Impacts of the invasive alien *Heracleum mantegazzianum* on native plant-pollinator interactions

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Contents

1. Summary

Pollination is one of the most essential ecosystems services, it is crucial to the reproduction of most flowering plants, and plays an important role in crop production. This fundamental ecosystem service is threatened by the ongoing global change, which includes climatic change, changes in land use, and the introduction and spread of alien species. Alien plants may have a negative impact on native plants when they compete for pollination services. Effects of competition for pollinators may have an impact on the quantity as well as the quality of pollination. The quantity of pollination adresses the number of visits a plant receives, while the quality of pollination describes the number of transferred pollen grains. The complex interactions of these factors determines the outcome of seed set for a plant. Ultimately, a negtive affection of these components may lead to a reduction of plant fitness. The fact that alien plants often have large showy inflorescences as they were commonly introduced as ornamentals makes them potentially superior competitors. Alien plants have been shown to affect the quantity as well as the quality of co-flowering native species. Furthermore, it has to be taken into consideration that species do not interact in a vacuum, plants and pollinators form a mutualistic interaction network. While there is evidence that alien plants are well-integrated into interaction networks, there is still a demand to know if this integration translates into effects on the quality of pollination and reproductive success of a community of co-flowering plants.

Aim of this thesis was to scrutinize the impacts of the alien invasive plant *Heracleum mantegazzianum* on native plant-pollinator systems. Due to its tall growth and large compound inflorescences *H. mantegazzianum* definitively has the potential to affect the pollination of native plants. In order to find out about the pollinators of the invader a field study was conducted, which included observation of flowers and measurements of pollinator efficiency. The same measurements were made for the native closely related *Heracleum sphondylium* in order to detect an overlap of pollinator faunas. An experimental garden setup was used in order to determine the effect of the invader on insect visitation and set seed of an array of co-flowering plants. Additionally, I used a network approach to explore the impact of *H. mantegazzianum* on two- and one-mode network parameters. Furthermore, the transport of alien pollen was quantified and network parameters of networks based on visitation, interaction and pollen transfer were compared.

Results show that the large inflorescences of the invader were highly attractive to a broad range of insects, yet there were just a few insects truly important pollinators, most of all the honeybee *Apis mellifera*. There was low potential for competition between the two *Heracleum*-species, yet the invader might have a potential to influence native plant-pollinator interactions due to its association with the super-generalist *A. mellifera*. However, results of the experimental garden revealed that visitation rates of co-flowering plants were (although statistically non-significant) generally enhanced, and the effect on seed set was neutral. *H. mantegazzianum* was found not only to be well integrated, but dominant in invaded visitation networks. Nevertheless, in combination with the results for seed set it was concluded that the impact of the invader was not detrimental to the invaded plant-pollinator system. Additionally, I could show that, while flower visitors of *H. mantegazzianum* were less constant than on other plants and there were plant-to-plant interactions for all co-flowering plants, still little alien pollen was transferred. Nevertheless, there was a potentially competitive effect of conspecific pollen loss depending on the plant species. Network analysis showed that the alien plant was only dominant in terms of visitation but not in terms of interspecific pollen potentially transferred. This highlights that both, the quantity and the quality component, need to be assessed to create an adequate estimate on the impact of an invader on plant-pollinator systems.

2. General Introduction

2.1 Pollination by animals – Nature's service industries

The manifold adaptions of plants and animals to the mutualism pollination provide some of the most remarkable phenomena in nature. Pollination by animals has sparked the interest of many scientists and its importance as ecosystem function has long been recognized (Sprengel 1793, Darwin 1876, Müller 1873, Knuth 1898, Faegri and van der Pijl 1971, Proctor et al. 1996). The vast majority of angiosperms (87.5%) relies on pollination by animals (Ollerton et al. 2011). For cultivated plants the numbers that need biotic vectors in order to be fertilized are 84% in Europe (Wilock and Neiland 2002) and 35% worldwide (Klein et al. 2007). Therefore, pollination does not only sustain ecosystem functioning, but is an example where nature provides valuable services to mankind. The fact that this ecosystem service is threatened by human activities (Kearns et al. 1998) makes pollination an important field of ecological research, today. In order to understand how pollination is affected by a changing planet it is necessary to look at the relationship of plants and their pollinators in more detail. Plants as sessile organisms are dependent on vectors to promote the movement of male gametes to their female counterparts. While there are several mechanisms that allow plants to set seed without pollen transfer, sexual reproduction is essential for the long-term sustainability of plant populations (Wilcock and Neiland 2002). Furthermore, outcrossing promotes parental fitness due to inbreeding effects caused by selfing (Husband and Schemske 1996). Vectors that carry pollen can be abiotic like wind or water, but in many cases plants employ animals as their pollen vectors (see above). From the plant's perspective it is favorable to optimize the number of pollen grains that are received (female fitness) as well as the number of pollen grains transported to other conspecific individuals (male fitness). The number of visiting animals as well as the number of pollen grains an animal is able to transfer are both important factors for an optimal pollination. These two factors are also addressed as the quantity and quality component of pollination (Herrera 1987, 1989). Moreover, reproductive success is not only determined by the interactions of a plant and its pollinators. Plants may compete for pollination services when they share pollinators (e.g. Robertson 1895, Hocking 1968, Levin and Anderson 1970, Mosquin 1970). In contrast to competition for abiotic resources like light or nutrients competition for pollination acts over long distances. Furthermore, it affects the reproduction of competing plants directly; an impact on pollination may translate into an impact on plant fitness. Both components of pollination, quality and quantity, can be negatively affected by the presence of co-flowering competitors. An impact on the quantity component manifests itself in a reduction of visitation rates for a plant in the presence of a superior competitor as animals are lured to the more promising rewards. The impacts on quality component are a bit more complex: Pollinator sharing may lead to the deposition of heterospecific pollen on plants receptive organs and to the loss of conspecific pollen to other plants. The deposition of heterospecific pollen may lead to clogging of stigmas, allelopathic inhibition of pollen germination, and usurpation of ovules (Waser and Fugate 1986, Galen and Gregory 1989, Morales and Traveset 2008 and references cited therein). Heterospecific pollen deposition has an impact on the female fitness, while the loss of pollen to other plants negatively affects male fitness, when pollen grains are "wrongly" transferred to other plants (pollen wastage) (Waser 1986), reducing the number of pollen transported to other conspecific plants (Campbell and Motten 1985). Studies have shown that this may lead to a negative impact on seed set (Waser and Fugate 1986, Caruso and Alfaro 2000). Besides a reduction of seed set this may also affect outcrossing negatively (Campbell 1985, Bell et al. 2005). The impact of a competing plant species does not necessarily manifest itself in both components of pollination in the same way. Highly attractive plants may increase the visitation rates of co-flowering species (Thomson 1978, Johnson et al. 2003, Moeller 2004, Ghazoul 2006). However, this so-called magnet species effect may increase heterospecific pollen transfer (Rathcke 1983, Morales and Traveset 2008), when pollinators frequently switch between the magnet species and co-flowering plants. Nevertheless, the relationship and the evolution of plant-animal interaction are not entirely determined by achieving optimal fertilization of the plants, but also by the demands of foraging animals. The floral rewards that plants offer reach from pollen and nectar to oil and resins (Faegri and van der Pijl 1979, Proctor et al. 1996). As diverse as the rewards offered are the animals, which are used as pollinators, including: insects, birds, bats, and small mammals (Buchmann and Nabhan 1997). However, most pollination is conducted by insects foraging for nectar and pollen (Richards 1997). These animals need floral resources for themselves or in order to feed their larvae. The fact that animals are highly mobile adds further to the complexity of the interaction of plants and animals. An insect foraging on flowers strives to maximize its energy intake per foraging bout, while plants must provide ample rewards to encourage floral visitors on the one hand. On the other hand a surplus of rewards would cause less movement between plants and thus less outcrossing or even robbing of pollen and nectar, which would be a waste of resources. These "energetics of pollination" influence the evolution of plants and their floral visitors (Heinrich 1975).

Over the course of evolution plants have developed many mechanisms to optimize both quantity and quality of pollination as well as animals have adapted to optimally exploit floral resources. In some cases this evolution lead to extreme forms of specialization, for instance in yuccas (Pellmyr et al. 1996) or figs (Machado et al. 2001, Weiblen et al. 2000). Nevertheless, most plants have a rather generalized mode of pollination (Waser et al. 1996, but see Johnson and Steiner 2000) and use less extraordinary strategies to enhance the quantity and quality of pollen transfer. These strategies include mechanical isolation (Grant 1994) (e.g. the deposition of pollen on different parts of pollinators' bodies), differences in phenology (Rathcke 1988, Sih and Baltus 1987, Macior 1971) or even differences in timing of pollen release (Stone et al. 1998). Animals have developed strategies to forage optimally on the given floral resources and efficiently handle flowers with different morphologies. One strategy to optimize foraging behavior is flower constancy, the capacity of insects to restrict visits to a certain plant species and skip other rewarding resources (Waser 1986, Chittka et al. 1999). The most prominent example for flower constant behavior are honeybees (Grant 1950, Free 1963). Bumblebees exhibit flower constancy as well (Free 1970) and it was also found for syrphids (Goulson and Wright 1998). Moreover, flower constant pollinators are able to adapt their behavior depending on plant density (Kunin 1997, Bosch and Waser 2001) as well as pollinator density (Fontaine et al. 2008). In general, plants profit from flower constant pollinators, nevertheless pollinators may also developed strategies that are to the plants' disadvantage such as robbing of floral resources (Bronstein 2001).

Despite all adaptions pollen limitation, which means a shortage of received pollen grains, is not uncommon for plant populations (Burd 1994, Larson and Barett 2000, Ashman et al. 2004). Fluctuations in pollinator abundance and behavior as well as the interference with other plants may lead to pollination failure (Wilcock and Neiland 2002). Human-made global change, which comprises invasions of alien organisms, may bring about new challenges for plants competing for pollinators (Mitchell et al. 2009).

2.2 Alien plant invasions - When beauties become beasts

The human impact on ecosystems alters the functioning of these systems on a global scale (Vitoussek et al. 1997). This global change is threat to the persistence of biodiversity and ecosystem functioning. Along with the change of land use and global warming go invasions of alien organisms (Vitousek et al. 1996). Biological invasions are considered one of the biggest threats to biodiversity (Mack et al. 2000). Furthermore, the spread of invasive species is facilitated by human made disturbances like over-grazing, fires or soil disturbance (Hobbs and Huenneke 1992). Invasions are not only detrimental in ecological terms, but they also cause significant economic losses (Pimentel et al. 2005) and are a potential threat for human health and well-being (Soulé 1992, Pejchar and Mooney 2009). Alien plants are often found to have negative effects on native species, when they compete for resources (Levine et al. 2003). Furthermore, they reduce species richness of invaded plant communities (Gaertner et al. 2009, Hejda et al. 2009). Yet the impact of invasive species of may reach even farther, alien plants are able to change soil nutrient cycles (Ehrenfeld 2003, 2010) and thus alter ecosystem functioning. Besides effects of alien plants due to competition for abiotic resources, non-native species may as well have an impact on species interactions like pollination (Tylianakis et al. 2008). Plant pollinator systems are threatened by the loss of biodiversity, as functional biodiversity is important for their persistence (Fontaine et al. 2006). Climate change and alien plants lead to interactions that further threaten plant pollinator interactions (Schweiger et al. 2010). An example for such an effect is the decline of wild pollinator faunas due to loss of biodiversity caused by an invasive plant (Moron et al. 2009). Besides such an indirect impact there is also the possibility that alien plants compete directly with natives for pollination services. This is of course dependent on the mode of reproduction of the alien plants. In theory, plants that are autogamous or unspecialized in their pollination are thought to be more invasive (Baker 1965, 1974). Specialized plants should have a low chance of encountering their required interaction partners in a new environment. Nevertheless, there are just a few cases were a lack of suitable pollinators limits seed set for alien plants (Richardson et al. 2000 and references therein). There is even evidence that plants show invasiveness despite a specialized pollination system (Rodger et al. 2010). When alien plants co-opt the services of native pollinators (e.g. Stout et al. 2006) the possibility of competition for pollinators with co-flowering native species arises. Sharing of pollinators may lead to a disruption of evolved mutualisms between native plants and their pollinators (Traveset and Richardson 2006, Bjerknes et al. 2007).

Additionally, alien plants often possess large and showy, because they were often introduced as ornamentals (Stout and Morales 2009). As the size of inflorescences often determines the attractiveness to visiting insects (Campbell 1989, Ohara and Higashi 1994, Conner and Rush 1996), alien plants have the distinct potential to act as superior competitors and bring about negative effects for native species. Both components of pollination may be affected by alien plants. Chittka and Schürkens (2001) found a reduction of visitation rates for the native *Stachys palustris* caused by the invasive *Impatiens glandulifera*. The alien *Lythrum salicaria* was found to have a negative effect on seed set of a native congener due to a reduction of visitation rates and an effect of heterospecific pollen transfer (Brown and Mitchell 2001, Brown et al. 2002). In a field study the invasive *Euphorbia esula* was found to reduce the deposition of conspecific pollen on stigmas of co-flowering native species (Larson et al. 2006). There are also examples where the effect of alien plants on pollination of native species was neutral or positive (Moragues and Traveset 2005, Totland et al. 2006, Bartomeus et al. 2008b). Alien plants may even become a valuable food source for native pollinators (Tepedino et al. 2008). Nevertheless, a recent meta-analysis found a predominantly negative pollinator-mediated effect of invasive species (Morales and Traveset 2009). There is need for further research on this subject for two reasons. The first is that pollination is, for reasons pointed out above, a prime function of plant reproduction and ecosystem maintenance. The second is that since the processes, which drive global change, like the growth of human population and the increase of traffic due to globalization, are likely to intensify, it is plausible that the threat to biodiversity by invasions will also increase. Indeed, numbers of alien species are increasing in Europe and North America (Pimentel et al. 2005, Lambdon et al. 2008). Among these is the invasive problematic weed *Heracleum mantegazzianum*, to which this study is dedicated.

2.2.1 Study species *Heracleum mantegazzianum* – Blossoming public enemy

H. mantegazzianum is characterized by its tall growth, which can be up to 5 m, and its large, white inflorescences, which are compound umbels containing up to 80 000 flowers (Tiley et al. 1996). This plant is regarded as one of the most obnoxious invasive weeds in Europe (Pyšek et al. 1998). The origin of *H. mantegazzianum* is the Caucasus. Once introduced as ornamental and honey plant it escaped gardens and parks and spread rapidly in Central Europe (Pyšek and Pyšek 1995), the British Isles (Tiley et al. 1996), and parts of North America (Page et al. 2006). Besides the potential to threat native plant communities (Pyšek and Pyšek 1995, Thiele and

Otte 2008), *H. mantegazzianum* is a risk to human health as some of its contents, furanocoumarins, are phototoxic, causing severe burns in combination with sunlight (Drever and Hunter 1970). Furthermore, risk of erosion on invaded riverbanks is enhanced due to the fact that the plant is monocarpic (Tiley et al. 1996, Caffrey 1999). Today, there is plenty information about *H. mantegazzianum*, ranging from population life-cycle reproductive behavior to phenology or genetic analyses (Perglová 2007, Pergl et al. 2006, Hüls et al. 2007, Walker et al. 2003, Jahodová et al. 2007). However, information on insect visitation of *H. mantegazzianum* is limited to one study (Grace and Nelson 1981) and there is no information on which animals provide pollination to this plant. *H. mantegazzianum* is nevertheless dependent on pollinators to achieve a considerable seed-set (Perglová 2007). Due to the sheer size of its inflorescences, mass flowering (Perglová 2007) and the presumably generalist mode of pollination potentially interacting with many native flower visiting species *H. mantegazzianum* has the potential to affect native plant pollination. *Heracleum* species are known as cornucopian species (Corbet 2006) that are highly attractive to visiting insects and likely to cause competition for co-flowering plants (Mosquin 1971).

Plate 2.1: Typical stand of *Heracleum mantegazzianum* on a meadow in Bielefeld

2.3 Ecological Networks – Exploring complexity

Species do not interact in a vacuum, but they are linked to other species by interactions. These interactions can be antagonistic like predation and parasitism or mutualistic like seed dispersal and pollination. Interactions of plants and their pollinators can be described as mutualistic interaction networks (Bascompte and Jordano 2007). These networks are mathematically based on graph theory, which describes the pairwise interactions of a set of objects. The interactions in a network can be directed or undirected. Foodwebs, where one species gets eaten by another have directed interactions, while mutualisms, like plant-pollinator or plant-seed-disperser, are undirected (Jordano 1987). Furthermore, the frequency interactions can be included in a network, these networks are called weighted or quantitative networks. Another distinction between networks is, whether they are one-mode or two-mode. In a one-mode network there is only one group of interaction partners. In a two-mode network the interaction partners from two group and interact only with members of the opposite group (Borgatti and Everett 1997). Plant-pollinator networks are two-mode, as they consist of two groups, the plants and the pollinators. Nevertheless, two-mode networks are often projected into one-mode networks, (Olesen et al. 2006), in order to find effects between members of a certain group. In case of a two-mode plant-pollinator network this leads to a one-mode plant and a one-mode pollinator network. These networks can be used to interpret competitive effects between species, for instance plant species competing for pollination services. There are some features that are typical for mutualistic interaction networks. They are heterogeneous, which means that most species have few links, some have more connections than expected by chance. They are determined by weak asymmetric links among species, which means generalist animals interact with specialist plants and vice versa (Bascompte and Jordano 2007). Furthermore, they are often highly nested (Bascompte et al. 2003). Nestedness describes the fact that interaction partners of specialized species form a sub-set of the interaction partners of generalized species. A good example for nestedness is the composition of island communities. When there are several islands with different distances to the mainland, one would expect the island closest to the mainland to hold the most species. When the island farther from the mainland contain fewer species, but these are also present in the nearer islands, then the island community shows nestedness. Nestedness is often used to describe pollination networks, in this study it is relevant because it can be perceived as a measure of order in a system (Jordano et al. 2006), a possible impact of an invasive species could be to decrease nestedness and create a less ordered system. Another index often used to describe networks is connectance, which is the proportion of realized links to possible links. In a plant-pollinator network it is the sum of all occurring plant-pollinator interactions divided by the product of the numbers of plant and animal species (Dunne et al. 2002). The impact of an alien species could lead to lower connectance when the alien plant usurps links from native species (Aizen et al. 2008). While nestedness and connectance are properties of two-mode networks, there are also measurements available to describe one-mode networks, such as centrality scores. Originally centrality scores were used in social science to explore networks of human communication (Freeman 1979). Recently, they were applied to ecological networks in order to describe the potential of plants to influence other plants via pollinators and to find keystone species or hubs (Martín González et al. 2010). The first is expressed as closeness centrality, which is defined as the inverse sum of shortest distances from one node to all the other nodes. Plants with a high closeness might cause effects that easily "ripple" through the whole network. The second is expressed as betweenness. Betweenness describes the property of some node to connect parts of a network that would be otherwise unconnected and is defined on how many shortest paths connecting two other nodes a node lies. Plants with high betweenness form keystone species important for the overall function and stability of networks.

In order to understand the impacts of an alien plant on a native plant-pollinator system correctly it is necessary to use a network-based approach. A start has been made in discerning the effect of aliens on plant pollinator networks a decade ago (Memmott and Waser 2002, Olesen et al. 2002) and other studies followed. Still, this field of research is just fledgling and there is need for further studies (Burkle and Alarcón 2011). So far, studies found that alien plants were well integrated into mutualistic networks by generalist pollinators (Vilà et al. 2009, Padrón 2009). In some cases aliens caused a detrimental effect on mutualistic interactions of native plants and pollinators (Aizen et al. 2008). Nevertheless, most studies that use a network approach are based on visitation data, which of course simplifies plant-pollinator interactions and the interplay of the different components. In the few cases were a measurement of pollen transportation by insects was included alien plants often dominated the plant-pollinator networks they invaded (Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008a). Yet unknown is, if the effect of an alien plant on plant-pollinator interactions can be perceived in the quantity and quality component of pollination as well as the reproductive success.

2.4 Aims and objectives

Aim of this study is to scrutinize the impact of the alien invasive plant *H. mantegazzianum* on native plant-pollinator interactions. The first step was to determine the pollinators of the invader. For this purpose I conducted a field study, which included observation of flowers and measurements of pollinator efficiency. The same measurements were made for the native closely related *Heracleum sphondylium* as to detect an overlap of pollinator faunas. Furthermore, the degree of ecological specialization for each species was determined in order to estimate the impact of the alien plant on native plant-pollinator systems. The results are presented in the third chapter of this thesis. Furthermore, the impact of *H. mantegazzianum* on the reproductive success of a plant community were explored. This was done by an experimental garden setup. Additionally, I used a network approach to explore the impact of *H. mantegazzianum* on two- and one-mode network parameters. The results are presented in the fourth chapter of this thesis. Finally, I explored the impacts of of *H. mantegazzianum* on the behavior of pollinators and pollen transfer in a plant community and the influence of the alien plant on pollen transfer networks. For this purpose I used an experimental garden setup in order to test, whether floral constancy limits alien pollen carryover, or if the domination of the alien in terms of visitation translates into high amount of heterospecific pollen transfer for co-flowering species. Furthermore, two-mode and one-mode network parameters of networks based on visitation, actual interaction and pollen transport were explored. The results are presented in the fifth chapter of this thesis.

Plate 2.2: Feeding on the cornucopia. *Rhagonycha fulva* on *Heracleum sphondylium*

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3. Pollination of the invasive alien *Heracleum mantegazzianum* in comparison to the native *Heracleum sphondylium*. Is there potential for competition?

3.1 Abstract

While *Heracleum mantegazzianum* is one of the most ill-famed and most fought invasive species in Europe, yet little is known about its interaction with flower visiting insects and the pollination biology of this invader. In order to learn more about these aspects a field study was conducted and the pollinator importance of insect visitors was determined. Results were compared with findings from the native, closely related *H. sphondylium*. Furthermore, it was determined, whether both plants are similar in their degree of ecological and functional generalization. Results show that the large inflorescences of the invader are highly attractive to a broad range of insects, yet there are just a few insects truly important pollinators, most of all the honeybee *A. mellifera*. *H. sphondylium* is mostly pollinated by a more variable set of Dipterans, whereas honeybees are virtually absent from this plant. In conclusion, there was a low potential for competition effects between the two *Heracleum*-species, yet the invader might have a potential to influence native plant-pollinator interactions due to its association with the super-generalist *A. mellifera*.

3.2 Introduction

Biological invasions have a severe impact on global biodiversity (Mack et al. 2000) and are a major topic in ecological research (Richardson and Pyšek 2006). Numbers of alien plant species in Europe are increasing (Lambdon et al. 2008) and some of them have a significant impact on native plant communities (Hejda et al. 2009, Gaertner et al. 2009). Besides effects of alien plants due to competition for abiotic resources, non-native species may as well have an impact on species interactions like pollination (Tylianakis et al. 2008). Pollination is an important ecosystem service that is threatened by human influence (Kearns et al. 1998). It is crucial to the vast majority of angiosperms (Ollerton et al. 2011). Alien plants may disrupt the evolved mutualisms between native plants and their pollinators by competing for pollination services (reviewed in: Traveset and Richardson 2006, Bjerknes et al. 2007). Pollination of plants is determined by two components, commonly addressed as quantity and quality (Herrera 1987, 1989). Quantity is the number of visiting pollinators, and quality the number of conspecific pollen grains that are transferred. Alien plants are able to influence both components often with a negative impact on native plant species (Chittka and Schürkens 2001, Brown et al. 2002, Larson et al. 2006). The invasive species in these studies were often characterized by large showy inflorescences, which is typical for alien plants as they were often introduced as ornamentals (Stout and Morales 2009). Since the size of inflorescences often determines the attractiveness to visiting insects (Campbell 1989, Ohara and Higashi 1994, Conner and Rush 1996), alien plants have the distinct potential to act as superior competitors and bring about negative effects for native species. In this regard, the alien invasive plant *H. mantegazzianum* definitively has the potential to influence native plant pollinator interactions, as it is Europe's largest herbaceous plant with large compound umbels, which are up to 80 cm in diameter (Tiley et al. 1996). However, information on insect visitation of *H. mantegazzianum* is limited to one study (Grace and Nelson 1981) and there is no information on which animals provide pollination to this plant. Nevertheless, *H. mantegazzianum* is dependent on pollinators to achieve a considerable seed-set (Perglová 2007). As pointed out above negative effects for native plants may arise when alien species co-opt the services of native pollinators and share pollinators with native plants. These effects might be most pronounced on a morphologically similar co-flowering native species with less showy inflorescences (e.g. Brown and Mitchell 2001). My hypothesis was that *H. mantegazzianum* shares pollinators with *Heracleum sphondylium*, a plant native to Europe. *H. sphondylium* is closely related to the invader, but has significantly smaller inflorescences. It is plausible that competitive pollinator-mediated effects occur between these plants. Furthermore, hybridization of *H. mantegazzianum* and *H. sphondylium*, although it occurs infrequently, has been reported (Stewart and Grace 1984, Tiley et al. 1996 and references therein).

Besides possible effects of competition for pollinators the scrutiny of the pollination of the two *Heracleum*-species offers the opportunity to shed light on the mode of pollination of generalist plant species with less-sophisticated floral morphology. Generalist plant species have often been overlooked, although they are of great value for insect diversity or network stability (Olesen et al. 2007, Martín González et al. 2010). The reason for this underestimation of generalist plant families might be that pollination biology is often dedicated to specialist-interactions and the evolution of specialization (Armbruster 2006). However, there is a distinction between the process to evolve towards specialization, which is called evolutionary specialization, and the contemporary ecological state of specialization or generalization a species has, called ecological specialization (Armbruster 2006). Ollerton et al. (2007) defined ecological generalization by the number of effective pollinators a plant interacts with. In addition, they used the term functional generalization, which refers to higher taxonomic levels (e.g. bird-pollinated, fly-pollinated). In their terms an ecologically generalized plant might reveal functional specialization. Until now the genus *Heracleum* has been described as super-generalist, cornucopian (Corbet 2006) and labeled as "promiscuous" in literature (Sheppard 1991, Perglová 2007). However, it is important to distinguish between visitors and pollinators (Pellmyr 2002). This can be quite challenging for Apiaceae due to their floral morphology. Umbels consist of many small white flowers rendering a direct method (allowing a singular visit by a pollinator on a previously bagged flower) as proposed by Spears (1983) impossible. Also, Apiaceae are often dichogamous, predominantly protandric (Bell 1971), although protogyny also occurs (Webb 1984). There is evidence that dichogamy and insect behavior influence pollinator efficiency for Apiaceae (Zych 2002, 2007). Yet, only a few other studies include differences of pollinator attraction due to different sexual stages of Apiaceae (but see Schlessman et al. 2004, Davila and Wardle 2007). Other studies show that not all visitors are equally important pollinators on Apiaceae (Lamborn and Ollerton 2000, Zych 2002, 2007). Even a form of specialization called "cryptic specialization" (Bell 1971, Lindsey 1984, Lindsey and Bell 1985) was found: Despite a broad spectrum of visitors and open floral rewards subtle modifications in floral morphology allow only a few insect species to be pollinators.

Aims of this study are:

1. To determine which animals provide pollination service to the alien invader *H. mantegazzianum* with regard to its particular floral traits.
2. To explore, whether there is an overlap of the pollinator communities of the native and the invasive species of *Heracleum* and assess the potential for competitive effects due to pollinator sharing.
3. To find out if the alien plant species has a different number of effective pollinators than the native species and thus to determine their degree of ecological generalization and if there is a difference in that degree.

3.3 Methods and Materials

3.3.1 Plant species

Heracleum mantegazzianum (Apiaceae), Giant Hogweed, is an up to 5 m tall monocarpic weed native to the West-Caucasus (Mandenova 1950, quoted from Tiley et al. 1996) that has been naturalized in many countries of Central Europe and North America. Inflorescences are compound umbels. One plant can carry up to 80 000 small white flowers (Tiley et al. 1996). Reproduction is amphimictic, flowers are hermaphrodite, protandrous, insect-pollinated and self-fertile (Tiley et al. 1996, Perglová 2007). Flowering occurs from June to August with a peak in early July (Tiley et al. 1996).

Heracleum sphondylium (Apiaceae), Hogweed, is a perennial plant occurring in most European countries except the extreme North, parts of the Mediterranean and some Atlantic and Mediterranean Islands (Sheppard 1991). The plant reaches heights up to 2 m. Flowers are small, white and protandrous and are visited by a broad range of insects (Knuth 1898, Drabble and Drabble 1927, Zych 2002, 2007). Several subspecies of *Heracleum sphondylium* exist (Sheppard 1991). In this case I refer to subspecies *Heracleum sphondylium sphondylium*. The main flowering period is from June to September (Sheppard 1991).

3.3.2 Study sites

Field studies were carried out on 6 sites invaded by *H. mantegazzianum* and 5 sites where *H. sphondylium* was present. All field sites were within a 20 km radius around the campus of Bielefeld University, Bielefeld, Germany. All field sites were either roadsides or nutrient rich, often ruderalized, meadows.

3.3.3 Field observations

Observations were carried out from June to August 2008. Flowering of the two plant species did not overlap on my sites in this year, *H. sphondylium* started flowering a week after *H. mantegazzianum* had ceased. Each observation unit lasted 10 minutes, in which I recorded flower visiting insect species and flowering phase (male or female). In case of *H. mantegazzianum* this method often required a ladder in order to view the whole umbel. Insects were grouped into morphospecies. Observation units where carried out between 0800 and 1900 hours, since this was the main activity phase of flower visiting insects. Primary umbels were chosen for observations as they are mainly responsible for seed production (Sheppard 1991, Tiley et al. 1996, Perglová

2007). A total of 354 observation units (59 hours) were conducted on *H. mantegazzianum* and 337 observation units (ca. 56 hours) were conducted on *H. sphondylium*. In order to provide additional data and to detect any inter-seasonal changes in the pollinator communities I conducted a smaller survey of the pollinator community of the two *Heracleum*-species in 2010. I caught insects using a glass jar on a transect walk on one site, where both *H. mantegazzianum* and *H. sphondylium* occurred (flowering of *H. sphondylium* started three days after flowering of *H. mantegazzianum* had ceased). Insects were killed with ethyl acetate and put in a deep freezer (-20°C) for later analysis.

3.3.4 Insect pollen loads

Insects were caught in random intervals at each day in the field. Glass jars were used to catch specimen, which were killed with ethyl acetate and stored in glass vials that contained 75% alcohol to wash the pollen off their bodies. A total of 203 specimens was caught. Bees that carried pollen in their corbiculae were not sampled, as they carried a lot of pollen that was not available for pollination. Since no exact amount of alcohol could be measured under field conditions, the alcohol was allowed to evaporate from the glass vials after field sampling and was replaced by exactly 1 ml of 75% alcohol. Two sub samples of 0.1 ml of this solution were used to count the number of pollen grains using a Bürker hemocytometer (Paul Marienfeld GmbH and Co. KG, Lauda-Königshofen, Germany). I counted both pollen from the plant the insect was caught on as well as pollen from other plants, however, I used only the counts for con-specific pollen for latter analysis. As the washing method used in 2008 proofed to be rather time-consuming and laborious I used a fuchsin cube to dab pollen off the defrosted insects (Kearns and Inouye 1993) in 2010. The fuchsin cube was melted on a microscope slide and the pollen was counted.

3.3.5 Pollinator importance index

In order to assess pollinator importance direct measurements of pollinator effectiveness (as described by Spears 1983) are thought to be the best method (Pellmyr 2002). However, this method is rather impractical for *H. mantegazzianum* because of the plant height and the minuteness of the flowers. Instead, I combined several indirect measurements to calculate an index of pollinator importance. Indices based on indirect measures have also been used by comparable studies (Lindsey 1984, Lamborn and Ollerton 2000, Zych 2002, 2007).

I used PII = A x C x L to measure the importance of a given insect species as pollinator. A is the relative abundance of an insect species. C for constancy is not meant as floral constancy, but describes the preference of an insect for male or female umbels. Pollinator efficiency would be reduced, if a visiting insect species would for instance predominantly forage for pollen, as this would result in low pollen carryover to flowers in female stage. My calculation of the constancy is based on the observations I made on female and male umbels. I regarded an insect that visits both sexual stages equally often the best pollinator. In order to have a constancy value that ranges from 0 (the insect visits one sexual phase exclusively and does not contribute to pollination) and 1 (visits both stages equally often), I calculated the relation of visits to male and visits to female umbels as well as its reciprocal and used the value that was smaller than 1.

$$C = f/m \text{ if } f/m < 1 \text{ or } m/f \text{ if } f/m > 1$$

L describes the pollen load. In order to include this measure in the index for pollinator importance the relative pollen load was calculated by relating the average pollen load of an insect species to the combined pollen load of all insects (Lindsey and Bell 1984). Insects that had a relative abundance less than 3% were excluded from the computation of pollinator importance. This was done, because too few rare flower visitors were caught to provide a good database for pollen counts.

3.3.6 Data analysis

Statistical analysis was conducted using R statistical language version 2.12.1 (R Development Core Team 2010) and the vegan package version 1.17-10 (Oksanen et al. 2011). I used nonparametric tests, as data could not be transformed to meet the assumption of normality. Kruskal-Wallis test and multiple comparison post-hoc test after Siegel and Castellan (1988), implemented in the R-package pgirmess version 1.5.1 (Giraudoux 2011) were used to detect differences between pollen loads. Chi-square test was used to test the overall effect of preference for sexual stages. I used error corrected multiple chi-square test as post-hoc tests, with an error correction proposed by Benjamini and Hochberg (1995). Dissimilarities in visitor and pollinator assembly were calculated using the Morisita-Horn index (Krebs 1998). Since there were more observation units on male umbels than on female umbels of *H. sphondylium*, I used a re-sampling method based on the bootstrap procedure (Krebs 1998) in order to achieve the same sample size for the calculation of C. The mean of 10 000 random samples with the size of the smaller set (“female”) was drawn from the larger set (“male”) and used in the calculation.

3.4 Results

3.4.1 Visitation

Visitation rates of *H. mantegazzianum* were significantly higher than of *H. sphondylium* in 2008 (Fig. 3.1). However, not all insects showed a preference for *H. mantegazzianum*. From the 24 morphospecies only a few showed no difference in their abundance on either plant. Most striking is the difference in the abundance of *A. mellifera*, which made up 25% of all visits to *H. mantegazzianum*, but hardly ever occurred on *H. sphondylium* (Fig. 3.2). Visitation of *H. mantegazzianum* in 2010 was clearly dominated by *A. mellifera* (56% of all insects caught) (Fig. 3.3). *H. sphondylium* showed an almost evenly distributed array of visiting insect species with Syrphini being the most common (20.35%) (Fig. 3.3).

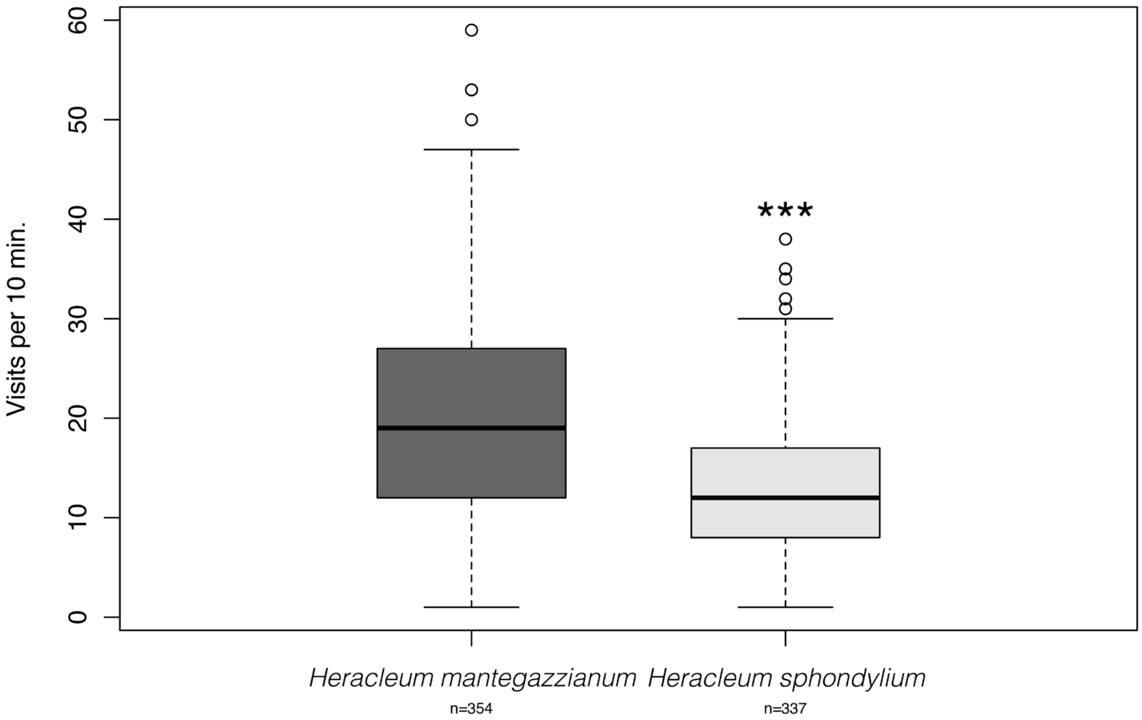

Figure 3.1: Number of insect visitors during 10 min. observation units of the two *Heracleum* species (data from 2008). *** indicates significant statistical difference (Wilcoxon rank sum test, W = 82761, $p < 0.001$)

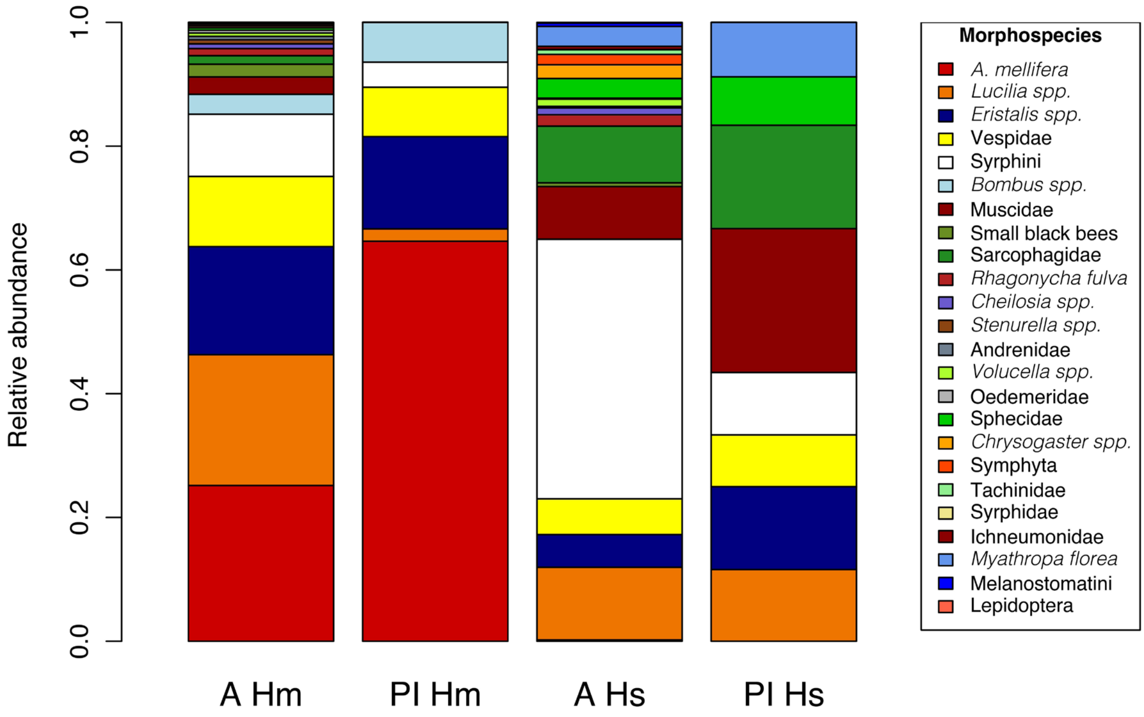

Figure 3.2: Relative abundance (A) and relative pollinator importance (PI) of insect visitors of *H. mantegazzianum* (Hm) and *H. sphondylium* (Hs) (data from 2008).

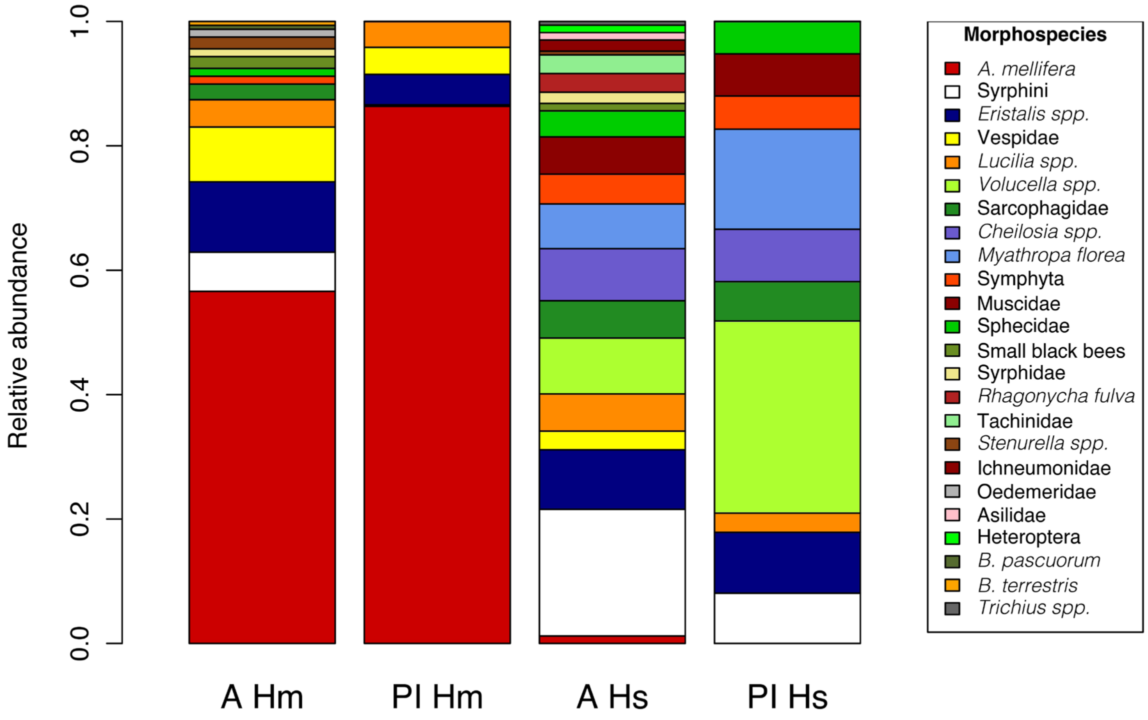

Figure 3.3: Relative abundance (A) and relative pollinator importance (PI) of insect visitors of *H. mantegazzianum* (Hm) and *H. sphondylium* (data from 2010).

3.4.2 Constancy

The preference of insects for one sexual stage over another is expressed as the ratio of the visits of each morphospecies on either male or female umbels. Fig. 3.4 a, b show this ratio for the data of 2008. The width of the bars of the mosaic plots shows the abundance of each morphospecies. For *H. mantegazzianum* Syrphini were significantly more often found on male inflorescences, while *Lucilia* spp. and Vespidae clearly preferred the female stage. Honeybees showed a preference for male umbels, while bumblebees and *Eristalis* spp. showed no bias. The distribution of visits to each sexual stage of *H. sphondylium* was more even. Only Syrphini visited female umbels significantly more frequently. In 2010 there was no statistically significant effect of the preference of insects for any sexual phase (Fig. 3.5 a, b). However, there was a tendency of some insect groups (*Eristalis* spp., Syrphini) to prefer the male stages of inflorescences of *H. mantegazzianum*, with the exception of *Lucilia* spp., which seemed to prefer female flowers. Due to the small sample size of each important group visiting *H. sphondylium* there was no statistical basis to prove any difference in animal visitation of any sexual phase. The largest group of insect visitors, Syrphini, showed a slight preference for male inflorescences.

3.4.3 Insect pollen loads

Pollen loads ranged from individuals that carried virtually no pollen grains up to quite high pollen loads (Fig. 3.4 c, d) in 2008. Nevertheless, some insects were better vectors for pollen than others. *A. mellifera* carried most *H. mantegazzianum*-pollen, significantly more than *Lucilia* spp. and Vespidae, which had the lowest pollen loads. None of the insects caught on *H. sphondylium* reached the levels of pollen load of *A. mellifera* on *H. mantegazzianum*. While differences were less pronounced for the insects on *H. sphondylium*, Syrphini and *Lucilia* spp. showed a tendency for rather low pollen loads. The observed number of pollen grains on both plant species in 2010 was much greater than pollen loads counted in 2008. This is due to the different methods used in each year. The observed differences in the pollen carrying capacities of each insect group, however, remain largely the same. Pollen loads of *A. mellifera* caught on *H. mantegazzianum* were significantly higher than the pollen loads of Syrphini and Vespidae (Fig 3.5 c). For *H. sphondylium* there was significant difference between a group of morphospecies consisting of *Myathropa florea*, Symphyta and *Volucella* spp. with high pollen loads and a group of morphospecies that had low pollen loads consisting of by Syrphini and *Lucilia* ssp. (Fig 3.5 d).

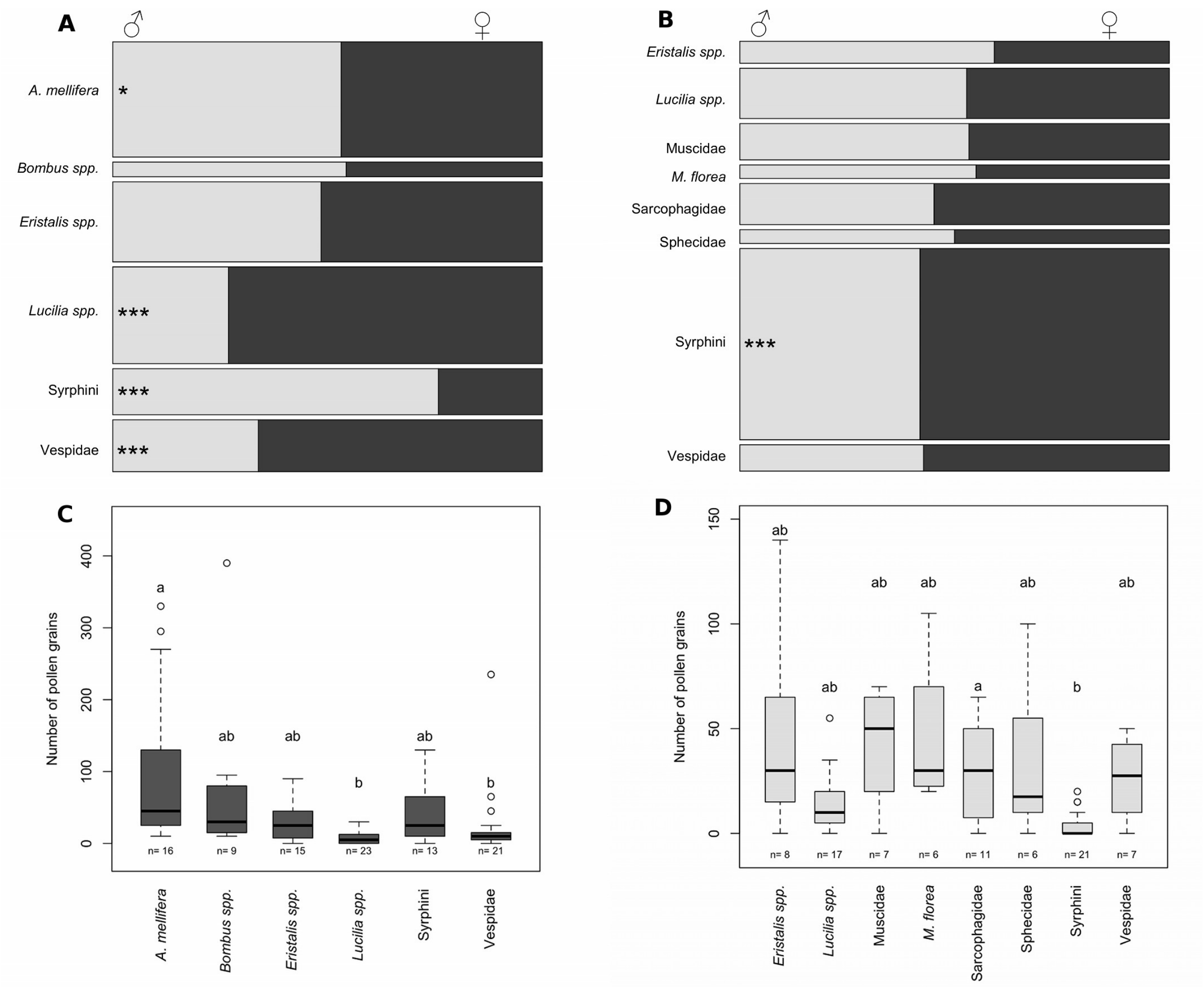

Figure 3.4 a-d: a) Relative visits of insects to male (lightgrey) or female (darkgrey) umbels of *H. mantegazzianum* in 2008. Different size of bars shows relative abundance of morphospecies. *** indicates significant statistical difference (Chi-Square test, $\chi^2 = 572.96$, $p < 0.001$). **b)** ditto for *H. sphondylium*. (Chi-Square test, $\chi^2 = 38.35$, $p < 0.001$) **c)** Pollen loads of insects caught on *H. mantegazzianum*, letters indicate significant statistical differences, (Kruskal-Wallis test, $H = 31.25$, $p < 0.001$). **d)** ditto for *H. sphondylium* (Kruskal-Wallis test, $H = 22.58$, $p < 0.001$). Mind different scales.

3.4.4 Pollinator importance

The most important pollinator for *H. mantegazzianum* in 2008 was *A. mellifera* exceeding the value of any other insect species by far (Fig 3.2). While Syrphini dominated the visits to *H. sphondylium*, these insects did not stand out in their pollinator importance. Their contribution was more or less equal to the other insect species. The overlap (based on the Morisita-Horn Index) between the relative abundance of insect visitors between the two plants was 46.15% and the overlap of the important pollinators was 11.15%. In 2010 *A. mellifera* was not only the most common visitor of *H. mantegazzianum* but was by far the most important pollinator for this plant (Fig. 3.3). While the contribution of *Lucilia* spp., *Eristalis* spp. and Vespidae was small, Syrphini were negligible as pollinators. For *H. sphondylium Volucella* spp. played an important role as pollinator, although it was not the most abundant visitor. Other insects form a group of more or less equally important pollinators. In comparison, these results show even more a difference in the visiting insect fauna and the important pollinators of both plant species (Fig 3.3). The percentage of overlap (based on the Morisita-Horn index) for visitors between both plant species was 17.74% and 1.38% for important pollinators in 2010.

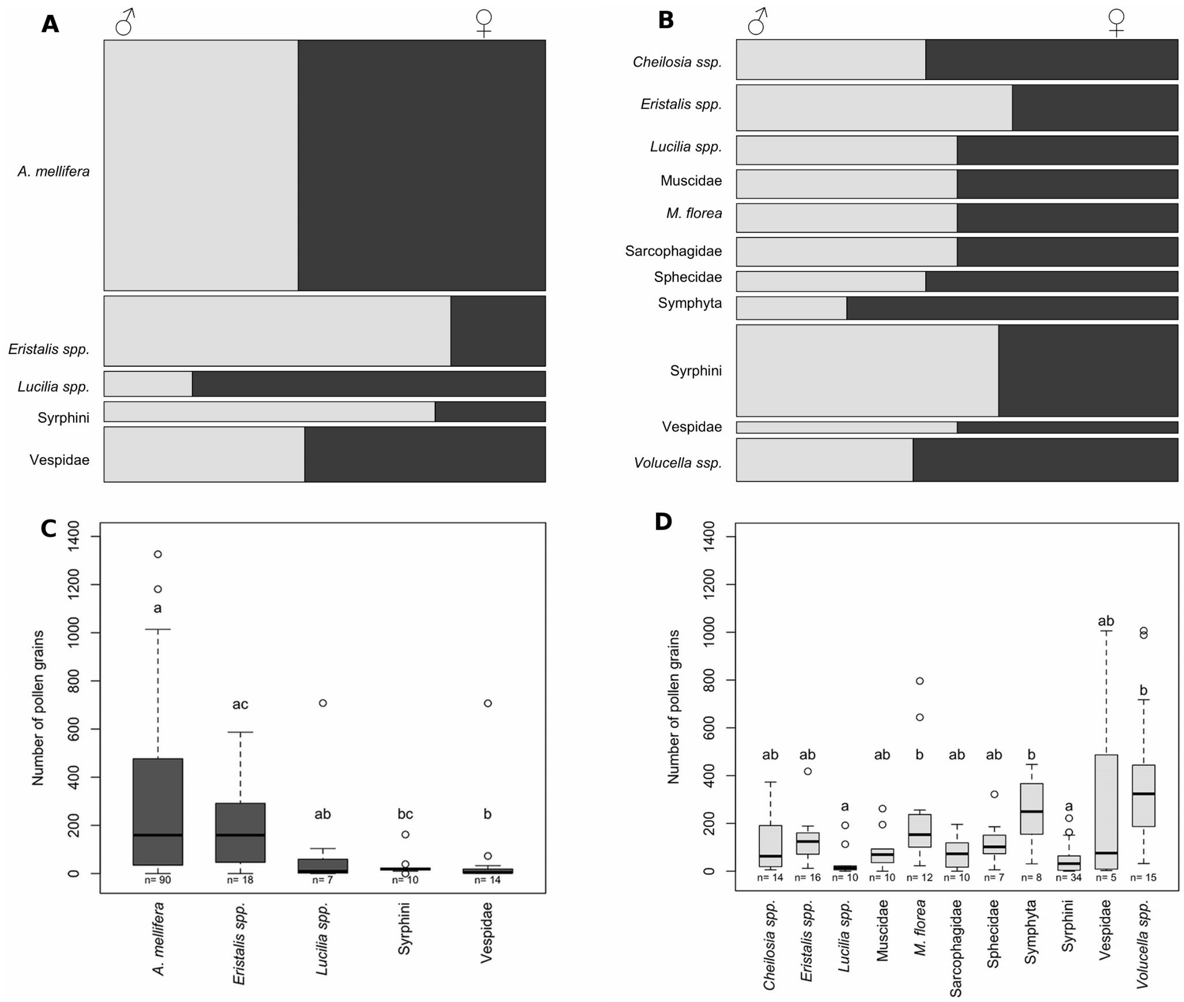

Figure 3.5 a-d: a) Relative visits of insects to male (lightgrey) or female (darkgrey) umbels of *H. mantegazzianum* in 2010. Different size of bars shows relative abundance of morphospecies. *** indicates significant statistical difference (Chi-Square test, $\chi^2 = 7$, $p = 0.135$). **b)** ditto for *H. sphondylium*. (Chi-Square test, $\chi^2 = 6.27$, $p = 0.791$) **c)** Pollen loads of insects caught on *H. mantegazzianum*, letters indicate significant statistical differences, (Kruskal-Wallis test, $H = 26.16$, $p < 0.001$). **d)** ditto for *H. sphondylium* (Kruskal-Wallis test, $H = 54$, $p < 0.001$). Mind different scales.

3.4.5 Differences between seasons

Both seasons (2008 and 2010) showed the importance of *A. mellifera* for *H. mantegazzianum*. It exceeded the efficiency as pollinator of any other morphospecies by far. Similarity between important pollinators of *H. mantegazzianum* between seasons was 94.2%. Furthermore, honeybees hardly ever visited *H. sphondylium* in any season. In both years pollination of *H. sphondylium* was provided by several different morphospecies. Although there was some variation in the composition of this group of pollinators (congruence of important pollinators was 46%), most of them were Dipterans and there was not a big variation in their pollination efficiency.

3.5 Discussion

3.5.1 Pollinators and pollinator importance

A. mellifera is the most abundant, most effective (in terms of pollen transfer) and most important pollinator for *H. mantegazzianum*. Other studies of *H. mantegazzianum* also reveal high levels of honeybee visitation (Grace and Nelson 1981, Nielsen et al. 2008), while Apiaceae in general are typically associated with dipteran pollinators (Larson et al. 2001). Dipteran visitors on *H. mantegazzianum* are heterogeneous in their importance as pollinators. Drone flies (*Eristalis* spp.), which are known to be effective pollinators for other plants (Gómez and Zamora 1999, Pérez-Bañón et al. 2007) provide valuable pollination service for *H. mantegazzianum*. Syrphini and *Lucillia* spp. are of lesser importance as pollinators caused by a bias against sexual stages or modest pollen carrying capacity or both. Low pollen loads for small syrphids and calliphorid flies have often shown in other studies on other Apiaceae or (closely related) Araliaceae (Lamborn and Ollerton 2000, Zych 2007, Pérez-Bañón et al. 2007, Jacobs et al. 2010). Nevertheless, they are effective in pollination of some crops (Clement et al. 2007, Jauker and Wolters 2008) and are important pollinators in the field, when they show high abundances (Lamborn and Ollerton 2000, Zych 2007, Jacobs et al. 2010). Differences in resource availability may explain the preference for male or female umbels by certain insect groups. There is evidence that floral rewards are different in each sexual stage of dichogamous plants (Bell et al. 1984, Snow and Grove 1995, Aizen and Basilio 1998). For instance, nectar secretion of caraway (*Carvum carvi*) is raised 1.5 fold during female stages (Langenberger and Davis 2002). If a similar pattern occurred for *Heracleum*, it might explain the preference of some insects (especially *Lucilia* spp.) for female stages. Beside nectar there is also pollen as resource insects forage on. Syrphids are long known to feed on pollen (Müller 1873), the species in my study are known to be generalist pollen feeders (Haslett 1989) and *Heracleum* is amongst their most-important food sources (Branquart and Hemptinne 2000). Additionally, Syrphini feed almost exclusively on pollen while *Eristalis* spp. tend to include more nectar in their diet (Gilbert 1985). This would at least explain the pattern of visits to male and female flowers of these syrphid species on *H. mantegazzianum*. Compared to the invasive plant species the pollinator community of the native *H. sphondylium* is more diverse, especially in the season of 2010, where pollinators include eleven different morphospecies. Most striking is the absence of *A. mellifera*. Honeybees are also absent or found infrequently on *H. sphondylium* in other studies (Knuth 1898, Grace and Nelson 1981, Zych 2002, 2007). Syrphini are the most abundant morphospecies in both years, however their effectiveness is limited by their low pollen carrying capacity. Interestingly, Syrphini prefer female flowers when they visit *H. sphondylium*, which is opposite to their behavior on *H. mantegazzianum* (a preference of the male stage). An explanation might be provided by the different feeding behavior of different sexes. Female syrphids need pollen in order to lay eggs (Irvin et al. 1999 and references therein), while the males feed on energy-rich nectar in order to pursue the females (Golding and Edmunds 1999). At the time when *H. sphondylium* was flowering there were possibly more male Syrphini present than female. The community of important pollinators of *H. sphondylium* also showed more temporal fluctuation than for *H. mantegazzianum*, which was also reported from Zych (2002, 2007) in studies on the pollination of *H. sphondylium*.

In conclusion, this study reveals that a substantial part of the pollination of *H. mantegazzianum* was done by honeybees, its importance exceeded the pollinator importance of any other abundant insect species by far. Pollinator importance of *H. sphondylium* was distributed more evenly and the group of important pollinators was more variable in time. My results show the complexity of the interplay of the so-called quantity and quality interactions of a plant-pollinator system (Herrera 1987, 1989). On the one hand I found one most abundant visitor, which also had the highest overall effectiveness (i.e. *A. mellifera*) on the other hand *Lucillia* spp. was very abundant, but due to their low effectiveness they were of low importance to the pollination of *H. mantegazzianum* (the importance of honeybees was 30-fold). Additionally, my findings are in contrast to the opinion that pollinator importance is mainly predicted by visitation rates (Vázquez et al. 2005, Sahil and Conner 2006).

3.5.2 Potential impact of *H. mantegazzianum* on native plant-pollinator interactions

While *H. mantegazzianum* has higher visitation rates and is undoubtedly more attractive than its native counterpart, there is not much overlap in their pollinator communities. This is despite the fact that both plants are morphologically similar and closely related. In contrast to my results a study on alien and native *Senecio* (species which also have open inflorescences and a highly generalist) found a high overlap of insect visitors (Vanparys et al. 2008). It is unlikely that competition effects appear between the two *Heracleum*-species, when they do not share pollinators.

Nevertheless, there are many other ways that *H. mantegazzianum* might influence native plant-pollinator interactions. Nielsen et al. (2008) found a slight facilitation effect on visitation rates for *Mimulus guttatus* growing in close vicinity of *H. mantegazzianum*, but no effect on seed set, which is rather unsurprising if one considers the completely different floral morphologies. Due to the generalist foraging behavior of *A. mellifera* the possible impacts of *H. mantegazzianum* are not limited to just one plant species, as alien plants are often integrated into plant pollinator-networks by (super-)generalist pollinators (Richardson et al. 2000, Memmot and Waser 2002). Honeybees are recognized to exert major influence on the interaction in invaded plant-pollinator networks (Kaiser-Bunbury et al. 2011). Often, both plant species and honeybees are alien and act as mutualists (Barthell et al. 2001, Stout et al. 2002, Morales and Aizen 2006), a process described as invasional meltdown by Simberloff and von Holle (1999). However, this is not the case in the system I studied. *A. mellifera* is not only native to Germany (Michener 2000), but it is most probably also native to the origin of *H. mantegazzianum*, the Caucasus region (Ruttner 1988 and references therein). Nevertheless, in a study dedicated to the impacts of alien *Impatiens glandulifera* on a plant pollinator network in England a facilitation effect on visitation rates of native plants was found, but a negative effect due to high alien pollen loads mediated by *A. mellifera* was concluded (Lopezaraiza-Mikel et al. 2007).

3.5.3 Ecological generalization of the two *Heracleum*-species

From a botanist's viewpoint both plants show a textbook example of being highly generalist, as they attract a wide range of insect visitors and there are no morphological barriers that exclude visiting insects from anthers or stigma. This is reflected in the diversity of visiting insect species of both plants. Both plants fit the description of Corbet (2006) as allophilous and cornucopian. However, I found no evidence that the open flowers allow all insects to be equally good pollinators, so while hardly being "monogamous" the two *Heracleum*-species are not less specialized in their pollination (Faegri and van der Pijl 1979, Proctor et al. 1996), or even "promiscuous" (Grant 1949). The degree of ecological generalization of the pollination of *H. sphondylium* is higher than of *H. mantegazzianum*. Or to put it in another way: *H. mantegazzianum* is ecologically more specialized than *H. sphondylium*. If one thinks further and considers different functional groups in pollination (Fenster et al. 2004) there is functional specialization in both plants. *H. mantegazzianum* relies mainly on the honeybee for pollination, while *H. sphondylium* is pollinated mostly by Dipterans (also see Zych 2002, 2007, Lopezaraiza-Mikel et al. 2007).

Alas, due to the apparent lack of floral modification and the fact that there are inter-annual fluctuations of insect populations observations of pollinator importance of one season can only provide a snapshot. Temporal variation of important pollinators has been shown for other Apiaceae (Lamborn and Ollerton 2000, Zych 2007, Davila and Wardle 2007) as well as for other systems (e.g. Fishbein and Venable 1996, Price et al. 2005). Herrera (2005) concluded that generalization is not a species-level trait but can be regarded as local phenomenon. However, variation in the pollinator community of *H. sphondylium* is greater than of *H. mantegazzianum*, where the honeybee remains dominant in all years. *A. mellifera* is ubiquitous in the studied area and less likely to show variation in population size. Furthermore, it has to be taken into consideration, that there might be subtle clues for insects to differentiate between different Apiaceae species. It has been suggested that the different heights of *H. mantegazzianum* and *H. sphondylium* and the risk of predation might account for different visitor assemblies (Grace and Nelson 1981). Ollerton et al. (2007) describe the minute amount of nectar produced by *Daucus carota* as a filter to exclude larger bees in order to occupy the less-exploited pollinator niche of small Dipterans. Although data on the nectar composition of *Heracleum* is basically not existent (but see Corbet et al. 1979), there is evidence that *H. mantegazzianum* produces more nectar and pollen per flower than *H. sphondylium* (Höwing 2008). Bigger inflorescences (and the typical dense stands of *H. mantegazzianum*) and thus more resources could explain the fidelity of honeybees to this plant (Goulson 1999, Corbet 2006). Another hint for insects is of course floral scent. While differences in the composition of floral scent has been shown for Apiaceae (Borg-Karlson 1993, Tollsten et al. 1994), I do not have any data on scents of the two *Heracleum*-species, beside the personal observation of the distinct sweet smell associated with stands of *H. mantegazzianum.*

My results support the view that a lack of morphological specialization does not automatically lead to highly generalist pollination. Furthermore, besides all variation, distinct patterns in pollinator importance can manifest themselves even in two closely related generalist plant species.

3.5.4 Conclusion

The data indicate that *H. mantegazzianum* in spite of its broad range of insect visitors relies mainly on *A. mellifera* as pollinator, which is in contrast to the native species *H. sphondylium*. While competition effects between these two plant species are unlikely to occur, there is a potential of the invader to interact with other native plant species via the honeybee. Future studies to determine this impact should be based on a network approach in order to account for the generalist foraging behavior of the invader's main pollinating agent *A. mellifera*.

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4. Impact of the invasive alien *Heracleum mantegazzianum* on reproduction and the network structure of a community of co-flowering plants

4.1 Abstract

The invasive *Heracleum mantegazzianum* is an alien plant with large rewarding inflorescences with the potential to disrupt pollinating services for co-flowering species. Furthermore, its main pollination agents are super-generalist honeybees potentially linking the plant to many others in a community. An experimental garden setup was used in order to scrutinize the effect of the invader on insect visitation and set seed of an array of co-flowering plants. Additionally, I used a network approach to explore the impact of *H. mantegazzianum* on two- and one-mode network parameters. While visitation rates of co-flowering plants were (although statistically non-significant) generally enhanced, the effect on seed set was neutral. *H. mantegazzianum* was found not only to be well integrated but dominant in invaded networks. Nevertheless, in combination with the results for seed set it was concluded that the impact of the invader was not detrimental to the invaded plant pollinator system.

4.2 Introduction

The human impact on ecosystems alters the functioning of these systems on a global scale (Vitoussek et al. 1997). Climatic change, changes in land use and the spread of alien species are the more prominent facets of this ongoing global change. With the alterations of the functions of the thus affected ecosystems goes along a possible alteration of their ecosystem services. One of these "public services" of nature under pressure by anthropogenic influence is pollination (Kearns et al. 1998). Pollination is critical to most plants as it is estimated that 88% of flowering angiosperms rely on biotic pollination (Ollerton et al. 2011). Plant pollinator systems are threatened by the loss of biodiversity, as functional biodiversity is important for their persistence (Fontaine et al. 2006). Among the biggest threats to biodiversity are biological invasions (Mack et al. 2000). Climate change and alien plants lead to interactions that further threaten plant pollinator interactions (Schweiger et al. 2010).

Furthermore, it has been shown that alien plants are able to directly influence native species by competing for pollinators (reviewed in: Traveset and Richardson 2006, Bjerknes et al. 2007).

Competition for pollinators works via two components commonly addressed as quality and quantity, which are intermingled by complex mechanisms (for a review see: Mitchell et al. 2009). Quantity describes the number of visits by pollinators that a plant receives while quality refers to the number of pollen grains that are received. Alien plants have been shown to negatively affect seed set through the quantity component (e.g. Chittka and Schürkens 2001, Ghazoul 2004, Brown et al. 2002) as well as the quality component (e.g. Kandori et al. 2009).

Nevertheless, the effects of pollinator sharing do not necessarily have to be negative. Plants may also have a facilitative effect on co-flowering species (Thomson 1978, Johnson et al. 2003, Moeller 2004, Ghazoul 2006). Visitation rates may be enhanced in the presence of an attractive plant and plots with a bigger floral display attract more visitors (Hegland and Totland 2005) as visitors that are drawn to the plots visually may also visit less prominent co-flowering species. This effect is often referred to as the magnet-species effect (Laverty 1992). In many cases alien plants often have large showy inflorescences as they were often introduced as ornamentals (Stout and Morales 2009) and were indeed found to be acting as a magnet species (Lopezaraiza-Mikel et al. 2007). However, enhanced visitation rates and pollinator sharing also increase the risk of improper pollen transfer, which may reduce reproductive success (Rathcke 1983, Morales and Traveset 2008). There is evidence from the field that, while more insects are attracted to invaded field sites they also carry high amounts of alien pollen (Lopezaraiza-Mikel et al. 2007).

Alas, most of the studies that scrutinized the impact of alien plants were based rather on single pairwise interactions than on a community approach. Interaction of species, however, occurs in a community context. Introduced plants can play a role in shaping plant communities via plant pollinator interactions (Sargent and Ackerly 2007). These multiple interactions are of no small complexity and can be perceived as mutualistic networks (Jordano 1987, Bascompte and Jordano 2007). Prominent features of mutualistic networks are their heterogeneity (most species have few links, some have more connections than expected by chance), nestedness (specialist interact with subsets of generalists' interaction partners) and that they are determined by weak asymmetric links among species (generalist animals interact with specialist plants and vice versa) (Bascompte and Jordano 2007). Networks as a means to describe the interactions among species have proven a valuable tool for ecologists (Thompson 2006). Knowledge about the topology of a network reveals information about its dynamics and stability (Strogatz 2001). Thus, it is necessary to use a network-based approach to explore the pollinator-mediated impact of alien plants.

A start has been made in discerning the effect of aliens on plant pollinator networks a decade ago (Memmott and Waser 2002, Olesen et al. 2002) and other studies followed. Still, this is just a fledgling field of research and there is need for further studies (Burkle and Alarcón 2011). So far, studies found that alien plants were well integrated into mutualistic networks by generalist pollinators (Vilà et al. 2009, Padrón 2010). Alien plants often dominate the plant-pollinator networks they invade (Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008a, b) sometimes to a point where they cause a detrimental effect on mutualistic interactions of native plants and pollinators (Aizen et al. 2008). Nevertheless, there is no study that combines investigation of network parameters and the impact on seed set. This is important, because ultimately seed production and seedling establishment determines the impact on plant populations (Turnbull et al. 2000).
Aim of this study is, to quantify the effects of an alien invasive plant on visitation and seed-set of native plants as well as on network topology. The parameters scrutinized were nestedness and connectance. Connectance is the quotient of realized links and all possible links (Dunne et al. 2002), when the alien "usurps" links from native species this should lead to lower connectance. Nestedness can be perceived as a measure of order in a system (Jordano et al. 2006). A possible impact of an invasive species could be to decrease nestedness and create a less ordered system. Furthermore, centrality scores were employed in order to analyze the importance of plant species in a network (Martín González et al. 2010). The alien plant I focused on was *Heracleum mantegazzianum*, the Giant Hogweed. This plant is regarded as one of the most obnoxious alien invaders in Europe (Pyšek et al. 1998). It has the potential to act as magnet species as it is characterized by very large inflorescences and it is visited by a diverse array of insects. Moreover, super-generalist honeybees play a central role in its pollination (see chapter 3), so this plant is potentially linked to many others in a community. Network analysis is usually used in whole communities of plants and their flower visitors. Here I used an experimental garden setup for a network approach in order to investigate the influence of an invasive species on co-flowering plants. The following key question were addressed:

1. Is there an impact of *H. mantegazzianum* on the visitation rates and seed set of co-flowering plants in a community? I hypothesized that there are differences in the impact for the different plant species depending on the way a plant is pollinated (morphology, level of generalization etc.), plants with a high level of pollinator sharing with *H. mantegazzianum* are likely to be the most affected.

2. Is there a difference in the number and identity of visiting insect species in invaded and uninvaded plots? My hypothesis was, that *H. mantegazzianum* acts as magnet species, but that this effect is also dependent on the identity of the visiting insect species.

3. How does the invader change the architecture of a plant-visitor network?

When the alien plant "usurps" links from co-flowering species connectance is likely to decrease, while the presence of a super-generalist alien might increase nestedness. Furthermore, it is plausible that the super-generalist alien has high centrality scores indicating that it is a keystone of invaded networks. Whether this leads to the detriment of invaded networks was a question left open.

4.3 Materials and Methods

4.3.1 Plant species

Heracleum mantegazzianum (Apiaceae), Giant Hogweed, is an up to 5 m tall monocarpic weed that has been naturalized in many countries of Central Europe and North America. For further information see Tiley et al. (1996).

I selected focal plants to form a gradient, based on their floral morphology, from plants that are specialized in their pollination to plants that have a generalized mode of pollination. The following seven plant species were used as focal species (order of species is ascending from the morphologically most specialized to the most generalized):

Linaria vulgaris (Plantaginaceae), Common Toadflax is a perennial plant, which can grow to 90 cm in height. Its pale yellow flowers consist of a lower and upper lip that shuts the flowers, thus permitting only strong insects like bumblebees to pollinate.

Lotus corniculatus (Fabaceae) is a herbaceous perennial; the yellow flowers have the morphology typical for the family. Plants grow up to 30 cm.

Salvia nemorosa (Lamiaceae) is a perennial herbaceous plant that grows up to 50 cm. Flowers are zygomorphic consisting of an upper and lower lip, blue to violet and arranged in whorls.

Digitalis purpurea (Plantaginaceae), Common Foxglove is an herbaceous biennial. Plants can be up to 2 m tall; flowers are pink, tubular, zygomorphic and arranged in dense inflorescences.

Campanula poscharskyana (Campanulaceae) is a perennial plant with open violet colored flowers, plants are trailing and can grow up to 30 cm.

Lythrum salicaria (Lythraceae), Purple Loosestrife is a perennial herbaceous plant that grows up to 1.5 m. Flowers are red to purple and arranged in dense clusters. Furthermore, flowers possess heterostyly. This plant has been the focus research recently as it is invasive in North America and has negative pollinator-mediated effect on native congeners (Brown and Mitchell 2001, Brown et al. 2002).

Scabiosa japonica (Dipsacaceae) is an annual plant that reaches heights up to 30 cm. Flowers are small, pale violet and arranged in heads that are ca. 4 cm in diameter.

All plants will be referred to by their genus from here on. Some of the plant species were raised from seeds (*D. purpurea, L. corniculatus, L. vulgaris*) while others had to be bought from local plant nurseries (*C. poscharskyana, L. salicaria, S. nemorosa, S. japonica*).

4.3.2 Experimental garden setup

The idea behind the garden experiment was to create artificial networks in the way of an addition experiment keeping density of co-flowering focal species constant, so that effects are not confounded with density effects (Mitchell et al. 2009).

I selected a meadow situated on the campus of the Bielefeld University, Bielefeld. Six study sites (plots) were created on this meadow. The meadow was mown prior to the installment of the plots. The minimum of space between to sites was 4 m, which was found sufficient space to avoid alien pollen carryover by other studies (Montgomery 2009, Takakura et al. 2011). Furthermore, several tall oak trees that grew on the whole site provided further separation. I created an artificial network on each of the plots by arranging eight pots of each plant species in a circular design. Four plants of each species were put together as a patch and patches were randomly arranged in a circle of ca. 3 m diameter. For most plants I used two patches (i.e. a total of eight pots), except for *C. poscharskyana* and *L. corniculatus* where a lack of plants only provided one patch with four respectively six plants. Instead of whole *H. mantegazzianum* plants I used umbels that I cut off in a nearby field site and placed into water buckets. A previous study revealed that umbels are a good surrogate for whole *H. mantegazzianum* plants (Himmler 2008) Umbels lasted about a week and were replaced as necessary. Five buckets with umbels of *H. mantegazzianum* were placed in the center of each plots that served as invaded treatment. This space was left empty in the control treatment. Furthermore, I counted the open inflorescences at the beginning of my experiment, when a plot had less open inflorescences than another I added additional pots to ensure homogeneity between plots. In total each plot contained about 50 potted plants. I continued to count open inflorescences throughout the experiment; the deviation for each plant species and plot was between ± 1.3 - 10% depending on the plant species.

4.3.3 Insect visitation

Observations started with the flowering period of *H. mantegazzianum* in the end of June and lasted until the middle of July 2009. In order to have data for all plots during different times a day by rotating the plot that observations started on each day and then continued with the other plots in numerical order. Plots were watched continuously during the activity phase of insects (usually between 0800 and 1800 hours). In each plot a patch of a plant species was randomly selected and watched for 3 minutes recording all floral visitors. This was repeated until all plant species in a network were sampled. As most plants were represented in two patches and each plot was usually sampled at least twice a day I chose the patch that was not watched before in the second run. A total of 1196 observation units (ca. 60 hours) were conducted. I calculated the mean visitation of all insects for each plant species during 3 minutes. Additionally, I formed groups of insects based on their morphology and behavior and calculated the overall insect visitation for each plot as further described below (see section 4.3.6 Data analysis). Based on the total numbers of visiting insect species I calculated the similarity for the visitor fauna of each plant species and *H. mantegazzianum* based on the cumulated numbers of visits in the invaded plots by using the Morisita-Horn index (Krebs 1998). The similarity was expressed as percentage of congruence.

4.3.4 Reproductive success

For some plants I removed all open flowers a day before the start of the experiment and left only buds, which mostly started flowering the next day. I marked the stems of plants, where a removal of flowers would have caused damage, with a ribbon in order to differentiate between flowers that were possibly fertilized prior to the start of my experiment in order to exclude them from analysis. After the end of the experiment, I calculated the numbers of flowers that were open during my experiment, by counting the number of fruits and the scars left on the stems by flowers that did not develop fruit. In the case of *S. japonica* I collected the total flower head and calculated the number of fertilized and not fertilized flowers. Fruits were collected, dried and seeds were counted. Due to the enormous effort of counting seeds I selected a subset of 12 plants per species and treatment (four plants for each plot). As a measure for reproductive success the ratio of seeds per flower for each plant was calculated.

4.3.5 Network parameters

I created two types of networks from the observational data: One-mode and two-mode networks. Two-mode data describe the interaction of two sets of interaction partners (here animals and plants). Such a network is also called a quantitative bipartite network. It is created by putting the sums of all visits for all plants in a matrix (plants x animals). I calculated degree (number of interacting insects) and the normalized degree (percentage of interacting insect) for each plant species using two-mode data. Further indices for two-mode networks were connectance and nestedness. I calculated the "classical" nestedness index (Rodríguez-Girónes and Santamaría 2006) that describes nestedness as temperature ranging from 0 (perfect nestedness) to 100 (perfect chaos). I used (Nestedness-100)/100 to create an index ranging from 1 (perfect nestedness) to 0 (perfect chaos) to facilitate comparability with an additional nestedness index I used that included the weight of interactions (Galeano et al. 2009). I tested connectance and nestedness against a null model of random associations (1000 runs, Patefield 1981) in order to evaluate whether stochastic processes or particular mechanisms produced structural patterns.

Two-mode data can be transformed into one-mode (Olesen et al. 2006). One-mode networks describe the interactions of entities that belong to the same set (here: plants). I used one-mode data to calculate betweenness and closeness for each plant species. Theses so-called centrality scores were first introduced by Freeman (1979) and used in social networks. Recently they have been employed to identify plant species that are important for the overall coherence of a network (keystone species) (Martín González 2010). In my study I used an algorithm proposed by Opsahl et al. (2009) that via a tuning parameter called alpha, is able to incorporate both number of connected nodes and tie weight (the strength of interactions). In this study I used an alpha of 0.5 to place an equal weight on tie strength and number of nodes. Closeness is based on the shortest path between a plant species and the other species. A high closeness describes the fact that such a species can easily influence others in a network. Betweenness is the sum of shortest paths between all plant species that pass through a certain plant species. A plant with a betweenness higher than zero connects parts of a network that otherwise would be unconnected, thus forming hubs or keystone species.

4.3.6 Data analysis

All data analysis was carried out using R statistical language version 2.13.0 (R Development Core Team 2011). The packages bipartite 1.16 (Dormann et al. 2009), tnet 3.0.5 (Opsahl 2009) and vegan 1.17-10 (Oksanen et al. 2011) were used. As data was not normally distributed and could not be transformed to meet the criteria of normal distribution non-parametric tests were used throughout. The statistical significance of the influence of the invader was tested with a test developed by Scheirer et al. (1976). This test can be regarded as a non-parametric equivalent to a two-way ANOVA. I programed this test into R following Sokal and Rohlf (1995). The fact that in many observation units no visits were recorded posed a problem that I tried to overcome by comparing the sums of observed visits by each insect group for each plot. I used a re-sampling technique based on the bootstrap procedure (Krebs 1998) to create sample of the same size. The mean of 10 000 random draws without replacement with the size of the smallest sample for each plot was employed to create such equally sized samples. The same technique was used for the data I created visitation networks with. A drawback of calculating sums of insect visitation for each plot is the resulting low sample size of three for each treatment, which prevented the use of any post-hoc tests for these data. However, I could not come up with more replicates, because of the high effort of maintaining and sampling artificially created networks.

Congruence of networks was tested using Procrustes analysis, which employs an algorithm that minimizes the sum of squares of distances between corresponding points of two matrices (Jackson 1995, Peres-Neto and Jackson 2001, Alarcón 2008 et al.). I used the same (plants x animals) matrices as I used to calculate two-mode networks, albeit, in order to avoid multiple comparisons, I created cumulative networks, which means I added observations I made for each treatment, thus creating one control network and one invaded network. Furthermore, Procrustes analysis is able to calculate the deviation between individual points. These residuals indicate which plant was subject to the highest amount of change between treatments. The significance of the result was tested by a permutation test implemented in the protest function of the vegan package of R (10 000 permutations). All data are presented ± standard error unless stated otherwise.

4.4 Results

4.4.1 Visitation and seed set

Figure 4.1 shows mean visitation rates plotted against the mean seed set per flower for each plant species. (Unfortunately, I was not able to measure the seed set for *C. poscharskyana*, so this plant species is left out of this graphic. Visitation (mean visits in 3 min) was 0.78 (± 0.063) in networks without *H. mantegazzianum* and 0.76 (± 0.059) in networks with the invader). The idea behind this way of presentation is to differentiate between a facilitative, neutral or competitive effect of the invader on other plant species. Facilitation would manifest itself in enhanced visitation rates and enhanced seed set; the data point would lie further to the upper right compared to the control treatment. Competition would cause the opposite effect. However, my experiments revealed no statistical significant differences between the treatments (Tab. 4.1). Rates of seed set were not significantly different for any plant (Tab. 4.1). Seed set of *L. corniculatus* was slightly reduced, while visitation rates remained constant. There was a marginal reduction of seed set and visitation rates for *S. nemorosa*. In summary, there was no plant that produced significantly less seed when *H. mantegazzianum* was present, and there was a tendency for some plants (*D.*

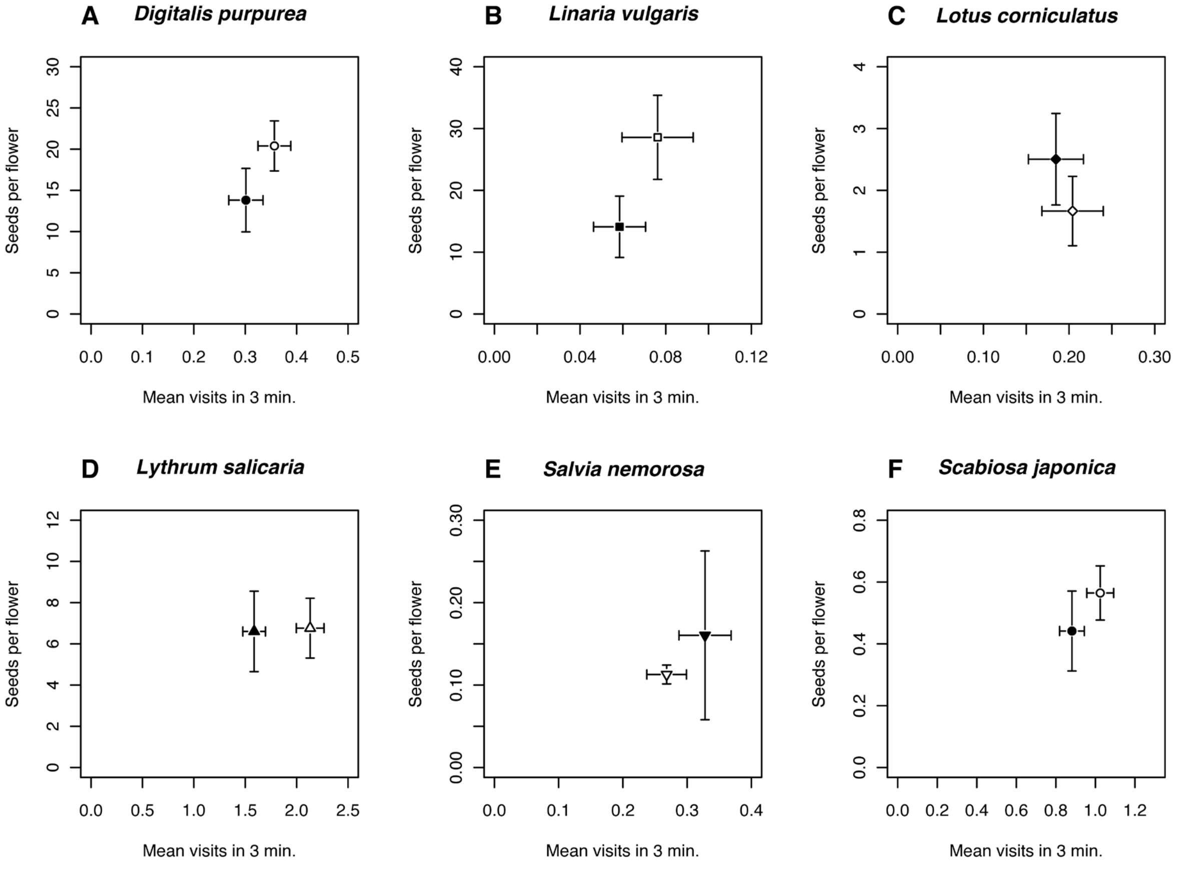

Figure 4.1 a-f: Average visitation (x-axis) and seed set (y-axis) of native plant species. Black symbols indicate control, white the invaded treatment. n = 12 for seed set and n = 74-83 for visitation. ± SE. Mind different scales.

purpurea, L. vulgaris, S. japonica) of an enhancement of visitation rates in combination with *H. mantegazzianum*. Most pronounced was this tendency for *L. salicaria*, where the presence of *H. mantegazzianum* lead to an increase in visitation of roughly 35%. Furthermore, *L. salicaria* was also the plant with the highest proportion of visitors shared with *H. mantegazzianum* (Tab. 4.2). *S. japonica* and *C. poscharskyana* also showed a high percentages of visitor sharing. The other plant species shared markedly less than half of their visitors with the invader. The lowest proportion of sharing had *L. vulgaris*.

Table 4.1: Results of the statistical analysis (Scheirer-Ray-Hare test) for visitation, seed set of plants, and overall insect visitation. The interaction term was not significant in any analysis and is not shown here.

	Sum of squares	H	Degrees of freedom	p
Visitation				
Plant species	84419441.55	707.6172	6	≤ 0.001
Treatment	153578.6902	1.2873	1	0.8493
Seed set				
Plant species	3543.3333	31.9219	5	0
Treatment	18.7778	0.1692	1	0.4423
Overall visitation				
Insect morphospecies	9857.5833	39.8286	8	≤ 0.001
Treatment	1791.1296	7.2369	1	0.0298

Table 4.2: Percentage of visitor sharing between *H. mantegazzianum* and native species based on Morisita-Horn index

	Overlap of visitor faunas with *H. mantegazzianum* [%]
Linaria vulgaris	14.5
Lotus corniculatus	18.1
Digitalis purpurea	21.4
Salvia nemorosa	36.9
Campanula poscharskyana	69.4
Scabiose japonica	72.1
Lythrum salicaria	77.7

4.4.2 Overall insect visitation

There was a statistical significant difference between the total number of visits between invaded and uninvaded plots (Tab. 4.1). This was mainly due to visits on umbels of the invasive species (Fig. 4.2). There was no difference in the magnitude of visitation of co-flowering plants with or without *H. mantegazzianum.* Different insect groups showed a different reaction to the presence of the alien plant species: Syrphini and honeybees were frequently found visiting both the invader and other plant species. While there was an increase in their overall presence in study sites with the invader (more than three-fold for honeybees), their visitation to the co-flowering plant species remained constant. Other insects like bumblebees, solitary bees (mostly Halictidae and Andrenidae) or Lepidoptera showed little or no affection for *H. mantegazzianum*. There was a slight increase in their visitation in networks with the invader, but the proportion of visits to the invader was small. Syrphidae, wasps, Coleoptera, and flies (= Calliphoridae, Muscidae, Sarcophagidae, Tachinidae) were only marginally present in networks without *H. mantegazzianum*, but showed a pronounced increase in their numbers in networks with the invader. This increase was solely caused by visits to *H. mantegazzianum*.

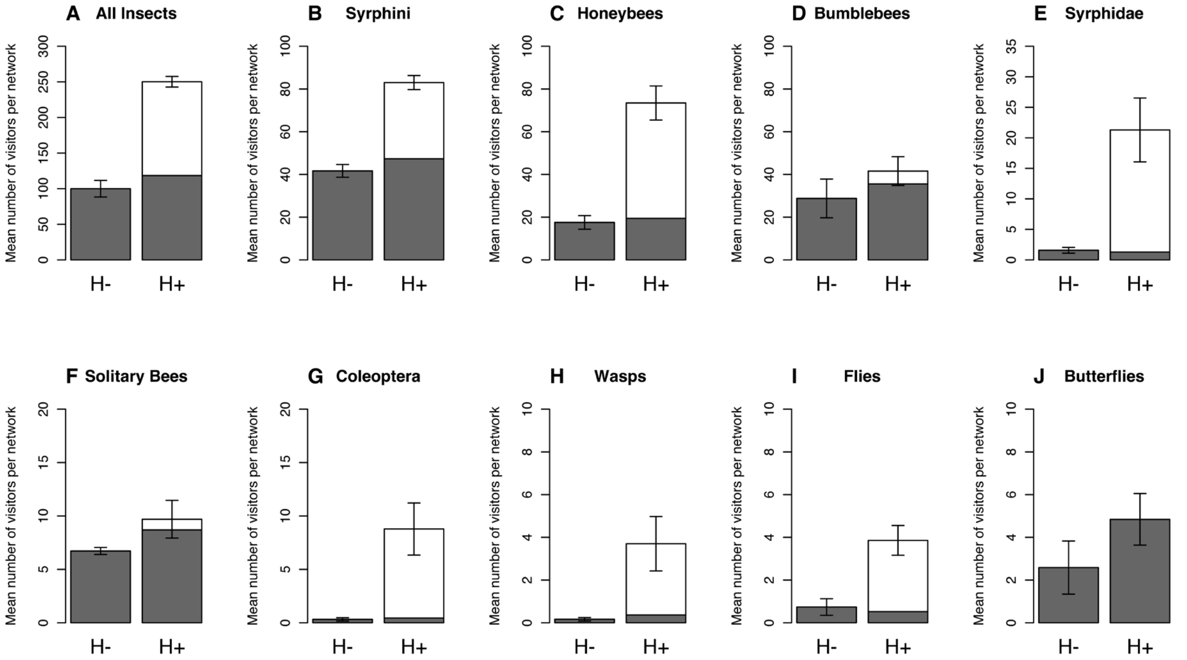

Figure 4.2 a-j: Mean visitation rates of insect groups in control (H-) and invaded plots (H+). Visits to native plants are shaded grey, visits to *H. mantegazzianum* white. Error bars show standard error for the total visitation (n = 3). Mind different scales.

4.4.3 Network Parameters

All calculated two-mode network parameters were significantly different from randomly arranged data produced by null models. Connectance in networks with *H. mantegazzianum* was lower than in the networks where the invader was not present (Tab. 4.3). The "classical" nestedness temperature indicator showed no difference between the invaded and the control treatment. The weighted index showed a slight increase of nestedness for the network containing the alien. There were minimal fluctuations in the degree (the total number of insect species a plant interacts with) of plants growing with or without the invader (Tab. 4.4), however there was no statistical difference in the degree of co-flowering plants between invaded and control plots (Scheirer-Ray-Hare test p > 0.05). Note that, while there was a tendency that degree (i.e. the number of interacting insect species) of most plant species decreased slightly, *S. japonica* interacted with more species when the invader is present (Tab. 4.4). The normalized degree (the percentage of interacting and occurring insects) of co-flowering plants was not significantly

Table 4.3: Two-mode parameters for control and invaded networks. Data show the mean of the 3 replicates for each treatment. ± SD

Connectance		**Nestedness**		**weighted Nestedness**	
control	invaded	control	invaded	control	invaded
0.40 ± 0.01	0.34 ± 0.03	21.51 ± 7.60	21.07 ± 1.75	0.46 ± 0.15	0.57 ± 0.06

Table 4.4: Degree (number of interaction partners) and normalized degree (ratio of interaction partners and available interaction partners) for plant species in control and invaded networks. Data show the mean of the 3 replicates for each treatment ± SD

	Degree		**normalized Degree**	
	control	invaded	control	invaded
C. poscharskyana	9.00 ± 2.00	8.00 ± 1.00	0.51 ± 0.09	0.35 ± 0.06
Digitalis purpurea	7.33 ± 0.58	6.00 ± 0.00	0.42 ± 0.04	0.26 ± 0.01
H. mantegazzianum	-	13.33 ± 2.31	-	0.58 ± 0.08
Linaria vulgaris	2.67 ± 0.58	3.00 ± 1.00	0.15 ± 0.02	0.13 ± 0.04
Lotus corniculatus	4 00 ± 1.00	4.00 ± 1.00	0.22 ± 0.02	0.17 ± 0.05
Lythrum salicaria	9.33 ± 1.15	9.33 ± 1.00	0.54 ± 0.11	0.41 ± 0.09
Salvia nemorosa	6.67 ± 2.52	6.00 ± 2.08	0.38 ± 0.14	0.26 ± 0.05
Scabiosa japonica	10.33 ± 3.21	12.67 ± 2.08	0.58 ± 0.08	0.55 ± 0.07

different between control and invaded plots. A high normalized degree indicates a high level of generalization. It was generally lower for co-flowering plants in invaded networks, but not significantly different in the mean (Scheirer-Ray-Hare test $p > 0.05$). In control plots *S. japonica* was the most generalized plant, while *H. mantegazzianum* had the highest normalized degree in invaded plots.

4.4.4 Centrality

In networks without the invader *L. salicaria* had the highest closeness i.e. was the species that had the highest potential to influence other plant species. While there was no significant effect on overall closeness of co-flowering plants (Scheirer-Ray-Hare test $p > 0.05$), there were changes on the species level due to the presence of the invader. Closeness of *L. salicaria* was lower than the closeness of *H. mantegazzianum* in invaded networks. Betweenness for most plants was zero, which indicated that they were not important as keystone species or hubs. *L. salicaria* was a keystone species both in the presence and absence of the invader, although its importance was somewhat diminished when *H. mantegazzianum* is present (Tab. 4.5). *H. mantegazzianum* also showed a non-zero betweenness which indicated that it played a role as keystone species in invaded networks. Figure 4.3 shows a projection of (cumulative) one-mode networks that underline the importance of *H. mantegazzianum* in an invaded network.

Table 4.5: Centrality scores for plant species in control and invaded networks. Data show the mean of the 3 replicates for each treatment. ± SD

	Closeness		**Betweenness**	
	control	invaded	control	invaded
C. poscharskyana	0.17 ± 0.03	0.12 ± 0.01	0	0
Digitalis purpurea	0.13 ± 0.01	0.10 ± 0.00	0	0
H. mantegazzianum	-	0.28 ± 0.04	-	3 ± 2
Linaria vulgaris	0.07 ± 0.00	0.05 ± 0.01	0	0
Lotus corniculatus	0.11 ± 0.04	0.08 ± 0.01	0	0
Lythrum salicaria	0.31 ± 0.04	0.22 ± 0.00	5 ± 2	1 ± 1
Salvia nemorosa	0.14 ± 0.04	0.09 ± 0.02	0	0
Scabiosa japonica	0.19 ± 0.01	0.14 ± 0.02	0	0

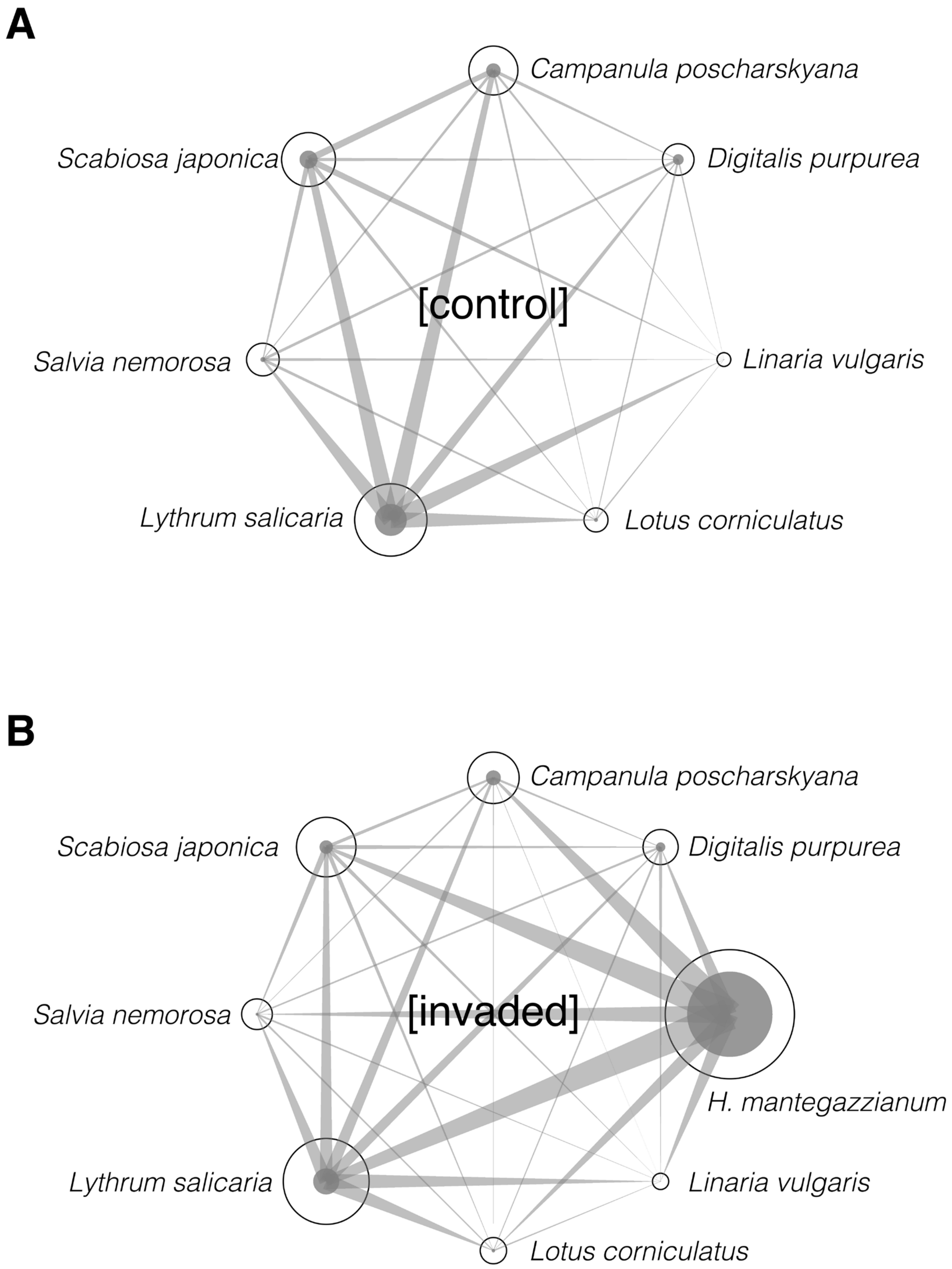

Figure 4.3 a, b: Projection of cumulative one-mode networks for the control and the invaded treatment following Morris et al. 2005. Thickness of lines indicates strength of interactions, size of nodes the total number of visits grains found for a species in a network.

4.4.5 Network congruence

The percentage of congruence between the control and the invaded network was weak (16.71%) and not significant (p = 0.367). This indicates that there was no correlation in the patterns of insect visitation in the control and the invaded network. Residuals of Procrustes analysis are shown in Table 4.6 the values show the deviation of two corresponding points i.e. for which plant the visitation data changed the most under the influence of *H. mantegazzianum*. *L. salicaria* showed the highest residual, indicating that the highest amount of change occursed on this plant.

Table 4.6: Results for Procrustes analysis. Residuals indicate the deviation between corresponding points, in this case the differences for each plant species between the control and invaded network.

	Residuals
Campanula poscharskyana	0.247
Digitalis purpurea	0.209
Linaria vulgaris	0.241
Lotus corniculatus	0.210
Lythrum salicaria	0.619
Salvia nemorosa	0.170
Scabiosa japonica	0.292
Congruence [%]: 16.71 (p = 0.367)	

4.5 Discussion

4.5.1 Visitation and seed set

H. mantegazzianum did not affect the reproductive success of co-flowering plant species. There were neither competitive effects, nor was there evidence for facilitation, because strictly speaking facilitation does only occur when seed set is increased (Feldman et al. 2004). However, visitation rates for some plants were enhanced, this effect is most pronounced for *L. salicaria* where the presence of *H. mantegazzianum* lead to a 35% increase of visitation rates. It is possible that the lack of power of the non-parametric statistics that were used prevented me from finding any significance. Nevertheless, the enhancement of visitation rates for *L. salicaria* did not translate into a gain in seed set. It seems that the pool of potential pollinators was not limited. Since the most common visitors to my plots were Syrphini, honeybees and bumblebees, a limitation would indeed be very much unlikely as these animals appear in large numbers and are virtually ubiquitous. Also, it has to be taken into consideration that, while individual visitation rates varied, the plants in my experiment received a considerable amount of visits, mostly from social insects, so it is plausible that these plants were not pollinator limited.

Nevertheless, altered visitation rates for *L. salicaria* and changes in the degree and level of generalization for other plants indicated a change in the interactions of the community caused by the presence of *H. mantegazzianum*. This supports the view of other studies that the floral context can influence interaction patterns in a community of plants and pollinators (Lázaro et al. 2009, Flanagan et al. 2011). Alas, when the reproductive success of plants is not affected these changes are of little ecological consequence at least on a short timescale. Additionally, seed set could be more robust than visitation: the impact of an alien plant on visitation does not necessarily translate into an impact on seed set (Totland et al. 2006, Bartomeus et al. 2010). Dietzsch et al. (2011) proposed a robust breeding system, which means a system that is not sensitive to a reduction of visitation, as a mechanism that avoided that the negative influence of an alien plant on *Digitalis purpurea* (which was also present in my networks) translated into seed set.

My results are in contrast with a recent meta-analysis (Morales and Traveset 2009), which found a predominantly negative effect of alien plants on the reproduction of native plants. However, a study that explored the impact of *H. mantegazzianum* on co-flowering *Mimulus*-plants found an effect very similar to my data, a slight enhancement of visitation rates and a neutral effect on seed set (Nielsen et al. 2008). Most evidence of negative effects,however, comes from pairwise interaction studies, and the effect of an alien plant may differ, dependent on the native species. For instance, Larson et al. (2006) found that the infestation with the alien *Euphorbia esula* resulted in a range of effects on visitation rates dependent on the identity of the native plant and the season. Similar results were found for the invasive *Carprobrotus* spp.,where the effect on visitation of co-flowering natives ranged from facilitative to competitive, but the effect on seedset was neutral (Moragues and Traveset 2005, Jakobsson et al. 2008). Recently, Kaiser-Bunbury et al. (2011) found that the presence of alien plants did not reduce fruit set of native plants and that it even may enhance fruit set for some species. While community wide studies arguably lack the precision of a pairwise approach (Morales and Aizen 2006), my data and other evidence suggest that alien plants do not generally have a negative impact on the reproductive success of native plant communities.

4.5.2 Overall insect visitation

While the number of total visits was doubled in plots containing *H. mantegazzianum*, overall visitation to co-flowering plants remained constant. The additional visitors visited almost exclusively the invader. A similar effect was found by Totland et al. (2006), albeit they also recorded a decrease in visitation to native plants, which was not the case in my study. Furthermore, different insect groups responded differently to the presence of *H. mantegazzianum*. I propose different foraging strategies of insect groups as a plausible explanation for the perceived pattern. The ability to react appropriately to changes in resource availability in order to maximize energy intake is described by optimal foraging theory (OFT) (Emlen 1966, MacArthur and Pianka 1966). Flower constancy, the capacity of insects to restrict visit to a certain flower and skip other rewarding resources (Waser 1986, Chittka et al. 1999) as a means to optimize foraging behavior has been shown for honeybees, bumblebees as well as syrphids (Grant 1950, Free 1963, 1970, Goulson and Wright 1998). Nevertheless, flower constancy does not mean that an animal visits one plant species exclusively, as it is dependent on plant density (Kunin 1997, Kunin and Iwasa 1996, Bosch and Waser 2001), as well as pollinator density (Fontaine et al. 2008, Inouye 1978). It is conceivable that *H. mantegazzianum* as highly rewarding, cornucopian, species (Mosquin 1971, Corbet 2006, chapter 3) causes flower constant visitors, especially honeybees, to concentrate on this resource. Floral constancy of most of the visiting insect species might limit transitions of foraging insects from one plant to another. When honeybees recruited additional workers that visit *H. mantegazzianum* and predominantly stayed true to this resource this could explain the absence of any effects on seed set, as this would neither affect the quantity nor the quality of insect visitation. Flower constancy has been used by other studies to explain limited competitive effects between plants that share pollinators (McGuire and Armbruster 1991, Feldman 2008, Yang et al. 2007, Ollerton et al. 2007). In contrast to my findings there are studies that show negative effects on seed set caused by honeybees (Brown and Mitchell 2001, Brown et al. 2002). Alas, these experiments used arrays of similar flowers (namely two *Lythrum* species), which may have caused honeybees to forage among them indiscriminately (Kunin 1993, Klinkhamer et al. 2001). Nevertheless, my experiment was designed to study the quantity component of pollination; the quality component was only accessed indirectly in terms of seed set. Alternatively, it is possible that heterospecific pollen transfer occurs, but has no effect on seed set (Montgomery 2009, Tscheulin et al. 2009). In contrast to this hypothesis seed set of plants hand-pollinated with *H. mantegazzianum* pollen was found to be negatively affected (Nielsen et al. 2008). The challenge for future studies will be to quantify the amount of alien pollen transferred to co-flowering species.

4.5.3 Network parameters

H. mantegazzianum was not only well integrated into the plant-pollinator network, but found to be dominating plant pollinator interactions. Centrality measures indicated not only its importance as a keystone species in the network, but also point to a reduced importance of the other plants. This and the low congruence in the Procrustes analysis indicate that the invader was able to change the structure of a plant pollinator network. However, other network parameters like connectance or nestedness remained largely unchanged in the presence of the invader. Co-flowering plants did not interact with less insect species in invaded plots. One plant species (*S. japonica*) even had more interaction partners when *H. mantegazzianum* was present. In the invaded networks there were more insects groups present than in the networks without the invader. However, these additional insect groups tend to visit *H. mantegazzianum* almost exclusively. This leads to a decrease of the normalized degree of co-flowering plant species. They become apparently more specialized in terms of numbers of interaction partners, because they interact with less of the "available" insect groups. This was also the reason why I found a slightly lower connectance in invaded plots.

Many of my findings are in congruence with other studies on the impact of alien plants on pollination networks. Alien plants are mostly well integrated in native pollination networks (e.g. Memmott and Waser 2002, Morales and Aizen 2006, Bartomeus et al. 2008a, b). Additionally, super-generalist aliens often act as keystone or core species (Aizen et al. 2008, Valdovinos 2009, Vilà et al. 2009). In my case I believe it is logical that *H. mantegazzianum* had this role when I look at the part that other super-generalist plant species, especially Apiaceae, play in pollination networks (Olesen et al. 2007, Martín González et al. 2010). Some authors pointed out that super-generalist aliens become keystones at the expense of a changed network architecture causing detriment to those networks (Aizen et al. 2008). On the other hand, studies that simulated the removal of alien plants found that established alien plants are important for the persistence of pollination networks (Carvalheiro et al. 2008, Valdovinos et al. 2009). A changed network structure might also be a more robust structure. In this regard nestedness is mentioned as a feature that increases robustness of pollination networks (Bascompte 2003, Memmott et al. 2004, Jordano et al. 2006). While the impact of the invader in my study on nestedness is not pronounced, it rather increased than reduced it. Super-generalist aliens increased nestedness pattern in other studies (Bartomeus 2008a, Padrón et al. 2009). This is not an unexpected effect. A species that is very generalized will naturally enhance the effect that specialized species interact with a subset of the interaction partners of generalized species (i.e. form a nested pattern). Nevertheless, as *H. mantegazzianum* is also important as connector it might increase the tolerance of the invaded network to species extinctions.

Another negative impact of alien plants is the shift of links from native to alien plants (Aizen et al. 2008). This was not found in my study, I argue that the invader simply creates new links without a loss of links for native plants (Padrón et al. 2009). Also, as pointed out above, higher densities might lead to partitioning of resources by insect visitors, which would provide another view than usurpation of links for the same pattern. When this happens, without an impact on reproductive success for invaded plant communities (as in my study) it is arguable to call this effect detrimental. Nevertheless, Aizen et al. (2008) studied systems where alien plants and alien pollinators occurred. These invader complexes (e.g. Barthell et al. 2001) might be more destructive than a single alien plant species (Vilà et al. 2009). On the other hand, recent studies reveal that alien plants and alien pollinators do not necessarily have a negative impact on native reproduction success or cause detriment to plant pollinator networks (Kaiser-Bunbury and Müller 2009, Kaiser-Bunbury et al. 2011). In conclusion, while my data indicates that *H. mantegazzianum* has no detrimental effect on plant-pollinator networks and other studies report similar effects, it is unclear if this is generally the case for all alien plants. Furthermore, it has to be considered that other effects like alien abundance (Muñoz and Cavieres 2008, Dietzsch et al. 2011), spatial scale (Cariveau and Norton 2009, Yang et al. 2011), or landscape parameters (Bartomeus et al. 2010) might influence the outcome of competition for pollination of alien and native plants.

4.5.4 Conclusion

H. mantegazzianum was able to change the network structure of invaded communities but without any impact on reproductive success of co-flowering plants. As an explanation I propose two factors: No limitation of the pool of potential pollinators and floral constancy of the most important insect groups. The invaded plant community is likely to persist, as both facilitative and competitive effects could lead to a change in plant community assembly (Sargent and Ackerly 2007). There is need to address the lack of information how insect behavior really affects interaction and heterospecific pollen transfer in order to verify my assumptions. A more precise understanding of the inner workings of a plant-pollinator network exposed to invasion would lead to a more precise estimation of the impacts of *H. mantegazzianum* and other alien plants on native plant pollinator interactions.

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5. Impacts of the invasive alien *Heracleum mantegazzianum* on the quality of pollination and pollen transport networks

5.1 Abstract

Previous studies found the alien invasive plant *Heracleum mantegazzianum* not only to be highly visited but also dominating invaded visitation webs. However, the neutral effect of the invader on reproductive success raised further questions on how the alien affects interspecific pollen transfer. In this study I used an experimental garden setup in order to test, whether floral constancy limits alien pollen carryover, or if the domination of the alien in terms of visitation translates into high amount of heterospecific pollen transport to co-flowering species. Furthermore, two-mode and one-mode network parameters of networks based on visitation, actual interaction and interspecific pollen transfer were explored. Results show that while flower visitors of *H. mantegazzianum* are less constant than on other plants and there are plant-to-plant interactions for all co-flowering plants, still little alien pollen is transport. Nevertheless, there is a potentially competitive effect of conspecific pollen loss depending on the plant species. Network analysis shows that the alien plant is only dominant in terms of visitation but not in terms of interspecific pollen transport. This highlights that both, the quantity and the quality component, need to be assessed to create a complete picture on the impact of an invader on plant-pollinator systems.

5.2 Introduction

Pollination by animals is one of the most fundamental ecosystem services, essential for the reproduction of nearly 90 % of all angiosperms (Ollerton et al. 2011). Two components determine the interactions of a plant and its pollinators. The first is commonly addressed as quantity component and describes the number of visits by pollinators on a certain plant (Herrera 1989). The second called the quality component describes the pollination efficiency of the different flower visitors (Herrera 1987), and is often investigated by the number of pollen grains, which pollinators are able to deposit on a plant's receptive organ. Both components may be affected by competition for pollinators. Plants may compete for pollinators, when they use the same animals as pollen vectors (pollinator sharing), flower at the same time and have no other separating mechanisms (Levin and Anderson 1970, Rathcke 1983). Mechanisms, which avoid competitive effects caused by shared pollinators, include evolutionary displacement of floral characters (e.g.

Armbruster et al. 1994), spatial separation of plant species (e.g. Kephart 1983), or flower constancy of shared pollinators (e.g. Ollerton et al. 2007). Nevertheless, competition for pollination services seems to be a commonplace challenge for plants (Mitchell et al. 2009). Competitive effects have an impact on the quantity component by reducing visitation for the competitively inferior plant as pollinators are "usurped" by the superior plant. Ultimately, this may lead to a reduction in fertilization and seed set. The impacts on quality components are a bit more complex: Pollinator sharing may lead to the deposition of heterospecific pollen on plants' receptive organs and to the loss of conspecific pollen, which might be deposited on the receptive organs of other plants. Negative impacts, which appear under heterospecific pollen transfer, include: clogging, stigma closure, allelopathic inhibition of pollen germination and usurpation of ovules (Waser and Fugate 1986, Galen and Gregory 1989, Morales and Traveset 2008 and references cited therein). Heterospecific pollen deposition has an impact on the female fitness, while the loss of pollen to other plants negatively affects male fitness, when pollen grains are "wrongly" transferred to other plants (pollen wastage) (Waser 1986), reducing the number of pollen transported to other conspecific plants (Campbell and Motten 1985). Studies have shown that this may lead to a negative impact on seed set (Waser and Fugate 1986, Caruso and Alfaro 2000). Besides a reduction of seed set this may also affect outcrossing negatively (Campbell 1985, Bell et al. 2005). The impact of a competing plant species is not necessarily perceived in both components of pollination in the same way. Furthermore, there might be also positive effects of co-flowering plants. For example, highly attractive plants may increase the visitation rates of co-flowering species (Thomson 1978, Johnson et al. 2003, Moeller 2004, Ghazoul 2006). However, this so-called magnet species effect may increase heterospecific pollen transfer (Rathcke 1983, Morales and Traveset 2008), when pollinators frequently switch between the magnet species and co-flowering plants.

Alien plants, which are mostly pollination generalists with large showy inflorescences as they were often introduced as ornamentals (Stout and Morales 2009), are most likely to cause competition for pollination services, which may lead to disruption of interaction patterns of native plants and their pollinators (reviewed in: Richardson and Traveset 2006, Bjerknes et al. 2007). Seed set may be negatively affected by alien plants through the quantity component (e.g. Chittka and Schürkens 2001, Ghazoul 2004, Brown et al. 2002) as well as the quality component (e.g. Kandori et al. 2009). Alien plants have been found to dominate pollen transportation in invaded sites (Lopezaraiza-Mikel et al. 2007). In a recent review of interspecific pollen transfer, Morales and Traveset (2008) conclude that the dominance of alien plants in pollen transport translates in magnitudes of heterospecific pollen transfer that will impair pollination. Other studies show that heterospecific pollen deposition by an alien reduced seed set of a native plant (Brown and Mitchell 2001, Flanagan et al. 2009, Matsumoto et al. 2010, Da Silva and Sargent 2011, but see Moragues and Traveset 2005, Tscheulin et al. 2009). However, species do not interact in a vacuum, but in the context of interaction networks (Bascompte and Jordano, 2007). Studies found aliens plants well integrated into mutualistic networks by generalist pollinators (Vilà et al. 2009, Padrón 2010). Alien plants often dominate the plant-pollinator networks they invade (Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008a,b) sometimes to a point where they cause a detrimental effect on mutualistic interactions of native plants and their pollinators (Aizen et al. 2008). Alas, most networks studies are based on visitation rather than on pollen transfer (but see Forup and Memmott 2005, Gibson et al. 2006, Bartomeus et al. 2008a, Alarcòn 2010). The information that is available today is restricted to the integration of alien into visitation networks, but little is known how this really affects the patterns of hetero- and conspecific pollen transfer (the quality of pollination) and ultimately reproductive success.

Aim of this study is to scrutinize the impact of the alien *Heracleum mantegazzianum* on hetero- and conspecific pollen transfer for co-flowering plants. Furthermore, I used a network approach to explore, if the alien was able to change the pollen transport pattern in a community-context. In a previous study I found the alien *H. mantegazzianum* attracting more insects to invaded plots and slightly enhancing the visitation rates of co-flowering species (chapter 4). Although high levels of pollinator sharing were detected, at least for some of the focal species, was not lowered for native species (chapter 4). I hypothesized that the floral constancy of the invader's main pollinator *A. mellifera* limited interactions (and pollen carryover) between the alien and co-flowering plants. Alternatively it is possible that alien pollen is transferred to co-flowering species, but it does not affect seed set, although Nielsen et al. (2008) found a negative effect of *H. mantegazzianum* pollen on the seed set of *Mimulus guttatus*-plants hand-pollinated with *H. mantegazzianum* pollen. Furthermore, *H. mantegazzainum* was found to dominate and change visitation webs and to be a keystone species invaded networks (chapter 4). My aim was to investigate whether this dominance is also found in webs based on actual interaction (i.e. only contains insect that carry pollen between at least two plant species), or interspecific pollen transport (a web based on heterospecific pollen as interaction strength).

The following key question were scrutinized by the means of an experimental garden setup:

1. How does pollinator behavior influence plant-to-plant interactions in a plant-pollinator system invaded by the alien plant species *H. mantegazzianum*?

It was hypothesized that visitors (especially honeybees) to *H. mantegazzianum* show significant flower constancy to this "cornucopian" resource, thus limiting interactions between the alien and co-flowering plants.

2. How does the alien plant affect interspecific pollen transfer?

Especially when Hypothesis 1 proofs to be falsified, it is possible that the presence of *H. mantegazzianum* leads to an increase of heterospecific pollen transport and to a reduction of conspecific pollen transport for co-flowering plants.

3. How does the presence of *H. mantegazzianum* affect a interaction network based on pollen transport? As pointed out above, *H. mantegazzianum* is a well-integrated keystone species in visitation networks. The interplay of the factors of the first two question will determine whether this domination in visitation webs translates into the same in pollen transport networks.

5.3 Materials and Methods

5.3.1 Plant species

Heracleum mantegazzianum (Apiaceae), Giant Hogweed, is an up to 5 m tall monocarpic weed that has been naturalized in many countries of Central Europe and North America. For further information see Tiley et al. 1996.

The following seven plant species were used as focal species:

Campanula poscharskyana (Campanulaceae) is a perennial plant with open violet colored flowers, plants are trailing and can grow up to 30 cm.

Centaurea cyanus (Asteraceae), Cornflower, is an annual plant, which flowers are blue and arranged in capitula 1.5–3 cm in diameter, with a ring of a few large, spreading ray florets surrounding a central cluster of disc florets. Plants reach heights of 100 cm.

Digitalis purpurea (Plantaginaceae), Common Foxglove is a herbaceous biennial. Plants are up to 2 m tall; flowers are pink, tubular, zygomorphic and arranged in dense inflorescences.

Lupinus polyphyllus (Fabaceae), Garden Lupine, grows up to 150 cm and is a perennial plant native to North America naturalized in Germany, flowers are zygomorphic and of a deep violet.

Nepeta cataria (Laminacae), Catnip, is perennial plant up to 60 cm tall, flowers are violet and zygomorphic.

Phacelia tanacetifolia (Boraginaceae) is an annual plant growing up to 120 cm native to North America; flowers are blue, bell-shaped and arranged in dense inflorescences.

Salvia officinalis (Laminaceae), Garden Sage, is a perennial plant, which grows up to 60 cm. Flowers are pink and zygomorphic.

Scabiosa japonica (Dipsacaceae) is an annual plant that reaches heights up to 30 cm. Flowers are small, pale violet and arranged in heads that are ca. 4 cm in diameter.

H. mantegazzianum plants were extracted from a field site nearby the campus of Bielefeld University in May a year prior to the experiment. They were planted in pots and overwintered on the site of the experiment. Some of the focal plants were cultivated from seeds in the spring of the same year (*C. cyanus, P. tanacetifolia*), or consisted of plants that were cultivated a year earlier (*S. officinalis*), while other plants were bought from local plant nurseries (*C. poscharskyana, D. purpurea, L. polyphyllus, N. cataria, S. japonica*).

5.3.2 Experimental garden setup

The idea behind the garden experiment was to create artificial networks in the way of an addition experiment keeping density of co-flowering focal species constant, so that effects are not confounded with density effects (Mitchell et al. 2009).

I selected a meadow situated on the campus of the Bielefeld University. Six study sites (plots) were created on this meadow. The meadow was mown prior to the installment of the plots. The minimum of space between to sites was 4 m, which was found sufficient space to avoid alien pollen carryover by other studies (Montgomery 2009, Takakura et al. 2011). Furthermore, several tall oak trees that grew on the whole site provided further separation. I created an artificial network on each of the plots by arranging eight pots of each plant species in a circular design. 4 plants of each species were put together as a patch and patches were randomly arranged in a circle of ca. 3 m diameter. As the number of available plants was low for *S. japonica* and *C. poscharskyana* only one patch (four pots) of these species was used in each network. Five pots with blooming *H. mantegazzianum* plants were assigned to each of the three invaded networks and placed in the middle, whereas this space was left free in the control treatment. Furthermore, I counted the open inflorescences at the beginning of my experiment, when a pot had less open inflorescences than another I added additional pots of a certain plant species to ensure homogeneity between plots. In total each plot contained between 56-60 potted plants. I continued to count open inflorescences throughout the experiment; the deviation for each plant species and plot was between ± 1-9.6 % depending on the plant species.

5.3.3 Sampling of insect pollen loads

H. mantegazzianum plants started blooming in the end of June 2010. Sampling started on 25th of June and lasted until 11th of July 2010. Each network was sampled by walking a round transect for an hour catching each insect that was spotted on a flower. Species were morphotyped and the identity of the plant species they were caught on was recorded. Insects were caught in glass jars. These jars had perforated lids so that the vapors of ethyl acetate could enter the jar when it was placed over a killing jar containing gypsum that was saturated with the substance. The thus euthanized insect were put in a -20 °C freezer for later analysis. Jars used to catch insect were carefully wiped with alcohol to avoid contamination. A fuchsin gel cube was used to dap pollen off the bodies of defrosted insects (Kearns and Inouye 1993). It was carefully avoided to sample pollen that was attached to corbiculae of bees. The fuchsin cube was melted on a microscope slide and the pollen was counted. Pollen was identified using a microscope and a reference collection of pollen of the plant species used in the experiment. A total of 670 insects was caught and analyzed.

5.3.4 Interaction and pollen transport

Insect pollen loads in combination with the identity of the plant species an insect was caught on were used in order to find out which plant species interact with each other. That means an interaction for each plant was recorded when an animal was caught at that plant or was found carrying pollen of that plant. As pollinators often carried more than one pollen species a total of 1051 plant-to-plant interactions was recorded. For each plant I calculated the proportion of interactions that were heterospecific. Heterospecific pollen that was potentially transferred was calculated in a similar fashion: The total number of pollen grains that were heterospecific was assessed for all insects that interacted with a plant species.

5.3.5 Constancy index

In order to describe the floral constancy of foraging insects I used an index adapted from Jacob's preference index (Jacobs 1974) by Gegear and Laverty (2005). This index incorporates the general preference of a certain insect species for a certain resource and shows whether insects deliberately choose to or not to re-visited a plant species. It is calculated as CI = (c-e)/(c+e-2ce), where c is the proportion of conspecific interactions and e is the expected frequency of interactions (i.e. the proportion of visits carried out by all the individuals to certain plant species). An index above zero indicates flower constant behavior, whereas values below zero show inconstant foraging behavior, and zero values indicate random foraging. I calculated this index for each plant and each functional group (e.g. bumblebees) of foraging insects. Basis for this analysis were all insects that were either caught on a certain plant species or carried pollen of that plant. I calculated the relative abundance of all those individuals that carried either pollen of another plant species or were caught on another plant species.

5.3.6 Network parameters

Three different types of network were created from the gathered data: A visitation, an interaction and a (interspecific) pollen transport network. The first was based on the abundances of insect caught on each plant species. In the second I only used insects that showed interaction between at least plant species, that means either insects that carried at least two different kinds of pollen grains or were caught at a plant species carrying heterospecific pollen. The same data was used to create the last network, but instead of the abundance of each insect morphospecies the total number of transported heterospecific pollen grains was used as interaction strength. For each network parameters based on two-mode and one mode data were created. Two-mode data describe the interaction of two sets of interaction partners (here animals and plants). Such a network is also called a bipartite network. It is created by putting the sums of all visits for all plants in a matrix (plants x animals). Indices for two-mode networks used in this study were connectance and nestedness. Connectance is the quotient of realized links and all possible links (Dunne et al. 2002). Nestedness is a typical feature of plant-pollinator networks (Bascompte 2003). It describes the fact that the interaction partners of the most specialized species are a subset of the interaction partners of the most generalized species. Nestedness can be perceived as a measure of order in a system (Jordano et al. 2006). A possible impact of an invasive species could be to decrease nestedness and create a less ordered system. I calculated the “classical” nestedness index (Rodríguez-Girónes and Santamaría 2006) that describes nestedness as temperature ranging from 0 (perfect nestedness) to 100 (perfect chaos). I used (N-100)/100 to create an index ranging from 1 (perfect nestedness) to 0 (perfect chaos) to facilitate comparability with an additional nestedness index I used that included the weight of interactions (Galeano et al. 2009). I tested connectance and nestedness against a null model of random associations (1000 runs; Patefield 1981) in order to evaluate whether stochastic processes or particular mechanisms produced structural patterns

Two-mode data can be transformed into one-mode (Olesen et al. 2006). One-mode networks describe the interactions of entities that belong to the same set (here: plants). I used one-mode data to calculate betweenness and closeness for each plant species. These so-called centrality scores were first introduced by Freeman (1979) and used in social networks. Recently they have been employed to identify plant species that are important for the overall coherence of a network (keystone species) (Martín González et al. 2010). In my study I used an algorithm proposed by Opsahl et al. (2009) that via a tuning parameter called alpha, is able to incorporate both number of connected nodes and tie weight. In this study I used an alpha of 0.5 to place an equal weight on tie strength and number of nodes. Closeness is based on the shortest path between a plant species and the other species. A high closeness describes the fact that such a species can easily influence others in a network. Betweenness is the sum of shortest paths between all plant species that pass through a certain plant species. A plant with a betweenness higher than zero connects parts of a network that otherwise would be unconnected, thus forming hubs or keystone species.

5.3.7 Data analysis

All data analysis was carried out using R statistical language version 2.13.0 (R Development Core Team 2011). The packages bipartite 1.16 (Dormann et al. 2009), tnet 3.0.5 (Opsahl 2009) and vegan 1.17-10 (Oksanen et al. 2011) were used. As data was not normally distributed and could not be transformed to meet the criteria of normal distribution nom-parametric test were used throughout. The effect of the influence of the invader on plant-plant interactions was tested by using a χ^2-test. The statistical significance of the influence of the invader on pollen loads was tested with a test developed by Scheirer et al. (1976). This test can be regarded as a non-parametric equivalent to a two-way ANOVA. I programed this test into R following Sokal and Rohlf

(1995). Post-hoc testing was done by using multiple Wilcoxon rank sum tests including an error correction contrived by Benjamini and Hochberg (1995).

Congruence of networks were compared using Procrustes analysis, which employs an algorithm that minimizes the sum of squares of distances between corresponding points of two matrices (Jackson 1995, Peres-Neto and Jackson 2001, Alarcón et al. 2008). I used the same (plants x animals) matrices as I used to calculate two-mode networks, albeit, in order to avoid multiple comparisons, I created cumulative networks, which means I added observations I made for each treatment, thus creating one control network and one invaded network. The significance of the result was tested by a permutation test implemented in the protest function of the vegan package of R (10 000 permutations).

All data are presented ± standard error unless stated otherwise.

5.4 Results

5.4.1 Pollinator behavior and plant interactions

The pollinator constancy index (CI) describes the behavior of foraging insects (Tab. 5.1). Honeybees mostly displayed flower constant behavior, except when foraging on *S. japonica* (Tab. 5.1). Other pollinators exhibited a rather inconsistent pattern of foraging behavior. Especially bumblebees displayed a range of behavior from high levels of constancy to inconstancy, depending on the plant species. Furthermore, pollinators of *H. mantegazzianum* were not especially flower constant. In some cases pollinator behavior changed when *H. mantegazzianum* was present, but there was no consistent pattern of a reaction to the invasive plant. Interestingly, most foragers on *H. mantegazzianum* exhibited inconstancy, which means a tendency to interact with a heterospecific plant after an interaction with the invader. Furthermore, the constancy of honeybees to *H. mantegazzianum* was, compared to other plant species, rather low.

From the plant's perspective the different foraging patterns and the abundance of pollinating species led to a number of heterospecific interactions. The relative abundance of heterospecific interactions for all plants is displayed in Fig. 5.1. It can be read as the percentage of all visiting insects that potentially carried heterospecific pollen to a plant species they visited. For the invaded treatment (H+) the whole bar shows the total interaction with other plants, whereas the fraction of interaction with the alien plant is shown in white. The results of this analysis were tested for statistic significance by a Chi-Square test presented in Tab. 5.2. Interactions were significantly

Table 5.1: Constancy index for each functional insect groups and plant species. Values > 0 indicate flower constant, < 0 inconstant, and 0 random foraging behavior. Numbers in grey indicate n < 10.

control	Honey-bees	Bumble-bees	Flies	Solitary bees	Syrphidae	Syrphini	Vespidae
Centaurea cyanus	0.05	0.06	-1.00	-1.00	-1.00	0.10	-1.00
C. poscharskyana	0.20	-1.00	-	-1.00	-	-	-
Digitalis purpurea	0.89	0.81	-	1.00	-	-	-
Lupinus polyphyllus	0.98	0.35	-	1.00	-	-	-
Nepeta cataria	0.29	-0.01	-	-1.00	-	-0.27	-
P. tanacetifolia	0.79	-0.01	-1.00	-0.16	-	0.38	-
Scabiosa japonica	-1.00	-1.00	-1.00	0.82	-1.00	-1.00	-1.00
Salvia officinalis	0.98	0.05	-	-	-	-1.00	-
invaded	Honey-bees	Bumble-bees	Flies	Solitary bees	Syrphidae	Syrphini	Vespidae
Centaurea cyanus	0.18	-0.53	-1.00	-	-1.00	-0.22	-
C. poscharskyana	0.65	-1.00	-1.00	0.60	-	-1.00	-
Digitalis purpurea	0.91	0.88	-	1.00	-	-	-
H. mantegazzianum	0.29	-0.13	-0.43	0.64	-0.36	-0.65	-0.15
Lupinus polyphyllus	0.80	0.40	-	1.00	-	-	-
Nepeta cataria	0.37	-1.00	-	-	-1.00	-1.00	-
P.tanacetifolia	0.32	-0.08	-1.00	1.00	-1.00	0.03	-1.00
Scabiosa japonica	-0.08	-1.00	-1.00	-	-1.00	-1.00	-
Salvia officinalis	-1.00	0.90	-	-	-	-	-

Table 5.2: Results of the statistical analysis for plant-to-plant interaction (Chi-Square test) and pollen loads (Scheirer-Ray-Hare test). The interaction term was not significant in any analysis and is not shown here.

	χ^2		**Degrees of freedom**	**p**
Interaction				
Plant species	57.936		8	≤ 0.001
Treatment	0.647		1	0.421
	Sum of squares	**H**	**Degrees of freedom**	**p**
Heterospecific pollen loads				
Plant species	2704713.58	46.83	7	≤ 0.001
Treatment	31559.36	0.55	1	0.715
Total conspecific pollen loads				
Plant species	8969865.34	155.31	7	≤ 0.001
Treatment	213472.50	3.70	1	0.213
Pure conspecific pollen loads				
Plant species	1925295.45	33.34	7	≤ 0.001
Treatment	372605.52	6.45	1	0.046

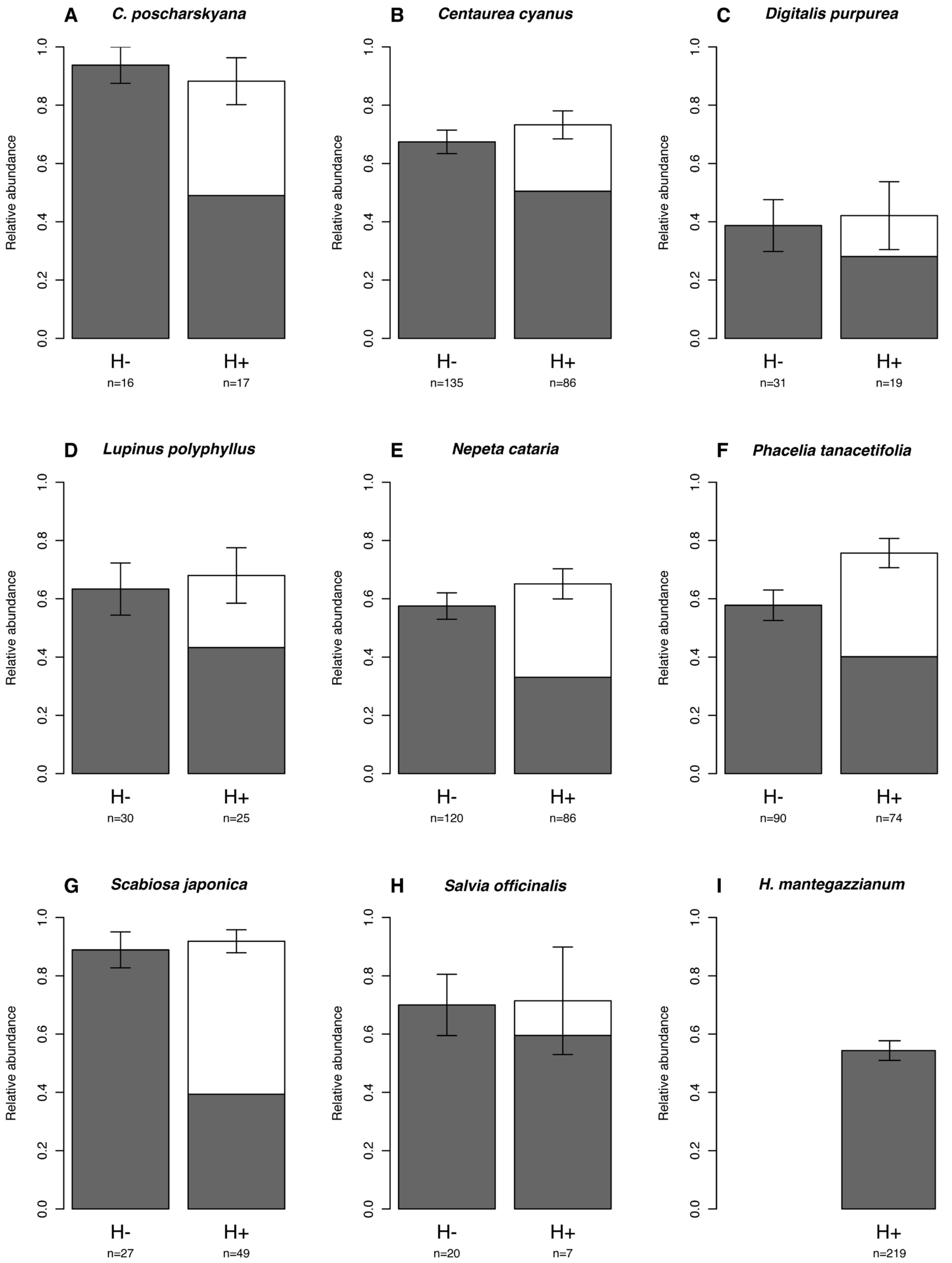

Figure 5.1 a-i: Average relative abundance of heterospecific interactions for all plant species for the control (H-) and the invaded treatment (H+). The proportion of interactions with the alien plant is shown in white. ± SE

different for the different plant species. While all plants interacted with other plants, there were some plants where the interaction with other plants occurred in less than 50% of the cases (*D. purpurea*) and other where nearly all interactions were with other plants (*C. poscharskyana, S. japonica*). All plants showed considerable interaction with the alien. However, the magnitude of alien interactions differed with the plant species. *S. officinalis* and *D. purpurea* experienced the lowest levels, with 12% resp. 14% of all interactions being with the alien, while *S. japonica* had the highest value with 52% of all interactions being with *H. mantegazzianum*. Values of other plants ranged between 25 and 35%. However, the presence of *H. mantegazzianum* did not alter the overall pattern of interaction for focal species. There was no statistical significant influence by the presence of the invader on the overall effect of interactions (Tab 5.2). While there was interaction with the alien for all plants, it did not account for more heterospecific interaction in most cases. Nevertheless, *P. tanacetifolia* showed a tendency for more heterospecific interactions, when *H. mantegazzianum* was present. Furthermore, *H. mantegazzianum* showed a value of 0.54. That means that of all animals that had an interaction with *H. mantegazzianum* 54% also interacted with co-flowering species. In other words 46% of all its visitors interacted solely with the invader.

5.4.2 Heterospecific pollen transport

Fig. 5.2 was calculated the same way as Fig. 5.1 only that it shows the heterospecific pollen loads potentially received by each plant instead of interactions. The results of the Scheirer-Ray-Hare test are presented in Tab. 5.2. While the overall effect of potential reception of heterospecific pollen was significantly different for each plant species, it did not change when *H. mantegazzianum* was present. However, there was a tendency for some plants that the total amount of heterospecific pollen was lower, when the invader was present. The fraction of *H. mantegazzianum* pollen that was potentially transferred to a certain plant species is shown in white. Compared to the relative abundance of interactions with the alien most plants experienced rather small alien pollen loads that were potentially transferred.

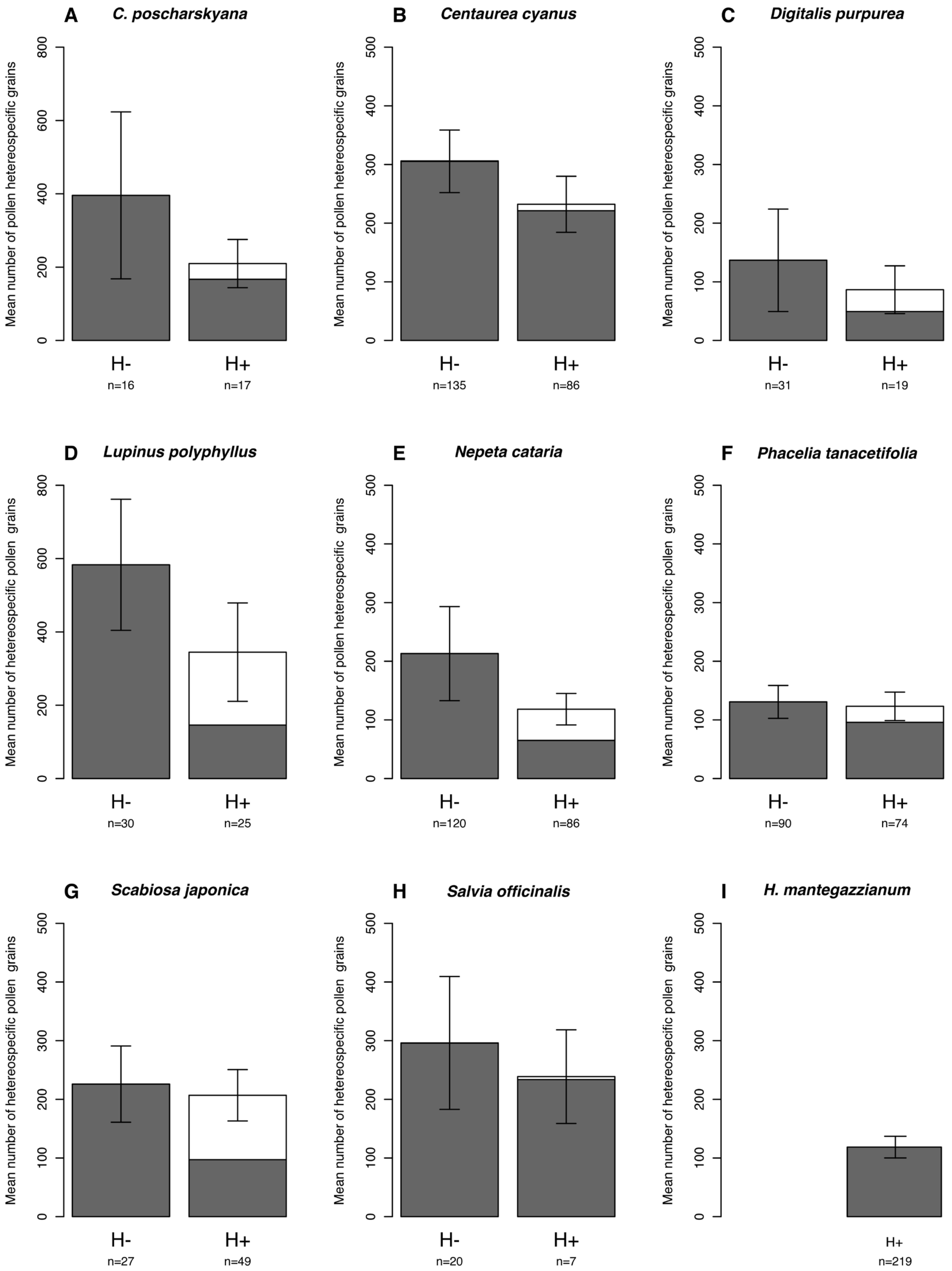

Figure 5.2 a-i: Average number of heterospecific pollen grains potentially transferred to each plant species for the control (H-) and the invaded treatment (H+). The proportion of *H. mantegazzianum* pollen is shown in white. ± SE. Mind different scales.

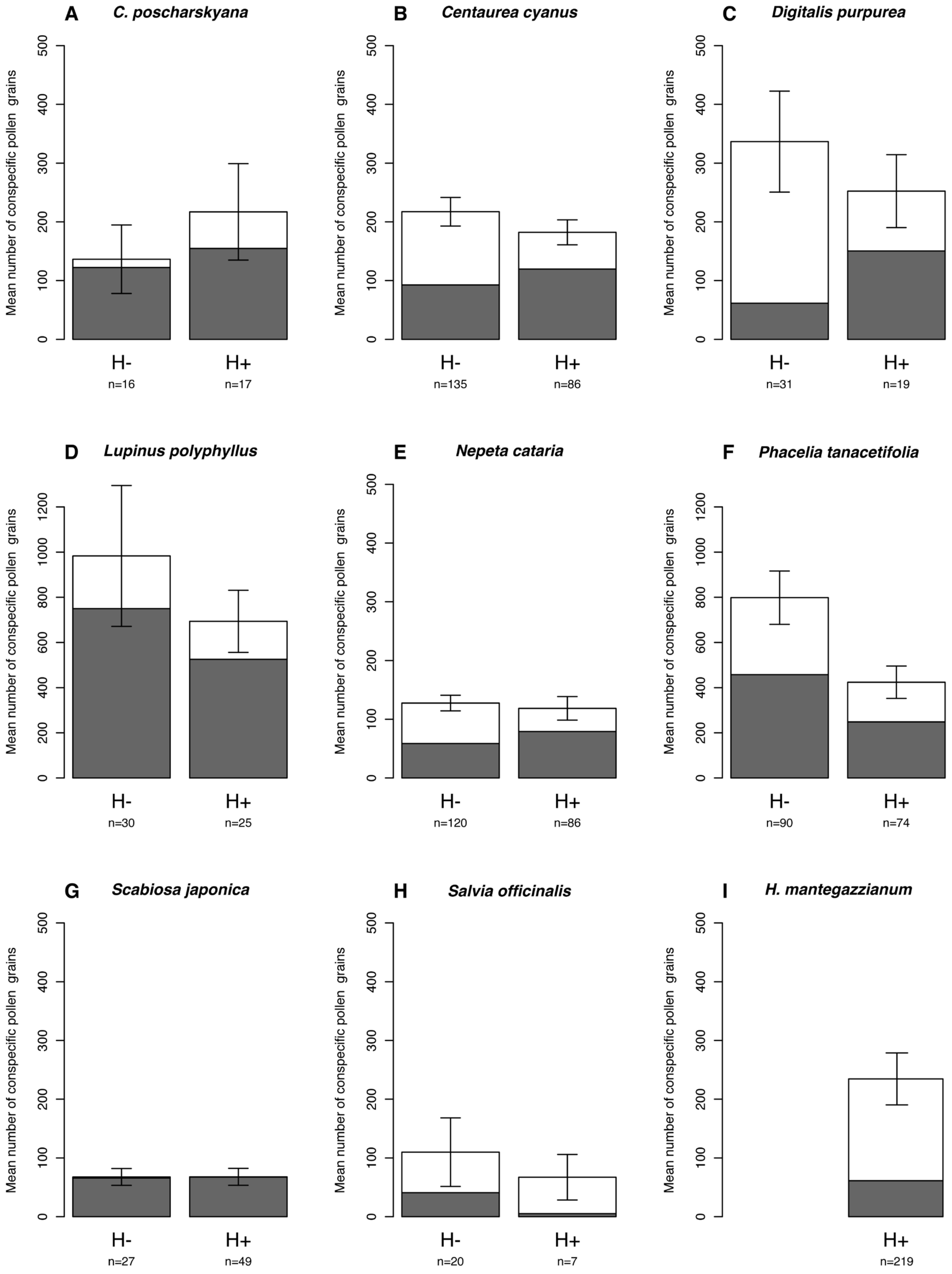

Figure 5.3 a-i: Average number of conspecific pollen grains potentially transferred to each plant species for the control (H-) and the invaded treatment (H+). The proportion of pollen that was found the only pollen species an insect was carrying (pure load) is shown in white. ± SE. Mind different scales.

5.4.3 Conspecific pollen transport

Similar to the approach for heterospecific pollen transport I calculated the number of potentially transferred conspecific pollen grains (Fig. 5.3). In this case, the bar shows the mean of the total amount of conspecific pollen, while the fraction in grey indicates the amount of conspecific pollen that was received by an animal that interacted with more than one plant species. The white area shows the fraction of conspecific pollen that was received as a pure pollen load. A pollen load was considered pure when an animal only carried pollen of the plant that it was caught on. These pure loads are possibly valuable for the plant in two ways: First, it may enhance female fitness by increasing the chance of fertilization and reducing negative effects by heterospecific pollen, second it potentially increases male fitness. When animals are not in contact with other plants no conspecific pollen is deposited on other plant species (and thus, wasted). Second, a high level of pure pollen loads indicates not only visitors with a high flower constancy, but also a high amount of pollen that is not spread in the system, limiting the competitive effects by heterospecific pollen transfer. The presence of the invader had no significant influence on the number of conspecific pollen grains for each plant (see Tab. 5.2). There was a statistically significant influence of the invader on pure pollen loads, however, post-hoc testing revealed only a marginally significant difference in pure pollen loads for *P. tanacetifolia* (Wilcoxon test W = 2681, $p_{corr} = 0.058$) and no significant differences for other species. In general, *P. tanacetifolia* was the plant that showed the most pronounced effect of the presence of *H. mantegazzianum*: More heterospecific interactions and lower conspecific pollen loads, which can also be seen in the differences in the representation of *P. tanacetifolia* in Fig. 5.4 e, f.

5.4.4 Network parameters

Three different kinds of networks were created. The first was "classically" based on observations or in this case of animals that were caught. The strength of the interactions was based on the number of individuals that were caught. For the second type I counted only these animals that interacted with more than one plant species that means I excluded those animals that visited only one plant species and carried only pollen of that kind. The third type was calculated in a similar fashion only that pollen loads were used as strength of interactions.

Tab.5. 3 shows the two-mode parameters for different types of networks. In some cases there was no significant difference to randomly arranged data, these values are printed in grey. Networks based on interactions for instance exhibited neither significant connectance nor nestedness or weighted nestedness. I cannot tell, if the lack of difference from randomly arranged data was due to the way the networks were calculated or caused by chance. The only type of network where significant values for all parameters for at least two networks of each treatment were found was the network based on pollen transport. In these networks there was a tendency for connectance to be lower in invaded networks, while nestedness and weighted nestedness remained rather unchanged between treatments.

Table 5.3: Two-mode network parameters for different types of network and treatments. Each parameter was calculated for each replication of the control (C) and the invaded treatment (I), numbers in grey show values that have no significant difference to randomly arranged data created by nullmodels. ± SD.

Visitation	**Connectance**	**Nestedness**	**weighted Nestedness**
C1	0.43	0.54	0.16
C2	0.45	0.62	0.24
C3	0.32	0.74	0.40
Mean	0.40 ± 0.07	0.63 ± 0.10	0.27 ± 0.12
I1	0.26	0.79	0.56
I2	0.30	0.86	0.79
I3	0.34	0.74	0.63
Mean	0.30 ± 0.04	0.80 ± 0.06	0.66 ± 0.12

Interaction	**Connectance**	**Nestedness**	**weighted Nestedness**
C1	0.65	0.91	0.66
C2	0.53	0.85	0.61
C3	0.49	0.76	0.47
Mean	0.55 ± 0.08	0.84 ± 0.08	0.58 ± 0.10
I1	0.42	0.75	0.61
I2	0.54	0.88	0.75
I3	0.38	0.80	0.72
Mean	0.45 ± 0.08	0.81 ± 0.07	0.69 ± 0.04

Pollen transport	**Connectance**	**Nestedness**	**weighted Nestedness**
C1	0.63	0.91	0.70
C2	0.52	0.89	0.45
C3	0.46	0.73	0.26
Mean	0.53 ± 0.08	0.84 ± 0.10	0.47 ± 0.22
I1	0.41	0.76	0.51
I2	0.51	0.86	0.59
I3	0.37	0.78	0.59
Mean	0.43 ± 0.07	0.80 ± 0.05	0.56 ± 0.04

Table 5.4: One-mode parameters for each plant species in the different types of networks and treatment. Values presented are the mean of the three replications per treatment ± SD.

Closeness	**Visitation**		**Interaction**		**Pollen transport**	
	control	invaded	control	invaded	control	invaded
Centaurea cyanus	0.22 ± 0.04	0.17 ± 0.07	0.23 ± 0.04	0.18 ± 0.00	0.19 ± 0.02	0.17 ± 0.02
C. poscharskyana	-	0.08	0.10 ± 0.02	0.08 ± 0.02	0.08 ± 0.03	0.08 ± 0.07
Digitalis purpurea	0.13 ± 0.05	0.14	0.09 ± 0.03	0.07 ± 0.01	0.06 ± 0.03	0.09 ± 0.05
H. mantegazzianum	-	0.34 ± 0.05	-	0.22 ± 0.01	-	0.18 ± 0.01
L. polyphyllus	0.10 ± 0.01	0.11	0.10 ± 0.01	0.10 ± 0.02	0.19 ± 0.06	0.15 ± 0.04
Nepeta cataria	0.29 ± 0.03	0.27 ± 0.04	0.20 ± 0.02	0.18 ± 0.01	0.15 ± 0.05	0.16 ± 0.01
P. tanacetifolia	0.20 ± 0.02	0.15 ± 0.04	0.17 ± 0.01	0.15 ± 0.02	0.30 ± 0.07	0.24 ± 0.05
Scabiosa japonica	0.08 ± 0.02	0.11 ± 0.01	0.11 ± 0.01	0.13 ± 0.01	0.07 ± 0.04	0.09 ± 0.01
Salvia officinalis	0.11 ± 0.02	0.08	0.09 ± 0.02	0.07 ± 0.01	0.05 ± 0.02	0.02 ± 0.00

Betweenness	**Visitation**		**Interaction**		**Pollen transport**	
	control	invaded	control	invaded	control	invaded
Centaurea cyanus	0.67 ± 0.58	0	3.67 ± 3.51	0	4.00 ± 3.61	0.33 ± 0.58
C. poscharskyana	-	0	0	0	0	0
Digitalis purpurea	0	0	0	0	0	0
H. mantegazzianum	-	0.33 ± 0.58	-	2.33 ± 2.08	-	0
L. polyphyllus	0	0	0	0	0	0
Nepeta cataria	2.33 ± 2.52	0	1.33 ± 2.31	0	0.33 ± 0.58	0
P. tanacetifolia	0.67 ± 1.15	0.33 ± 0.58	2.00 ± 3.46	0	7.33 ± 4.16	8.00 ± 7.21
Scabiosa japonica	0	0	0	0	0	0
Salvia officinalis	0	0	0	0	0	0

One-mode networks express the competition between plants: Based on visitation they show the potential of plants to draw visitors away from other plants (quantity component). Based on interaction they show the potential for competitive effects on the quality component (heterospecific pollen transfer, conspecific pollen loss). Based on heterospecific pollen transport they show the actual magnitude of interspecific pollen transport. One-mode parameters that were calculated for the different networks were closeness and betweenness (Tab. 5.4). Closeness shows how well a plant is connected to others and indicates a possibility of influencing other plant species. Betweenness values greater than zero indicate plants that connect different parts of networks i.e. are "hubs" or "keystones". There was no significant influence of the invader on closeness of native plants for the calculations based on visitation, interaction or pollen transport (Scheirer-Ray-Hare test, $p > 0.05$). Species that had high visitation rates, but introduced low amounts of pollen into the system (for instance *N. cataria*) had high closeness values in the visitation network. Other plants like *P. tanacetifolia* and *L. polyphyllus* had higher closeness values in the pollen transport network than in the visitation network, because of the high amount of pollen that these plants introduced into the system. *H. mantegazzianum* fell in the former category: Its closeness exceeded that of other plants in the visitation network, but ranged among others in the pollen transport network. *C. cyanus*, *P. tanacetifolia* and *N. cataria* were keystone species in the control treatment, indifferent on what the network calculation was based on (Tab. 5.4). *N. cataria* was only a keystone species when the invader was absent, while *P. tanacetifolia* always had this status except for the invaded network based on interaction. *H. mantegazzianum* was a keystone species, for calculations based on visitation or interaction, but not so in pollen transport networks. In these networks *P. tanacetifolia* and *C. cyanus* were keystones and remained so, when the invader was present. A visualization of one-mode networks is given in Fig. 5.4.

5.4.5 Network congruence

Results from the Procrustes analysis indicated that there was low congruence between the control and invaded networks for networks that were calculated on the basis of visitation or interaction (Tab. 5.5). For networks that were based on pollen transport there was a significant congruence between treatments. Furthermore, interaction and visitation networks showed significant congruence, which was not the case for pollen transport networks for either comparison.

Table 5.5: Results of the Procrustes analysis. Comparisons between cumulative networks between the different treatments and the different types of networks.

Comparison control - invaded	**Congruence [%]**	**p**
Visitation	12.49	0.393
Interaction	28.04	0.168
Pollen transport	59.14	0.003

Comparison of different types	**control**		**invaded**	
	Congruence [%]	**p**	**Congruence [%]**	**p**
Visitation – Interaction	73.52	0.0354	78.59	≤ 0.001
Visitation – Pollen transport	15.41	0.3438	26.95	0.214
Interaction – Pollen transport	28.18	0.2064	42.07	0.082

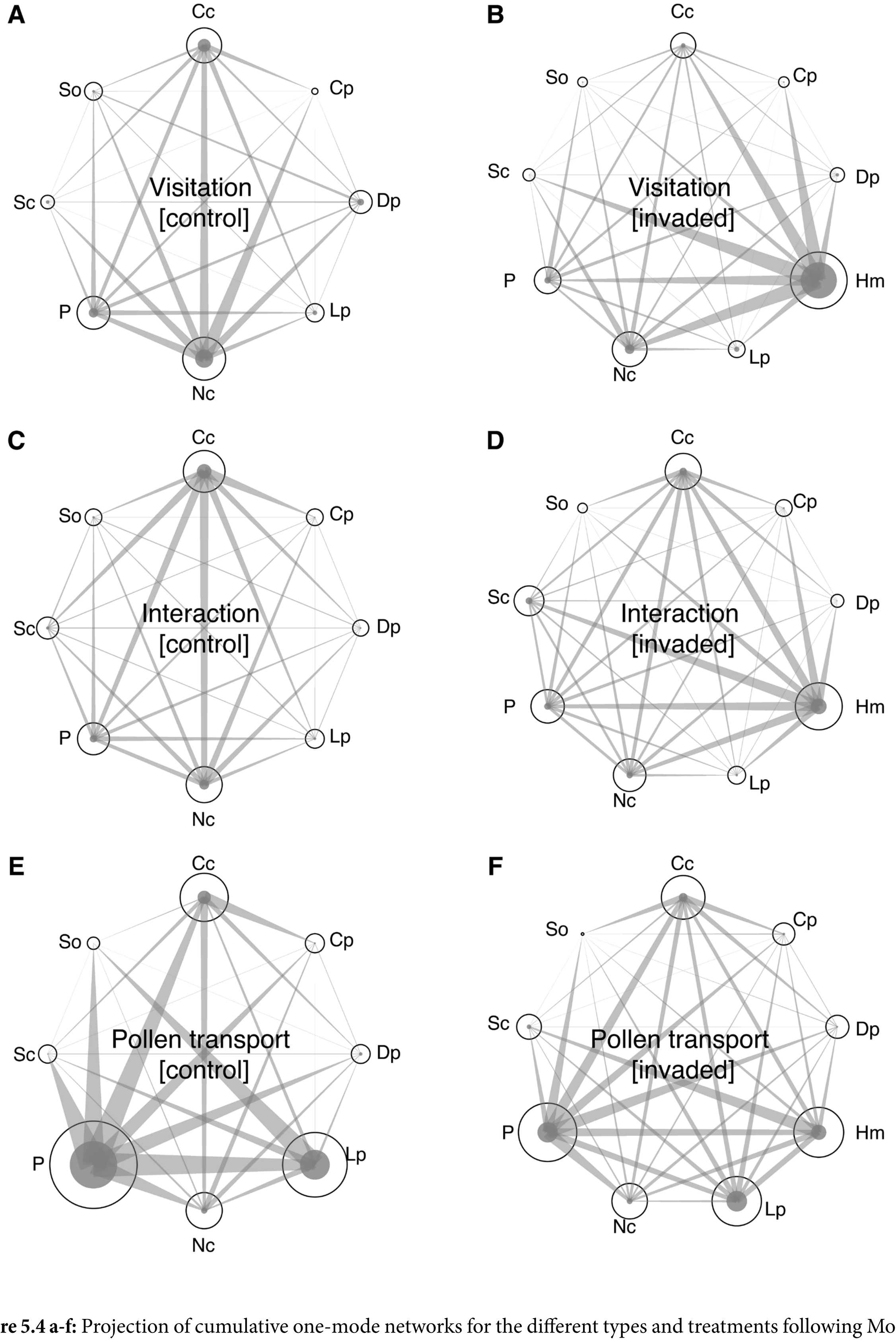

Figure 5.4 a-f: Projection of cumulative one-mode networks for the different types and treatments following Morris et al. 2005. Thickness of lines indicates strength of interactions, size of nodes the total number of visits/interactions/pollen grains found for a species. Cc: *Centaurea cyanus*, Cp: *Campanula poscharskyana*, Dp: *Digitalis purpurea*, Hm: *Heracleum mantegazzianum*, Lp: *Lupinus polyphyllus*, Nc: *Nepeta cataria*, P: *Phacelia tanacetifolia*, Sc: *Scabiosa japonica,* So: *Salvia officinalis*.

5.5 Discussion

5.5.1 Interaction and pollinator behavior

While honeybees showed flower constancy in general, their constancy in visits to *H. mantegazzianum* was rather low. Furthermore, all plants showed considerable interaction with the invader. The fact that despite the high abundance of potentially flower constant honeybees and bumblebees there was still considerable heterospecific interaction seems contradictory. However, it has to be considered that there are differences between the species level of specialization and the specialization of individuals (Araújo et al. 2008, 2010). Flower constancy of honeybees is a trait of the individual (Wells and Wells 1983). There are some individuals (5-35 %, Seeley 1983) acting as scouts that show a highly generalized pattern of foraging in order to find new foraging opportunities (Lindauer 1952, Seely 1983). In my study flower constancy was assessed at the species level, that honeybees showed flower constancy at the species level does not rule out that there were individuals that caused interspecific movement between plants.

Foraging bumblebees are known to show variable behavior in order to respond optimally to fluctuating resources. While they specialize individually on rewarding flowers (major), they also retain visits to other flowers (minor) (Heinrich 1976). Furthermore, depletion of rewarding resources by competing foragers causes bumblebees to switch their preferences (Heinrich 1979). The superimposition of the individual response to the resources offered by the different plant species causes most likely the variation of foraging behavior that was recorded in this study. The interesting point is that the invader did not account for more heterospecific interactions. In other words: The relative number of animals that potentially transferred foreign pollen remained the same, only that some of them carried pollen of *H. mantegazzianum*. In conclusion, the level of interactions with the alien was not determined by the floral constancy of insects visiting *H. mantegazzianum*, but individually different for each plant species. While differences in floral constancy might explain differences in the magnitude of heterospecific interactions (compare *D. purpurea* and *S. japonica*), I have to reject the hypothesis that interaction of the alien and focal species were limited due to floral constancy to *H. mantegazzianum*. My results are in accordance with other studies that show that there is interspecific pollinator movement and potential for competition in a system dominated by social bees (Kephart 1983, Flanagan et al. 2011). Nevertheless, the magnitude of interaction with the alien varied for each plant species, so it seems likely that the competitive effect by an alien plant is dependent on the plant species and the identity of its pollinators. This is supported by the range of native-alien plant interactions reported by other studies (24-70%) (Brown et al. 2002, Totland et al. 2006, Bartomeus 2008a, Flanagan et al. 2009, 2011).

5.5.2 Heterospecific pollen transport, loss of conspecific pollen

Interactions between plants via pollinators convey valuable information about the structure of a plant-pollinator system; however, crucial for the impact of competition on plant reproduction are not pollinator movements but their impact on pollen transfer (Campbell and Motten 1985). *H. mantegazzianum* pollen did not dominate in the pollen loads found on insects interacting with co-flowering plants. In most cases alien pollen loads are rather small compared to the total amount of heterospecific pollen. There was even a tendency for some plants to experience smaller heterospecific pollen loads when the invader is present. This is in contrast to the findings of Lopezaraiza-Mikel et al. (2007), who found the alien *Impatiens glandulifera* dominating insect pollen loads. Furthermore, my experiment only measured pollen that was transported by insects not the pollen that was actually transferred to co-flowering plants. It is plausible that only a small part of alien pollen found on pollinators' bodies is really deposited on the stigmas of co-flowering plants. Studies that explored the deposition of alien pollen on native stigmas often found that there was a low amount of alien pollen transferred to native reproductive parts (Moragues and Traveset 2005, Jakobsson et al. 2008, Larson et al. 2006, Dietzsch et al. 2011). Bartomeus et al. (2008a) detected high amounts of alien pollen on pollinators' bodies yet low deposition on native stigmas. Placement of heterospecific pollen on stigmas can be avoided by like differences in floral morphology, placement on pollinators' body or timing of pollen release (Brown and Kodric-Brown 1979, Armbruster et al. 1994, Stone et al. 1998, Muchala and Potts 2007). Moreover, the number of pollen grains carried on pollinators' bodies is not necessarily correlated with the number of pollen deposited on stigmas (Adler and Irwin 2006).

In conclusion, the hypothesis that *H. mantegazzianum* pollen dominates the invaded plant-pollinator system leading to high rates of alien pollen potentially transferred has to be rejected. There is, however, an impact of the alien on conspecific pollen that is potentially transferred. While the amount of heterospecific pollen potentially transferred to *H. mantegazzianum* is rather low, conspecific pollen of co-flowering plants does not need to be actually transferred to the invader to be wasted. It was shown that conspecific pollen of a focal plant was lost due to the grooming behavior of pollinators when visiting an alien plant (Flanagan et al. 2009). Furthermore, the fact that pollinators include *H. mantegazzianum* in their foraging schemes might facilitate pollen los due to other forces (e.g. wind) (Inouye et al. 1994, Johnson et al. 2005). I found the impact on conspecific pollen transport to be species dependent: some plants suffered no loss of conspecific pollen, while *P. tanacetifolia* displayed the most pronounced effect. Larson et al. (2006) explored the impact of the alien *Euphorbia esula* on the pollination of a community of plants and found a similar effect: The loss of conspecific pollen depended on the plant species and was more pronounced than the deposition of heterospecific pollen. Other studies that scrutinized the impact of alien plants via pairwise interactions come to contrasting results. The alien *Carduus nutans* caused more heterospecific and less conspecific pollen to be deposited on the stigmas of a co-flowering native, yet there was no significant impact on seed set (Cariveau and Norton 2009). The deposition of conspecific pollen of a native species was lowered by the invasive *Rhododendron ponticum*, but there was no significant impact on seed set (Dietzsch et al. 2011). *Lythrum salicaria* has been reported to have a negative impact on the seed set of native plants by the loss of conspecific pollen (Flanagan et al. 2009). While it is generally thought that conspecific pollen loss is more likely to cause negative effects than heterospecific pollen deposition (Campbell and Motten 1985, Feinsinger et al. 1991, Murcia and Feinsinger 1996, Morales and Traveset 2008), the effect on the impact on the pollination of a plant seems to be dependent on the identity of the alien plant, the native (focal) species and, most likely, the pollinators' identity. Furthermore, some of the studies cited above as well as other studies (e.g. Caruso 1999) imply that loss of conspecific pollen does not necessarily have a negative impact on plant fitness. There seems to be some leeway before a reduction of the deposition of conspecific pollen grains actually translates into negative effects for plant reproduction (Totland et al. 2006). Taken the neutral effect on seed set and the effects found in this study together the impact of *H. mantegazzianum* on co-flowering plants seems less dramatic. However, there still might be an impact on the quality of seed set as the effects of conspecific pollen loss may have an effect on outcrossing rates (Campbell 1985, Bell et al. 2005). Additionally, other environmental factors could enhance competitive effects. Changes in pollinator behavior due to changes in plant abundance might have an impact on the outcome of competition (Levin and Anderson 1970, Yang et al. 2010), as well as fluctuations in pollinator communities have been shown to have an impact on pollen transfer (Gómez et al. 2010).

5.5.3 Network parameters

The two-mode parameters calculated for this study did not present a solid basis for the discussion of the impact of *H. mantegazzianum* on a plant-pollinator network. In many cases I was not able to detect a significant difference from randomly arranged data created by nullmodels. In case of the pollen transport, where most parameters for most networks showed significance, I found little differences for the invaded and the control treatment for these parameters. The problem with these overall measures could be that they are to broad to detect an effect caused by a single alien species, despite an obvious potential for competition (compare Pádron et al. 2009). However, focus of this study is the impact of the alien plant on competition for the quality component of pollination. One-mode data seems better suited to scrutinize this impact on the network-level. The calculated one-mode parameters revealed that the role of some plants is different depending on type of network. This is especially true for *H. mantegazzianum*: The invader was dominant in a visitation-based network, but ranged among the other plants in a network based on pollen transport. The network parameters underline the fact that, while *H. mantegazzianum* was highly visited and all plant species showed interaction with the invader, still little alien pollen was transported. *H. mantegazzianum* does dominate visitation webs, but does not dominate or even "inundate" pollen transport webs as found by Lopezaraiza-Mikel et al. (2007) for *I. glandulifera* and hypothesized by Morales and Traveset (2008) for other alien plants. Pollen transport webs exhibited significant congruence between the control and invasive treatment, indicating that *H. mantegazzianum* did not change the patterns of interspecific pollen transport. The results of this study show, however, that the alien plant was well integrated into the plant-pollinator networks. This was also found for other alien plants (Morales and Aizen 2006, Bartomeus et al. 2008b, Vilà et al. 2009), while these data were based on observation, I could actually proof that there is really interaction (in form of pollen transport) between the alien and the other plants in a network. Nevertheless, there is no evidence that the integration of the alien plant *H. mantegazzianum* causes a detrimental effect on plant- pollinator networks. In general, there are studies that do report a negative impact by an alien plant on pollination networks (e.g. Aizen et al. 2008), while others show that aliens integrate without necessarily causing detriment (e.g. Kaiser-Bunbury and Müller 2009, Kaiser-Bunbury et al. 2011). The great complexity of plant-animal interactions makes it obviously hard to predict a general trend of the impact of alien plants. The findings of this study that a super-generalist, highly visited plant has an impact on visitation, but not on pollen transport, adds further to this complexity. Furthermore, I believe that it is essential for future studies to include a measurement of pollen transport (or better stigmatic pollen deposition) in order to fully understand the quantity and quality component of pollination. Additionally, I could show that one-mode data is indeed a valuable tool for pollination biologist (see also Olesen et al. 2002, Pádron et al. 2009, Martín González et al. 2010).

5.5.4 Conclusion

The impact of *H. mantegazzianum* on plant-pollinator systems cannot be deduced from its appearance as highly generalized, cornucopian plant species: The fact that the invader is an exceptionally attractive plant does not translate automatically into strong competition effects for other plants. Nevertheless, while the effects of the invader are not straightaway catastrophic, there are hints that it does cause competitive effects for co-flowering plants by potentially lowering conspecific pollen transfer. These effects vary depending on the plant species. The key for the understanding of the impact of alien invasion on pollination seems to lie in the fact that this problem has many facets and is experienced differently on different scales (e.g. individual vs. community) (see also Dupont et al. 2011). The challenge for future studies will be to incorporate these different levels of impact as well as the different mechanisms that determine competition for pollination in order to come to a general conclusion about plant invasions.

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6. General Discussion

Aim of this thesis was to investigate, whether the invasion by *H. mantegazzianum* has pollinator-mediated effects on co-flowering plant species. I characterized the pollinator fauna of the invader and compared it to a native congener. Additionally, I used an experimental garden setup for a network-based approach of the impacts of the invasive species on quantity and quality of pollination. On the following pages I will not only try to synthesize the results from the different experiments, but I will also provide some general considerations to the impact of alien organisms as well as a few critical thoughts to my approach.

6.1 The impact of *H. mantegazzianum* on plant-pollinator interactions

H. mantegazzianum was highly attractive to flower visiting insects, which can be seen both in the magnitude of visitation rates a well as in the diversity of its visitor fauna. The most abundant visitor, the honeybee, was also the most important pollinator of the invader. Due to the association with this super-generalist forager *H. mantegazzianum* was well integrated into a network of co-flowering plants. Insects switched frequently between the invasive plant and co-flowering species. The invader was able to change visitation webs and plays a dominant role in invaded networks. Hence, *H. mantegazzianum* seems to meet the prerequisites to severely disturb plant-pollinator interactions. However, my results revealed no significant negative effect caused by the alien. I found a neutral effect on the quantity component of pollination, which means there was no significant change in visitation rates for co-flowering plants in the presence of the invader. Some plants showed even a tendency for an enhancement of visitation rates. There was no evidence that the reproductive success of co-flowering plants was affected. The fact that insects switched between the invader and co-flowering plants did not lead to a higher amount of heterospecific pollen transported. There was, however, evidence that some plants might receive less conspecific pollen when growing together with *H. mantegazzianum*. The interesting point is that the functioning of the plant-pollinator system was not severely affected in the presence of a highly attractive super-generalist plant species. It seems that plant-pollinator systems have certain resilience against invasions (see also Kaiser-Bunbury and Müller 2009, Kaiser-Bunbury et al. 2011). Vilà et al. (2009) concluded from a Europe-wide survey that the dominance of alien plants in visitation does not translate into changes of connectance, linkage level and nestedness. Aizen et al. (2008) found effects in linkage and connectivity in networks where several species, plants as well as pollinators, were alien. It is possible that effects on measurements like connectance only become evident after a severe impact by alien organisms. The introduction of a single plant species seems to be buffered by the invaded plant system and less detrimental than the impact of several alien organisms (plants and pollinators) that even might facilitate each other (Simberloff 2006). The overall negative pollinator-mediated effect of alien plants that was found by Morales and Traveset (2009) was based on a meta-analysis of studies mainly based on pairwise comparisons of native and alien species. While community wide studies arguably lack the precision of a pairwise approach (Morales and Aizen 2006), it is nevertheless plausible that the impact on the reproduction of plants in a community is less severe. Furthermore, it has to be taken into consideration that pollinator mediated effects are dependent on the identity of the alien species as well as the native species. In some cases studies conducted so far indicate a negative influence of the alien plant, this is the case for instance for *Lythrum salicaria*, which is invasive in North America (Brown and Mitchell 2001, Brown et al. 2002, Flangan et al. 2009, 2010 DaSilva and Sargent 2011). For other invasive species like *Impatiens glandulifera* (Chittka and Schürkens 2001, Lopezaraiza-Mikel et al. 2007, Vilà et al. 2009, Nienhuis et al. 2009, Bartomeus et al. 2010) or *Carpobrotus* ssp. (Moragues and Traveset 2005, Jakobsson et al. 2007, Bartomeus 2008a, b, Vilà et al. 2009) effects range from negative over neutral to facilitative and there is no evidence for a general negative effect on native plant-pollinator systems. The integration of *H. mantegazzianum* may also have positive effects for the invaded plant-pollinator system. Super-generalist aliens often act as keystone or core species (Aizen et al. 2008, Valdovinos 2009, Vilà et al. 2009). Established alien plants can be important for the persistence of pollination networks (Carvalheiro et al. 2008, Valdovinos et al. 2009). Super-generalist aliens increased nestedness pattern in other studies (Bartomeus 2008a, Padrón et al. 2009). Nestedness is regarded as a feature that increases robustness of pollination networks (Bascompte et al. 2003, Memmott et al. 2004, Jordano et al. 2006). A changed network structure might also be a more robust structure. *H. mantegazzianum* might increase the tolerance of the invaded network to species extinctions. Nonetheless, due to the complexity of plant pollinator interactions positive effects might be canceled out by simultaneously occurring negative effects. Enhanced visitation rates, for instance, may go along with high alien pollen loads (Lopezaraiza-Mikel et al. 2007). While this was not the case with *H. mantegazzianum*, there was still evidence that the invader causes loss of conspecific pollen for at least one plant species. While reproduction of co-flowering species was unaffected, there still might be an impact on the quality of seed set as the effects of conspecific pollen loss may have an effect on outcrossing rates (Campbell 1985, Bell et al. 2005). Additionally, other environmental factors could enhance competitive effects. Changes in pollinator behavior due to changes in plant abundance might have an impact on the outcome of competition (Levin and Anderson 1970, Yang et al. 2011), as well as fluctuations in pollinator communities have been shown to have an impact on pollen transfer (Gómez et al. 2010). In conclusion, it definitively would be inconsiderate to play down the impacts of *H. mantegazzianum* that I found in my thesis, but it seems that the overall function of the plant-pollinator system is retained, which makes it likely that invaded plant communities may persist.

Beside an impact on native plant communities there is also the impact on native pollinators to consider. From the pollinator's perspective *H. mantegazzianum* might provide an additional source of floral resources. The main visitor to *H. mantegazzianum* is the honeybee, which is an important pollen vector for many other plants. Furthermore, honeybees possess economic value due to their pollination services to agricultural plants and honey production (Kearns et al. 1998, Klein et al. 2007). Other invasive plants are able to supply resources to generalist bees (comparable to mass-flowering crops) or fill phenological gaps (Tepedino et al. 2008, Stout and Morales 2009). This is especially true for *H. mantegazzianum* as it shows a kind of mass flowering (Perglová 2007) and it flowers at a time of the year where natural resources are scarce for bees. *Imaptiens glandulifera*, which is invasive in Central Europe, provides valuable food sources for bees (Starý and Tkalcú 1998, Schürkens and Chittka 2001) and might increase bumblebee colony fitness similar to mass flowering crops (Bartomeus et al. 2010). Super-generalist weedy plants provide resources in disturbed habitats with few native flowering species (Williams et al. 2011). Beside honeybees other insects that forage on *H. mantegazzianum* also provide valuable services. *Episyrphus balteatus* (Syrphini), for instance, is of value as pest-control against aphids (Pineda et al. 2007, Tenhumberg and Poehling 2000). *H. mantegazzianum* might as other Apiaceae (Olesen et al. 2007, Zych 2007) have a value as food source and support for local insect diversity, especially in the light of a possible decline of pollinators (Biesmeijer et al. 2006). The dense populations of *H. mantegazzianum* that occur locally are of course a threat to plant biodiversity, but on the other hand the are also an abundant source of nectar and pollen for foraging insects. There is, however, a caution: Yet unknown is, if the effects on pollination services of massive flowering stands of *H. mantegazzianum* will be similar to the results of this thesis that was based on a medium level of invasion.

6.2 The menace of alien plants - a question of perception

The traditional view that aliens generally have a negative influence on native ecosystems does not adequately characterize the complexity of biological invasions (Goodenough 2010). A recent meta-analysis (Vilà et al. 2011) revealed that, while alien species have significant impacts on the ecosystems they invade, these impacts are always context-dependent. Nevertheless, an a priori assessment of the impact of an alien organism is impossible to achieve, especially as other environmental factors might determine whether aliens become problematic or not. Furthermore, it is unclear at what point an alien organism becomes problematic. Research dedicated to invasive plants should at best provide information for ecological conservation and wildlife management. In this regard, it is necessary to assess the potential of an alien species to damage ecosystem functioning, threat human health or cause economic loss. *H. mantegazzianum* exemplifies how an invasive plant may have an impact on many different levels. Undoubtedly, *H. mantegazzianum* has the potential to affect human health negatively. The results of this thesis indicate that pollinator-mediated effects are not to such an extent that a call for an intensification of the control of *H. mantegazzianum* would be justified. Furthermore, studies show that *H. mantegazzianum* has only little impact on the diversity of local plant populations and most stands of this species are not dominant (Thiele and Otte 2006, 2008). Efforts could be saved to control a plant that might even be valuable resource to flower-visiting insects. The removal of alien plants is not always the most sensible or cost-efficient solution (Ewel and Putz 2004). Furthermore, there is the sentiment that in a profoundly disturbed environment (like Central Europe) the distinction of alien and native plant hardly makes sense and that society needs to develop a new way to manage the really harmful species, despite their origin (Thompson and Davis 2011). Due to the ongoing transformation of the planet by human activity more and more ecosystems will be turned into “novel ecosystems” with new species combinations and interactions (Hobbs et al. 2006, 2009). In theses systems non-native organisms may even partially compensate for the loss of native pollinators and thus help to maintain ecosystem functioning (Pattemore and Wilcove 2011). Nonetheless, in the end it is not up to scientists to make decisions, whether efforts should be made to fight invasive species. We all have to make a decision how we want to cope with a changing biota on a changing planet.

6.3 Limitations of this study, directions of future research

We are a long way from a true understanding of the complexity of plant-pollinator interactions. While network approaches are a useful tool to analyze these interactions, they provide nothing more than just an estimate. I could show that the patterns of visitation and the patterns of pollen transport in a plant-animal network do not necessarily correlate. In addition, transported pollen on insect bodies does not necessarily reach the plants' reproductive organs and if fruit set, seed set, or seed quality is affected by any of these aforementioned factors is yet a completely different matter. In addition, it has been shown that individual plants and pollinators form highly complex sub-networks (Dupont et al. 2011), which is adding to the complication of providing a profound understanding of plant-pollinator interactions. Nevertheless, such understanding will be necessary to protect an ecosystem service so essential as pollination in the future. The growth of human population continues and so will global change and biological invasions. For the maintenance of plant-pollinator interactions this will lead to new challenges as not only the numbers and abundance of alien organisms in ecosystems are likely to increase, but a change of many environmental factors is also to be expected. Alien abundance (Muñoz and Cavieres 2008, Dietzsch et al. 2011), or landscape parameters (Bartomeus et al. 2010) might influence the outcome of competition for pollination of alien and native plants. Future studies should include the effects of multiple alien species on plant-pollinator interactions, as well as an increase of the abundance of non-native organisms. Furthermore, research is required whether the impacts of an alien plant on pollination are context dependent, for instance if climate change or land use have an influence on the effects of an alien plant. Additionally, long-term monitoring of plant-pollinator systems is necessary, as they have been shown to exhibit temporal variability (e.g. Fishbein and Venable 1996, Price et al. 2005).

In conclusion, while a long time has passed since the groundbreaking discoveries of Christian Konrad Sprengel (1793), scientific research still has a long way to go in order to truly discover nature's secret of plant-pollinator interactions.

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7. Appendix

Table 7.1: Statistical difference between visits to male and female umbels for each morphospecies in 2008 corresponding to Fig 3.4 a, b. p_{corr} shows p-values corrected for multiple comparisons after Benjamini and Hochberg (1995).

H. mantegazzianum	χ^2	**p**	**p_{corr}**
A. mellifera	7.270	0.0072	0.0110
Bombus spp.	1.739	0.1872	0.2247
Eristalis spp.	1.094	0.2955	0.2955
Lucilia spp.	321.089	< 0.001	< 0.001
Syrphini	192.200	< 0.001	< 0.001
Vespidae	83.990	< 0.001	< 0.001
H. sphondylium	χ^2	**p**	**p_{corr}**
Eristalis spp.	5.496	0.019058	0.076231
Lucilia spp.	1.208	0.271574	0.333778
Muscidae	1.193	0.274536	0.333778
M. florea	1.110	0.292056	0.333778
Sarcophagidae	2.846	0.091552	0.183103
Sphecidae	0	0.99763	0.99763
Syrphini	36.730	< 0.001	< 0.001
Vespidae	4.109	0.042655	0.113746

Table 7.2 a: Statistical difference between insect pollen loads in 2008 of *H. mantegazzianum* corresponding to Fig 3.4 c. Multiple comprisons after Kruskal-Wallis test after Siegel and Castellan (1988). Note that this test is not able to compute exact p-values, but shows whether p is below a certain threshold.

H. mantegazzianum			
Comparison	**observed difference**	**critical difference**	**p**
A. mellifera – *Bombus* spp.	6.76	34.42	> 0.05
A. mellifera – *Eristalis* spp.	22.060	29.69	> 0.05
A. mellifera – *Lucilia* spp.	44.31	26.89	< 0.001
A. mellifera - Syrphini	15.93	30.84	> 0.05
A. mellifera - Vespidae	34.23	27.41	< 0.01
Bombus spp.- *Eristalis* spp.	15.30	34.83	> 0.05
Bombus spp. – *Lucilia* spp.	37.55	32.48	< 0.05
Bombus spp. - Syrphini	9.17	35.82	> 0.05
Bombus spp. - Vespidae	27.47	32.91	> 0.05
Eristalis spp. – *Lucilia* spp.	22.25	27.41	> 0.05
Eristalis spp. - Syrphini	6.12	31.30	> 0.05
Eristalis spp. - Vespidae	12.17	27.92	> 0.05
Lucilia spp - Syrphini	28.37	28.66	> 0.05
Lucilia spp - Vespidae	10.07	24.93	> 0.05
Syrphini - Vespidae	18.29	29.15	> 0.05

Table 7.2 b: Statistical difference between insect pollen loads in 2008 of *H. sphondylium* corresponding to Fig 3.4 d. Multiple comprisons after Kruskal-Wallis test after Siegel and Castellan (1988). Note that this test is not able to compute exact p-values, but shows whether p is below a certain threshold.

H. sphondylium

Comparison	observed difference	critical difference	p
Eristalis spp.- *Lucilia* spp.	14.14	33.25	> 0.05
Eristalis spp. - Muscidae	2.25	43.85	> 0.05
Eristalis spp. - *M. florea*	6.87	43.85	> 0.05
Eristalis spp. - Sarcophagidae	2.68	35.26	> 0.05
Eristalis spp. -Sphecidae	4.58	39.58	> 0.05
Eristalis spp. - Syrphini	27.66	32.53	> 0.05
Eristalis spp. - Vespidae	5.5	43.85	> 0.05
Lucilia spp. - Muscidae	16.39	36.33	> 0.05
Lucilia spp. - *M. florea*	21.02	36.33	> 0.05
Lucilia spp. - Sarcophagidae	11.46	25.29	> 0.05
Lucilia spp. - Sphecidae	9.56	31.04	> 0.05
Lucilia spp. - Syrphini	13.51	21.32	> 0.05
Lucilia spp. - Vespidae	8.64	36.33	> 0.05
Muscidae - *M. florea*	4.62	46.22	> 0.05
Muscidae - Sarcophagidae	4.93	38.17	> 0.05
Muscidae - Sphecidae	6.83	42.19	> 0.05
Muscidae - Syrphini	29.91	35.66	> 0.05
Muscidae - Vespidae	7.75	46.22	> 0.05
M. florea - Sarcophagidae	9.55	38.17	> 0.05
M. florea - Sphecidae	11.45	42.19	> 0.05
M. florea - Syrphini	34.54	35.66	> 0.05
M.florea - Vespidae	12.37	46.22	> 0.05
Sarcophagidae - Sphecidae	1.901	33.17	> 0.05
Sarcophagidae - Syrphini	24.98	24.33	< 0.05
Sarcophagidae - Vespidae	2.81	38.17	> 0.05
Sphecidae - Syrphini	23.08	30.26	> 0.05
Sphecidae - Vespidae	0.91	42.19	> 0.05
Syrphini - Vespidae	22.16	35.66	> 0.05

Table 7.3 a: Statistical difference between insect pollen loads in 2010 of *H. mantegazzianum* corresponding to Fig 3.5 c. Multiple comprisons after Kruskal-Wallis test after Siegel and Castellan (1988). Note that this test is not able to compute exact p-values, but shows whether p is below a certain threshold.

H. mantegazzianum			
Comparison	**observed difference**	**critical difference**	**p**
A. mellifera - Eristalis spp.	2.18	29.19	> 0.05
A. mellifera - Lucilia spp.	37.01	44.36	> 0.05
A. mellifera - Syrphini	39.51	37.68	< 0.05
A. mellifera - Vespidae	46.33	32.48	< 0.001
Eristalis spp. - *Lucilia* spp.	34.83	50.35	> 0.05
Eristalis spp. - Syrphini	37.32	44.58	> 0.05
Eristalis spp. - Vespidae	44.15	40.28	< 0.05
Lucilia spp. - Syrphini	2.49	55.71	> 0.05
Lucilia spp. - Vespidae	9.32	52.33	> 0.05
Syrphini - Vespidae	6.83	46.80	> 0.05

Table 7.3 b: Statistical difference between between insect pollen loads in 2010 of *H. sphondylium* corresponding to Fig 3.5 d. Multiple comprisons after Kruskal-Wallis test after Siegel and Castellan (1988). Note that this test is not able to compute exact p-values, but shows whether p is below a certain threshold.

H. sphondylium

Comparison	**observed difference**	**critical difference**	**p**
Cheilosia spp. - *Eristalis* spp.	14.39	49.59	> 0.05
Cheilosia spp. - *Lucilia* spp.	30.66	56.10	> 0.05
Cheilosia spp. - Muscidae	3.61	56.10	> 0.05
Cheilosia spp. - *M. florea*	29.27	53.31	> 0.05
Cheilosia spp. - Sarcophagidae	5.76	56.10	> 0.05
Cheilosia spp. - Sphecidae	10.50	62.72	> 0.05
Cheilosia spp. - Symphyta	41.46	60.05	> 0.05
Cheilosia spp. - Syrphini	22.96	43.03	> 0.05
Cheilosia spp. - Vespidae	8.14	70.59	> 0.05
Cheilosia spp. - Volucella spp.	49.18	50.35	> 0.05
Eristalis spp. - *Lucilia* spp.	45.05	54.62	> 0.05
Eristalis spp. - *Muscidae*	18.00	54.62	> 0.05
Eristalis spp. - *M. florea*	14.88	51.75	> 0.05
Eristalis spp. - Sarcophagidae	20.15	54.62	> 0.05
Eristalis spp. - Sphecidae	3.89	61.40	> 0.05
Eristalis spp. - Symphyta	27.06	58.67	> 0.05
Eristalis spp. - Syrphini	37.35	41.08	> 0.05
Eristalis spp. - Vespidae	6.25	69.42	> 0.05
Eristalis spp. - *Volucella* spp.	34.78	48.70	> 0.05
Lucilia spp. - Muscidae	27.05	60.60	> 0.05
Lucilia spp. - *M. florea*	59.93	58.02	< 0.05
Lucilia spp. - Sarcophagidae	24.90	60.60	> 0.05
Lucilia spp. - Sphecidae	41.16	66.78	> 0.05
Lucilia spp. - Symphyta	72.11	64.27	< 0.05
Lucilia spp. - Syrphini	7.70	48.74	> 0.05
Lucilia spp. - Vespidae	38.80	74.22	> 0.05
Lucilia spp. - Volucella spp.	79.83	55.32	< 0.001
Muscidae - *M. florea*	32.88	58.02	> 0.05
Muscidae - Sarcophagidae	2.15	60.60	> 0.05
Muscidae - Sphecidae	14.11	66.78	> 0.05
Muscidae - Symphyta	45.06	64.27	> 0.05
Muscidae - Syrphini	19.35	48.74	> 0.05
Muscidae - Vespidae	11.75	74.22	> 0.05
Muscidae - *Volucella* spp.	52.78	55.32	> 0.05
M. florea - Sarcophagidae	35.03	58.02	> 0.05
M. florea - Sphecidae	18.77	64.44	> 0.05

Table 7.3 b: continued

H. sphondylium			
Comparison	**observed difference**	**critical difference**	**p**
M. florea - Symphyta	12.19	61.85	> 0.05
M. florea - Syrphini	52.23	45.50	< 0.01
M. florea - Vespidae	21.13	72.13	> 0.05
M. florea - *Volucella* spp.	19.91	52.48	> 0.05
Sarcophagidae - Sphecidae	16.26	66.78	> 0.05
Sarcophagidae - Symphyta	47.21	64.27	> 0.05
Sarcophagidae - Syrphini	17.20	48.74	> 0.05
Sarcophagidae - Vespidae	13.90	74.22	> 0.05
Sarcophagidae - *Volucella* spp.	54.93	55.32	> 0.05
Sphecidae - Symphyta	30.96	70.13	> 0.05
Sphecidae - Syrphini	33.46	56.24	> 0.05
Sphecidae - Vespidae	2.36	79.34	> 0.05
Sphecidae - *Volucella* spp.	38.68	62.02	> 0.05
Symphyta - Syrphini	64.42	53.25	< 0.01
Symphyta - Vespidae	33.31	77.25	> 0.05
Symphyta - *Volucella* spp.	7.72	59.32	> 0.05
Syrphini - Vespidae	31.10	64.90	> 0.05
Syrphini - *Volucella* spp.	72.14	42.00	< 0.001
Vespidae - *Volucella* spp.	41.03	69.97	> 0.05

Table 7.4: Statistical difference between the invaded and the control treatment of pure conspecific pollen loads each plant species coresponding to Fig 5.3. Wilcoxon rank sum test. p_{corr} shows p-values corrected for multiple comparisons after Benjamini and Hochberg (1995).

	W	**p**	**p_{corr}**
Centaurea cyanus	144.5	0.563	1
C. poscharskyana	5102	0.046	0.367
Digitalis purpurea	255	0.412	1
Lupinus polyphyllus	353.5	0.676	1
Nepeta cataria	4639.5	0.157	1
Phacelia tanacetifolia	2681	0.007	0.058
Scabiosa japonica	650	0.667	1
Salvia officinalis	75.5	0.719	1

Table 7.5: Residuals of the Procrustes analysis for the different treatments and types of networks corresponding to the analysis presented in chapter 5.

	Visitation control - invaded	Interaction control - invaded	Pollen transport control - invaded
Centaurea cyanus	0.31	0.49	0.17
C. poscharskyana	0.18	0.16	0.11
Digitalis purpurea	0.10	0.09	0.07
Lupinus polyphyllus	0.14	0.13	0.25
Nepeta cataria	0.66	0.31	0.20
Phacelia tanacetifolia	0.14	0.15	0.34
Scabiosa japonica	0.15	0.05	0.07
Salvia officinalis	0.12	0.09	0.12

control	Visitation - Interaction	Visitation - Pollen transport	Interaction - Pollen transport
Centaurea cyanus	0.27	0.23	0.11
C. poscharskyana	0.15	0.22	0.15
Digitalis purpurea	0.07	0.14	0.17
Lupinus polyphyllus	0.06	0.17	0.42
Nepeta cataria	0.37	0.76	0.19
Phacelia tanacetifolia	0.10	0.14	0.59
Scabiosa japonica	0.08	0.15	0.14
Salvia officinalis	0.05	0.17	0.20

invaded	Visitation - Interaction	Visitation - Pollen transport	Interaction - Pollen transport
Centaurea cyanus	0.29	0.10	0.12
C. poscharskyana	0.04	0.12	0.12
Digitalis purpurea	0.07	0.13	0.12
Lupinus polyphyllus	0.04	0.23	0.42
Nepeta cataria	0.09	0.30	0.11
Phacelia tanacetifolia	0.13	0.33	0.50
Scabiosa japonica	0.17	0.11	0.19
Salvia officinalis	0.07	0.13	0.16

Table 7.6: Grouping of morphospecies, these morphospecies were used throughout the experiments unless otherwise stated.

Morphospecies	**Species**
A. mellifera	-
Andrenidae	*Andrena* sp.
Asilidae	undetermined species
Bombus spp.	*Bombus terrestris, Bombus pratorum, Bombus pascuorum Bombus* sp.
Cheilosia spp.	*Cheilosia illustrata, Cheilosia fasciata, Cheilosia* sp.
Chrysogaster spp.	undetermined species
Eristalis spp.	*Eristalis tenax, Eristalis pertinax, Eristalis* sp.
Heteroptera	undetermined species
Ichneumonidae	undetermined species
Lepidoptera	Hesperiidae, Lycaenidae, *Pieris* sp.
Lucilia spp.	*Lucilia sp*. and other Calliphoridae
Megachilidae	*Anthidium sp*. and other undetermined species
Melanostomatini	*Melastoma mellinum* and other undetermined species
Muscidae	undetermined species
Myathropa florea	-
Oedemeridae	undetermined species
Rhagonycha fulva	-
Sarcophagidae	undetermined species
Small black bees	e.g. *Hylaeus* sp., *Lasioglossum* sp. other undetermined species of the same habitus
Sphecidae	*Philanthus triangulum, Crabo cribarius, Ectemnius* sp., other undetermined species
Stenurella spp.	undetermined species
Symphyta	*Tenthredo sp*. and other undetermined species
Syrphidae	other undetermined Syrphidae
Syrphini	*Episyrphus balteatus*, *Syrphus* sp., other undetermined species
Tachinidae	undetermined species
Trichius sp.	undetermined species
Vespidae	*Dolichiovespula sp., Vespula* sp.*, Polistes* sp.
Volucella spp.	*Volucella bombylans, Volucella pellucens*

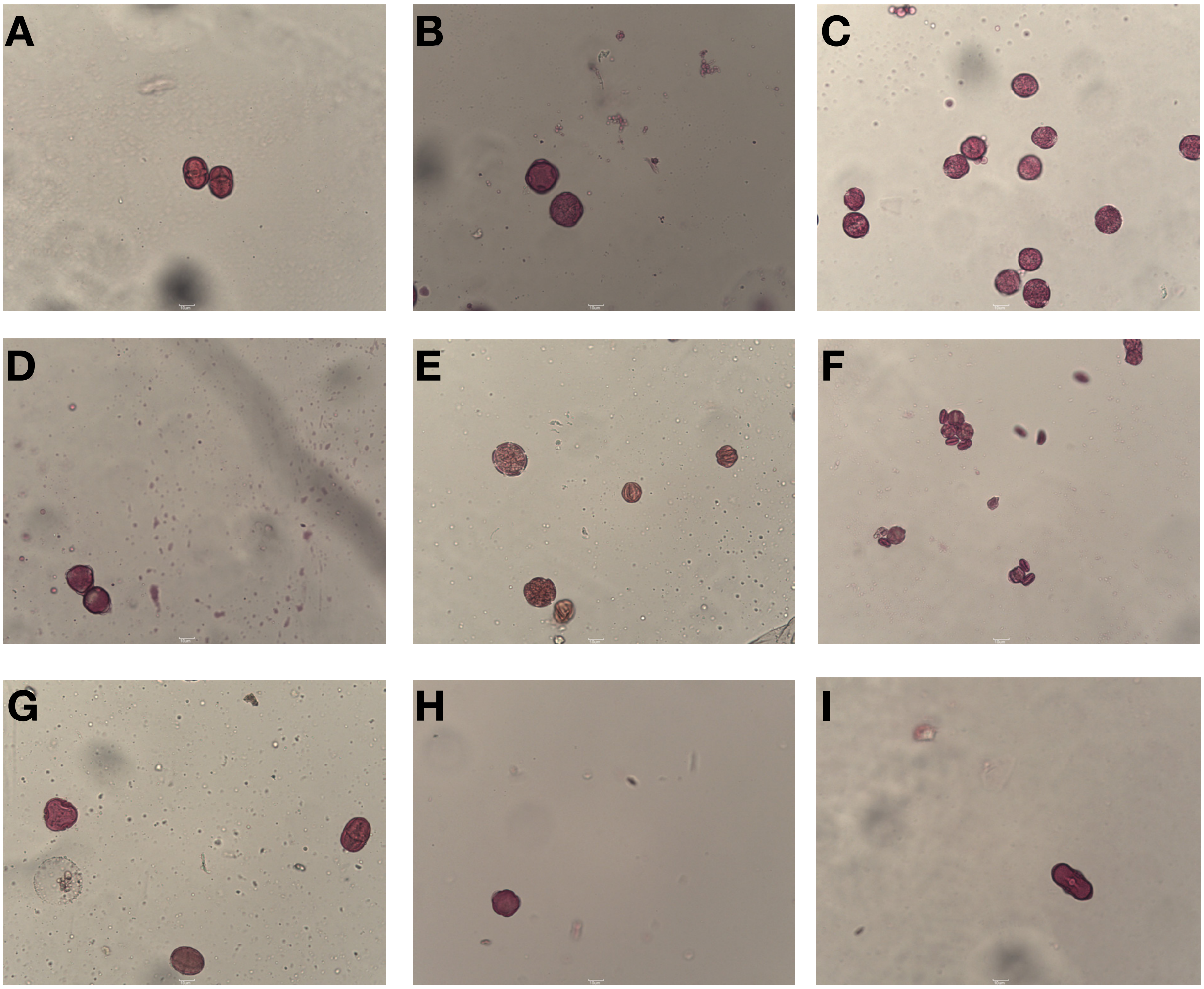

Plate 7.1 a-i: Fuchsin-stained pollen grains of the different plant species under a light microscope (40 x magnification). A: *Centaurea cyanus*, B: *Campanula poscharskyana*, C: *Digitalis purpurea*, D: *Lupinus polyphyllus*, E: *Nepeta cataria*, F: *Phacelia tanacetifolia*, G: *Scabiosa japonica,* H: *Salvia officinalis,* I: *Heracleum mantegazzianum*.

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Erklärung

Ich versichere, dass ich diese Arbeit selbständig verfasst, keine anderen Quellen und Hilfsmittel als die angegebenen benutzt und die Stellen der Arbeit, die anderen Werken dem Wortlaut oder Sinn nach entnommen sind, kenntlich gemacht habe. Die Arbeit hat in dieser oder ähnlicher Form keiner anderen Prüfungsbehörde vorgelegen.

Bielefeld, den 12. Dezember 2011

Ulrich Zumkier