist and are readily visited by native pollinators (Traveset and Richardson 2006). This scenario may cause pollinators to change their foraging decisions, potentially leading to changes in network structure (Ghazoul 2004, Aizen et al. 2008), and ultimately modifying pollen transfer patterns, with potential consequences on the reproductive success of native plants (Lopezaraiza-Mikel et al. 2007, Morales and Traveset 2009, Vanbergen et al. 2018). In some cases, invasive plant species may compete for pollinators with native species (Brown et al. 2002, Bartomeus et al. 2008). In other cases, invasive plants may act as magnet species, attracting pollinators to the community and promoting higher visitation rates to other plants via spill over (Moragues and Traveset 2005, Bartomeus et al. 2008, Molina-Montenegro et al. 2008).

However, plant invasions usually represent extreme scenarios in which the local community is strongly dominated by an alien species that often produces large amounts of floral resources compared to the native species (*e.g.* Chittka and Schürkens 2001). Therefore, it is difficult to discern whether changes in plant–pollinator interactions are attributable to changes in plant composition *per se* or to a massive increase in floral resource availability. In this study, we are interested in changes in plant community composition involving native species. We experimentally manipulate patches of a natural scrubland community by introducing a native plant (simulating a range expansion) and then assess the ability of the plant–pollinator community to rearrange its interactions and the short-term ecological consequences on the reproduction of resident plants. Importantly, we control for the amount of floral resources introduced. We have two objectives: 1) to analyse the effects of the arrival of a new species on the pollinator community, plant–pollinator interactions and the structure of the plant–pollinator network; and 2) to evaluate the consequences of these changes on pollination (pollen deposition on the stigmas) and plant reproductive success (fruit and seed set).

We work in natural communities dominated by the shrub *Cistus salviifolius* in which we introduce the co-flowering congeneric *C. albidus*. *C. albidus* usually occurs at lower altitudes than *C. salviifolius* (Bolós et al. 2005). Therefore, our manipulation mimics an elevational shift, a common phenomenon under the current climate change scenario (Kelly and Goulden 2008). Additionally, our manipulation is plausible because both plants coexist in other areas (Trabaud and Oustric 1989, Bosch 1992, Bosch et al. 2009). *C. albidus* produces more pollen and nectar per flower than *C. salviifolius* and attracts more and larger pollinators (Bosch 1992). Consequently, we envision three possible outcomes. First, *C. albidus* could draw pollinators away from *C. salviifolius* and/or other resident plant species. Depending on the magnitude of this effect, it could result in reduced pollination and reproductive success. Studies on plant invasions have shown that interspecific competition for pollinators often results in decreased connectivity of native species (Aizen et al. 2008, Kaiser-Bunbury et al. 2011). Thus, under this scenario we would expect an overall decrease in generalization. Second, *C. albidus* could act as a magnet species and attract new pollinators. Then, *C. albidus* could share them with the local community, thus acting as a facilitator. This spill-over effect could enhance pollination and reproductive success of the resident plant species. However, given that *C. albidus* produces large amounts of pollen and attracts large pollinators, which carry and deposit large amounts of pollen (Bosch 1992, Willmer and Finlayson 2014), this scenario could also result in increased heterospecific pollen deposition. Under this scenario we would expect an increase in generalization (Valdovinos et al. 2009) and network nestedness (Traveset et al. 2013), as well as a decrease in network modularity (Santos et al. 2012, Albrecht et al. 2014). Alternatively (third scenario), *C. albidus* could attract new pollinators but not share them with the other plants, with no effects on pollination and reproductive success of the resident community. This scenario would favour the appearance of a new network module dominated by *C. albidus*.

1.2. Material and Methods

1.2.1. Study area and site selection

The study was conducted in Montseny Natural Park (Barcelona, NE Spain) in 2016, and comprised an area of 32km^2 between 432 and 818 m a.s.l. (Supplemental Material (SM) Chapter 1: Table SM1). The climate in the area is sub-Mediterranean, with a mean annual temperature of 13.8 ºC and a mean rainfall of 649 mm.

The area is occupied by a matrix of dense Mediterranean holm oak (*Quercus ilex*) forests with scattered patches of Mediterranean scrubland. We selected 18 of these patches (henceforth plots) measuring ~ 500 m^2 (range: 200-900 m^2) (SM Chapter 1: Fig. SM1). All plots were dominated by *Cistus salviifolius* and included some subdominant species such as *Lavandula stoechas* and *Thymus vulgaris*. Distance between nearest plots was ~ 900 m (range 387-2487 m). This distance is assumed to encompass the foraging range of most pollinator species (Greenleaf et al. 2007). All plots were surrounded by dense forest (> 95% of the landscape cover within a 250 m radius). To further isolate plots, before the beginning of the flowering period we removed all flowering plants within a 50 m buffer from the periphery of each plot.

1.2.2. Introduction of *Cistus albidus*

Plots were distributed between the two treatments (colonized, control) based on plant community composition, flowering phenology and geographical distribution (SM Chapter 1: Table SM1, Fig. SM1). As a result, plots of the two treatments did not differ in flower abundance, flower richness, flower diversity (t-test, $|t| < 0.93$, $P > 0.36$ in all 3 cases), flower composition (PERMANOVA, pseudo-$F_{1,16} = 0.71$, $P = 0.74$) or spatial distribution (test on spatial homogeneity of group dispersion, $F_{1,16} = 0.40$, $P = 0.54$).

Potted *C. albidus* individuals with open flowers were introduced in 9 of the 18 plots (colonized plots) when *C. salviifolius* started to bloom (mid-April). *C. albidus* pots (~ 15 per plot) were intermixed with *C. salviifolius* individuals. The remainder of the plots (n = 9) were left unmanipulated (control plots).

C. salviifolius and *C. albidus* flowers are actinomorphic and have a similar structure. However, *C. albidus* flowers are pink (as opposed to white in *C. salviifolius*), slightly larger, and produce approximately twice as much pollen and nectar (Bosch 1992). To avoid the potentially confounding effect of a massive increase in floral resources, we matched *C. albidus* floral resources (pollen and nectar) to those of the local *C. salviifolius* population in each colonized plot. Therefore, the number of introduced *C. albidus* flowers (~ 80 flowers/plot, range: 56-104) was approximately half the number of *C. salviifolius* flowers (~ 150 flowers/plot, range: 106-195 flowers/plot). To allow pollinators to adjust to the new flower context, pollinator surveys were conducted 3 days after the introduction of *C. albidus*. Early in the morning, before starting the pollinator surveys, we further adjusted the number of *C. salviifolius* and *C. albidus* flowers to the desired 2:1 ratio by either adding or removing *C. albidus* flowers.

1.2.3. Pollinator surveys

Pollinator surveys were conducted between 24 April and 5 May. Each plot was surveyed by 2-3 observers throughout a day, from 09:30 until 14:30. This period encompasses the entire life span of individual *C. salviifolius* and *C. albidus* flowers (Bosch 1992). We sampled 2-3 plots per day. Sampling dates did not vary between control and colonized plots (Wilcoxon test, $W = 41$, $P = 1$).

Early in the morning, before starting the pollinator survey, all open flowers in the plot were counted. Pollinator surveys consisted of several rounds (~ 11 rounds/plot, range 6 – 20 rounds) in which we recorded all pollinators contacting the reproductive organs of the flowers. Some pollinators were captured for later identification in the laboratory. Usually, all flowers in the plot were surveyed in each round. However, when a plant species was very abundant, subsets of flowers were surveyed. On the other hand, to record a sufficiently large number of interactions in rare plant species, these were surveyed more frequently. We define visitation rate as the number of pollinators visiting a plant species divided by the number of flowers surveyed, and interaction frequency as the visitation rate of a pollinator species to a plant species multiplied by the flower abundance (number of open flowers) of that plant species. We use interaction frequency as a measure of interaction strength (e.g. Vázquez et al. 2005). We define abundance of a pollinator species as the sum of the frequencies of all interactions in which this pollinator species is involved.

We recorded 188 pollinator species. Most of them were rare (166 species accounted for less than 1% of total pollinator abundance). To facilitate comparison across plots and because similar pollinators are expected to have similar effects on pollination, pollinator species were grouped into 17 functional groups based on taxonomic, morphometric and abundance criteria (Gómez et al 2010). The 17 pollinator groups were: 1) honeybees (*Apis mellifera*); 2) bumblebees (mostly *Bombus terrestris*); 3) short-tongued small bees (< 10 mm long) (STSB); 4) short-tongued large bees (> 10 mm long) (STLB); 5) long-tongued small bees (LTSB); 6) long-tongued large bees (LTLB); 7) hoverflies; 8) beeflies; 9) flies; 10) ants; 11) butterflies; 12) wasps; 13) true bugs; 14) grasshoppers; 15) small (< 5 mm long) beetles; 16) medium-sized (5-10 mm long) beetles; 17) large (> 10 mm long) beetles. Unless otherwise indicated, analyses were conducted using pollinator functional groups.

1.2.4. Stigma pollen loads

To evaluate pollination, we measured pollen deposition on the stigmas of *C. salviifolius* (present in all plots), *L. stoechas* (present in 7 control and 7 colonized plots), *T. vulgaris* female morph (henceforth *T. vulgaris* F, 6 control and 6 colonized plots) and *T. vulgaris* hermaphroditic morph (henceforth *T. vulgaris* H, 6 control and 5 colonized plots). For each of these species/morphs (henceforth focal plants) we tagged 10 size-representative individuals distributed across the plot. Early in the morning, before pollinators were active, we marked 6 newly-opened (unvisited) flowers on each tagged individual. In *L.*

stoechas the probability that a flower will set a fruit depends on its position within the inflorescence (Muñoz and Devesa 1987). For this reason, in this species we marked only central flowers located in the most basal part of the inflorescences.

At the end of the pollinator survey, and just before *C. salviifolius* flowers started losing their petals and closing their sepals, we collected the stigmas of 2 marked flowers of each of the 10 tagged individuals per focal plant. By working with newly-opened flowers and collecting them at the end of the day, we ensured that pollen deposition was directly attributable to the visitation patterns observed during the pollinator survey. Stigma collection was done with extreme caution to avoid accidental pollen self-deposition. Stigmas were placed individually on a layer of fuchsine-stained gelatine (Beattie 1971) in Eppendorf tubes and kept at 4ºC until processed. The remaining 4 marked flowers per individual were left for later assessment of fruit and seed set.

Collected stigmas were mounted on glass slides, and pollen grains were identified and counted (all pollen grains in *L. stoechas, T. vulgaris* F and *T. vulgaris* H; ca. 75 % of the stigma surface in *C. salviifolius*) at 300X by the Palynological Service of Universitat Autònoma de Barcelona (http://sct.uab.cat/lap/).

1.2.5. Fruit- and seed-set

L. stoechas and *T. vulgaris* flowers remain open and receptive for 3-4 days (Muñoz and Devesa 1987, Arnan et al. 2014). For this reason, and to extend the potential effects of *C. albidus* on pollinator visitation and reproductive success of focal plants, potted *C. albidus* were left in the field for three days following the pollinator surveys.

We collected the fruits of the 4 marked flowers left on each tagged individual at the beginning of the fruit-ripening period (*C. salviifolius* and *T. vulgaris*: 1 month after bloom; *L. stoechas*: 4 months after bloom). In the laboratory, we opened these fruits and counted viable and unviable seeds. Small, pale-coloured seeds without endosperm were considered unviable.

1.2.6. Data analyses

Pollinator community

To compare the pollinator community of control and colonized plots we analysed overall pollinator species abundance, richness, diversity (Shannon index) and composition, and the abundance of each pollinator functional group. Pollinator abundance data were log-transformed to meet model assumptions. Because pollinator abundance and flower abundance were highly correlated (r = 0.91), abundance data were analysed with ANCOVAs, with treatment (control and colonized plots) as fixed factor and flower abundance as a covariate. In the analysis of pollinator functional group abundance we applied the Benjamini-Hochberg method for multiple test comparisons. Pollinator species richness (log-transformed) and diversity were analysed with t-tests, and pollinator species composition with PERMANOVA (Bray-Curtis dissimilarity index).

Plant–pollinator interaction patterns

We compared overall visitation rates at the plot level and in focal plants (*C. salviifolius*, *L. stoechas*, *T. vulgaris* F and *T. vulgaris* H). We used Wilcoxon tests because data were not normally distributed and could not be appropriately transformed. In addition, we compared pollinator group composition of each focal plant between control and colonized plots with PERMANOVA (Bray-Curtis dissimilarity index). To detect which pollinator groups differed between control and colonized plots, we calculated the contribution of each pollinator group to the observed dissimilarity with a SIMPER analysis.

Network structure

We built a plant–pollinator network for each plot with the interaction frequency data. To characterize overall network generalization, we calculated H_2' (Blüthgen et al. 2006), plant generality (weighted mean number of pollinator species visiting a plant species) and pollinator generality (weighted mean number of plant species visited by a pollinator species) (Bersier et al. 2002). We also characterized specialization of focal plant species and pollinator functional groups using d' (Blüthgen et al. 2006). We conducted *t*-tests to compare the values of these metrics between control and colonized plots. Comparisons of pollinator functional group d' were conducted with Wilcoxon tests followed by Benjamini-Hochberg corrections.

For each network we calculated nestedness using the Weighted Nestedness metric based on Overlap and Decreasing Fill (*WNODF*) (Almeida-Neto and Ulrich 2010). To assess the significance of nestedness in each network we built a null model in which 1000 networks were generated by setting the probability of interaction between two species proportional to their relative abundances (Vázquez et al. 2007). Then, the observed value was compared with the 95% confidence interval of the null distribution. Nestedness values of control and colonized networks were compared with a *t*-test. Finally, to analyse the effect of *C. albidus* on network nestedness we calculated the contribution of *C. albidus* to the observed nestedness (Saavedra et al. 2011).

We calculated the modularity of each network using Consensus Modularity (Gómez et al. 2014). This script uses the *QuanBiMo* algorithm (Dormann and Strauss 2013) and returns a number of modules (*nQ*), a modularity index (*Q*), and its significance by comparison to a null model. The number of modules and the modularity index of control and colonized networks were compared with *t*-tests or Wilcoxon tests depending on data distribution. To synthesise the modularity patterns observed, we pooled together the data of all control and all colonized local networks to build a control metanetwork and a colonized metanetwork.

Pollination and plant reproductive success

To study the functional consequences of the introduction of *C. albidus* we compared pollination (amount of conspecific and heterospecific pollen grains deposited on the stigmas) and plant reproductive success (fruit and seed set) of focal plants in control and colonized plots.

We conducted generalized linear mixed models on the number of conspecific pollen grains deposited on the stigmas (Poisson family for *C. salviifolius* and, due to the high frequency of zeros, negative binomial family for *L. stoechas, T. vulgaris* F and *T.*

vulgaris H), with treatment (control vs colonized) as fixed factor and plot and individual plant (nested within plot) as random factors. We used a similar procedure to analyse heterospecific pollen grain deposition with zero-inflated negative binomial family models. Heterospecific pollen grains could belong to *C. albidus* or to resident species. To discriminate between these two types of heterospecific deposition we analysed heterospecific pollen composition with PERMANOVA (Bray-Curtis dissimilarity index). Rare pollen species (< 1% of total pollen grains) were grouped into a single category (*other*), and a dummy variable (a = 0.01) was added to allow model convergence. To detect which heterospecific pollen types differed between control and colonized plots, we calculated the contribution of each heterospecific pollen type to the observed dissimilarity with a SIMPER analysis.

Fruit set was calculated as the proportion of flowers (4 marked flowers on 10 individuals per focal plant) that formed at least one seed. We used generalized linear mixed models (binomial family) on the proportion of flowers producing fruits (1: yes, 0: no), with treatment as fixed factor and plot and individual (nested within plot) as random factors. *C. salviifolius* flowers have a variable number of ovules, whereas *L. stoechas* and *T. vulgaris* flowers have 4 ovules. We tested differences between treatments in seed set (number of seeds / fruit) with generalized linear mixed models (Poisson family) on seed number, with treatment as fixed factor and plot and individual (nested in plot) as random factors.

All analyses were conducted in R (R Core Team, 2018). We used the package *vegan* (Oksanen et al. 2018) for multivariate statistics, *Bipartite* (Dormann et al. 2008) for network analyses and *lme4* (Bates et al. 2015) and *glmmADMB* (Skaug et al. 2016) for linear models. All means are followed by ± SE.

1.3. Results

1.3.1. Pollinator community

The introduction of *Cistus albidus* did not alter pollinator abundance ($F_{1,15} = 0.21$, $P = 0.65$), species richness ($t_{14.7} = -0.41$, $P = 0.68$), diversity ($t_{15.7} = -0.26$, $P = 0.80$), or composition (pseudo-$F_{1,16} = 0.73$, $P = 0.76$). However, bumblebee abundance increased 3.2-fold in colonized plots (control plots: 0.99 ± 0.40 individuals/plot; colonized plots: 3.15 ± 1.10; $F_{1,15} = 12.06$, $P = 0.003$). These differences in bumblebee abundance persisted when visits recorded on *C. albidus* were excluded from the analysis (colonized plots: 2.57 ± 0.88; $F_{1,15} = 7.62$, $P = 0.015$), indicating that bumblebees attracted to the colonized plots visited not only *C. albidus* but also other plants in the community. There were no differences between treatments in the abundance of the other pollinator groups (SM Chapter 1: Table SM2).

1.3.2. Plant–pollinator interaction patterns

C. albidus was visited mostly by honeybees (43% of the visits), followed by hoverflies (17%), short-tongued small bees (mostly *Lasioglossum* spp., 10%), short-tongued large bees (mostly *Andrena* spp., 5%), bumblebees (9%), and small beetles (7%) (SM Chapter 1: Fig. SM2).

Visitation rate at the plot level did not differ between treatments (control plots: 0.29 ± 0.10 individuals / 100 flowers; colonized plots: 0.26 ± 0.05; $W = 39$, $P = 0.93$), and visitation rates of the focal plants were also similar in the two treatments (all $W < 36$, $P > 0.43$). However, pollinator composition of *Lavandula stoechas* changed in colonized plots (pseudo-$F_{1,12} = 2.12$, $P = 0.04$). Bumblebees increased their visitation rate 1.7-fold (control plots: 0.015 ± 0.01 individuals / 100 flowers; colonized plots: 0.026 ± 0.005; SIMPER, $P = 0.015$) and became the most important pollinator group of this plant in colonized plots (Fig. 1). Pollinator composition did not vary in *Thymus vulgaris* F (pseudo-$F_{1,11} = 0.67$, $P = 0.77$), *T. vulgaris* H (pseudo-$F_{1,9} = 0.58$, $P = 0.77$), or *C. salviifolius* (pseudo-$F_{1,16} = 0.32$, $P = 0.95$). Bumblebee visitation rate to *C. salviifolius* was 7-fold greater in colonized plots (marginally significant trend; control plots: 0.011 ± 0.008 individuals / 100 flowers; colonized plots: 0.068 ± 0.03; SIMPER, $P = 0.086$), but bumblebees remained an infrequent visitor of *C. salviifolius* (Fig. 1).

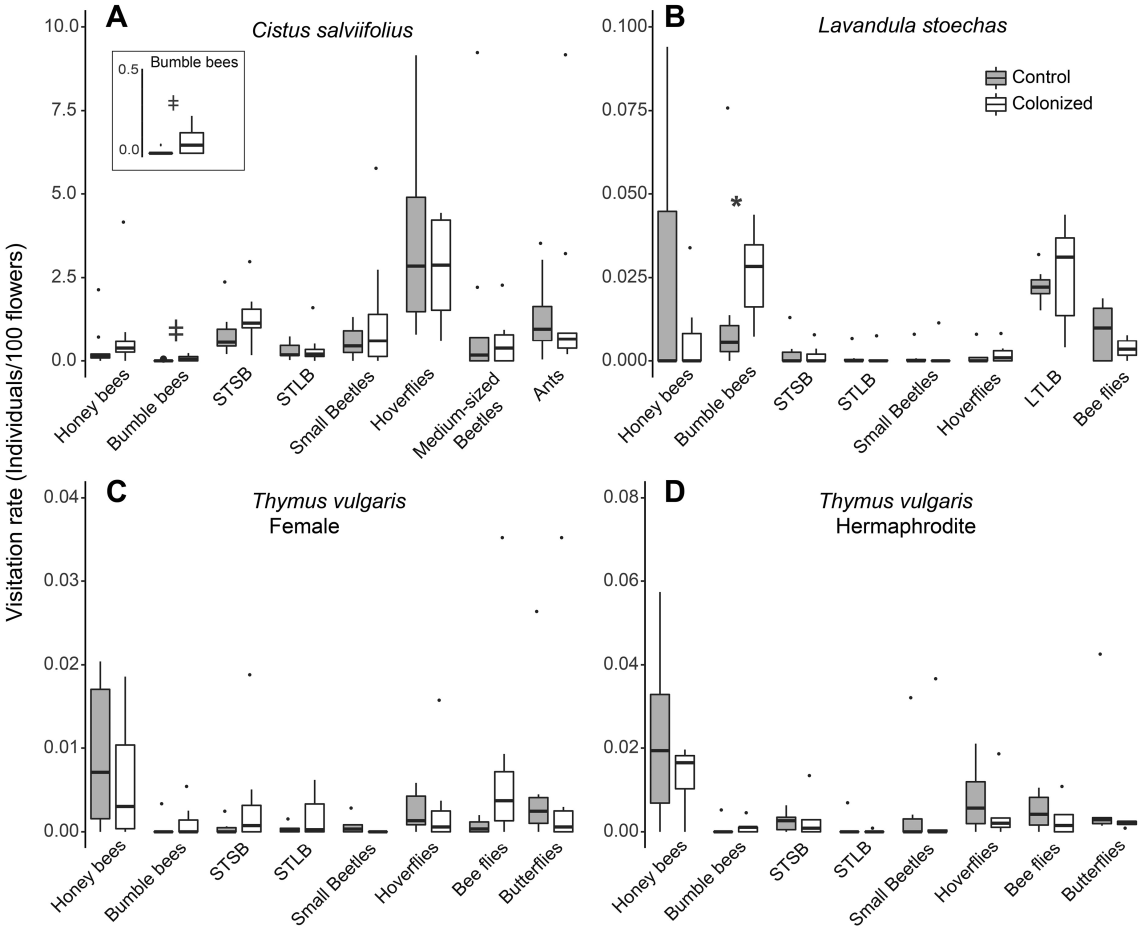

Fig. 1 Visitation rate (pollinator individuals per 100 flowers) of the main pollinator groups to focal plants in control (grey) and colonized (white) plots. Significant (*, *P* < 0.05) and marginally significant (ǂ, *P* < 0.1) differences from SIMPER analyses are indicated. STSB: Short-Tongued Small Bees, STLB: Short-Tongued Large Bees, LTLB: Long-Tongued Large Bees.

1.3.3. Network structure

Network and species generalization

Network specialization (H_2') decreased 0.80-fold from control to colonized networks (Table 1). Plant generality remained unaltered but pollinator generality increased 1.5-fold (Table 1). These differences became non-significant when we removed *C. albidus* from the networks of the colonized plots, indicating that the increase in generalization was primarily driven by the interactions involving the introduced plant (Table 1).

Species specialization (*d'*) decreased 0.39-fold in *C.salviifolius* and 0.5-fold in *T. vulgaris* F (Table 1) but did not change in *L. stoechas* and *T. vulgaris* H (Table 1). In colonized networks *C. albidus* showed the lowest specialization ($d' = 0.10 \pm 0.04$) (Table 1). Specialization (*d'*) did not change in any pollinator functional group (SM Chapter 1: Table SM3).

Table 1 Measures of network specialization (H_2'), trophic level generalization (plant and pollinator generality) and species specialization (d') in control and colonized networks (N = 9 per treatment).

	Control networks		Colonized networks			
Metric	mean	SE	mean	SE	*t*	*P*
Network specialization (H_2')	0.51	0.02	0.41	0.03	2.68	**0.018 §**
Plant Generality	4.34	0.48	4.62	0.40	-0.45	0.66
Pollinator Generality	1.97	0.15	2.96	0.24	-3.44	**0.004 §**
Species specialization (d')						
Cistus salviifolius	0.33	0.07	0.13	0.05	2.31	**0.036**
Lavandula stoechas	0.56	0.07	0.43	0.06	1.37	0.20
Thymus vulgaris F	0.28	0.03	0.14	0.05	2.49	**0.031**
Thymus vulgaris H	0.23	0.06	0.27	0.12	-0.34	0.74
Cistus albidus	-	-	0.10	0.04	-	-

See SM Chapter 1: Table SM3 for d' values of pollinator functional groups.

§ non-significant when *C. albidus* visits are removed from the analysis.

Network nestedness and modularity

All control and colonized networks were significantly less nested than random webs (SM Chapter 1: Table SM4). However, nestedness tended to increase from control to colonized networks (*WNODF*; control plots: 27.6 ± 2.3; colonized plots: 32.2 ± 1; $t = -1.85$, $P = 0.09$). *C. albidus* tended to be a positive contributor to network nestedness (individual nestedness contribution = 0.54 ± 0.39; Wilcoxon test on contribution greater than 0, $V = 36$, $P = 0.06$), and clearly belonged to the core of supergeneralist species (Fig. 2B). This core also included the four focal plants and *Euphorbia characias* in both control and colonized plots (Fig. 2A, B).

All control and colonized networks were significantly modular (SM Chapter 1: Table SM5). Control and colonized networks had similar levels of modularity (*Q* index; control plots: 0.33 ± 0.04; colonized plots: 0.34 ± 0.03; t = -0.16, P = 0.87) and a similar number of modules (*nQ*; control plots: 3.40 ± 0.29; colonized plots: 3.80 ± 0.15; W = 34, P = 0.50). However, module composition of the control and colonized metanetworks showed some important differences (Fig. 2C, D). The control metanetwork had 3 modules (Fig. 2C). Module *a* included *C. salviifolius* and other plant species visited by hoverflies, beetles (small, medium-sized and large) and short-tongued bees (small and large). Module *b* included *L. stoechas* and *T. vulgaris* (both morphs) and other plant species visited by beeflies, bumblebees, butterflies, honeybees and long-tongued bees (small and large). Module *c* included *Euphorbia characias* and other plant species visited by ants and flies (Fig. 2C). In the colonized metanetwork modules *a* and *c* were almost identical to modules *a* and *c* of the control metanetwork (Fig. 2D). However, the introduction of *C. albidus* caused module *b* to split into two modules. Module *b1*included *T. vulgaris* (both morphs) and *C. albidus*, with the honeybee as the most important pollinator, followed by beeflies and butterflies. *L. stoechas* was included in a separate module (*b2*) visited by bumblebees and long-tongued bees (small and large) (Fig. 2D).

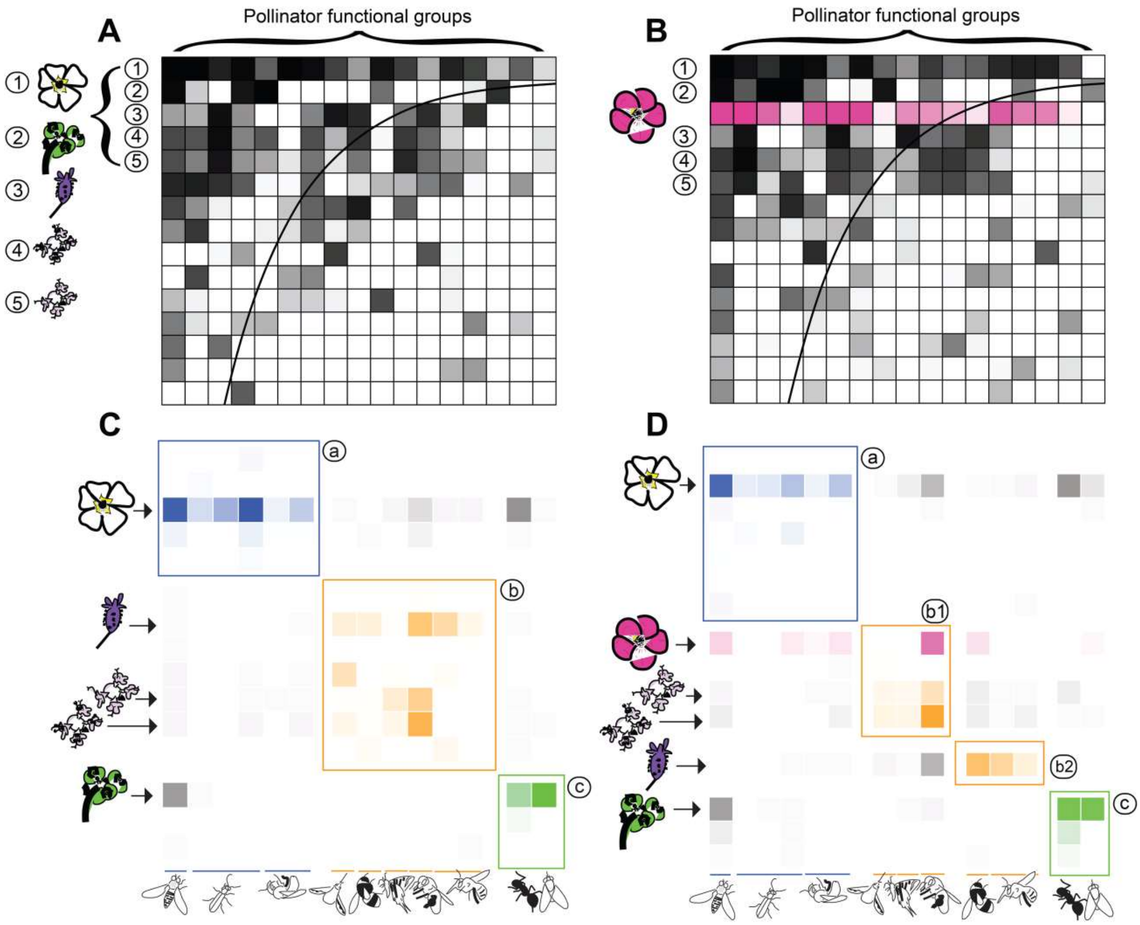

Fig. 2 Nested (A, B) and modular (C, D) matrices of control (A, C) and colonized (B, D) metanetworks (N = 9 local networks per treatment). Colour intensity denotes interaction frequency. In nested matrices (A, B), the solid line represents the isocline of perfect nestedness, and plants forming the core of supergeneralist species are indicated by numbers (1. *Cistus salviifolius*, 2. *Euphorbia characias*, 3. *Lavandula stoechas*, 4. *Thymus vulgaris* H, 5. *Thymus vulgaris* F, plus *Cistus albidus* (pink flower in B)). In modular matrices (C, D) interactions within each module are coloured differently (blue, orange, green), and pollinator groups are, from left to right in C: hoverflies, beetles (small, medium-sized and large), short-tonged bees (small and large), beeflies, bumblebees, butterflies, honeybees, long-tonged bees (small and large), ants and flies. *Cistus albidus* interactions are shown in pink. For clarity, only the 15 most-connected plant species and the 14 most-connected pollinator groups are shown.

1.3.4. Pollination and plant reproductive success

Pollination

None of the four focal plants showed differences in conspecific pollen stigma loads between control and colonized plots (all $|z| < 1.54$, $P > 0.12$) (Fig. 3, A-D). In contrast, heterospecific pollen deposition in two focal plants, *C. salviifolius* and *L. stoechas,* was greater in colonized plots ($z = 4.51$, $P < 0.001$ and $z = 2.59$, $P = 0.01$, respectively) (Fig. 3E, F). However, even in these two species, heterospecific pollen loads were a small fraction of overall pollen loads (0.4 ± 0.1 % and 2.4 ± 1.1, respectively).

Composition of heterospecific pollen loads in *C. salviifolius*, *L. stoechas* and *T. vulgaris* F changed between control and colonized plots (all $F > 4.4$, $P < 0.003$). These changes were mediated mainly by *C. albidus* pollen (Fig. 3, E-H), but heterospecific deposition of *T. vulgaris* H, *L. stoechas*, and *other* (non-focal plants) pollen also increased (SIMPER, p-values between 0.001 and 0.06).

Plant reproductive success

The introduction of *C. albidus* affected the reproductive success of two of the four focal plants. In colonized plots, the fruit set of *T. vulgaris* F increased 1.32-fold ($z = 2.36$, $P = 0.018$) (Fig. 3K), whereas seed set of *L. stoechas* tended to decrease 0.83-fold ($z = -1.77$, $P = 0.077$) (Fig. 3N).

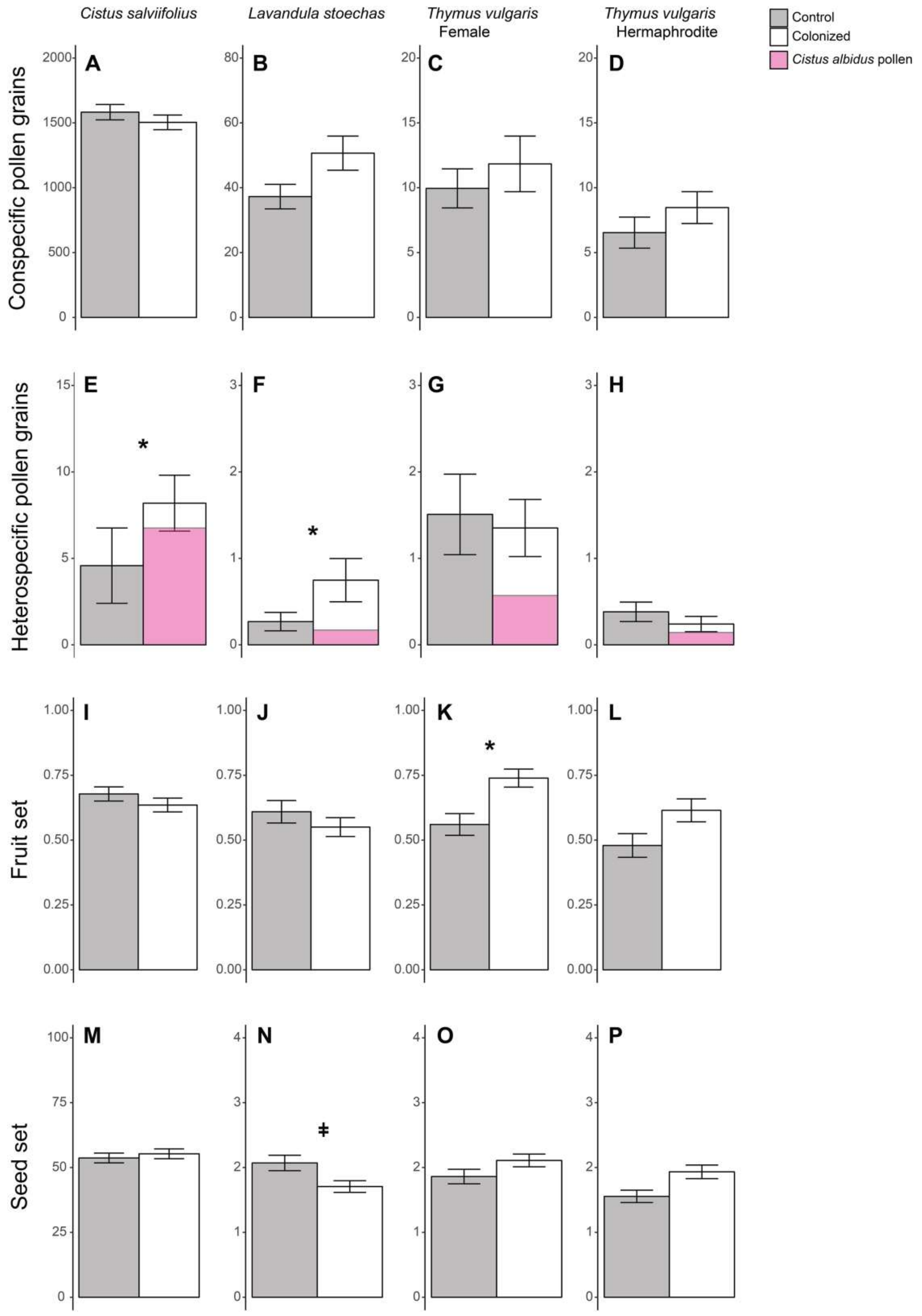

Fig. 3 Conspecific (A-D) and heterospecific (E-H) pollen grains deposited on the stigmas, and fruit set (% of flowers that developed into fruits) (I-L) and seed set (number of seeds per fruit) (M-P), of focal plants in control (grey) and colonized (white) plots (mean ± SE). Significant (*, $P < 0.05$) and marginally significant (ǂ, $P < 0.1$) differences are indicated.

1.4. Discussion

The experimental introduction of *Cistus albidus* had important consequences for local plant–pollinator communities. First, it caused an increase in bumblebee abundance that, importantly, did not only involve visitation to *C. albidus*, but also to other plants. Second, it affected the structure of plant–pollinator networks. The pollinator trophic level and some focal plant species became more generalized, resulting in a generalization increase at the network level. The introduction of *C. albidus* also increased network nestedness and modified the arrangement of plants and pollinators in modules. Ultimately, all these changes resulted in higher heterospecific pollen deposition and contrasting effects on the reproductive success of some focal plants. Overall, these results fall within our second envisioned scenario, in which *C. albidus* acts as a magnet species, facilitating interactions to other plants through spill-over and promoting generalization.

1.4.1. Effects on the pollinator community and plant–pollinator interaction patterns

Bumblebees increased their abundance three-fold in colonized plots, resulting in increased visitation to *Lavandula stoechas* and, to a certain extent, *C. salviifolius*. Because *C. albidus* was introduced three days before the surveys, this result implies that bumblebees were able to locate the introduced plant in a relatively short period of time. Bumblebees have long foraging ranges (up to 3km) and are known to select patches with high floral rewards (Goulson 2010). In our study, bumblebees visited recently-opened *C. albidus* flowers early in the morning when anthers were fully loaded with pollen. Later in the day, as *C. albidus* pollen was rapidly depleted, bumblebees switched to visiting *L. stoechas* for nectar collection.

1.4.2. Effects on network structure

The introduction of *C. albidus* fostered generalization of the overall network (decrease in H_2') and at the pollinator trophic level (increase in pollinator generality). These changes were mostly a consequence of new interactions involving *C. albidus*, but generalization also increased in two of the four focal plants, *C. salviifolius* and *Thymus vulgaris* F. Several studies have analysed the effects of plant invasions on the structure of plant–pollinator interactions. In some cases, invasive species increase generalization (Valdovinos et al. 2009), but other studies have found opposite results (Aizen et al. 2008, Kaiser-Bunbury et al. 2011). These discrepancies may be explained by the level of dominance of the invasive species in terms of floral resources. At high levels of dominance, competition for pollinators and decrease in generalization are expected to occur (Ratchke 1983, Bjerknes et al. 2007, Muñoz and Cavieres 2008). Because invasive plants usually produce large amounts of floral resources and become strongly dominant, it is not surprising that competition for pollinators and negative effects on generalization are a common outcome in plant invasion studies (Morales and Traveset 2009). By contrast, we worked with native species and deliberately maintained the levels of introduced floral resources similar to those of resident species. At these low levels of dominance, facilitation and increased generalization are expected (Ratchke 1983, Ghazoul et al. 2006, Muñoz and Cavieres 2008).

C. albidus generated new strong interactions and was an important component of the core of supergeneralist species, thus contributing to an increase in network nestedness. New species are more likely to be incorporated into local communities when they interact with resident generalist species, resulting in reduced effective competition and ultimately enhancing the number of coexisting species (Bastolla et al. 2009, Thébault and Fontaine 2010). Ultimately, generalization and network nestedness are expected to foster stability against perturbation events such as plant and pollinator extinctions (Waser et al. 1996, Thébault and Fontaine 2010).

Contrary to our expectations, the introduction of *C. albidus* did not result in decreased network modularity, but it had important effects on the arrangement of plant–pollinator interactions, causing a module of the control metanetwork to split into two in the colonized metanetwork. This result was mediated by the increase in the interaction frequency between bumblebees and *L. stoechas*. Because modules are considered coevolutionary units (Olesen et al. 2007), module reorganization at the regional level could imply changes in the selective pressures of local, isolated plant populations, with potential consequences on evolutionary dynamics.

1.4.3. Effects on pollen deposition

Although *C. albidus* acted as a facilitator of certain interactions to focal plants, it did not affect conspecific pollen loads, a result that is consistent with the fact that overall (all pollinators) visitation rates did not change for any of the four focal plants. It is important to note that to avoid introducing large amounts of *C. albidus* pollen we adjusted the number of *C. albidus* flowers to the existing floral resources in each plot.

The impact of the arrival of a new plant on both conspecific and heterospecific pollen deposition patterns of resident plants is likely to increase if the newcoming plant becomes dominant over time, as seen in many instances of exotic plant introductions (Morales and Traveset 2008, Dietzsch 2011).

On the other hand, we found a significant increment in heterospecific pollen deposition in two of the four focal plants. Most of this heterospecific deposition involved *C. albidus* pollen. *C. albidus* produces large amounts of pollen (Bosch 1992) and was the most generalized plant species in the network, sharing the most abundant pollinators with focal plants and thus acting as a hub-donor (*sensu* Tur et al. 2016). However, changes in heterospecific deposition were also mediated by pollens of other plants in the community. This result is consistent with the above-mentioned increase in generalization and suggests changes in pollinator floral fidelity (Morales and Traveset 2008).

1.4.4. Effects on plant reproductive success

Under a scenario of *C. albidus* facilitating interactions to resident plants, we envisioned either a positive effect on reproductive success by means of increased conspecific pollen deposition, or a negative effect by means of increased heterospecific pollen deposition. However, we found no changes in conspecific pollen deposition and the increase in heterospecific pollen deposition was too low to result in stigma clogging (Ashman and Arceo-Gómez 2013). Consequently, we hypothesize that the observed changes in the reproductive success of focal plants were mediated by changes in the quality of the conspecific pollen deposited (Aizen and Harder 2007).

The seed set of *L. stoechas* trended towards a decrease in colonized plots. This plant species was mostly visited by honeybees in control plots and by bumblebees in colonized plots. Honeybees and bumblebees show important differences in foraging behaviour. Compared to the honeybee, bumblebees visit more flowers per individual plant (Arnan et al. 2014), a behaviour that results in increased geitonogamy (Karron et al. 2009), potentially lowering seed set (de Jong et al. 1993). To establish whether bumblebees also visited more flowers per individual in *L. stoechas*, we conducted an independent pollinator survey in the same study area in which we measured the number of flowers visited by bumblebees and honeybees on *L. stoechas* individuals. Bumblebees visited more than twice (117 ± 26.7) as many flowers as honeybees (52.7 ± 10.7) (GLMM, $z = 33.7$, $P < 0.001$) per individual. This result suggests that the shift in the major pollinator of *L. stoechas* resulted in increased deposition of geitonogamous pollen, ultimately leading to reduced reproductive success. An *ad hoc* analysis of *L. stoechas* fruits of the tagged plants of the control and colonized plots confirmed that seed set was negatively correlated to bumblebee visitation (proportion of bumblebee visits: GLM, $F_{1,12} = 5.1$, $P = 0.04$; $r = -0.55$; bumblebee visitation rate: GLM, $F_{1,12} = 3.4$, $P = 0.09$; $r = -0.47$).

On the other hand, fruit set of *T. vulgaris* F increased in colonized plots. Again, because we found no differences in conspecific pollen loads between control and colonized plots, we hypothesize that this change in reproductive success was mediated by changes in conspecific pollen quality. *T. vulgaris* F pollinator-generalization increased in colonized plots and various studies have found a positive relationship between pollinator diversity and plant reproductive success (Gómez et al. 2007, Perfectti et al. 2009, Albrecht et al. 2012). Different pollinator species have different foraging behaviours, notably in terms of distances flown between consecutively-visited plants (Herrera 1987a, 1987b), resulting in different outcrossing distances. Therefore, pollinator diversity entails genetic diversity of pollen loads and increased chances of reaching optimal outcrossing distances (Waddington 1983, Waser and Price 1991), potentially leading to increased reproductive success (Niesenbaum 1999, Paschke et al. 2002).

1.4.5. Concluding remarks

We show that the arrival of a native plant into a natural community may affect the pollinator community, plant–pollinator interactions, network structure, pollination and plant reproductive success even when the new plant is not overly dominant. Our experiment simulates a process that is becoming increasingly frequent under the current scenario of climate change in which some plants are rapidly modifying their distribution along elevational gradients (*e.g.* Kelly and Goulden 2008), leading to changes in the flowering "theater". Our results demonstrate that ecological relationships between plants and pollinators are rapidly rearranged in response to novel situations, and the observed changes in plant reproductive success suggest that these shifts in interaction patterns may have long-term evolutionary consequences. In addition, our study establishes a relationship between network structure and function (see also Gómez et al. 2011, Gómez and Perfectti 2012). In our study, the relationship between network structure and pollination and plant reproductive success appears to be mediated by differences among pollinators in foraging behavior (abundance of pollinators that differ in number of flowers visited per individual plant, outcrossing distances) leading to changes in pollen quality. Pollen quality, as opposed to pollen quantity, is increasingly being signaled as a factor limiting plant reproductive success (Aizen and Harder 2007, Arceo-Gómez and Ashman 2014). Therefore, we encourage pollination ecologists to further explore the link between pollinator foraging behavior, plant–pollinator network structure and the quality component of pollination (*e.g.* Valverde et al. 2019) to improve our understanding of the relationship between interaction patterns and plant reproductive success.

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CHAPTER 2

Patch size affects the structure of host-parasitoid communities and their interaction networks: a study with cavity-nesting bees and wasps

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Manuscript in preparation

Abstract

The species-area and the link-area relationships establish that species and interaction richness increase with habitat area, and both relationships are supported by strong empirical evidence. However, information on how area size may affect interaction network structure is mostly lacking. In these study we analyze the structure of cavity-nesting bee-wasp communities and their nest associates (henceforth hosts and parasitoids) as well as their interaction networks in habitat patches of three size categories (small, ~0.1 ha; medium, ~5 ha; and large, sites of continuous habitat, akin to the mainland in island biogeography studies). Our objective is to test several species-area, link-area and network-area hypotheses based on previous theoretical and empirical studies. In partial agreement with our hypothesis, species and interaction richness increased from small to medium patches, but not from medium to large patches. Contrary to our expectations, richness of the higher trophic level (parasitoids) was not more affected by patch size than the lower trophic level (hosts), and interaction richness was not more affected by patch size than species richness. In partial agreement with our hypothesis, host, parasitoid and interaction communities of small patches were nested subsets of those in medium and large patches, but we did not find a nested structure between medium and large patches. Links per species increased with patch size, and host vulnerability was higher in large patches than in the other two size classes. Parasitism rate did not follow any patch-size-mediated trend. Based on network-area theory, we expected network specialization and modularity to increase with patch size, but these expectations were not met. Network specialization and modularity did not follow clear size-related trends. On the other hand, and in agreement with our hypothesis, the number of modules increased with patch size. Our study is in partial agreement with the species-area and the link-area relationships. However, our results are mostly in disagreement with the predictions of the network-area relationship. We suggest that community impoverishment in small patches may result in severe trophic constraints, leading to high ecological specialization and modularity in small patches. Our results have important implications for conservation, since medium patches contain levels of species and interaction diversity similar to those of “mainland sites”.

Keywords: habitat fragmentation, host-parasitoid interactions, link–area relationship, nested communities, network-area relationship, network structure, species–area relationship

2.1. Introduction

The species-area relationship is one of the most ancient and robust laws in ecology (Arrhenius 1921, Lawton 1999). The increase in species richness with increasing area is a widespread pattern that can be explained by two mechanisms. The first mechanism relies on the habitat-diversity hypothesis, which states that large areas contain a greater diversity of habitats and therefore host a larger number of associated species (Williams 1964). The second mechanism is related to the theory of island biogeography, which states that, in an equilibrium situation, extinction rate is inversely related to population size, which is proportional to habitat area (MacArthur and Wilson 1967). In sum, this relationship predicts greater richness in larger areas (Connor and McCoy 1979).

In principle, a local community (*sensu* Leibold et al. 2004) should reflect regional diversity (Ricklefs 1987). However, because patch size varies and different species have different traits, the composition and structure of local communities may vary as a result of environmental filtering and dispersal barriers (Hanski et al. 1995, van Nouhuys and Hanski 2002, Cornell and Harrison 2014). As large patches usually hold more species-rich and densely populated communities (*e.g.* Aizen and Feinsinger 1994), communities from small patches are expected to be nested subsets of communities from large patches (*sensu* Patterson 1987). However, community local composition is also affected by other components of environmental variation, leading to differences among patches of different sizes as a result of species turnover (Baselga et al. 2010). Highly mobile generalist species, with greater colonization ability and capable of exploiting a wide variety of resources, may be able to colonize more patches and a greater variety of patch sizes (Dennis et al. 2000). Specialist species, on the other hand, tend to be locally rare and restricted to large patches (Tscharntke et al. 2002a, Rand and Tscharntke 2007, Öckinger et al. 2010). However, resources may easily become limiting in small patches (Dennis et al. 2003). In this context, specialist species may have a competitive advantage over generalist species, potentially leading to a situation of codominance (colonization-competition tradeoff; Maurer 1990, Tilman 1994, Morris 1996) resulting in increased community evenness. Importantly, the species-area relationship is steeper at higher trophic levels (Holt et al. 1999), meaning that these tend to be more affected by patch size than lower trophic levels. Thus, as stated by the *productive space hypothesis*, large patches are expected to accommodate more trophic levels and more individuals and species of higher trophic levels (Schoener 1989).

Organisms are not isolated entities, they establish interactions with other organisms in the community. In agreement with the species-area relationship and the scaling of the number of interactions (links) with species richness, the link-area relationship states that the number of links also increases linearly with area (Brose et al. 2004). Sabatino and collaborators (2010) found that interaction richness increased with patch size twice faster than species richness, but this faster increase may be attenuated as a consequence of dietary specialization in larger patches (Burkle and Knight 2012). As a consequence, links per species are expected to increase in large patches, leading to higher levels of function (Steffan-Dewenter and Tscharntke 2002). For example, various studies have found higher levels of predation/parasitism in large patches (Kruess and Tcharntke 1994, Thies and Tscharntke1999).

Interactions among species within a community can be arranged in networks describing the identity and the strength of each interaction. Through its above-mentioned effects on community structure and species composition, patch size is expected to have profound effects on network structure. However, in comparison to the large body of literature addressing the effect of patch size on species richness and, to a lesser extent, species interactions, information on the relationship between patch size and network structure is scarce.

Galiana and collaborators (2018) explored the relationship between area and food web network structure from a theoretical perspective. Their study shows that, based on the *trophic theory of island biogeography* (Gravel et al. 2011), generalist species may be preferentially selected in small patches, and therefore small patches should contain more generalized networks. By contrast, large patches, which contain more resources and therefore more associated specialist species, should host more specialized networks, which ultimately may lead to higher levels of modularity and a greater number of modules per network (Galiana et al. 2018). Empirical studies relating patch size and network structure are scarce (Gonzalez et al. 2011). In a study system composed of grasslands habitats of different sizes, Aizen et al. (2012) found that mutualistic networks in small patches were nested subsets of networks from large patches. In agreement with the predictions of Galiana et al. (2018), they also found that rare interactions and those involving specialist species were more prone to disappear in small patches. On the other hand, and in contrast to the theoretical expectations of Galiana et al. (2018), Spiesman and Inouye (2013) and Traveset et al. (2018) found that, sandhill and marshland habitat loss resulted in more specialized and modular mutualistic networks. These results may be indicative of a loss of generalist species and/or an increase in interactions between specialist species (Traveset et al. 2018). Finally, Laurindo et al. (2019) found no differences in bat-fruit network specialization and modularity between continuous (> 1000 ha) and fragmented (~350 ha surrounded by unfavorable habitat) forests.

In this study, we surveyed nests of cavity-nesting bees and wasps (henceforth CNBW) and their nest associates (parasitoids, cleptoparasites, predators and scavengers; henceforth parasitoids) in patches of open habitat within a dense forest matrix. Previous studies have demonstrated that CNBW communities are much richer and abundant in open habitats than in dense forests (Osorio et al. 2015). Our aim was to analyze the relationship between patch size and the structure of the host and parasitoid communities as well as the structure of their interaction networks. We have the following hypotheses: 1) host, parasitoid and interaction richness will increase with patch size; parasitoid richness will increase faster than host richness, and interaction richness will increase faster than species richness; 2) host and parasitoid evenness will decrease with patch size; as a consequence, interaction evenness will decrease with patch size; 3) local species/interaction composition will have a nested structure, with communities of smaller patches being subsets of communities of larger patches; 4) links per species, host vulnerability and parasitism rate will increase with patch size; parasitoid generality will decrease with patch size; 5) network specialization, network modularity and number of network modules will increase with patch size.

2.2. Material and Methods

2.2.1. Study area and site selection

The study was conducted in the Montseny Natural Park (Barcelona, NE Spain, 41°47'N 2°24'E) in 2016. The study area comprised 270 km^2 between 192 and 1235 m a.s.l. (Table SM1, Fig. SM1). The climate in the area is sub-Mediterranean, with a mean annual temperature of 13.8 ºC and a mean annual rainfall of 649 mm.

The natural vegetation of the park comprises dense forests of *Quercus ilex* with almost no understory of flowering plants (Bolòs 1983). This forest matrix is interrupted by scattered clearings of various sizes resulting from logging, extensive grazing and low-intensity agroforestry farming. In contrast to the forest matrix, these clearings (including scrublands and grasslands) host a high diversity of flowering plants. At the higher altitudes the forest has been replaced by meadows, and in the valleys surrounding the park, by a mosaic of seminatural habitats (scrubland and grassland), farmland and small urban areas.

We selected 42 sites of open habitat (favorable to CNBW; Osorio et al. 2015) grouped into three patch size categories: small, medium and large (14 sites per size category; Table SM1, Fig. SM1).

Small patches (mean ± SE: 0.15 ± 0.03 ha, range: 0.02 – 0.4 ha) were mostly clearings resulting from logging activities and contained no buildings (Fig. SM2a). Medium patches (5.65 ± 0.64 ha; 2 – 11.2 ha) were mostly farm complexes and contained at least one old building (Fig. SM2b). Both small and medium patches were surrounded by dense forest matrix (unfavorable to CNBW; Osorio et al. 2015) at least within a 500-m-buffer (Fig. SM2a-b). The third size category (large patches) was composed of sites located in very large areas of open habitat in the valleys and the higher altitude meadows. Although they were not proper patches, in the sense that they were not surrounded by forest matrix, we use the term "large patches" for convenience. All large patches contained buildings and their surroundings (500-m-buffer) contained > 50% of open favorable habitat (Fig. SM2c). These sites were expected to host the highest richness of CNBWs and to provide a good measure of the regional pool of species and interactions (akin to the mainland in island biogeography; MacArthur and Wilson 1967). To confirm that the forest matrix was unfavorable to CNBW, we sampled 5 additional sites within the forest (Fig. SM1). These sites yielded very few nests and almost no interactions with parasitoids (see below).

Distance between contiguous patches was ~ 1400 m (range: 456-4439 m) (Fig. SM1). This distance encompasses the foraging range of most CNBW species (Gathman and Tscharntke 2002, Guédot et al. 2009, Zurbuchen et al. 2010). Satellite imagery revealed few landscape changes in the selected patches for at least the last 30 years (Fig. SM2).

2.2.2. Trap-nesting

To obtain CNBW nests we installed one nesting station in each patch. Each nesting station consisted of seven drilled wood blocks (10 x 10 x 15 cm). Each block had 25 inserted paper straws of a given diameter (2, 3, 4, 5, 6, 7, and 8 mm), amounting to 175 cavities per station. Paper straw length was 5 cm for the 2- and 3-mm diameters, 9 cm for the 4-, 5- and 6-mm diameters, 12 cm for the 7-mm diameter, and 15 cm for the 8-mm diameter. Nesting stations were attached to trees or to farm buildings wherever these were available at ~ 150 cm above the ground, facing southeast. We placed bands of sticky glue at the base of each nesting station to avoid predation by ants and earwigs.

Every two weeks throughout the nesting season (March-October) we collected paper straws with completed nests and replaced them with empty paper straws, so that cavities of all sizes would be available throughout the nesting season. Collected nests were kept in an incubator simulating temperatures of the study area. In October nests were transferred to a 4 ºC chamber for wintering. At the beginning of the spring, nests were incubated at room temperature (~ 20 ºC) to enhance host and parasitoid development and emergence. Nests were then dissected and host identity, number of cells per nest, number of parasitized cells and parasitoid identity were noted.

2.2.3. Data analyses

For each patch size category, we evaluated sampling completeness by building individual-based rarefaction curves for host and parasitoid richness (Chao and Chiu 2016). We did not include interaction richness in these analyses due to its inherent interpretative difficulties (Jordano 2016). Observed and expected richness were similar both for hosts and parasitoids (Table SM2; Fig. SM3).

Spatial autocorrelation

The spatial distribution of study sites was constrained by the availability of patch sizes across the Park and its surroundings. To test for possible spatial and altitudinal autocorrelation in community composition we conducted Mantel correlograms. We first generated a matrix of geographical distances and a matrix of altitudinal distances between patches using Euclidean distances. We then generated a matrix of species composition (hosts + parasitoids) dissimilarities between patches, using the quantitative Bray-Curtis index. To control for potential effects of patch size category on species composition, correlograms were conducted separately for small, medium and large patches. We found no spatial or altitudinal autocorrelation (all $|r| < 0.2$ and $P > 0.05$) at all distance classes and patch size categories. Therefore, we did not include spatial coordinates in further analyses.

Hypothesis 1. Host, parasitoid and interaction richness will increase with patch size; parasitoid richness will increase faster than host richness, and interaction richness will increase faster than species richness.

We compared host and parasitoid richness across patch size categories with ANOVA's followed by *posthoc* Tukey's tests. Because parasitoid richness was highly correlated to host richness ($r = 0.70$, $P < 0.001$), we reanalyzed parasitoid richness with ANCOVA's including host richness as a covariate. Differences in interaction richness (number of different links present in a local network) across patch size categories were analyzed with Kruskal-Wallis tests because the residuals did not meet model assumptions, followed by *posthoc* Dunn's tests. Because interaction richness is affected by network size (hosts species x parasitoid species) (Dormann et al. 2009), we rerun the analysis with ANCOVA's including network size (log-transformed) as a covariate.

To test whether parasitoid richness increased with patch size faster than host richness, we run a model with richness as the response variable and the interaction between trophic level (host vs parasitoid) and patch size category as the explanatory variable. We run this model three times, comparing small vs medium, medium vs large and small vs large patches. We followed the same approach to test whether interaction richness increased with patch size faster than species richness, running a model with richness as the response variable and the interaction between entities (species (hosts + parasitoids) vs interactions) and patch size category as the explanatory variable.

Hypothesis 2. Host and parasitoid evenness will decrease with patch size; as a consequence, interaction evenness will decrease with patch size.

To visualize community structure and dominance patterns within each patch size category, we built host and parasitoid rank-abundance curves using the mean relative abundance of each species. Then we calculated species evenness using Hurlbert's PIE, which measures the probability that two randomly sampled individuals from the community belong to two different species (Hurlbert 1971).

We followed the same procedure for interactions. We used interaction frequency as a measure of "interaction abundance".

Differences across patch size categories in host, parasitoid, and interaction evenness were analyzed with Kruskal-Wallis tests because the residuals did not meet model assumptions, followed by *posthoc* Dunn's tests. Because parasitoid diversity was not correlated to host diversity (Spearman's $\rho = 0.07$, $P = 0.64$), we did not include host diversity as a covariate in the parasitoid diversity model.

Hypothesis 3. Local species/interaction composition will have a nested structure, with communities of smaller patches being subsets of communities of larger patches.

We assessed species/interaction nestedness with the temperature metric (Atmar and Patterson 1993). This metric is rooted in the theory of island biogeography and has been extensively used to quantify community nestedness (Ulrich et al. 2009). We used the algorithm BINMATNEST (Rodríguez-Gironés and Santamaría 2006) which calculates a line of perfect order for the community matrix above which all occurrences are expected. Absences above the line of perfect order and presences below it increase matrix temperature proportionally to the distance from the line. Matrix temperature ranges from 0 for a perfectly nested organization to 100 for a non-nested matrix. Then, again using BINMATNEST we calculated the ordering of rows and columns that minimizes matrix temperature ("packed matrix"). The statistical significance of the matrix temperature is compared to a null model in which the probability of occupancy is proportional to the richness of the site and the occurrence of the species or the interaction (Bascompte et al. 2003). Importantly, the ordering of the matrix (e.g. the rank of the sites) is ecologically meaningful (Rodríguez-Gironés and Santamaría 2006).

We used host, parasitoid, and interaction matrices in which each row represents a site (of a given patch size category) and each column a species or an interaction, and cells are filled with species and interaction occurrence (1: present, 0: absent). Each site was assigned its rank in the "packed matrix". If, as hypothesized, small patches are nested subsets of communities of larger patches, rank small patches > rank medium patches > rank large patches. Differences across patch size categories in rank values were analyzed with Kruskal-Wallis followed by *posthoc* Dunn's tests.

Some species and interactions contribute positively to nestedness, whereas others, called idiosyncratic, contribute negatively and therefore tend to increase matrix temperature (Atmar and Patterson 1993). We visually inspected host, parasitoid and interaction packed matrices to detect idiosyncratic species/interactions within in each patch size category.

Hypothesis 4. Links per species, host vulnerability and parasitism rate will increase with patch size; parasitoid generality will decrease with patch size.

We calculated links per species as the number of links divided by the number of species in each plot (*e.g.* Olesen and Jordano 2002). We also calculated host vulnerability (weighted mean of the number of parasitoid species attacking a host species) and parasitoid generality (weighted mean of the number of host species attacked by a parasitoid species) (Bersier et al. 2002). We then compared links per species, host vulnerability and parasitoid generality across patch size categories with ANOVA's followed by *posthoc* Tukey's tests. Parasitoid generality data were log-transformed to meet model assumptions. Because links per species, host vulnerability and parasitoid generality are affected by network size (Dormann et al. 2009), we rerun these analyses with ANCOVA's including network size (log-transformed) as a covariate.

We calculated parasitism rate of each nest as the proportion of parasitized cells. Then we compared parasitism rate across patch size categories using a betaregression model (link = logit). Site and host species were included as random factors. Because betaregression operates with open intervals and to avoid the presence of 0s and 1s, we transformed the data following Smithson and Verkuilen (2006). Model significance was assessed with a Wald test.

Hypothesis 5. Network specialization, network modularity and number of network modules will increase with patch size.

We built a host-parasitoid network for each site (henceforth local network) using interaction frequency data, *i.e.*, number of cells of a host species parasitized by a parasitoid species.

Network specialization was calculated using the H_2' index. H_2' uses interaction frequency data to analyze the degree of specialization between the lower and the higher trophic level and is not affected by network size (Blüthgen et al. 2006). H_2' ranges from 0 for extreme generalization to 1 for extreme specialization (Blüthgen et al. 2006). Differences across patch size categories in H_2' were analyzed with ANOVA followed by *posthoc* Tukey's tests.

Modularity (Newman 2006) was calculated using the quantitative algorithm of Becket (2016). For each local network the algorithm was re-run 100 times to stabilize modularity computation, obtaining a modularity index (*Q*) and a number of network modules (*nQ*). *Q* is proportional to the number and isolation of network modules and ranges from 0 for networks with a random configuration to 1 for networks composed by perfect compartments. To test whether the modular structure of each local network differed from a random organization, we build a null model in which 1000 networks were generated using the Patefield's algorithm (Patefield 1981), which randomizes observations keeping row and column sums constant. Then, the observed value of modularity was compared with the 95% confidence interval of the null distribution of random modularity values. Differences across patch size categories in Q were analyzed with ANOVA followed by *posthoc* Tukey's tests. Only values of networks that were significantly modular were included in these analyses.

Because modularity may be affected by network size (Olesen et al. 2007), we also calculated relative modularity (Q'). $Q' = (Q - \bar{Q}_{null})/\sigma Q_{null}$, where $\bar{Q}_{null}$ and σQ_{null} are the mean and the standard deviation of the modularity values obtained with the null model. Relative modularity can thus be interpreted as the extent to which network structure differs from a random network. Differences in relative modularity (Q') were analyzed with ANOVA's followed by *posthoc* Tukey's tests.

Differences across patch size categories in number of network modules (*nQ*) were also analyzed with ANOVA followed by *posthoc* Tukey's tests. In the analysis of the number of network modules, networks that were not significantly modular were assigned 1 module by definition. To account for the potential effects of network size on number of network modules we reanalyzed *nQ* with ANCOVA including network size (log-transformed) as covariate.

Statistical software and reported values

All analyses were conducted in R v4.0.2 (R Core Team, 2019). We used the package *iNEXT* (Hsieh and Chao 2020) for rarefaction curves, *vegan* (Oksanen et al. 2019) for spatial autocorrelation analyses, *vegan* and *BINMATNEST* (C++ program; Rodríguez-Gironés and Santamaría 2006) for community nested structure analyses, *betareg*

(Cribari-Neto and Zeileis 2010) for betaregression models, and *bipartite* (Dormann et al. 2008, Dormann et al. 2009) for network analyses. All means are followed by ± SE.

2.3. Results

We obtained 4833 nests, amounting to 16804 cells. These nests were built by 44 bee and wasp species and hosted 47 parasitoid species. As many as 2855 cells from 1474 nests (of 34 host species) were parasitized (17.0 % cell parasitism; 30.5 % nest parasitism), resulting in 164 specific host-parasitoid interactions (Table 1). The low number of nests and cells produced in the five forest sites confirmed that the forest matrix was not a favorable habitat for CNBW communities (Table 1).

Table 1 Overall description of the CNBW community across patch size categories.

	Sites	Nests produced	Cells produced	Host richness	Parasitoid richness	Interaction richness
Small patches	14	609	1906	27	23	56
Medium patches	14	2058	7173	29	33	86
Large patches	14	2166	7725	32	34	97
Total	42	4833	16804	44	47	164
Forest matrix	5	28	64	4	1	1

Hypothesis 1. Host, parasitoid and interaction richness will increase with patch size; parasitoid richness will increase faster than host richness, and interaction richness will increase faster than species richness.

Patch size affected host richness ($F_{2,39} = 8.76$, $P < 0.001$), which, in partial agreement with our hypothesis, increased from small to medium patches but showed no differences between medium and large patches (Fig. 1a).

The effect of patch size on the structure of parasitoid communities followed the same pattern ($F_{2,39} = 4.57$, $P = 0.016$) (Fig.1b). However, differences in parasitoid richness between patch size categories disappeared after controlling for host richness ($F_{2,38} = 1.67$, $P = 0.20$).

Patch size affected interaction richness ($X^2_{(2,\ 42)} = 13.67$, $P = 0.001$), which again increased from small to medium patches with no differences between medium and large patches (Fig. 1e). However, these differences narrowly failed significance after controlling for network size ($F_{2,38} = 2.64$, $P = 0.085$).

In contrast to our expectations, parasitoid richness did not increase with patch size faster than host richness (Table 2). Similarly, interaction richness did not increase faster than species richness (Table 2).

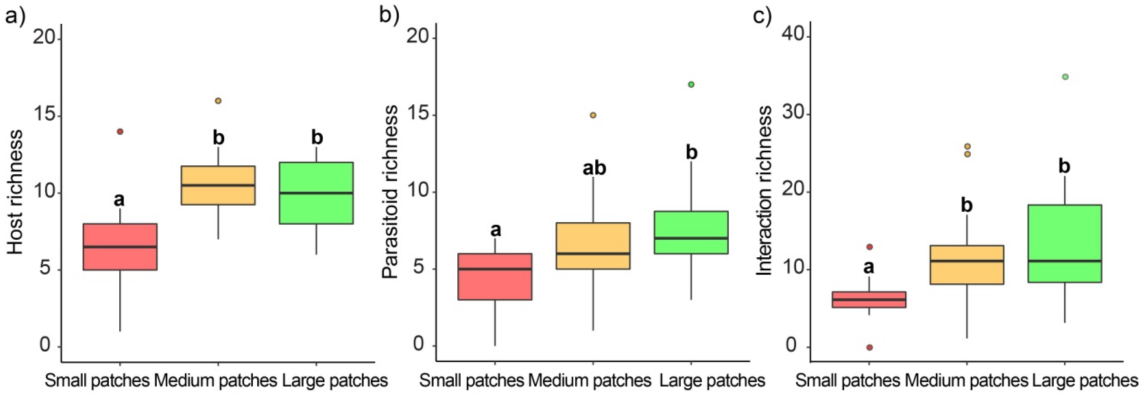

Fig. 1 Host richness (a), parasitoid richness (b), and interaction richness (c) in small, medium, and large patches (N = 14 per patch size category). Different letters denote significant differences at $P < 0.05$ (Tukey's test for (a, b), Dunn's test for (c)). Differences in parasitoid richness (b) disappear when host richness is included as a covariate. Differences in interaction richness (c) narrowly failed significance when network size is included as a covariate.

Table 2 Comparison of the standardized slopes of the relationships of patch size with host and parasitoid richness, and with species (host + parasitoid) and interaction richness (N = 14 per patch size category).

Contrast	*z* hosts	*z* parasitoids	$F_{1,52}$	*P*	*z* species	*z* interactions	$F_{1,52}$	*P*
Small vs Medium	3.86 ± 0.18	2.36 ± 1.16	1.05	0.31	6.21 ± 1.94	5.82 ± 2.42	0.02	0.90
Medium vs Large	-0.71 ± 0.18	1.07± 1.16	1.27	0.27	0.36 ± 1.94	1.57 ± 2.42	0.12	0.73
Small vs Large	3.14 ± 0.18	3.43± 1.16	0.04	0.85	6.57 ± 1.94	7.43 ± 2.42	0.08	0.78

Hypothesis 2. Host and parasitoid evenness will decrease with patch size; as a consequence, interaction evenness will decrease with patch size.

Rank-abundance curves showed that the relative abundance of the most dominant host species increased with patch size (Fig. 2a). The most dominant host species in large patches (*Osmia caerulescens*) was also the most dominant in medium patches but dropped to rank 6 in small patches, where the most dominant host species were *Trypoxylon* sp. and *O. submicans* (Fig. 2a, Fig. 3a-c).

In partial agreement with our hypothesis, host evenness differed between patch size categories ($X^2_{(2, 42)} = 8.6$, $P = 0.01$), decreasing from small and medium patches to large patches (Fig. 2b).

As opposed to hosts, rank-abundance curves of parasitoid species were quite similar across patch size categories, with a slight increase in dominance in medium patches (Fig. 2c). The most dominant parasitoid species in large patches (*Trichodes alvearius*) was also the most dominant in medium patches (together with *Sapyga quinquepunctata*) but dropped to rank 3 in small patches, where the most dominant parasitoid species was Tachinidae sp.1 (Fig. 2c, Fig. 3a-c).

Differences in parasitoid evenness between patch size categories narrowly failed significance ($X^2_{(2, 42)} = 5.35$, $P = 0.069$) (Fig. 2d). The *posthoc* analysis did yield significant differences but these did not follow the hypothesized trend of decreased evenness with patch size. Medium patches had lower evenness than large patches, and small patches did not differ from medium and large patches (Fig. 2d).

Rank-abundance curves of interactions were almost identical across patch size categories (Fig. 2e). Not surprisingly, the most dominant interactions involved the most dominant host and parasitoid species (Fig. 2e, Fig. 3a-c).

Contrary to our expectation, interaction evenness did not differ between patch size categories ($X^2_{(2, 41)} = 0.58$, $P = 0.75$) (Fig. 2f).

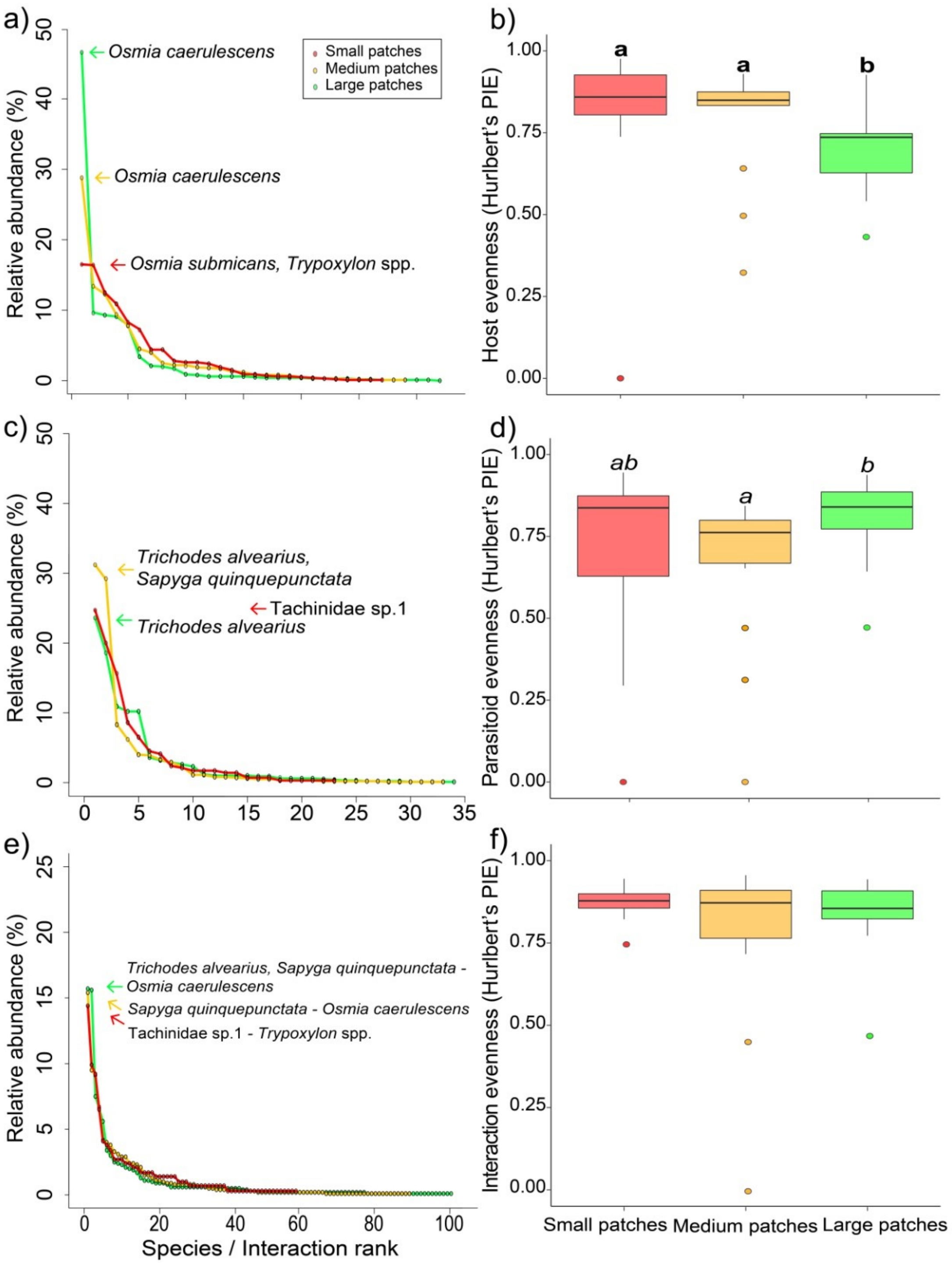

Fig. 2 Rank-abundance curves (a, c, e) and species evenness (Hurlbert's PIE) (b, d, f) for hosts (a, b), parasitoids (c, d) and interactions (e, f) in small, medium and large patches (N = 14 per patch size category). In rank-abundance curves each dot represents a species/interaction, and the most dominant species/interaction is indicated for each patch size category. In evenness plots different letters denote significant differences (in bold $P < 0.05$, in italics $P < 0.10$; Dunn's test).

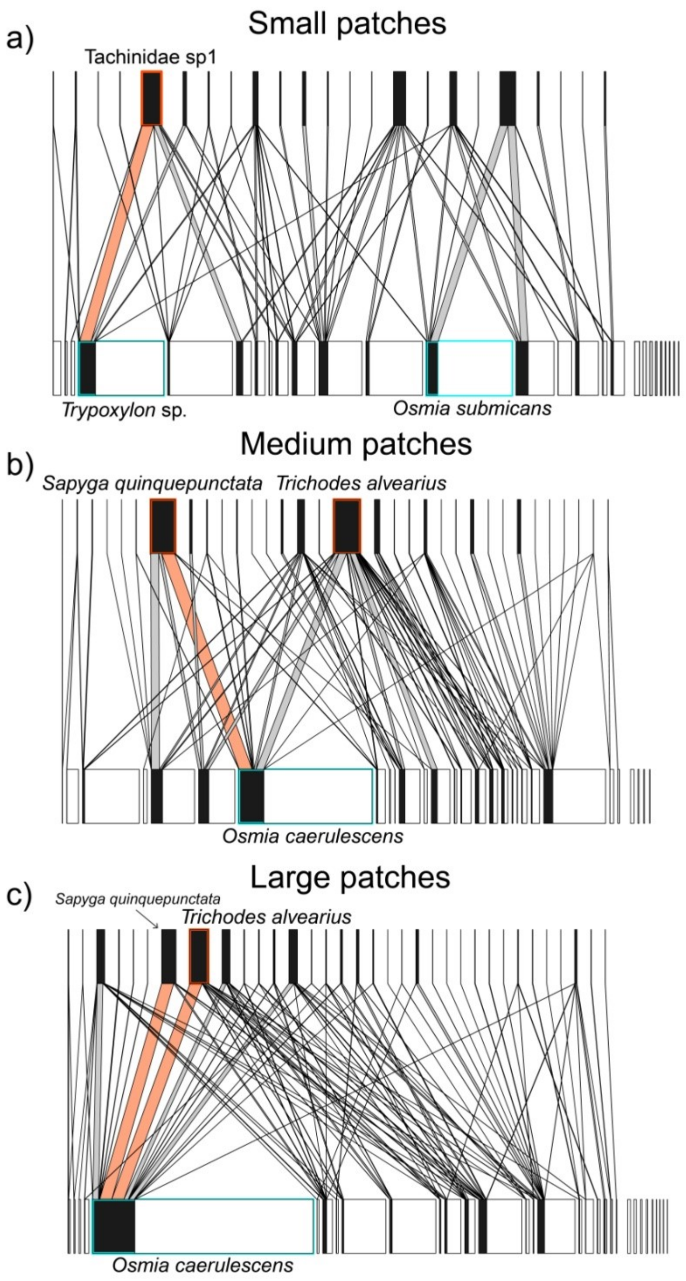

Fig. 3 Metanetworks of small (a), medium (b) and large (c) patches (N = 14 per patch size category), depicting community an interaction structure. Bars at the top represent parasitoid abundance (number of parasitized cells) and bars at the bottom host abundance (number of host cells, including parasitized (black) and non-parasitized (white) cells). Non-parasitized host species are represented at the bottom right-hand corner. Width of links denotes interaction frequency. Bars and links are at the same scale within a metanetwork but not between metanetworks. For each metanetwork, the most dominant host species (blue), parasitoid species (orange) and interaction (pale orange) are indicated.

Hypothesis 3. Local species/interaction composition will have a nested structure, with communities of smaller patches being subsets of communities of larger patches.

Nestedness temperature for host, parasitoid and interaction packed matrices was 19.3, 14.2 and 10.6, respectively (Figure 4a-c). These temperatures were significantly lower than those obtained in the respective null models (all $P < 0.001$) and therefore host, parasitoid and interaction communities showed a nested structure (Figure 4a-c).

In addition, there was a significant effect of patch size category in the ranking of sites in the nested packed matrix of host ($X^2_{(2, 42)} = 10.63$, $P = 0.005$), parasitoid ($X^2_{(2, 42)} = 10.23$, $P = 0.006$) and interaction ($X^2_{(2, 42)} = 11.23$, $P = 0.004$) communities (Figure 4a-c). For the three communities, small patches had higher ranks than medium and large patches (Dunn's tests, all $P < 0.018$), but medium and large patches had similar ranks (Dunn's tests, all $P > 0.41$) (Figure 4a-c). That is, host, parasitoid and interaction communities of small patches were nested subsets of communities of medium and large patches.

The packed matrices revealed a certain prevalence of idiosyncratic (contributing negatively to nestedness) host species in small patches (Figure 4a). These include species that are rare or non-existing in medium and large patches (*Megachile rotundata*, *Psenulus fuscipennis* and Pompilidae Gen. sp.), but also species abundant in other patch size categories (*Osmia bicornis,* found mainly in medium and large patches, and *Pison atrum,* found mainly in small and medium patches). Similarly, idiosyncratic parasitoid species were mostly found in medium patches (Figure 4b). These include species that are unique to medium patches (*Hybomischos* sp.2, *Omalus* sp.8, Brachonidae Gen. sp.2 and Chalcididae Gen. sp.1), but also found in other patch size categories (*Meloe* sp. in medium and large patches, and Tachinidae sp.1 in small and medium patches). By contrast, the incidence of idiosyncratic interactions was similar in all three patch size categories (Figure 4c) (*Anthrax trifasciatus – Hylaeus communis* and *Coelioxys inermis – Megachile centuncularis* (unique to large patches), Tachinidae sp.1 – *Pison atrum* (found in small and medium patches), and *Anthrax anthrax – Osmia leaiana* (unique to small patches)).

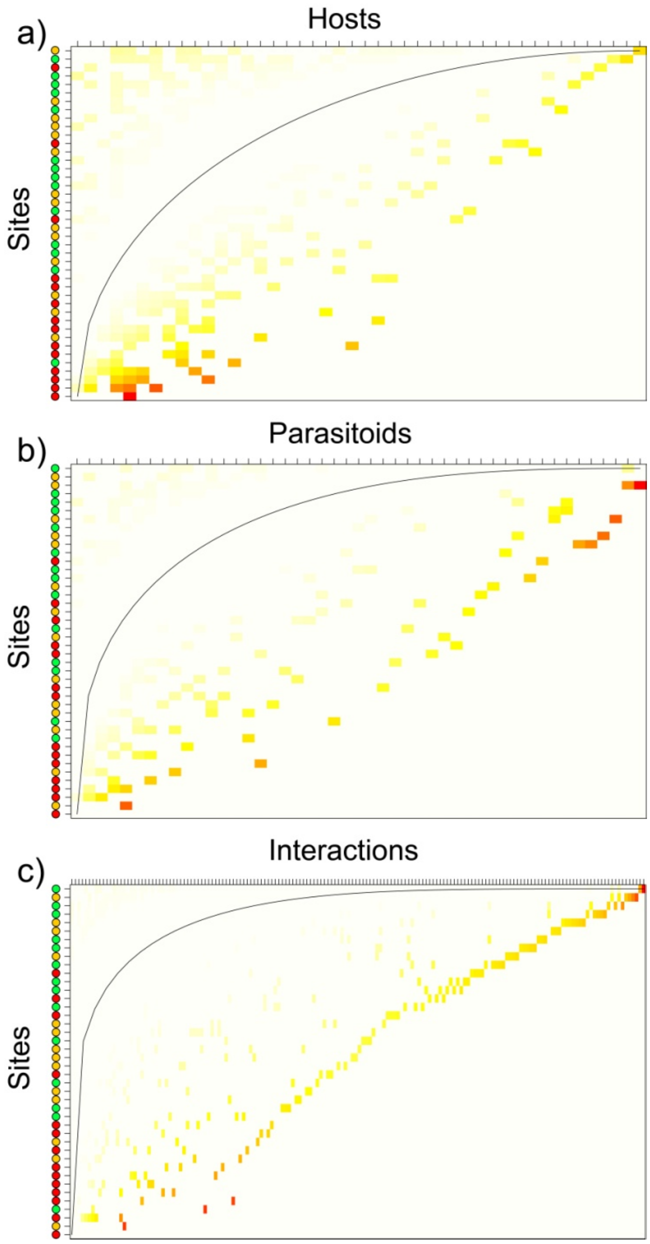

Fig. 4 Nestedness packed matrices for host (a), parasitoid (b) and interaction (c) communities based on the temperature metric. Each row represents a site of a given patch size categories (red: small; orange: medium; green: large; N = 14 sites per patch size category), and columns correspond to species / interactions. Sites and species / interactions are ordered so to minimize matrix temperature and the line of perfect order is drawn for each matrix. Unexpected absences (cells above the line) and occurrences (below the line) increase matrix temperature proportionally to their distance from the line. Color intensity is proportional to the temperature a cell exerts on matrix temperature. Species and interactions with high temperature may be viewed as idiosyncratic.

Hypothesis 4. Links per species, host vulnerability and parasitism rate will increase with patch size; parasitoid generality will decrease with patch size.

Links per species tended to differ between patch size categories ($F_{2,\ 39} = 3.08$, $P = 0.057$) and, in partial agreement with our hypothesis, were lower in small than in large patches, with no differences between medium patches and the other two patch size categories (Figure 5a). However, these differences disappeared after controlling for network size ($F_{2,38} = 0.57$, $P = 0.57$).

Host vulnerability differed between patch size categories ($F_{2,\ 39} = 6.94$, $P = 0.003$) and, in partial agreement with our hypothesis, increased from small and medium patches to large patches (Fig.5b). These differences persisted after controlling for network size ($F_{2,38} = 4.18$, $P = 0.02$). On the other hand, and in contrast to our hypothesis, parasitoid generality did not differ between patch size categories ($F_{2,38} = 1.85$, $P = 0.17$) (Fig.5c).

Parasitism rate differed between patch size categories (Wald test, $X^2_{(2,4747)} = 8.71$, $P = 0.013$), but did not follow the hypothesized pattern associated to patch size (Fig. 5d). Parasitism rate was higher in medium than in large patches, but small patches did not differ from medium and large patches (Fig. 5d).

Hypothesis 5. Network specialization, network modularity and number of network modules will increase with patch size.

Differences across patch size categories in network specialization (H_2') narrowly failed significance ($F_{2,37}$ = 2.79, P = 0.074). At any rate, the trend observed (a decrease from small to medium patches, with no differences between large patches and the other two patch size categories) did not confirm our hypothesis (Fig. 5e).

Three local networks (two from small patches and one from medium patches) were too small to compute modularity, and two small-patch networks were not significantly modular (Table S2). The remaining networks (12 from small, 13 from medium and all 14 from large patches) were more modular than random webs (Table S2).

Network modularity (Q) differed between patch size categories ($F_{2,35}$ = 3.35, P= 0.047) but, contrary to our hypothesis, decreased from small to medium and large patches (Fig. 5f). These differences disappeared when Q values of the two non-significantly modular networks from small patches were considered ($F_{2,37}$ = 1.07, P = 0.36). Network relative modularity (Q', which quantifies to what extent network modularity differs from random) differed between patch size categories ($F_{2,36}$ = 5.60, P = 0.008), increasing from small to medium patches, with no differences between medium and large patches (Fig. 5g) .

Number of network modules differed between patch size categories ($F_{2,39}$ = 2.83, P = 0.002) and, in partial agreement with our hypothesis, increased from small to large patches, with no differences between medium patches and the two other patch size categories (Fig. 5h). However, the effect of patch size on number of network modules disappeared after controlling for network size ($F_{2,38}$ = 0.34, P = 0.71).

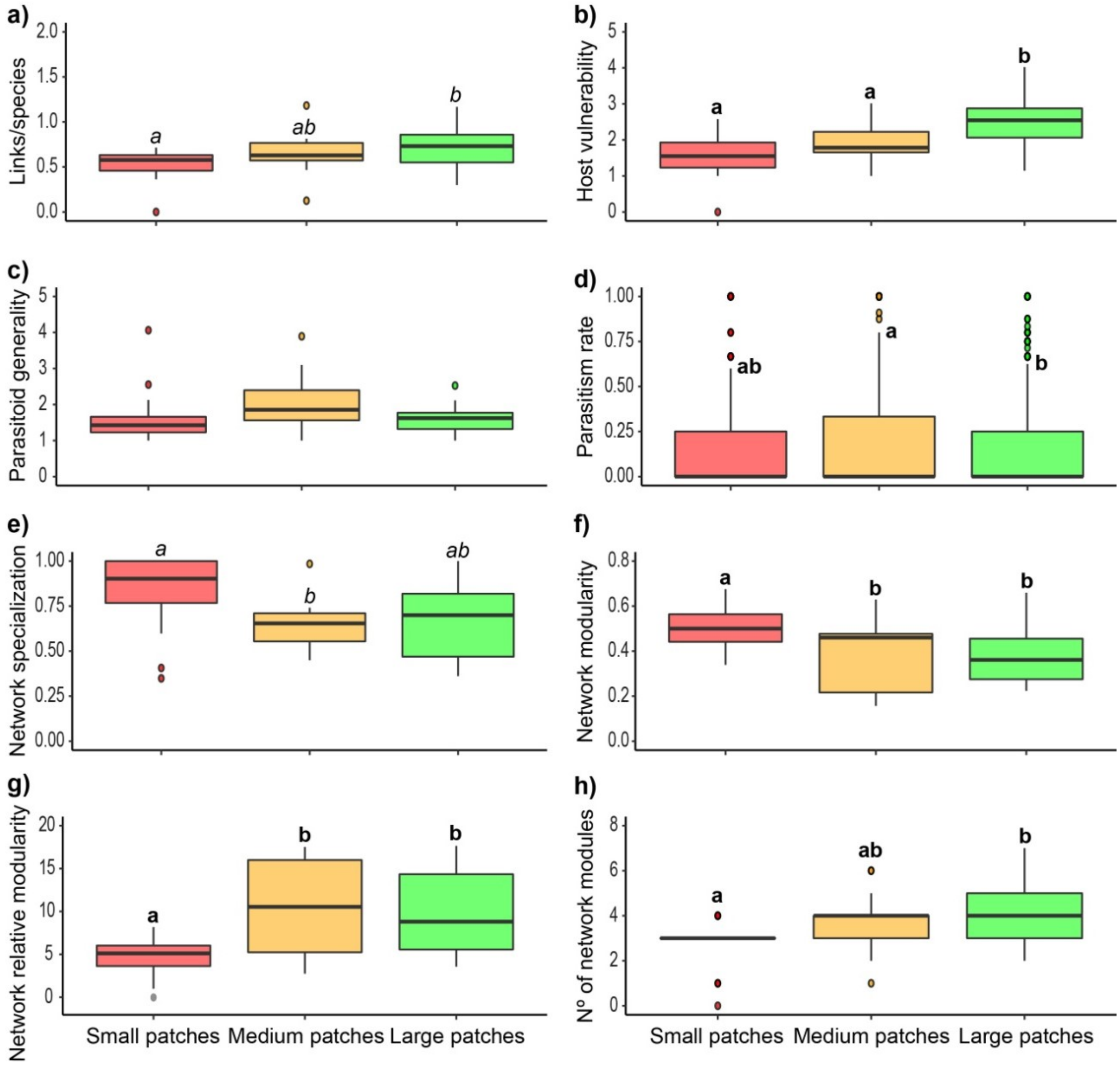

Figure 5 Number of links per species (a), host vulnerability (weighted mean number of parasitoid species attacking a host species) (b), parasitoid generality (weighted mean number of host species attacked by a parasitoid species) (c), parasitism rate (mean proportion of parasitized cells in each nest) (d), network specialization (H_2') (e), network modularity (Q) (f), network relative modularity (Q') (g) and number of network modules (nQ) (h) in small, medium and large patches (N = 14 sites per patch size category). Different letters denote significant differences (in bold $P < 0.05$, in italics $P < 0.10$; Tukey's test for (a-b, e-h), Wald test for (d)). When network size is included as a covariate, differences in number of links per species (a) and number of network modules (h) fail significance, whereas host vulnerability (b) remains significant.

2.4. Discussion

The general objective of this study was to establish whether CNBW communities and their interactions with parasitoids conformed to the predictions of the species-area, link-area and network-area relationships. For the most part, predictions regarding species-area and link-area relationships were partially met, but predictions regarding network-area relationships were mostly not met.

Hypothesis 1. Host, parasitoid and interaction richness will increase with patch size; parasitoid richness will increase faster than host richness, and interaction richness will increase faster than species richness.

A previous study (Steffan-Dewenter 2003) tested the species-area relationship in CNBW communities. Using a patch-size range that closely coincided with the size of our small and medium patches, and in agreement with our results, that study supported the species-area relationship (Steffan-Dewenter 2003). However, we used a wider patch size range and found that medium and large patches showed similar richness of hosts and parasitoids. The species-area relationship relies on two assumptions. The first assumption is the existence of a threshold below which area and energetic requirements of a focal species are not met, and the second is the existence of an asymptotic level of richness derived from the regional pool of species (Lomolino 2000). Thus, our results suggest that host and parasitoid populations overcome extinction thresholds in medium patches (Fahrig 2001). In other words, hosts and parasitoids find enough resources in medium patches to generate stable populations and communities (Fahrig 2013). The lack of differences in species richness between medium (~ 5ha) and large ("continental") patches suggests that medium patches contain the same amount and diversity of resources as large patches in the spatial scale at which CNBW experience their landscape, which ranges between 150 and 600 m (*e.g.* Gathman and Tschartnke 2002). On the other hand, probably due to resource scarcity, small patches (~ 0.1 ha) harbor clearly impoverished communities in comparison with the regional pool of species.

Because most parasitoids are totally dependent on relatively narrow ranges of specific hosts, parasitoids and hosts followed similar richness patterns (see also Osorio et al. 2015, Torné-Noguera et al. 2020).

Accordingly, and in agreement with the theoretical predictions of the link-area relationship (Brose et al. 2004), host-parasitoid interaction richness followed the same pattern as species richness, increasing from small to medium patches but with no differences between medium and large patches.

In contrast to our hypothesis, parasitoid richness did not increase faster than host richness with patch size. Our original prediction relies on the assumptions of parasitoid trophic specialization and energetic constraints of higher trophic levels (Holt et al. 1999). However, the effect of patch size on parasitoid and host richness may be similar if: a) parasitoid populations are enhanced in large patches resulting in increased top-down control of hosts. Positive relationships between parasitoid richness and host richness were found within each patch size category (Pearson's $r > 0.52$, $P < 0.057$), suggesting a generalized bottom-up control of parasitoid communities; b) Parasitoid communities contain highly mobile and generalist species. The parasitoid community was characterized by widely distributed species across all patch size categories (70% of parasitoid species occurring in at least 3 sites occurred across the three patch size categories). Thus, in our study, parasitoid and host species seems to be similarly affected by patch size because top-down control of hosts was absent and because parasitoid community contained widely distributed species.

Again in contrast to our hypothesis, interaction richness in our study did not increase faster than species richness with patch size. This means that, on average, the gain of one species results in the gain of one interaction. In other words, as species richness increases with patch size, only a small fraction of the new potential interactions is realized, corroborating the specialized nature of host-parasitoid relationships (*e.g.* Hawkins et al. 1994).

Hypothesis 2. Host and parasitoid evenness will decrease with patch size; as a consequence, interaction evenness will decrease with patch size.

In partial agreement with our hypothesis, host evenness was lowest in large patches. This is mostly due to the strong dominance of *Osmia caerulescens* (Megachilidae) in large patches. *O. caerulescens* is well known to be a highly synanthropic species, and has been found to be particularly abundant in agricultural and urban environments (Westrich 1989, Falk and Lewington 2015, Rosas-Ramos et al. 2016). The fact that, in contrast to most other CNB species which are univoltine, *O. caerulescens* produces two generations per year (Taséi 1972, Westrich 1990, Vicens et al. 1993), may further have contributed to its high abundance in large patches.

As for parasitoids, and in contrast to our hypothesis, the lowest evenness was found in medium patches as a result of the strong dominance of the two most abundant parasitoid species in our study, *Trichodes alvearius* (Cleridae) and *Sapyga quinquepunctata* (Sapygidae). Schüepp et al. (2011) found that parasitoid communities of CNBW were positively affected by proximity to forest habitats. Both small and medium patches are open habitats surrounded by forest matrix. While in small patches the general scarcity of resources may prevent the enhancement of parasitoid populations, in medium patches the forest edge may act as a habitat with complementary resources for parasitoids (Ries and Sisk 2004). A complementary explanation for the observed pattern is that the high densities of *O. caerulescens* in large patches may sustain high densities of multiple parasitoid species (Steffan-Dewenter and Schiele 2008). These species of parasitoids comprise both generalist (*Anthrax anthrax* and *Melittobia acasta*; beefly and eulophid wasp, respectively) and specialist (*Chaetodactylus* sp.; parasitic mite) species.

As for interactions, in contrast to our hypothesis, evenness was unaffected by patch size. Our hypothesis was based on the expectation that both host and parasitoid evenness would decrease with patch size. Since this expectation was partially met for hosts and not met for parasitoids, and since host dominance was accompanied by new strong interactions, it is not surprising that interaction evenness was unrelated to patch size.

Hypothesis 3. Local species/interaction composition will have a nested structure, with communities of smaller patches being nested subsets of communities of larger patches.

In agreement with our hypothesis, communities of small patches were nested substets of communities of medium and large patches. Community nestedness patterns are mainly determined by selective immigrations and extinctions (Lomolino 1996). Highly mobile and generalist species, with high migration and colonization abilities, are found everywhere, whereas species with low dispersal capacities and high habitat / diet specialization are restricted to large areas, a situation that generates community nestedness (Dennis et al. 2012). These latter species may be unable to colonize small patches and, if they do, they may be incapable of maintaining successful populations, either as a consequence of the absence of a specific resource or as a consequence of stochastic extinctions. Thus, since in our study communities of medium patches were not nested subsets of communities from large patches, minimum habitat size for population persistence at the community level seems to be found in medium patches (Shaffer 1981, Fahrig 2007).

We also found that interactions of small patches were nested subsets of interactions of medium and large patches. Aizen et al. (2012) found a similar pattern which was explained by the non-random loss of rare interactions and those involving specialist partners in small fragments. That is, small patches may contain ubiquitous interactions as well as interactions involving generalist species, whereas medium and large patches may also host rare interactions and interactions between specialist species. The fact that, in our study, interaction communities of medium patches were not nested subsets of communities from large patches is not surprising given the absence of differences between these two patch size categories in species and interaction richness.

We found a high proportion of unique species (~20%) and interactions (~40%) to each patch category (Table S3). This feature implies a certain level of species turnover that potentially reduces the nested structure of communities. Species and interactions that decrease community nestedness are known as idiosyncratic (Atmar and Patterson 1993). We detected some idiosyncratic species of hosts in small patches, some idiosyncratic species of parasitoids in medium patches, and some idiosyncratic interactions across patch size categories. In some cases these species and interactions were rare and unique to a patch size category. However, in other cases, especially for hosts in small patches, they were idiosyncratic because they were particularly abundant in that patch size category. Idiosyncratic species and interactions, thus, are expected to result from the inclusion of a wider range of spatial variability beyond habitat size, such as specific habitat or resource requirements and/or interaction rewiring (Poisot et al. 2015).

Hypothesis 4. Links per species, host vulnerability and parasitism rate will increase with patch size; parasitoid generality will decrease with patch size.

In agreement with our hypothesis, links per species increased with patch size. However, host vulnerability increased only in large patches in relation to the other two size categories. Host vulnerability is expected to be related to parasitoid diversity patterns (*e.g.* Maunsell et al. 2015). While parasitoid richness increased with patch size, host vulnerability increased only in large patches. This pattern might be related to the fact that, in general, parasitoid species were able to attain high densities only in large patches (resulting in high parasitoid evenness), and therefore more species of parasitoids attacked host species in large patches.

Because generalist parasitoids are expected to be preferentially selected in small patches (Galiana et al. 2018), we hypothesized that parasitoid generality would decrease with patch size (*e.g.* Cagnolo et al. 2009). However, parasitoid generality was unaffected by patch size. A plausible explanation is that, in small patches, evolutionary generalist species may behave as ecological specialists due to reduced host diversity (Holt and

Lawton 1993). In addition, even when a range of valid hosts are available not only specialist parasitoids may be gained, but even generalist parasitoids may reduce their host spectrum by selecting preferred or abundant hosts, thus behaving as ecological specialists (Devictor et al. 2010, Armbruster 2017).

Parasitism rate did not follow any clear patch size mediated trend. The highest parasitism rate was found in medium patches (but only in comparison to large patches). Since parasitism rate is positively related to parasitoid diversity (*e.g.* Tylianakis et al. 2006), it is surprising that parasitism rate did not follow a similar pattern to parasitoid richness or host vulnerability. Because parasitism rate followed the same pattern as parasitoid evenness, so we provide related mechanisms. Thus, we suggest that the existence of an ecotone between the open habitat and the forest matrix may have fostered an *edge effect* by which rates of parasitism are enhanced (Fagan et al. 1999). Schüepp et al. 2011 found higher parasitism rate in host-parasitoid networks close to forest edges. Mechanisms explaining these edge effects include cross-boundary subsidies, in which parasitoid populations may be fostered by complementary resources present in forest edges, and ecological traps, if hosts use edge resources (*e.g.* dead logs as nesting sites) that ultimately attract parasitoids (Gates and Gysel 1978, Fagan et al. 1999). Edge effects would be expected to be even stronger in small patches, but host and parasitoid loss in small patches may have prevented potential interactions to occur, maintaining similar levels of parasitism with respect to medium and large patches. Alternatively, the high parasitism rate in medium patches could be related to the strong dominance of the parasitoid *T. alvearius* in this patch size category. *T. alvearius* is a generalist predatory beetle that attacked almost all host species in our study (Fig. 3) (see also Osorio et al. 2015, Torné-Noguera et al. 2020). This species often destroys all the cells within a nest, resulting in increased mortality in comparison to other parasitoids. Both *T. alvearius* abundance and relative abundance were correlated to parasitism rate (Spearman's $\rho = 0.46$, $P = 0.002$; $\rho = 0.47$, $P = 0.002$; respectively). Some studies have found that food webs dominated by a few parasitoid species result in enhanced host population regulation (Hawkins et al. 1999, Tylianakis et al. 2007). The fact that parasitoid evenness was lowest in medium patches in our study supports this relationship.

Hypothesis 5. Network specialization, network modularity and number of network modules will increase with patch size.

In contrast to our hypothesis, network specialization decreased from small to medium patches, with large patches showing no differences with the other two patch size categories. As stated above, due to impoverishment of the host community, generalist parasitoids may have access to a limited range of hosts in small patches, and thus become ecological specialists (Holt and Lawton 1993, Armbruster 2017). This mechanism can explain why the few empirical studies available found a correspondence between high network specializationand habitat loss (Spiesman and Inouye 2013, Traveset et al. 2018). In medium patches generalist parasitoid species are able to encounter more potential hosts, resulting in decreased network specialization. The intermediate H_2' values found in large patches may be explained by two opposite trends. On the one hand, by the presence of realized generalist species. On the other hand, by the presence of specialist species engaging in stronger interactions with their partners (Steffan-Dewenter and Tscharntke 2002, Tscharntke et al. 2002a, Aizen et al.

2012). That is, network specialization may reflect the presence of exclusiveness between interacting partners only in the largest patches (Blüthgen et al. 2008).

Contrary to our hypothesis, network modularity decreased with patch size, but only from small to medium patches, with medium and large patches showing similar network modularity. In principle, network specialization is related to network modularity (Dormann and Strauss 2014). Thus, as stated before, highest modularity in small patches may actually reflect high interaction constraints between partners rather than true evolutionary specialization between them. In other words, high modularity in small patches could be related to a high degree of isolation between modules as a consequence of a scarcity of highly connected species. Because of ecological and phylogenetical constraints, antagonistic networks tend to be highly compartmentalized (Cagnolo et al. 2011, Poulin et al. 2011). However, and in agreement with findings of Grass et al. (2018), host-parasitoid modularity is negatively affected by host richness, which would explain the high modularity found in small patches.

To account for potential effects of network size on network modularity, we also calculated relative modularity, that is, network modularity relative to a null model. Relative modularity increased from small to medium and large patches. Thus, network relative modularity followed a trend (increase with patch size) opposite to network modularity (decrease with patch size), so that small patches had the highest network modularity but were the least structured networks among patch size categories. In other words, networks from small patches seem to have high modularity simply by virtue of their size, because interacting partners are heavily constrained by partner availability. In contrast, networks from medium and large patches had lower network modularity, but much higher modularity than expected according to their size, because interactions are strongly structured.

In agreement with our hypothesis, the number of network modules increased with area. However, because differences in network modules between patch size categories disappeared after correcting for network size, network modules likely increased with patch size simply because larger patches contain more species and therefore a greater variety of species associations (Olesen et al. 2007, Ramos-Jiliberto et al. 2010). This work demonstrates that, besides species- and link- area relationships, other units of measure related to network structure, such as network modules, also scale with area. Because network modules can be regarded as co-evolutionary units (Thompson 1982, Olesen et al. 2007), this result suggests that larger areas may contain greater potential for evolutionary dynamics.

Interestingly, the observed patterns in modularity mean that the highest level of network stability is found in small patches (Thébault and Fontaine 2010). That is because the absence of highly connected species, which otherwise may decrease network modularity, decreases apparent competition and the probability of network collapse (Thébault and Fontaine 2010). Paradoxically, this result entails that the highest level of stability is found in the simplest and poorer species community and adds to the long-standing debate of diversity-stability relationships in ecosystems (May 1973, McCann 2000). However, community impoverishment in small patches may indicate that hosts and parasitoids may not be able to maintain levels of ecosystem function (pollination, biological control and population regulation) comparable to those in large patches and mainland sites (Tylianakis et al. 2006, Steffan-Dewenter and Westphal 2008).

Implications for conservation

The species-area relationship has long been explored and used for conservation purposes (*e.g.* Pimm et al. 1995). Although there is a need to understand the effect of the different drivers of global change on species interactions (Tylianakis et al. 2008), ecologists have only started to understand how ecological networks scale with area (Galiana et al. 2018), and therefore how habitat loss or fragmentation may affect the web of life. Our study is one of the first empirical works addressing the relationship between network structure and area.

Two important implications for conservation ecology emerge from our study. First, medium patches (~ 5 ha) contain as much species and interaction richness as large patches (continuous habitat). Therefore, a proper selection of medium patches may suffice to represent the regional pool of species and interactions, and to maintain good levels of ecosystem function and services (pollination and arthropod population regulation). In Mediterranean ecosystems forest encroachment is threatening open habitats within forest matrices (Cervera et al. 2019). This encroachment results in biodiversity reservoirs being concentrated in continuous habitats, which in turn are subjected to increasing agricultural intensification and urbanization (Vanbergen and Insect Pollinators Initiative 2013). A return to traditional extensive agricultural and livestock farming practices, would help to recover areas of open habitats within forest matrices, and could be a good conservation strategy to ensure biodiversity and ecosystem function. Second, although communities and interactions of small patches were nested subsets of communities and interactions of medium and large patches, some idiosyncratic species and interactions were also found in small patches. Thus, even small patches may have some conservation value (Tscharntke et al. 2002b). The modular structure of small-patch interaction networks seems to confer viability to these communities. We conclude that an appropriate combination of medium and small patches should achieve maximum spatial heterogeneity and therefore constitute and adequate conservation program in our system (Simberloff and Abele 1982).

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GENERAL DISCUSSION

GENERAL DISCUSSION

Ecological communities are highly variable as a consequence of a diverse array of ecological processes and environmental variation operating over short periods of time and over relatively small spatial scales. Because species interact between them, changes in ecological communities are likely to result in changes in interaction patterns and network structure. Finally, because species interactions determine function (e.g. pollination and predation), changes in interaction patterns and network structure may have far reaching consequences on ecosystem functioning. Understanding this process is of special interest in a global change scenario, as climate change is modifying species distributions and habitat loss is causing community simplification (Vitousek 1994).

In this thesis I aimed to understand the role of community and habitat variability on ecological communities, species interactions, interaction networks, and ecosystem function. I tried to elucidate this by conducting two field experiments and assessing the effects of changes in plant community composition on plant-pollinator networks and the effects of patch size on host-parasitoid networks.

The goal of this general discussion is to put the results of the two experiments of this thesis in the context in which they are embedded in order to generate a general framework to predict the responses of natural communities to plant colonization and a framework for the network structure-area relationship. We also aim to compare the responses of mutualistic and antagonistic networks to changes.

Changes in plant community composition affect pollinator communities, plant-pollinator interactions, network structure, pollination, and plant reproductive success

Community changes involving native species are frequent, include biologically and ecologically (*e.g.* in terms of adaptations and relative abundances) similar species (Micheli et al. 1999), and are becoming more important in a context of climate change in which species are modifying their distribution ranges (Kelly and Goulden 2008).

Can we predict plant-pollinator community wide effects of changes in plant community composition?

The case of experimental colonization of Cistus albidus

Cistus albidus is a Mediterranean flowering shrub species with specific traits. In this section we argue that community responses after the experimental colonization of *C. albidus* of native communities are mostly predictable based on its traits.

C. albidus is an early spring flowering plant with large, actinomorphic pink flowers that produce large amounts of pollen and nectar (Bosch 1992). It was primarily visited by honeybees, a managed, abundant, eusocial supergeneralist species; and attracted bumble bees, a large wild species with similar ecological features and high energetic requirements. Pollinators with high energetic requirements show floral preferences for flowers with high floral rewards (Heinrich 1975), which tend to be associated to floral characteristics such as large sizes and UV-Blue colours (Menzel and Shmida 1993, Giurfa 1995, Raine and Chittka 2007, Reverté et al. 2016) like those found in *C. albidus*.

Floral characteristics of *C. albidus* are related to species generalization levels (Ollerton et al. 2007). That is, because *C. albidus* interacted with all pollinators present in the community, overall network and pollinator generalization increased; and because it interacted heavily with abundant, generalist pollinators but also with rare, specialist species, network nestedness also increased. Because of the increase in generalization and nestedness due to *C. albidus* interactions, and because *C. albidus* produces large amounts of pollen, *C. albidus* became a pollen donnor (*sensu* Tur et al. 2016), dominating heterospecific pollen transfer. In spite of this, conspeficic pollen loads on native stigmas did not change, and increased heterospecific pollen loads on native stigmas were marginal. This suggests that, on the one hand, spillover to resident plants was relatively low and, on the other hand that, although at the species level all pollinators interacted with *C. albidus*, individual foragers might show high levels of floral constancy (Morales and Traveset 2008).

Supergeneralists species tend to reduce network modularity, merging network modules together (Albrecht et al. 2014). *C. albidus* acted as a supergeneralist but, probably as a consequence of its moderate relative abundance, their interactions were proportional (in degree and in frequency) to other species in the community. Thus, effects of *C. albidus* on network modularity were restricted to the heavy increase in visitation of the newcomer bumble bees to the native plant *Lavandula stoechas*, which resulted in a new network module. This change apparently translated into an increase of geitonogamous pollen on *L. stoechas* stigmas, resulting in a decrease in seed set.

Thus, for *L. stoechas*, the general pattern of facilitation generated by *C. albidus* contrasts with the negative output in reproductive success. Indeed, the indirect effects of *C. albidus* on *L. stoechas* reproductive success seems to be mediated by the floral preferences and the foraging behavior of bumble bees (Balfour et al. 2013, Benachour 2017) and by the floral display of *L. stoechas*. Similarly, although the positive output in reproductive success of *Thymus vulgaris* F is in accordance with the facilitation pattern that *C. albidus* exerted in the community, this output seems to be mediated by a positive diversity-function response as a consequence of an specific reproductive biology, *i.e.*, a female of a geitonogamous species being pollen-limited (Widén and Widén 1990, Knight et al. 2005). That is because *C. salviifolius* generalization also increased but reproductive success was unaltered, probably because large amounts of pollen production in this species prevents the species from heavy pollen limitation. To sum up, the effects on reproductive success were species specific and not related to general community-wide effects.

Different ecological contexts may induce different community wide and species-specific responses

Ecological processes such as plant colonization of local communities may generate novel plant-pollinator communities, new interactions and different network structures, and ultimately modify pollination and reproductive success of resident plant species.

Colonizing plants may represent a diverse array of taxa, with a diversity of flower structures and reproductive strategies, which may in turn end up in communities with a diverse array of plants that contain ecologically diverse pollinators. The characteristics of the colonizing plant, as well as the native plant-pollinator community, may determine the most likely output at the community and at the species level (Fig. 1).

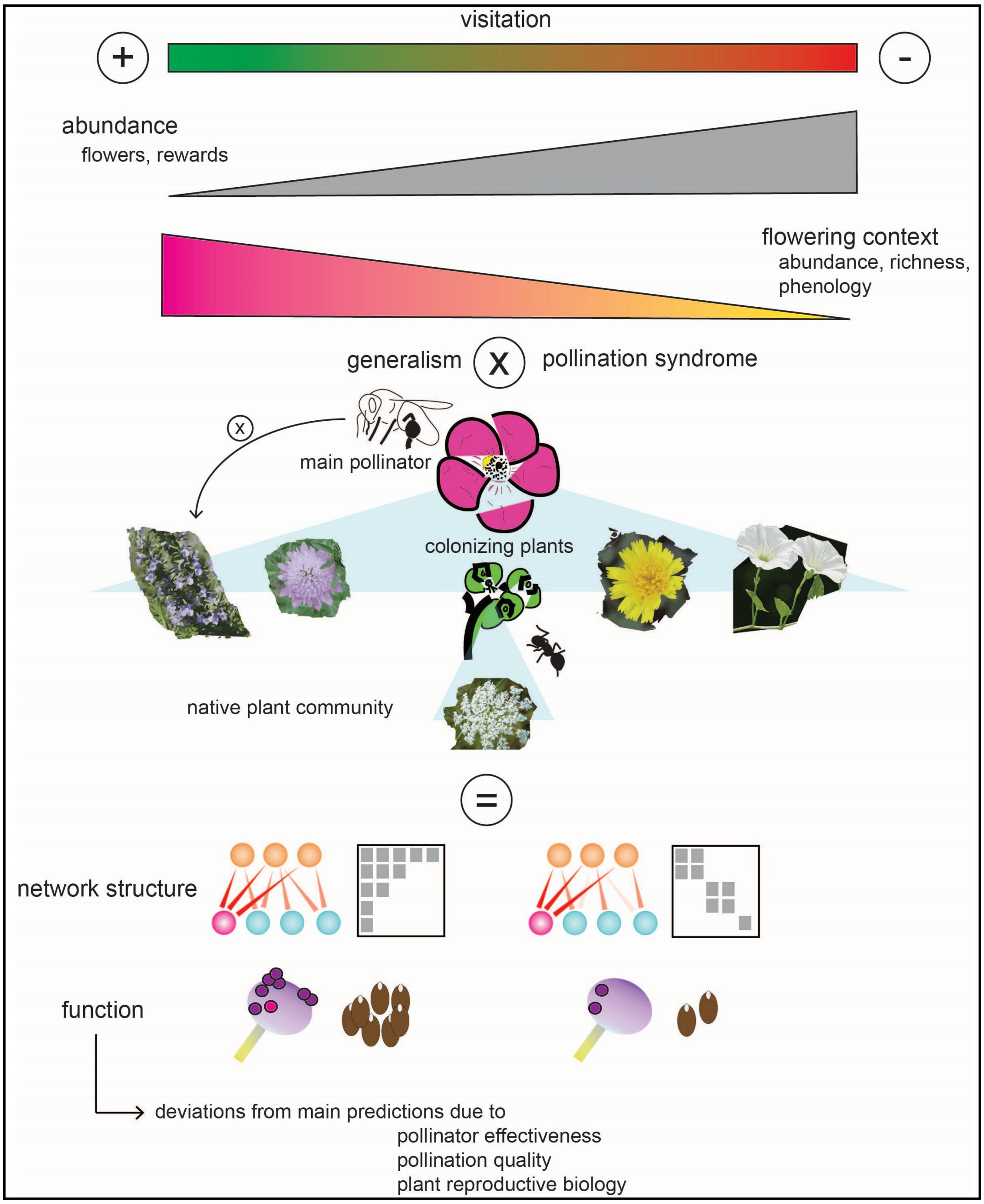


Fig. 1 General framework for the effects of changes in plant community composition on ecological communities. Facilitation of visits or competition for pollinators is mainly determined by the relative abundance of the colonizing plant. The degree of generalism of the colonizing plant may determine the extent of community wide effects, and its pollination syndrome which plant species are most likely to affect through shared pollinators. On this basis network structure and pollen deposition patterns are highly predictable. However, reproductive success may be conditioned by pollinator effectiveness, by the quality component of pollination and by plant reproductive biology.

First, and probably the most important factor, is the relative abundance of the colonizing plant (*e.g.* number of flowers). If colonizing plants exhibit low to moderate relative abundances there might be a positive effect on plant diversity, which may result in pollinator facilitation (Ratchke 1983, Gazhoul 2006). Contrary, at high relative abundances, the plant community might be dominated by the colonizing plant, and the most probable output is competition for pollinators, as usually seen in plant invasion studies (Ratchke 1983, Muñoz and Cavieres 2008, Morales and Traveset 2009).

Second, a factor that may condition community wide effects is the flowering context. One can easily notice the profound change in flowering community colors throughout the year (Arnold et al. 2009). In spring plant communities tend to be diverse, and there are more flowers than pollinators, *i.e.*, flowers compete for pollinators (Shmida and Dafni 1989). In summer plant communities are less diverse, and there are more pollinators than flowers, *i.e.*, pollinators compete for flowers. Accordingly, in spring, the *flowering market* in most Mediterranean communities is characterized by large, purple flowers with large floral rewards, *i.e.*, high investment in pollinator advertisement. In contrast, in summer flowers are characterized by small, white flowers with low floral rewards (Shmida and Dafni 1989, Bosch et al. 1997). Bartomeus et al. 2008a suggested that pollinators choose the most rewarding species only when resources at the community level are scarce. Thus, in spring, the arrival of a colonizing plant –showy and moderately abundant- may facilitate interactions to flowers that otherwise would not be visited, whereas in summer may monopolize the pollinators of the community (Bartomeus et al. 2008a, Russo et al. 2019).

Third, community wide effects may be related to the degree of generalism of the newcomer plant. Generalist plants can interact with a diverse array of pollinators, and therefore are easily incorporated into the colonized communities (Traveset and Richardson 2014). Therefore, generalist plants, which share pollinators with most of the rest of the plants in the community, are expected to have the potential to either facilitate or compete for pollinators at the community wide level (Russo et al. 2014). Specialist plant species, on the other hand, have a more restricted potential. On the one hand, if they experience an asymmetric specialization, they would interact with the most generalist species of pollinators (Ashworth et al. 2004). If so, the specialist plant would be rapidly incorporated in the community, and because generalist pollinators are also abundant (Fort et al. 2016), its effect on the community would be minimal. On the other hand, if the plant is in reciprocal specialization with a given pollinator (either at the species or at the functional group level), two possible outcomes are possible. First, the colonizing plant does not find its pollinator, a situation that can lead to the local extinction of the plant. Second, the colonizing plant may encounter its specialized pollinator, establishing a tight relationship (Liu and Pemberton 2010). If the colonizing plant is functionally similar and preferred over a resident species, competition might be restricted to that resident species.

Fourth, plants with similar flower characteristics (size, symmetry, colour) tend to interact with similar pollinators, a pattern that is called *pollination syndromes* (Fenster et al. 2004). Although plant-pollinator systems are highly generalists (Waser et al. 1996), one can easily realize that different kinds of flowers are usually associated to different kinds of flower visitors. Thus, the most important pollinator (or functional group of pollinators) of the colonizing plant (*e.g.* Larsson 2005) may channel the potential effects that this plant may have on the rest of the plant community (magnet effect, spill over, pollinator facilitation or pollinator competition). Community wide effects and specific species responses to the presence of the colonizing plant might thus be related to flower similarity and therefore to pollinator overlap (Gibson et al. 2012), but also to phylogenetic similarity (Morales and Traveset 2009). Because pollinators show multiple and variable characteristics (*e.g.* Willmer and Stone 2004), the specific traits of the pollinator may ultimately determine the extent and direction of the consequences on function (Herrera 1987, Herrera 1989).

Fifth, the production of pollen and nectar per flower. Together with flower abundance, floral rewards per flower unit may determine the magnitude of the magnet effect as well as the facilitation/competition effect that the colonizing plant may exert to the pollinator and the native plant community, respectively (*e.g.* Thomson 1988). Colonizing plants with high pollen production are therefore likely to become, provided they are generalists, pollen donors (*sensu* Tur et al. 2016). Because they are in turn expected to be visited by large pollinators, which are capable of transporting large amounts of pollen (Bosch 1992, Willmer and Finlayson 2014), this situation may lead to the domination of pollen transport networks (Lopezaraiza-Mikel et al. 2007), with potential risk for heterospecific pollen deposition (Brown and Mitchell 2001). However, there is an astonishing amount of evidence that heterospecific pollen deposition is marginal, even when the colonizing species is dominant (*e.g.* Bartomeus et al. 2008b, Dietzsch et al. 2011, Ashman and Arceo-González 2013; but see Briggs et al. 2016). Individual foragers of the most important pollinators, bees, show high levels of floral constancy and specialization (Goulson 1999, Brosi 2016), especially eusocial bees (Wells and Wells 1986), which usually dominate plant-pollinator communities (*e.g.* Reverté et al. 2019). Actually, potential heterospecific pollen transfer might occur if colonizing plants produce large amounts of nectar in comparison to pollen. Whereas bees foraging for pollen are highly constant, bees foraging for nectar usually visits several flowers of several species in a single bout (*personal observation*).

Regarding network structure, facilitation of interactions may lead to the realization of interactions involving not only the colonizing plant but other species already present in the native community, increasing overall network connectance and generalization (Valdovinos et al. 2009, Hernández-Castellano et al. 2020). If plants and pollinators engage in more and stronger interactions, interaction asymmetries are expected to increase, fostering an increase in network nestedness (Traveset et al. 2013, Stouffer et al. 2014, Hernández-Castellano et al. 2020). Because network nestedness and modularity are inversely related (Fortuna et al. 2010), network modularity may decrease and network modules may become strongly connected to each other, blurring the compartmentalized network structure (Santos et al. 2012, Albrecht et al. 2014). Competition (*e.g.* pollinator exclusion) may lead to the opposite pattern, *i.e.*, network nestedness may decrease and network modularity may increase (Valido et al. 2019). Colonizing plants might also form new modules either through new attracted pollinators to the community or through generalist pollinators usurped to native plants (Albrecht et al. 2014). In general, the network role of the colonizing plant would be similar to that played in its original distribution range (Emer et al. 2016).

Facilitation of interactions leads to increased visitation and may lead to increased conspecific pollen deposition (Ashman et al. 2020). Contrary, competition for pollinators leads to decreased visitation and may lead to decreased conspecific pollen deposition (Mitchell et al. 2009). Thus, facilitation could lead to an increase in reproductive success (*e.g.* Feldman 2008), whereas competition could lead to a decrease in reproductive success (*e.g.* Brown et al. 2002) if reproductive success is pollen-limited.

However, pollination and reproductive success may be affected not only by the quantity but also by the quality of pollination (Aizen and Harder 2007). Although visitation and conspecific pollen loads might remain unaltered, the genetic quality of the pollen delivered on stigmas may be altered as a consequence of changes in plant-pollinator interactions, with important consequences on plant reproduction (Alonso et al. 2012). In that situation, network structure might be useful to shed light into reproductive success patterns. For instance, network generalization might be related to high genetic diversity reaching plant stigmas (Gómez et al. 2011). Similiary, whereas network nestedness could be associated to pollinator sharing, network modularity and network module composition may point to a tight relationship with a given species of pollinator (Hernández-Castellano et al. 2020) that might be altering the quality of the delivered pollen.

Depending on the reproductive biology of the plant species and its degree of pollen limitation, the quantity and the quality of pollination may have contrasting results in the reproductive output (Bjerknes et al. 2007). Thus, plants which are totally dependent on pollinators and obligate outcrossing species are expected to experience more changes in reproductive success than plants that have the capacity to self (Lundgren et al. 2013).

In sum, the relative abundance of floral resources of the colonizing plant and the flowering context may determine the sign and magnitude of either positive or negative effects on plant-pollinator interactions (*e.g.* Moragues and Traveset 2005). The degree of generalism and the pollination syndrome of the colonizing plant may determine the potential to interact with the whole plant community and with specific plants via shared pollinators. These characteristics may suffice to predict network structure and pollen deposition patterns. However, due to the importance of the quality component of pollination and to diverse plant biologies, reproductive success is highly unpredictable and species-specific.

We thus encourage ecologists to study the relationship between pollinator foraging behavior and network structure (Gómez et al. 2011, Tur et al. 2014), and between pollinator foraging behavior and the quality component of pollination (Valverde et al. 2019), to improve our understanding of the relationship between interaction patterns and plant reproductive success.

Changes in patch size affect host-parasitoid communities, host-parasitoid interactions, network structure, and parasitism

In this section we merge the results of our second experiment with the current body of knowledge, including empirical examples and theoretical expectations, to develop a framework for the network-area relationship.

Towards a comprehensive framework for the network-area relationship

Larger areas contain more abundant and diverse resources, and therefore species richness is expected to increase with area (*e.g.* Steffan-Dewenter 2003) (Fig. 2a). Small pathes might be highly influenced by local processes other than area that result in insufficient levels of resources to maintain stable populations (see *small island effect*, Lomolino 2000). As area increases, species may gradually overcome extinction thresholds (Fahrig 2001), and therefore species richness may increase very rapidly with increasing area. Species richness increases with area may gradually decrease when habitat size contains enough resources to host a community as rich as communities from the continent. Once the species asymptote is reached, increasingly large areas may simply contain similar species richness, and the level of species gain might be so weak as a consequence of species interactions (Cornell and Lawton 1992). Due to the trophic specialization of parasitoids and because of energetic constraints, parasitoids would be more affected by area than hosts (Holt et al. 1999) (Fig. 2a). However, both trophic levels might be similarly affected if parasitoid communities contain a considerable proportion of widely distributed generalist species (Holt et al. 1999).

Larger areas contain more interactions because number of interactions scale with number of species (Brose et al. 2004) (Fig. 2b). Because one species can establish several interactions with several species in the network, number of interactions is expected to increase more rapidly with area than number of species (Sabatino et al. 2010) (Fig. 2b). However, interactions and species might be similarly affected if specialist species are gradually gained and therefore only a small proportion of interactions are realized (Burkle and Knight 2012). Thus, links per species may increase with area (Galiana et al. unpublished data), but hosts and parasitoids may not be similarly affected (Fig. 2c). Host vulnerability may increase linearly with area because larger areas contain more parasitoids and more links. For parasitoids, though, the preferential selection of generalist species in small patches may not translate into a linear decrease in parasitoid generality with patch size. In small patches, impoverished host communities may prevent generalist parasitoid species from interacting with many potential preys. This situation may lead parasitoid species to behave as ecological specialists (Holt and Lawton 1993, Armbruster 2017). Parasitoid generality may increase as parasitoids have gradually more access to complex host communities as area increases (Devictor et al. 2010), but may decrease at the same pace as evolutionary specialist parasitoid species appear in larger areas (Galiana et al. 2018). This may yield a convex response of parasitoid generality with area (Fig. 2c).

How does network structure scale with area? In small patches, the generalized ecological specialization due to a heavy impoverishment of potentially interacting species may yield high levels of network specialization (Fig. 2d). As area increases, more interacting partners are available and generalist species may actually interact with many species, decreasing network specialization (Hernández-Castellano et al. Chapter 2). Large areas may contain more specialist parasitoid species associated to large populations of specialist host species, yielding new strong specialized interactions and increasing network specialization (Galiana et al. 2018, Gómez-Martínez et al. 2020). This may yield a concave response of network specialization with area (Fig. 2d). Network modularity may follow a similar pattern to network specialization because both variables are intimately related (Dormann and Strauss 2014) (Fig 2e). However, depending on the degree and the interaction frequency of interactions involving generalist species, as well as their role as connectors, specialization and modularity might not reach or exceed levels found in small patches. This process may explain why the scarce empirical evidence available suggests that the most specialized and modular networks are found in small habitats (Spiesman and Inouye 2013, Traveset et al. 2018, Hernández-Castellano et al. Chapter 2), where the most impoverished communities are found (Grass et al. 2018, Hernández-Castellano et al. Chapter 2). This framework incorporates the few empirical examples available and the theoretical expectations of increased specialization and modularity with area (Galiana et al. 2018).

Finally, provided that the specialized nature of host-parasitoid networks (Hawkins 1994) remains constant across scales, the number of network modules is likely to increase linearly with area because larger areas contain more species and therefore more species associations (Fig. 2f). Similarly, the inclusion of a wider range of spatial variability might also result in more species associations as a consequence of interaction rewiring (Poisot et al. 2015).

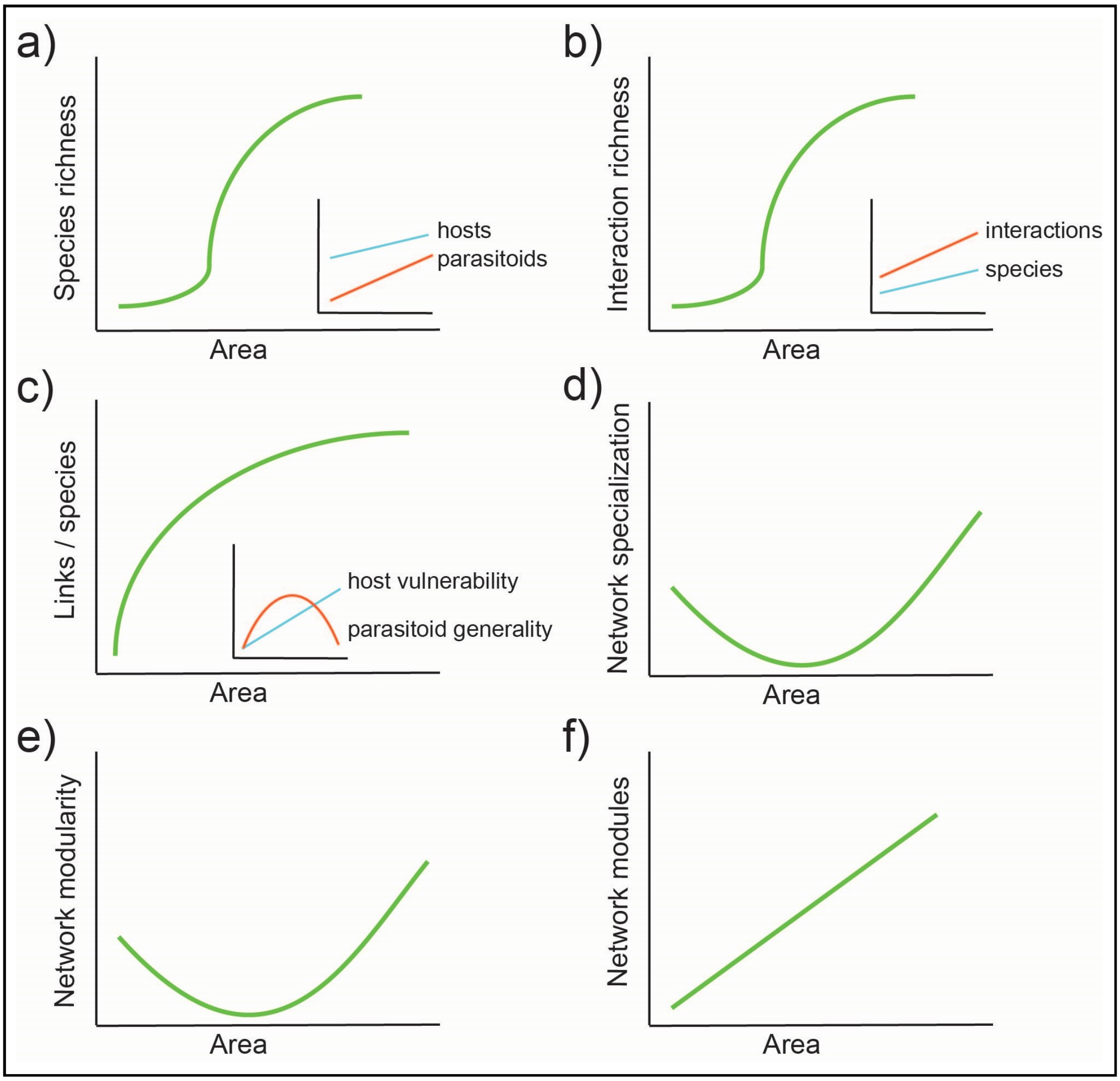


Fig. 2 General framework for the network-area relationship. Species (a) and interactions (b) scale in a similar fashion with area. Parasitoids are more affected by area than hosts (a) and interactions are more affected by area than species (b) (for simplification lineal relationships are drawn). As a consequence, number of links per species increase with area, with hosts being attacked gradually by more parasitoids and with parasitoids showing ecological and evolutionary specialization at small and large areas, respectively (c). Network specialization is determined by community impoverishment in small patches, which result in few potential interactions; as area increases realized generalists are found and the contribution of reciprocal specialization is expected to increase gradually with area (d). Network modularity follows a similar pattern to network specialization (e), and network modules increase linearly with area because more species associations are found (f).

We encourage ecologists to generate empirical evidence regarding the network structure-area relationship. The framework provided in this study, which tries to merge empirical evidence with theoretical expectations, can be used as a starting point, and consequently ratified, refuted, or modified according to the emerging body of knowledge.

Implications for conservation biology

The species-area relationship has long been used for conservation purposes, including the designation of natural reserves (Simberloff and Abele 1982, Pimm et al. 1995). In addition, current drivers of global change are affecting not only species but also interactions (Tylianakis et al. 2008). Therefore, understanding how ecological networks respond to changes in habitat area is important for the conservation of communities of interacting species and their related ecosystem functions.

Stability

In our study the highest network specialization and modularity was found in small patches. According to our study and to our developed framework on the network-area relationship, similar or actually higher levels of network specialization and modularity could only be reached in the largest areas. Specialization and modularity characterize antagonistic networks (Wcislo and Cane 1996, Cagnolo et al. 2011). These network variables are intimately related to antagonistic network stability, as network specialization and modularity prevent the spread of interactions because networks are compartmentalized, and thus apparent competition between hosts is reduced (Thébault and Fontaine 2011). In small patches, though, high levels of stability are expected to be reached simply by virtue of network size, because in impoverished communities species can actually interact with few partners and therefore network configuration is highly constrained. In contrast, large patches may have high levels of stability because interacting networks are built upon highly structured complex communities, *i.e.*, there are diverse species organized in multiple compartments of interacting species. Thus, network structure may prevent community collapse in small patches, whereas in large patches it may foster complexity and, ultimately, function (Tylianakis et al. 2006, Steffan-Dewenter and Whestpal 2008).

Diversity

A small patch would have little conservation value with respect to a large patch provided that the species community and the interactions of the small patch were a nested subset of those of the large patch (Patterson 1987). If species communities and interactions networks differ in composition not only due to richness but as a consequence of species and interaction turnover (either produced by species turnover or rewiring), deviations from perfect nestedness are likely. If so, idiosyncratic species and interactions may occur even in small patches and therefore conservation efforts should also target small sites (Atmar and Patterson 1993). Moreover, the species-area and the link-area relationships are useful to determine which habitat size is adequate to represent communities and networks as rich and complex as communities and networks from the continent (Cornell and Lawton 1992, Fahrig 2007). This habitat size reference may thus be useful to determine conservation efforts.

Function

Parasitism is the main mortality factor of CNBW (Hawkins 1994). Parasitism is an ecosystem function that is related to population regulation and therefore to community diversity (*e.g.* Paine 1966). The positive relationship between parasitism rate and area has been corroborated in multiple empirical works (Kruess and Tscharntke 1994, 2000; Thies and Tscharntke 1999). Diverse parasitoid communities, which are usually found in large patches, can strengthen parasitism rates (Tylianakis et al. 2006, Fenoglio et al. 2012). Specialist parasitoid species, which are usually found in large patches, also increase functional complementarity of the parasitoid community and have a strong influence on parasitism rates (Fenoglio et al. 2012, Peralta et al. 2014). However, higher parasitism rate is not always found in large areas (Steffan-Dewenter 2003, Steffan-Dewenter and Schiele 2008). Parasitism rate can also be promoted in highly altered habitats where a single parasitoid dominates the interaction network (Hawkins et al. 1999, Tylianakis et al. 2007). Generalist parasitoids can also be effective host population regulators, especially in diverse communities (Symondson et al. 2002, Tylianakis and Binzer 2014), but also generalist predators (Stiling and Cornelissen 2005). For this reason, parasitism rates are likely to be affected beyond attributes regarding habitat area. Other aspects such as surrounding landscapes (Thies et al. 2003, Klein et al. 2006), habitat structure (Schüepp et al. 2011) and species-specific attributes of particular parasitoid species (Hernández-Castellano et al. Chapter 2) must be taken into account to shed light into parasitism patterns in relation to habitat area. Thus, the relationship between community complexity, network structure and parasitism, remains unclear (*e.g.* Gagic et al. 2011). A decrease in network connectivity, which may result in a modular structure, may reduce host vulnerability as well as apparent competition between hosts, eventually reducing parasitism rate (Holt 1977, Cardinale et al. 2003, Frost et al. 2016).

Parallelisms and divergences in the response of mutualistic and antagonistic networks to changes

Mutualistic and antagonistic networks differ fundamentally in the interaction type and therefore in the consequences for their interacting partners. The study systems of this thesis are pollinators in general and solitary bees and wasps in particular. For pollinators we studied their mutualistic interactions with plants. For solitary bees and wasps we studied their antagonistic interactions with parasitoids. For both types of networks we studied their response to changes. Although the experimental setting and the questions addressed are different, both experiments are based in the increase in the availability of resources. In addition, in both cases the variables explored are based in community composition, interaction patterns, network structure, and ecosystem function. We may thus explore to what extent and in which direction the response of different kinds of networks involving pollinators differ, and if these results are in general accordance to the available body of knowledge.

The case of plant-pollinator and host-parasitoid networks at the Montseny Natural Park

At the Montseny Natural Park plant-pollinator communities were faced with the arrival of a new plant. The new plant was not overly abundant so this arrival represents a change in species composition (addition of a species) rather than a change in flower abundance (addition of flowers was adjusted to local floral resources). Host-parasitoid communities were faced with increasing amounts of habitat. Although responses were representative up to a threshold, in this section we point to general patterns for convenience.

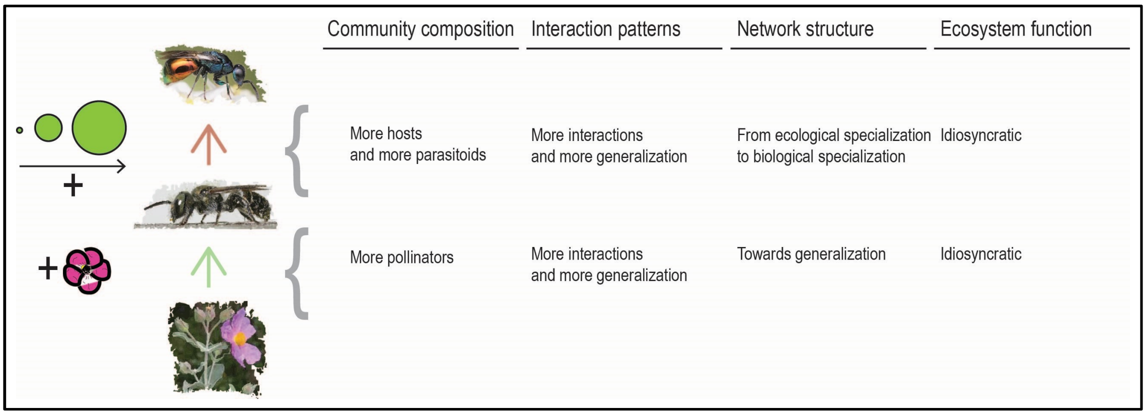
Regarding community composition, both types of networks responded in the same direction when resources were added (Fig. 3). On the one hand, the addition of *C. albidus* translated into a bumblebee abundance increase. On the other hand, increasing habitat area translated into an increase in host and parasitoid richness. Plants, pollinators and parasitoids conform consecutive trophic levels, and therefore they are expected to be highly dependent and covary between them (Potts et al. 2003, Osorio et al. 2015). Thus, the positive response of both mutualistic and antagonistic networks to an increase of resources is thermodynamically predictable in the terms that an increase in the abundance and / or richness in a given trophic level will lead to an increase in the abundance and / or richness of the consecutive trophic level (Lindeman 1942, Schneider and Kay 1994) (Figure 3).

Regarding interaction patterns, both types of networks responded similarly when resources were added (Fig. 3). The increase in the abundance of bumblebees translated into an increase in the frequency of interactions involving this species, but also in an overall increase in species and pollinator generalization. The increase in the abundance and richness of hosts and parasitoids translated into an increase in interactions, but also in an increase in host vulnerability. This pattern is in accordance to the scaling law of species and interactions (Cohen and Briand 1984, Martinez 1992) (Figure 3).

Regarding network structure, mutualistic and antagonistic networks differ in the extent and direction of their responses (Fig. 3). First of all, it must be said that changes in network structure in our experiments were weak in magnitude and significance. The structure of ecological networks has been previously demonstrated to be not only a pervasive but a stable feature of most communities (Petanidou et al. 2008, Vilà et al. 2009). At any rate, the addition of *C. albidus* resulted in an increase in network generalization as well as network nestedness. Increasing habitat area resulted in a complex pattern. Because interactions are ecologically constrained in small patches, network specialization and modularity decreased at first as parasitoids have gradually more access to more hosts. However, as communities become more complex, networks become more structured, and intermediate levels of network specialization were found in large patches. In our proposed framework we suspect that higher values of specialization and modularity are expected if the contribution of specialist species become progressively higher and the number of network modules continues to increase linearly with area. This suggests that the addition of resources in mutualistic and antagonistic networks may ultimately lead to more structured networks and, particularly, to network attributes that foster stability of each type of networks (Bastolla et al. 2009, Thébault and Fontaine 2011) (Fig. 3).

Regarding ecosystem function, mutualistic and antagonistic networks responded in a highly idiosyncratic manner (Fig. 3). In mutualistic networks, facilitation of interactions is likely to generate positive responses in pollination and reproduction of plants (*e.g.*

Feldman et al. 2008). In antagonistic networks, larger patches are likely to contain higher parasitism (*e.g.* Kruess and Tscharntke 1994). However, in our experiments, both types of networks showed species-specific responses in all directions and patterns that are not related to the main factor of study (Fig. 3).



Community composition	Interaction patterns	Network structure	Ecosystem function
More hosts and more parasitoids	More interactions and more generalization	From ecological specialization to biological specialization	Idiosyncratic
More pollinators	More interactions and more generalization	Towards generalization	Idiosyncratic

Fig. 3 The response of mutualistic (green arrow) and antagonistic (red arrow) networks to the addition of resources on community composition, interaction patterns, network structure, and ecosystem function.

Differential features and responses of mutualistic and antagonistic networks

Mutualistic and antagonistic networks have different structure as a consequence of ecological and evolutionary processes. As such, mutualistic networks show nested patterns that can be related to differential species abundances, whereas antagonistic networks show modular patterns as a consequence of coevolutionary histories and constraints (and vice versa) (Lewinsohn et al. 2006, Wardhaugh et al. 2015). Thus, the specialization structure among different types of networks fundamentally differs. In mutualistic networks specialist species interact with generalist species, and interactions between specialist species are absent, whereas in antagonistic networks reciprocal specialization between species or between groups of species is widespread (Guimarães et al. 2006). This pattern is likely the result of differential directions in natural selection. Mutualistic interactions favor the development of multispecies networks, whereas antagonistic interactions favor the compartmentalization through coevolution, generating modules of species engaged in arms races (Thompson 2005, Guimarães et al. 2006). For this reason, mutualistic partners usually engage in multiple interactions with a wide array of species, whereas antagonistic partners interact with few species that are closely phylogenetically related (Fontaine et al. 2009). Similarly, the stability of mutualistic and antagonistic networks is intimately related to the type of architecture that characterizes each type of network (Thébault and Fontaine 2011).

We are aware of only two empirical works which compare the response of mutualistic and antagonistic networks to changes. Grass and collaborators (2018) worked in grassland fragments of variable size and landscape features. They found effects on network structure of plant-pollinator and host-parasitoid communities mediated by species richness. Pollinator richness increased network modularity in plant-pollinator networks, whereas host richness decreased network modularity in host-parasitoid networks. They hypothesized that richer pollinator communities may reflect high functional diversity and therefore more species associations that may ultimately yield high modularity. However, they gave no specific interpretation for modularity patterns in host-parasitoid networks (Grass et al. 2018).

Morrison and Dirzo (2020) worked in a gradient of agricultural intensification. They found that plant-pollinator networks were always more nested and less modular than host-parasitoid networks. As agricultural intensification increased, species richness of plants, pollinators and herbivores decreased, and in both plant-pollinator and plant-herbivore networks, network nestedness increased, whereas network modularity decreased. They hypothesized that the prevalence of abundant and generalist species in intensively managed crops are responsible for the observed patterns in plant-pollinator network structure (Morrison and Dirzo 2020). Although they gave no specific information for patterns in plant-herbivore networks, it is assumable that the former mechanism is also applicable.

Taking together, both studies they reached similar conclusions regarding the responses of mutualistic networks: an increase in species richness leads to less nested and more modular networks. However, they reached contrasting conclusions regarding the responses of antagonistic networks: Grass et al. (2018) found that an increase in species richness leads to less modular neworks, whereas Morrison and Dirzo (2020) found that richer communities host more modular networks. We relate this difference to the fact that they study different kinds of antagonistic networks. Grass et al. (2018) studied host-parasitoid networks, whereas Morrison and Dirzo (2020) studied plant-herbivore networks. We therefore suggest that different patterns in antagonistic networks response might be related to different degrees of specialization, because herbivores are typically more specialized in their diets than parasitoids *sensu lato* (*e.g.* Cagnolo et al. 2009, Cagnolo et al. 2011). Thus, increased richness in host-parasitoid networks may result in an increase of potential partners, whereas increased richness in plant-herbivore networks may result in more associations between specialist species.

In our study on plant-pollinator networks, the addition of resources (a species of plant) translated into an increase in overall network generalization and nestedness, but pollinator richness was unaffected. Despite the facilitative effect on species interactions that the addition of resources may have, spatio-temporal heterogeneity is expected to result in a diversity of species associations and, as a consequence, in an increase in network modules (e.g. Morente-López et al. 2018). However, in highly generalized systems, the positive relationship between network modules and modularity is elusive (Olesen et al. 2007). A combined effect with the decrease in interaction asymmetry (and therefore nestedness) as a consequence of more even pollinator communities may lead to higher modularity values (Bascompte et al. 2003, Krishna et al. 2008).

In our study on host-parasitoid networks, our results parallel those found by Grass et al. (2018), which study the same types of communities. We thus suggest that the mechanisms behind network specialization (and therefore network modularity) with resource availability might be the same: high ecological specialization in small patches, followed by an increase in generalization. However, as hypothesized, we might expect a concomitant increase in network specialization if evolutionary specialists are gradually gained, which may ultimately lead to similar patterns to those found by Morrison and Dirzo (2020) with plant-herbivore networks.

Concluding remarks

Darwin (1859) referred to the diversity of species and interactions as the *entangled bank*. More than a century later, Lawton (1999) stated that community ecology is a *mess*. Communities are complex and variable. However, their responses to changes are predictable in their more fundamental aspects of organization (species and interactions). Interaction networks, indeed, give additional and important information about community assembly and structuring (*e.g.* Yodzis 1998), and allow for important generalizations to be made. Despite its recent development and empirical knowledge gaps, network structure is also generally predictable and, importantly, related to system stability. Despite the predictions and empirical examples available, the consequences of the reorganization of ecological communities in ecosystem function remain highly contingent. In this sense, it is possible that the disentanglement of complexity remains practically impossible for now.

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General Conclusions

Chapter 1

- We demonstrated that the arrival of a new plant have profound effects on plant-pollinator communities even when the new plant is a native species and is not overly dominant.
- The colonizing plant acted as a magnet species, attracting bumblebees to the colonized communities and facilitating interactions to other plants through spillover. The colonizing plant acted as a supergeneralist species, increasing plant, pollinator and network generalization, as well as network nestedness.
- Facilitation and generalization patterns through shared pollinators resulted in increased heterospecific pollen deposition on the stigmas of resident plants, although its magnitude was too low to potentially affect reproductive success.
- The colonizing plant also modified the composition of network modules. This alteration was mainly driven by the increased interaction frequency between bumblebees and some resident plants.
- The colonizing plant did not modify conspecific pollen loads on the stigmas of resident plants. However, reproductive success of two resident species was affected. Thus, the colonizing plant likely affected the quality of the pollen deposited through its effects on plant-pollinator interactions.

- One resident plant species showed increased reproductive success in colonized plots. This is likely to result from an increase in pollen load genetic diversity (mixture of pollen grains from different outcrossing distances) mediated by increased pollinator diversity.
- Another resident plant species showed decreased reproductive success in colonized plots. This is likely to result from a shift in the major pollinator (from honeybees to bumblebees). Bumblebees visit twice as many flowers as honeybees per individual plant, potentially increasing deposition of geitonogamous pollen.
- Our results establish a relationship between network structure and function that is mediated by differences among pollinators in foraging behaviour.

Chapter 2

- We demonstrated that patch size has profound effects on communities of cavity-nesting bees and wasps (hosts) and their nests associates (parasitoids).
- Host, parasitoid, and interaction richness increased from small to medium patches, but not from medium to large patches. Species communities and interaction networks from small patches were nested subsets of those in medium and large patches. Idiosyncratic species/ interactions were present in all patch size categories.

- These results have important implications for conservation. Medium patches contain as many species and interactions as large patches, and therefore this habitat size (~5 ha) may suffice to maintain high levels of diversity and ecosystem function (pollination and arthropod population regulation). In addition, even small patches may have some conservation value.
- Links per species increased with patch size, but parasitism rate did not follow any patch-size mediated trend. Parasitism rate seems to be influenced by features not necessarily related to patch size such as edge effects and parasitoid traits.
- Contrary to our expectation, network specialization decreased from small to medium patches, but network specialization of large patches did not differ from that of small and medium patches. We suggest that community impoverishment in small patches may limit the range of host species available to generalist parasitoids, leading to high ecological specialization.
- Also contrary to our expectation, network modularity decreased from small to medium and large patches. Importantly, the modular structure in small patches may confer robustness, preventing these impoverished communities to collapse.
- The number of network modules increased with patch size. This pattern was mainly mediated by an increase in network size. This work demonstrates that, besides species or links, other units of measure related to network structure also scale with area.
- Overall, our results are in partial agreement with the species-area and the link-area relationships, and mostly in disagreement with the predictions of the network-area relationship.

Conclusiones Generales

Capítulo 1

- Demostramos que la llegada de una nueva planta tiene efectos profundos en las comunidades planta-polinizador incluso cuando la nueva planta es una especie autóctona y no es excesivamente dominante.
- La planta colonizadora actuó como una especie imán, atrayendo a abejorros a las comunidades colonizadas y facilitando las interacciones a las otras plantas a través de un efecto de derrame.
- Los patrones de facilitación y generalización mediados por los polinizadores compartidos resultaron en un incremento de la deposición de polen heterospecífico en los estigmas de las plantas residentes, aunque la magnitud fue muy pequeña para afectar potencialmente al éxito reproductivo.
- La planta colonizadora también modificó la composición de los módulos de la red. Esta alteración fue principalmente impulsada por el incremento en la frecuencia de interacción entre los abejorros y algunas plantas residentes.
- La planta colonizadora no modificó las cargas de polen conespecífico en los estigmas de las plantas residentes. Sin embargo, el éxito reproductivo en dos plantas residentes se vio afectado. Por lo tanto, la planta colonizadora posiblemente afectó la calidad del polen depositado a través de sus efectos sobre las interacciones planta-polinizador.

- Una especie de planta residente mostró un incremento en el éxito reproductivo en las parcelas colonizadas. Posiblemente esto sea debido a un incremento en la diversidad genética de la carga de polen (mezcla de granos de polen de diferentes distancias de cruzamiento) mediada por un incremento en la diversidad de polinizadores.
- Otra especie de planta residente mostró una disminución en el éxito reproductivo en las parcelas colonizadas. Posiblemente esto sea debido al cambio en el polinizador más importante (de abejas de la miel a abejorros). Los abejorros visitan el doble de flores por individuo de planta que las abejas de la miel, incrementando potencialmente la deposición de polen geitonogámico.
- Nuestros resultados establecen una relación entre la estructura de la red y la función que está mediada por las diferencias en el comportamiento de forrageo de los polinizadores.

Capítulo 2

- Demostramos que el tamaño del parche tiene efectos profundos sobre las comunidades de abejas y avispas nidificantes en cavidades preestablecidas (huéspedes) y su fauna asociada (parasitoides).

- La riqueza de huéspedes, parasitoides, e interacctiones incremento de los parches pequeños a los medianos. Las comunidades de especies y las redes de interacciones de los parches pequeños resultaron ser subconjuntos anidados de las de los parches medianos y grandes. Se encontraron especies e interacciones idiosincráticas en todas las categorías de tamaño de parche.
- Estos resultados tienen implicaciones importantes para la conservación. Los parches medianos contienen tantas especies e interacciones como los parches grandes, y por lo tanto este tamaño de hábitat (~5 ha) podría ser suficiente para mantener niveles altos de diversidad y función ecosistémica (polinización y regulación de las poblaciones de artrópodos). Además, incluso los parches pequeños podrían tener un determinado valor de conservación.
- Los enlaces por especie incrementaron con el tamaño del parche, pero la tasa de parasitismo no siguió ninguna tendencia mediada por el tamaño del parche. La tasa de parasitismo parece estar influenciada por características no necesariamente relacionadas con el tamaño del parche, como los efectos de eje y los rasgos de los parasitoides.
- En oposición a nuestras expectativas, la especialización de la red disminuyó de los parches pequeños a los medianos, pero la especialización de la red de los parches grandes no difirió de la de los parches pequeños y medianos. Sugerimos que el empobrecimiento de las comunidades en los parches pequeños podrían limitar el rango de huéspedes disponibles para los parasitoides generalistas, produciendo una alta especialización ecológica.

- También en oposición a nuestras expectativas, la modularidad de la red disminuyó de los parches pequeños a los medianos y grandes. Importantemente, la estructura modular en los parches pequeños podría conferir robustez, previniendo el colapso en estas comunidades empobrecidas.
- El número de módulos de la red incrementó con el tamaño del parche. Este patrón fue principalmente mediado por un incremento en el tamaño de la red. Este trabajo demuestra que, más allá de las especies o los enlaces, otras unidades de medida relacionadas con la estructura de la red también escalan con el área.
- En general, nuestros resultados están en parcial acuerdo con las relaciones especies-área y enlaces-área, y mayoritariamente en desacuerdo con las predicciones de la relación estructura de la red-área.

Supplemental Material Chapter 1

Table SM1 Characteristics of the study plots before the addition of *Cistus albidus*.

Plot number	Plot code	Treatment	X coordinate	Y coordinate	Altitude (m)	Area (m^2)	Survey date	Flower abundance	Flower richness	Flower diversity (*H'*)
1	CC1	Control	450818	4619602	517	350	24/4/2016	16703	6	1.33
2	CC2	Control	444132	4620633	660	600	24/4/2016	25097	7	1.39
3	CC3	Control	444896	4619860	610	250	5/5/2016	64623	10	1.50
4	CC4	Control	448346	4618727	550	450	25/4/2016	63814	5	0.92
5	CC5	Control	448884	4620264	818	350	4/5/2016	1929	4	0.91
6	CC6	Control	449626	4622244	568	500	26/4/2016	8105	17	1.70
7	CC7	Control	444510	4620242	595	700	5/5/2016	34423	27	1.63
8	CC8	Control	448742	4621772	747	700	4/5/2016	5978	10	0.60
9	CC9	Control	448954	4623483	432	400	3/5/2016	65159	7	1.07
10	CT1	Colonized	449704	4619104	625	700	24/4/2016	83564	8	1.24
11	CT2	Colonized	444391	4621475	780	200	25/4/2016	5055	6	1.40
12	CT3	Colonized	444859	4617373	588	650	25/4/2016	13476	11	1.61
13	CT4	Colonized	449505	4620230	712	500	4/5/2016	131224	11	1.38

Table SM1 (continued).

Plot number	Plot code	Treatment	X coordinate	Y coordinate	Altitude (m)	Area (m^2)	Survey date	Flower abundance	Flower richness	Flower diversity (*H'*)
14	CT5	Colonized	449184	4619284	685	900	3/5/2016	221811	18	1.23
15	CT6	Colonized	448170	4623189	680	700	26/4/2016	13872	19	1.10
16	CT7	Colonized	444490	4620780	660	500	2/5/2016	7543	17	1.96
17	CT8	Colonized	448495	4622102	762	500	5/5/2016	6049	14	1.68
18	CT9	Colonized	452372	4621519	762	300	5/5/2016	3340	5	0.64

Table SM2 Abundance (mean ± SE number of individuals) of pollinator functional groups in control vs colonized plots (N = 9 per treatment). Significant results ($P < 0.05$) are shown in bold. Model: ANCOVA with treatment as fixed factor and flower abundance as a covariate. Flower abundance had no effect on hoverflies, medium-sized beetles, large beetles, short-tonged small bees, short-tonged large bees, wasps and grasshoppers, a marginal positive effect on small beetles ($P = 0.06$), and a significant positive effect ($P < 0.05$) on the rest of pollinator functional groups.

Functional group	Control	Colonized	$F_{1,15}$	P
Honey bees	5.94 ± 2.69	9.17 ± 4.07	0.18	0.68
Bumble bees	0.99 ± 0.40	3.15 ± 1.10	12.06	**0.003**
Short-Tongued Small Bees	2.65 ± 0.75	3.09 ± 0.55	0.23	0.64
Short-Tongued Large Bees	0.87 ± 0.22	1.17 ± 0.32	1.07	0.32
Long-Tongued Small Bees	0.73 ± 0.20	1.16 ± 0.68	0.02	0.88
Long-Tongued Large Bees	1.83 ± 0.54	1.51 ± 0.38	0.32	0.58
Hoverflies	10.33 ± 2.47	9.62 ± 1.86	0.06	0.82
Bee flies	1.69 ± 0.64	1.18 ± 0.44	0.70	0.41
Flies	3.66 ± 3.12	8.16 ± 6.80	0.02	0.89
Ants	4.30 ± 0.96	6.44 ± 3.09	0.85	0.37
Butterflies	1.24 ± 0.42	1.29 ± 0.56	0.68	0.42
Small Beetles	8.84 ± 4.56	3.29 ± 1.18	1.51	0.24
Medium-sized Beetles	2.99 ± 1.96	0.99 ± 0.40	1.03	0.33
Large Beetles	1.64 ± 0.93	0.86 ± 0.44	0.25	0.62
Wasps	0.06 ± 0.05	0.12 ± 0.07	1.44	0.25
True bugs	0.38 ± 0.35	1.56 ± 0.95	1.79	0.20
Grasshoppers	0.21 ± 0.10	0.40 ± 0.12	3.02	0.10

Table SM3 Specialization (*d'*) (mean ± SE) of the main pollinator groups in control and colonized networks (N = 9 per treatment) and results of Wilcoxon tests comparing the two treatments (control and colonized networks).

Specialization (*d'*)	Control networks		Colonized networks			
	mean	SE	mean	SE	*W*	*P*
Honey bees	0.29	0.08	0.21	0.06	47	0.59
Bumble bees	0.37	0.1	0.35	0.06	42	0.93
Short-Tongued Small Bees	0.07	0.04	0.04	0.03	49.5	0.37
Short-Tongued Large Bees	0.04	0.06	0.06	0.04	36	0.65
Long-Tongued Small Bees	0.22	0.11	0.13	0.06	40	0.42
Long-Tongued Large Bees	0.49	0.07	0.33	0.06	56	0.19
Hoverflies	0.1	0.04	0.09	0.05	47	0.59
Bee flies	0.44	0.1	0.21	0.07	53.5	0.10
Flies	0.2	0.09	0.31	0.08	28.5	0.31
Ants	0.18	0.08	0.18	0.07	39	0.93
Butterflies	0.23	0.09	0.12	0.07	46	0.34
Small Beetles	0.26	0.07	0.18	0.06	49.5	0.45
Medium-sized Beetles	0.17	0.07	0.08	0.04	32	0.34
Large Beetles	0.01	0.001	0.05	0.03	17.5	0.74

Table SM4 Nestedness values (*WNODF*) of control and colonized networks (N = 9 per treatment). All networks were significantly less nested than random networks.

Control network	*WNODF*	*P*	Colonized network	*WNODF*	*P*
CC1	32.4	**0.001**	CT1	33.3	**<0.001**
CC2	26.2	< **0.001**	CT2	28.9	< **0.001**
CC3	29.1	< **0.001**	CT3	28.8	< **0.001**
CC4	20.9	< **0.001**	CT4	29.9	< **0.001**
CC5	34.8	**0.003**	CT5	36.6	< **0.001**
CC6	21.9	< **0.001**	CT6	34.3	< **0.001**
CC7	15.8	< **0.001**	CT7	31.8	< **0.001**
CC8	36.1	**0.003**	CT8	30	< **0.001**
CC9	31.1	< **0.001**	CT9	36.6	< **0.001**

Table SM5 Modularity index (*Q*) and number of modules (*nQ*) of control and colonized networks (N = 9 per treatment). All networks were significantly modular.

Control network	*Q*	*nQ*	*z*	*P*	Colonized network	*Q*	*nQ*	*z*	*P*
CC1	0.18	4	70.7	< **0.05**	CT1	0.41	4	147.8	< **0.05**
CC2	0.22	4	112.7	< **0.05**	CT2	0.27	4	44.7	< **0.05**
CC3	0.52	4	189.6	< **0.05**	CT3	0.49	4	183.6	< **0.05**
CC4	0.2	2	69	< **0.05**	CT4	0.41	3	147.1	< **0.05**
CC5	0.24	3	59.6	< **0.05**	CT5	0.41	3	214.9	< **0.05**
CC6	0.36	4	74.4	< **0.05**	CT6	0.23	4	56.1	< **0.05**
CC7	0.51	4	84.6	< **0.05**	CT7	0.21	4	28.7	< **0.05**
CC8	0.35	4	58.7	< **0.05**	CT8	0.36	4	60	< **0.05**
CC9	0.43	2	178.5	< **0.05**	CT9	0.3	4	48.4	< **0.05**

Fig. SM1 Map of the study area indicating the location of control (grey dots) and colonized (white dots) plots.

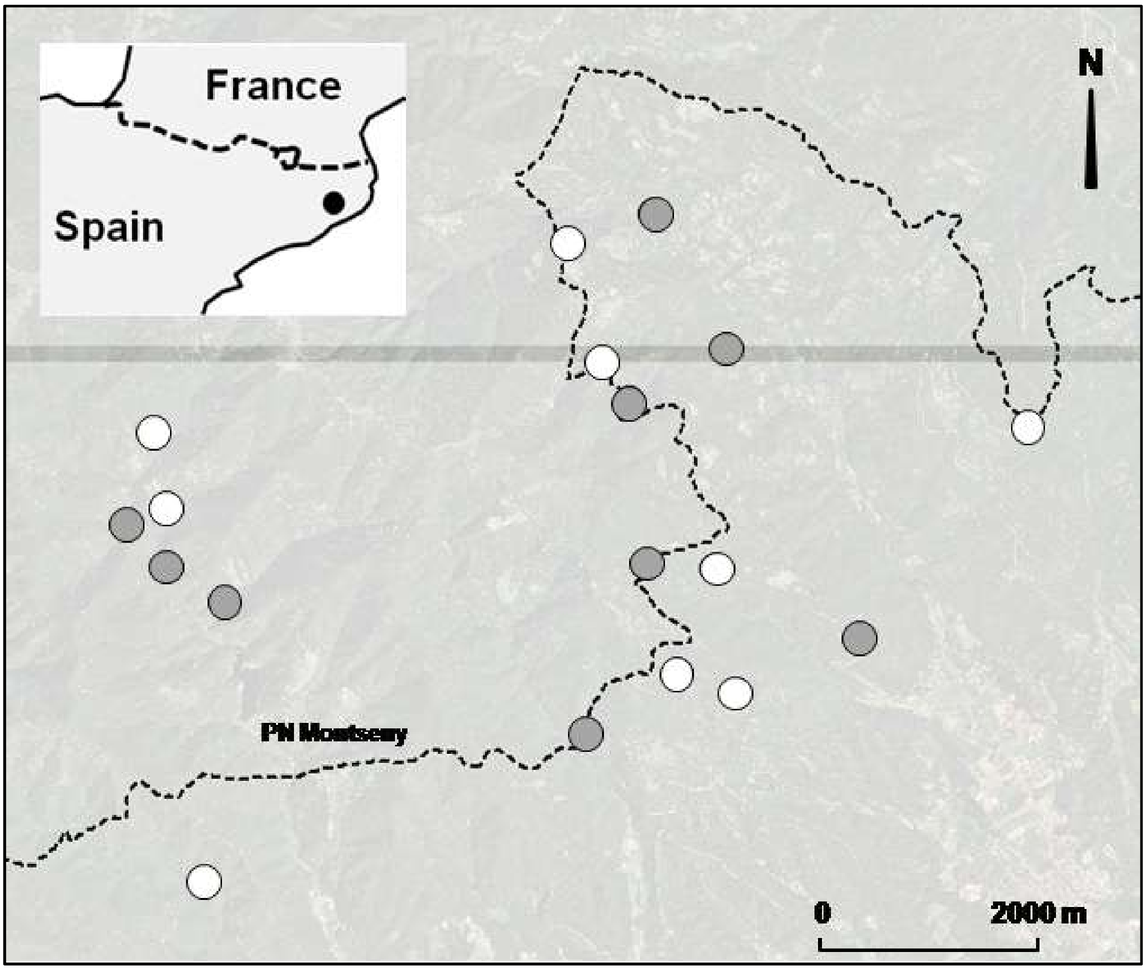
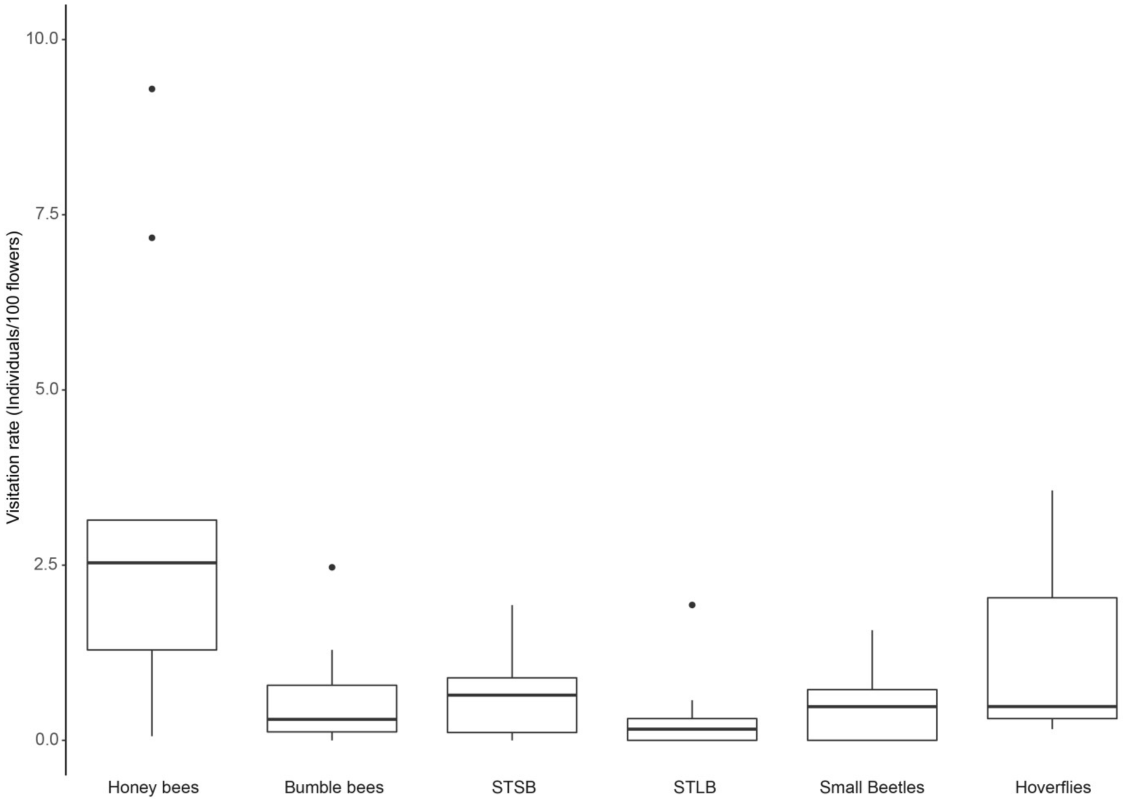


Fig. SM2 Visitation rate (pollinator individuals per 100 flowers) of the main pollinator groups to *Cistus albidus*. STSB: short-tongued small bees; STLB: short-tongued large bees.



Supplemental Material Chapter 2

Table SM1 Characteristics of the 42 study sites.

Plot number	Patch size category	Patch size (ha)	X coordinate	Y coordinate	Altitude (m)
1	Small	0.02	455487	4620140	479
2	Small	0.04	456765	4621551	638
3	Small	0.1	444862	4617385	590
4	Small	0.15	443195	4627997	771
5	Small	0.08	444322	4619877	730
6	Small	0.06	446792	4619549	959
7	Small	0.4	444568	4621501	743
8	Small	0.24	448265	4623542	509
9	Small	0.25	442882	4625440	1037
10	Small	0.2	442640	4626862	922
11	Small	0.33	446583	4624026	1111
12	Small	0.06	448753	4624739	631
13	Small	0.07	450794	4626015	713
14	Small	0.05	456689	4622001	808
15	Medium	5.6	443325	4628719	955
16	Medium	4.4	444392	4627311	985
17	Medium	9.2	446031	4618221	568
18	Medium	7	445847	4619414	755
19	Medium	1.95	444365	4621013	689
20	Medium	4.6	447601	4620081	780

Table SM1 (continued).

Plot number	Patch size category	Patch size (ha)	X coordinate	Y coordinate	Altitude (m)
21	Medium	2.6	440720	4626176	488
22	Medium	6	448539	4622574	689
23	Medium	6	447046	4623424	837
24	Medium	5	447752	4623820	683
25	Medium	11.2	447596	4626505	902
26	Medium	5.2	444426	4629152	875
27	Medium	6.2	456202	4621282	673
28	Medium	4.1	443567	4625112	1131
29	Large	> 40	437003	4634971	559
30	Large	> 40	451101	4611028	198
31	Large	> 40	448508	4610399	198
32	Large	> 40	441188	4630809	769
33	Large	> 40	444187	4613538	277
34	Large	> 40	442536	4612069	261
35	Large	> 40	452887	4616542	227
36	Large	> 40	439725	4636928	549
37	Large	> 40	440918	4611690	192
38	Large	> 40	443100	4610742	252
39	Large	> 40	444610	4622572	1235
40	Large	> 40	444242	4625105	1187
41	Large	> 40	437996	4630853	610
42	Large	> 40	438431	4633885	586

Table SM2 Observed and expected (mean ± SE) host and parasitoid richness, observed interaction richness and unique species/interactions in each patch size category.

	Observed host richness	Unique host species	Expected host richness	Observed parasitoid richness	Unique parasitoid species	Expected parasitoid richness	Observed interaction richness	Unique interactions
Small patches	27	5 (19%)	27	23	4 (17%)	29 ± 6.5	56	19 (34%)
Medium patches	29	3 (10%)	29	33	8 (24%)	39 ± 6.5	86	36 (42%)
Large patches	32	9 (28%)	32	34	8 (24%)	46 ± 17.1	97	54 (56%)

Table SM3 Network modularity index (Q), number of network modules (nQ), and relative modularity (Q') in local networks of small, large and mainland patches (N = 14 local networks per patch size category). Modular structure was compared to a randomized null model (in bold significant results at $P < 0.05$). Relative modularity (Q') is calculated as a z-score with the observed values and the random values generated with the null model.

Small patch	Q	nQ	Q'	P	Medium patch	Q	nQ	Q'	P	Large patch	Q	nQ	Q'	P
CX01	0.50	3	NA	NA	CG01	0.38	3	16.94	**< 0.001**	OB01	0.55	5	10.25	**< 0.001**
CX02	0.35	3	3.34	**< 0.001**	CG02	0.46	6	15.99	**< 0.001**	OB02	0.36	3	6.69	**< 0.001**
CX03	0.45	3	4.98	**< 0.001**	CG03	0.22	4	10.54	**< 0.001**	OB03	0.37	4	14.62	**< 0.001**
CX04	0.56	3	5.25	**< 0.001**	CG04	0.16	2	4.88	**< 0.001**	OB04	0.66	6	14.84	**< 0.001**
CX05	0.60	3	5.65	**< 0.001**	CG05	0.26	3	4.41	**< 0.001**	OB05	0.32	4	5.51	**< 0.001**
CX06	0.68	4	6.83	**< 0.001**	CG06	0.48	4	10.64	**< 0.001**	OB06	0.42	7	13.47	**< 0.001**
CX07	0.23	4	-0.03	0.35	CG07	0.16	5	8.36	**< 0.001**	OB07	0.31	3	5.73	**< 0.001**
CX08	0.44	4	7.40	**< 0.001**	CG08	0.47	4	15.99	**< 0.001**	OB08	0.26	2	7.37	**< 0.001**
CX09	0.50	3	4.64	**< 0.001**	CG09	NA	1	NA	NA	OB09	0.58	4	11.55	**< 0.001**
CX10	0.56	3	5.75	**< 0.001**	CG10	0.63	4	17.52	**< 0.001**	OB10	0.26	3	3.57	**0.001**

Table SM3 (continued).

Small patch	*Q*	*nQ*	*Q'*	*P*	Medium patch	*Q*	*nQ*	*Q'*	*P*	Large patch	*Q*	*nQ*	*Q'*	*P*
CX11	0.57	3	3.73	**< 0.001**	CG11	0.49	4	2.74	**0.01**	OB11	0.36	3	4.35	**< 0.001**
CX12	0.11	2	0.99	0.15	CG12	0.47	6	5.74	**< 0.001**	OB12	0.22	3	4.64	**< 0.001**
CX13	0.34	4	8.18	**< 0.001**	CG13	0.19	3	5.24	**< 0.001**	OB13	0.47	6	17.64	**< 0.001**
CX14	NA	0	NA	NA	CG14	0.48	4	11.10	**< 0.001**	OB14	0.24	5	15.46	**< 0.001**

Fig. SM1 Map of the study area indicating the location of small (red circles), medium (orange) and large (green) patches (N = 14 per patch size category), and the location of 5 forest-matrix sites (white circles). Montseny Natural Park limits are indicated by a blue dotted line.

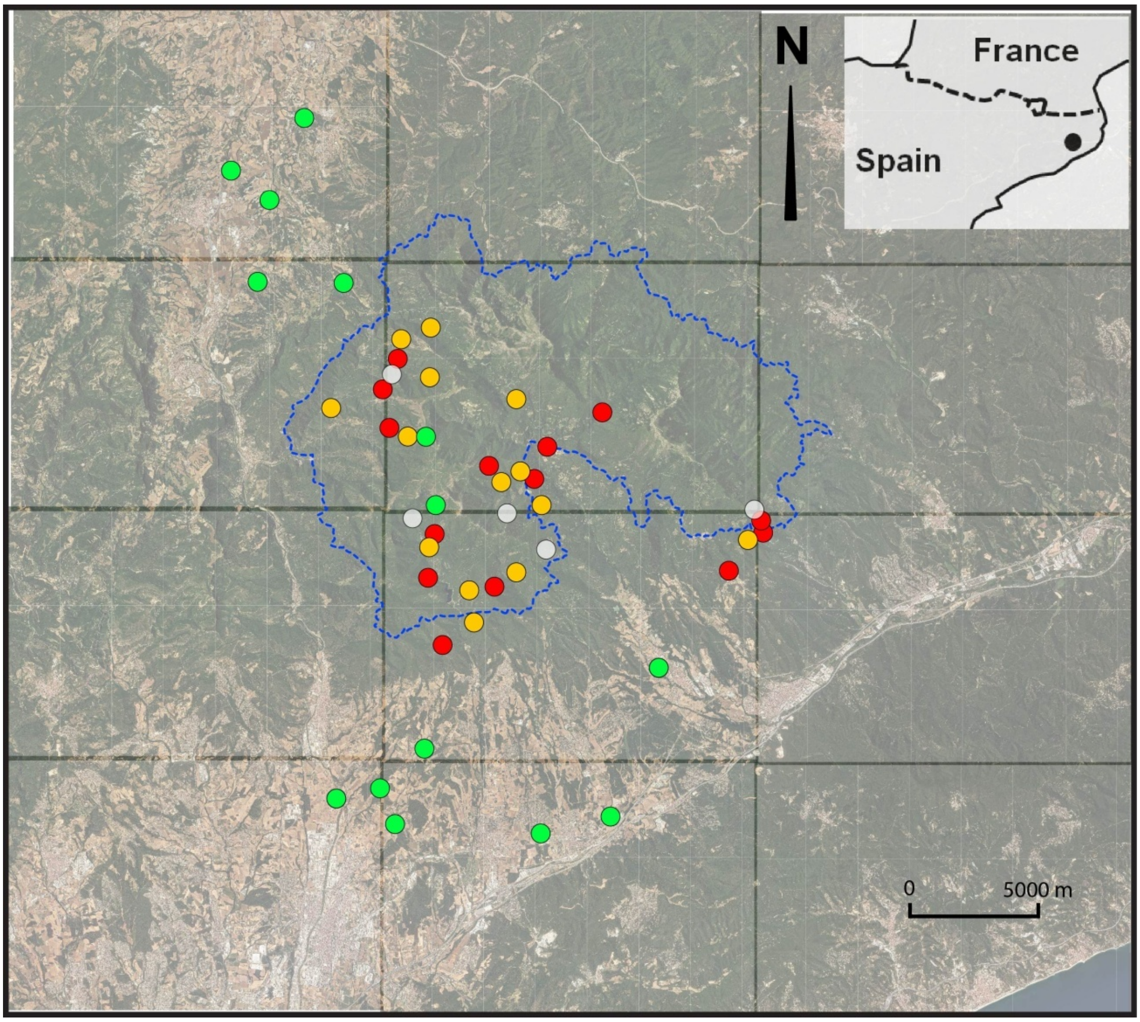


Fig. SM2 Examples of a) small, b) medium and c) large patches. For each category a recent (2016) and an old (1986) aerial images are provided to illustrate the scarcity of landscape changes in the last 30 years. Source: Institut Cartogràfic i Geològic de Catalunya (ICGC), www.icc.cat/vissir3/.

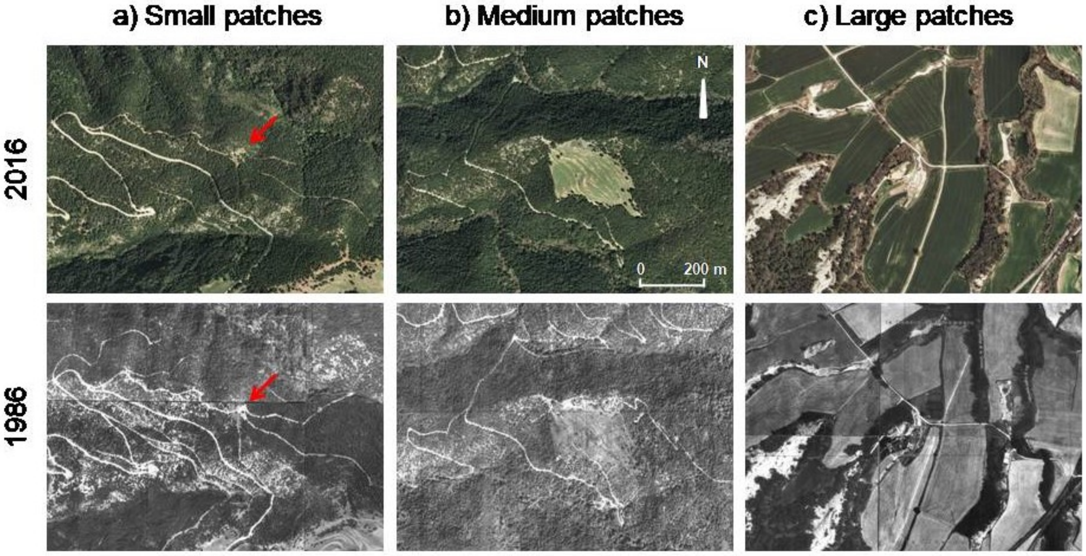
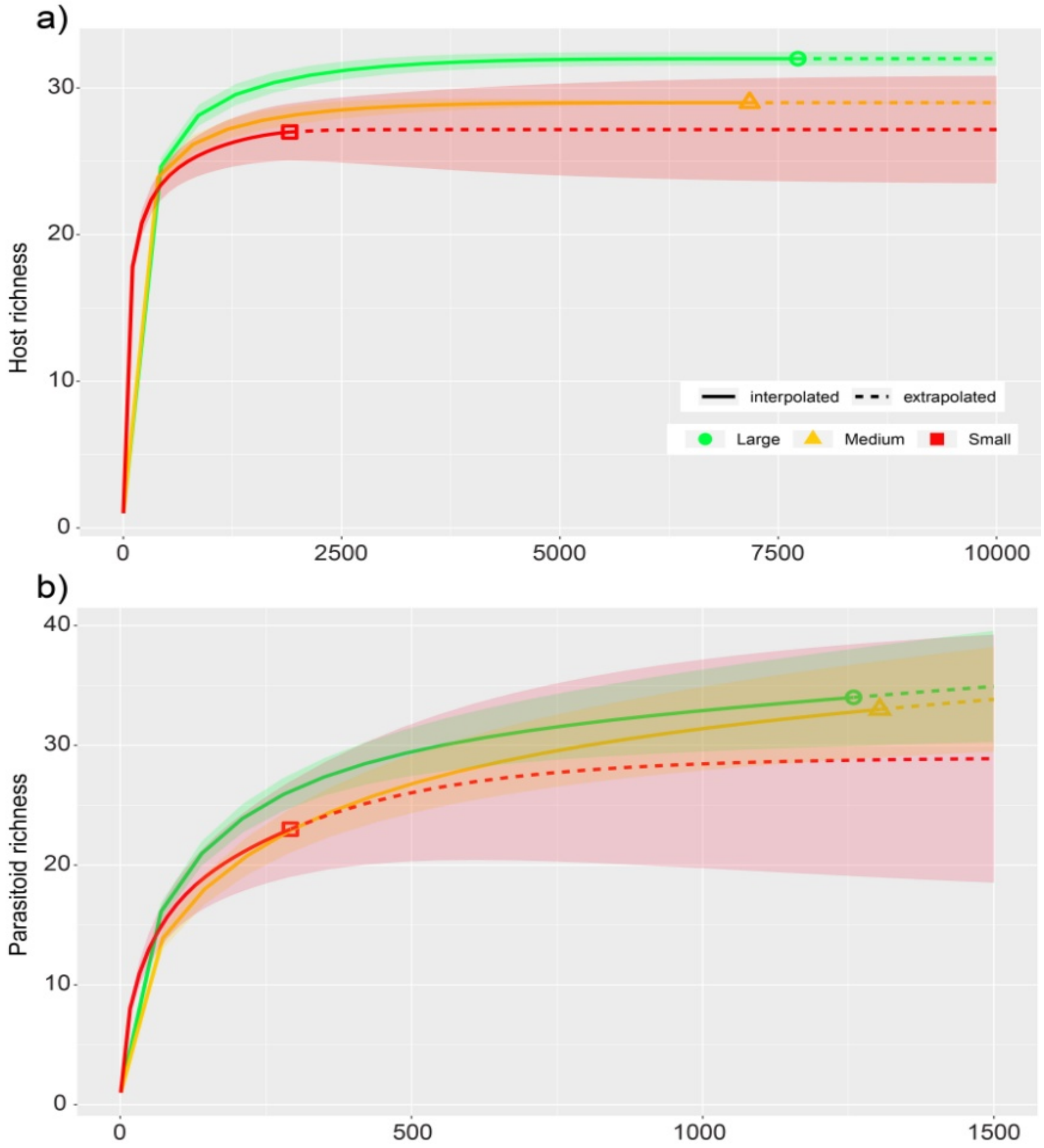


Fig SM3 Rarefaction curves of a) host and b) parasitoid richness, based on Hill number *q* = 0, in small, medium and large patches (N = 14 per patch size category). Extrapolations (broken lines) are based on the number of individuals/interactions to reach total sampling coverage. 95% confidence intervals are based on bootstrapping standard errors.



“Dondequiera que haya conocimiento,

dondequiera que haya virtud,

dondequiera que haya belleza,

él encontrará un hogar”

R.W. Emerson, en el funeral de H.D. Thoreau, 1862

Ecological communities are variable as a consequence of multiple ecological processes and diverse sources of environmental variation. However, current climate change and habitat loss are eroding biodiversity at an alarming rate. In this PhD thesis I analyze the effects of changes in plant communities and habitat size on plant-pollinator and host-parasitoid networks. I tackle these issues with field experiments, and I address both fundamental (responses in species composition and interaction patterns) and applied (consequences on function: pollination, reproduction, and parasitism) questions. Based on the current body of knowledge, I provide a general framework to predict community-wide and species-specific responses to plant colonization of native communities. Similarly, based on the species-area (the most robust law in ecology) and the link-area relationships, I provide a framework for the network-area relationship.

Cover: *An entangled bank is not a mess, or the Ionian Enchantment triumph* (Carlos Hernández-Castellano)