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Bottom-up effects in plant-insect networks: the role of plant communities in structuring insect communities

Kate Pereira Maia

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy in the Faculty of Science

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Abstract

Biodiversity is associated with important ecosystem processes and functions. However, many species are currently threatened by human activities, making ecological restoration a major tool in conservation biology. An important component of biodiversity are the interactions between species as these provide ecological functions and services. In terrestrial systems restoration usually starts with the restoration of plant communities, as plants serve directly or indirectly as a resource for upper trophic levels. Ecological networks provide a powerful tool for describing, analysing and understanding whole communities in a restoration context, for example they can be used to identify structurally important species and to measure community robustness. In this thesis, I use plant-insect networks from natural and agricultural systems, to investigate how plant communities support biodiversity at higher trophic levels. I do this by identifying keystone resources for insect herbivores and parasitoids, and by showing that keystone roles are performed by few plant species and that these roles are context dependent. Using a field experiment, I then evaluate whether plant species network roles, *i.e.* central vs. peripheral, can be used to restore pollinator communities, and found that central plant species attracted a higher richness and abundance of pollinators than peripheral species. Finally, I test the robustness of pollination and herbivory networks to the loss of plant species, accounting for differences in network structure and natural history between both systems. I found that herbivory networks tend to be more robust than pollination networks to plant extinctions, but that the inverse is true when interaction rewiring is considered. Together, these three approaches extend both our current understanding of bottom-up effects in plant-insect networks and the potential to undertake restoration that targets more than one trophic level.

Dedication

"Mas sei, que uma dor assim pungente
Não há de ser inutilmente
A esperança
Dança na corda bamba de sombrinha
E em cada passo dessa linha pode se machucar
Azar, a esperança equilibrista
Sabe que o show de todo artista tem que continuar"

- Aldir Blanc

Ao povo brasileiro

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Finally and most important, I would like to thank my family for their unconditional support and for helping me to get here, specially to my parents.

Author’s Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Kate Pereira Maia
Bristol, November 2018

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Chapter 1 Introduction

Besides its intrinsic value, biodiversity positively affects ecological communities in many ways. For example, increasing biodiversity leads to more efficient use of ecosystem resources, is associated with higher ecosystem persistence and stability, and prevents ecological invasion at local scales (McCann, 2000; Kennedy et al., 2002; Cardinale et al., 2006; Gravel et al., 2011). Increasing biodiversity seems also to be positively associated with the provision of ecosystem services (Balvanera et al., 2006; Harrison et al., 2014; Winfree et al., 2015). Despite its importance, biodiversity and, consequently, the persistence of ecological communities, is being threatened by human activities, which include intensification of agriculture, climate change, deforestation, and habitat fragmentation (Sala et al., 2000; Tilman, 2001; Hanski, 2005; Bellard et al., 2012; Ledger et al., 2012; Laurance et al., 2014). Such activities result not only in the loss of species, but also in the loss of another crucial component of ecological communities, the interactions that connect species in nature (Aizen et al., 2008a; Tylianakis et al., 2008; Laliberté and Tylianakis, 2010). Ecological interactions appear to be an extremely fragile component of biodiversity since interactions can be lost before species are lost (Tylianakis et al., 2008; Valiente-Banuet et al., 2015). Studies suggest that interactions are lost at a faster pace than species (Albrecht et al., 2007; Valiente-Banuet et al., 2015) and that habitat modification might alter species interactions even when it does not affect species themselves (Tylianakis et al., 2007). Therefore, it is essential to consider ecological interactions as a component of biodiversity when both evaluating the impact of human activities and developing methods to mitigate the impacts of biodiversity loss.

The main tools which are capable of mitigating the negative impacts of human activity on biodiversity are conservation and ecological restoration (Mace, 2014; Possingham et al., 2015; Brudvig, 2017). Often seen as ostensibly similar, since both are challenged by the unprecedented rate and magnitude of environmental change (Steffen et al., 2007; Hooke and Martín-Duque, 2012), conservation and restoration have different aims and practices (Young, 2000; Wiens and Hobbs, 2015). While conservation is concerned with preserving the least degraded areas in order to maintain their current status, restoration is focused on heavily degraded areas with the aim of recovering some of its value to biodiversity (Mace, 2014; Wiens and Hobbs, 2015). In order to meet our goals on biodiversity conservation, both methods need to be combined (Possingham et al., 2015). With 80% of the world's surface showing evidence of human activity (Ellis and Ramankutty, 2008), and one third of ecosystems heavily degraded (Millennium Ecosystem Assessment, 2005), passive protection of ecosystems is not enough as protected areas do not adequately cover all biomes or taxa (Rodrigues et al., 2004; Venter et al., 2014; Watson et al., 2014). In this sense, ecological restoration should become a primary focus of biodiversity management.

A large part of ecological restoration research and practice in terrestrial systems has focused on the plant community to achieve restoration goals (Young, 2000; Young et al., 2005). In natural systems, even when natural regeneration methods are selected, some assistance to re-stablish the plant community may be required (Chazdon and Guariguata, 2016). Similarly, in agricultural systems, successful biodiversity stewardship schemes have focused on increasing the provision of limited resources for targeted taxa (Winspear et al., 2010; Dicks et al., 2015). For several taxa, at least some of these resources are provided either directly or indirectly by the plant community (Walker et al., 2008; Vaudo et al., 2015). The focus on the plant community relies on the assumption that after its establishment, the arthropod community will naturally regenerate (Forup et al., 2008; Woodcock et al., 2010; Jellinek et al., 2013), but it is also supported by a large amount of evidence suggesting strong bottom-up effect in terrestrial systems (Scherber et al., 2010). As a result, ecological restoration which started as a botanical discipline, has now expanded to target multiple trophic levels (Henson et al., 2009), the interactions between species across different levels (Forup et al., 2008; Memmott, 2009) and ecosystem services (Rey Benayas et al., 2009; Rey Benayas and Bullock, 2012), which often result from these interactions (Tylianakis et al., 2010).

In this thesis, I explore the role of plant communities in supporting upper trophic levels, specifically pollinators, insect herbivores and parasitoids, in natural and agricultural systems. For that, I use ecological networks in three complementary approaches – the analysis of a large dataset from the literature, a manipulative field experiment and simulation modelling. From the network data, I sought to extract information from extant plant-insect communities which could inform the creation of new plant communities with the focus of reaching positive effects for the biodiversity of insects and their interactions with plants. In what follows I introduce the main concepts which underpin the three studies in this thesis: ecological restoration, bottom-up effects and ecological networks. I finish the *Introduction* by outlining what has been investigated in each chapter.

1.1 The era of ecological restoration: challenges and changes

"*In art, restoration involves recapturing an objects aesthetic value.*
In ecology, the stakes are arguably much higher (…)"
Roberts, Stone and Sugden (2009)

Ecological restoration is the intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability (SER 2004). Its goals are to re-establish a range of desirable attributes of natural systems (Brudvig, 2011), mainly native species composition, ecosystem functions and stability (SER, 2004; Shackelford et al., 2013). Ecological restoration is currently considered humankind's primary option for increasing biodiversity (Brudvig, 2011). Additionally, the United Nations Environmental Programme argues that restoration should be considered as a method to address environmental issues such as carbon sequestration and mitigation of climate change, and social issues like poverty (Nellemann and Concoran, 2010).

Ecological restoration experienced four main paradigms: restoration to guide the recovery of degraded systems, restoration as a compensation for habitat loss (frequently performed by industries to offset the destruction of natural ecosystems), restoration to provide ecosystem services and restoration to promote community resilience (Suding, 2011). These paradigms reflect the ongoing change of a field, which originally focused on the recovery of pristine habitats (Hobbs et al., 2009), using historical systems as reference (Swetnam et al., 1999; Balaguer et al., 2014) and by mainly focusing on species composition (Brudvig, 2011; Perring et al., 2015). However, the recognition that humans have been interacting and modifying ecosystems for thousands of years (Ellis et al., 2013), makes the concept of pristine environments hard to grasp. Additionally, historical targets have proven hard to achieve, since factors such as climate, available species pools - due to extinctions and invasions - and human activities have changed. An additional challenge is that humans are expected to continue modifying their surroundings at increasing rates (Tilman et al., 2011). These future environmental changes will possibly make targets focused on species composition harder to achieve and more transient.

Due to the challenges posed to previous ecological restoration paradigms, and the developments of ecological theory, the practice of ecological restoration has evolved and adapted in several ways (Shackelford et al., 2013). Such transformations include: (i) broader definitions of endpoints which have moved solely from species composition to incorporate other aspects such as ecosystem function and desired dynamics (Suding, 2011; Zirbel et al., 2017), (ii) the adoption of new measures of biodiversity which now encapsulate more than taxonomy and species richness to include, for example, phylogenetic composition (Barak et al., 2017), and (iii) the search for mechanisms affecting outcomes (Zirbel et al., 2017). For instance, current restoration models incorporate site-level factors, landscape-level factors and historical contingencies (Brudvig, 2011), which are expected to move the field towards a predictive science. In terrestrial systems, ecological restoration has also moved from a strictly botanical science, to the development of management which focuses on additional trophic levels. One example, is the creation on flower patches specifically designed to target pollinators (Hopwood, 2008; Morandin and Kremen, 2013; Harmon-Threatt and Hendrix, 2015). Concomitantly, ecological restoration has incorporated in its practice knowledge and tools from other fields of ecology (Palmer et al., 1997; Young et al., 2005; Montoya et al., 2012). One such field is the study of ecological networks, which captures the multitrophic and functional purpose of current restoration schemes.

1.2 Bottom-up effects and its importance on plant-insect systems

"*... the removal of higher trophic levels leaves lower levels intact (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all.*"
Hunter and Price (1992)

One question that has arisen in the 60's, with the publication of "the world is green" proposition (Hairston et al., 1960), is whether ecological communities are structured by bottom-up forces, meaning that populations are limited by their resources, or by top-down forces, if populations are controlled by their predators (Hunter and Price, 1992; Chase et al., 2000; Koricheva et al., 2000; Walker and Jones, 2001). For decades, much empirical work has provided evidence pointing in one direction or the other (Price et al., 1980; Walker and Jones, 2001), or even showing that both mechanisms act together (Huryn, 1998; Chase et al., 2000; Aquilino et al., 2005). For instance, in the same community each mechanism can occur at different scales, *e.g.*

within and between-habitats (Wulff, 2017) or in different trophic levels (Hoekman, 2011). Currently, ecologists agree that bottom-up and top-down forces interact in complicated ways when structuring ecological communities (Chase et al. 2000), and that the relative importance of one mechanism or another is frequently context and system dependent (Hunter and Price 1992), and therefore varying across space and time.

Despite being harder to detect than top-down forces, due to a time lag in its effects (Smith et al., 2010; Wulff, 2017), there is extensive evidence of bottom-up forces particularly in terrestrial systems where they are believed to be more important (Hunter and Price, 1992; Schmitz et al., 2000; Halaj et al., 2001; Walker et al., 2008). In terrestrial systems, the effects of the plant assemblage were found to reach not only herbivores (Siemann, 1998; Koricheva et al., 2000; Schaffers et al., 2008; Welti et al., 2017) but higher trophic levels (Bukovinszky et al., 2008; Scherber et al., 2010; Kos et al., 2011; Schuldt and Scherer-Lorenzen, 2014). Specifically, researchers sought to understand if increasing plant diversity is associated with increases in insect diversity and abundance. The effect of different measures of plant diversity on upper trophic levels have been investigated, such as the effects of plant richness (Koricheva et al., 2000; Scherber et al., 2010; Dinnage et al., 2012; Welti et al., 2017), functional diversity (Koricheva et al. 2000, Scherber et al. 2010), phylogenetic diversity (Dinnage et al. 2012, Pellissier et al. 2013), structural diversity (Lawton 1983, Holmquist et al. 2014) or diversity of plant traits (Pywell et al., 2003; Pellissier et al., 2013; Fornoff et al., 2017). Most of these empirical studies suggest that insect abundance and diversity respond to some aspects of plant diversity.

Insect herbivores are an extremely diverse group, representing a large proportion of terrestrial species (Price, 2002; Novotny et al., 2004). Herbivores are an important link in terrestrial ecosystems serving as resource for several groups, for example to parasitoid species which provide the service of pest control – but also affecting plant populations (Carson and

Root, 1999). In fact, the richness of plant species can indirectly, through herbivores, affect the richness and phylogenetic composition of the parasitoid community (Nascimento et al., 2015). Insect herbivores have adapted to interact with virtually every single plant part (Memmott et al., 2000; Almeida-Neto et al., 2011; Schallhart et al., 2012; Volf et al., 2015). To avoid such high predation pressure, plants have evolved a multitude of counter defences which have pushed herbivores into specialisation (Forister et al., 2015). Such coevolutionary arms races between plants and herbivores might explain the reason that oligotrophic herbivores - species which feed on more than one host plant - usually feed on closely related species (Novotny and Basset, 2005; Fontaine and Thébault, 2015). In that sense, an important feature of plant communities affecting plant-herbivore interactions, is their phylogenetic composition (Weiblen et al., 2006; Whitfeld et al., 2012; Pellissier et al., 2013; Forister et al., 2015). Moreover, the effect of plant community phylogenetic composition can cascade up, also affecting predators and parasitoids (Dinnage et al., 2012).

Pollination is an important ecosystem service provided mainly by insect species. It is estimated that 75% of crops species (Klein et al., 2003) and 87.5% of flowering plant species (Ollerton et al., 2011) depend on animal pollination, making their current decline extremely concerning (Potts et al., 2010; Carvalheiro et al., 2013; Dicks et al., 2013). There is extensive evidence suggesting that pollinators can be resource limited, and that the lack of diverse and sufficient resource habitats is an important cause of current pollinator declines (Carvell et al., 2006; Roulston and Goodell, 2011; Vanbergen and The Insect Pollinators Initiative, 2013; Ollerton et al., 2014). Specifically, the observed declines of flower resources could make insects more prone to the lethal effect of diseases and pesticides (Goulson et al., 2015), potentially due to reduced immunocompetence (Alaux et al., 2010). Pollinator diversity – both richness and abundance - are known to respond to the number of flowering species and individuals (Potts et al., 2010; Hudewenz et al., 2012; Orford et al., 2016). Additionally, in a biodiversity experiment, not only pollinator richness, but also flower visitation, increased with richness and abundance of flowers (Hudewenz et al., 2012). In another experiment, pollinator functional diversity increased with plant richness positively affecting the stability of pollination services (Orford et al., 2016). Therefore, the creation of appropriate flower habitats will likely support diverse pollinator communities, securing an important aspect of ecosystem function and an important service.

1.3 Ecological networks: a measure of ecological function and a tool for restoration

"*It is interesting to contemplate an entangled bank,* (…)*, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.*"
Darwin (1859)

Ecological networks have been intensively studied for the past 20 years, greatly advancing our understanding on the structure and functioning of ecological communities (Poisot et al., 2016). By using tools from other fields such as social and computer sciences (Newman, 2003), ecologists are able to study interactions at the community level in a single framework, making them systematic and comparable (Delmas et al., 2018). In an ecological network, nodes – usually species – are connected by links whenever species interact. More recently, these links became weighted by including information on the frequency or strength of interactions between species (Vázquez et al., 2005, 2015). By looking at ecological communities as networks, ecologists were able to describe and better understand the emerging and often repeated structural properties of ecological communities (Bascompte et al., 2006; Fortuna et al., 2010; Dáttilo et al., 2016) and to identify key species for community structure (Mello et al., 2015).

Additionally, the study of species interactions, through the use of network tools, has shed light on the importance of network structure for the stability (Bastolla et al., 2009; Thébault and Fontaine, 2010), sensitivity to invasion (Valdovinos et al., 2018) and extinction (Burgos et al., 2007; Stouffer and Bascompte, 2011) in ecological communities. This knowledge is very relevant for applied fields such as conservation and ecological restoration (Harvey et al., 2017).

Plant-pollinator and plant-herbivore-parasitoid systems were some of the first types of ecological networks to be studied (Jordano, 1987; Memmott et al., 1994; Memmott, 1999). As both interaction types also support important ecosystem services – pollination and pest control (Crowder et al., 2010; Campbell et al., 2012) - understanding their structure and dynamics is of applied interest as well. In terms of network structure, we know that pollination networks are nested (Bascompte et al., 2003), *i.e.* formed by a core of generalist species with which specialist species interact. Herbivory networks instead, are frequently modular (Thébault and Fontaine, 2010; Cagnolo et al., 2011), a pattern in which sets of species interact more frequently among each other than with other species in the network (Olesen et al., 2007). These structural patterns can affect species coexistence (Bastolla et al., 2009), network persistence (Burgos et al., 2007; Stouffer and Bascompte, 2011) and even evolutionary dynamics (Guimarães et al., 2011).

Pollination and herbivory networks have been studied in terms of their stability and robustness (Memmott et al., 2004; Thébault and Fontaine, 2010; Allesina and Tang, 2012; Sauve et al., 2014; Welti et al., 2017). Robustness measures how resistant a network is to the loss of species (Dunne et al., 2002; Memmott et al., 2004). In this approach, species in one trophic level are sequentially removed and coextinctions in another trophic level are quantified (Dunne et al., 2002). The original method, which was static and based strictly on network topology, has evolved to incorporate stochasticity (Vieira and Almeida-Neto, 2015; Traveset et al., 2017), dynamics at the species and network levels (Ramos-Jiliberto et al., 2012; Pearse and Altermatt, 2013; Valdovinos et al., 2013), and information on the natural history of the system to inform realistic extinction sequences (Pearse and Altermatt, 2013; Astegiano et al., 2015; Berg et al., 2015).

Network tools have been used to address ecological questions with practical applications. For instance, some studies looked at how network structure responds to invasive species (Lopezaraiza–Mikel et al., 2007; Bartomeus et al., 2008; Traveset et al., 2013) and to habitat fragmentation (Hagen et al., 2012; Emer et al., 2013, 2018). The effect of different management practices in agricultural systems has also been explored with the use of ecological networks (Macfadyen et al., 2009a; Orford et al., 2016). Finally, ecological networks have been used to evaluate the effects of ecological restoration (Cusser and Goodell, 2013). For instance, several studies have compared the structure of restored communities with the one of target or reference sites (Forup and Memmott, 2005; Forup et al., 2008; Williams, 2011; Ribeiro da Silva et al., 2015; Rodewald et al., 2015; Kaiser-Bunbury et al., 2017), or between different restoration treatments (Atkinson et al., 2015). As some ecosystems services are the result of species interactions rather than of species composition (Harvey et al., 2017), the study of how agricultural management practices and restoration strategies affect network structure, can also inform us about the recovery of services provided by these species.

By explicitly exploring alternative restoration strategies and comparing the resulting outcomes, recent studies have gone a step further providing us with mechanistic information that can move restoration from a site-specific enterprise into a predictive practice (Brudvig, 2017). Devoto et al. (2012) investigated how order of plant species introduction – either maximising convergence or complementarity - affects conservation outcomes. Using a theoretical framework, LaBar et al. (2014) have investigated the effect of several species introduction scenarios following species extinctions in pollination networks. For instance, they show that the number of species introduced is more important, for resulting species richness, than the strategy used for species selection and that the introduction of generalist species will result in stable communities (LaBar et al., 2014). Finally, since restoration is considered the acid test for ecological theory (Bradshaw, 1987), *i.e.* “if we do not understand the processes at work in an ecosystem we are unlikely to be able to reconstruct it” (Bradshaw, 1996), combining ecological networks with restoration data can teach us how communities are assembled. For instance, Ponisio et al. (2017), using an 8-year restoration dataset, found that pollination networks were assembled thorough a different process than previously thought. According to their study, in pollination networks the most persistent species are not generalists, as predicted by the preferential attachment hypothesis, but are species with highly dynamic network roles (Ponisio et al., 2017).

1.4 Thesis structure

The overarching aim of work described in this thesis was to ask how ecological networks can usefully inform the creation or restoration of plant communities when the intention is to positively affect additional trophic levels such as pollinators, insect herbivores and parasitoids. For that, I developed three studies which are complementary in topic and method. The first data chapter focuses on plant-herbivore-parasitoid interactions, while the second data chapter focuses on interactions between plants and pollinators; and in the third and final data chapter, I compare both types of networks. In terms of approach I combine data analysis of a large empirical dataset from the literature (Chapter 2), a field experiment (Chapter 3) and a simulation model (Chapter 4). Below, I briefly describe each chapter and outline how each data chapter connects with the three underpinning topics:

Chapter 1: In the Introduction, I provide an overview of the literature about the three guiding and unifying topics of the work presented in this thesis: ecological restoration, bottom-up effects in community ecology and ecological networks. The chapter ends with an overview of the thesis structure.

Chapter 2: In the first data chapter I used a combination of null models and species-level network metrics to identify keystone plant resources for herbivores and parasitoids in agricultural systems. The term keystone species, originally referred to top predator species (Paine, 1969), is today applied more generally to species that disproportionally affect the rest of the community relative to their abundances (Watson and Herring, 2012). I used a dataset from the literature comprising 20 replicate plant-herbivore-parasitoid networks, which allowed the exploration of context dependency on plant species keystone roles. Additionally, I investigated the consistency of plants roles across trophic levels and the effect of plant phylogenetic relatedness on plant’s network roles. Keystone plant species are a restoration target, as these plants have a high potential of reaching positive results for biodiversity and ecosystem services (Pocock et al., 2012).

Chapter 3: In this chapter, I tested whether plant species centrality roles in plant-pollinator networks are good indicators of their ability to restore interactions between plants and pollinators. To do this, I calculated the centrality role of plant species in 17 published pollination networks and selected five central and five peripheral species. Then, I experimentally introduced the selected species into replicate plots and recorded their interactions with pollinators. I then tested the effect of central and peripheral plant species introduction on the pollinator and resident plant community and on network structure. Central plant species could be the focus of restoration programmes when focusing on pollinators (Martín González et al., 2010) as these could increase the richness and abundance of pollinators available for resident plant species.

Chapter 4: In the last data chapter, I brought together herbivory and pollination networks to investigate how differences in network structure and on the natural history between both interaction types affects the dynamics and robustness of these systems to the loss of plant species. For this, I used a large empirical dataset comprising 17 herbivory and 26 pollination networks and an adaptive network model. I explicitly investigate how the different population feedbacks – the reciprocal demographic effects between plants and insects – and level of generalisation – higher in pollination than in herbivory networks – between the two interaction types affect network collapse. I suggest that improving our understanding of how communities collapse might help explain how plant communities can be better engineered to support biodiversity.

Chapter 5: In the discussion I summarise the main findings of the work presented in this thesis and I discuss the implications of the main results of my studies. I also suggest future directions for research.

Chapter 2

The identification of keystone resource plant species in plant-insect food webs

2.1 Introduction

Ecological networks have been used to understand both the structure and the function of natural and managed communities (Laliberté and Tylianakis, 2010; Peralta et al., 2014; Rodewald et al., 2015; Ruggera et al., 2016). For example, they have been used to test the efficacy of pest control on farms under different management regimes (Macfadyen et al., 2009a), assess the impact of alien species (Bartomeus et al., 2008) and test the success of restoration (Kaiser-Bunbury et al., 2017). Networks provide a powerful tool for identifying species of structural importance in ecological communities (Mello et al., 2015; Dehling et al., 2016) and can be used to identify plants species that act as keystone species (Pocock et al., 2012); keystone species being those which have a disproportionately large effect on network structure and function relative to their abundance (Paine, 1969; Watson and Herring, 2012). In pristine communities, identifying keystone species can help to focus conservation programs on specific taxa with large impacts on the overall community (Diaz-Martin et al., 2014; Mello et al., 2015; Traveset et al., 2017). Similarly, detecting and fostering keystones in degraded habitats could provide a real impetus at the start of a restoration programme, as degraded habitats make up one third of the world's ecosystems (Millennium Ecosystem Assessment, 2005) and their restoring is a priority in many countries (Suding, 2011).

In terrestrial systems, restoration usually starts with the creation of a plant community or with the addition of plant species to existing communities. However, only a few restoration studies investigate the effects of individual plant species on the next trophic level (Moir et al., 2010; Barton et al., 2013; Schuldt and Scherer-Lorenzen, 2014). Highlighting potential keystone species that have a large effect over higher trophic levels could help to focus restoration, as these plants may have a high potential to augment biodiversity and improve ecosystem services (Pocock et al., 2012). Furthermore, understanding when and why plant species act as keystones would provide us with invaluable knowledge on the mechanisms structuring communities and on the functioning of ecosystems (Simberloff, 1998). Since the context in which species are found varies from site to site, the roles species play might also vary. Ecological restoration would therefore benefit, not only from the identification of keystone resources, but also from insights on which traits and ecological contexts are associated with being a keystone species, as this information could greatly increase the predictive power of restoration schemes (Brudvig, 2017).

Species' roles in ecological networks are frequently a result of how attributes of a focal species relate to attributes of other species in the community, the most obvious being species relative abundance (Cagnolo et al., 2011; Fort et al., 2016). Similarly, pollinator species with similar traits to the community trait average interact with more plant species than pollinators with unique traits (Coux et al., 2016). Likewise, the composition of the plant community could affect the importance of each plant species for herbivores and, consequently, plant species' roles in herbivory networks. For instance, co-occurring host species could result in mutual increased herbivory by attracting and supporting large populations of herbivores and, in turn, could end up sharing important roles as keystone resources in herbivory networks. Moreover, the impact of plants can reach more than one trophic level (Bukovinszky et al., 2008) and, by sustaining large populations of herbivores, plant species could indirectly support parasitoid species and the service of pest control.

Plant-herbivore interactions are known to be phylogenetically conserved, that is, insect herbivores tend to feed on closely related host species (Novotny and Basset, 2005; Elias et al., 2013; Fontaine and Thébault, 2015; Bergamini et al., 2017). Castagneyrol et al. (2014) showed that plant phylogenetic proximity drives herbivore response to plant diversity, so that herbivores respond not only to the abundance of their focal hosts, but also to the abundance of related host species (Castagneyrol et al., 2014). Therefore, the phylogenetic context in which plant species are found could be an important determinant of plant species roles in herbivory networks, and it could also explain how these roles vary across networks. Understanding how the phylogenetic context of the plant community affects plant species roles could be a powerful tool when designing plant communities with the purpose of restoring consumer insect communities.

Here, I use 20 plant-herbivore-parasitoid networks collected in the West of England (Macfadyen et al., 2009a) to identify keystone plant resources for herbivores and parasitoids. Specifically, I ask the following questions: 1) How common are keystone resource species in the 20 networks, and are species with keystone roles consistent across networks?; 2) Are plant species roles conserved across trophic levels, *i.e.* do important plants for herbivores also support parasitoids?; 3) What is the role of phylogenetic context in explaining plant species roles?

2.2 Material and Methods

2.2.1 The focal habitat

Farmland is an important habitat for biodiversity given the large area it occupies (Aizen et al., 2008b) and its potential to support high levels of ecosystem services (Billeter et al., 2008; Schneiders et al., 2012). However, most farmland does not live up to its biodiversity potential (Benton et al., 2003) and understanding how to improve farmland habitats for biodiversity is an important aim for restoration ecology in many parts of the world both for conservation and for the provision of ecosystem services (Kleijn et al., 2006; Jellinek et al., 2013; Morandin and Kremen, 2013; Banks-Leite et al., 2014). Moreover, farms could be straightforward systems to manage given that a large part of their plant community is already under human control. Thus, ecological restoration is both pertinent and pragmatic in these habitats.

2.2.2 The network dataset

The network data was originally collected to study differences in biodiversity and pest control between conventional and organic farms (Macfadyen et al., 2009a). The dataset consists of 10 pairs of plant-herbivore-parasitoid interaction networks (Table S 2-1), each corresponding to a pair of neighbouring organic and conventional farms, all located in the South West of England (Gibson et al., 2007). Insect herbivores, external (Lepidoptera larvae) and internal feeders (Diptera and Lepidoptera larvae), were collected on plants in all farm habitats using transects with size proportional to habitat area. Herbivores were reared and their parasitoids were added to the networks. Each plant species was assigned an abundance category in each sampling event ranging from 1 to 4 based on its transect cover. Plants in category 1 were present once to a few times in the whole transect, plants in category 2 could be easily spotted but still occupied less than 10% of the transect area, plants in category 3 occupied between 11 and 50% of transect area, and plants in category 4 occupied more than 50% of transect area. At the end of 11 sampling events over the course of two years, categories were summed, and each plant species received one relative abundance value. For purposes of analysis, I divided the 20 tri-trophic plant-herbivore-parasitoid networks into plant-herbivore and plant-parasitoid networks (Pocock et al., 2012). While the former depicts direct interactions, the latter describes indirect interactions between plants and pest enemies as, ultimately, plants influence higher trophic levels (Bukovinszky et al., 2008) and have the potential of interacting indirectly with parasitoids in a mutually beneficial way (Kaplan et al., 2016).

2.2.3 How common are keystone resource species in the 20 networks, and are species with keystone roles consistent across networks?

I identify keystone species within plant communities as those species which have the strongest influence on upper trophic levels compared to null expectations. To do that, I first describe plant species' network roles with the quantitative species-level metric *strength*. S*trength* is based on the dependences of consumers on a resource species, therefore describing how important a resource is to its consumers (Bascompte et al., 2006):

$$strength_i^P = \sum_{j=1}^{NA} d_{ij}^A \tag{1}$$

where *NA* is the number of insect species in the network, d_{ij}^A is the dependence of insect species *j* on plant *i*. *Strength* increases both with the number of insect species that feed on a focal plant, and with how dependent on that plant species insect species are. The dependence of insect species *j* on plant species *i* is a measure of the proportion the insect's diet on *i*:

$$d_{ij}^A = \frac{I_{ij}}{\sum_{i=1}^{NP} I_{ij}} \tag{2}$$

where I_{ij} is the frequency of interactions between *j* and *i* and *NP* is the number of plant species in the network.

Not all plant species with high *strength*, however, can be considered keystones since high *strength* is expected for highly abundant species (Vázquez et al., 2009a). Indeed, high abundance is a good indicator of a species' ecological success and abundant species are likely to have large effects over the community. However, from a restoration perspective, it is useful to identify plant species with a disproportionately high *strength* (*i.e.* support more species and individuals than expected based on its abundance), as these do not necessarily need to be highly abundant to attract consumers. Therefore, I also calculated the *keystone role* of each plant species in each network by comparing its observed *strength* with a null expectation based on its relative abundance. I generated the null expectation for each plant species using the *econullnetr* R package (R Core Team, 2017; Vaughan et al., 2017), which is designed to identify resource preferences by consumers (here plants and insects). The null model operates at the level of individual consumers: each insect individual selects a plant species based on the plant's relative abundance. Interactions distributed at the individual level are then summarised at the species level. I ran the null model 1000 times for each network, and defined the *keystone role* of plant *i* in farm *k* as the standardised effect size of its *strength*:

$$keystone\ role_{ik} = \frac{strength_{ik} - \overline{strength_k}}{sd(strength_k)} \tag{3}$$

where $strength_{ik}$ is the *strength* of species *i* in farm *k*, and $\overline{strength_{in}}$ and $sd(strength_{in})$ are the average and standard deviation of the *strength* of plant species *i* in the null networks generated for farm *k*, respectively. Finally, as a categorical measure of species' *keystone role*, each plant species was assigned one of three statuses: (i) keystone species: whose observed *strength* was above the upper confidence interval of its null expectation, (ii) average species: whose observed *strength* was between the confidence intervals of its null expectation, and (iii) underused species: whose observed *strength* was below the lower confidence interval of its null expectation.

Plant species with high values of *strength*, even if with a low value for *keystone role*, are expected to be important for network structure since they are strongly connected to a variety of insect species. Therefore, to investigate whether keystone species have high *strength* I tested the association between species status (keystone, average or underused, as explanatory variable) and species *strength* (the response variable) using linear mixed models (LMM). Random effect structure was selected with Akaike Information Criteria (Zuur et al., 2009) among: (i) no random effect, (ii) species identity, (iii) farm, and (iv) both species identity and farm. The relationship between *strength* and species status was tested using likelihood ratio tests that compared the selected model with an equivalent model omitting species status.

2.2.4 Are plant species roles conserved across trophic levels, i.e. important plants for herbivores also support parasitoids?

To test whether plant species' role is conserved across trophic levels (whether keystones resources are the same for herbivores and parasitoids), I did two analyses. First, I tested whether plant species' *strength* and *keystone role* in plant-herbivore networks (explanatory variable) are associated with their *strengths* and *keystone roles* in plant-parasitoid networks, at a local scale (in each farm) with LMMs. Random effect structure was selected among: (i) no random effect, (ii) species identity, (iii) farm and (iv) species identity and farm as random intercept. I estimate the variance explained by the model ($R^2LMM_{(fix+rand)}$), and the proportion attributed to fixed ($R^2LMM_{(fix)}$) and random effects ($R^2LMM_{(rand)}$) following (Nakagawa and Schielzeth, 2013), using the *MuMIm* R package (Barton, 2013). Second, I tested whether plant species' roles in plant-parasitoid networks can be predicted by their roles in plant-herbivore networks at a regional scale, following the jack-knifing method used by

Emer et al. (2016). I started by averaging the role (*strengths* and *keystone role*) of each species in plant-herbivore and plant-parasitoid networks across all farms. I then fitted two linear regressions relating species mean *strength* and *keystone role* between plant-herbivore and plant-parasitoid networks and tested the fit of the linear regressions (Zuur et al., 2009). Then, to validate the linear regressions, I refitted the linear regression after systematically removing each species and used the coefficients of the new regression to predict the role of the removed species in plant-parasitoid networks from its mean role in plant-herbivore networks. I compared the observed mean values in plant-parasitoid networks with the predicted values using Pearson's correlations tests.

2.2.5 What is the role of phylogenetic context in explaining plant species roles?

To test whether plant species with high *strength* values are phylogenetically proximate to other plant species present in the plant community, I modelled plant species *strength* as a function of phylogenetic relatedness and relative abundance as a covariate. To obtain a phylogenetic tree for the plant assemblage of each farm I pruned a dated European phylogeny that includes 4685 plant species and was constructed to serve as a reference phylogeny for ecological and evolutionary studies (Durka and Michalski, 2012). Since the network dataset included some plant species that were not identified to species level (29 out of 137), I followed a simple set of rules that allowed me to include most of these species in the analysis (Table S 2-2). Species were included in the analysis only if identification was at least at the genus level and I dealt with species identified to genus in the network data set in two ways: (i) species that were the only representatives of that genus in the data (*e.g. Trifolium* sp.) were represented by their genus in the resulting phylogenetic tree; (ii) species that co-occurred with congeneric species, also identified only to genus (*e.g. Trifolium* sp. 1, *Trifolium* sp. 2) were replaced by one species in that genus drawn from the pool of species in the phylogenetic tree that were likely to occur in the study area according to Botanical Society of Britain and Ireland (bsbi.org), this resulting in multiple phylogenetic trees. To decide between the multiple trees, I tested their coefficient of concordance with the *ape* R package (Paradis et al., 2004). As concordance levels were high (Table S 2-3), I randomly selected one of the possible trees for these networks.

To characterise the phylogenetic context of each plant species in each network, I adapted two commonly used indices that describe phylogenetic relatedness of each plant species to the other species in the plant community (Li et al., 2015a, 2015b). Mean phylogenetic distance (MPD_{ab}) is the average of how distant each plant species is to all other plant species in the network, weighted by species abundances:

$$MPD_{ab_i} = \sum_{j=1}^{S_P} d_{ij} * a_j \tag{4}$$

where S_P is the number of plant species in the community, d_{ij} is the distance between species *i* and *j*, and a_j is the relative abundance of species *j*. Low MPD_{ab} values indicate that the focal plant co-occurs with closely related species and/or that distantly related species are rare. Nearest phylogenetic distance (NPD_{ab}) measures how distant each plant species is to its closest relative in the community, weighted by its closest relative abundance:

$$NPD_{ab_i} = d_{ik} * a_k \tag{5}$$

where d_{ik} is the distance between *i* and its closest relative *k*, and a_k is the relative abundance of species *k*. Low NPD_{ab} values indicate that the focal species co-occurs with a very close relative. These metrics are complementary in revealing the ways in which a species is related to the rest of the community: a species can co-occur with a close relative but still be far from most other species, or the inverse.

Insect herbivores feed on related plant species (Cagnolo et al., 2011; Elias et al., 2013; Bergamini et al., 2017). To my knowledge, the phylogenetic signal of plant-parasitoid interactions has never been tested, but parasitoid species often feed on closely related herbivores, even if the phylogenetic signal is weaker than in plant-herbivore networks (Cagnolo et al., 2011; Elias et al., 2013). Therefore, to understand if and how phylogenetic context affect plant species role in plant-herbivore and plant-parasitoid networks, I used four LMMs, two for each network type. These models had species *strength* as response variable, phylogenetic context (NPD_{ab} and MPD_{ab} in separate models) as explanatory variables and relative abundance as a covariate, since species abundance is known to affect species roles in ecological networks (Cagnolo et al., 2011; Fort et al., 2016). Random structures were selected among: (i) no random effect, (ii) species identity, (iii) farm and (iv) species identity with farm. Species *strength* was boxcox transformed, while NPD_{ab} and relative abundance were log transformed. I then used hierarchical partitioning to calculate the relative importance of phylogenetic context and relative abundance in explaining plant species roles with the *hier.part* R package (Chevan and Sutherland, 1991; Walsh and MacNally, 2013). Each observation corresponds to the occurrence of a species in a farm. However, four observations from plant-herbivore networks (out of 580) and two from the plant-parasitoid networks (out of 320) were of phylogenetically isolated species (Figure S 2-1). These are the two fern species *Phyllitis scolopendrium* (renamed as *Asplenium scolopendrium*) and *Pteridium aquilinum*, and the conifer *Taxus baccata*: the only non-Angiosperm species in the data set (Table S 2-4). A careful inspection of their phylogenetic context shows that they can be considered outliers for those metrics (Figure S 2-2 and Figure S 2-3) and were therefore excluded from this analysis.

2.3 Results

The plant-herbivore networks had on average 30 plant species (range = 21 to 41), 63 insect species (range = 44 to 83) and were very sparse, with an average connectance of 0.042 (± 0.007 SD). Plant-parasitoid networks were smaller with 17 plant species (range = 11 to 23) and 37 insect species (range = 26 to 58) on average, and less sparse with an average connectance of 0.092 (± 0.018 SD).

2.3.1 How common are keystone resource species in the 20 networks, and are species with keystone roles consistent across networks?

I found keystone plant resources in all plant-herbivore and plant-parasitoid networks (Figure 2-1). Plant-herbivore networks had relatively fewer keystone species on average (Mean ± SD: 4.05 ± 1.57, range = 1 to 8; 13.3% ± 4.3, range = 4.2% to 20%) than plant-parasitoid networks (Mean ± SD: 2.6 ± 0.88, range = 1 to 4; 15.6% ± 5.5, range = 5.9% to 25%). Underused species were also common (Figure 2-1), being present in all plant-herbivore networks (Mean ± SD: 4.7 ± 2.43, range = 1 to 11; 15.2% ± 6.8, range = 4.8% to 31%) and in 19 out of 20 plant-parasitoid networks (Mean ± SD: 2.9 ± 1.45, range = 0 to 5; 16.7% ± 7.1, range = 0% to 27%). In both network types, there was no difference in the proportion of keystone (plant-herbivore: t = 1.96, df = 9, p = 0.08; plant-parasitoid: t = 1.02, df = 9, p = 0.34) or underused species (plant-herbivore: t = 2.01, df = 9, p = 0.07; plant-parasitoid: t = 1.43, df = 9, p = 0.19) between organic and conventional farms.

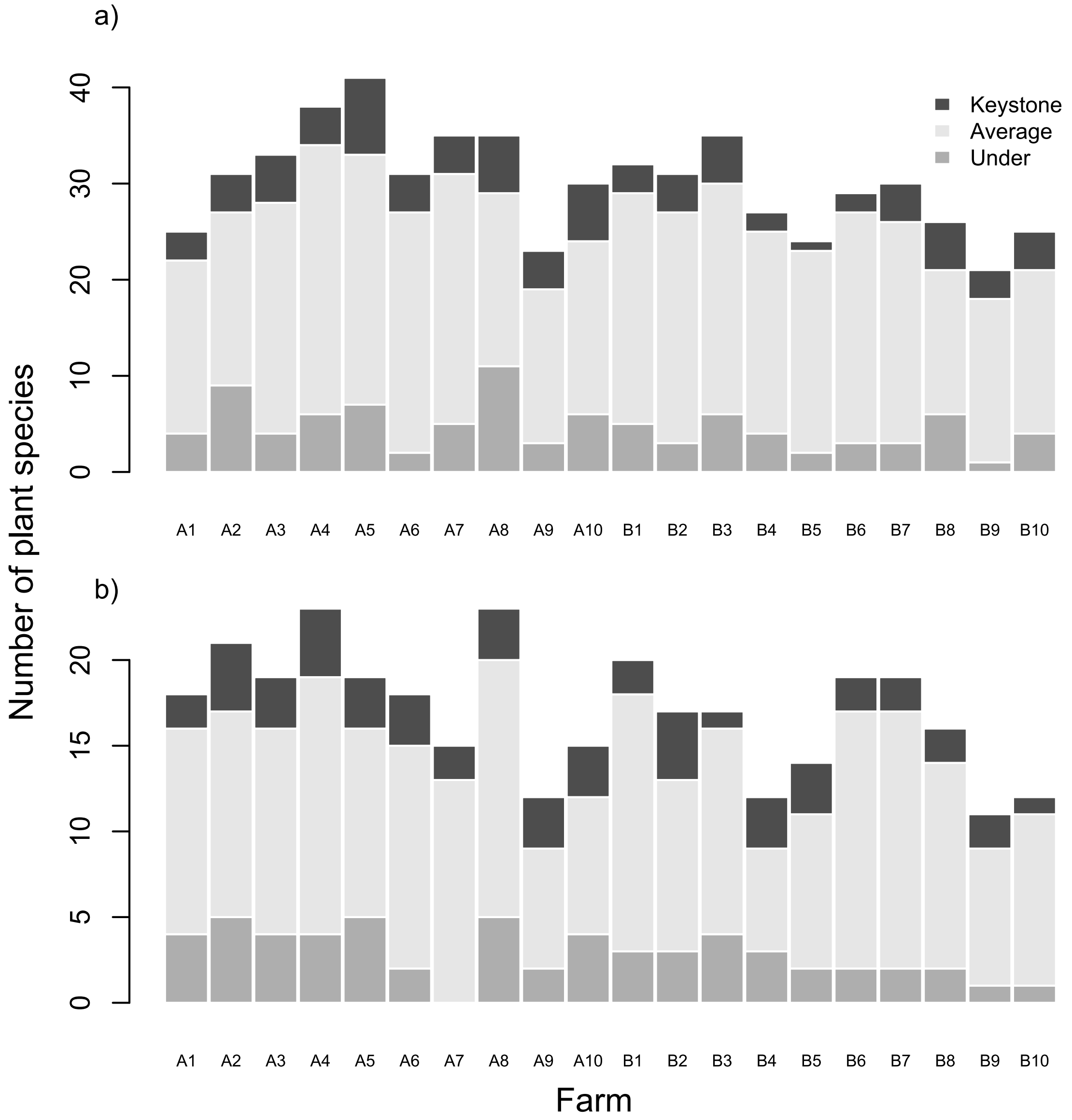

Figure 2-1 Distribution of plant species in: a) plant-herbivore and b) plant-parasitoid networks (networks correspond to farms labelled A1 to A10 and B1 to B10). Overperforming species (Keystone: above null model confidence intervals) are in dark grey, average species (Average: between null model confidence intervals) are in light grey and underused species (Under: below null model confidence intervals) are in medium grey.

Of the 137 plant species present in the 20 plant-herbivore networks, only 18 (13%) acted as a keystone resources in at least one plant-herbivore network. While 27 out of the 89 (30%) plant species present in the plant-parasitoid networks acted as keystone resources in at least one plant-parasitoid network. These plant species were not consistently keystones: on average, they are keystones in 62% of the plant-herbivore networks (± 33, range = 1% to 100%)

and in 42% (± 33, range = 5% to 100%) of the plant-parasitoid networks in which they are present. Keystone species are listed in Table S 2-5 and Table S 2-6. The observed *strength* of keystone species was higher than of non-keystone species (plant-herbivore networks: $\chi^2(2) = 209.84$, $p < 0.001$; plant-parasitoid networks: $\chi^2(2) = 168.52$, $p < 0.001$), and keystones occur in most classes of relative abundance for both network types (Figure S 2-4).

2.3.2 Are plant species roles conserved across trophic levels, i.e. important plants for herbivores also support parasitoids?

I found that both plants' *strength* and *keystone roles* are conserved across trophic levels at the farm scale ($\chi^2(1) = 106.87$, $p < 0.001$ and $\chi^2(1) = 55.56$, $p < 0.001$, respectively; Figure 2-2a-b). In both models, the fixed effect (plant's roles in plant-herbivore networks) was responsible for more than half of the variance of the full model (*strength*: $R^2LMM_{(fix+rand)} = 0.55$, $R^2LMM_{(fix)} = 0.35$, $R^2LMM_{(rand)} = 0.2$; *keystone roles*: $R^2LMM_{(fix+rand)} = 0.48$, $R^2LMM_{(fix)} = 0.25$, $R^2LMM_{(rand)} = 0.23$). Thus, on average, plant species that were important resources for herbivores were also important resources for parasitoids in each farm. Species identity was selected as random effect in both models. I also found that, regionally (*i.e.* using the jack-knifing method), both species' *strength* ($F_{1,87} = 38.14$, $R^2 = 0.3$, $p < 0.001$) and *keystone role* ($F_{1,87} = 42.48$, $R^2 = 0.33$, $p < 0.001$) in plant-parasitoid networks could be predicted from its average role in plant-herbivore networks (Figure 2-2c-d). The model validation shows that predicted values of *strength* ($t = 5.7$, $p < 0.001$, $r = 0.52$) and *keystone role* ($t = 5.97$, $p < 0.001$, $r = 0.54$) for plant-parasitoid networks are highly correlated to the observed mean values of these metrics.

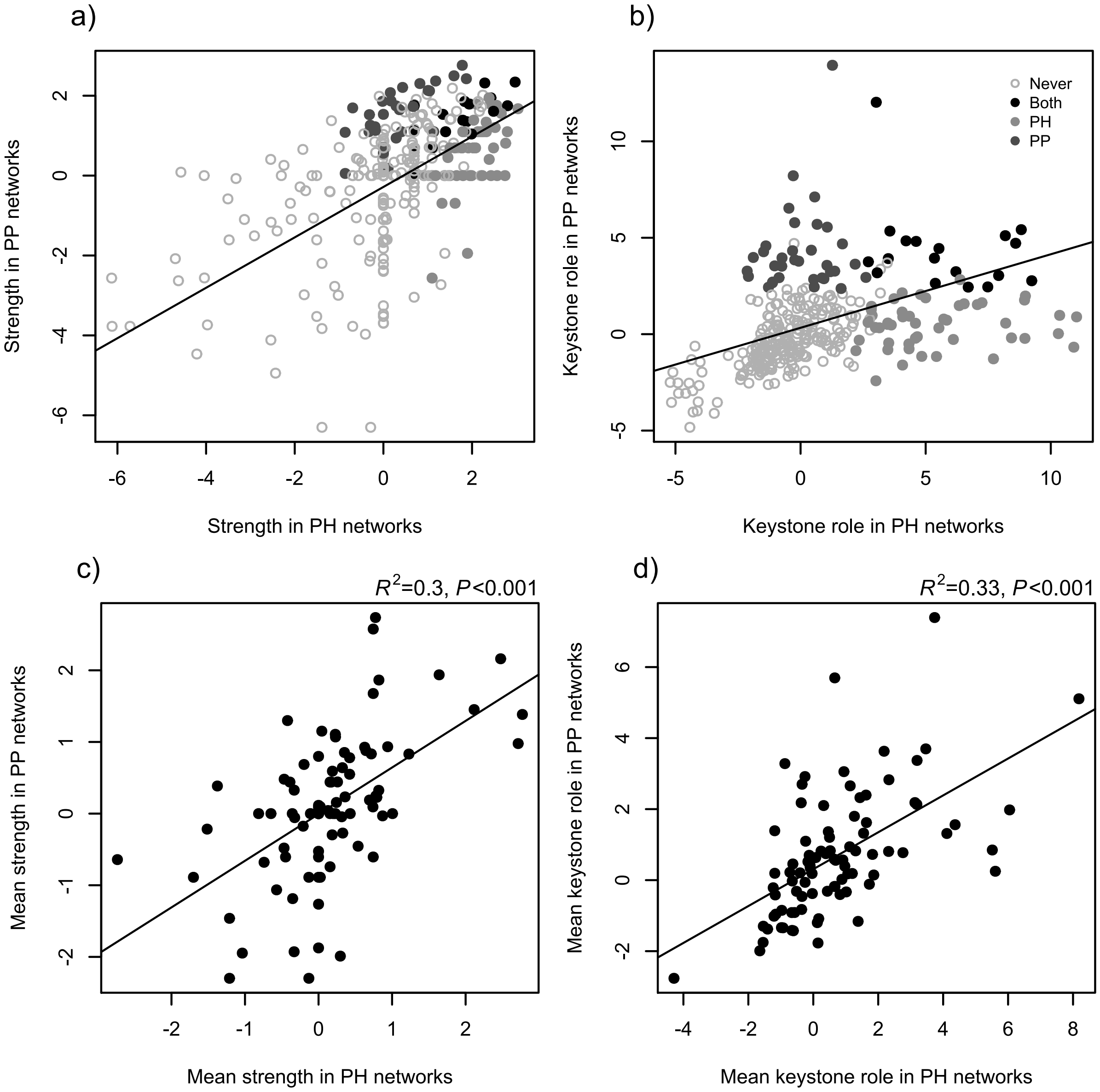

Figure 2-2 Relationship between plant species roles in plant-herbivore (PH) and plant-parasitoid (PP) networks: a) strength and b) keystone role. Each dot represents a species on a farm. Unfilled dots are species that are not keystones in either the PH or PP networks of a given farm (Never), in black are species that are keystones in both the PH and PP networks of a given farm (Both), in light grey are species that are only keystones in the PH network of a given farm (PH) and in dark grey are species that are only keystones in the PP network of a given farm (PP). Linear regression between c) mean species strength and d) mean species keystone role in PH and PP networks; each dot represents the average role of a species across all farms in which that species occurs.

2.3.3 What is the role of phylogenetic context in explaining plant species roles?

Species *strength* was a function of its phylogenetic context in plant-herbivore networks (Table 2-1). Specifically, the average phylogenetic distance to all other plant species in the community (MPD_{ab}), but not the distance to its closest neighbour (NPD_{ab}), negatively affects plant *strength* (Figure 2-3; Table 2-1) and explains 17% of the variance in the model. Additionally, relative abundance is positively associated with the *strength* of plant species in plant-herbivore and plant-parasitoid networks (Table 2-1). Even if MPD_{ab}, in plant-herbivore networks, and abundance in both network types, affect plant species *strength*, keystone plant species were distributed across a large range of relative abundances and phylogenetic isolation on each farm (Figure 2-3, Figure S 2-5 and Figure S 2-6).

Table 2-1 Results of the linear mixed-effects models (LMM) testing whether plant species relative abundance and phylogenetic context (nearest phylogenetic distance, NPDab, and mean phylogenetic distance, MPDab) are associated to plant species strength in plant-herbivore and plant-parasitoid networks. For both metrics, the random structure selected with Akaike Information Criteria (AIC) included only species identity. Estimates, t and p values and the percentage of explained variance attributed to each fixed effect (% R^2) composing the final model.

	Fixed-effect	**Estimate**	**t**	**p**	**% R^2**
Plant-Herbivore	Abundance	+0.37	7.48	<0.001	83%
	MPD_{ab}	-0.007	-2.33	0.02	17%
Plant-Parasitoid	Abundance	+0.42	5.46	<0.001	-

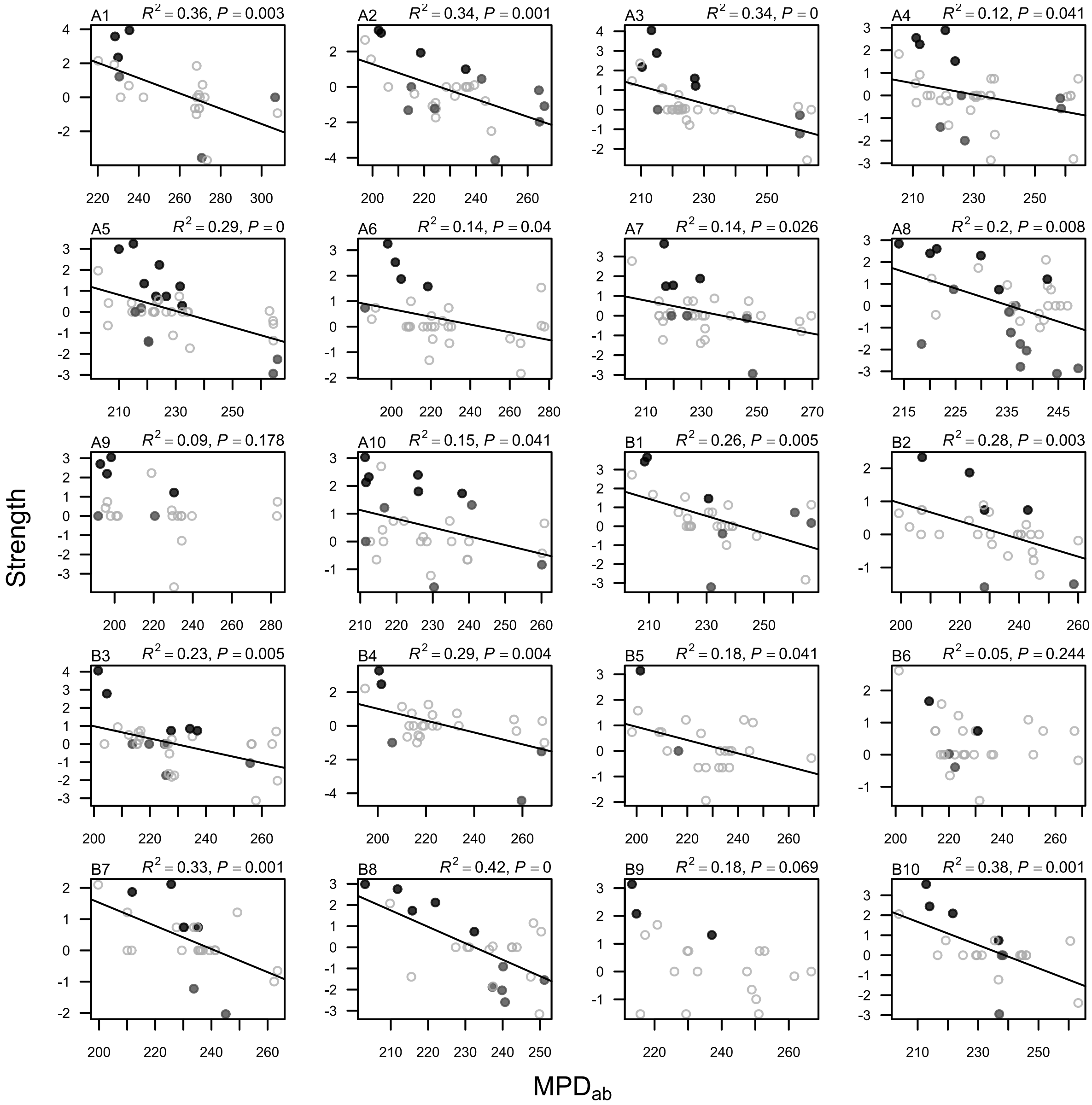

Figure 2-3 Results of linear mixed models (LMM) between plant species strength and weighted mean phylogenetic distance to other plant species (MPDab) performed individually for each plant-herbivore network (network codes - A1 to A10 and B1 to B10 – in the top left corner of each plot). Each dot represents a species in a farm, in dark grey are overperforming species (keystone species: above null model confidence intervals) and in lighter grey are underused species (below null model confidence intervals). Strength values were boxcox transformed. Lines of best fit are drawn for statistically significant models.

2.4 Discussion

The results show that keystone plant resources for insects are widespread in farms, but that relatively few plant species play keystone roles and that being a keystone plant is context dependent rather than an absolute species attribute. I also found that plant species with important roles in plant-herbivore networks also had important roles in plant-parasitoid networks. Finally, I found that the most important plant species for network structure are not only abundant but are also closely related to other plant species in plant-herbivore networks. In what follows I first address the limitations of this study, and then consider the original questions, putting the results in the context of previous findings.

2.4.1 Limitations

There are two main limitations in this study. First, better quality abundance data for plant species would have been desirable. While an ordinal scale was used, there are a number of advantages in the plant data: they were collected at the same time, using the same methods and with the same sampling effort (all factors which vary in many studies involving multiple networks). The networks are also from a relatively small area making both, plant and insect communities, comparable and the study of variation on species roles possible. In mitigation for this possible limitation I show that the ordinal abundance measure used correlates highly with estimated percentage plant cover (Figure S 2-7). Second, with truly independent abundance data for herbivores, I would have a more precise estimate of plant species roles in plant-parasitoid networks, and on how those roles are mediated by herbivore diversity. However, collecting insect abundance data independently from interaction data remains challenging (Maldonado et al., 2013). Therefore, I dealt with this problem by connecting parasitoids directly to plants, an approach used by Pocock et al. (2012) and that can highlight how plant species could potentially support pest control.

2.4.2 Keystone species in farmland systems

The high potential of the keystone species concept for conservation (Simberloff, 1998) led to the use of ecological networks as a tool for identifying keystone species (Mello et al., 2015; Zhao et al., 2016; Traveset et al., 2017). Even if the concept was originally created for top predators (Paine, 1995), the importance of bottom-up effects on the structure of plant insect communities (Dinnage et al., 2012; Pellissier et al., 2013; Holmquist et al., 2014) suggests that keystones also exist among plants. I found that keystone resource species are pervasive in agricultural systems, but so are underused species, and that keystone species are not simply rare species with moderate values of *strength* but include important species for network structure serving as a frequent food source for several insect species. Two of the results suggest that plant species identity matters for the roles plant species play in plant-herbivore and plant-parasitoid networks. First, for both plant-herbivore and plant-parasitoid networks, the pool of keystone species (and of underused species) was small including less than a third of plant species in the regional pool. Second, in several analyses, species identity was selected as a random effect while farm was not, suggesting that species roles varied more between species than within species between farms.

Plant species identity, however, did not fully explain the role played by plant species in plant-herbivore and plant-parasitoid networks, since species roles varied across networks. The challenge faced by community ecologists is understanding when and why species play important ecological roles. Community composition has the potential of affecting interaction occurrence (Lázaro et al., 2009; Yguel et al., 2011; Donoso et al., 2017) and consequently species roles in ecological communities. Since context dependency of species performance has tremendous implications for ecological restoration (Perring et al., 2015), understanding which compositional features of ecological communities are important for different interaction types would be an important step towards increasing the predictive power of restoration ecology. For instance, phenotypic disparity and phylogenetic relatedness interact to affect the success of nurse-based restoration, based on facilitative interaction between plants (Verdú et al., 2011), while diverse communities of predators with complementary feeding niches increase attack rates and control of aphid pests (Northfield et al., 2010). Here, I show that plant relatedness - how close a species is, on average, to all other plant species in the community (MPD_{ab}), but not the distance to its closest neighbour (NPD_{ab}) - affects plant-herbivore interactions so that the most important plant species for herbivores are closely related to other species in the plant community. Possibly, plant species co-occurred with small sets of related co-hosts in farms, so that MPD_{ab} better described herbivore host choices than $NPD_{ab.}$ Conversely, plant relatedness did not affect plant-parasitoid interactions. Even if parasitoids tend to feed on related herbivores and herbivores on related plants (Cagnolo et al., 2011; Elias et al., 2013), phylogenetic signal is not necessarily symmetrical, and related herbivores do not feed on related plants (Elias et al., 2013; Fontaine and Thébault, 2015), explaining the lack of effect of plant relatedness on plant-parasitoid interactions. As parasitoid diversity reduces temporal variation in pest control (Macfadyen et al., 2011a), focusing on keystone plant species for parasitoids might facilitate the restoration of pest control.

Despite the observed importance of plant abundance and phylogenetic relatedness (only in plant-herbivore networks) in explaining plant species *strength*, it is important to note that keystone plant species were distributed across a large range of relative abundances and phylogenetic isolation on each farm (Figure 2-3, Figure S 2-5 and Figure S 2-6), suggesting that phylogenetic context and species abundance are not enough to predict which plant species will have the status of keystones in farms.

This study highlights the benefit of studying multiple interaction types in combination (Fontaine et al., 2011; Pocock et al., 2012; Dáttilo et al., 2016). Plant species roles were conserved across trophic levels – correlated in plant-herbivore and plant-parasitoid networks -

across two different scales: locally since important plant species for herbivores in a farm were also important for parasitoids in that farm, and regionally since I was able to predict average plant species importance for parasitoids based on their average importance for herbivores across farms. These are promising results as they suggest that two additional trophic levels could benefit from management of one single level (Scherber et al., 2010; Hudewenz et al., 2012). If plant species roles are conserved across different types of interaction networks, the loss of few plant species could jeopardize multiple ecosystem services (Albrecht et al., 2014). On the other hand, the high correlation of plants' degrees – their number of interaction partners and another way of describing species network roles - in a pollination and herbivory network had a stabilising effect on the system (Sauve et al. 2016), suggesting that multiple interaction systems could benefit from sharing keystone species.

2.4.3 Conclusions

The intensification of agriculture is a key driver of the current biodiversity crisis we face (Foley et al., 2005). In many countries, agricultural systems occupy a very large proportion of the land area (50% in France, Spain and the Netherlands and 70% in the UK and South Africa; World Bank, 2015), the best approaches to promote biodiversity at a large scale (Phalan et al., 2011a; Tscharntke et al., 2012) and at a small scale (*e.g.* within farms) need to be identified. Since habitat creation is a large part of management at a small scale in agricultural systems (Rey Benayas and Bullock, 2012; Morandin et al., 2016), the results suggest that practitioners should take heed of the interplay between species abundance and network roles. The results are also interesting from a theoretical perspective, as the identification of keystones can help to elucidate how species traits and ecological contexts interact to allow the emergence of key ecological roles. The keystone concept was created in 1960's but the quest for keystones remains important nearly 60 years later, as the identification of these species represent a win-

win situation: it improves our understanding of community structure and functioning and can potentially reverse biodiversity declines which are highest in agro-ecosystems.

2.5 Supplementary Material

Table S 2-1 The dataset used for analysis, consisting of pairs of plant-herbivore (PH) and plant-parasitoid (PP) networks collected in 20 farms in the southwest of England (Macfadyen et al. 2009a). Each row corresponds to a farm and includes information about the two networks (one of each interaction type: PH and PP) collected in that farm. The codes are as follows: Farm = code name of each farm; Treat = farm management (C=conventional and O=organic); Type = type of network (PH or PP); Insect = number of herbivore species in the PH networks and of parasitoid species in the PP networks; Plant = number of plant species in the PH and PP networks, C = connectance of the PH and PP networks.

Farm	**Treat.**	**Type**	**Insect**	**Plant**	**C**	**Type**	**Insect**	**Plant**	**C**
A1	O	PH	78	25	0.05	PP	45	18	0.09
A2	O	PH	61	31	0.05	PP	43	21	0.08
A3	O	PH	83	33	0.04	PP	39	19	0.07
A4	O	PH	66	38	0.03	PP	46	23	0.07
A5	O	PH	80	41	0.03	PP	44	19	0.09
A6	O	PH	62	31	0.04	PP	33	18	0.09
A7	O	PH	70	35	0.04	PP	33	15	0.10
A8	O	PH	73	35	0.04	PP	58	23	0.08
A9	O	PH	56	23	0.05	PP	28	12	0.10
A10	O	PH	81	30	0.04	PP	43	15	0.10
B1	C	PH	83	32	0.04	PP	45	20	0.08
B2	C	PH	45	31	0.04	PP	30	17	0.10
B3	C	PH	68	35	0.04	PP	37	17	0.10
B4	C	PH	55	27	0.05	PP	27	12	0.14
B5	C	PH	44	24	0.05	PP	29	14	0.12
B6	C	PH	54	29	0.04	PP	34	19	0.07
B7	C	PH	52	30	0.04	PP	39	19	0.07
B8	C	PH	54	26	0.05	PP	36	16	0.10
B9	C	PH	46	21	0.06	PP	26	11	0.11
B10	C	PH	58	25	0.05	PP	29	12	0.10

Table S 2-2 Plant species with low resolution identification (*i.e.* not to species level) in the network dataset or absent in the phylogenetic dataset. Plant species names, number of networks (PH for plant-herbivore and PP for plant-parasitoid) in which they are present, identification issue (Unknown=unknown species, Family=only identified to family, Aggregated=muliple species of the same genus, Genus=only identified to genus, Variety=crop variety, Unavailable=species not present in the phylogeny dataset and Hybrid=hybrid of two species) and solution used (either Removed or the name of the phylogeny branch used).

Species Name (network data)	PH	PP	Problem	Solution
UKP39[1]	1	-	Unknown	Removed
Asteraceae[1]	1	-	Family	Removed
Grass[1]	20	20	Family	Removed
Avena spp.[2]	9	7	Aggregated	*Avena*
Rumex spp.[3]	19	4	Aggregated	*R. acetosella* *R. conglomeratus* *R. crispus* *R. obtusifolius* *R. sanguineus*
Taraxacum spp.[2]	6	3	Aggregated	*Taraxacum*
Trifolium spp.[3]	19	13	Aggregated	*T. campestre* *T. dubium* *T. fragiferum* *T. hybridum* *T. medium* *T. micranthum* *T. striatum* *T. aestivum*
Arctium sp.[2]	5	3	Genus	*Arctium*
Brassica sp.[4]	1	1	Genus	*Brassica elongata*
Brassica unknown[4]	1	1	Genus	*Brassica elongata*
Carduus sp.[2]	1	-	Genus	*Carduus*
Cerastium sp.[3]	1	1	Genus	*C. diffusum* *C. pumilum* *C. semidecandrum* *C. tomentosum*
Cirsium sp.[3]	0	-	Genus	*C. acaule*

				C. eriophorum
				C. palustre
Lamium sp.[3]	2	-	Genus	*L. amplexicaule*
				L. hybridum
				L. maculatum
Lathyrus sp.[2]	1	1	Genus	*Lathyrus*
Lupinus sp.[2]	3	1	Genus	*Lupinus*
Malus sp.[5]	2	-	Genus	*Malus domestica*
Prunus sp.[3]	2	-	Genus	*P. domestica*
				P. laurocerasus
				P. lusitânica
Ranunculus sp.[3]	2	2	Genus	*R. auricomus*
				R. bulbosus
				R. flammula
				R. lingua
				R. sceleratus
Rosa sp.[2]	3	1	Genus	*Rosa*
Salix sp.[2]	2	-	Genus	*Salix*
Silene sp.[3]	3	-	Genus	*S. flos-cuculi*
				S. latifolia
				S. vulgaris
Triticum sp.[2]	18	17	Genus	*Triticum*
Viola sp.[2]	2	1	Genus	*Viola*
Brassica oleracea (Acephala Group)[6]	2	2	Variety	*Brassica oleracea*
Brassica oleracea (Italica Group)[6]	1	1	Variety	*Brassica oleracea*
Cynara scolymus[7]	1	1	Unavailable	*Cynara cardunculus*
Tilia vulgaris/europaea[8]	2	-	Unavailable	*Tilia x vulgaris*
X *Triticosecale*[9]	4	5	Hybrid	*Triticum aestivum*
				Secale cereale

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[1] Species with identification up to family level were removed

[2] Species with identification at the genus level and that are the only occurrences of that genus in the network dataset were replaced by their genus branch

[3] Species with identification at the genus level but that are not the only occurrences of that genus in the network dataset were replaced by a set of possible species that were both: (i)

present in the phylogenetic tree and (ii) known to occur in the study area (Botanical Society of Britain and Ireland, bsbi.org)

[4] Do not co-occur in any network, replaced *Brassica elongata*

[5] Replaced by *Malus domestica* (Botanical Society of Britain and Ireland, bsbi.org)

[6] Do not co-occur in any network, replaced by *Brassica oleracea*

[7] Replaced by *Cynara cardunculus*

[8] Replaced by *Tilia x vulgaris*

[9] X *Triticosecale* is a hybrid of species from a *Triticum* and a *Secale* species, and only one species from each genus (*Triticum aestivum* and *Secale cereale*) were available in the phylogenetic dataset. Since *Triticum aestivum* and *Secale cereale* never co-occur in the network dataset, each replaced *X Triticosecale* in networks where the other species was present

Table S 2-3 Results of the concordance analysis between distance matrices (N=number of distance matrices, each corresponding to a phylogenetic tree) for 10 plant-herbivore and 4 plant-parasitoid networks. Networks were collected in farms identified by a code (Farm). Concordance analysis: values for Kendall's coefficient of concordance (W) between matrices, and tests of concordance values using permutations (p-value). *A posteriori* analysis for the contributions of individual matrices to overall concordance: mean mantel (Mantel), mean p-value and mean corrected p-value (Cor. P-value, Holm method) across alternative matrices for each network. *Cases of non-significance after Holm correction: since W values are as high as for other matrices, non-significance was assumed to be due to the large number of alternative matrices (N).

Plant-herbivore						
		Concordance		**Contribution of indiv. matrices**		
Farm	**N**	**W**	**p-value**	**Mantel**	**p-value**	**Cor. p-value**
A1	175	0.9997	<0.001	0.9997	<0.001	0.17*
A2	140	0.9987	<0.001	0.9987	<0.001	0.14*
A4	7	0.9995	<0.001	0.9994	<0.001	0.007
A5	21	0.9995	<0.001	0.9994	<0.001	0.02
A6	7	0.9995	<0.001	0.9994	<0.001	0.007
B1	5	0.9997	<0.001	0.9996	<0.001	0.005
B2	3	1	<0.001	1	<0.001	0.003
B3	3	0.9998	<0.001	0.9998	<0.001	0.003
B8	5	0.9989	<0.001	0.9986	<0.001	0.005
B9	3	0.9998	<0.001	0.9997	<0.001	0.003
Plant-parasitoid						
A1	35	0.9994	<0.001	0.9994	<0.001	0.03
A2	35	0.9995	<0.001	0.9995	<0.001	0.03
A4	7	0.9994	<0.001	0.9992	<0.001	0.007
A10	2	0.9975	<0.001	0.9950	<0.001	0.002

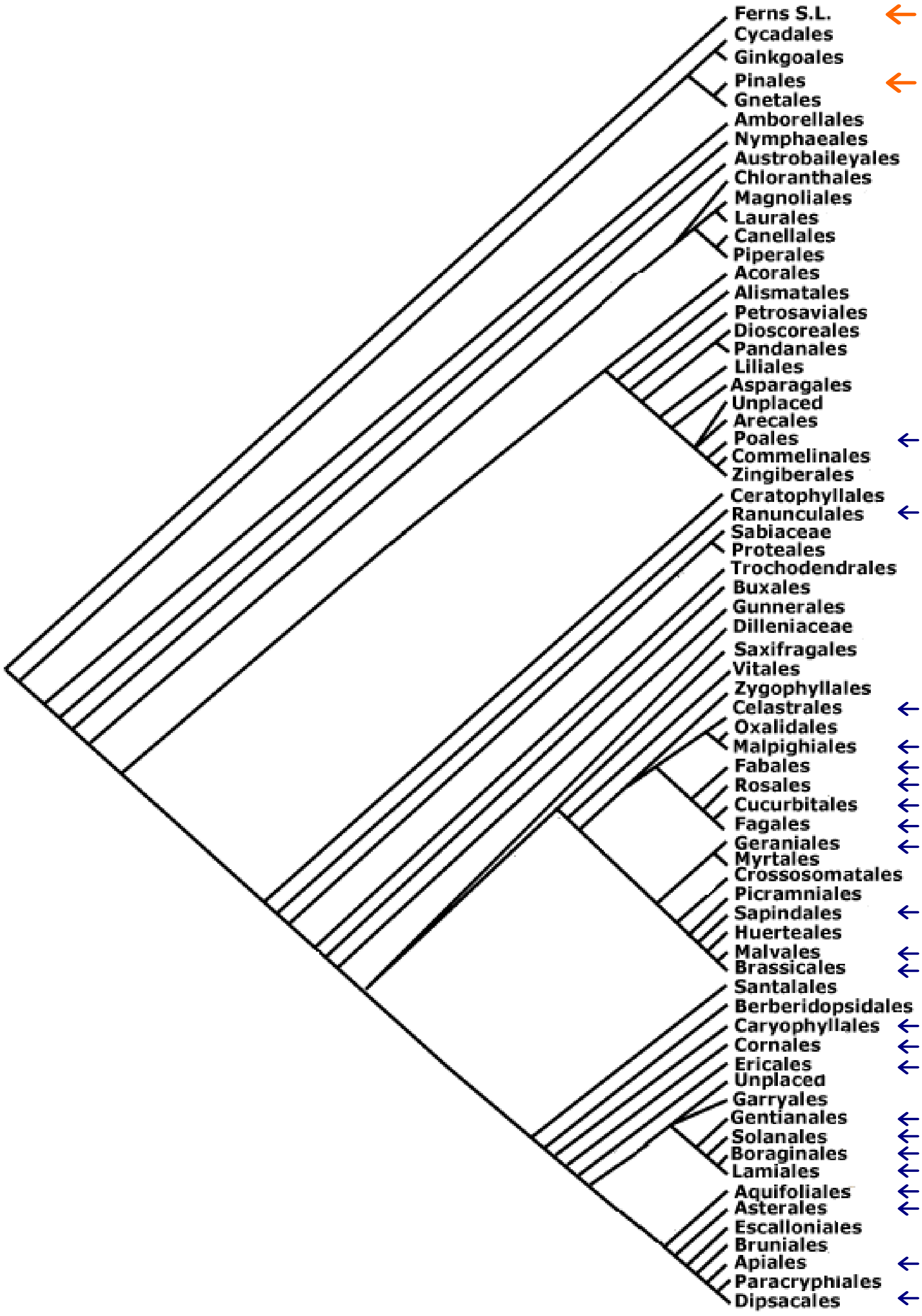


Figure S 2-1 Phylogenetic tree extracted from the Angiosperm Phylogeny Website (www.mobot.org/MOBOT/research/APweb/) including angiosperm plant orders and non-angiosperm groups: Ferns, Cycadales, Gynkgoales, Pinales and Gnetales. With blue arrows are highlighted the orders that include most plant species in the dataset. In orange are highlighted the groups including phylogenetically isolated species in the dataset: the two species of fern *Phyllitis scolopendrium* (current *Asplenium scolopendrium*) and *Pteridium aquilinum*, and the conifer species *Taxus baccata* in Pinales.

Table S 2-4 List of occurrences (combination of plant species per farm) excluded from the phylogenetic context analysis (question 3) due to extreme phylogenetic isolation. Species names, corresponding farm names of the plant-herbivore and plant-parasitoid networks in from which plant species were removed and, in parenthesis, the metrics of phylogenetic relatedness for which plant species are outliers (NPD_{ab}=nearest phylogenetic distance; MPD_{ab}=mean phylogenetic distance). * Formerly known as *Asplenium scolopendrium.*

Species	**Plant-Herbivore**	**Plant-Parasitoid**
*Phyllitis scolopendrium**	B1 (NPD_{ab}/MPD_{ab})	B1 (MPD_{ab})
Pteridium aquilinum	A1 (MPD_{ab})	-
Pteridium aquilinum	B9 (NPD_{ab}/MPD_{ab})	-
Taxus baccata	A4 (NPD_{ab}/MPD_{ab})	A4 (MPD_{ab})

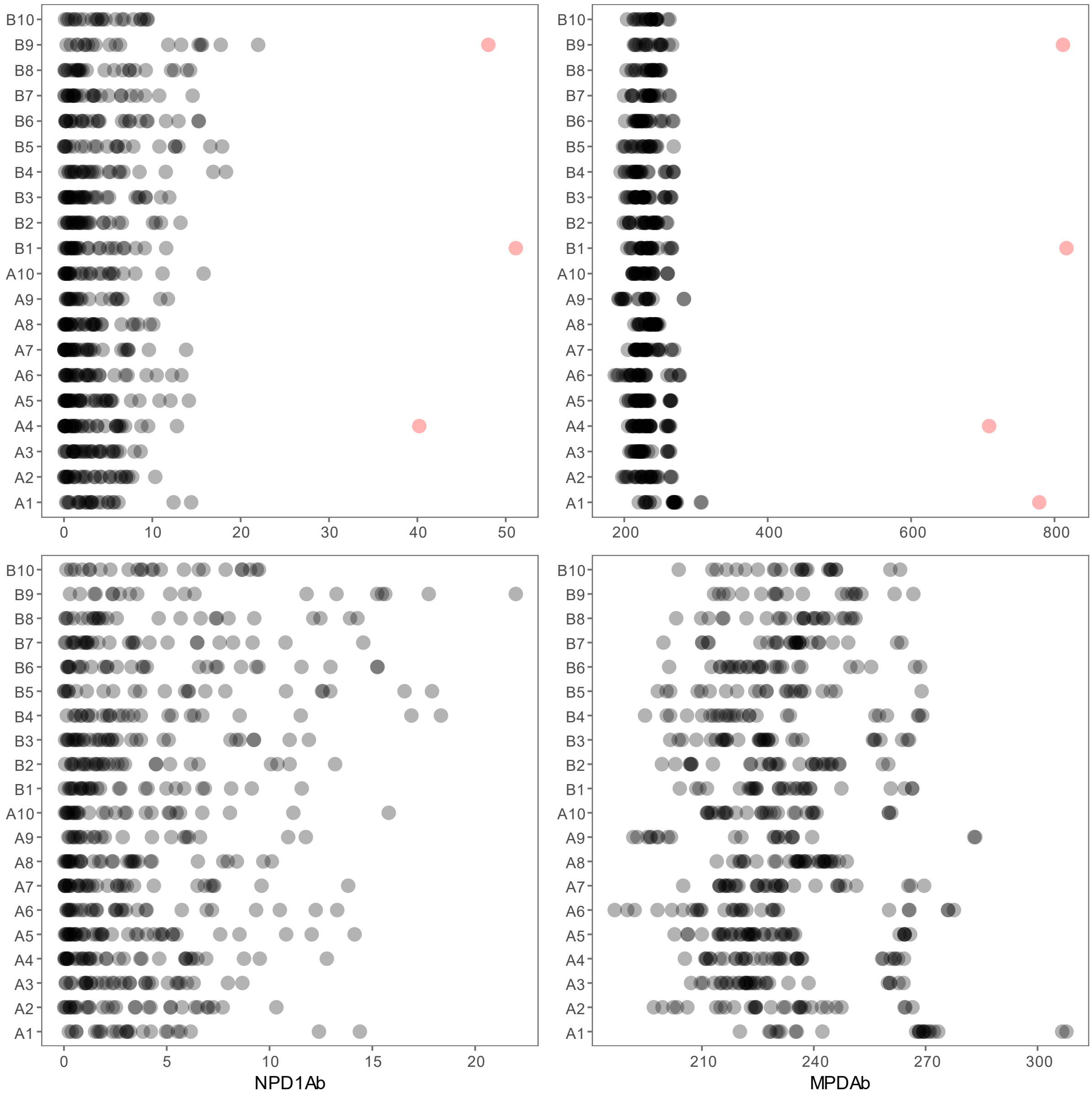


Figure S 2-2 Cleveland dotplots of the phylogenetic context metrics NPDab (nearest phylogenetic distance; a and c) and MPDab (mean phylogenetic distance; b and d) from plant-herbivore networks. Each dot represents a species in a farm (y axis) with their corresponding metric values (x axis). In red are occurrences (species per farm) considered outliers for that metric and, therefore, that were removed from the analysis. a) and b) Cleveland plots before the removal of outliers; c) and d) Cleveland plots after the removal of outliers.

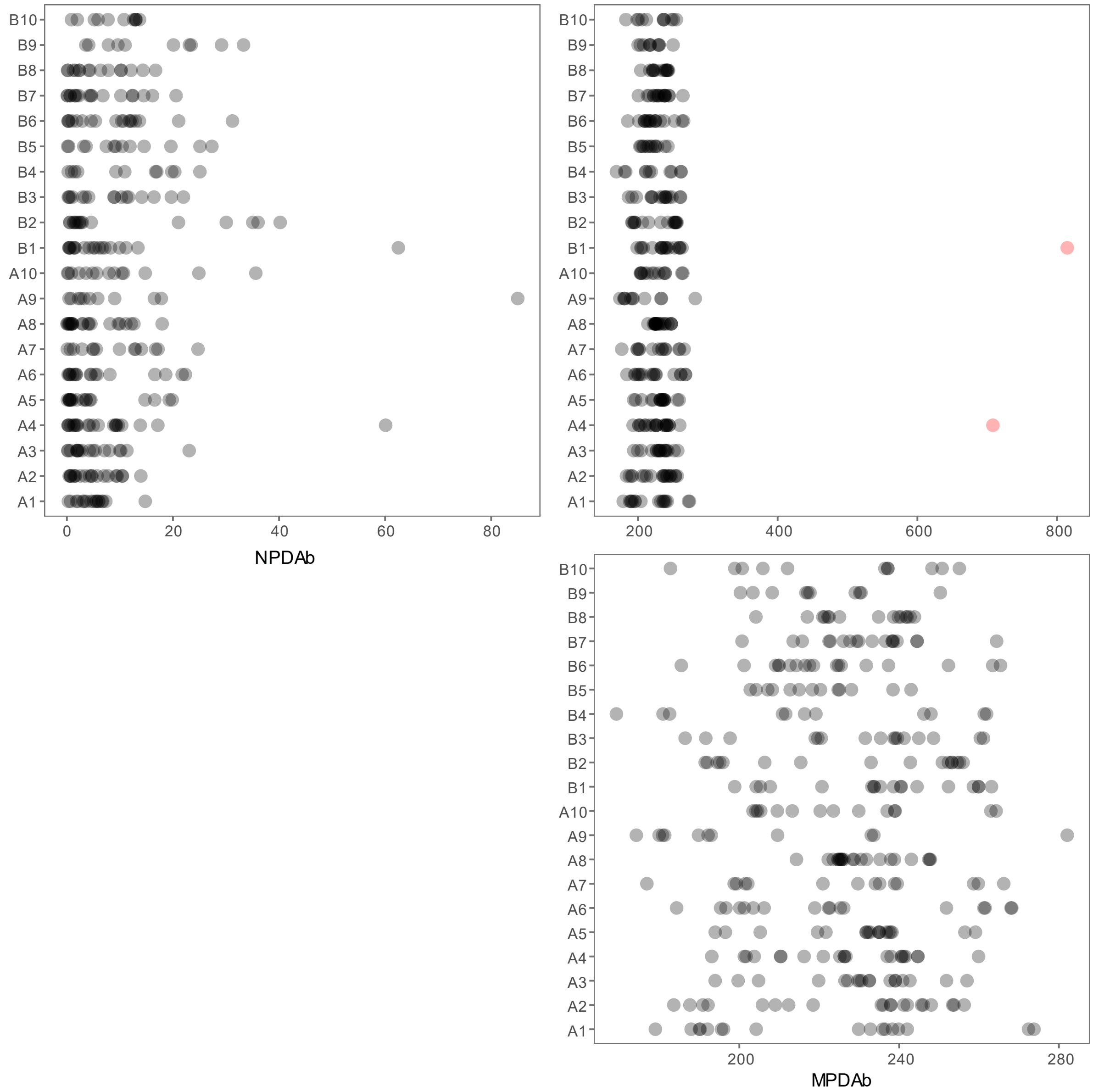


Figure S 2-3 Cleveland dotplots of the phylogenetic context metrics NPDab (nearest phylogenetic distance; a) and MPDab (mean phylogenetic distance; b and d) from plant-parasitoid networks. Each dot represents a species in a farm (y axis) with their corresponding metric values (x axis). In red are occurrences (species per farm) considered outliers for that metric and, therefore, that were removed from the analysis. a) and b) Cleveland plots before the removal of outliers; d) Cleveland plot after the removal of outliers. Plot c) not included since no species had an extreme value of NPDab nor was removed from the analysis.

Table S 2-5 List of the 137 plant species present in the 20 plant-herbivore networks. Networks are named after their corresponding farms (A1-A10 and B1-B10). When species are present in a network, cells correspond to species status: K are keystone species, A are average species and U are underused species. When absent from a network, cells are filled with (-). Species that play a keystone role in at least one farm are marked in bold.

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Acer campestre	-	K	A	A	A	A	A	A	K	K	A	-	A	A	-	-	A	-	-	-
Acer platanoides	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acer pseudoplatanus	-	-	-	A	-	-	-	-	A	-	-	-	-	A	-	-	-	-	A	-
Achillea millefolium	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Alopecurus myosuroides	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Angelica sylvestris	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Anthriscus sylvestris	-	-	A	A	A	-	A	A	-	A	A	-	A	A	U	A	A	A	A	U
Apium nodiflorum	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Arctium sp.	-	-	A	A	-	-	-	-	-	-	A	A	A	-	-	-	-	-	-	-
Arrhenatherum elatius	-	-	-	-	-	-	-	-	A	-	-	A	-	-	-	-	-	-	-	-
Asteracae unknown	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Atriplex patula	-	-	-	A	-	A	-	-	-	-	-	-	-	-	A	-	-	-	-	-
Avena spp.	U	-	-	A	U	A	A	-	A	-	-	A	A	-	A	-	-	-	-	-
Brachypodium sylvaticum	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Brassica juncea	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brassica napus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	A	-	-	-	-
Brassica nigra	-	-	-	-	-	-	A	-	-	-	-	-	-	-	A	-	-	-	-	-
Brassica oleracea (Acephala)	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	A	-	-	-

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Brassica oleracea (Italica)	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
***Brassica rapa* sp.**	-	-	-	-	-	-	-	-	-	-	-	K	K	-	-	-	K	-	-	-
***Brassica* sp.**	-	-	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brassica unknown	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Bryonia dioica	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-
Calystegia sepium	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cannabis sativa	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Capsella bursa-pastoris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-
Carduus sp.	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carpinus betulus	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-
Cerastium fontanum	-	A	-	-	-	A	-	A	A	-	-	-	-	-	-	-	-	-	-	-
Cerastium glomeratum	-	A	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-
Cerastium sp.	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chenopodium album	-	A	-	-	-	-	-	-	-	-	-	-	A	-	A	A	A	-	-	K
Chenopodium polyspermum	-	-	-	-	-	-	-	K	-	-	-	-	K	-	-	-	-	-	-	-
Cirsium arvense	-	-	A	U	A	A	A	U	-	A	A	-	A	A	-	A	A	A	-	-
Cirsium vulgare	-	A	-	A	A	A	A	-	-	A	-	-	-	-	-	A	-	-	-	-
Clematis vitalba	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	A	-	-	-	-
Convolvulus arvensis	-	A	A	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-
Cornus sanguinea	-	-	A	-	-	-	-	-	-	-	A	-	-	-	-	-	-	A	-	A

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Coronopus squamatus	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-
Corylus avellana	K	K	K	K	K	-	K	K	-	K	K	K	-	A	A	-	K	K	K	K
Crataegus monogyna	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	A	A	K	K	K
Cynara scolymus	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Dactylis glomerata	-	-	-	A	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Euonymus europaeus	-	-	A	-	K	-	-	-	-	-	-	-	K	-	-	-	-	-	-	-
Fagus sylvatica	-	-	-	K	A	K	A	-	-	-	-	-	-	-	-	K	-	-	-	-
Fraxinus excelsior	A	-	-	A	-	A	A	-	-	-	-	-	-	A	A	A	A	-	-	-
Galeopsis tetrahit	-	-	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galium aparine	-	-	-	-	-	-	A	U	-	-	-	-	-	-	-	-	-	-	-	-
Geranium dissectum	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-
Geranium robertianum	-	-	-	-	-	A	-	-	-	A	-	-	-	-	A	-	-	A	-	-
Geum rivale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-
Geum urbanum	-	-	-	-	-	-	-	-	A	A	-	A	-	-	-	A	-	-	-	-
Glechoma hederacea	A	-	A	U	U	A	-	A	-	A	A	-	U	A	-	U	U	U	A	-
Grass unknown	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
Heracleum sphondylium	A	A	A	A	A	-	A	-	A	-	A	A	U	A	A	-	A	-	A	A
Holcus lanatus	A	U	-	-	-	-	U	A	-	A	-	A	A	A	-	-	U	U	-	-
Hordeum vulgare	-	-	U	U	A	-	A	A	-	-	U	U	A	U	A	A	A	U	-	-
Hypericum perforatum	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-

	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
Ilex aquifolium	A	A	-	-	A	-	-	A	-	-	-	A	-	-	-	-	-	-	-	-
Juglans regia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A
Kickxia spuria	-	-	-	A	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lamiastrum galeobdolon	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Lamium álbum	-	-	-	-	A	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-
Lamium purpureum	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lamium sp.	-	-	-	-	A	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Lapsana communis	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Lathyrus sp.	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leucanthemum vulgare	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ligustrum vulgare	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-
Lolium multiflorum	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Lolium perene	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	U
Lonicera periclymenum	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lupinus sp.	-	-	A	-	A	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Malus sp.	A	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-
Malus sylvestris	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Medicago sativa	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-
Mercurialis perennis	-	-	-	A	-	A	-	-	-	U	-	A	-	-	-	-	-	-	-	A
Myosotis arvensis	-	-	-	-	U	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
Papaver rhoeas	-	-	-	A	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllitis scolopendrium	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Plantago major	-	-	A	-	-	-	-	-	A	A	A	-	-	-	-	-	-	-	-	-
Poa annua	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-	-	-	-	-	-
Poa trivialis	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-	-	-	A	-	-
Polygonum aviculare	-	-	-	-	-	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-
Primula vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A
Prunus avium	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-
Prunus cerasifera	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-
Prunus sp.	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	A	-
Prunus spinosa	K	K	K	A	K	K	K	K	K	K	K	A	K	K	A	A	K	K	K	K
Pteridium aquilinum	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-
Quercus robur	A	A	K	-	K	-	A	-	-	K	U	K	-	A	-	-	-	-	-	-
Ranunculus acris	U	A	-	A	-	A	A	U	-	-	-	-	A	A	-	-	-	A	-	-
Ranunculus ficaria	-	U	A	-	A	-	-	U	A	-	A	A	-	U	-	-	A	U	-	A
Ranunculus repens	A	U	A	A	A	A	A	A	A	U	U	U	A	A	-	A	A	A	A	A
Ranunculus sp.	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Raphanus raphanistrum	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhamnus cathartica	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-
***Rosa* sp.**	-	A	-	-	K	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Rubus fruticosus	A	A	A	A	-	A	A	U	A	U	A	A	A	U	A	-	A	A	A	A
Rumex acetosa	A	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	A	-	-
Rumex spp.	A	U	U	U	U	A	A	A	U	U	U	A	U	A	A	-	A	A	A	A
Salix sp.	-	-	-	-	-	-	-	A	-	-	A	-	-	-	-	-	-	-	-	-
Sambucus nigra	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	U	-	-	A	-
Secale cereale	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecio jacobaea	-	-	-	-	-	-	-	-	A	-	-	A	-	-	-	A	-	-	-	A
Senecio vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	A	-	-	-
Silene dioica	A	-	A	-	-	-	-	-	-	-	-	A	A	-	-	-	-	-	A	-
Silene sp.	-	-	-	-	-	-	-	-	A	-	-	A	-	-	-	-	A	-	-	-
Sinapis arvensis	-	-	-	-	-	-	-	-	A	A	-	-	-	-	A	-	-	-	-	-
Solanum dulcamara	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Sonchus arvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-
Sonchus asper	-	-	A	A	A	A	A	-	-	-	-	A	A	-	A	-	A	K	-	-
Sonchus oleraceus	-	-	-	A	-	-	A	-	-	A	A	-	-	-	-	-	-	-	-	A
Stachys sylvatica	A	-	A	-	A	A	-	-	-	A	-	A	-	A	A	A	-	-	-	-
Stellaria graminea	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Stellaria media	-	U	A	-	U	-	-	-	-	-	-	-	A	-	-	A	-	-	A	A
Taraxacum spp.	-	-	-	-	-	A	A	-	-	-	A	-	-	A	-	A	-	A	-	-
Taxus baccata	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Tilia vulgaris/europaea	-	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium pratense	A	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium repens	-	A	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium spp.	U	U	A	A	A	U	U	U	U	A	A	A	U	A	-	A	A	A	A	A
Triticum sp.	-	U	U	U	U	A	U	U	-	U	A	A	U	A	A	A	A	U	A	U
ukP39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-
Ulmus procera	-	-	A	-	-	-	K	A	-	-	-	A	A	-	-	K	A	A	-	-
Urtica dioica	A	A	A	K	K	K	A	K	K	K	A	A	A	A	A	A	A	K	A	A
Valeriana officinalis	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Veronica montana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A
Veronica persica	-	A	-	-	-	-	U	-	-	-	-	-	A	-	-	-	-	-	-	-
Veronica serpyllifolia	-	-	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viburnum lantana	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-
Vicia faba	-	-	-	-	A	A	-	-	A	-	A	-	-	-	A	A	-	-	-	-
Vicia sativa	-	-	-	-	-	-	-	-	A	-	-	-	A	-	-	-	-	-	-	-
Vicia sepium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	K	-	-	-
Viola sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	A
X Triticosecale	-	U	-	-	-	A	-	U	-	A	-	-	-	-	-	-	-	-	-	-
Zea mays	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	A	A	A	A	A

Table S 2-6 List of the 89 plant species present in the 20 plant-parasitoid networks. Networks are named after their corresponding farms (A1-A10 and B1-B10). When species are present in a network, cells correspond to species status: K are keystone species, A are average species and U are underused species. When absent from a network, cells are filled with (-). Species that play a *keystone role* in at least one farm are marked in bold.

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Acer campestre	-	A	-	A	-	-	-	-	K	A	A	-	-	-	-	-	-	-	-	-
Alopecurus myosuroides	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Angelica sylvestris	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Anthriscus sylvestris	-	-	-	A	A	-	-	A	-	-	-	-	A	A	A	A	A	A	-	-
Arctium sp.	-	-	A	A	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Arrhenatherum elatius	-	-	-	-	-	-	-	-	A	-	-	A	-	-	-	-	-	-	-	-
Atriplex patula	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
***Avena* spp.**	A	-	-	A	U	-	A	-	-	-	-	A	U	-	K	-	-	-	-	-
Brassica juncea	-	-	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brassica napus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	A	-	-	-	-
Brassica nigra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-
Brassica oleracea(Acephala)	-	-	-	-	-	-	-	K	-	-	-	-	-	-	-	-	A	-	-	-
Brassica oleracea (Italica)	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
***Brassica rapa* sp.**	-	-	-	-	-	-	-	-	-	-	-	K	K	-	-	-	K	-	-	-
***Brassica* sp.**	-	-	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brassica unknown	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Calystegia sepium	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Capsella bursa-pastoris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Cerastium glomeratum	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-
Cerastium sp.	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chenopodium album	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	A	-	-	-
Chenopodium polyspermum	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium arvense	-	-	-	A	-	-	A	A	-	U	A	-	-	-	-	A	-	A	-	-
Cirsium vulgare	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	A	-	-	-	-
Clematis vitalba	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-
Convolvulus arvensis	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cornus sanguinea	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Coronopus squamatus	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-
Corylus avellane	K	A	K	A	K	-	A	A	-	-	-	-	-	-	-	-	K	A	A	A
Crataegus monogyna	A	K	A	U	A	A	A	A	A	K	K	-	A	A	A	U	A	A	K	A
Cynara scolymus	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Dactylis glomerata	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-	-	-	-	-	-
Euonymus europaeus	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fagus sylvatica	-	-	-	K	-	A	-	-	-	-	-	-	-	-	-	A	-	-	-	-
Fraxinus excelsior	-	-	-	A	-	A	-	-	-	-	-	-	-	-	K	-	-	-	-	-
Galeopsis tetrahit	-	-	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geum rivale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-
Glechoma hederacea	-	-	A	-	-	-	-	-	-	-	U	-	-	-	-	-	-	A	-	-

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Grass unknown	U	U	U	U	U	U	A	U	U	U	U	U	U	U	U	A	A	A	U	U
Heracleum sphondylium	A	A	-	-	A	-	A	-	-	-	A	K	-	-	A	-	A	-	-	A
Holcus lanatus	A	A	-	-	-	-	-	A	-	A	-	U	A	-	-	-	A	U	-	-
Hordeum vulgare	-	-	U	A	A	-	-	A	-	-	K	A	-	U	K	-	A	U	-	-
Ilex aquifolium	A	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kickxia spuria	-	-	-	K	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lathyrus sp.	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lolium multiflorum	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Lolium perenne	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-	-	-	-	-	-
Lonicera periclymenum	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lupinus sp.	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Medicago sativa	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-
Papaver rhoeas	-	-	-	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllitis scolopendrium	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Plantago major	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	-
Poa annua	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-	-	-	-	-	-
Poa trivialis	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-	-	-	-	-	-
Prunus spinosa	A	A	-	-	-	-	-	A	A	A	A	-	A	A	A	-	A	A	A	A
Quercus robur	A	A	A	-	-	-	-	-	-	K	-	A	-	A	-	-	-	-	-	-
Ranunculus acris	A	K	-	-	-	A	K	A	-	-	-	-	A	K	-	-	-	A	-	-

	A1	**A2**	**A3**	**A4**	**A5**	**A6**	**A7**	**A8**	**A9**	**A10**	**B1**	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**
Ranunculus ficaria	-	-	A	-	A	-	-	A	A	-	A	K	-	-	-	-	-	A	-	A
Ranunculus repens	K	K	K	K	A	K	K	K	K	K	A	A	A	K	-	K	U	K	K	K
Ranunculus sp.	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rosa sp.	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubus fruticosus	U	U	-	A	-	A	A	-	-	A	A	A	-	-	-	-	-	-	-	-
Rumex acetosa	U	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex spp.	-	-	-	-	-	-	-	A	-	U	-	-	-	-	-	-	A	-	A	-
Secale cereale	-	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senecio vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	U	-	-	-	A	-	-	-
Silene dioica	-	-	A	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-
Sinapis arvensis	-	-	-	-	-	-	-	-	K	A	-	-	-	-	-	-	-	-	-	-
Sonchus arvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	K	-	-	-	-
Sonchus asper	-	-	A	A	-	A	A	-	-	-	-	-	A	-	A	-	A	K	-	-
Sonchus oleraceus	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A
Stachys sylvatica	-	-	A	-	A	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-
Stellaria media	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	U	-	-	-	-
Taraxacum spp.	-	-	-	-	-	U	-	-	-	-	-	-	-	U	-	A	-	-	-	-
Taxus baccata	-	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium pratense	A	-	-	K	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium repens	-	U	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
***Trifolium* spp.**	U	U	U	U	U	-	A	A	U	U	U	-	-	K	-	-	-	-	A	A
***Triticum* sp.**	-	A	U	U	U	A	A	A	-	-	A	K	A	A	A	A	A	A	A	A
Ulmus procera	-	-	-	-	-	-	A	A	-	-	-	-	-	-	-	A	-	-	-	-
Urtica dioica	A	A	A	A	U	A	A	K	A	A	A	U	A	A	-	A	U	A	A	A
Veronica persica	-	A	-	-	-	-	-	-	-	-	-	-	U	-	-	-	-	-	-	-
Veronica serpyllifolia	-	-	-	-	A	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vicia faba	-	-	-	-	-	K	-	-	A	-	-	-	-	-	U	A	-	-	-	-
Vicia sativa	-	-	-	-	-	-	-	-	A	-	-	-	A	-	-	-	-	-	-	-
Viola sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-
X Triticosecale	-	U	-	-	-	A	-	-	-	A	-	-	-	-	-	-	-	-	-	-
Zea mays	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	A	A	A	A

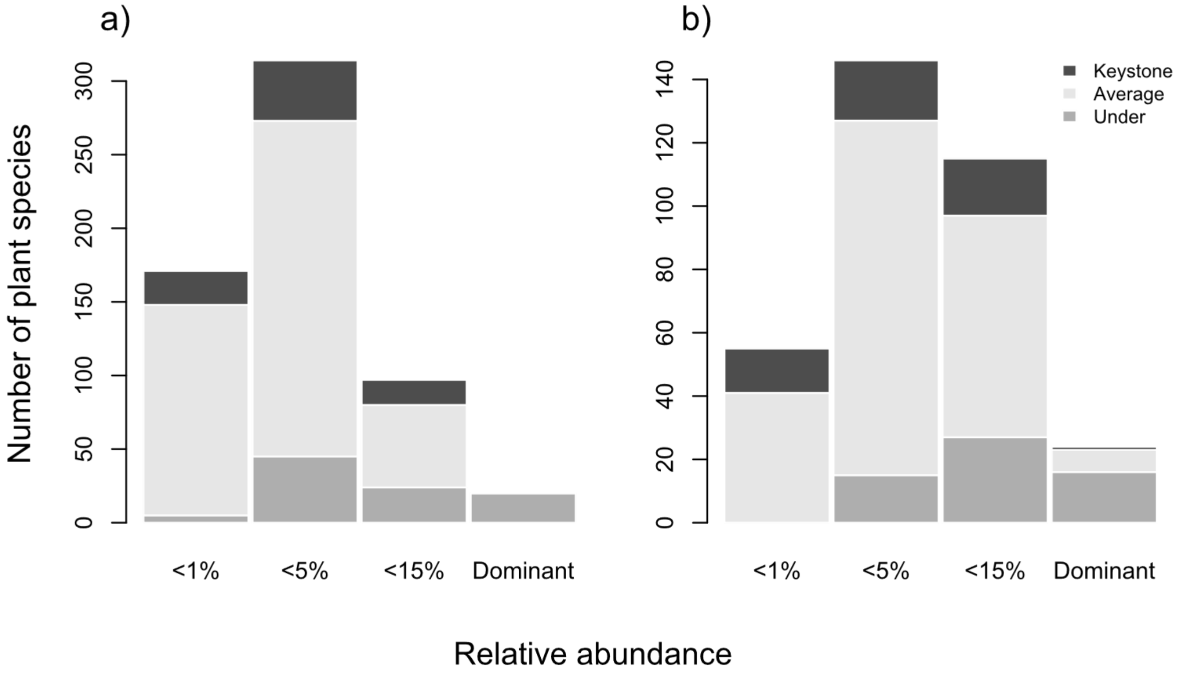


Figure S 2-4 Distribution of plant species across different classes of relative abundance in a) plant-herbivore and b) plant-parasitoid networks. Overperforming species (Keystone: above null model confidence intervals) are in dark grey, average species (Average: between null model confidence intervals) are in light grey and underused species (Under: below null model confidence intervals) are in medium grey.

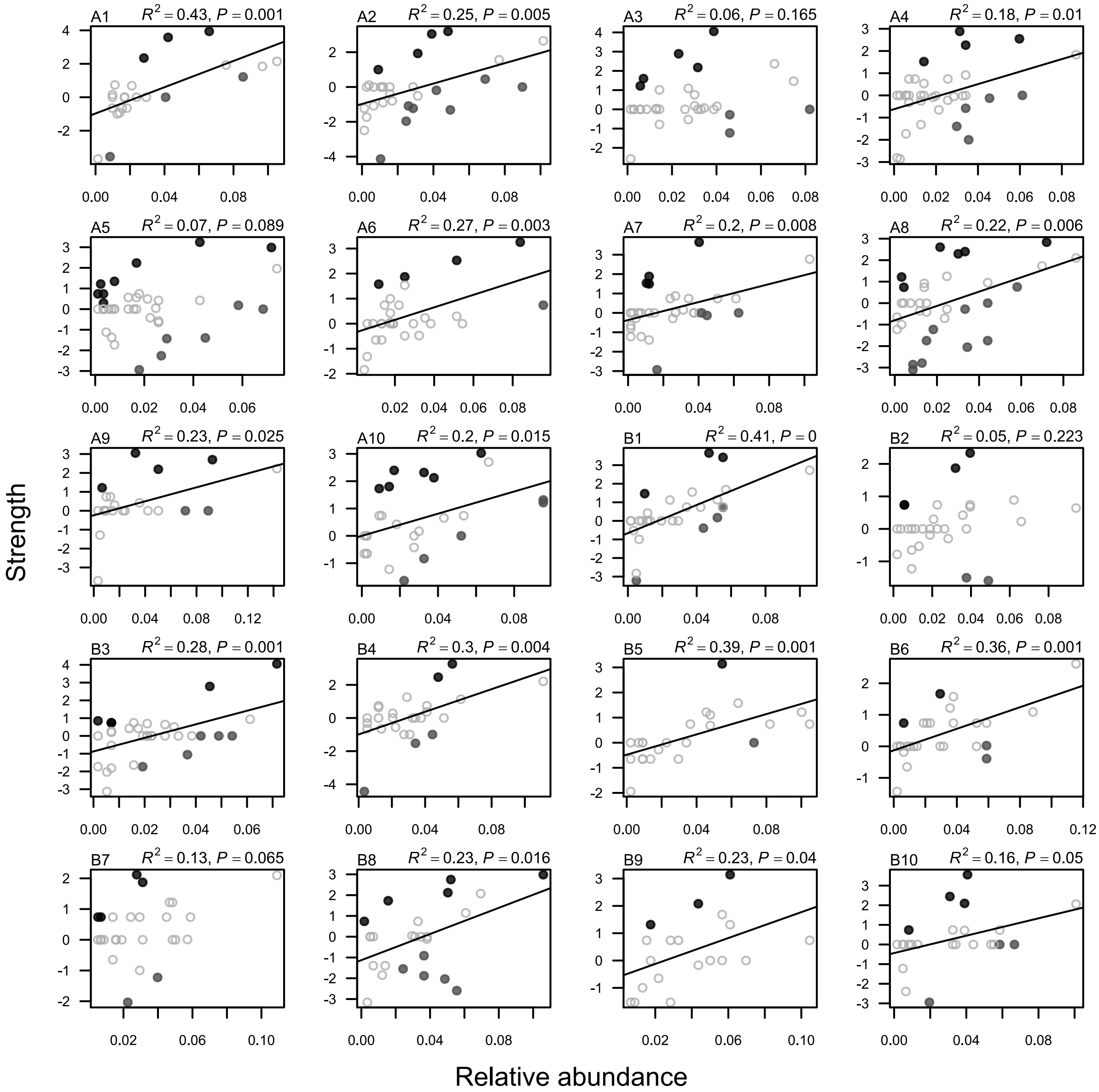


Figure S 2-5 Results of linear models (LMs) between plant species strength and relative abundance performed individually for each plant-herbivore network (network codes - A1 to A10 and B1 to B10 – in the top left corner of each plot). Each dot represents a species in a farm, in dark grey are overperforming species (keystone species: above null model confidence intervals) and in lighter grey are underused species (below null model confidence intervals). Strength values were boxcox transformed. Lines of best fit are drawn for statistically significant models.

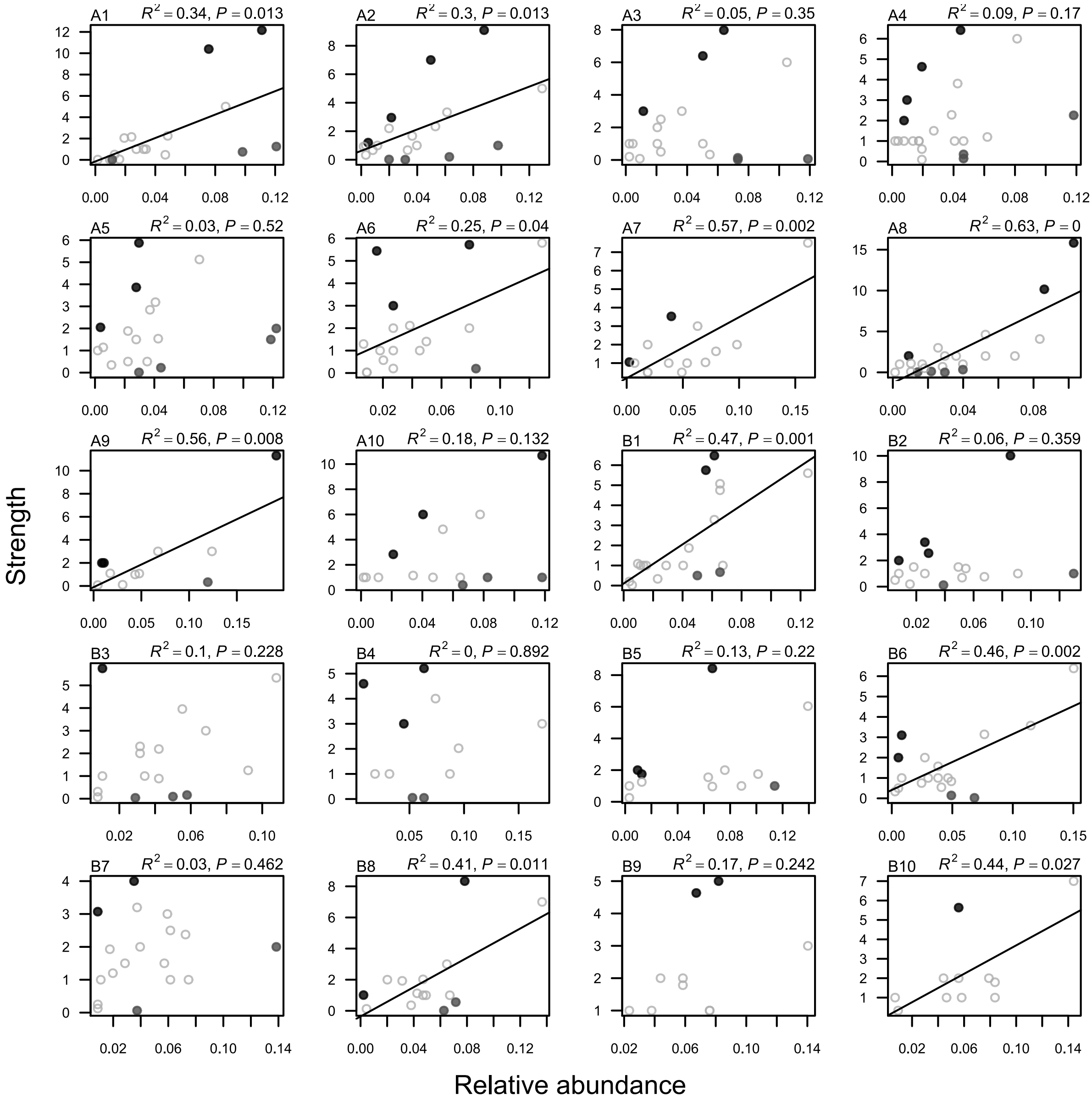


Figure S 2-6 Results of linear models (LMs) between plant species strength and relative abundance performed individually for each plant-parasitoid network (network codes - A1 to A10 and B1 to B10 – in the top left corner of each plot). Each dot represents a species in a farm, in dark grey are overperforming species (keystone species: above null model confidence intervals) and in lighter grey are underused species (below null model confidence intervals). Strength values were boxcox transformed. Lines of best fit are only drawn for statistically significant models.

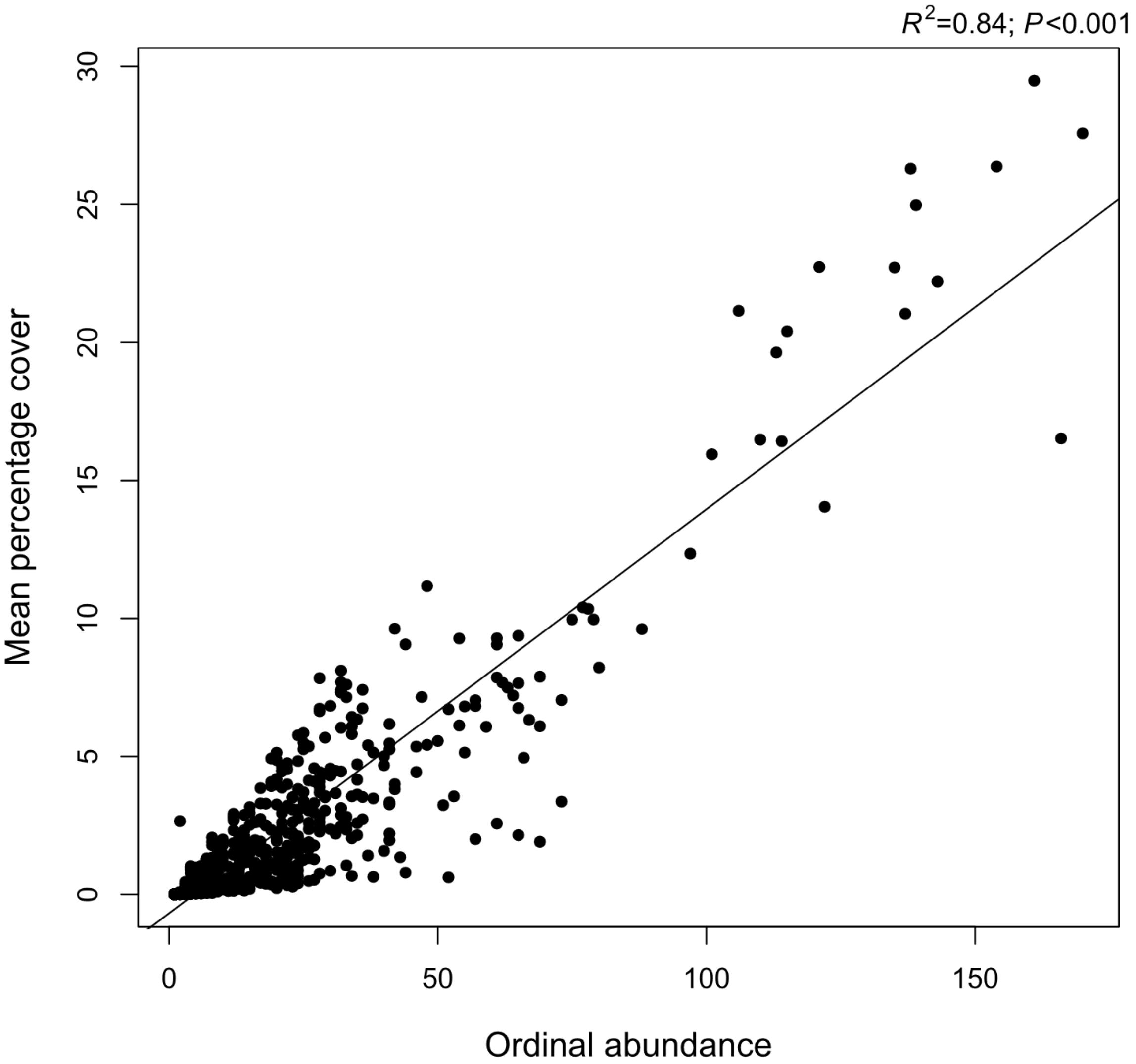


Figure S 2-7 Relationship between the measure of ordinal plant abundance used and estimated mean percentage plant cover, which was calculated by assuming that each species was at the mean of its category of percentage cover.

Chapter 3

Plant species roles in pollination networks: an experimental approach.

Glossary

Network core: Region of a network where species are densely connected.

Core species: Species that belong to the network core, *i.e.* species that interact with several species inside and potentially outside the network core.

Generalist species: Species which interact with a large set of mutualist species when compared to other species in the community.

Specialist species: Species which interact with a small set of mutualist species when compared to other species in the community.

Centrality: Group of species-level metrics which identify the most important species for information flow (*i.e.* disturbance, selective pressures, population changes) due to their position in the network.

Central species: The five plant species with high levels of centrality which were selected to be introduced in the experimental plots.

Peripheral species: The five plant species with low levels of centrality which were selected to be introduced in the experimental plots.

Introduced species: Central and Peripheral plant species selected to be planted in the experimental plots.

Resident species: Plant species naturally occurring in the experimental plots.

Normalised degree (ND): Species-level metric which describes the level of generalisation/specialisation of a species, *i.e.* the proportion of pollinator species a plant species interacts with.

Closeness centrality (CC): Species-level metric which describes whether species are on average close, in number of links, to other species in the network.

Betweenness centrality (BC): Species-level metric which describes whether species are frequently in between the shortest distances, in number of links, connecting species pairs in the network.

Partner diversity: Species-level metric which describes whether the interactions of a species are evenly distributed across interaction partners.

Closeness centralisation: Network-level metric which describes whether information flow in a network is controlled by one or few species, *i.e.* there are few central and several peripheral species.

Nestedness: Network-level metric which describes whether interactions of specialist species are a subset of interactions of generalist species.

Interaction evenness: Network-level metric which describes whether interaction strength (in terms of interaction frequency) is evenly distributed between species pairs in the network.

3.1 Introduction

Pollination is an important ecosystem service, provided mainly by insect pollinators. It is estimated that 75% of crops species (Klein et al., 2003) and 87.5% of flowering plant species in general (Ollerton et al., 2011) depend on animal pollination, and in recent years the demand for crop pollination by insects has tripled (Aizen and Harder, 2009). However, current pollinator declines caused mainly by habitat loss (Potts et al., 2010), farming intensification (Sanchez-Bayo and Goka, 2014) and insect diseases (Goulson et al., 2015) could disrupt pollination services. To ensure the integrity of natural ecosystems (Ashman et al., 2004; Aguilar et al., 2006) and the productivity of insect-dependent crops (Klein et al., 2007), healthy pollinator populations need to be supported.

Decreasing floral resources due to habitat loss and degradation are a key contributor to current pollinator declines (Carvell et al., 2006; Kleijn and Raemakers, 2008; Roulston and Goodell, 2011). Even when non-lethal, the lack of good feeding habitat can make insects more prone to more harmful stressors such as diseases and pesticides (Alaux et al., 2010; Goulson et al., 2015). Therefore, flower planting schemes are an important strategy to recover pollination function in both agricultural (Pywell et al., 2005) and urban areas (Blackmore and Goulson, 2014). Since diverse pollinator communities increase the quality and stability of pollination services (Hoehn et al., 2008; Winfree and Kremen, 2009; Albrecht et al., 2012; Orford et al., 2016), plant species which are able to attract and support a high diversity and abundance of pollinators need to be identified (Dixon, 2009).

Currently, species lists for seed mixes and planting plans are put together using expert knowledge rather than rigorous field trials on how a community of plants interacts with a community of pollinators. Ecological networks can be used to identify species with structural and functional importance in pollination systems (Martín González et al., 2010; Coux et al., 2016). Pollination systems are formed by a core of well-connected generalist plant and insect species with which many specialist species interact (Bascompte et al., 2003). This structure is thought to promote network robustness and to increase the resilience of pollination networks due to high levels of redundancy (Memmott et al., 2004; Burgos et al., 2007; Bastolla et al., 2009; Song et al., 2017). Since species forming the network core are structurally and functionally important in pollination systems (Vázquez and Aizen, 2004; Coux et al., 2016), ecological restoration could focus on core plant species. My aim in this study is to explore how the plant species with differing network roles in natural plant-pollinator communities perform in replicate experimental conditions.

Core plant species usually have high levels of centrality, *i.e.* they interact with a high proportion of pollinator species, having a high chance of being at short distances to most species in the network and between other species shortest distances (Martín González et al., 2010). Central plant species in pollination networks might, therefore, provide a shortcut when the ultimate aim of restoring plant communities is to restore pollinator communities. Given that plant species share and compete for pollinators, the effect of introducing new plants to recover pollination function could also affect the resident plant species. Introducing plant species with high centrality (potentially species presenting attractive traits), for instance, might benefit resident plant species due to pollinator spill-over (Morandin and Kremen, 2013; Blaauw et al., 2014). Individuals from a non-rewarding orchid species, for instance, had higher pollination success when in proximity to highly rewarding species (Johnson et al., 2003). Alternatively, the attractiveness of central plants species to pollinators could result in lower visitation to resident plant species. For instance, visitation to resident plant species might be positively affected by higher richness and diversity of neighbouring flowers, but negatively affected by the generalisation level of neighbouring plants (Lázaro et al., 2009). If we are to fully understand the impact of using central plant species to recover pollination function, in addition to studying their impact on pollinators, we also need to assess their effect on resident plant species and on emerging network structure, as this affects community function and persistence (Tylianakis et al., 2010).

In my study I use a field experiment to test whether species roles in pollination networks can be used to identify plant species with the most potential to recover plant-pollinator communities. Specifically, I ask three questions: 1) Do central plant species attract a higher diversity of pollinators than peripheral species? Since high centrality is a measure of structural importance, I expect central plant species to attract higher pollinator diversity than peripheral species; 2) After introduction, which network roles are occupied by the introduced species, and how does species introduction affect the resident plant species' network roles? I expect central species, but not peripheral species, to occupy the most important network roles by monopolising interactions with pollinators; consequently, I also expect resident plant species to have lower structural importance in networks with introduced central species when compared to networks with introduced peripheral species; 3) Does the introduction of peripheral and central species promote a different network structure? I expect interactions to be concentrated by few species in networks with introduced central species, making these networks more centralised, more nested - *i.e.* with a stronger core of generalists with which specialist species interact - and with lower levels of interaction evenness than networks with introduced peripheral species.

3.2 Material and Methods

My study has three components. Focusing on published pollination networks collected in English meadows, I first quantified the centrality of each plant species and selected five central and five peripheral plant species. I then introduced the selected species into experimental plots where I collected visitation data for both introduced and resident plant species. Finally, I constructed pollination networks for the experimental plots with the visitation data, to test the impact of the introduced plants on pollinators, resident plants and on network structure.

3.2.1 Identifying central and peripheral plant species in plant-pollinator networks

To identify central and peripheral plant species in natural plant-pollinator communities, I investigated the roles of plant species in 17 published plant-pollinator networks (Table S 3-1). All these networks were collected in English meadows, most of them (15 out of 17) in southwest England, these being networks from similar systems to my intended experimental plots. I removed grass species from the analysis since they are wind pollinated, even if pollinators do feed on their pollen (Orford et al., 2016).

I used three centrality metrics which are commonly studied in combination given their complementary properties (Martín González et al., 2010; Emer et al., 2016). The three metrics are binary, *i.e.* not accounting for the frequency of interaction between species. *Normalized degree* is the number of species each species interacts with, divided by the number of possible interacting partners (here, the number of pollinator species in the network), this describing the level of species generalisation. The two other centrality measures are calculated based on the unipartite projection (plant-plant) of bipartite (plant-pollinator) networks, in which plant species are connected if they share pollinators. *Closeness centrality* is the mean shortest distance (measured in number of interactions) between a focal plant species and all other plant species in the network. Plant species with high closeness centrality share pollinators with other plants (Freeman, 1979; Martín González et al., 2010) having a high niche overlap with other plant species (Carvalheiro et al., 2014). *Betweenness centrality* is the proportion of the shortest paths (in number of interactions) connecting all plant species pairs in the network crossing a focal species. Species with high betweenness centrality increase network cohesiveness by connecting parts of the network that would be isolated (Freeman, 1979; Martín González et al., 2010). All centrality metrics were calculated using *bipartite* R package (Dormann et al., 2008; Dormann, 2011; R Core Team, 2017).

Central species may present attractive traits for pollinators, for instance by providing high nectar content (Cusser and Goodell, 2014). Alternatively, high centrality may be due to sampling bias, that is when abundant species are sampled more than rarer species (Vázquez et al., 2009b; Gibson et al., 2011). To control for the latter scenario and to focus on species whose centrality measures truly reflect attractiveness to pollinators, I compared the observed centrality of each plant species in each network with a null expectation. I generated 1000 null network counterparts for each empirical network using a null model in which plants and pollinators were assigned interactions in proportion to their relative abundances but keeping connectance constant (Vázquez et al., 2007). The probability of an interaction between plant *i* and pollinator *j* is:

$$p_{ij} = p_i * p_{j,} \tag{1}$$

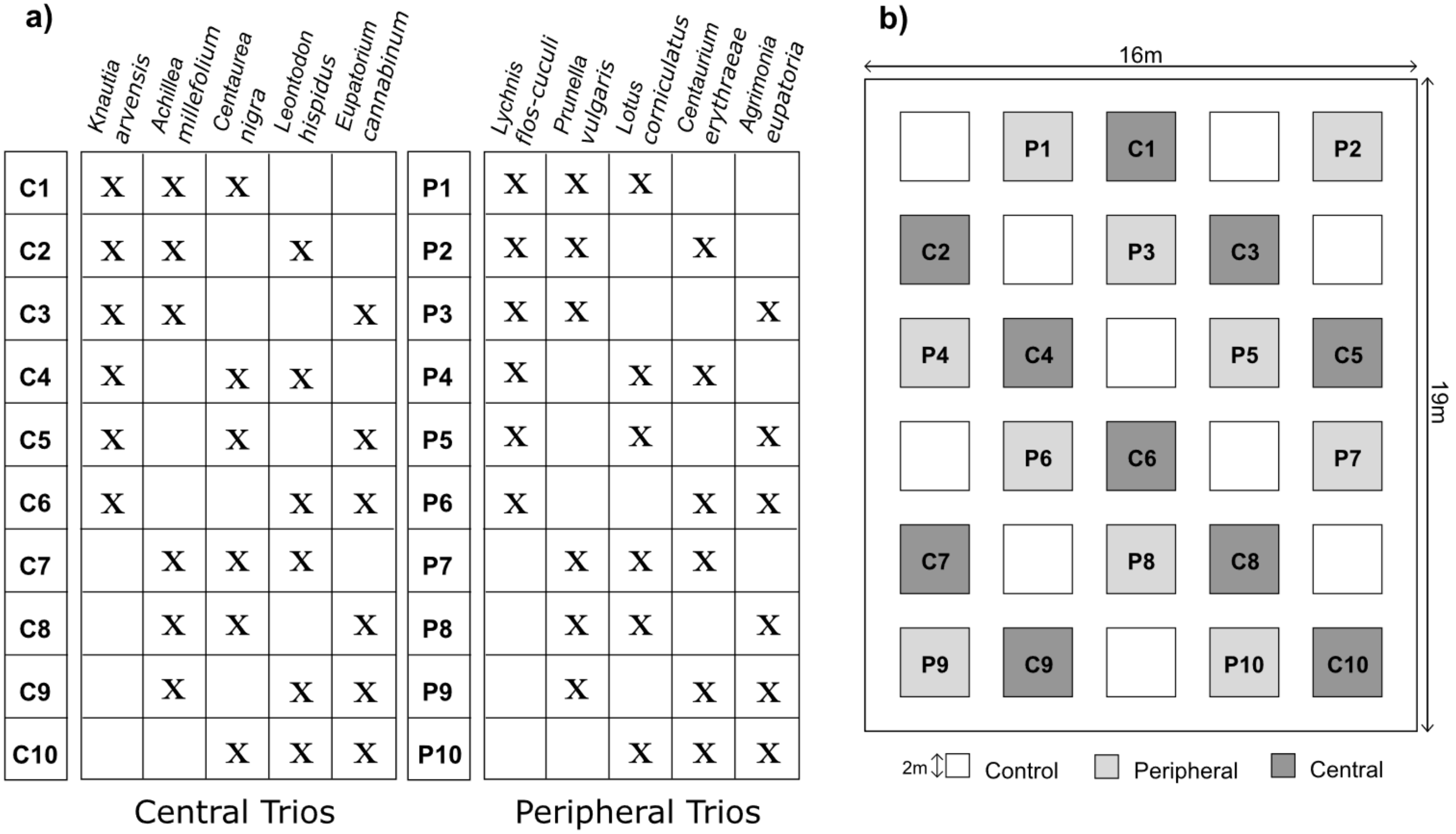
where p_i is the abundance of plant species *i* relative to all other plant species in the network, and p_j is the abundance of pollinator species *j* relative to all other pollinator species in the network. Plant species abundances were measured as floral abundance in the original datasets. As plant relative abundance information was not directly available for three datasets (DS, DH and M, Table S 3-1), I extracted this information from the network plots available in the original publications. As I did not have independent abundance measures for pollinator species, I used interaction frequency as a proxy. Then, I compared the three observed centrality metrics of species *i* in empirical network *k* to the centrality of species *i* in all null counterparts of *k* using standardised effect sizes (SES):

$$SES_{ik} = \frac{c_{ik} - \overline{c_{in}}}{\mathrm{sd}(c_{in})}, \tag{2}$$

where SES_{ik} is the standardised effect size of species *i* in network k, c_{ik} is the centrality metric of species *i* in empirical network k, and $\overline{c_{in}}$ and $sd(c_{in})$ are the average and standard deviation of plant species' i centralities in the null counterparts of k, respectively. I averaged the three SES (one for each centrality metric) of each species in each network, and then averaged the SES of each species across networks, so that each plant species was assigned one SES value. This approach provided each plant species with a single value which was straightforward to compare across networks and species, and easily interpretable since positive SES values represent species whose observed centrality is above null model expectation and vice versa. I ranked the 60 plant species present in the 17 networks by their SES values (Table S 3-2). Finally, I selected five plant species from the top 20 ranked species (central species) and five from the bottom 20 (peripheral species) as focal species whose community role would be tested in a field experiment (Table S 3-2; Figure 3-1). Their flowering time and availability from wildflower suppliers were the main criteria used for selection, with species flowering in July and August being preferred; co-flowering being essential for the experiment. These criteria resulted in my central species being *Achillea millefolium*, *Centaurea nigra*, *Eupatorium cannabinum*, *Knautia arvensis* and *Leontodon hispidus* and peripheral species being *Agrimonia eupatoria*, *Centaurium erythraea*, *Lotus corniculatus*, *Lychnis flos-cuculi* and *Prunella vulgaris*.

3.2.2 Experimental design and sampling procedure

My experimental plots were in two adjacent areas of grassland in Bristol, UK (51°48'N, 2°62'W) separated by large buildings, and the two plots (Plot A and Plot B) were c. 370 m apart. Resident plant species were uniformly distributed in both plots (see Table S 3-4 for a list of species found in each plot and their centrality rank positions). Each of the two plots had 30 subplots, 2m x 2m in size, these providing the experimental replicates: 10 of these were planted with central species, 10 with peripheral species and 10 were left as controls (Figure 3-1). To avoid the effect of particularly attractive or unattractive species confounding my results (as I would not be able to separate a treatment effect from a species effect) I introduced three central or peripheral species in each subplot, this providing 10 unique trios per treatment in both plots (Figure 3-1a). In October 2016, I planted the 10 trios of both treatments (Figure 3-1b), reducing the immediate competition from the resident plants by using weed mats (40 cm x 40 cm) around each experimental plant to allow them to establish. Weed mats were also placed in control subplots. From June to September 2017 I sampled and collected the pollinators in Plot A 22 times and in Plot B 20 times using timed observations, such that each subplot was observed for 15 minutes per sampling occasion. Weekly, I counted flower units of all flowering species (resident and introduced) in control, peripheral and central subplots. A flower unit was defined as one or more flowers that insects could access without flying (Carvalheiro et al., 2008; Baude et al., 2016), *e.g.* for Asteraceae a flower unit is a whole inflorescence while in Fabaceae it is one flower. Therefore, even if a floral unit represents a different number of flowers for different plant species, it is defined from the insect's perspective what, in the context of this study, is a more accurate measure of floral abundance (Carvalheiro et al., 2008). At the end of the season, all insects were identified by taxonomists.



	Knautia arvensis	*Achillea millefolium*	*Centaurea nigra*	*Leontodon hispidus*	*Eupatorium cannabinum*
C1	X	X	X		
C2	X	X		X	
C3	X	X			X
C4	X		X	X	
C5	X		X		X
C6	X			X	X
C7		X	X	X	
C8		X	X		X
C9		X		X	X
C10			X	X	X

Central Trios

	Lychnis flos-cuculi	*Prunella vulgaris*	*Lotus corniculatus*	*Centaurium erythraeae*	*Agrimonia eupatoria*
P1	X	X	X		
P2	X	X		X	
P3	X	X			X
P4	X		X	X	
P5	X		X		X
P6	X			X	X
P7		X	X	X	
P8		X	X		X
P9		X		X	X
P10			X	X	X

Peripheral Trios

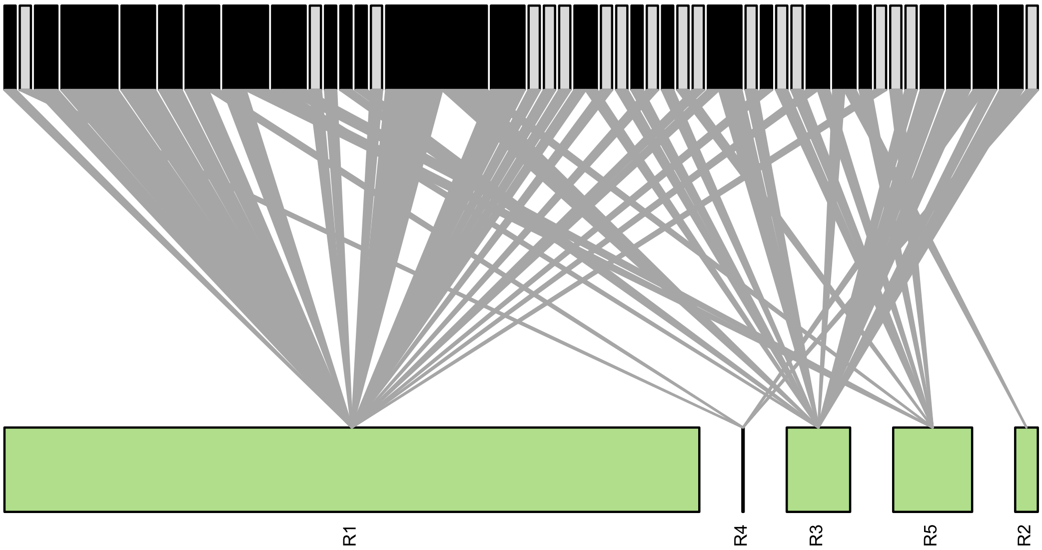
Figure 3-1 a) Ten trios of central (C1 to C10) and peripheral (P1 to P10) plant species; central species: *Knautia arvensis*, *Achillea millefolium*, *Centauria nigra*, *Leontodon hispidus*, and *Eupatorium cannabinum*; peripheral species: *Lychnis flos-cuculi*, *Prunella vulgaris*, *Lotus corniculatus*, *Centaurium erythraea* and *Agrimonia eupatoria*. Species belonging to each trio are marked with an X. b) Experimental plot: white squares represent control subplots, light grey squares represent peripheral subplots (P1 to P10) and darker grey squares represent central subplots (C1 to C10). Plant trios from P1 to P10 and C1 to C10 were planted in the corresponding peripheral and central subplots.

3.2.3 Calculating network metrics

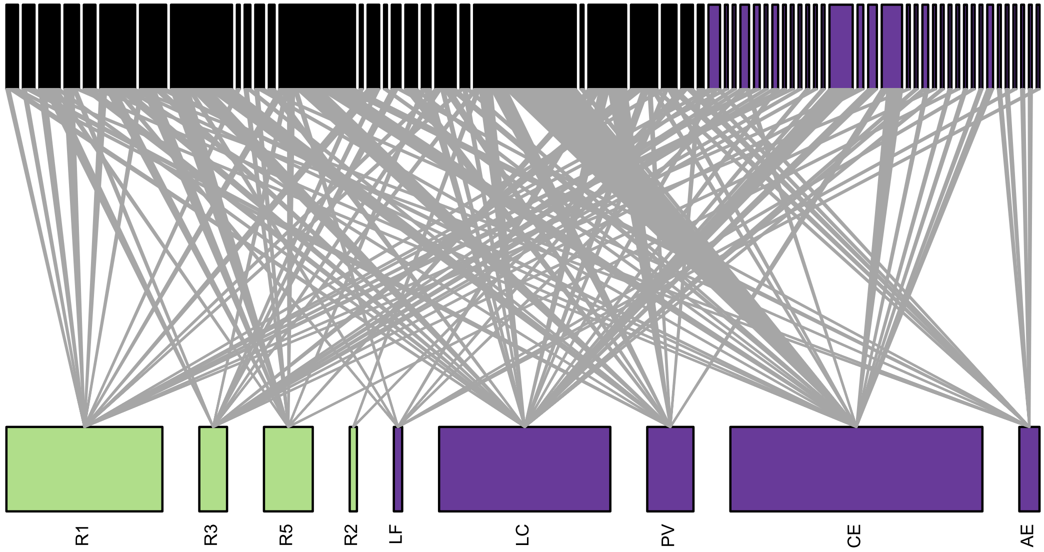
I constructed one quantitative pollination network per subplot, so that the interactions sampled in control, peripheral and central subplots resulted in 20 control, 20 peripheral and 20 central networks, respectively, 10 of each treatment from each experimental plot (Figure 3-2 and Figure S 3-1). All species-level and network-level metrics described below were calculated with *bipartite* and *sna* R packages (Dormann et al., 2009; Dormann, 2011; Butts, 2016).

To test whether the species network roles measured from the published networks hold under experimental conditions, and to investigate how central and peripheral plant species affect resident species I used three species-level metrics: two centrality measures used earlier – normalised degree and closeness centrality - along with partner diversity, a quantitative metric that accounts for the frequency of interactions between species. I chose these three metrics as they have a clear meaning even in small networks. Additionally, in this analysis I calculated closeness centrality straight from the bipartite network (instead of using the unipartite projection as above), in order to get meaningful distances in these smaller networks. Partner diversity is the Shannon diversity index calculated for the interactions of each species, high values indicating even spread of interactions across partners and low values indicating interactions being dominated by few partner species. Since I expect central species, but not peripheral species, to monopolise pollinators, I expect central species to have higher normalised degree, closeness centrality and partner diversity than resident plant species in central networks, while peripheral species will have similar network roles to resident species in peripheral networks. Additionally, I expect resident species to have decreasing values of normalised degree, closeness centrality and partner diversity from control, to peripheral to central networks.

a) Control network



b) Peripheral network



c) Central network

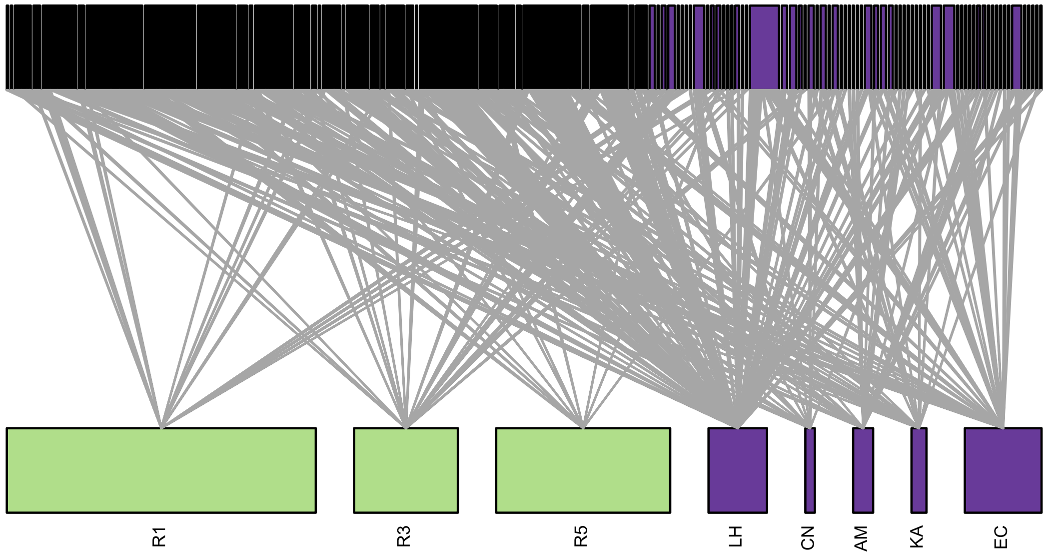


Figure 3-2 Quantitative pollination networks of a) control, b) peripheral and c) central treatments of Plot A (see Figure S 3-1 for Plot B). The networks depicted show interaction data pooled across all subplots for each treatment in this plot, although analyses were conducted on a per-subplot-per-plot basis. For each network, the lower rectangles represent plant species abundance, the upper rectangles represent insect species abundance and link widths represent interaction frequency between species pairs. In purple are the introduced plant species along with the insect species which only appear in peripheral and/or central subplots. In light grey (control network) are insect species only observed in control subplots. Codes for introduced plant species: KA=*Knautia arvensis*, AM=*Achillea millefolium*, CN=*Centauria nigra*, LH=*Leontodon hispidus*, EC=*Eupatorium cannabinum*, LF=*Lychnis flos-cuculi*, PV=*Prunella vulgaris*, LC=*Lotus corniculatus*, CE=*Centaurium erythraea*, AE=*Agrimonia eupatoria*. Resident species were numbered from R1 to R5 and names are given in Table S 3-4.

To investigate how peripheral and central plant species affect the network structure of my experimental networks I used three network-level metrics: closeness centralisation, nestedness and interaction evenness. The first two metrics are binary, while the third is quantitative. Closeness centralisation, is a network-level metric based on the species-level metric closeness centrality, and it measures the difference between the centrality of each species to the maximum centrality value of the network (Freeman, 1979; Butts, 2016). I calculate nestedness, which measures the extent to which the interactions of specialist species are a subset of interactions of generalist species, with the metric NODF (Almeida-Neto et al., 2008). Interaction evenness is similar to partner diversity but calculated at the network-level, measuring the equitability of network interactions and describing whether the frequency of interactions are evenly distributed or if a handful of interactions dominate the network (Tylianakis et al., 2007). Since I expect central species to occupy the most important network roles when introduced by monopolising interactions with pollinators, I expect the central networks to have a higher centralisation and nestedness, but lower interaction evenness than peripheral networks.

3.2.4 Do central plant species attract a higher diversity of pollinators than peripheral species?

To test whether subplots with introduced central plant species attract a higher abundance and richness of pollinators than subplots with introduced peripheral species, I used general linear mixed models (GLMM) with a Poisson distribution. To account for the variation in flowers abundance present in each subplot (Figure S 3-2, Table S 3-3), I included floral abundance as an offset variable (Reitan and Nielsen, 2016). Fixed effects were both treatment and plant richness in the subplot since plant richness, in addition to abundance, could affect pollinator richness and abundance (Potts et al., 2003; Orford et al., 2016). Each observation corresponded to data collected from each subplot during each sampling event. To account for the repeated measures of each subplot and for the multiple subplots from each plot, I included subplot nested in experimental plot as a random effect. The significance of fixed effects was assessed with likelihood ratio tests as these represent a good trade-off between reliability and simplicity. The effect of treatment was further investigated with Tukey tests using the *emmeans* R package (Lenth, 2018).

3.2.5 After introduction, which network roles are occupied by the introduced species, and how does species introduction affect resident plant species' network roles?

To investigate the network roles played by introduced species in my experimental networks, I compared the network roles (normalised degree, closeness centrality and partner diversity) of introduced species versus resident in peripheral and central networks. I expect central, but not peripheral species, to occupy the most important roles in their networks when compared to resident species in those networks. For this analysis, species-level metrics were used in three separate models linear mixed models (LMM) as response variables. The interaction between species status (resident versus introduced) and treatment, plus species abundance were included as fixed effects. Random effect structure was selected with Akaike Information Criteria (AIC, Zuur et al., 2009), and potential structures were: no random effect, species identity and network identity nested in experimental plot.

To test the effect of species introduction on resident species roles, I compared the network roles of resident species among control, peripheral and central networks. I expect decreasing metric values for resident species from control to peripheral to central networks. Species-level metrics were used in three separate linear mixed models as response variables. I included treatment and species abundance as fixed effects. Random effect structure was selected with AIC, and potential structures were: no random effect, species identity and network identity nested in experimental plot. In both analyses, the significance of fixed effects was assessed with likelihood ratio tests and the effect of treatment was further investigated with Tukey tests using *emmeans* R package (Lenth, 2018).

3.2.6 Does the introduction of peripheral and central species promote a different network structure?

To investigate the effect of species introduction on network structure I performed separate linear mixed models (LMM) for each network-level metric (closeness centralisation, nestedness and interaction evenness). Four control networks were excluded from all analysis due their small size (Table S 3-5). Since network metrics are dependent on number of species in the network (Song et al., 2017), and number of species was likely to vary across treatments, the metric values were normalized. Interaction evenness is normalised when calculated in *bipartite* R package (Dormann et al., 2009). Closeness centralisation was normalised by comparing the observed value of each network with the theoretical maximum centralisation for that network (Butts, 2016). Observed nestedness values were normalised following (Song et al., 2017). For 32 networks, maximum nestedness values were assessed by iterative search. For those networks, interactions were initially randomised 1000 times and maximum nestedness values kept. Maximum nestedness values were then searched in up to one million randomised networks, in steps of ten-fold increase in number of randomisations, whenever a 5% or higher increase in maximum nestedness was observed. Ten (of the fifty-six) networks were excluded from the nestedness analysis (Table S 3-5) as both their observed and maximum nestedness values were zero and could not be normalised. After normalisation, none of the network-level metrics correlated with network size (Figure S 3-3). Models for each network-level metric had treatment as fixed effect and random effect structure was selected with AIC from the alternative structures: no random effect and experimental plot.

3.3 Results

In total 1876 insects and 171 insect species were collected from the two plots: 910 insects and 129 species in Plot A, and 966 insects and 108 species in Plot B (Table S 3-6). In addition to the 10 species of plant which were added to the plots, a further 17 plant species were found growing naturally in the plots, 8 in Plot A and 14 in Plot B (Table S 3-4).

3.3.1 Do central plant species attract a higher diversity of pollinators than peripheral species?

In both plots, the observed abundance and richness of pollinators increased from control to peripheral to central subplots (Figure 3-3a-b). The models show that treatment had a significant effect on both pollinator abundance ($\chi^2(_2) = 50.77$, $p < 0.001$) and richness ($\chi^2(_2) = 48.12$, $p < 0.001$). As the offset variable included in the models accounts for differences in subplot floral abundance between treatments, the models show that peripheral subplots attracted significantly fewer insect individuals and species than control subplots, while central subplots attracted significantly more insect individuals and species than both peripheral and control subplots (Figure 3-3c-d). Plant richness had a negative effect on insect abundance and richness (abundance: $\chi^2(_1) = 25.1$, $p < 0.001$; richness: $\chi^2(_1) = 23.21$, $p < 0.001$).

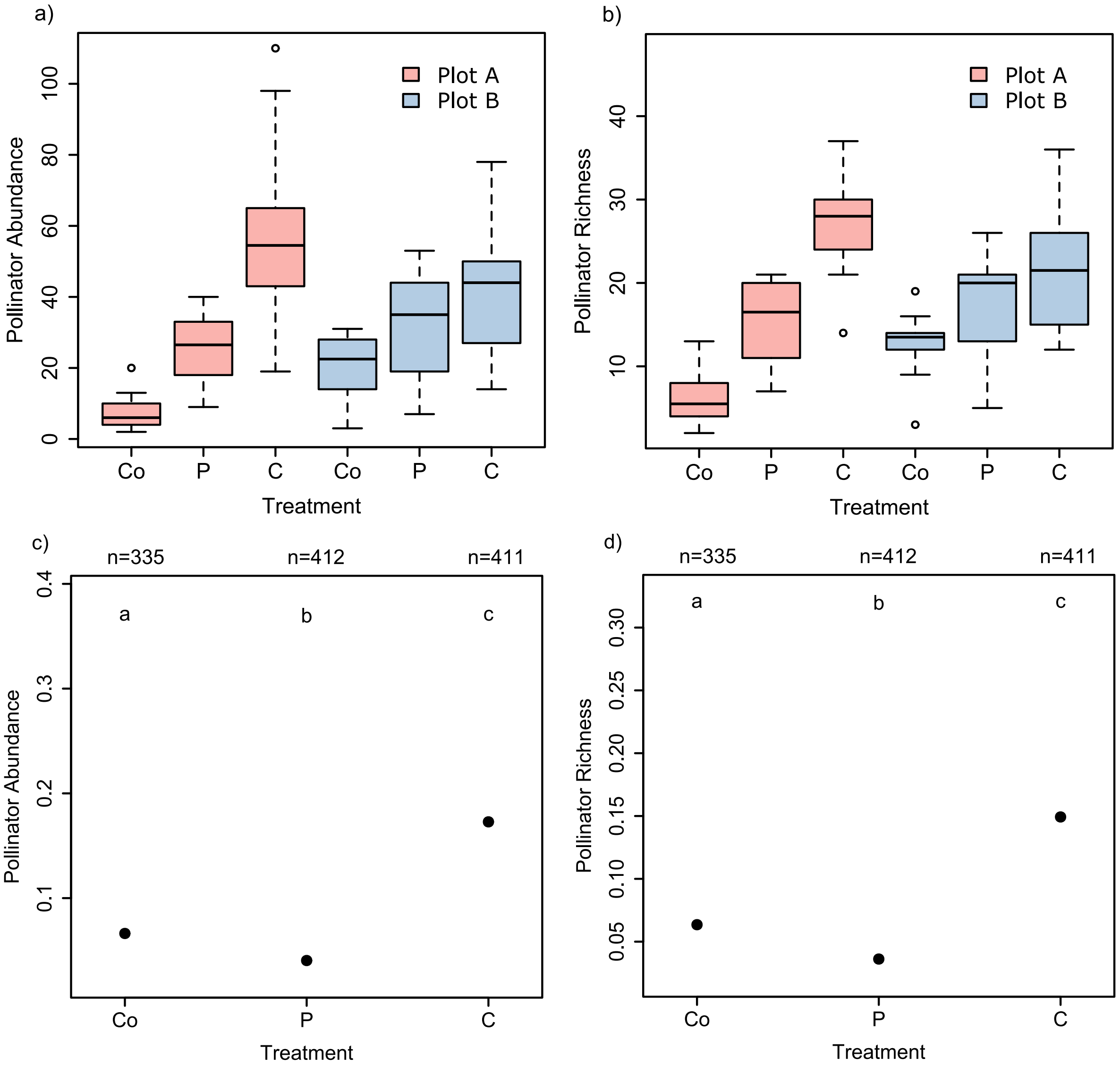


Figure 3-3 a) Pollinator abundance – raw data; b) Pollinator species richness – raw data; c) Pollinator abundance – model estimates; d) Pollinator species richness – model estimates per treatment in each subplot. Treatments are coded as follows: Control - Co, Peripheral - P, Central - C. Different letters indicate statistically different treatments.

3.3.2 After introduction, which network roles are occupied by the introduced species, and how does species introduction affect resident plant species' network roles?

Experimental networks had on average 4.12 flowering plant species (min = 1, max = 9; mean plant species in control = 2.6, peripheral = 5.1 and central = 4.65 networks) and 16.8

insect species (min = 2, max = 37; mean insect species in control = 9.45, peripheral = 16.35 and central = 24.65 networks; Table S 3-5). As expected, introduced central species had significantly higher values of normalised degree ($p < 0.01$), closeness centrality ($p = 0.03$) and partner diversity ($p < 0.01$) than resident species in central networks, while introduced peripheral species had similar values for all metrics to resident species in peripheral networks (normalised degree: $p = 0.97$; closeness centrality: $p = 0.99$; partner diversity: $p = 0.98$; Figure 3-4a-c). Floral abundance had a positive effect on all species-level metrics (normalised degree: $\chi^2(_1) = 16.86$, $p < 0.001$; partner diversity: $\chi^2(_1) = 30.88$, $p < 0.001$; closeness centrality: $\chi^2(_1) = 21.59$, $p < 0.001$). For normalised degree, only species identity was included in the selected random structure, while for partner diversity and closeness centrality both species identity and network identity nested in experimental plot were included.

Treatment had a significant effect on resident species normalised degree ($\chi^2(_2) = 47.14$, $p < 0.001$). Resident plant species in central networks were visited by significantly fewer insect species than those in control networks ($p < 0.01$), but the difference between resident species in central and peripheral networks was only marginal and not significant ($p = 0.054$; Figure 3-4d). Resident plant species had similar values of closeness centrality and partner diversity in networks of all treatments (Figure 3-4e-f). Floral abundance had a positive effect on all species level metrics (normalised degree: $\chi^2(_1) = 18.63$, $p < 0.001$; partner diversity: $\chi^2(_1) = 25.16$, $p < 0.001$; closeness centrality: $F(_1) = 12.65$, $p < 0.001$). For normalised degree and partner diversity, only species identity was included in the selected random structure, while for closeness centrality no random structure was selected.

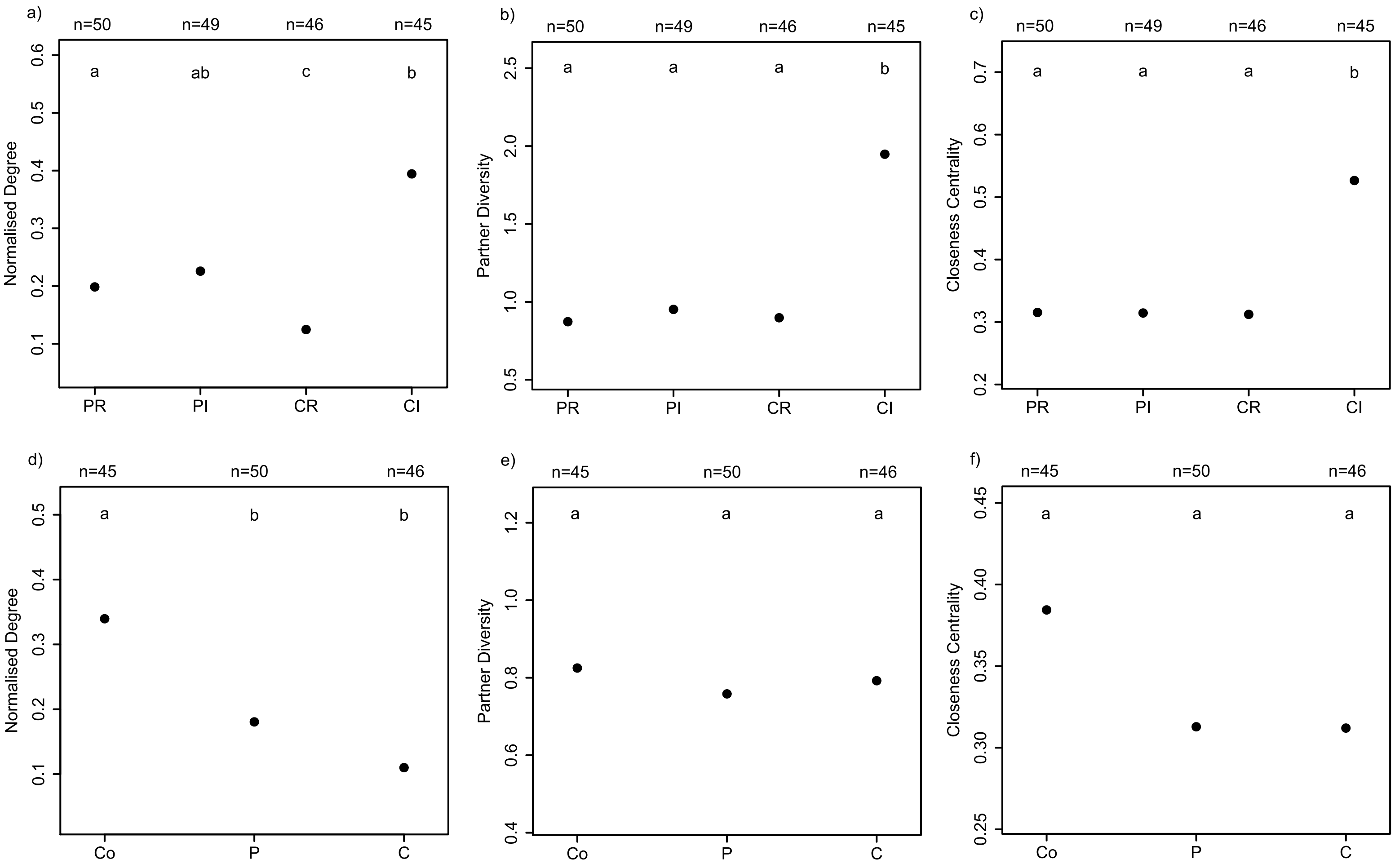


Figure 3-4 Network roles (model estimates) of resident and introduced species in peripheral and central networks: a) normalized degree, b) partner diversity and c) closeness centrality. PR and PI are resident and introduced species in peripheral networks, and CR and CI are resident and introduced species in central networks. Network roles (model estimates) of resident species in control (Co), peripheral (P) and central (C) networks: d) normalized degree, e) partner diversity and f) closeness centrality. Different letters represent statistically different treatments.

3.3.3 Does the introduction of peripheral and central species promote a different network structure?

At the network level, I expected the introduction of central species to increase network centralisation and nestedness, but to decrease interaction evenness. Centralisation was lower in peripheral than in central networks, but central networks were not more centralised than control networks ($F(2) = 7.85$, $p = 0.001$; Figure 3-5a). But contrary to my expectation, interaction evenness was higher in central than in peripheral networks but no different to control networks ($F(2) = 3.86$, $p = 0.03$; Figure 3-5c). Finally, the introduction of neither peripheral nor central species affected nestedness ($F(2) = 0.41$, $p = 0.66$; Figure 3-5b).

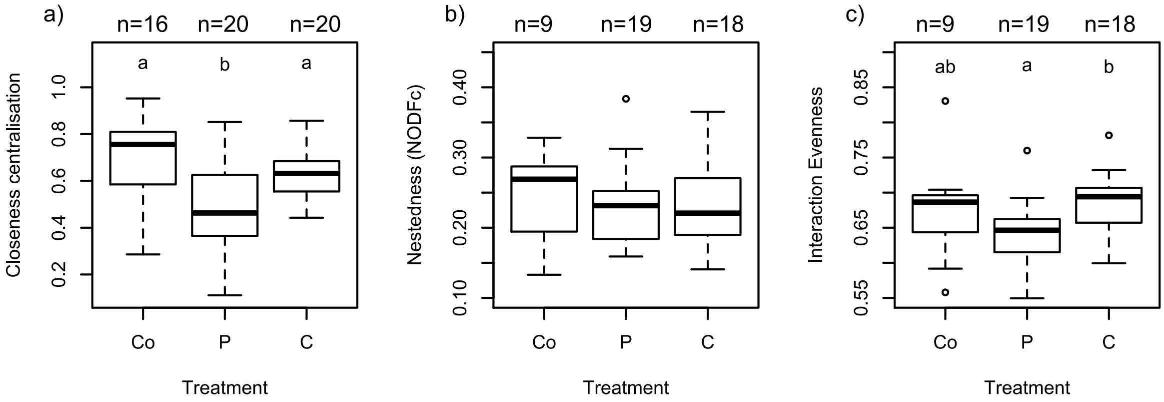


Figure 3-5 Network-level structure of plant-pollinator interactions across treatments. a) closeness centralisation, b) nestedness (measured with NODFc) and c) interaction evenness. Different letters represent statistically different treatments. Code for treatment: Co=control, P=peripheral, C=central.

3.4 Discussion

To my knowledge, this is the first field test of species network roles. As predicted, I found that central plant species attracted a higher richness and abundance of pollinators than peripheral species, and that central plant species occupy the most important network roles after introduction, while peripheral species do not. The high attractiveness of central species to pollinators, however, does not seem to negatively affect resident plant species network roles.

Finally, I found that the introduction of central species did not affect network structure, while the introduction of peripheral species decreased network centralisation, and peripheral networks had lower interaction evenness than central networks. In what follows I first address the limitations of my study, and then consider my results in the context of previous findings.

3.4.1 Limitations

There are two main limitations in my study. First, as the spatial scale of the study is small, I observed behavioural rather than populational responses, and spill-over of pollinators between subplots of different treatments might have occurred. If spill-over did occur from central to peripheral and control subplots, then the higher pollinator diversity found in central subplots is a conservative result; but the small difference in results regarding species roles and network structure between treatments should be interpreted with caution. Second, my experiment is a short term one, run for one field season only. While there is no obvious reason why running the experiment in spring or in the autumn would affect the results, it would be good to have a greater degree of spatial and temporal variation, the former perhaps using plant communities from very different systems and the latter including data from different years.

3.4.2 Plant species roles in ecological networks.

I found that central plant species attracted a significantly higher abundance and richness of pollinators than peripheral species. Therefore, for this system, plant species network roles in natural communities accurately predicted their importance for pollinators in the experimental arrays, and likely in other plantings. I did not control for variation in species morphology or nectar content between treatments, even if these attributes are known to mediate plant-pollinator interactions (Stang et al., 2006; Santamaría and Rodríguez-Gironés, 2007; Junker et al., 2013; Lihoreau et al., 2016). Flowers with more accessible nectar tubes could be visited by a wider range of insect species than flowers with less accessible tubes (Stang et al., 2006; Campbell et al., 2012), and plants with higher nectar content potentially receive more visits than species with lower network content (Lihoreau et al., 2016). Together with high abundance (Fort et al., 2016), attractive traits such generalist flower morphologies and higher nectar concentration are likely associated to central roles of plant species in pollination networks. Evaluating which morphological traits is associated with plant species centrality, while not the focus of this study, would be an interesting future study and an important contribution to flower planting schemes.

I expected central, but not peripheral, species to occupy the most important roles in their networks, by outcompeting resident species and concentrating most interactions for themselves (Bjerknes et al., 2007; Morales and Traveset, 2009). Indeed, I found that plant species' original roles did hold under experimental conditions: the central species I added became the species with the most important network roles in experimental conditions whereas peripheral species continued to act as peripheral in the experiment. However, the introduction of central and peripheral species affected resident species similarly: resident species interacted with fewer pollinator species in both central and peripheral networks than in control networks. Therefore, the increase in plant neighbourhood richness but not the level of generalisation of neighbouring species, negatively affected the generalisation of resident plant species, the opposite pattern found for two plant species by Lázaro et al. (2009). Resident species' closeness centrality and partner diversity remained unaffected by the introduction of either central or peripheral species. Therefore, despite negatively affecting the richness of pollinators visiting resident species (normalised degree), introduced central species did not appear to monopolise interactions at the expense of resident plant species since resident species presented similar network roles in peripheral and central networks. This suggests that it was the increase in species richness (from control to peripheral and central) that affected the normalised degree of the resident plants, rather than the centrality of the introduced species. The potential for a flowering species to influence its neighbours depends on its reward availability and accessibility (Carvalheiro et al., 2014) but measuring at the community scale whether this influence is positive or negative is challenging. Increased visitation due to an attractive neighbour will likely benefit pollen limited species (Laverty, 1992; Johnson et al., 2003) but, if stigmas get clogged by hetero-specific pollen, the net effect of co-occurring with attractive neighbours might be detrimental to the focal plant (Fang and Huang, 2013). That said, stigma clogging by attractive neighbours is not inevitable (*e.g.* Emer et al., 2015) and the overall impact of adding plants to communities will be only truly understood when seed-set and recruitment are measured.

Central species were attractive to pollinators and caused a decrease in the number of interaction partners of resident species, however their introduction did not increase network centralisation or nestedness, as expected (Aizen et al., 2008a; Bartomeus et al., 2008). On the other hand, the introduction of peripheral species decreased network centralisation (compared to control and central networks) and interaction evenness (compared to central networks). Introduced central species may have simply replaced the previous central species present in the subplots maintaining network centralisation, while peripheral species by occupying similar network roles of resident species (Figure 3-4c) promoted networks with a more evenly distributed number of interaction partners among species (lower centralisation). Even if unexpected, the lower interaction evenness results for peripheral than for central networks also agree with results found at the species level: central species presented high levels of partner diversity (Figure 3-4b) without affecting the partner diversity of resident species (Figure 3-4e), suggesting that the high and even number of visitation received by central species was not obtained at the expense of resident species. In antagonistic networks, perturbations such as habitat modification and species invasions have been associated with both decreased

(Tylianakis et al., 2007) and increased (Lopez-Nunez et al., 2017) interaction evenness. In contrast interaction evenness was unaffected by an invasive plant species in pollination networks (Tiedeken and Stout, 2015). The role of interaction evenness on community functioning and stability is not fully understood: while evenness of species abundance is often associated with enhanced community functioning and resilience (Hillebrand et al., 2008; Crowder et al., 2010), theoretical work suggests that the presence of weak interactions in the network has a stabilizing effect (McCann et al., 1998; Berlow, 1999). Looking forward, further work is needed to elucidate how levels of interaction evenness are associated with community functioning and persistence over time.

3.4.3 Conclusion

To be able to predict community structure shows that we truly understand the rules by which communities are assembled. Here, plant species network roles were accurately predicted using their roles in published empirical networks: the introduction of central species attracted a higher richness and abundance of pollinators and central species occupied the most important network roles. That said, my expectations for their effect on resident plant species and network structures, however, were not met. Given that most restoration projects start at the plant community (Montoya et al., 2012), being able to select the plants with the highest potential to promote community level properties would be very useful. If network roles could be used to predict the most important plants in promoting network properties such as robustness and resilience this would be very useful indeed as these are key network statistics in successful conservation (Mace, 2014). As our knowledge on the structure and dynamics of ecological networks increases, more field experiments are needed to test our understanding of the parameters we identify and measure. Pollination networks are a good system for this approach, since they have been thoroughly studied (Bascompte and Jordano, 2007; Burkle and Alarcón, 2011), they are straightforward to manipulate (*e.g.* Brosi and Briggs, 2013) and are under severe threat (Santamaría et al., 2016).

3.5 Supplementary Material

Table S 3-1 Networks used to select central and peripheral plant species to be introduced in the field experiment. Code representing each network, "Network"; source of the network, "Reference"; location and date of data collection, "Area" and "Year"; number of plant and pollinator species in the network, "Plants" and "Poll." respectively. In parenthesis is the original number of species, and outside the parenthesis the final number of species after grass removal.

Network	**Reference**	**Area**	**Year**	**Plants**	**Poll.**
DH	Dicks et al. 2002	Norfolk	1999	16 (17)	60 (61)
DS	Dicks et al. 2002	Norfolk	1999	16	36
M	Memmott 1999	Bristol	1997	15	37
FM1	Forup & Memmott 2005	Bristol	2000	6	24
FM2	Forup & Memmott 2005	Bristol	2000	12	28
FM3	Forup & Memmott 2005	Bristol	2000	11	53
FM4	Forup & Memmott 2005	Bristol	2000	24 (25)	79
OAC	Orford unpublished	Bristol	2012	13 (24)	44 (57)
OB1	Orford et al. 2016	Bristol	2012/13	8 (13)	32 (39)
OB2	Orford et al. 2016	Gloucestershire	2012/13	10 (17)	40 (49)
OB4	Orford et al. 2016	Gloucestershire	2012/13	12 (20)	56 (66)
OB5	Orford et al. 2016	Gloucestershire	2012/13	8 (11)	13 (21)
OB6	Orford et al. 2016	Gloucestershire	2012/13	7 (16)	37 (53)
OB7	Orford et al. 2016	Somerset	2012/13	13 (15)	37 (38)
OB8	Orford et al. 2016	Somerset	2012/13	10 (15)	56 (59)
OB9	Orford et al. 2016	Somerset	2012/13	5 (8)	24 (30)
OB10	Orford et al. 2016	Somerset	2012/13	6 (9)	12 (17)

Table S 3-2 Combined list of plant species from the 17 networks used to select central and peripheral species. Species are ranked from the highest to the lowest mean centrality (Mean), the average of their normalised degree (ND), closeness (CC) and betweenness centrality (BC) values. Central species are among the top 20 ranked species (rank 1 to 20), and peripheral species are among the bottom 20 ranked species (rank 41 to 60). Selected central and peripheral species are marked with an asterisc.

Rank	**Plant species**	**ND**	**CC**	**BC**	**Mean**
1	*Ranunculus bulbosus*	16.8282	0.9889	3.3298	7.0489
2*	*Knautia arvensis*	8.9253	2.2419	3.2802	4.8158
3	*Cirsium palustre*	3.2416	1.2234	9.7428	4.7359
4	*Heracleum sphondylium*	8.7714	0.4521	4.8000	4.6745
5*	*Achillea millefolium*	8.0222	0.5761	3.5378	4.0453
6	*Torilis japonica*	8.1474	2.0562	1.0941	3.7659
7	*Cirsium* sp.	10.3732	0.7704	-0.1012	3.6808
8	*Cirsium vulgare*	9.8341	0.4960	0.0000	3.4434
9	*Filipendula ulmaria*	5.5974	1.3268	2.5850	3.1697
10	*Taraxacum officinale* agg.	5.9127	0.8356	2.5850	3.1111
11	*Angelica sylvestris*	5.7228	0.8348	1.5754	2.7110
12	*Orchis morio*	2.4086	1.1170	4.3661	2.6306
13*	*Eupatorium cannabinum*	5.7167	1.2646	-0.0674	2.3046
14*	*Leontodon hispidus*	4.4813	1.6445	0.0204	2.0487
15	*Senecio squalidus*	2.8558	1.3146	1.5615	1.9106
16	*Vicia cracca*	1.8867	1.4821	2.0015	1.7901
17	*Leontodon autumnalis*	3.5156	1.3590	0.4338	1.7695
18*	*Centaurea nigra*	3.3655	0.9336	0.7611	1.6867
19	*Hypochaeris radicata*	2.5932	0.7540	1.0529	1.4667
20	*Cirsium arvense*	3.4912	0.0706	0.6391	1.4003

21	*Crepis paludosa*	1.6948	0.5267	1.6716	1.2977
22	*Crepis capillaris*	2.7602	0.8413	0.2389	1.2801
23	*Geranium pratense*	3.1227	0.1692	-0.1021	1.0633
24	*Clematis vitalba*	1.8436	0.9923	0.0578	0.9646
25	*Daucus carota*	3.8048	-0.7814	-0.1313	0.9640
26	*Matricaria discoidea*	1.9119	1.1068	-0.1269	0.9639
27	*Cardamine pratensis*	3.6084	-1.0848	-0.1392	0.7948
28	*Stellaria media*	0.3827	-0.4707	2.0029	0.6383
29	*Aethusa cynapium*	2.2629	0.0690	-0.6484	0.5612
30	*Senecio jacobaea*	0.9885	-0.0548	0.3834	0.4390
31	*Crepis vesicaria*	-0.1147	0.8942	-0.0562	0.2411
32	*Leontodon saxatilis*	0.0646	0.7084	-0.3035	0.1565
33	*Trifolium pratense*	0.0203	0.2775	0.1622	0.1533
34	*Leucanthemum vulgare*	0.4406	0.1965	-0.2150	0.1407
35	*Conopodium majus*	-0.3937	0.8408	-0.1561	0.0970
36	*Vicia sativa*	0.7273	-0.5399	0.0155	0.0676
37	*Galium verum*	0.4313	-0.4818	0.0221	-0.0095
38	*Crepis biennis*	-1.4728	0.7655	0.4898	-0.0725
39	*Lathyrus pratensis*	-0.5821	-0.5440	0.8770	-0.0830
40	*Ranunculus acris*	-0.4876	0.6001	-0.4617	-0.1164
41	*Ranunculus repens*	-0.3811	-0.0703	-0.5137	-0.3217
42	*Bellis perennis*	-0.7265	0.0053	-0.5654	-0.4289
43*	*Lychnis flos-cuculi*	-0.9421	-0.1462	-0.3888	-0.4924
44	*Rubus fruticosus*	-0.7774	-0.5462	-0.2893	-0.5376

45	*Capsella bursa-pastoris*	-0.3015	-0.7844	-0.7466	-0.6109
46	*Linum catharticum*	-3.0493	0.6906	-0.4979	-0.9522
47	*Chamerion angustifolium*	-1.7357	-0.3496	-1.0237	-1.0363
48*	*Prunella vulgaris*	-0.5681	-4.5321	1.2126	-1.2958
49	*Anthriscus sylvestris*	-1.1473	-2.4819	-0.2985	-1.3092
50	*Trifolium repens*	-1.9882	-1.4629	-0.8758	-1.4423
51*	*Centaurium erythraea*	-1.1010	-2.9669	-0.3925	-1.4868
52*	*Lotus corniculatus*	-1.7755	-2.3617	-0.4386	-1.5252
53	*Cerastium fontanum*	-1.4057	-3.9529	-0.3235	-1.8941
54	*Convolvulus arvensis*	-3.1206	-1.6361	-0.9614	-1.9061
55	*Primula veris*	-3.7091	-1.3857	-1.5606	-2.2184
56*	*Agrimonia eupatoria*	-5.4423	-0.9766	-0.9990	-2.4726
57	*Trifolium dubium*	-5.7070	-1.3290	-1.4040	-2.8133
58	*Rhinanthus minor*	-3.9828	-3.4876	-1.5085	-2.9930
59	*Euphrasia officinalis*	-4.3050	-4.9308	-1.2691	-3.5016
60	*Medicago lupulina*	-4.8170	-5.0114	-1.2181	-3.6822

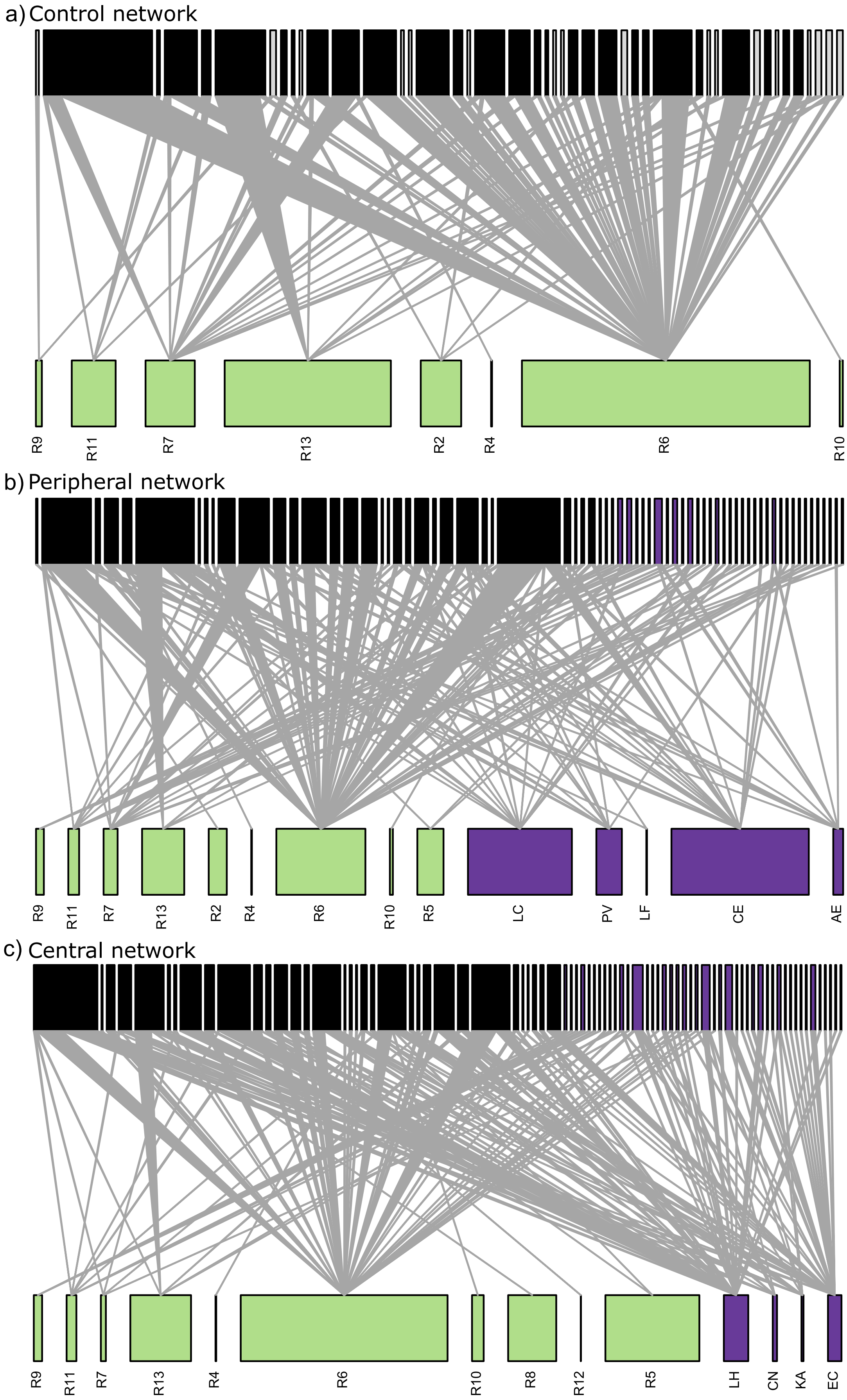

a) Control network
R9
R11
R7
R13
R2
R4
R6
R10
b) Peripheral network
R9
R11
R7
R13
R2
R4
R6
R10
R5
LC
PV
LF
CE
AE
c) Central network
R9
R11
R7
R13
R4
R6
R10
R8
R12
R5
LH
CN
KA
EC

Figure S 3-1 Quantitative pollination networks of a) control, b) peripheral and c) central treatments of Plot B. The networks depicted show interaction data pooled across all subplots for each treatment in this plot, although analyses were conducted on a per-subplot-per-plot basis. For each network, lower bars represent plant species abundance, top bars represent insect species abundance and link widths represent interaction frequency between species pairs. In purple are introduced plant species and insect species that only appear in peripheral and central subplots. In light grey (control network) are insect species only observed in control subplots. Codes for introduced plant species: KA=*Knautia arvensis*, AM=*Achillea millefolium*, CN=*Centauria nigra*, LH=*Leontodon hispidus*, EC=*Eupatorium cannabinum*, LF=*Lychnis flos-cuculi*, PV=*Prunella vulgaris*, LC=*Lotus corniculatus*, CE=*Centaurium erythraea*, AE=*Agrimonia eupatoria*. Resident species were numbered from R1 to R13 and names are given in Table S 3-4.

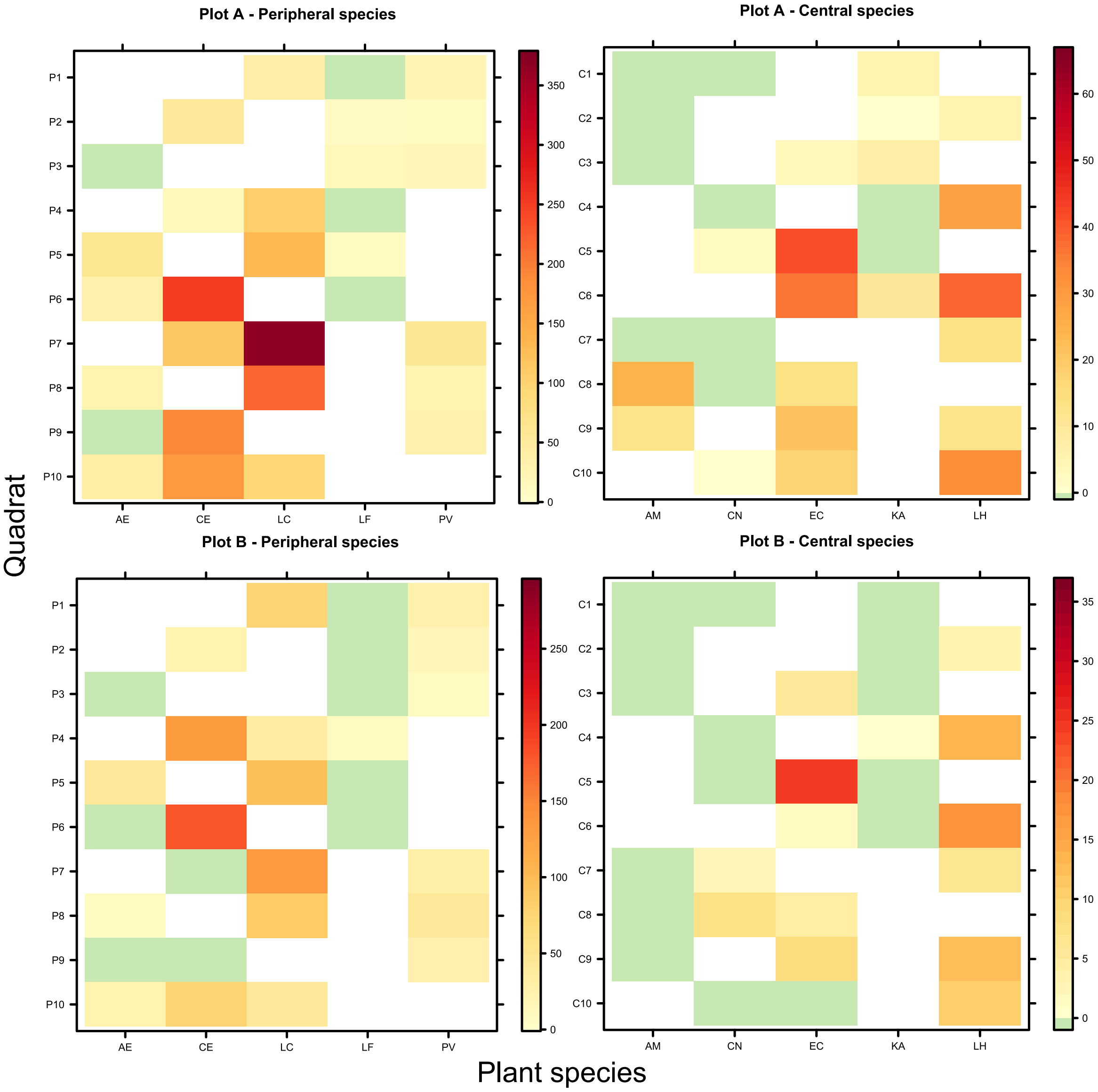


Figure S 3-2 Flowers abundance per introduced species across subplots (Quadrat) in Plot A and Plot B. Species codes: AE=*Agrimonia eupatoria*, AM=*Achillea millefolium*, CE=*Centaurium erythraea*, CN=*Centauria nigra*, EC=*Eupatorium cannabinum*, KA=*Knautia arvensis*, LC=*Lotus corniculatus*, LF=*Lychnis flos-cuculi*, LH=*Leontodon hispidus*, PV=*Prunella vulgaris*. Peripheral subplots are marked as P1 to P10 and central subplots as C1 to C10. Squares are white when that species was not assigned to that subplot, light green when the species assigned to that subplot did not flower, and ranging from light yellow to dark red in proportion to the number of flowers of that species in that subplot.

Table S 3-3 Flowering success of central and peripheral species: species name and number of individual plants of each species (out of the total 18 individuals of each species) that successfully flowered in Plots A and B.

Central species	**Plot A**	**Plot B**	**Peripheral species**	**Plot A**	**Plot B**
Achillea millefolium	3	0	*Agrimonia eupatoria*	9	8
Centaurea nigra	10	6	*Centaurium erythraea*	17	16
Eupatorium cannabinum	17	11	*Lotus corniculatus*	18	18
Knautia arvensis	11	4	*Lychnis flos-cuculi*	7	1
Leontodon hispidus	18	17	*Prunella vulgaris*	18	17

Table S 3-4 List of resident plant species in the experimental plots. Codes R1 to R13 are assigned to species which were observed receiving insect visits and correspond to codes used in Figures 3-2 and S 3-1. Species family, name, their occurrence in experimental plots A and/or B (marked with an X) and centrality rank (see Table S 3-2).

Code	**Family**	**Species**	**Plot A**	**Plot B**	**Rank**
R1	Asteraceae	*Bellis perennis*	X		42
-	Convolvulaceae	*Calystegia silvatica*		X	
R2	Caryophyllaceae	*Cerastium fontanum*	X	X	53
R6	Convolvulaceae	*Convolvulus arvensis*		X	54
R7	Asteraceae	*Crepis capillaris*		X	22
R8	Geraniaceae	*Geranium dissectum*		X	
-	Geraniaceae	*Geranium molle*	X		
R9	Apiaceae	*Heracleum sphondylium*		X	4
R10	Fabaceae	*Lathyrus pratensis*		X	39
-	Plantaginaceae	*Plantago lanceolata*	X	X	
R11	Ranunculaceae	*Ranunculus acris*		X	40
R3	Ranunculaceae	*Ranunculus repens*	X		41
R4	Asteraceae	*Taraxacum officinale agg.*	X	X	10
R12	Asteraceae	*Tragopogon pratensis*		X	
R13	Fabaceae	*Trifolium pratense*		X	33
R5	Fabaceae	*Trifolium repens*	X	X	50
-	Plantaginaceae	*Veronica persica*	X	X	

Table S 3-5 Number of plant and insect species per network. Each network corresponds to one subplot: 10 (subplots 1 to 10) per treatment (control, peripheral, central) per plot (Plot A, Plot B) resulting in 60 pollination networks. Four control networks were excluded from all network-level analysis (question 3) due to their small size (marked in light grey). Ten additional networks were excluded from nestedness analysis since their nestedness values could not be normalised (marked in dark grey).

Plot	**Subplot**	**Control**		**Peripheral**		**Central**	
		Insects	**Plants**	**Insects**	**Plants**	**Insects**	**Plants**
Plot A	1	4	3	7	4	29	5
Plot A	2	2	1	10	5	21	4
Plot A	3	2	2	11	4	14	4
Plot A	4	6	2	16	3	27	3
Plot A	5	5	2	20	5	24	5
Plot A	6	13	3	17	5	37	5
Plot A	7	8	3	17	5	27	4
Plot A	8	8	3	20	6	30	6
Plot A	9	10	3	14	6	29	5
Plot A	10	5	1	21	6	36	4
Plot B	1	12	4	5	3	14	5
Plot B	2	19	3	20	5	26	3
Plot B	3	14	1	20	5	36	5
Plot B	4	12	2	26	6	22	5
Plot B	5	14	4	21	6	21	4
Plot B	6	14	3	22	9	20	7
Plot B	7	9	3	12	4	27	6
Plot B	8	16	4	14	6	12	4
Plot B	9	3	2	21	5	26	6
Plot B	10	13	3	13	4	15	3

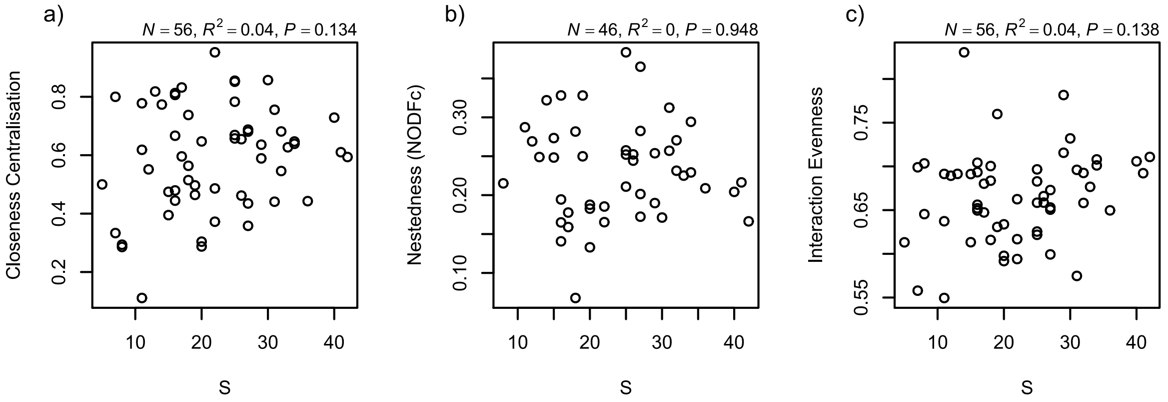


Figure S 3-3 Relationship between network-level metrics and network size (S) after metrics were normalized. a) Closeness centralisation, b) Nestedness and c) Interaction Evenness. Network size is the sum of plant and insect species. Ten out of 56 networks were removed from nestedness analysis due to non-meaningful NODF (nestedness metric) values.

Table S 3-6 List of insect species collected in the field experiment. Order, species name and number of individuals collected in plots A and B.

Order	**Species**	**Plot A**	**Plot B**
Coleoptera	*Altica* sp.	1	0
Coleoptera	*Amara familiaris*	1	0
Coleoptera	*Coccinella septempunctata*	0	2
Coleoptera	*Corizus hyoscyami*	0	1
Coleoptera	*Meligethes* sp.	20	7
Coleoptera	*Oedemera nobilis*	0	3
Coleoptera	*Rhagonycha fulva*	1	10
Coleoptera	*Tachyporus nitidulus*	1	0
Diptera	*Anthomyia liturata*	8	0
Diptera	*Botanophila* sp.	16	5
Diptera	*Botanophila striolata*	54	0
Diptera	*Brachicoma devia*	0	1
Diptera	*Cheilosia albitarsis*	1	1
Diptera	*Cheilosia bergenstammi*	1	0
Diptera	*Cheilosia impressa*	0	1
Diptera	*Cheilosia pagana*	11	0
Diptera	*Chloromyia formosa*	2	0
Diptera	*Chromatomyia milii*	1	0
Diptera	*Chrysotoxum bicinctum*	0	16
Diptera	*Chrysotoxum festivum*	1	5
Diptera	*Chrysotoxum vernale*	1	0
Diptera	*Coenosia tigrina*	10	0
Diptera	*Dasysyrphus albostriatus*	1	1
Diptera	*Delia platura*	2	3
Diptera	*Delia* sp.	2	3
Diptera	*Dicraeus vagans*	0	1
Diptera	*Dolichopus trivialis*	1	0
Diptera	*Dolichopus ungulatus*	2	0
Diptera	*Empis albinervis*	0	1
Diptera	*Empis femorata*	2	0
Diptera	*Empis livida*	0	6

Diptera	*Empis* sp.	1	0
Diptera	*Epistrophe grossulariae*	1	0
Diptera	*Episyrphus balteatus*	80	84
Diptera	*Eriothrix rufomaculata*	5	13
Diptera	*Eristalis tenax*	9	2
Diptera	*Eumerus tuberculatus*	6	26
Diptera	*Eupeodes corollae*	10	26
Diptera	*Eupeodes latifasciatus*	7	4
Diptera	*Eupeodes latilunulatus*	1	0
Diptera	*Eupeodes luniger*	4	27
Diptera	*Fannia serena*	1	0
Diptera	*Fannia* sp.	0	1
Diptera	*Fernandia cuprea*	4	1
Diptera	*Helina parcepilosa*	0	1
Diptera	*Helina reversio*	1	0
Diptera	*Helina* sp.	1	1
Diptera	*Helina tetrastigma*	0	1
Diptera	*Helophilus pendulus*	9	4
Diptera	*Heringia heringi*	1	0
Diptera	*Hydrellia maura*	17	0
Diptera	*Limnia unguicornis*	0	1
Diptera	*Lonchoptera furcata*	1	1
Diptera	*Lucilia sericata*	16	7
Diptera	*Megaselia* sp.	0	1
Diptera	*Melanomya nana*	1	0
Diptera	*Melanostoma mellinum*	1	6
Diptera	*Melanostoma scalare*	7	0
Diptera	*Melastoma* sp.	1	0
Diptera	*Meliscaeva cinctella*	1	0
Diptera	*Merodon equestris*	7	5
Diptera	*Meromyza* sp.	0	2
Diptera	*Metopia* sp.	1	0
Diptera	*Myathropa florea*	1	2

Diptera	*Neoascia podagrica*	1	0
Diptera	*Ocytata pallipes*	0	2
Diptera	*Opomyza germinationis*	1	1
Diptera	*Opomyza petrei*	1	0
Diptera	*Oscinella frit*	0	4
Diptera	*Oscinella nitidissima*	2	0
Diptera	*Oscinella* sp.	0	1
Diptera	*Pachygaster atra*	1	0
Diptera	*Paragus haemorrhous*	0	1
Diptera	*Paragus* sp.	1	0
Diptera	*Paregle audacula*	1	0
Diptera	*Pegoplata aestiva*	33	57
Diptera	*Phaonia serva*	1	0
Diptera	*Phasia obesa*	0	1
Diptera	*Phasia pusilla*	0	2
Diptera	*Phora* sp.	0	1
Diptera	*Pipizella viduata*	5	2
Diptera	Pipunculidae sp.	0	1
Diptera	*Platycheirus albimanus*	46	38
Diptera	*Platycheirus scutatus*	6	1
Diptera	*Platycheirus* sp.	0	2
Diptera	*Platycheirus sticticus*	1	2
Diptera	*Pyrophaena rosarum*	1	0
Diptera	*Rhamphomyia variabilis*	7	1
Diptera	*Rhingia campestris*	1	0
Diptera	*Rhingia rostrata*	5	0
Diptera	*Rhinophora lepida*	9	1
Diptera	*Sarcophaga haemorrhoa*	1	0
Diptera	*Sarcophaga nigriventris*	3	2
Diptera	*Sarcophaga* sp.	2	1
Diptera	*Sarcophaga subvicina*	1	0
Diptera	*Sarcophaga variegata*	1	0
Diptera	*Scaeva pyrastri*	2	6

Diptera	*Scathophaga stercoraria*	1	5
Diptera	Sciaridae sp.	1	0
Diptera	*Sepsis* sp.	1	1
Diptera	*Sicus ferrugineus*	1	0
Diptera	*Siphona geniculata*	2	1
Diptera	*Siphona* sp.	0	1
Diptera	*Solieria* sp.	1	0
Diptera	*Sphaerophoria bankowskae*	0	2
Diptera	*Sphaerophoria menthastri*	3	10
Diptera	*Sphaerophoria scripta*	7	13
Diptera	*Sphaerophoria spp.*	23	23
Diptera	*Sphaerophoria taeniata*	0	7
Diptera	*Suillia variegata*	1	0
Diptera	*Syritta pipiens*	33	8
Diptera	*Syrphus ribesii*	31	17
Diptera	*Tetanocera elata*	1	0
Diptera	*Thecophora atra*	0	1
Diptera	*Volucella inanis*	2	0
Diptera	*Volucella pellucens*	3	0
Diptera	*Xanthogramma pedissequum*	2	3
Hymenoptera	*Ancistrocerus gazella*	0	1
Hymenoptera	*Andrena bicolor*	1	0
Hymenoptera	*Andrena dorsata*	0	1
Hymenoptera	*Andrena fulvago*	2	0
Hymenoptera	*Andrena minutula*	1	0
Hymenoptera	*Andrena semilaevis*	5	1
Hymenoptera	*Andrena* sp.	1	0
Hymenoptera	*Apis mellifera*	51	39
Hymenoptera	*Athalia* sp.	0	1
Hymenoptera	Aulacidae sp.	0	1
Hymenoptera	*Bombus hortorum*	1	2
Hymenoptera	*Bombus hypnorum*	1	0
Hymenoptera	*Bombus lapidarius*	25	20

Hymenoptera	*Bombus lucorum*	4	3
Hymenoptera	*Bombus pascuorum*	52	81
Hymenoptera	*Bombus pratorum*	1	0
Hymenoptera	*Bombus terrestris*	10	6
Hymenoptera	*Bombus psithyrus sp.*	1	0
Hymenoptera	Braconidae sp.	6	6
Hymenoptera	Chalcidoidea sp.	5	4
Hymenoptera	Gasteruptidae sp.	1	0
Hymenoptera	*Halictus rubicundus*	4	2
Hymenoptera	*Halictus tumulorum*	57	44
Hymenoptera	*Hylaeus hyalinatus*	2	0
Hymenoptera	Ichneumonidae sp.	1	3
Hymenoptera	*Lasioglossum albipes*	7	5
Hymenoptera	*Lasioglossum calceatum*	23	41
Hymenoptera	*Lasioglossum fulvicorne*	0	2
Hymenoptera	*Lasioglossum lativentris*	0	1
Hymenoptera	*Lasioglossum morio*	18	3
Hymenoptera	*Lasioglossum smaethmanellum*	5	126
Hymenoptera	*Lasioglossum* sp.	0	2
Hymenoptera	*Lasioglossum villosulum*	4	19
Hymenoptera	*Leucozonium leucozonium*	0	7
Hymenoptera	*Megachile centuncularis*	3	0
Hymenoptera	*Megachile ligniseca*	5	1
Hymenoptera	*Megachile willughbiella*	8	2
Hymenoptera	*Mellita leporina*	1	1
Hymenoptera	*Nomada fabriciana*	2	0
Hymenoptera	*Nomada flavoguttata*	1	0
Hymenoptera	*Osmia bicornis*	1	0
Hymenoptera	*Osmia caerulescens*	4	3
Hymenoptera	*Osmia leaiana*	8	0
Hymenoptera	*Sphecodes monilicornis*	2	1
Hymenoptera	*Tenthredo* sp.	0	5
Hymenoptera	*Vespula germanica*	1	0

Hymenoptera	*Vespula vulgaris*	1	0
Lepidoptera	*Maniola jurtina*	0	10
Lepidoptera	*Pararge aegeria*	1	0
Lepidoptera	*Pieris napi*	2	1
Lepidoptera	*Thymelicus lineola*	0	14
Lepidoptera	*Thymelicus sylvestris*	0	3
Miridae	Miridae sp.	0	1
Thysanoptera	Thysanoptera sp.	0	1

Chapter 4

The effect of generalisation and population feedbacks on the robustness of plant-insect assemblages: a comparison of pollination and herbivory networks

4.1 Introduction

Plant and insect species interact in many different ways: insects can defend plants from predators, disperse seeds or facilitate plant reproduction, whereas plant species often serve as food source and nesting substrate for many insect species (Del-Claro et al., 1996; Shepherd and Chapman, 1998; Coley et al., 2006; Requier et al., 2015). As both groups are extremely species-rich (RBG, 2016; Stork, 2018), plant-insect interactions represent a ubiquitous component of biodiversity. It has been estimated that more than 85% of flowering plant species depend on animals for pollination (Ollerton et al., 2011), the majority of those pollinators being insects. Similarly, plant-herbivore interactions are extremely diverse (Price, 2002), as insect herbivores were estimated to comprise to up to 6 million species (Novotny et al., 2002). Given their richness and abundance, the effects of insect pollinators and herbivores on plants will have widespread demographic and organisational consequences at the community level, turning the study of the structure, dynamics and resilience of plant-insect communities into a central aim in Ecology. As the effect of plant community composition and abundance distribution can propagate upwards through several trophic levels (Scherber et al., 2010), the study of how communities disassemble with the loss of plant species could generate insights into the obverse effect - how communities reassemble with plant species introduction (Tylianakis et al., 2018).

Ecological networks depict the interactions among species, visually each species is represented by nodes that are linked whenever species interact. Recurrent structural patterns have been described for ecological networks of different interaction types (Bascompte et al., 2003; Guimarães et al., 2007a; Donatti et al., 2011; Pires and Guimarães, 2013). For instance, the antagonistic networks formed by insect herbivores and plants often present modular structures (Thébault and Fontaine, 2010; Cagnolo et al., 2011), *i.e.* sets of species interact more among themselves than with the rest of species in the network. Networks depicting free-living mutualisms, such as those between plants and pollinators, can show both modular and nested structures (Bascompte et al., 2003; Olesen et al., 2007; Guimarães et al., 2007b). Nested networks comprise a highly connected core of generalist species, which interact with generalist and specialist species, whilst specialist species interact mostly with generalists. These types of structural patterns affect the dynamics and robustness of ecological networks in different ways (Dunne et al., 2002; Burgos et al., 2007; Thébault and Fontaine, 2010; Stouffer and Bascompte, 2011; Vieira and Almeida-Neto, 2015). For example, in pollination networks, nestedness increases the speed of community recovery after perturbations (Thébault and Fontaine, 2010), but facilitates network collapse to species loss (Burgos et al., 2007).

The structure of ecological networks is likely to reflect the natural history of ecological interactions (Guimarães et al., 2007b). Generalisation, for instance, could benefit pollinators and insect herbivores by increasing resource availability (Waser et al., 1996; Bernays and Minkenberg, 1997). However, the selective pressure imposed by plants defences on herbivores can result in an evolutionary arms race between the two groups favouring herbivore specialisation (Thompson, 2005). In fact, insect herbivores are often more specialised in resource use than pollinators (Fontaine et al., 2009). Pollinators, on the other hand, may optimize foraging gains and nutritional intakes by feeding on a wider range of resources (Alaux et al., 2010; Pasquale et al., 2013), leading to the high levels of generalisation observed for pollinators (Waser et al., 1996; Fontaine et al., 2009). Another key aspect of natural history that may explain differences in the structure of pollination and herbivory networks is the type of population feedback resulting from the interaction, (Thébault and Fontaine, 2010) *i.e.* the reciprocal demographic consequences of the interaction in terms of its effects on per capita growth rates. The reciprocally positive demographic effects of mutualisms could make extinction cascades more likely and longer in pollination systems than in herbivory, as plant population declines would lead to declines in pollinators, which would lead to further declines in plants and so on (Vieira and Almeida-Neto, 2015). In herbivory, however, as only herbivores benefit from the interaction, plant declines would lead to herbivore declines, but herbivore declines would not lead to plant declines, constraining the frequency and length of extinction cascades. Moreover, the population feedbacks and extinction cascades could interact with and change network structure to affect the resilience of these systems to perturbation (Thébault and Fontaine, 2010).

Ecological networks are not static, but rather they are dynamical systems in which species abundances and network structure reciprocally affect each other and vary over time (Poisot et al., 2015). Indeed, interaction rewiring, *i.e.* the switch of interactions from one partner to another, is widespread in free-living mutualisms, such as in pollination (Kaiser-Bunbury et al., 2010), in which the generalisation of several species leads to flexibility of interaction partners (Bascompte and Jordano, 2014). Interaction rewiring between plants and pollinators can occur over time (CaraDonna et al., 2017) and space (Carstensen et al., 2014;

Trøjelsgaard et al., 2015) as a consequence of and despite changes in species abundances (Carstensen et al., 2014; Trøjelsgaard et al., 2015; MacLeod et al., 2016). Interaction rewiring can also happen among locally specialist plant and pollinator species (Carstensen et al., 2014), and in more specialized interactions such as herbivory (Novotny, 2009). However, while interaction rewiring has been observed in insect herbivores (Auerbach and Simberloff, 1988; Murphy and Feeny, 2006), these host switches are often phylogenetically constrained and involve plant species within the same genus (Novotny and Basset, 2005; but see Agosta, 2006).

Adaptive network models (ANMs) are a class of dynamic network models which are useful for the study of reciprocal effects between population dynamics and interaction structure, as ANMs have two in-built sources of dynamics which feedback on each other. The local dynamics is the variation in species abundances over time, and the topological dynamics is the rewiring of interactions changing network structure (Gross and Blasius, 2008; Valdovinos et al., 2010; Ramos-Jiliberto et al., 2012). ANMs can therefore be used to investigate the consequences of the differing level of generalisation (as differing rewiring opportunities) and population feedbacks (as local dynamics), between pollination and herbivory for the robustness of these systems. Network robustness is an easy to interpret and broadly used network metric that quantifies how resistant ecological networks are to the loss of species (Memmott et al., 2004; Burgos et al., 2007).

Here I use ANMs to investigate how differences in the network structure, on the population feedbacks and on the level of generalisation (through rewiring opportunities), affect the dynamics and robustness of pollination and herbivory systems to species loss (Figure 4-1a). I do this using data from empirically derived networks. I predict that the positive and reciprocal demographic effects between plant and insect populations (population feedbacks) in pollination networks will result in more frequent and longer coextinction cascades in than in herbivory networks, this negatively affecting the robustness of pollination systems. I also predict a more limited range of rewiring opportunities in herbivory networks, this reducing their robustness. Finally, I investigate how the structure of pollination and herbivory networks interact with population feedbacks and rewiring opportunities to affect network robustness.

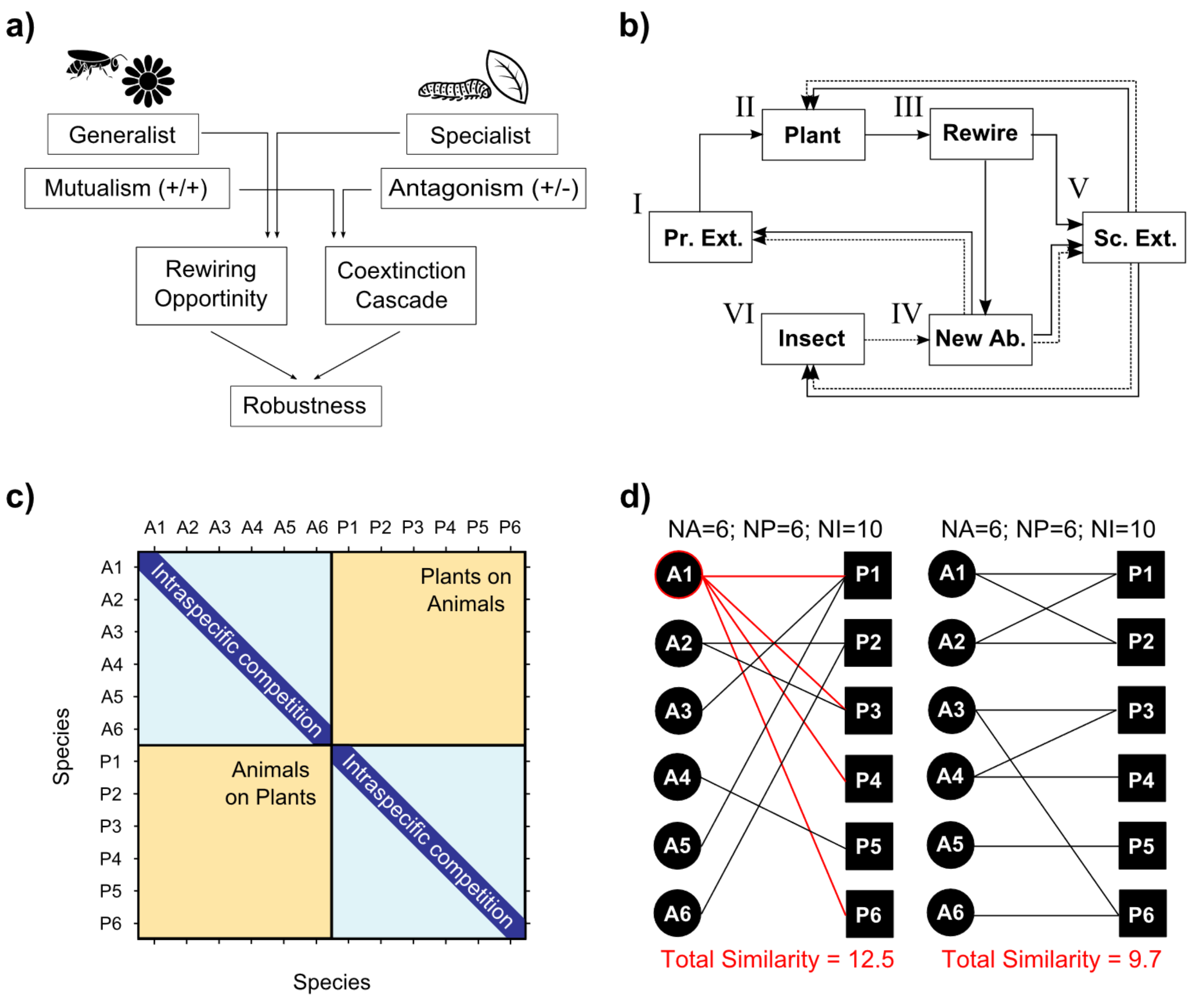


Figure 4-1 a) The level of generalisation of pollination and herbivory networks is expected to affect rewiring opportunities, while the population feedbacks (mutualism vs antagonism) are expected to affect coextinction cascades. Rewiring opportunities and coextinction cascades are expected to affect network robustness. b) Scheme of extinction cascades, normal arrows indicate consequences of the loss of plant species and dashed arrows indicate consequences of the loss of animal species. Cascades start with the primary extinction of a plant (I and II). Animals interacting with that plant have the chance of rewiring (III). If rewiring is successful, new abundances are calculated (IV), and if all new abundances are positive a new cascade begins (I). Species for which rewiring is unsuccessful or whose abundance reach zero suffer secondary extinctions (V). Secondary plant extinctions lead to a similar sequence of events than primary extinctions (I and II). Secondary animal extinctions lead directly to the calculation of new abundances (VI and IV). c) Square matrix **T** (eq. 2) of a network with six animal (A1 to A6) and six plant species (P1 to P6). **T** has information on the per capita effects of each interaction on the abundance of every species in the network, cells have the effect of the column species over the abundance of the row species. Yellow quadrats carry information of pollination or herbivory (ΓAP and ΓPA) and blue quadrants carry information of competition (ΩAA and ΩPP). I only explore the effect of intraspecific competition, in elements of the dark blue diagonal. d) Differing levels of generalisation can influence rewiring opportunities: both networks have the same number of animal (NA) and plant (NP) species, and of interactions (NI), but given the presence of a generalist species in the left network (A1 circled in red), the resulting sum of interaction similarities between animal pairs (total similarity) is higher in the left network than in the right network.

4.2 Material and Methods

4.2.1 Dataset

I compiled all the pollination networks found in two online datasets (Interaction Web Database and Web of Life), all the herbivory networks compiled by three previous studies (Fontaine et al., 2009; Pires and Guimarães, 2013; Fontaine and Thébault, 2015), and networks of both interactions types found by an independent search. From these, I selected a subset of networks excluding networks (i) in which animal species were not exclusively insects, (ii) that were both from the same interaction type and author, and (iii) which were collected over more than two years or across large scales (*e.g.* the whole country). This selection process resulted in 26 pollination and 17 herbivory networks from the literature (Table S 4-1). Networks of both interaction types are bipartite, depicting interactions between species in two sets, plants and insects, but not between species in the same set (*e.g.* between plants or between insects). Even if the frequency of interaction between species was available for some networks, I only used binary interaction information from these networks (following Dáttilo et al., 2016), as I am comparing different systems which are likely to vary in species abundances, detectability and data collection methods, all factors which could add noise to the results making the understanding of the mechanisms explicitly investigated harder. Below I first provide a general overview of the simulation procedure. Then, in the following sections I detail how the local and topological dynamics were incorporated in the simulation. I finish by describing the simulation scenarios and statistical analysis.

4.2.2 Simulation overview

Using the 43 networks, I simulate coextinction cascades following an initial primary extinction in which one plant species is randomly selected for removal (Figure 4-1b). One coextinction cascade encompasses all secondary extinctions following a primary extinction, including species from both trophic levels. I chose to eliminate plants in primary extinctions as insects are the active elements of interaction rewiring, and because the effect of plants on insects is positive in both pollination and herbivory systems this making comparison of network collapse straightforward. Following the primary extinction (Figure 4-1b; steps I and II), insect species previously interacting with the extinct plant have the opportunity to rewire (step III; section *4.2.4. Rewiring algorithm – Topological dynamics*). After changes on network structure due to species loss and rewiring, species abundances are recalculated and coextinctions computed (steps IV and V, respectively). Coextinctions can either be abundance-related - when abundances approach zero - or interaction-related - when species are disconnected from the network, except for plants in herbivory networks which can remain in the system even if disconnected. I used simulated abundance data (section *4.2.3. Model – Local dynamics*), as the interaction frequency recorded in the original dataset is not necessarily a reliable abundance measure (*e.g.* it can depend on the method of collection). Coextinctions are treated similarly to primary extinctions: the secondary extinction of a plant (step II), gives the insects feeding on that plant the opportunity of rewiring. If insects are lost though (step VI) plants do not rewire, as plants do not actively search for pollinators. Species abundances are recalculated after changes in network structure and any further coextinctions are computed. Coextinction cascades end when coextinctions lead to no further coextinctions, and a new cascade starts with the removal of another plant.

4.2.3 Model – Local dynamics

I use the model developed by Suweis et al. (2013). Interaction networks and interaction matrices (**M**) are interchangeable structures. In **M**, each animal species, $A = \{A_1, A_2, A_3... A_{Sn}\}$, is a row, each plant species, $P = \{P_1, P_2, P_3...P_{Sn}\}$, is a column, and $m_{ij} = 1$ when insect *i* and plant *j* interact, and $m_{ij} = 0$ otherwise. Species richness in the network is *SM* = *SA* + *SP*. At the beginning of the simulation, I randomly sampled species abundances from a lognormal distribution with mean $\mu = 1$ and standard deviation $\sigma = 1$. As an example, a random sample of 100.000 values drawn from this distribution has mean = 4.47, sd = 5.81 and ranges from 0.039 to 173.68, while abundance-related coextinctions happen when abundances reach 0.001. During the simulation, species abundances are an outcome of interactions established with other species (Eq. 1). In pollination networks, plants and animals are positively affected by interactions, while in herbivory networks only animals benefit while plants are negatively affected by animals. The population dynamics of species *i* can be described as a function of the per capita effects of ecological interactions on its abundance x_i:

$$\frac{d_{x_i}}{d_t} = x_i\left(a_i + \sum_{j}^{S_M} \mathbf{T}_{ij} x_j\right), \tag{1}$$

where a_i describes the intrinsic growth rate of species *i* in the absence of interactions, $\mathbf{T}_{ij}$ represents the effects of species *j* on species *i*, and x_j is the abundance of species *j*. I assumed a type I functional response for both interaction types (Suweis et al., 2013).

The square matrix **T** (Figure 4-1c) of dimensions *SM* × *SM* includes information on the per capita effects of each interaction on the abundance of species *i* ($\mathbf{T}_{ij}$ in eq. 1):

$$T = \begin{bmatrix} \Omega_{AA} & \Gamma_{AP} \\ \Gamma_{PA} & \Omega_{PP} \end{bmatrix} = \begin{bmatrix} d & \omega_{1,2} & \cdots & \omega_{1,S_A} & \gamma_{1,S_A+1} & \cdots & \cdots & \gamma_{1,S_M} \\ \omega_{2,1} & d & \cdots & \cdots & \gamma_{2,S_A+1} & \cdots & \cdots & \cdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \omega_{S_A,1} & \vdots & \cdots & d & \gamma_{S_A,S_A+1} & \cdots & \cdots & \gamma_{S_A,S_M} \\ \gamma_{S_A+1,1} & \cdots & \cdots & \cdots & d & \omega_{S_A+1,S_A+2} & \cdots & \omega_{S_A+1,S_M} \\ \gamma_{S_A+2,1} & \cdots & \cdots & \cdots & \cdots & d & \cdots & \omega_{S_A+2,S_M} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \gamma_{S_M,1} & \cdots & \cdots & \cdots & \omega_{S_M,S_A+1} & \cdots & \cdots & d \end{bmatrix} \tag{2}$$

Quadrats Γ_{AP} and Γ_{PA} describe the per capita effects of pollination or herbivory on species abundances, whereas quadrats Ω_{AA} and Ω_{PP} summarize the per capita effects of competition. Diagonal elements represent intraspecific competition, *dii* = 1. Quadrat Γ_{AP} is built from the interaction matrix **M:** considering a pair of species i $\{i \in A\}$ and j $\{j \in P\}$ that interact ($m_{ij} = 1$), if the effect of j on the abundance of i is positive, $\gamma_{ij} \sim -|\mathcal{N}(\mu,\sigma_\Gamma)|$; if it is negative, $\gamma_{ij} \sim |\mathcal{N}(\mu,\sigma_\Gamma)|$; where $\mathcal{N}(\mu,\sigma_\Gamma)$ is a the normal distribution with mean $\mu = 0$ and standard deviation $\sigma_\Gamma = 0.1$. This parameterization ensures that all networks are stable when simulation starts. Within Γ_{PA}, the effect of species i on the abundance of its partner j is defined by a different number: $\gamma_{ji} \sim -|(\mu,\sigma_\Gamma)|$ if the effect of the interaction is positive, and $\gamma_{ji} \sim |\mathcal{N}(\mu,\sigma_\Gamma)|$ if it is negative. Therefore, pollination is a symmetric interaction in sign but not in value (Bascompte and Jordano, 2014), whilst herbivory is asymmetric in sign and value. Quadrats describing the effects of interspecific competition (Ω_{AA} and Ω_{PP}) were set to zero, assuming that species do not suffer interspecific competition.

4.2.4 Rewiring algorithm – Topological dynamics

Insect species had a chance to rewire as a response to the extinction of a resource (plant) species. Rewiring opportunities for insect species are identified using a matrix of forbidden links, **R**, calculated from **M** (Figure 4-1d, Code S 4-1)**.** At the beginning of each simulation, I calculated the Jaccard similarity index of interactions between all insect pairs in the network. As interactions are partly determined by species attributes such as morphology, physiology and phenology (Cornell and Hawkins, 2003; Stang et al., 2006; Olesen et al., 2011; Cipollini and Peterson, 2018), I assume that species with high interaction similarity are likely to share those attributes and, therefore, to establish similar interactions. Thus, I used the interaction similarity of insect pairs as the probability each species in the pair had of mimicking the interactions of the other species in the pair. With increasing similarity, the probability of mimicking interactions increases but the number of available interactions - not shared by both species - decreases. Given the higher level of specialisation in herbivory compared to pollination networks, I expect a lower interaction overlap in herbivory networks, this reducing the probability of species mimicking interactions (Figure 4-1d). Thus, **R** incorporates the differences in generalisation between pollination and herbivory networks.

Following Ramos-Jiliberto et al. (2012), rewiring occurs as a two-step process: step 1 determines which of the insects that lost a resource will rewire and step 2 determines to which new plant species the insects rewire. As my goal was not to investigate different rewiring scenarios (Ramos-Jiliberto et al., 2012), I chose one scenario for each step. An insect species' probability of rewiring (Step 1) was inversely proportional to its total resource abundance. For that, the abundance of all resources (plant species) of each insect species was summed, resulting in a total resource abundance per insect species. Then, the total resource abundance of each insect was normalised by the highest value of total resource abundance, so that normalised resource abundances (n) ranged from 0 to 1. Finally, the rewiring probability of insect *i* was calculated as $p_i = 1 - n_i$. Therefore, insects feeding on the maximum abundance of resources will not rewire (p_i = 1 - 1 = 0), while insects which lost their last resource (p_i = 1 - 0 = 1) will rewire. Insects with intermediate abundance of resources have an intermediate probability of rewiring. Insects selected then rewire to a new species (Step 2), both respecting **R** and in proportion to plants' abundances.

4.2.5 Simulations scenarios

To unravel how population feedbacks, generalisation (through rewiring opportunities) and network structure affect the robustness of pollination and herbivory networks, I ran 12 simulation scenarios (Table 4-1). To separate the effect of network structure from both population feedbacks and generalisation, in half of the scenarios I ran simulations on empirical networks. For the remaining scenarios, I generated 100 null networks for each empirical network using a null model in which interactions were distributed in proportion to species degree, *i.e.* number of interaction partners (null model 2, Bascompte et al., 2003). Therefore, the resulting null networks had similar degree distribution to empirical networks, but not other potential structural properties, *e.g.* nestedness or modularity.

To investigate how differences in network structure between pollination and herbivory networks affect extinction cascades and network robustness (Objective 1), I initially ran four scenarios (Scenarios 1 to 4, Table 4-1). In scenarios 1 and 2 I ran 100 simulations using empirical pollination and herbivory networks, respectively, while in scenarios 2 and 4 I ran simulation using the null networks. In these four scenarios insects had no opportunity to rewire. By comparing scenarios 1 and 2 with 3 and 4 (*i.e.* empirical vs null network structures) I investigated how the empirical structure of pollination and herbivory networks affected the robustness of these systems. To investigate the effect of population feedbacks I repeated the same procedure, with four additional scenarios, but flipping the population feedbacks (local dynamics) between the two network types (Scenarios 5 to 8, Table 4-1) in order to identify the separate effects of network structure and of population feedbacks (Objective 2). Thus, in scenarios 5 to 8 I treated pollination networks as herbivory networks and herbivory networks as pollination networks. Finally, to explore the effect of rewiring opportunities, the four remaining scenarios (scenarios 9 to 12, Table 4-1) were similar to scenarios 1 to 4, but the insects had the opportunity to rewire (Objective 3). All code used to run simulations can be found in the Supplementary Material.

Table 4-1 Description of simulation scenarios (S1 to S12): network type (Int. Type: pollination or herbivory), structure of the network (Structure: empirical or null), population feedbacks (Feedback: original or reversed) and rewiring opportunities (Rewiring: on or off). Objectives for which each scenario was used (Obj. 1 to 3), are marked with an X.

Scenario	Int. Type	Structure	Feedback	Rewiring	Obj. 1	Obj. 2	Obj. 3
S1	Pollination	Empirical	Original	Off	X	X	X
S2	Herbivory	Empirical	Original	Off	X	X	X
S3	Pollination	Null	Original	Off	X	X	X
S4	Herbivory	Null	Original	Off	X	X	X
S5	Pollination	Empirical	Reversed	Off		X	
S6	Herbivory	Empirical	Reversed	Off		X	
S7	Pollination	Null	Reversed	Off		X	
S8	Herbivory	Null	Reversed	Off		X	
S9	Pollination	Empirical	Original	On			X
S10	Herbivory	Empirical	Original	On			X
S11	Pollination	Null	Original	On			X
S12	Herbivory	Null	Original	On			X

I calculated the robustness of networks for all 12 scenarios using the *bipartite* R package (Dormann et al., 2008, 2009; R Core Team, 2017). The robustness metric used is based on the attack tolerance curve, which describes the percentage of species in one set (*e.g.* insects) remaining in the network following the sequential removal of species in the other set (*e.g.* plants). The area under this curve results in an intuitive robustness measure (Burgos et al., 2007), since values approaching 1 indicate high robustness as most species in one set survived, even after the removal of a high proportion of species on the other set. Alternatively, values approaching 0 indicate low network robustness, since almost no species in one set survived the removal of a low proportion of species on other set.

For the first eight scenarios, I also calculated: (i) the probability of abundance-related secondary extinctions, *i.e.* the number of abundance-related secondary extinctions as a proportion of all secondary extinctions; (ii) the average length of coextinction cascades; (iii) the probability of coextinction cascades, *i.e.* of a primary extinction lead to at least one secondary extinction; and (iv) the probability of a long coextinction cascade, *i.e.* of a primary extinction lead to at a cascade of length three or more. The loss of plant species is likely to lead to coextinction of insects (cascades of length two) in networks of both interaction types, while further coextinctions (cascades of length three or more) show whether cascades continue to propagate across both trophic levels. I expect long cascades to be more common in pollination than in herbivory networks.

4.2.6 Statistical analysis

I investigated the effect of network structure on the robustness of pollination and herbivory networks using the results of scenarios 1 to 4 (Table 4-1) with a linear mixed model (LMM). The model had robustness as the response variable and the interaction between structure (empirical vs null) and interaction type (pollination vs herbivory) as fixed effects. I used the Akaike Information Criteria (AIC) to select between (i) no random structure and (ii) network identity as random effect (Zuur et al., 2009), and the *emmeans* R package (Lenth, 2018) to perform *a posteriori* Tukey tests. I then explored which, if any, of the network structural patterns (species richness, connectance, nestedness and modularity) were associated with changes (increase or decrease) in network robustness using linear models (LM). The models had the ratio between the robustness of empirical and null networks (robustness ratio) as response variable and the interaction between metrics values and interaction type as explanatory variables. The robustness ratio shows whether network structure is associated with increases (ratio > 1) or decreases (ratio < 1) in robustness.

Using data from the first eight scenarios (Table 4-1), I investigated the effect of population feedbacks, and its interaction with network structure, on the robustness of pollination and herbivory networks. With LMMs, I compared the robustness of empirical and null networks of both interaction types (scenarios 1 to 4) with their robustness when pollination networks were treated as herbivory, and herbivory networks treated as pollination (reversed local dynamics, scenarios 5 to 8). Since I expect the positive and reciprocal population feedbacks of pollination to cause longer and frequent coextinction cascades, I expect that, with reversed feedbacks, the robustness of pollination networks will increase while the robustness of herbivory networks will decrease. The two models (one for each network type) had robustness as response variable, and the interaction between structure (empirical or null) and population feedback (non-reversed or reversed) as fixed effects. I used AIC to select between (i) no random structure and (ii) network identity as random effect, and the *emmeans* R package to perform *a posteriori* Tukey tests.

To better understand how network structure and population feedbacks affect the robustness of pollination and herbivory networks, I further investigated (i) the probability of abundance-related secondary extinctions, and the (ii) length and (iii and iv) probability of coextinction cascades in the first eight simulation scenarios. The eight models (four response variables and two interaction types) had the interaction between structure (empirical or null) and population feedbacks (normal or reversed) as fixed effects. I used LMMs for all models but for the ones looking at the probability of long extinction cascades (iv), which was transformed into a binary variable and analysed with generalised linear mixed models (GLMMs) of the binomial family. The (i) probability of abundance-related extinctions and (iii) of extinction cascades were logit transformed. I used the AIC to select between (i) no random structure and (ii) network identity as random effect, and the *emmeans* R package to perform *a posteriori* Tukey tests.

Finally, I used one LMM to understand how differences in generalisation between pollination and herbivory networks (which influences rewiring opportunities) interact with network structure to affect network robustness. The model had as response variable the ratio between robustness in the last four scenarios (S9 to S12) and in the first four (S1 to S4). Scenarios 9 to 12 are equivalent to scenarios 1 to 4, but only in the former insects had the opportunity to rewire. The magnitude of the robustness ratio indicates the increase – and, less likely, the decrease - in network robustness when insects were allowed to rewire. The interaction between structure (empirical or null) and interaction type (pollination or herbivory) were the fixed effects. I used the AIC to select between (i) no random structure and (ii) network identity as random effect, and the *emmeans* R package to perform *a posteriori* Tukey tests.

4.3 Results

Pollination networks were larger than herbivory networks (Table S 4-1), with 136 ± 127.2 species on average (mean ± SD, min = 18, max = 451), while herbivory networks had on average 98.5 ± 138.4 species (mean ± SD, min = 17, max = 655). Nevertheless, species richness (t = 0.93, df = 36.9, p = 0.36) and connectance (proportion of realised interactions; t = 0.37, df = 32.4, p = 0.71) were statistically similar in pollination and herbivory networks (Figure S 4-1a-b). Surprisingly, nestedness was more common than modularity in both network types, as 21% (4 out of 19) of herbivory networks and 11.5% (3 out of 26) of pollination networks were significantly modular, while 68.4% (13 out of 19) of herbivory and all the pollination networks were significantly nested. Nevertheless, pollination networks were more nested than herbivory networks (t = 2.99, df = 42.8, p < 0.01), but both network types had similar values of modularity (t = 1.31, df = 31.1, p = 0.2; Figure S 4-1c-d).

Network structure negatively affected the robustness of both pollination and herbivory networks (Figure 4-2; t = 4.35, df = 43, p < 0.001) as the robustness of null networks was higher than the robustness of networks with empirical structure. The final model included network identity as a random effect. However, the *a posteriori* analysis revealed that the negative effect of structure on network robustness was only significant for pollination networks (Figure 4-2a; $p < 0.001$). The negative effect of network structure on robustness seems to be mainly associated with nestedness (Figure 4-3), since, with increasing nestedness (z-scored), the negative effect of network structure on the robustness was more pronounced ($F_{(3,41)} = 34.63$, $p < 0.001$), especially for pollination networks (Figure 4-3c; $t = 3.78$, $p < 0.001$).

Treating pollination as herbivory networks – switching population feedbacks between interaction types - significantly increased the robustness of pollination networks (Figure 4-2a; $t = 3.29$, $df = 75$, $p = 0.001$), of both empirical ($p < 0.001$) and null networks ($p = 0.03$), even if the effect was higher in empirical networks. Accordingly, treating herbivory networks as pollination had a negative effect on network robustness (Figure 4-2b; $t = 4.3$, $p < 0.001$) which was similar for empirical and null networks ($p < 0.001$). Only the pollination model had network identity as a random effect, while the herbivory model had no random effect selected. When further investigating how network structure and population feedbacks are associated to the length and probability of coextinction cascades, I found that cascades were mainly associated with population feedbacks (Table S 4-2; Figure S 4-2). There were more abundance-related extinctions in pollination networks treated as pollination (PP networks) than in pollination networks treated as herbivory (PH networks; Figure S 4-2a). Coextinctions cascades were longer in PP than in PH (Figure S 4-2c), while long cascades were much more likely in PP than PH (Figure S 4-2g). Similarly, for herbivory networks, cascades were longer when networks were treated as pollination (HP larger than HH; Figure S 4-2d) and the probability of coextinction cascades (of any length) was also higher in HP than HH (Figure S 4-2f, h). On the other hand, network structure was the main driver of cascade probabilities in pollination networks, being much more common in null networks than in empirical networks

(Figure S 4-2e). Finally, network structure and population feedbacks were similarly important for the occurrence of abundance-related extinctions in herbivory networks (Figure S 4-2b).

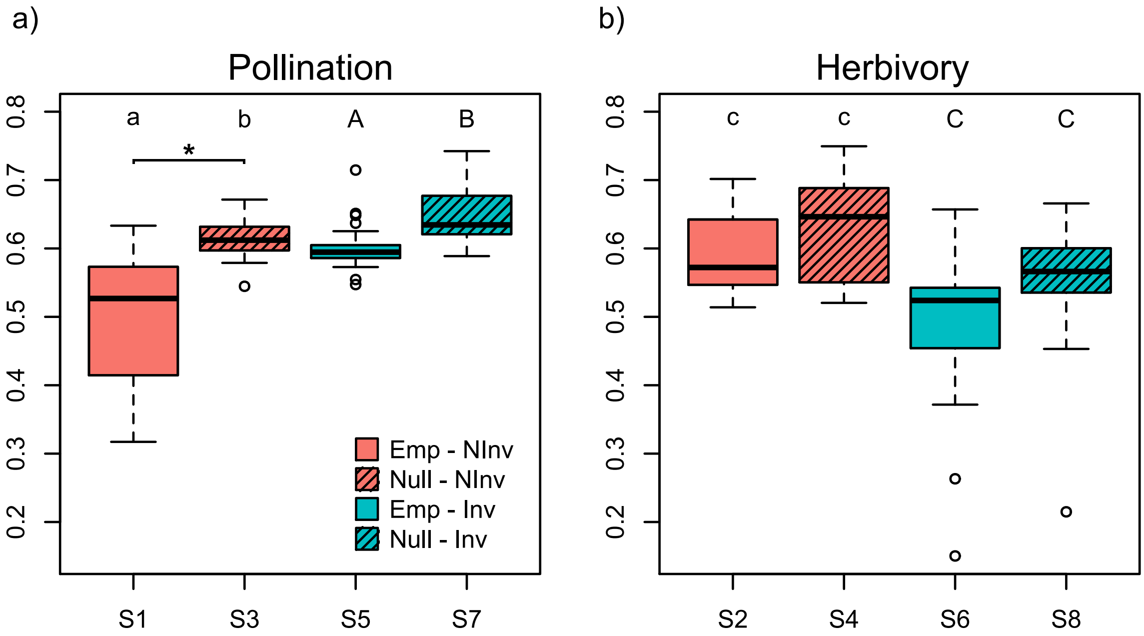


Figure 4-2 Robustness for a) pollination and b) herbivory networks in the first eight scenarios (S1 to S8). The striped boxes indicate scenarios in which null, instead of empirical, networks were used; blue boxes indicate scenarios in which population feedbacks were reversed and red boxes are non-reversed. Comparisons between empirical and null networks with non-reversed population feedbacks (S1 vs S3 and S2 vs S4; objective 1) with statistical significance ($p < 0.05$) are marked with an asterisk. Comparisons between non-reversed and reversed population feedbacks are represented by different letters (S1 and S5 vs S3 and S7 for pollination, and S2 and S6 vs S4 and S8 for herbivory; objective 2). Statistical significance ($p < 0.05$) is represented by the differences in letter case (A vs a). Description of simulation scenarios can be found in Table 4-1.

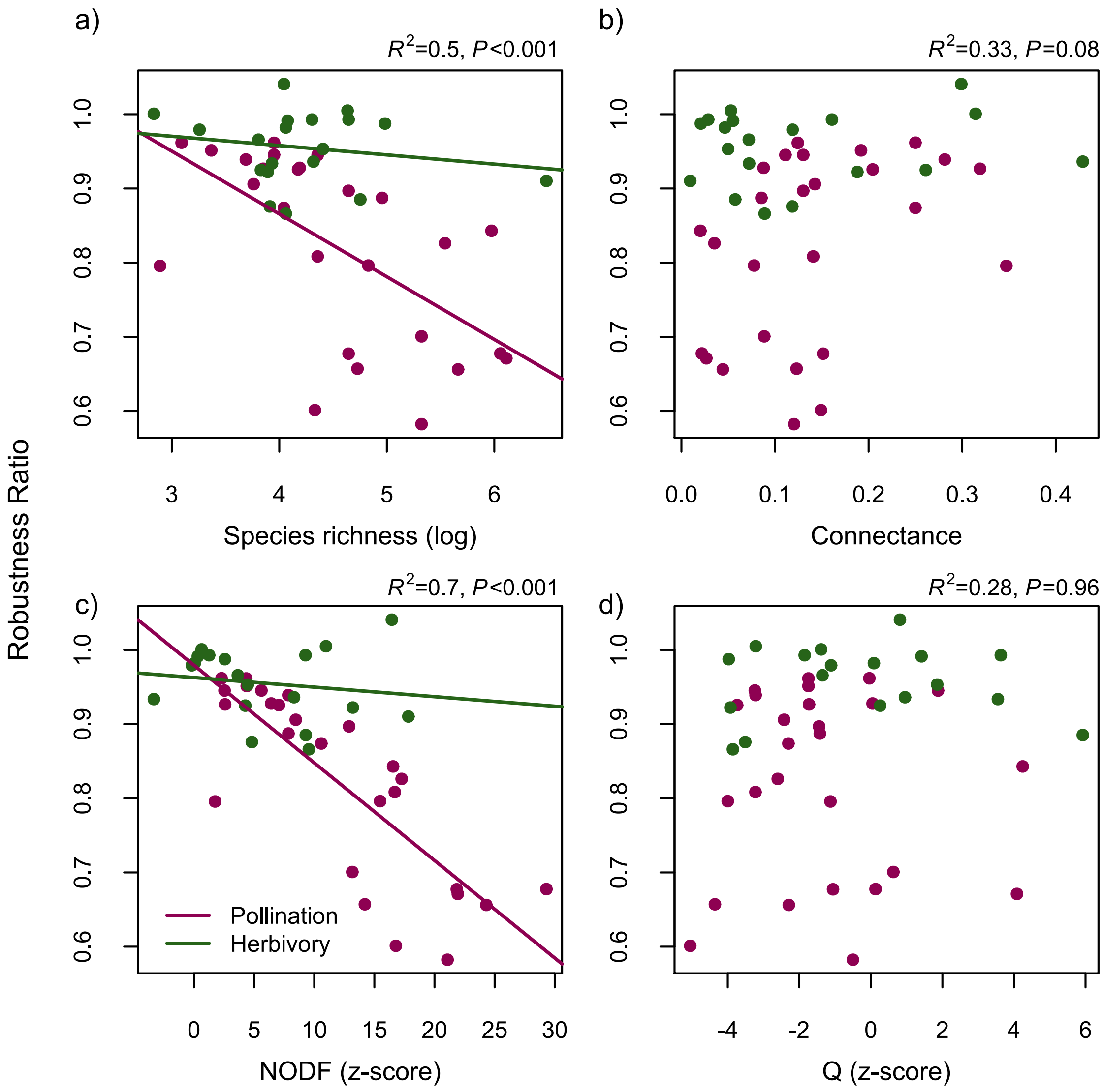


Figure 4-3 Relationship between the robustness ratio (between scenarios with empirical networks and scenarios with null networks; pollination: S1/S3; herbivory: S2/S4) and a) species richness (log), b) connectance, c) nestedness (z-scored values of NODF) and modularity (z-scored values of Q). Pink dots and lines represent pollination networks and green, herbivory.

Allowing insects to rewire, increased network robustness, on average, in all scenarios including empirical and null networks and networks of both interaction types (pollination and herbivory; Figure 4-4; t = 2.95, df = 43, p < 0.01). The largest increase observed was for empirical pollination networks, which increased on average 27% ± 20 (mean ± SD, min = 4%, max = 74%), followed by null pollination networks (13% ± 5, mean ± SD, min = 7%, max =

28%), and herbivory networks (empirical: 4% ± 4, mean ± SD, min = -4%, max = 11%; null: 2% ± 4, mean ± SD, min = -11%, max = 6%). Network structure had a significant effect in pollination networks, since empirical networks benefited more from opportunities of rewiring than null networks ($p < 0.001$), but it had no effect in herbivory networks ($p = 0.88$). Empirical pollination networks benefited more from rewiring opportunities than empirical herbivory networks ($p < 0.001$), but so did null pollination networks that had a higher increase in robustness than null herbivory networks ($p = 0.02$). One empirical and two null herbivory networks, had lower robustness when herbivores were allowed to rewire.

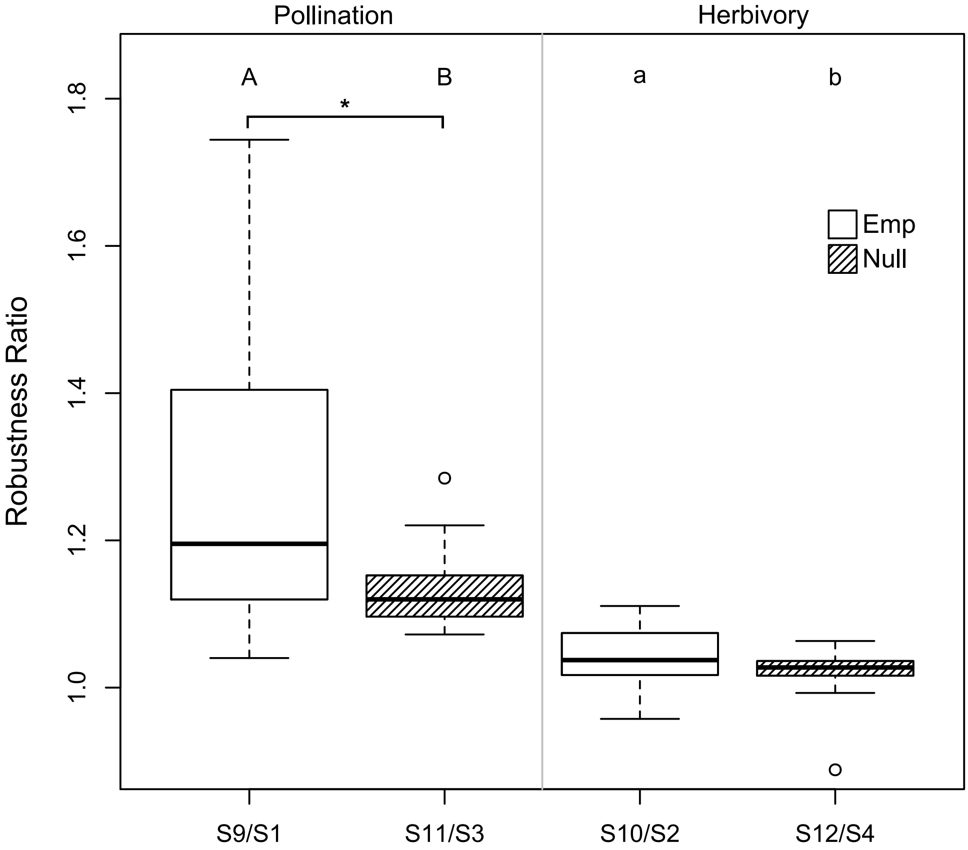


Figure 4-4 Ratio of robustness values for pollination and herbivory networks between the last and the first four scenarios (S9 to S12 and S1 to S4, respectively). The last scenarios are similar to the first four, but insects had the opportunity to rewire. Striped boxes indicate scenarios in which null, instead of empirical, networks were used. Comparisons between empirical and null networks of the same interaction type (S9/S1 vs S11/S3 and S10/S2 vs S12/S4; objective 1) with statistical significance ($p < 0.05$) are marked with an asterisk. Comparisons between networks of different interaction types but with similar structure (empirical: S9/S1 vs S10/S2 and null: S11/S3 vs S12/S4) are represented by different letters, and statistical significance ($p < 0.05$) by the difference in letter case (A vs a). Codes for simulation scenarios can be found in Table 4-1.

4.4 Discussion

Understanding how the natural history and network structure of different interaction types affect the dynamics and robustness of ecological communities to perturbation is very relevant to the study and application of conservation and restoration biology (Memmott, 2009; Montoya et al., 2012; Harvey et al., 2017). In this study, I found that herbivory networks tend to be more robust than pollination networks to plant extinctions due to two main reasons. First, pollination networks are more nested than herbivory networks, and nestedness is associated with decreasing levels of network robustness. Second, the reciprocal positive demographic effects of mutualisms, such as pollination, make coextinction cascades both more likely and longer in these systems, causing pollination networks to collapse faster. However, when taking into account the fact that network structure is not static, but that interaction rewiring is pervasive in real systems, both the higher generalisation level and the more nested structure of pollination networks increased the robustness of pollination when compared to herbivory systems. In what follows I first address the limitations of my study, and then consider the original objectives, putting my results in the context of previous findings.

4.4.1 Limitations

The population feedback results (Objective 2) were in accordance with my expectations. However, in my scenarios, I only included the effect of herbivory and pollination on species abundances (local dynamics), and it is likely that species populations will also respond to competitive interactions. However, I did not include interspecific competition in this version of the model to facilitate the initial interpretation of the effects of network structure, population feedbacks and generalisation on the robustness of pollination and herbivory networks. The model, however, was designed to also accommodate interspecific competition between plants and insects and in the future, competition scenarios such as resource competition for plants, apparent competition between plant species in herbivory networks (van Veen et al., 2006), and resource competition between insect species in pollination networks (Goulson and Sparrow, 2009) should be incorporated.

4.4.2 Robustness of pollination and herbivory networks

In the first four scenarios, which had no topological dynamics, *i.e.* insect species were not allowed to rewire, network structure negatively affected the robustness of pollination, but not of herbivory, networks. Networks of both interaction types had similar structural patterns to what had been found in previous studies: pollination networks were nested, more so than herbivory networks (Bascompte et al., 2003; Thébault and Fontaine, 2010), while herbivory networks were more modular than pollination networks, even if not significantly modular when compared to null networks (Thébault and Fontaine, 2010; Cagnolo et al., 2011). This differing structure, initially thought to result from the mutualism-antagonism dichotomy, is related with the degree of intimacy of the interaction types studied (Guimarães et al., 2007b; Pires and Guimarães, 2013), which is low in pollination systems, but either intermediate or high in most of the herbivory networks in this study (Pires and Guimarães, 2013). As the major structural difference observed between pollination and herbivory networks was in terms of nestedness, I will focus the discussion on this structural pattern.

Nestedness is thought to positively affect the resilience and stability of mutualistic networks (Memmott et al., 2004; Bastolla et al., 2009; Thébault and Fontaine, 2010; Rohr et al., 2014; but see Santamaría et al., 2016). Memmott et al. (2004) suggested that nestedness increased network robustness due to the asymmetry of interactions - specialists tend to interact with generalists – observed in nested networks. Burgos et al. (2007) specifically addressed the effect of nestedness on network robustness, having found that nestedness is positive for robustness only when primary extinctions happen from the least to the most connected species.

My results, therefore, agree with Burgos et al. (2007) since in this study primary extinctions followed a random sequence. When I explicitly explored the effect of nestedness on network robustness (Figure 4-3), I found that with increasing nestedness networks become less robust, specially pollination networks, since these networks reached levels of nestedness values not observed in herbivory networks (Figure 4-3, Figure S 4-1). Under a different approach, when investigating how network structure affect the stability of pollination and herbivory networks, Thébault and Fontaine (2010) found contrasting results for these two systems. Despite positively affecting the persistence of pollination systems, nestedness had a strong negative effect on the persistence of herbivory networks (Thébault and Fontaine, 2010). Nevertheless, it is hard to put my robustness results for herbivory networks into context since this approach is not commonly applied to herbivory systems (Pearse and Altermatt, 2013; Welti et al., 2017).

When allowing insects to rewire, pollination networks – both empirical and null – had larger increases in robustness than herbivory networks, as hypothesised (Figure 4-4). I expected that, the high level of generalisation in pollination systems (Waser et al., 1996; Fontaine et al., 2009), would lead to large topological flexibility resulting in a higher increase in the robustness of pollination than in herbivory networks. This hypothesis was corroborated, despite the presence of two exceptionally generalised herbivory networks, depicting interactions between plants and grasshoppers, which lack the extreme specialists typical of herbivory systems (Fontaine et al., 2009). Two obvious advantages associated with generalisation, when compared to specialisation, are the higher availability of potential resources (Tremmel and Mueller, 2013; Requier et al., 2015; Roger et al., 2017), and the nutritional benefits associated with a varied diet (Pasquale et al., 2013; Tremmel and Mueller, 2013; Malinga et al., 2018). The second might explain the higher generalisation of grasshoppers, when compared to other herbivores, since diet diversity positively affect the performance of grasshoppers (Bernays and Bright, 1993; Malinga et al., 2018) but not of other insect herbivores (Bernays and Minkenberg, 1997). Diverse diets can also benefit pollinators by facilitating opportunism (Roger et al., 2017) and by promoting increased immunity in some species (Alaux et al., 2010), even if generalisation might be constrained by morphology (Stang et al., 2006), phenology (Olesen et al., 2011) and behaviour (Gegear and Laverty, 2005).

Despite the larger increases in robustness observed for pollination networks, rewiring increased the robustness of networks of both interaction types (Figure 4-4). Despite the higher specialisation of herbivory networks, herbivore rewiring has been observed, even at ecological time scales due to ecological fitting (Agosta, 2006; Agosta and Klemens, 2008). Despite its pervasiveness in herbivory systems, ANMs and the effect of interaction rewiring on the dynamics and robustness of networks have mainly been applied to pollination systems (Ramos-Jiliberto et al., 2012; Valdovinos et al., 2013, 2016; CaraDonna et al., 2017), or in more generalised antagonistic systems such as food webs (Valdovinos et al., 2010; Curtsdotter et al., 2011; Gilljam et al., 2015). In most studies, rewiring increased the persistence of ecological communities (but see Gilljam et al., 2015). My results suggest that the higher increase in pollination robustness stems not only from its higher level of generalisation, but also from its higher nestedness, since the increase in robustness was higher in empirical than in null pollination networks (Figure 4-4). Moreover, generalised species can be composed by generalist and/or specialist individuals (Bernays and Minkenberg, 1997; Tur et al., 2014), so that interaction rewiring has the potential to represent both cases, as an individual behavioural change in the former and an evolutionary response in the latter.

4.4.3 Conclusion

Studying network robustness is crucial if we aim to understand how ecological communities respond to extinctions (Solé and Montoya, 2001). Here, I have attempted to disentangle how three different attributes, *i.e.* network structure, population feedbacks and species generalisation, affect the robustness of ecological networks. By investigating each attribute separately, and always comparing the same network between different scenarios, I was able to avoid confounding effects such as network size and connectance. I found that nestedness, a structural pattern common in networks of several interaction types (Bascompte et al., 2003; Guimarães et al., 2007a; Dáttilo et al., 2014), affects network robustness both negatively and positively when networks are treated as static and dynamical systems, respectively. The next steps in the study of network robustness are to investigate differing interaction types (Dáttilo et al., 2016), to continue adding realistic information on local and topological dynamics (Ramos-Jiliberto et al., 2012), extinction sequences (Astegiano et al., 2015; Vieira and Almeida-Neto, 2015; Santamaría et al., 2016) and competitive interactions, which will lead to indirect effects, and likely, to non trivial results. Combining real information about ecological systems with dynamical models will allow us to address applied conservation and restoration questions in a predictive way (Raimundo et al., 2018).

4.5 Supplementary Material

Table S 4-1 Dataset of empirical pollination (P1 to P26) and herbivory (H1 to H19) networks. Network code, reference, source (WoL=Web of Life Database; IWDB=Interaction Web Database), location, number of insect and plant species, network connetance (C), nestedness (NODF) and modularity (Q). Metric significance ($p < 0.05$) relative to 100 null networks is depicted by an asterisc.

Code	Reference	Source	Location	Insects	Plants	C	NODF	Q
P1	Kakutani et al. 1990	WoL (M_PL_054)	Japan	314	113	0.02	8.81*	0.50
P2	Kato et al. 1993	WoL (M_PL_056)	Japan	360	91	0.03	7.24*	0.49*
P3	Kato & Miura 1996	WoL (M_PL_055)	Japan	191	64	0.04	9.54*	0.50
P4	Forup & Memmott 2005 (M1)	Author	UK	37	15	0.12	19.26*	0.53
P5	Orford et al. 2016 (B1)	Author	UK	39	13	0.13	23.00*	0.51
P6	Pocock et al. 2012	Author	UK	241	47	0.04	17.71*	0.49
P7	Santos et al. 2010	IWDB	Brazil	25	51	0.15	46.36*	0.32
P8	Dicks et al 2002	WoL (M_PL_006)	UK	61	17	0.14	52.27*	0.40
P9	Elberling & Olesen 1999	WoL (M_PL_009)	Sweden	118	24	0.09	15.39*	0.49
P10	Ollerton et al. 2003	WoL (M_PL_013)	South Africa	56	9	0.20	35.49*	0.42
P11	Herrera 1988	WoL (M_PL_016)	Spain	179	26	0.09	21.98*	0.44
P12	Memmott 1999	WoL (M_PL_017)	UK	79	25	0.15	42.84*	0.33
P13	Inouye & Pyke 1988	WoL (M_PL_019)	Australia	85	40	0.08	19.31*	0.40
P14	Medan et al. 2002	WoL (M_PL_022)	Argentina	45	21	0.09	18.02*	0.60
P15	Mosquin & Martin 1967	WoL (M_PL_024)	Canada	18	11	0.19	32.07*	0.46
P16	Motten 1982	WoL (M_PL_025)	USA	44	13	0.25	51.26*	0.31

Code	Reference	Source	Location	Insects	Plants	C	NODF	Q
P17	Primack 1983	WoL (M_PL_027)	New Zealand	60	18	0.11	13.94*	0.54*
P18	Schemske et al. 1978	WoL (M_PL_032)	USA	33	7	0.28	56.66*	0.36
P19	Small 1976	WoL (M_PL_033)	Canada	34	13	0.32	40.96*	0.26
P20	Olesen Unpublished	WoL (M_PL_036)	Flores	12	10	0.25	35.96*	0.44
P21	Philipp et al. 2006	WoL (M_PL_042)	Galapagos	6	12	0.35	49.79*	0.35
P22	Lundgren & Olesen 2005	WoL (M_PL_045)	Greenland	26	17	0.14	32.22*	0.46
P23	Dupont & Olesen 2009	WoL (M_PL_047)	Denmark	186	19	0.12	29.96*	0.42
P24	Vázquez 2002	WoL (M_PL_051)	Argentina	90	14	0.13	30.01*	0.49
P25	Yamazaki & Kato 2003	WoL (M_PL_053)	Japan	294	99	0.02	4.71*	0.59*
P26	Bartomeus & Santamaría 2008	WoL (M_PL_058)	Spain	81	32	0.12	28.02*	0.32
H1	Basset & Samuelson 1996	Paper	New Guinea	36	10	0.26	38.23*	0.37
H2	Bluthgen et al. 2006	Paper	Borneo	12	38	0.12	22.12*	0.57
H3	Bodner et al. 2009		Ecuador	59	45	0.03	1.40	0.88
H4	Coley et al. 2006	Paper	Panama	45	37	0.05	6.47*	0.74
H5	Futuyma & Gould 1979	Paper	USA	57	18	0.43	58.43*	0.18
H6	Henneman & Memmott 2001 (P100)	Paper	Hawaii	26	32	0.09	28.50*	0.51
H7	Macfadyen et al. 2009a (A1)	Author	UK	78	25	0.05	10.24*	0.70
H8	Memmott et al. 1994	Paper	Costa Rica	92	54	0.02	0.68*	0.91
H9	Muller et al. 1999	Paper	UK	25	26	0.07	2.72	0.80*
H10	Nakagawa et al. 2003 – 1996	Data	Malaysia	29	20	0.19	53.00*	0.33

Code	**Reference**	**Source**	**Location**	**Insects**	**Plants**	**C**	**NODF**	**Q**
H11	Novotny et al. 2005	Paper	New Guinea	29	30	0.06	3.72	0.84
H12	Pocock et al. 2012 (aphid)	Author	UK	28	30	0.05	1.54	0.90
H13	Prado & Lewinsohn 2004	Paper	Brazil	35	81	0.06	13.24*	0.63*
H14	Rathcke 1976 – 1970	Paper	USA	10	7	0.31	33.28	0.38
H15	Tavakilian et al. 1997	Paper	French Guiana	353	302	0.01	2.11*	0.69*
H16	Tscharnatke et al. 2001	Paper	Germany	16	10	0.12	4.24	0.76
H17	Villa-Galaviz et al. 2012 (P42007)	Author	Mexico	27	18	0.07	6.18*	0.78
H18	Joern 1979	Wol (A_PH_004)	USA	22	52	0.16	30.4*	0.41*
H19	Ueckert & Hansen 1971	Paper	USA	14	43	0.3	69.3*	0.28

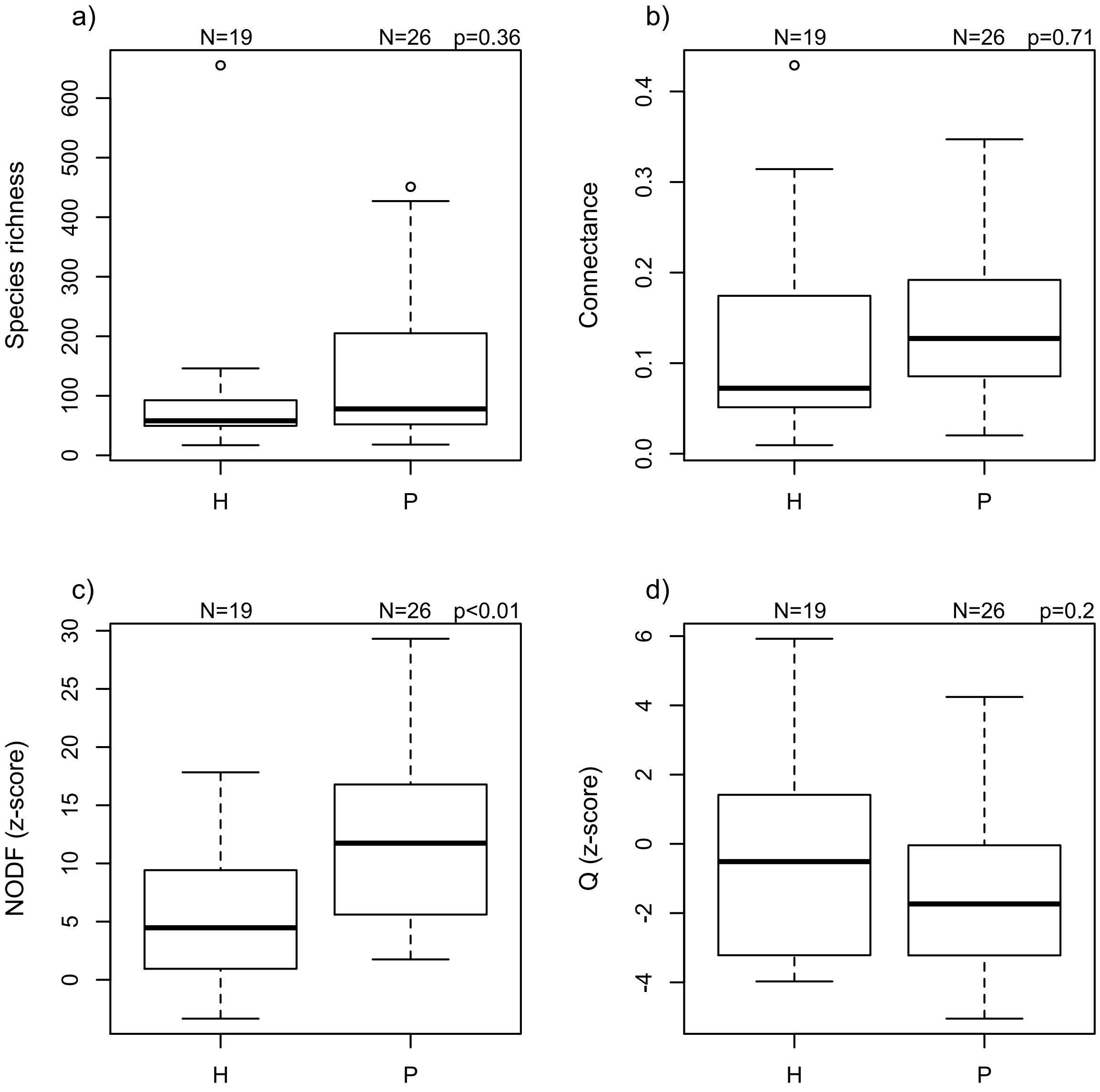


Figure S 4-1 a) Species richness, b) connectance, c) nestedness (z-scored values of NODF) and modularity (z-scored values of Q) of herbivory (H) and pollination (P) networks.

Table S 4-2 Results of the eight models investigating the effect of network structure and population feedbacks on (i) the probability of abundance-related extinctions, (ii) the length of coextinction cascades, (iii) the probability of coextinction cascades, and (iv) the probability of long coextinction cascades on pollination (P) and herbivory (H) networks. Linear mixed models were used, except for the two models on the probability of long cascades which were of the binomial family. Estimate (Est.), t and p-values of the effect of network structure, of reversing population feedbacks, and of the interaction between the two - only the results of the interaction are reported when the interaction was statistically significant ($p < 0.05$). All models had network identify as selected random effect.

	Structure			**Feedback**			**Interaction**		
Int. Type	**Est.**	**t**	**P**	**Est.**	**t**	**p**	**Est.**	**T**	**p**
Abundance-related extinction probability (logit-transformed)									
P	0.06	4.24	<0.001	-0.18	-12.24	<0.001	-	-	-
H	-0.008	-	-	0.007	-	-	-0.007	-2.22	0.03
Length of coextinction cascade									
P	-0.04	-	-	-0.05	-	-	-0.09	-21.6	<0.001
H	-0.02	-	-	0.07	-	-	0.04	8.3	<0.001
Coextinction cascade probability (logit-transformed)									
P	-0.85	-	-	-0.07	-	-	-0.19	-6.43	<0.001
H	-0.01	-0.78	0.43	0.3	18.75	<0.001	-	-	-
Long coextinction cascade probability (binomial)									
Int. Type	**Est.**	**z**	**P**	**Est.**	**z**	**p**	**Est.**	**Z**	**p**
P	0.9	-	-	-3.43	-	-	-0.94	-7.67	<0.001
H	0.44	5.5	<0.001	5.66	31.98	<0.001	-	-	-

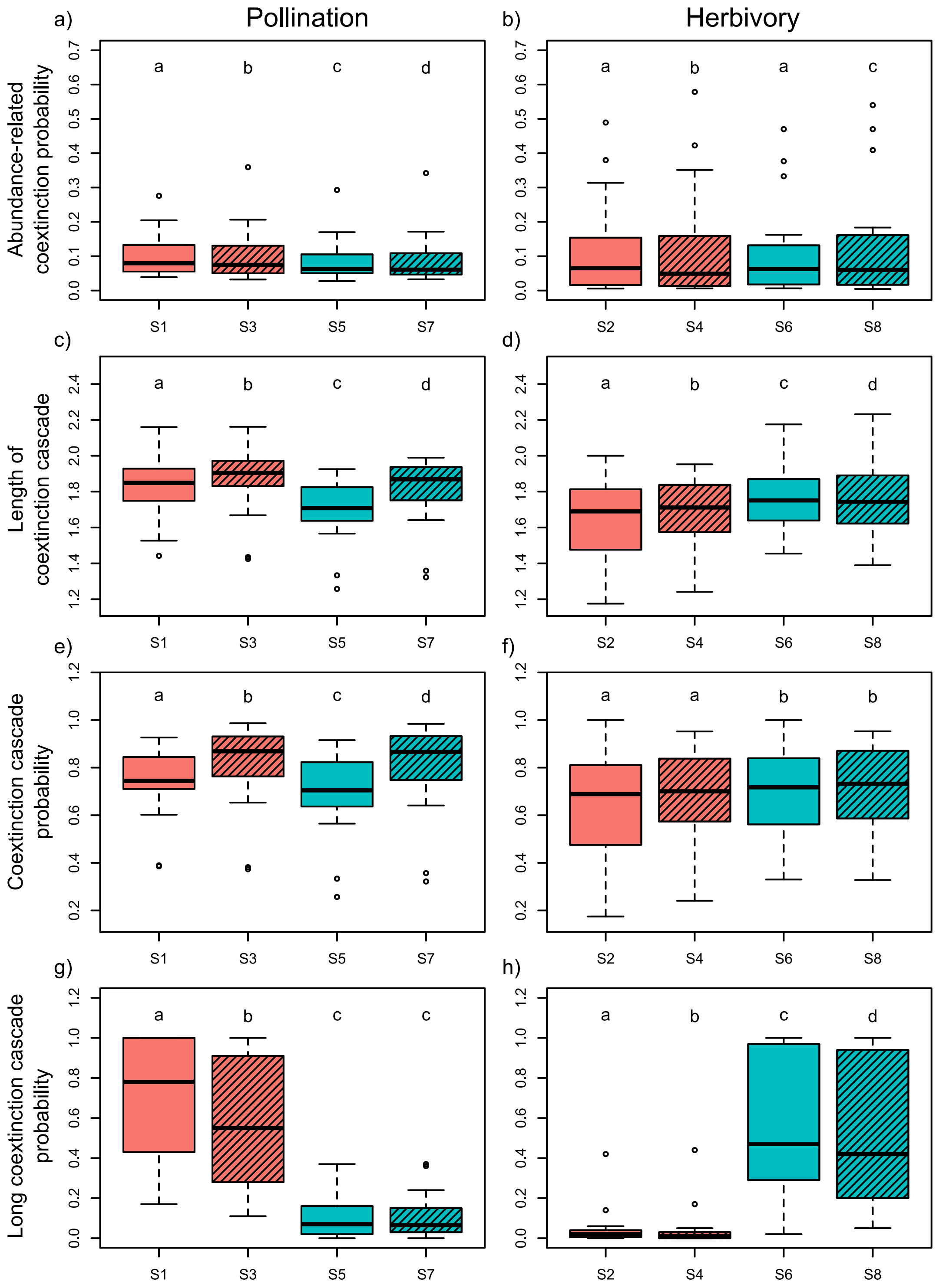


Figure S 4-2 Boxplots of the probability of abundance-related extinctions (a, b), the length of coextinction cascades (c, d), the probability of coextinction cascades (e, f), and the probability of long coextinction cascades (g, h), for pollination and herbivory networks in the eight first simulation scenarios (S1 to S8). Statistically different scenarios ($p < 0.05$) are marked with different letters. Codes for simulation scenarios can be found in Table 4-1.

Code S4-1. rew.rule is an auxiliary function that generates **R**, a matrix of forbidden links which describes the rewiring opportunities for insect species. Its single argument is **M**, the interaction matrix and it returns **R**. Requirements: *vegan* R package (Oksanen et al., 2017).

```
rew.rule <- function(M)
{
  rede <- M
  rede <- as.matrix(rede)

  PP <- 1-as.matrix(vegdist(rede, method="jaccard", binary=FALSE, diag=FALSE, upper=TRUE, na.rm = FALSE))

  pairs <- expand.grid(rownames(rede),rownames(rede))
  pairs <- pairs[pairs$Var1!=pairs$Var2,]

  for(j in 1:nrow(pairs))
  {
    prob <- PP[rownames(PP)==pairs$Var1[j],colnames(PP)==pairs$Var2[j]]
    exc.var1 <- which(M[rownames(M)==pairs$Var1[j],]==1&M[rownames(M)==pairs$Var2[j],]==0)
    exc.var2 <- which(M[rownames(M)==pairs$Var2[j],]==1&M[rownames(M)==pairs$Var1[j],]==0)
    rede[rownames(rede)==pairs$Var1[j], exc.var2] <- sample(c(1,0), length(exc.var2), prob=c(prob,1-
prob), replace=TRUE)
    rede[rownames(rede)==pairs$Var2[j], exc.var1] <- sample(c(1,0), length(exc.var1), prob=c(prob,1-
prob), replace=TRUE)
  }
  return(rede)
}
```

Code S4-2. sample.coin is an auxiliary function that samples which insects will rewire**.** Its two arguments are set, the set of insects that have lost a resource, and prob, a vector containing the rewiring probability for each insect in set. The function returns a vector of insect names which have been selected to rewire. Requirements: none.

```
sample.coin <- function(set, prob)
{
  res <- rep(NA, length(set))
  for(i in 1:length(set))
  {
    res[i] <- sample(c(1,0), 1, prob=c(prob[i], 1-prob[i]))
  }
  set <- set[res==1]
  return(set)
}
```

Code S4-3. AV.dom is an auxiliary function that creates the Jacobian matrix, **J,** regarding the equations describing the population dynamics of all species in the community, and calculates its dominant eigenvalue. Its three arguments are S, the number of species (plants and insects) in the interaction matrix **M**, Tab, the data frame in which species abundances are stored, and **MC,** where the information on the per capita effects of each interaction on the abundance of every species is stored. Therefore, **MC** is the equivalent of the square matrix **T**, but the name MC was adopted throughout the code to avoid conflicts with the programming language. The function returns the dominant eigenvalue of **J**. The results presented in this chapter did not require the use of this function, but the main function bip_cascade does. Requirements: none.

```
AV.dom <- function(S, TAb, MC)
{
  matriz.diag <- matrix(0,S,S)
  diag(matriz.diag) <- -TAb$abundance
  J <- matriz.diag%*%MC
  eigen <- eigen(J,only.values=TRUE)
  autovalores <- as.numeric(eigen$values)
  autovalores[(which(autovalores<10^-12&autovalores>0))] <- 0
  AVdom <- max(as.numeric(autovalores))
  return(AVdom)
}
```

Code S4-4. Lapla is an auxiliary function that creates the Laplacian matrix, **L**, regarding the interaction matrix **M**, which is used to calculate the number of components (NComp), size of the largest component (CSize), number of components with the largest component size (nLarge), and the algebraic connectivity (CA) of **M**. Its four arguments are **M**, the number of insect and plant species, nA and nP, and transp which states whether **M** is transposed or not. The function returns NComp, CSize, nLarge and CA. The results presented in this chapter did not require the use of this function, but the main function bip_cascade does. Requirements: *igraph* R package (Czárdi and Nepusz, 2006).

```
Lapla <- function(M, nA, nP, transp)
{
  if(transp==TRUE){M <- t(M)}
  q2 <- q4 <- M
  q1 <- mat.or.vec(nA, nA); q3 <- mat.or.vec(nP, nP)
  upper <- cbind(q1, q2); lower <- cbind(t(q4), q3)
  colnames(upper) <- colnames(lower) <- c(rownames(M), colnames(M))
  MQ <- as.matrix(rbind(upper, lower)); rownames(MQ) <-
  c(rownames(M), colnames(M))
  g <- graph_from_adjacency_matrix(MQ, "undirected")
  clu <- igraph::components(g)
  ncomp <- clu$no
  comp.sp <- groups(clu)
  c.size <- max(clu$csize)
  largclu <- which(clu$csize==max(clu$csize))
  conalg <- rep(NA, length(largclu))
  for(f in 1:length(largclu))
  {
    lc <- largclu[f]; lcsp <- comp.sp[[lc]]
    glc <- induced_subgraph(g, lcsp)
    laplaglc <- graph.laplacian(glc)
    eigenv <- eigen(laplaglc)$values
    conalg[f] <- eigenv[order(eigenv)][2]
  }
  conalg <- mean(conalg)
  return(data.frame(NComp=ncomp,CSize=c.size,nLarge=length(largclu),
  CA=conalg))
}
```

Code S4-5. holl1 is an auxiliary function that calculates the new abundances of every species after changes in networks structure. This function is used inside the *ode* function from *deSolve* R package. Its three arguments are t, a vector of time steps for which the function holl1 will be solved, y which is the vector storing the most recent values of species abundances, and parms, a list with the parameters used by holl1. The function returns a list with the newly calculated species abundances. Requirements: *deSolve* R package (Soetaert et al., 2010).

```
holl1 <- function(t, y, parms)
{
  with(parms, {
    dy <- y*(alpha - (MC%*%y))
    dy <- t(dy)
    return(list(dy))})
}
```

Code S4-6. bip_cascade is the main function used to simulate coextinction cascades in bipartite pollination and herbivory networks. It has 12 arguments: dir is the folder where source networks can be found, m.type is the type of matrix being used as source (pollination or herbivory), ext.target is the set of species targeted as primary extinctions (plants or insects, in this study all scenarios targeted plants), ext.scen is the scenario used to select species which will suffer primary extinctions (random, lowk or highk, in this study all scenarios were random), rew.logic determines whether rewiring will occur or not (TRUE or FALSE), rew.choice is the rewiring scenario used (always FALSE if rew.logic is FALSE, or either random or proportion if rew.logic is TRUE, in this study all scenarios with rew.logic = TRUE used proportion), comp.type is the competition scenario used (NC or CE, in this study all scenarios used NC), lnorm.mean and lnorm.sd are the mean and standard deviation of the lognormal distribution from which species abundances are sampled, strength is the standard deviation of the normal distribution from which the per capita effects of each interaction (stored in the square matrix **T**) on the abundance of every species are sampled, n.run is the number of simulations for each empirical network in dir.

```
bip_cascade <- function(dir, m.type, ext.target, ext.scen, rew.logic=FALSE, rew.choice=FALSE, comp.type,
lnorm.mean, lnorm.sd, strength, n.run=100){

  # Warning messages
  m.type <- as.character(m.type)
  if(!m.type %in% c("pol", "her")){return("Error: m.type must be pol or her")}
  ext.target <- as.character(ext.target)
  if(!ext.target %in% c("pla", "ins")){return("Error: ext.target must be pla or ins")}
  ext.scen <- as.character(ext.scen)
  if(!ext.scen %in% c("random", "lowk", "highk")){return("Error: ext.scen must be random, lowk or
  highk")}
  rew.logic<-as.logical(rew.logic)
  if(!is.logical(rew.logic)){return("Error: rew.logic must be logical")}
```

```r
if(rew.logic==TRUE){rew.choice <- as.character(rew.choice)}
if(rew.logic==TRUE){if(!rew.choice %in% c("random", "proportion")){return("Error: rew.choice must be
random or proportion")}}
comp.type <- as.character(comp.type)
if(!comp.type %in% c("NC", "CE")){return("Error: comp.type must be NC or CE")}
lnorm.mean <- as.numeric(lnorm.mean); lnorm.sd <- as.numeric(lnorm.sd); strength <-
as.numeric(strength)
is.wholenumber <- function(x, tol = .Machine$double.eps^0.5)  abs(x - round(x)) < tol

# Creates task name
if(m.type=="pol"){task <- paste("pol")} else {task <- paste("her")}
if(ext.scen=="lowk"){
  task <- paste(task, "_lk", sep="")
} else if(ext.scen=="highk"){
  task <- paste(task, "_hk", sep="")
} else {task <- paste(task, "_rd", sep="")}
if(rew.logic==FALSE){task <- paste(task, "_Nrew", sep="")}
if(rew.logic==TRUE)
{
  task <- paste(task, "_rew", sep="")
  if(rew.choice=="random"){task <- paste(task, "_rand", sep="")}
  if(rew.choice=="proportion"){task <- paste(task, "_prop", sep="")}
}
task <- paste(task, comp.type, sep="_"); task
```

```
# Sets up libraries and data
if("vegan" %in% rownames(installed.packages()) == FALSE) {install.packages("vegan")}
if("deSolve" %in% rownames(installed.packages()) == FALSE) {install.packages("deSolve")}
if("igraph" %in% rownames(installed.packages()) == FALSE) {install.packages("igraph")}
require(vegan); require(deSolve); require(igraph)
dir<-as.character(dir)
setwd(dir); redes <- list.files()
if(any(redes=="Results")){redes <- redes[-which(redes=="Results")]}

# Creates results folder inside network folder
mainDir <- paste("/Results")
dir.create(file.path(dir, mainDir), showWarnings = TRUE)
subDir <- paste(task, sep="")
mainDir <- paste(dir, "/Results", sep="")
dir.create(file.path(mainDir, subDir), showWarnings = TRUE)

# For each network in dir
for(z in 1:length(redes))
{
  print(z); setwd(dir)
  Mat <- as.matrix(read.table(redes[z], sep="\t", header=FALSE)); dim(Mat)
  rotulo <- strsplit(redes[z], ".txt")[[1]][1]
  setwd(file.path(mainDir, subDir))
```

```
for(k in 1:n.run)
{
 M <- Mat; M[M>1] <- 1
 nA=nrow(M); nP=ncol(M); S=nA+nP; C <- sum(M)/(nA*nP)
 namesA <- c(sprintf("A%d", 1:nA)); rownames(M) <- namesA
 namesP <- c(sprintf("P%d", 1:nP)); colnames(M) <- namesP

 # Creates abundance table TAb
 TAb <- data.frame(name=c(namesA, namesP), abundance=rlnorm(S, lnorm.mean, lnorm.sd))
 TAb_print <- matrix(TAb[,2], ncol=1); rownames(TAb_print) <- TAb[,1]; colnames(TAb_print) <-
 paste("i=0_j=0")
 write.table(t(TAb_print), file=paste(rotulo, "_TAb_", k, ".txt", sep=""), sep="\t", row.names=TRUE,
 col.names=TRUE)

 # Creates probability matrix P proportional to TAb
 AP <- matrix(rep(TAb[TAb$name %in% namesA,2], nP), nA, nP, byrow=FALSE)
 PP <- matrix(rep(TAb[TAb$name %in% namesP,2], nA), nA, nP, byrow=TRUE)
 P <- (AP*PP)/sum(AP*PP)
 rownames(P) <- rownames(M); colnames(P) <- colnames(M)

 # Creates rewire rule matrix
 rewM <- rew.rule(M)
 if(rew.logic==TRUE)
 {
```

```
  write.table(rewM, file=paste(rotulo, "_rewM_", k, ".txt", sep=""), sep="\t", col.names=TRUE,
row.names=TRUE)
  TRew_print <- data.frame(i=numeric(0), j=numeric(0), Ins=character(0), From=character(0),
To=character(0))
  write.table(TRew_print, file=paste(rotulo, "_TRew_", k, ".txt", sep=""), sep="\t",
row.names=TRUE, col.names=TRUE)
}

# Creates square matrix MC (per capita effect of every interaction on abundance of all species)
Q2 <- Q4 <- M
Q2[which(Q2==1)] <- -abs(rnorm(sum(M), 0, strength))
Q4[which(Q4==1)] <- -abs(rnorm(sum(M), 0, strength))
if(m.type=="her"){Q4 <- -Q4}
Q1 <- mat.or.vec(nA, nA); Q3 <- mat.or.vec(nP, nP)
if(comp.type=="CE")
{
  sampled.omegas <- runif(nA*nA)
  Q1[,] <- realized.interactions <- sampled.omegas < C
  Q1[Q1==1] <- abs(rnorm(sum(as.numeric(realized.interactions)), 0, strength))
  sampled.omegas <- runif(nP*nP)
  Q3[,] <- realized.interactions <- sampled.omegas < C
  Q3[Q3==1] <- abs(rnorm(sum(as.numeric(realized.interactions)), 0, strength))
}
```

```
upper <- cbind(Q1, Q2); lower <- cbind(t(Q4), Q3)
MC <- rbind(upper, lower); rownames(MC) <- colnames(MC) <- c(namesA, namesP)
diag(MC) <- 1
write.table(MC, file=paste(rotulo, "_MC_", k, ".txt", sep=""), sep="\t", col.names=TRUE,
 row.names=TRUE)

# Calculates alpha (intrinsec growth rate)
alpha <- MC%*%TAb$abundance; colnames(alpha) <- "alpha"

# Creates network info table TNet
AVdom <- AV.dom(S, TAb, MC)
N <- M; N[N!=0] <- 1
NODF <- as.numeric(nestednodf(N, order = TRUE)[[3]][3])
Lap <- Lapla(M, nA, nP, transp=FALSE)
TNet <- data.frame(i=0,j=0, AVdom=AVdom, NODF=NODF, C=C, NComp=Lap[1], CSize=Lap[2], nLarge=Lap[3],
 CA=Lap[4], nA=nA, nP=nP)
write.table(TNet, file=paste(rotulo, "_TNet_", k, ".txt", sep=""), sep="\t", col.names=TRUE,
 row.names=FALSE)

# Begining of simulation
AllSpp <- TAb[,1]

# Creates species extinction table TEx
TEx <- data.frame(i=numeric(0), j=numeric(0), name=character(0), ext_type=character(0))
```

```
write.table(TEx, file=paste(rotulo, "_TEx_", k, ".txt", sep=""), sep="\t")
bs <- seq(1, S, 1)

##### BIG FOR - Primary Extinction #####
i <- 1
while(i %in% 1:length(bs))
{
  if(ext.target=="pla"){target <- colSums(M)}else{target <- rowSums(M)}
  if(ext.scen=="lowk")
  {
    spp.min.degree <- which(target==min(target))
    if(length(spp.min.degree)>1){min.degree <- sample(spp.min.degree,1)} else {
      min.degree <- spp.min.degree}
    ext <- TAb[TAb$name==names(min.degree),]
  } else if(ext.scen=="highk") {
    spp.max.degree <- which(target==max(target))
    if(length(spp.max.degree)>1){max.degree <- sample(spp.max.degree,1)} else {
      max.degree <- spp.max.degree}
    ext <- TAb[TAb$name==names(max.degree),]
  } else {ext <- TAb[TAb$name==sample(names(target), 1),]}
  TEx <- rbind(TEx, data.frame(i=i, j=999, name=ext[1], ext_type="primaria"))

  ##### SMALL FOR - Executes extinctions (Prim or Sec) #####
  j <- 1; cascade=TRUE; break.cascade=FALSE
```

```
while(cascade==TRUE)
{
  ext.df <- TEx
  write.table(ext.df, file=paste(rotulo, "_TEx_", k, ".txt", sep=""), sep="\t", append=TRUE,
  col.names=FALSE, row.names=FALSE)

  for(n in 1:nrow(ext.df))
  {
    if(dim(M)[1]==1 && rownames(M)==ext.df[n,3] | dim(M)[2]==1 && colnames(M)==ext.df[n,3])
    {
      times <- seq(0, 10, by = 1)
      y <- TAb$abundance
      parms <- list(alpha=alpha, MC=MC)
      equilibrium <- FALSE

      while(equilibrium==FALSE)
      {
        res <- ode(y, times, holl1, parms)
        equi_test <- apply(rbind(res[,-1]),2,diff)<0.001
        if(all(equi_test))
        {
          y[y<=0.001] <- 0
          final_times <- seq(0, 100, by = 1)
          final_res <- ode(y, final_times, holl1, parms)
```

```
    final_equi_test <- apply(rbind(res[,-1],final_res[41:50,-1]),2,diff)<0.001
  if(all(final_equi_test)){TAb$abundance <- final_res[nrow(final_res),-1]; equilibrium <-
  TRUE} else {
      y <- final_res[nrow(final_res),-1]
    }
  } else {y <- res[nrow(res),-1]}
}

if(any(TAb$abundance<=0.001))
{
  TAb[TAb$abundance<=0.001,2] <- 0; ZERO <- TRUE
} else {ZERO <- FALSE}

ExtSpp <- AllSpp[!(AllSpp %in% TAb[,1])]
ExtSpp <- data.frame(name=ExtSpp, abundance=rep(0, length(ExtSpp)))
TAb_print <- rbind(do.call(data.frame, TAb), ExtSpp)
TAb_print <- TAb_print[match(AllSpp, TAb_print[,1]),]
TAb_print <- t(TAb_print[,2]); rownames(TAb_print) <- paste("i=",i,"_j=",j,sep="")
write.table(TAb_print, file=paste(rotulo, "_TAb_", k, ".txt", sep=""), append=TRUE,
sep="\t", row.names = TRUE, col.names=FALSE)

print("Fim da simulacao")
i <- length(bs)
break.cascade=TRUE
```

```
 break
}

if(ext.df[n,3] %in% namesP)
{
 transp <- TRUE; M <- t(M); P <- t(P); rewM <- t(rewM)

 if(rew.logic==TRUE)
 {
  pol_set <- names(which(M[rownames(M)==ext.df[n,3],]!=0))

  # Step1: Selects which insects will rewire
  if(length(pol_set)!=0)
  {
   step1 <- which(M!=0,arr.ind=TRUE); rownames(step1) <- NULL; step1 <- data.frame(step1)
   step1$pl.name <- rownames(M)[step1$row]
   step1$an.name <- colnames(M)[step1$col]
   step1$Ab <- TAb$abundance[match(step1$pl.name, TAb$name)]
   step1[step1$pl.name==ext.df[n,3],5] <- 0

   # rewire probability
   rew_prob <- tapply(step1$Ab, step1$an.name, sum)/max(tapply(step1$Ab, step1$an.name,
   sum))
```

```
  if(any(rew_prob=="NaN")){name <- names(rew_prob); rew_prob[rew_prob=="NaN"] <- 0;
  names(rew_prob) <- name}
  rew_prob <- 1-rew_prob; rew_prob <- rew_prob[match(pol_set,names(rew_prob))]
  pol_set <- sample.coin(pol_set, rew_prob)
}

if(rew.choice=="random")
{
  rewire <- M; rewire[] <- 1; rewire <- rewire/sum(rewire)
  rewire <- rewire*rewM
} else {rewire <- P*rewM}

rewire[which(M==1)] <- 0
rewire <- matrix(rewire[,which(colnames(rewire) %in% pol_set)], nrow=nrow(rewire),
dimnames=list(rownames(rewire), colnames(rewire)[which(colnames(rewire) %in% pol_set)]))
rewire <- t(rewire)
rewire <- matrix(rewire[which(rowSums(rewire)!=0),], ncol=ncol(rewire),
dimnames=list(rownames(rewire)[which(rowSums(rewire)!=0)], colnames(rewire)))

# Step 2: Selects to which plant will insects rewire
if(nrow(rewire)!=0)
{
  for(m in 1:nrow(rewire))
  {
```

```
        rewire_m <- rewire[m,]
        pol <- rownames(rewire)[m]
        new_int <- sample(colnames(rewire), 1, prob = rewire_m/sum(rewire_m))
        M[new_int, pol] <- 1
        MC[pol, new_int] <- -abs(rnorm(length(new_int), 0, strength))
        MC[new_int, pol] <- -abs(rnorm(length(new_int), 0, strength));
        if(m.type=="her"){MC[new_int, pol] <- -MC[new_int, pol]}
        TRew_print <- data.frame(i=i, j=j, Ins=pol, From=ext.df[n,3], To=new_int)
        write.table(TRew_print, file=paste(rotulo, "_TRew_", k, ".txt", sep=""), sep="\t",
        append=TRUE, col.names=FALSE, row.names=FALSE)
      }
    }
  }
} else {transp <- "oklahoma"}

M <- matrix(M[-which(rownames(M)==ext.df[n,3]),], ncol=ncol(M), dimnames=list(rownames(M)[-
which(rownames(M)==ext.df[n,3])], colnames(M)))
P <- matrix(P[-which(rownames(P)==ext.df[n,3]),], ncol=ncol(P), dimnames=list(rownames(P)[-
which(rownames(P)==ext.df[n,3])], colnames(P)))
MC <- MC[-which(rownames(MC)==ext.df[n,3]), -which(colnames(MC)==ext.df[n,3])]
rewM <- matrix(rewM[-which(rownames(rewM)==ext.df[n,3]),], ncol=ncol(rewM),
dimnames=list(rownames(rewM)[-which(rownames(rewM)==ext.df[n,3])], colnames(rewM)))
TAb <- TAb[-which(TAb$name==factor(ext.df[n,3], levels=levels(TAb$name))),]
```

```
  alpha <- matrix(alpha[-which(rownames(alpha)==ext.df[n,3]),], ncol=1,
  dimnames=list(rownames(alpha)[-which(rownames(alpha)==ext.df[n,3])]))

  if(transp==TRUE && n!=nrow(ext.df)){M <- t(M); P <- t(P); rewM <- t(rewM)}
}
if(break.cascade==TRUE){break.cascade==FALSE; break}

# New abundances
times <- seq(0, 10, by = 1)
y <- TAb$abundance
parms <- list(alpha=alpha, MC=MC)
equilibrium <- FALSE

while(equilibrium==FALSE)
{
  res <- ode(y, times, holl1, parms)
  equi_test <- apply(rbind(res[,-1]),2,diff)<0.001
  if(all(equi_test))
  {
    y[y<=0.001] <- 0
    final_times <- seq(0, 100, by = 1)
    final_res <- ode(y, final_times, holl1, parms)
    final_equi_test <- apply(rbind(res[,-1],final_res[41:50,-1]),2,diff)<0.001
```

```
    if(all(final_equi_test)){TAb$abundance <- final_res[nrow(final_res),-1]; equilibrium <-
    TRUE} else {
      y <- final_res[nrow(final_res),-1]
    }
  } else {y <- res[nrow(res),-1]}
}

if(any(TAb$abundance<=0.001))
{
  TAb[TAb$abundance<=0.001,2] <- 0; ZERO <- TRUE
} else {ZERO <- FALSE}

ExtSpp <- AllSpp[!(AllSpp %in% TAb[,1])]
ExtSpp <- data.frame(name=ExtSpp, abundance=rep(0, length(ExtSpp)))
TAb_print <- rbind(do.call(data.frame, TAb), ExtSpp)
TAb_print <- TAb_print[match(AllSpp, TAb_print[,1]),]
TAb_print <- t(TAb_print[,2]); rownames(TAb_print) <- paste("i=",i,"_j=",j,sep="")
write.table(TAb_print, file=paste(rotulo, "_TAb_", k, ".txt", sep=""), append=TRUE, sep="\t",
row.names = TRUE, col.names=FALSE)

nA <- nrow(TAb[TAb$name %in% namesA,]); nP <- nrow(TAb[TAb$name %in% namesP,])
AP <- matrix(rep(TAb[TAb$name %in% namesA,2], nP), nA, nP, byrow=FALSE)
PP <- matrix(rep(TAb[TAb$name %in% namesP,2], nA), nA, nP, byrow=TRUE)
P <- (AP*PP)/sum(AP*PP); if(any(is.nan(P))){P[is.nan(P)] <- 0}
```

```
rownames(P) <- TAb[TAb$name %in% namesA,1]; colnames(P) <- TAb[TAb$name %in% namesP,1]
if(transp==TRUE) {P <- t(P)}

S=(dim(M)[1]+dim(M)[2]); AVdom <- AV.dom(S, TAb, MC)
Lap <- Lapla(M, nA, nP, transp)
if(dim(M)[1]>1 & dim(M)[2]>1)
{
  N <- M; N[N!=0] <- 1
  NODF <- as.numeric(nestednodf(N, order = TRUE)[[3]][3])
  C <- sum(M)/(dim(M)[1]*dim(M)[2])
} else {NODF <- 999; C <- 999}

if(transp==TRUE){num_pla <- dim(M)[1]; num_pol <- dim(M)[2]} else {num_pla <- dim(M)[2];
num_pol <- dim(M)[1]}
TNet <- data.frame(i=i, j=j, AVdom=AVdom, NODF=NODF, C=C, NComp=Lap[1], CSize=Lap[2],
nLarge=Lap[3], CA=Lap[4], nA=num_pol, nP=num_pla)
write.table(TNet, file=paste(rotulo, "_TNet_", k, ".txt", sep=""), sep="\t", append=TRUE,
col.names=FALSE, row.names=FALSE)

# Secondary extinctions (next round)
if(any(rowSums(M)==0) | any(colSums(M)==0) | ZERO==TRUE)
{
  ext_int <- c(names(c(which(rowSums(M)==0), which(colSums(M)==0))))
```

```
            TEx_int <- data.frame(i=rep(i, length(ext_int)), j=rep(j, length(ext_int)), name=ext_int,
            ext_type=rep("sec_int", length(ext_int)))
            if(m.type=="her"){if(length(grep("P", TEx_int$name))!=0){TEx_int <- TEx_int[-grep("P",
            TEx_int$name),]}}
            ext_ab <- TAb$name[TAb$abundance==0]
            TEx_ab <- data.frame(i=rep(i, length(ext_ab)), j=rep(j, length(ext_ab)), name=ext_ab,
            ext_type=rep("sec_ab", length(ext_ab)))
            TEx <- rbind(TEx_int, TEx_ab)
            if(any(duplicated(TEx$name))){TEx <- TEx[-which(duplicated(TEx$name)),]}
            if(nrow(TEx)==0){cascade=FALSE}else{cascade=TRUE}
          } else {TEx <- data.frame(); cascade=FALSE}

          # End of small for
          if(transp==TRUE) {M <- t(M); P <- t(P); rewM <- t(rewM); transp <- "oklahoma"}
          if(dim(M)[1]==1 && dim(M)[2]==1)
          {
            print("Fim da simulacao")
            i <- length(bs); break
          } j <- j+1
        } i <- i+1
      }
    }
  }
}
```

Chapter 5 Discussion

Understanding how the interactions between plants and insects can inform the recovery of natural systems is a considerable challenge, especially when aiming at the restoration of multiple trophic levels and of ecosystem services (Memmott, 2009; Harvey et al., 2017). This thesis assessed the role of plant communities in structuring insect communities, specifically pollinators, herbivores and parasitoids. In this final Discussion chapter, I will summarise the main findings from the three studies presented, explaining their relevance and highlighting their limitations along with questions to be addressed by future studies.

5.1 What has been learnt?

The pressure on agricultural systems to feed a large population (Godfray et al., 2010) together with the increasing awareness about the negative impacts of agricultural intensification on biodiversity (Allan et al., 2015), have generated an extensive debate on how farms should be managed (Green et al., 2005; Fischer et al., 2008; Hodgson et al., 2010; Phalan et al., 2011a). Some suggest that, with intensive management, agricultural systems could occupy a smaller area, increasing the amount of land that can be spared for the conservation of natural environments (Phalan et al., 2011b). Alternatively, others propose that land for food production and biodiversity conservation should be shared, stating that biodiversity friendly management benefits not only the conservation of species but should also increase productivity, as crops depend on ecosystem services (Carvalheiro et al., 2011; Tscharntke et al., 2012).

The dataset used in Chapter 2 on plant-herbivore-parasitoid networks from 10 pairs of organic and conventionally managed farms has contributed to this debate. The data were originally collected to investigate how different management regimes affect plant and insect diversity and the service of pest control (Gibson et al., 2007; Macfadyen et al., 2009a, 2009b, 2011a, 2011b). For instance, these studies showed that, despite the higher richness of parasitoids in organic farms, the percentage of parasitism (suggesting pest control) was similar between management regimes (Macfadyen et al., 2009a), while the temporal stability of pest control was in fact higher within organic farms (Macfadyen et al., 2009a, 2011a).

In Chapter 2, I looked at this dataset from a new perspective. Instead of comparing management regimes or looking at the community-level network structure of the farms, I focused on the role of individual plant species. Specifically, I searched for keystone plant resources for insects in two trophic levels, using a traditional method in network studies, network metrics combined with null models (Dalsgaard et al., 2013; Trøjelsgaard and Olesen, 2013; Gilarranz et al., 2015; Sebastián-González et al., 2015), but this time applied to the structure of species-level interactions. This allowed me to separate which plant species were "preferred" (eaten more than expected), "avoided" (eaten less than expected) or eaten in proportion to their abundance. Since identifying food preferences can be difficult (King et al., 2010; Ibanez et al., 2013), this method will facilitate the study of neutral versus niche processes on species interactions at the level of whole-communities. I was also able to describe how species roles varied across communities, to show that plant species had conserved network roles across trophic levels and that the phylogenetic context of the plant community has a non-negligible effect on the interactions between plant and herbivores.

Researchers have acknowledged the disproportional importance of particular plant species for insects and other animals that depend on them, calling these species "keystone resources" (Peres, 2000; Watson, 2001; Watson and Herring, 2012; Anthelme et al., 2014; Diaz-Martin et al., 2014). These studies usually focused on one or few species, and decided which plant species were keystone resources *a priori*, based on specialist knowledge. For instance, keystone plant resources for vertebrates were defined in terms of their temporal non-redundancy and reliability, and on the size and abundance of the fruits produced (Diaz-Martin et al., 2014). The keystone role of mistletoes had, in fact, been empirically tested with the systematic removal of mistletoes from replicate plots (Watson and Herring, 2012). In this thesis, I contributed to the study of keystone plant resources by using a replicable methodological procedure, and my results contribute to the studies of biodiversity in agricultural systems and to geographical variation on species network roles.

In Chapter 3, I used a field experiment to test whether plant species roles in pollination networks could be used to promote the recovery of pollinator communities. I found that plant species network roles in natural pollination systems were a good indicator of their attractiveness to pollinators. One possible explanation for the consistent network roles observed for plant species in this study, is the high level of generalisation in pollination systems (Waser et al., 1996; Fontaine et al., 2009), which can make plant-pollinator interactions flexible in space and time (Olesen et al., 2008; Petanidou et al., 2008; Carstensen et al., 2014; Trøjelsgaard et al., 2015). Therefore, the likely turnover in the available pool of pollinator species from the original to the experimental locations, did not appear to affect the number of pollinator species able to visit introduced plants in the experimental plots, explaining their conserved network roles across space. The observed results, also suggest that the central network roles of the selected plant species potentially reflect generalised morphologies - i.e. traits which allow visitation by insects with a range of morphologies (Fontaine et al., 2005; Stang et al., 2006) - allowing central species to be visited by more insect species than peripheral plants regardless of the location. Generalised morphologies, combined with high rewards, as reported in Chapter 3, could explain why some plant species consistently present central network roles across communities, although further work is needed to confirm this.

In the same experiment, I also assessed whether plant species with different network roles had contrasting effects on the visitation received by resident plant species. I did this by comparing the network roles of resident species in treatments in which no species (control), peripheral or central plant species had been introduced. My results suggest that, despite the higher attractiveness of central species to pollinators, their effect on resident plants was not more damaging than the introduction of peripheral plants, as introducing peripheral and central species produced quite similar results. Visitation, however, is only the first step to be assessed, and if the effect on resident plants had been further investigated, different results could have been found. For instance, in a field experiment, a community with open flowers produced more seeds per fruit when visited by pollinators with short than with long mouth parts. However, this difference was compensated at the stage of recruitment which was similar with both pollinator types (Fontaine et al., 2005). My study would have benefitted from a more detailed exploration of the reproductive success of resident plant species. I considered looking at the pollen transported from introduced to resident species to infer negative effects on reproductive success. However, due to the difficulty in separating pollen from different species of the same family based in morphology (Moore et al., 1991), this idea was discarded.

The results of my experimental study suggest that pollination function was higher in central than in peripheral or control subplots, since high richness and abundance of pollinators are usually associated with higher pollination function (Albrecht et al., 2012; Garibaldi et al., 2013). However, pollination function can be measured directly with phytometer experiments. For instance, Orford et al. (2016) investigated pollination function promoted by different pasture plant communities and management regimes, by measuring the fruit and seed set, and weight and quality of fruits of three phytometer species. Following a similar procedure, I ran a further experiment where I added strawberry plants (*Fragaria* x *ananassa*) to each subplot, but I found no difference in strawberry weight across treatments. I did not include this result in the thesis however, as it could simply reflect the small spatial scale of the study, rather than a lack of treatment effect.

Most restoration studies which target insects explore whether the insect community had been re-established in restored sites, by comparing the pollinator (Tarrant et al., 2013; Sant’Anna et al., 2014) or herbivore (Rowe and Holland, 2013; Borchard and Fartmann, 2014) community with the ones from reference or historical sites. However, few restoration studies investigate the effects of individual plant species on the next trophic levels (Moir et al., 2010; Barton et al., 2013; Schuldt and Scherer-Lorenzen, 2014), even if there is ample evidence that not all plant species are equally important for herbivores and pollinators (Pywell et al., 2003; Barton et al., 2013). In Chapters 2 and 3, I followed the approach of Pocock et al. (2012), who suggested that ecological networks could be used to identify keystone species for restoration purposes, as these would have a high potential of reaching positive results for biodiversity and ecosystem services. My work added to this research field as, in addition to identifying the keystone species, as done by Pocock et al. (2012), in Chapter 3 I then tested the plants’ network roles using a field experiment and found it to be consistent in new combinations of species.

In Chapter 4, instead of focusing on single plant species which are important for insects, I investigated how whole plant-insect communities collapse with the loss of plant species. I have achieved this by specifically addressing observed differences between pollination and herbivory systems. Despite having been intensively studied, pollination and herbivory networks are still mostly studied separately. Several studies on herbivory networks have focused on understanding its frequently modular structure (Prado and Lewinsohn, 2004; Cagnolo et al., 2011; Elias et al., 2013; Pires and Guimarães, 2013; López-Carretero et al., 2014; Bergamini et al., 2017). While pollination networks have been intensively studied in terms of structure (Dalsgaard et al., 2013) and robustness to species loss (Astegiano et al., 2015; Santamaría et al., 2016), they have also been considered in terms of their temporal and spatial dynamics (Petanidou et al., 2008; Carstensen et al., 2014) and macroecological patterns (Trøjelsgaard and Olesen, 2013). When the two types of network are studied together, then it is possible to compare and contrast them showing, for instance, that phylogenetic conservatism if higher for plants in herbivory than in pollination networks (Fontaine and Thébault, 2015), and that asymmetric specialisation is more frequent in pollination than in herbivory systems (Thébault and Fontaine, 2008).

Having studied herbivory and pollination separately in Chapters 2 and 3, in Chapter 4 I asked how differences in natural history and network structure affected the robustness of both systems. First, I was interested in the different population feedbacks associated with mutualisms and antagonisms, which I expected to have profound consequences for extinction cascades. Second, I looked at differences in generalisation between the two systems, as I expected this to affect rewiring opportunities. There are several challenges involved in comparing networks of different interaction types (Thébault and Fontaine, 2008; Dáttilo et al., 2016), since the organisms involved in the interaction might vary in taxonomic resolution, the interaction could vary in the degree of intimacy and interactions may be sampled using different methods. All these factors are likely to affect network structure and interaction frequencies. By (i) focusing on similar groups in both types of network (plants and insects), (ii) using a design in which comparisons were made between scenarios, using the same network, instead of between networks, and (ii) adding simulated information strategically to avoid comparisons which could be misleading (e.g. species abundance), I was able to compare the robustness of both systems. This framework allowed me to avoid differences in network size, sampling methods and interaction strengths between interaction types, so that features of interest could then be isolated.

5.2 Future directions

The study of ecological networks can provide data which is very pertinent for the practice of conservation and ecological restoration. In this section I discuss how the data collection, including the one from my own field experiment, could be improved in future studies so that ecological theory and practice can become more aligned.

5.2.1 The identification of keystone resource plant species in plant-insect food webs

An obvious improvement to the study presented in Chapter 2 would be to have more detailed plant abundance data, and to have independently collected plant-herbivore and plant-parasitoid interactions. With this extra level of detail, the identification of keystone resources for both groups of insects would likely be more accurate. I am aware, however, of the challenges involved in adding these refinements to the collection of such intensive and well replicated datasets (in the original farm project the data collection already involved two years of field work, two full time staff and two seasonal field assistants). A further limitation is the short temporal scale of the study, as the data was collected over two years, which I then combined into one single dataset. In reality, studies involving field data at the community level with good replication will frequently present these sort of limitations, i.e. information will be less detailed than single-site studies. Nevertheless, both study types are equally important as they address different types of questions, single-site studies will provide detailed mechanistic explanations about the study systems (Danieli-Silva et al., 2012; Elias et al., 2013), while replicate and broad scale studies are the best way to identify patterns (Macfadyen et al., 2011b; Trøjelsgaard and Olesen, 2013).

Despite the challenges involved, data collected from longer temporal and larger spatial scales is needed if we aim to truly understand patterns and processes at the community level (Lawton, 1999). The reward for this can be high, for example, with a 8-year dataset on plant-pollinator interactions following hedgerow restoration, researchers were able to show how these communities reorganise over time, how reorganisation affected network structure and which network roles were occupied by the most persistent species across time (Ponisio et al., 2017). In reality, temporal and spatial scales are system dependant and here a careful choice of study system is helpful – for example it is logistically simpler to replicate an experimental system on hedgerow restoration than on woodland restoration.

5.2.2 Plant species roles in pollination networks: an experimental approach.

I sampled pollinator abundance and richness, and plant-pollinator interactions to test whether different plant treatments, central vs. peripheral plant species, attract a higher diversity of pollinators and to infer pollination function. Another way to measure diversity, however, which is closely connected with ecosystem functioning, is to measure the functional diversity (Cadotte et al., 2011). With data on plant species traits (e.g. colour, shape of floral tube, type of reward) and pollinator species traits (e.g. size, length of proboscis, phenology) I could have tested: a) whether central plants attract a higher functional diversity of pollinators, b) whether the functional diversity of pollinators was a response to the functional diversity of plants (instead of their network role) and, c) what is the effect of introducing functionally similar or dissimilar species over the community of resident plants and pollinators. Additionally, instead of inferring pollination function, I could have directly measured it using phytometer experiments, or by measuring seed production or seedling establishment of introduced and resident species (Fontaine et al., 2005; Brosi and Briggs, 2013). I suggest both improvements to be made in future field experiments on species network roles and alternative restoration treatments.

Another important point to be made is that for species network roles to be successfully applied in restoration or habitat creation schemes, other features of the selected plant species should be considered. Examples are: what are effort and cost required to manage these species, which species could be easily grown from seed and therefore could be added to seed mixes, and what is the phenology of the selected plants (Russo et al., 2013). For instance, plant species mixes encompassing a wide phenology would provide resources for pollinators for the whole season, and could be designed to provide for pollinators in periods of higher vulnerability (Kudo, 2014). Furthermore, with another year of experimentation I could have assessed how the community composition is likely to progress, for instance, whether central species are more likely to outcompete resident plants than peripheral species.

5.2.3 *The effect of generalisation and population feedbacks on the robustness of plant-insect assemblages: a comparison of pollination and herbivory networks*

An important limitation of the study presented in Chapter 4 is the absence of competitive interactions between plant species and between insect species. However, since the model was built to include such competitive interactions at a future stage, then plant species host to both herbivores and pollinators could compete for resources such as space, water and soil minerals. Resource competition between insect herbivores is thought to be low as plants are an abundant resource (Hairston et al., 1960; Tack et al., 2009; but see Denno et al., 1995; Kaplan and Denno, 2007). Insect pollinators, however, compete for flower resources (Goulson and Sparrow, 2009; Brosi and Briggs, 2013) and plants can compete for pollinators (Jakobsson et al., 2009). Apparent competition between plants is also a possibility in herbivory systems (van Veen et al., 2006). Therefore, the next step of this study is to include competition scenarios to explore how they affect robustness in these systems.

My robustness estimates are based on a number of assumptions about species abundance distributions, about the strength of interactions between species (*i.e.* the demographic effect of one species on another), and about the frequency of rewiring opportunities in each interaction type. These standardised assumptions between the two interactions types is what enables the two types of networks to be compared. However, increasing information on the natural history of species interactions is likely to produce increasingly realistic results (Traveset et al., 2017; Ramos–Jiliberto et al., 2018). For instance, if collection data is standardised between interaction types (*e.g.* similar sampling effort, standardised protocols on whether or not observed insects are removed or returned to the community) information on the interaction frequency could be made comparable between interactions types. With comparable interaction frequency information, field data on insect abundance could be used (rather than generating abundance data as was done in Chapter 4). Similarly, with increasing data availability on species traits, phenology and distribution (Morales-Castilla et al., 2015), more realistic rewiring opportunities for different species and interactions could be incorporated in future simulation studies. However, as detailed empirical data on species traits and on interaction strengths and plasticity at the community level is still very limited and I believe theoretical studies such as the one presented in Chapter 4 will continue to be relevant and informative for some time yet.

5.3 Final considerations

Throughout this thesis, I have repeatedly highlighted the degree of uncertainty associated with ecological restoration. Restoration schemes can end up with an unexpected composition of species and with lower levels of ecosystem functioning and services than reference communities (Henson et al., 2009; Audino et al., 2014; Barak et al., 2017). To address these uncertainties, it has been suggested that a mechanistic understanding of how communities assemble and persist and why some species more important community roles than others (*e.g.* keystones) should be pursed and incorporated into restoration practice (Suding, 2011; Brudvig, 2017). Aiming to contribute to this mechanistic understanding, in the second chapter of this thesis I looked for an association between plants species' local importance (*i.e. strength*) and relatedness to the remaining plant community. A mechanistic understanding of species roles and functioning should greatly improve the communication between ecological theory and practice. For instance, had a strong association between plant species' *strength* and relatedness been found, practitioners could be better advised on how to assemble plant communities with a focus on herbivores and parasitoids with a higher degree of certainty regarding the outcome.

When I experimentally tested, in the following chapter, whether plant species' centrality could predict their importance for pollinators, I favoured a phenomenological approach instead. A mechanistic approach would also have involved finding the features (*e.g.* traits) associated with plant species' centrality, so that species presenting those features could be used to increase the certainty of pollinator recovery. Despite the phenomenological approach used, my field experiment showed that central plant species attracted more pollinators than peripheral species, suggesting that plant species' centrality could serve as a shortcut to a mechanistic understanding, still benefiting the recovery of pollinator communities.

The high complexity of ecological communities hampers our complete understanding of how communities should be restored to better function and persist. Studies performed in academia can sometimes present spatial and temporal limitations, so that the practice of ecological restoration also feeds from these incomplete assessments. As it is not always straightforward to extrapolate results from smaller to larger scales, scientists can occasionally distance themselves from the debate on how to convert ecological theory into practice. For instance, one could argue that results from the second chapter of this thesis apply to a limited geographical range (southwest, UK), or that it is not certain that central plant species would more attractive to pollinators than peripheral ones had my field experiment been extended for another year. Studies performed at larger scales do indeed produced more general findings, but small-scale studies should still be communicated to practitioners and policy makers together with associated uncertainties and with strategies on how to deal with those uncertainties. To deal with restoration uncertainty, one suggestion would be to create heterogeneous restoration strategies (Benton et al., 2003; Baer et al., 2005; Suding, 2011; but see Palmer et al., 2010).

Heterogeneity allows the long-term persistence of systems at other levels of biological organisation (Agashe, 2009), so that heterogeneous restoration strategies (*e.g.* spatial heterogeneity in species composition or genotypes, and temporal heterogeneity in disturbance frequency) might result in long term persistence of restored ecosystems.

Focusing on the results presented in this thesis, a few suggestions to practitioners could be made. Despite the observed variation in plant species roles across farms, four species frequently acted as keystone resources for herbivores: *Corylus avellana* (common hazel), *Crataegus monogyna* (common hawthorn), *Prunus spinosa* (blackthorn) and *Urtica dioica* (common nettle). And if involved in more than 19000 herbivore observations in the dataset, these plant species were not associated to any of the crop pest species listed by the British Crop Production Council. For parasitoids, the most consistent keystone species were *Corylus avellana*, and *Ranunculus* species, specially *Ranunculus repens*. Together these species were associated to more than 50 parasitoid species. It can also be suggested that previously collected pollination networks should be used to identify plant species frequently playing central network roles, as these species could be used to increase pollinator diversity in pollinator poor sites. Despite not being the focus of my investigation, it could also be mentioned that four (out of five) central plant species used in the field experiment belonged to the Asteraceae family, while none of peripheral species did. This observation suggests that some shared aspect between Asteraceae species might explain their consistent central roles in pollination systems.

Scientists have been quantifying the importance of biodiversity for ecosystem function and services (Srivastava et al., 2012; Winfree et al., 2015; Soliveres et al., 2016) together with the fragility of ecological systems to human disturbance (Dirzo et al., 2014; Allan et al., 2015; Oliver et al., 2015). As the amount of threatened habitats continues to be high (Hansen et al., 2013), clear guidelines on how to manage ecosystems under different levels of degradation need to be developed (Tambosi et al., 2014). Ecological restoration is an extremely important strategy to recover highly or completely degraded systems (Chazdon, 2008; Forup et al., 2008; Fuentes-Montemayor et al., 2015). Ecological restoration has also been shown to be beneficial when dealing with invasive species (Heleno et al., 2010; Kaiser-Bunbury et al., 2017) or lost ecological functions. For instance, when important ecological functions have been lost and there are no locally occurring species able to execute that function, the introduction of new species into the community can be a good (Griffiths et al., 2011; Seddon et al., 2014; Svenning et al., 2016), but risky restoration strategy (Rubenstein et al., 2006; Butterfield et al., 2017). Under several circumstances, however, restoration should not be regarded as the first resource.

In ecosystems where the level of human degradation is low, and which harbours a high biodiversity and endemism, conservation should be the priority (Wiens and Hobbs, 2015). Protected areas can harbour higher species richness and abundance than unprotected areas (Gray et al., 2016), making a strong case for setting separate areas with the sole focus on conservation. An additional advantage of conserving existing areas is that its levels of biodiversity, ecosystem functioning, and the presence of rare and endemic species are known, while there is no guarantee that any of these properties could be restored or recreated anywhere, as an attempt to offset the degradation of existing areas (Maron et al., 2010; Sonter et al., 2014). As restored sites have frequently been observed to harbour lower biodiversity and functioning than reference areas even after long periods since restoration (Audino et al., 2014), offsetting should be treated as a second option to conservation whenever possible. Ultimately, we should be aiming at mitigating the causes of habitat degradation and, for that, we need to promote behavioural change of individuals and policy makers (Cowling, 2014).

5.4 Concluding remarks

Natural systems are subject to and the result of a combination forces, both deterministic and probabilistic, making the study of ecological communities a very exciting and somewhat challenging task. The outcome of these multiple forces are complex systems which require the combination of multiple approaches to be truly understood. In this thesis I used both field based and theoretical approaches to explore the role of plants in structuring ecological communities. While both approaches have their limitations, in combination they inform each other and provide a powerful strategy to address issues for both pure and applied ecology.

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