TECHNISCHE UNIVERSITÄT MÜNCHEN

Lehrstuhl für Terrestrische Ökologie

Department für Ökologie und Ökosystemmanagement

Metacommunity Ecology in a Plant–Herbivore System

Mohsen Mehrparvar

Vollständiger Abdruck der von der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt an der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr.rer.nat.)

genehmigten Dissertation.

Vorsitzender: Univ.-Prof. Dr. Boris Schröder

Prüfer der Dissertation:

1. Univ.-Prof. Dr. Wolfgang W. Weisser
2. Assist. Prof. Dr. Christoph Vorburger,
   ETH Zürich / Schweiz
3. Priv.-Doz. Dr. Thomas Hovestadt,
   Julius-Maximilians-Universität Würzburg

Die Dissertation wurde am 11.02.2013 bei der Technischen Universität München eingereicht und durch die Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am 07.06.2013 angenommen.

Table of Contents

SUMMARY iii

ZUSAMMENFASSUNG v

CHAPTER I 1

1- GENERAL INTRODUCTION.. 1

1-1- Metapopulation concept... 1

1-2- Core processes in metapopulations 2

1-2-1- Dispersal 3

1-2-2- Colonization 4

1-2-3- Extinction.. 5

1-3- Metacommunity ecology 6

1-4- Interspecific competition affects core processes 7

1-5- Aphids forming metacommunities.. 8

1-5-1- Aphids: life cycle, reproduction, morphs and dispersal............................ 9

1-5-2- Aphids natural enemies.. 11

1-5-3- Aphid–ant interactions 11

1-6- The study system... 12

1-6-1- The host plant.. 13

1-6-2- The aphid species.. 14

1-7- Objectives... 17

1-8- Manuscripts overview and authors contributions 18

CHAPTER II 23

2- Manuscript I.. 23

Multiple cues for winged morph production in an aphid metacommunity 23

CHAPTER III.. 37

3- Manuscript II 37

Species–sorting by a mutualist in a herbivore metacommunity: Ant–mediated reversal of competitive hierarchies 37

CHAPTER IV 67

4- Manuscript III 67

Mechanisms of species–sorting: Do aphids choose plants to avoid future competitive interactions? 67

CHAPTER V 89

5- Manuscript IV 89

Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing? 89

CHAPTER VI 99

6- Manuscript V 99

Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae) 99

CHAPTER VII 107

7- GENERAL DISCUSSION 107

7-1- Species interactions and their effects on metacommunity processes 107

7-1-1- Dispersal 108

7-1-2- Colonization 111

7-1-3- Extinction 112

7-2- Application of metacommunity ecology 114

7-3- Conclusion 116

LIST OF REFERENCES 119

ACKNOWLEDGMENTS 135

CURRICULUM VITAE 137

LIST OF PUBLICATIONS 141

SUMMARY

A metapopulation is defined as a set of spatially separated subpopulations, which are connected to each other by dispersal. In metapopulations, dispersal, colonization and extinction are the three main core processes that determine population dynamics and structure. A metacommunity will arise if two or more species that exhibit metapopulation structure occur in the same set of habitats, *a community of metapopulations*. Metacommunity theory explicitly addresses interactions among species at different spatial scales so that local and regional distributions and abundances of species are related to their interactions with each other. Having knowledge on core processes in metacommunities and the impacts of biological interactions on them potentially greatly assist efforts to manage biodiversity, ecosystem services, and natural resources specifically in the context of conservation ecology, crop protection and biological control.

The main aim of this thesis was to further understand the effects of biological interactions on metacommunity core processes, which ultimately shape metacommunity structure. In this study, three specialized tansy aphids (*Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanaceti*), all of which exhibit classical metapopulation structure, were used as a model system.

In chapter II, the effects of environmental factors and biological interactions on production of dispersal (winged) morphs of tansy aphids were studied. In this part of the study, it specifically tried to know more about the patterns of winged morph production of *M. tanacetaria* and *M. fuscoviride* during the growing season and also to look for differences between these species. It was also investigated whether maternal morph, crowding and presence of predators affected the production of dispersal morph. The results showed that *M. tanacetaria* produce winged morphs during the whole season while production of winged individuals in *M. fuscoviride* was limited to the first generations in the beginning of the season. The highest dispersal morphs production occurred in the third and fourth generations for both species. It was also found that the maternal morph could affect the production of winged offspring. Although winged mothers of both species produced a few winged offspring, unwinged mothers produced relatively more winged offspring. Crowding and the presence of predators caused a significant increase in proportion of winged morphs in *M. tanacetaria*, although there was no observable effect in *M. fuscoviride*. It was revealed that dispersal of community members was influenced by both species traits and specific habitat characteristics.

In chapter III, the outcomes of interspecific competition among the three specialized tansy aphid species were investigated, more especially whether the outcomes of such competition can be altered by the presence of mutualistic ants and predators. It was established that there are strong competitive interactions between tansy aphid species that could even lead to competitive exclusion. The presence of mutualistic ants considerably altered the competitive hierarchies among the aphid species. Predators affected the persistence time of aphid colonies; however, this was dependent on the ants' presence. In this system, competition can be considered as a key factor for structuring and dynamics of the metacommunity.

In chapter IV, it is tried to discover whether host choice by tansy aphids reflects the outcome of biological interactions with the other tansy aphid species and how the preference of these aphids is affected by the presence of conspecific or heterospecific aphids on the host plant. The results indicated that host plant choice by tansy aphids was affected by the presence of other aphids and previous aphid infestation of the host plants such that the aphids selected particular plants mostly to avoid future competitive interactions. Therefore, these interactions have the potential to influence the structure and dynamics of the metacommunity of these species.

In chapter V, different tansy aphid species were used as diet items to see if they have any effect on the survival and development of their predators. It was also explored whether there is any benefit of diet mixing for predators. Each aphid species, as prey, had different effects on the development and survival of predators; however, predators did not obtain any benefit when consuming a mixed diet.

In chapter VI, it was tried to answer this question that if the response of aphids to the presence of natural enemies by production of more winged offspring is a general strategy against all predators or just an evolutionary response to their specialist predators or parasitoids. It had been shown in previous studies that aphid specialist predators such as ladybirds and lacewings have considerable effects on wing induction in the pea aphid (*Acyrthosiphon pisum*), whilst the effect of generalist predators was unclear. In this study, pea aphid individuals were confronted by two different species of rove beetles (Staphylinidae) and the production of aphid winged offspring was investigated. The percentage of produced aphid winged offspring increased in the presence of both predator species. It was revealed that polyphagous predators that include aphids in their diet are also involved in the induction of aphid wing polyphenism.

Tansy–aphid metacommunity dynamics can be described mostly by the species–sorting perspective in which different aphid species preferentially sort into different habitats that create separate spatial niches through habitat heterogeneity. The present study shows that the metacommunity structure is influenced strongly by dispersal ability, strength of competitive interactions, availability of mutualistic partners and, of course, by the resident predator community. Putting all these results together creates a clearer picture of ongoing biological interactions in a plant–herbivore system and reveals that these interactions are central elements which have direct impacts on structuring a metacommunity through their effects on core processes. In such a system, small changes in habitat conditions can lead to distinct changes in metacommunity structure and diversity. In light of new knowledge about such systems, the experience gained can be used to effectively manage other natural metacommunity systems, more especially for purposes of conservation and biological control.

ZUSAMMENFASSUNG

Eine Metapopulation wird durch ein System von Populationen definiert, welche durch Ausbreitung miteinander verbunden sind. Ausbreitung, Kolonisierung und Aussterben sind die drei Hauptprozesse, welche die Dynamik und Struktur der Metapopulation bestimmen. Wenn Metapopulationen mehrerer Arten in denselben Habitaten vorkommen, bildet sich eine Metagemeinschaft, *eine Gemeinschaft von Metapopulationen*. Die Theorie der Metagemeinschaft befasst sich ausdrücklich mit Interaktionen zwischen Arten auf unterschiedlichen räumlichen Skalen, wobei die lokale und regionale Verteilung sowie die Häufigkeiten der Arten und ihre Wechselwirkungen untereinander in Beziehung zueinander gesetzt werden. Das Wissen über Kernprozesse in Metagemeinschaften und die Auswirkungen biologischer Interaktionen auf die Metagemeinschaft hilft uns besonders im Kontext von Naturschutzökologie, Pflanzenschutz und biologischer Schädlingsbekämpfung, die biologische Vielfalt, Ökosystemdienstleistungen und natürliche Ressourcen zu bewahren.

Das Ziel dieser Arbeit ist es biologische Wechselwirkungen und ihre Auswirkungen auf die Kernprozesse in Metagemeinschaften, welche letztlich die Struktur der Metagemeinschaft formen, genauer zu verstehen. Hierfür wurden drei Blattlausarten (*Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* und *Uroleucon tanaceti*) als Modellsystem verwendet, welche auf Rainfarn spezialisiert sind und eine klassische Metapoulationsstruktur aufweisen.

In Kapitel II wurden die Auswirkungen von Umweltfaktoren und biologischen Wechselwirkungen auf die Bildung von geflügelten Morphen der Rainfarn-Blattläuse untersucht. Insbesondere wurde versucht mehr über die Muster der Entwicklung geflügelter Morphen bei *M. tanacetaria* und *M. fuscoviride* während der Vegetationsperiode und die Unterschiede zwischen den beiden Arten zu erfahren. Es wurde ebenfalls untersucht ob die Eigenschaften der mütterlichen Morphe, eine große Populationsdichte oder die Anwesenheit von Räubern die Produktion von geflügelten Morphen beeinflusst. Die Ergebnisse zeigten, dass *M. tanacetaria* während der gesamten Vegetationsperiode geflügelte Morphen produziert, während die Produktion von geflügelten Individuen in *M. fuscoviride* auf die ersten Generationen zu Beginn der Vegetationsperiode begrenzt ist. Die Produktion von geflügelten Morphen war für beide Arten in der dritten und vierten Generation am größten. Des Weiteren kann die mütterlichen Morphe die Produktion von geflügelten Nachkommen beeinflussen. Obwohl geflügelte Mütter beider Spezies geflügelte Nachkommen produzierten, hatten flügellose Mütter relativ mehr geflügelten Nachwuchs. Eine hohe Populationsdichte und die Anwesenheit von Räubern verursachten einen signifikanten Anstieg des Anteils an geflügelten Morphen in *M. tanacetaria*, während kein Effekt auf *M. fuscoviride* gefunden wurde. Es konnte gezeigt werden, dass die spezifischen Eigenschaften der beiden Arten sowie die Charakteristiken des Lebensraumes die Verbreitung von Angehörigen der Gemeinschaften beeinflusst.

In Kapitel III wurde untersucht, welche Auswirkungen interspezifische Konkurrenz zwischen den drei auf Rainfarn spezialisierten Blattlausarten hat und ob diese durch die Anwesenheit von mutualistischen Ameisen oder von Räubern beeinflusst werden können. Es zeigte sich, dass es starke Konkurrenz zwischen den

Rainfarn-Blattlausarten gibt, welche sogar zur kompletten Ausgrenzung einer Art führen können. Die Anwesenheit von mutualistischen Ameisen veränderte die konkurrenzbedingte Hierarchie zwischen den Blattlausarten erheblich. Die Anwesenheit von Räubern beeinflusste die Lebenszeit der Blattlauskolonien, jedoch war dies abhängig von der Anwesenheit der Ameisen. In einem solchen System kann Konkurrenz folglich als Schlüsselfaktor für die Strukturierung und Dynamik der Metagemeinschaft betrachtet werden.

In Kapitel IV wurde getestet, ob die Wahl der Wirtspflanze bei Rainfarn-Blattläusen die biologischen Interaktionen mit anderen Rainfarn-Blattlausarten widerspiegelt und wie die Wahl der Blattläuse durch die Anwesenheit von Artgenossen oder artfremden Blattläusen beeinflusst wird. Die Ergebnisse zeigen, dass die Wahl der Wirtspflanze durch die Anwesenheit und den vorherigen Befall durch andere Blattläuse beeinflusst wird, so dass Blattläuse bestimmte Pflanzen auswählen, um zukünftige Konkurrenz zu vermeiden. Folglich können solche Interaktionen die Struktur und Dynamik der Metagemeinschaften dieser Arten beeinflussen.

In Kapitel V wurden verschiedene Rainfarn-Blattlausarten an deren Räuber verfüttert, um zu untersuchen wie sie deren Überleben und Entwicklung beeinflussen. Es wurde auch überprüft, ob eine gemischte Fütterung aus mehreren Blattlausarten einen Vorteil für die Räuber bietet. Die Fütterung hatte je nach Blattlausart unterschiedliche Effekte auf die Entwicklung und das Überleben der Räuber, die gemischte Fütterung brachte jedoch keinen Vorteil.

In Kapitel VI wurde untersucht, ob die Produktion von geflügelten Nachkommen als Reaktion auf die Anwesenheit von Räubern eine allgemeine Strategie gegen jegliche Art von Räubern oder eine evolutionäre Antwort auf spezialisierte Räuber und Parasiten darstellt. Frühere Studien hatten gezeigt, dass auf Blattläuse spezialisierte Räuber, wie Marienkäfer und Florfliegen, erheblichen Einfluss auf die Produktion von geflügelten Nachkommen bei der Erbsenblattlaus (*Acyrthosiphon pisum*) haben, während die Wirkung von Generalisten unklar war. In dieser Studie wurden Individuen der Erbsenblattlaus mit zwei verschiedenen Arten von Kurzflügelkäfern (Staphylinidae) konfrontiert und die Produktion von geflügelten Nachkommen untersucht. Die Ergebnisse zeigen, dass sich der Anteil an geflügelten Nachkommen bei Anwesenheit beider räuberischer Arten erhöht. Demnach beeinflussen polyphage Räuber, welche Blattläuse in ihre Ernährung einbeziehen, ebenfalls den Flügelpolymorphismus der Blattläuse.

Die Dynamik der Rainfarn-Blattlaus Metagemeinschaft kann hauptsächlich aus der *species-sorting perspective* beschrieben werden, nach welcher verschiedene Blattlausarten unterschiedliche Habitate bevorzugen, welche wiederum auf Grund heterogener Lebensräume räumlich getrennte Nischen bilden. Die vorliegende Studie zeigt, dass die Struktur der Metagemeinschaft stark von Ausbreitungsfähigkeit, Konkurrenz, Anwesenheit mutualistischer Partner und natürlich der ansässigen Räubergemeinschaft beeinflusst wird. Diese Ergebnisse ergeben zusammen ein klareres Bild der biologischen Interaktionen in Pflanze-Herbivoren-Systemen und zeigen, dass diese Interaktionen zentrale Elemente in Metagemeinschaften sind, da sie durch ihren Einfluss auf zentrale Prozesse deren Struktur beeinflussen. In einem solchen System können schon kleinste Änderungen des Lebensraumes zu deutlichen Veränderungen der Struktur und Diversität der Metagemeinschaft führen. Mit Hilfe der Erkenntnisse über diese Systeme können wir unsere Expertise erweitern um auch andere Systeme für Naturschutzzwecke oder biologische Schädlingsbekämpfung zu nutzen.

CHAPTER I

1- GENERAL INTRODUCTION

1-1- Metapopulation concept

Individuals within local populations interact with each other and, along with the results of these interactions together with the effect of environmental factors, these populations have a finite lifetime, i.e. have a certain probability of going extinct as a consequence of demographic stochasticity. Nevertheless, by looking at regional populations, it is found that overall, the populations are more persistent or even stable. Here the metapopulation concept helps to understand this dynamics and gives us the clearer resolution of these interactions.

A metapopulation can be seen as a population of populations, thus it is a set of spatially separated subpopulations that interact via migration and all have a finite lifetime (Hanski & Gilpin, 1991; Hanski, 1999; Hanski & Gaggiotti, 2004b). Basically, the metapopulation concept refers to certain important ecological phenomena including population turnover, extinction, and the establishment of new subpopulations (Hanski & Gaggiotti, 2004b; Leibold *et al.*, 2004). The metapopulation as a whole is often more stable than single subpopulations because of immigration of individuals from one subpopulation to habitat patches that were formerly occupied by other subpopulations which have become extinct (recolonization). It is also possible that some individuals immigrate to a small population and rescue it from extinction (rescue effect) (Gotelli, 1991; Gaggiotti & Hanski, 2004).

The term *metapopulation* was coined by Levins in 1969 when he provided a simple model to investigate the basic dynamics properties of metapopulations. At that time, he distinguished between the dynamics of a single population and a set of subpopulations and recognised that a fraction of the local habitat could be occupied by local populations at a time, i.e. occupancy model. However, the processes referred to in Levins (1969), i.e. the idea of metapopulation structure and dynamics, were already long known beforehand (Hanski & Gilpin, 1991). For example, Wright (1940) was curious about the evolutionary implications of patchy population structure, whilst Andrewartha & Birch (1954) strongly supported for the metapopulation view that local populations could frequently go extinct, and that local habitats could be empty or recolonized. MacArthur & Wilson (1967) presented a theory based on the extinction and colonization processes, as determinants of species diversity on islands. After Levins' pioneering work, the metapopulation idea and its perspectives developed considerably.

1-2- Core processes in metapopulations

The core processes concerning metapopulations are dispersal, colonization of new local populations and population extinction (Hanski & Gilpin, 1991; Hanski, 1998; Clobert *et al.*, 2004; Hanski & Gaggiotti, 2004b). The study of how these processes, acting together, affect the dynamics, structure and the evolution of local populations and metapopulations is crucial to a better understanding of the environment and the management of natural resources.

1-2-1- Dispersal

Dispersal of individuals among patches of habitats as a determinant of colonization–extinction is a critical component of metapopulation dynamics (Clobert *et al.*, 2004). Within a metapopulation, all patches are partly exchanging individuals due to dispersal, even those that are already occupied. Re–colonization of empty habitat patches, in which the population is already extinct, only takes place as a result of dispersal. In addition, extinction probability is certainly affected by increasing dispersal through emigration and is decreased by immigration (i.e. rescue effect) (Hanski, 1999; Clobert *et al.*, 2004; Gaggiotti & Hanski, 2004).

There is increasing evidence to show that the departure of an individual from its natal patch is dependent on numerous factors and that individuals do not choose to settle in a new habitat at random (Kokko *et al.*, 2001; Clobert *et al.*, 2004). Multiple biotic and abiotic factors are responsible for promoting dispersal (migration). Habitat–specific factors such as temperature, food, natural enemies and interspecific competition, mating related factors including inbreeding avoidance, and social factors such as intraspecific competition and local high population density or imminent extinction, may be considered as local factors initiating dispersal (Zera & Denno, 1997; Seymour *et al.*, 2003; Clobert *et al.*, 2004; Bates *et al.*, 2006; Yee *et al.*, 2009). In addition, there are other factors that can affect dispersal, not only at the local scale (i.e. within local populations) but also at the metapopulation scale. For example, recolonization of empty habitats determined by the migration distances travelled by individuals, which by itself determines the spatial scale of the metapopulation (Clobert *et al.*, 2004). Population density is one of the most prominent factors influencing the dispersal rate. It can be seen both as an indication of intraspecific competition and as a sign of habitat quality (e.g. Müller *et al.*, 2001; Clobert *et al.*, 2004; Nowicki & Vrabec, 2011).

Dispersal has three phases: emigration, transience and settlement (immigration), all of which play an important role in successful transfer of individuals in the metapopulation (Clobert *et al.*, 2004). Indeed, departure and settlement decisions depend on habitat quality in terms of food resources, amount of refuges, predators, parasites and conspecific and heterospecific competitors. Most species studied are found to have a state–dependent dispersal response to changes in habitat quality; among such species aphids are well–documented examples (Mackay & Wellington, 1977; Weisser *et al.*, 1999; Sloggett & Weisser, 2002; Kunert & Weisser, 2003; Clobert *et al.*, 2004). One of the considerable causes for dispersal morph production in aphids is the presence of their natural enemies. Numerous studies have focused on the effects of specialist aphid predators such as ladybirds, lacewings and hoverfly larvae on their aphid prey using the model species, the pea aphid *Acyrthosiphon pisum* Harris (e.g. Dixon & Agarwala, 1999; Weisser *et al.*, 1999; Kunert & Weisser, 2003). However, studies on the other aphid species and also the effects of generalist predators like predatory bugs and rove beetles, are very rare. It is not clear yet if this is a general strategy of aphids against all predators or just an evolutionary response to their specialist predators or parasitoids.

Dispersal in many taxa is often characterized by special mechanisms, e.g. wings in the case of aphids, which enhance their ability to disperse. In many organisms, production of disperser individuals among the population is condition dependent. For example, when host plant quality is reduced, aphids start to produce winged individuals that are specialized for dispersal (Johnson, 1966; Sutherland, 1969b; Müller *et al.*, 2001).

1-2-2- Colonization

Colonization is a fundamental process in metapopulation ecology (Gaggiotti *et al.*, 2002), defined as starting with the arrival of an immigrant and ending when the extinction probability of the population is no longer dependent on the immigrant properties (Ebenhard, 1991). Colonization ability of a species is critical to its survival in a patchy habitat. Several factors could potentially affect the probability of successful colonization of habitats, such as the number of colonizers, the reproductive mode of the organism in question (asexual reproduction vs. sexual reproduction), the reproductive value of colonisers, their niche breath and the presence of competitors (Cole, 1983; Bengtsson, 1991; Ebenhard, 1991; Hanski, 1999). Finding suitable habitats for settlement by immigrants is very important for a successful colonization and consequently population increase. So here, occupancy of the habitat by conspecific or heterospecific individuals is crucial such that it could lead to future competitive or facilitative interactions. Therefore, any biotic and abiotic factors that influence the probability of successful colonization of a species in suitable habitats will be influential in understanding the metapopulation dynamics of that species.

1-2-3- Extinction

Extinction also plays an important role in metapopulation dynamics. Many processes naturally contribute to extinctions in metapopulations. The main drivers for extinction of local populations in a metapopulation are demographic and environment stochasticities; however, extinction could come about by deterministic causes, such as natural enemies and interspecific competition (Bengtsson, 1989; Harrison, 1991; Hanski, 1998; Weisser & Härri, 2005). A fundamental criterion in metapopulation modelling is that the risk of population extinction increases with decreasing population size. In other words, the size of a local population plays a key role in its extinction probability, so that the larger the local population, the lower the probability of extinction (e.g. Weisser & Härri, 2005), a fact directly related to the operation of Allee effect in small subpopulations (e.g. aphid colonies on plant) within metapopulations (Amarasekare, 1998; Stephens *et al.*, 1999). Indeed, most metapopulations exhibit considerable variations in the size and quality of their habitat patches and these have a great impact on the size of local populations (Hanski & Gilpin, 1991; Harrison, 1991). Nevertheless, the size of a local population is also affected by many other factors including the rate of dispersal, competitive interactions, the activity of predators and parasitoids, and disease events.

1-3- Metacommunity ecology

A metacommunity forms when two or more species are confined to the same set of habitat patches and are connected by the dispersal of at least one of the component species. In other words, if two or more species that exhibit metapopulation structure occur in the same set of habitats they form a metacommunity, *a community of metapopulations* (Hanski & Gilpin, 1991; Wilson, 1992; Holyoak *et al.*, 2005b; Leibold, 2009). Hanski and Gilpin (1997) used the term metacommunity as an equivalent for *multispecies metapopulation*. Therefore, all the processes that shape and structure a metapopulation will still have their important roles within a metacommunity. Metacommunity ecology explicitly addresses interactions among species at different spatial scales so that local and regional distributions and abundances of species are related to their interactions with each other. If the species interact as competitors, mutualists, facilitators in successional processes or predator–prey, then the presence of one species in a habitat patch influences the extinction and colonization probability of another species, and this ultimately could affect their distribution at local and regional scales (Hanski & Gilpin, 1991; Leibold *et al.*, 2004; Hoopes *et al.*, 2005).

One of the pioneering works on metacommunities was published by Wilson (1992). He posited the idea in his influential theoretical paper that complex interactions between species can themselves provide a source of endogenous variation that affects diversity in spatial scales. Another influential paper on metacommunity concepts is the review by Leibold *et al.* (2004) which specifically discusses how species interactions may influence – or be influenced by – the spatial dynamics of individual metapopulations. There are different approaches toward metacommunity dynamics which differ in their assumptions about dispersal rates and the amount of environmental heterogeneity. Leibold *et al.* (2004) in their seminal review synthesized these paradigms into a common framework or unifying theme. They classify four metacommunity paradigms, as defined in Table 1-1. These perspectives each describes specific processes that are useful for predicting empirical community patterns.

Table 1-1: Metacommunity paradigms defined by Leibold *et al.* (2004).

Metacommunity paradigms	Definition
Patch dynamics perspective	This assumes that patches are identical and that each patch is capable of containing populations. Patches may be occupied or unoccupied. Local species diversity is limited by dispersal. Spatial dynamics are dominated by local extinction and colonization.
Species–sorting perspective	This emphasizes the resource gradients or patch types cause sufficiently strong differences in the local demography of species and the outcomes of local species' interactions that patch quality and dispersal jointly affect local community composition. This perspective emphasizes spatial niche separation above and beyond spatial dynamics. Dispersal is important because it allows compositional changes to track changes in local environmental conditions.
Mass–effect perspective	This focuses on the effect of immigration and emigration on local population dynamics. In such a system, species can be rescued from local competitive exclusion in communities where they are bad competitors, by immigrate from communities where they are good competitors. This perspective emphasizes the role that spatial dynamics affect local population densities.
Neutral perspective	Here, all species are similar in their competitive ability, movement and fitness. Population interactions among species consist of random walks that alter relative frequencies of species. The dynamics of species diversity are then derived both from probabilities of species loss (extinction, emigration) and gain (immigration, speciation).

1-4- Interspecific competition affects core processes

As mentioned earlier, interspecific competition can lead to considerable effects on ongoing processes in metapopulations such as dispersal, colonization and extinction (Bengtsson, 1991). Therefore, competition could be considered as a key factor in structuring and dynamics of a metacommunity. In a metacommunity, where a set of ecologically similar species are present, interactions between resident individuals in habitat patches and potential colonists are likely to be competitive. Generally, if the species do interact with each other as competitors or even facilitators, then the presence of one species may influence the extinction or colonization probabilities of another species, thereby influencing its regional distribution. These kinds of interspecific interactions could in the longer term lead to coexistence or extinction of certain species which finally shape the metacommunity assembly. At the metacommunity level, two competitors which cannot coexist locally may nonetheless coexist as competing metapopulations (Slatkin, 1974; Hanski, 1983). Essentially, coexistence could be based on heterogeneous distributions of individuals as a function of habitat heterogeneity. Here, the key mechanisms are competitive exclusion rates and relative dispersal abilities of the species (Hanski & Gilpin, 1991). Empirical evidences for this possible coexistence are reviewed by Bengtsson (1991).

1-5- Aphids forming metacommunities

The metapopulation concept (and coupled with this, the metacommunity concept) have attracted much interest in the past few decades. There are numerous studies on this topic on different organisms such that many aspects of ecology have been investigated, including multitrophic interactions, conservation and evolution (e.g. see Hanski & Gaggiotti, 2004a). Overviewing the literatures on this topic reveals that the majority of the metapopulation studies in terrestrial ecosystems are biased towards the use of butterfly species (Lepidoptera) as models, as performed especially by Hanski and his colleagues (e.g. Thomas & Hanski, 1997; Hanski, 1998; Saccheri *et al.*, 1998; Hanski, 1999; Harrison *et al.*, 2011). Among insects, aphids (Hemiptera: Sternorrhyncha) are also ideal organisms to study the metapopulation and metacommunity concepts. A considerable number of aphid species are supposed to exhibit metapopulation structure, since they live in discrete patchy habitats with a restricted diet breath, i.e., feed on restricted number of host plants and these plants are essentially “islands of resources” leading to habitat spatial heterogeneity. Having specialized life cycles, short generation times, asexual reproduction and specialized morph for dispersal are the other prominent characteristics of aphids which make them suitable organisms for this kind of studies. However, there are considerably fewer studies on aphids in comparison with butterflies. The work performed by Addicott (1978c) is one of the foremost studies on aphid metapopulation dynamics, whilst Weisser and his colleagues are among the very few scientists who have focused intensively on aphids metapopulation and metacommunity (e.g. Weisser, 2000; Massonnet *et al.*, 2002; Weisser & Härri, 2005; Zheng *et al.*, 2009; Loxdale *et al.*, 2011).

1-5-1- Aphids: life cycle, reproduction, morphs and dispersal

Aphids are small (1-10 mm. in length), soft–bodied insects which feed on the phloem of their plant hosts using mouthparts comprising piercing stylets (Miyazaki, 1987b). These insects exhibit a various range of relatively complicated life cycles. Each has a number of different stages and for each stage there are one or more specialist morphs. These morphs are adapted for specific purposes in the life cycle (Williams & Dixon, 2007). They breed predominantly by apomictic parthenogenesis whereby largely genetically identical offspring are produced mitotically by a process involving "telescoping of generations" (see Blackman, 1987; Dixon, 1998).

The life cycles of aphids can be divided into two types based on how they utilize their host plant: 1) Non host–alternating life cycle (monoecious or autoecious) in which the aphids feed and reproduce on either one host plant or a few closely related plants during the year. They can produce eggs on the same group of host plants that is fed on by all of the parthenogenetic generations. 2) Host–alternating life cycle (heteroecious) in which aphids have two distinct types of host plants i.e. primary host plants which are mostly woody (e.g. Rosaceae) and secondary host plants which are herbaceous. In aphid species which retain an autumnal sexual phase, following mating of the sexual morphs, overwintering is achieved as cold–hardy eggs on the primary host, whilst in the following spring and summer, winged asexual females are produced and migrate back to the secondary host where they produce numerous parthenogenetic generations. In the autumn, winged forms (males and pre–sexual females or gynoparae) are induced within the asexual lineages as a result of the short day length and low temperature conditions, and migrate back to the primary host and thereupon lay eggs, thus completing the life cycle (and in effect resetting it) (Kawada, 1987; Dixon, 1998; Blackman & Eastop, 2000; Williams & Dixon, 2007). In terms of egg production in aphids, there are two types of life cycles. Some aphid species are holocyclic, meaning that they produce eggs in their annual life cycles, although some other species never produce eggs and overwinter as asexual females (virginoparae) or as nymphs; this group are described as anholocyclic. In between, there are some aphid species that show both holocycly and anholocycly (Dixon, 1998; Simon *et al.*, 2002; Williams & Dixon, 2007). In species with a sexual phase, at the beginning of the spring, the first morph to hatch from the overwintering egg is termed the *fundatrix* (i.e. first asexual female or initial asexual lineage stem mother); these morphs begin to reproduce by parthenogenesis and give birth to other parthenogenetic females that establish several generations during the year. An aphid's lifespan within an asexual lineage is generally short and within a relatively few days (usually 7-10) soon become adult (Kawada, 1987; Dixon, 1998).

In aphids, various types of morphs occur in relation to biological characters in their life cycle. There could be five or even more different adult female phenotypes in the life cycle of an aphid lineage, as found in connection with heterogony and host alternation. Different morphs are specialized for different tasks such as reproduction, dispersal, and surviving severe or less favorable climatic or nutritional conditions (Kawada, 1987; Miyazaki, 1987a). One of the most common morphs in aphids is the winged morph, specialized for dispersal. The two main advantages of producing winged dispersal morphs in aphids are migration and dispersal between different host plants, and escape from adverse environmental conditions (Kawada, 1987; Dixon, 1998). In a metapopulation setting, dispersal is even more important as each plant is essentially an island of resource separated by unsuitable habitat that the aphids have to navigate before reaching the next suitable plant.

1-5-2- Aphids natural enemies

Aphids are attacked by many natural enemies. As shown in many studies, these can, and often do, drastically influence aphids population structure and fitness in different ways (Dixon, 1998). In the metacommunity context, two aspects of the natural enemies' influence are more important. Firstly, there is the effect of natural enemies on population extinction such that natural enemies could be considered as an effective driver for extinction of aphid populations. In a metacommunity, where there are several aphid species in a habitat patch and which share common predators, the suitability of a species as prey could cause *apparent competition* which in turn could potentially lead to extinction of that species (Morin, 1999). Secondly, the effect of natural enemies on dispersal of aphids such that predation or the risk of predation has knock–on effects on prey dispersal (e.g. Weisser *et al.*, 1999; Weisser, 2001). It has long been shown that the presence of predators in a habitat patch induces the production of winged morphs among an aphid colony which thereby allows them to escape from predators, or reduce the risk of predation (Dixon & Agarwala, 1999; Weisser *et al.*, 1999).

1-5-3- Aphid–ant interactions

Mutualistic interaction between aphids and ants is one of the classical examples of mutualism (Keller & Gordon, 2010). There are numerous studies which focus on ant–aphid interactions, many of which indicate that ants are beneficial to aphids (e.g. Dixon, 1998; Stadler & Dixon, 1999; Flatt & Weisser, 2000). Aphids provide honeydew to ants (which is rich in carbohydrates) and in return gain protection against natural enemies, especially predators and parasitoids (Sudd, 1987; Renault *et al.*, 2005; Stadler & Dixon, 2008). In addition, there are further advantages for aphids being attended by ants, for example when ants collect honeydew they actually clean the immediate environment which thereby prevents the aphids sticking to their own honeydew, and perhaps also from being covered with honeydew, whilst it also decreases the likelihood of growth of fumagine fungi. Several lines of evidence show that ant attendance improves aphids reproductive performance, and promotes developmental rates, and colony growth (Flatt & Weisser, 2000; Fischer *et al.*, 2001; Stadler & Dixon, 2008). Aphid species that are attended by ants exhibit two types of mutualistic relationships: facultative mutualism in which aphids are able to survive without ants so that they engage in mutualism when ants are present, and obligate mutualism in which aphids need ants for their survival. However, the relationship between ants and aphids is not always mutualistic; in some cases ants prey upon aphids (Sudd, 1987; Billick *et al.*, 2007), for example, the sycamore aphid *Drepanosiphum platanoides* (Schrank) is frequently preyed by the wood ant, *Formica rufa* (L.) (Skinner, 1980).

Mutualistic aphids–ants interactions could have a crucial impact on the metacommunity dynamics of aphids and potentially might also alter the ongoing metacommunity processes. For example, tending by ants of an aphid species may cause the extinction of other competitor aphid species (Addicott, 1978a). Ant attendance also could have an effect on extinction of tending aphid populations, for example, Addicott (1978c) showed that the populations of three species of aphids of the genus *Aphis* tended by ants had lower extinction rates than untended populations of the same species. In another study, Tilles & Wood (1982) revealed that colonies of *Cinara* spp. infesting white fir were more likely to go extinct if not attended by ants.

1-6- The study system

The present thesis focuses on the specialized aphids of the tansy plant as a good model for studying metapopulation and metacommunity processes. These aphids exhibit the preconditions for investigating metapopulation structure i.e.

feeding on a certain host plant species which occurs as a discrete patchily distributed resource (Weisser, 2000; Massonnet *et al.*, 2002; Loxdale *et al.*, 2011).

1-6-1- The host plant

Tansy, *Tanacetum vulgare* L. (Asteraceae) (Fig. 1-1) is a perennial herbaceous composite plant native to Europe and Asia (Mitich, 1992). It grows as isolated patches or stands of single plants on riverbanks, wastelands and along roadsides. The individual plants comprise a largely genetically identical genet with up to 70 flowering ramets (shoots) (but usually much fewer). Plants can reproduce both sexually by producing tiny seeds and clonally underground via stolons. In the field, tansy plants are easily recognized and a few to several

Figure 1-1: Tansy, *Tanacetum vulgare* (Asteraceae). The picture was taken in the summer when the flower head was fully developed. Photo: The author.

hundred plants can be found at any particular site. These sites are often separated from one another by vegetation unsuitable for the survival of its specialized aphids. At the end of the autumn, the above–ground ramets dry off and die until the next spring whereupon new ramets emerge from the soil.

1-6-2- The aphid species

Tansy, as with most other plants, is attacked by herbivorous insects, including aphids. Tansy hosts more than 23 aphid species globally (Blackman & Eastop, 2006; Holman, 2009), including three specialist tansy feeders: *Macrosiphoniella tanacetaria* (Kaltenbach) (Fig. 1-2), *Metopeurum fuscoviride* Stroyan (Fig. 1-3) and *Uroleucon tanaceti* (L.) (Fig. 1-4) (Hemiptera: Aphididae) which are the special objects of this study. These aphids are cyclical parthenogens, i.e. numerous parthenogenetic generations are followed by a single autumnal/winter sexual generation within the annual life cycle (Massonnet *et al.*, 2002; Weisser & Härri, 2005; Loxdale *et al.*, 2011). Alate (winged) asexual females are produced especially in the spring and summer months and then fly off to colonize new plants. Sexual morphs (winged/wingless males and wingless oviparae) are induced in autumn under the influence of short day and low temperature conditions and mate on tansy. Like other holocyclic aphids, after mating with males, the oviparae lay diapausing eggs which hatch the following spring and initiate new asexual lineages, but since the aphids are monoecious, on the same host plant.

Macrosiphoniella tanacetaria is 3.2–4.1 mm long with green to dark greyish green body, dusted with fine wax powder, with black antennae, legs, siphunculi and cauda (Fig. 1-2). This species is monoecious and holocyclic with wingless oviparae and winged males. The distribution of this species includes Europe, Morocco, West Asia, Siberia and it has been introduced to North and South America (Blackman & Eastop, 2006). It is not ant–attended (Stadler, 2004) and feeds in loose colonies mainly on the new shoots and flowering head of the host plant.

Figure 1-2: *Macrosiphoniella tanacetaria*: a wingless viviparous female with two 4th instar nymphs in the summer with green colour (up) and a colony consisting several wingless viviparous females with their offspring in the autumn with dark grayish green colour (down). Photo: The author.

Metopeurum fuscoviride is dark brown to black with body length of 1.8-2.9 mm. Abdomen have a black central patch which disappears in preserved specimens (Fig. 1-3). This species is also monoecious and holocyclic but unlike *M. tanacetaria* and *U. tanaceti*, produces both wingless oviparae and males in late autumn. Its distribution includes Europe, West Siberia and Central Asia (Blackman & Eastop, 2006). This species is obligatory myrmecophilous aphid and is commonly attended by the black garden ant, *Lasius niger* (L.) (Mackauer & Völkl, 1993; Flatt & Weisser, 2000), as well as – more rarely – other species, especially the red ant, *Myrmica rubra* (L.) and the wood ant, *Formica rufa* L. (Loxdale *et al.*, 2011). *Metopeurum fuscoviride* is a stem feeder, feeding in more compact colonies near the apex of the ramets but can also occupy (at least to a certain extent) the same feeding niche as *M. tanacetaria* (although mixed colonies have not been observed).

Figure 1-3: A colony of *Metopeurum fuscoviride* consisting of wingless and winged viviparous females with their offspring attended by mutualistic ants. Photo: The author.

Uroleucon tanaceti is bright red or reddish brown, with yellowish, black–banded antennae and legs, brown–black siphunculi and yellow cauda (Fig. 1-4). Body length is 2.2–3.4 mm. This species is also monoecious and holocyclic with wingless oviparae but with winged males (pers. obs.). Its distribution includes Europe, West Siberia, Central Asia, the eastern Himalayas and North America (Blackman & Eastop, 2006). It feeds mainly on the underside of the lower leaves of its host plant and is also a non–ant attended species. The parts of the plant infested by *U. tanaceti* soon becomes yellow, which is an indication that aphid–plant co–evolution of this particular species is not yet very advanced (Nowak & Komor, 2010).

Figure 1-4: A colony of *Uroleucon tanaceti* comprising a wingless viviparous female with both winged and wingless offspring. Photo: The author.

1-7- Objectives

The general aim of this study was to increase knowledge about metapopulation and metacommunity processes and involving biological interactions that shape the structure and assembly of a herbivore metacommunity in patchy habitats using tansy aphids as a model system.

More specifically, the objectives were to:

A) Study the seasonal life cycle and appearance timing of dispersal morphs of specialized tansy aphids during the growing season.

B) Explore the effects of maternal morph and environmental factors, such as crowding and the presence of predators, on induction of dispersal morph in tansy aphids which ultimately affect the dispersal among habitat patches.

C) Investigate the outcomes of interspecific competition among the three aforementioned specialized tansy aphids and how the outcome is altered (or not) by the presence of mutualistic ants and predators, and how it eventually shapes the metacommunity structure of these aphids.

D) Understand the colonization strategies that tansy aphids use for host plant selection with emphasis on the effects of biological interactions on host plant choice.
E) Study the suitability and effects of different aphid species as prey on development and survival of their predators and to discern whether or not there is any diet mixing benefit for predators.
F) Investigate if the response/s of aphids to the presence of natural enemies by production of more winged offspring is a general strategy against all predators or just it is an evolutionary response to their specialist predators.

1-8- Manuscripts overview and authors contributions

This thesis contains five manuscripts. A brief summary of each manuscript along with the authors contributions is given below.

1-8-1- Manuscript I

Mehrparvar, M., Zytynska, S. E. & Weisser, W. W. Multiple cues for winged morph production in an aphid metacommunity. Published in *PLoS ONE,* 8(3): e58323.

In this manuscript, some of the main factors that stimulate and affect the production of winged aphid individuals, which are specialized for dispersal between habitat patches, were studied. Here, we particularly focused on the winged morph production patterns in the two specialized tansy aphids, *M. tanacetaria* and *M. fuscoviride*, throughout the growing season, whilst the effects of maternal morph, crowding and predator presence on the production of winged morphs were also investigated. This study provided a more detailed picture of the population dynamics and dispersal of these aphids, which are among the most important phenomena in the metacommunity ecology.

MM, SEZ and WWW conceived and designed the experiments. MM performed the experiments. MM and SEZ analyzed the data. MM wrote the manuscript, which was edited by SEZ and WWW.

1-8-2- Manuscript II

Mehrparvar, M., Balog, A. & Weisser, W. W. Species–sorting by a mutualist in a herbivore metacommunity: Ant–mediated reversal of competitive hierarchies. In preparation for submission to *Ecology Letters*.

This manuscript describes the interspecific competition, one of the most important factors that shapes metacommunity structure and assembly, among the three specialized tansy aphids with special focus on the roles of mutualistic ants and predators on the outcome of these competitive interactions. In this study, a greenhouse experiment, in the absence of predators, was performed to determine the effects of two mutualistic ant species on the competition outcome among the three aphid species. In a field experiment, the outcome of competitive interactions was evaluated in the presence of both mutualistic ants and predators.

MM and WWW conceived and designed the experiments. MM and AB performed the experiments. MM analyzed the data. MM wrote the manuscript, which was edited by WWW.

1-8-3- Manuscript III

Mehrparvar, M., Mansouri, S. M. & Weisser, W. W. Mechanisms of species–sorting: Do aphids choose plants to avoid future competitive interactions? Submitted to *Ecological Entomology*.

This manuscript concerns findings on the colonization strategies that the three specialized tansy aphids use to choose their host plant, which ultimately creates their metacommunity structure. Here, emphasis was on competitive interactions as a determinant factor that affect colonization of immigrants. Winged and unwinged forms of aphids were used to test their choices toward occupied/unoccupied and previously infested/uninfested plants by conspecific or heterospecific individuals. An additional experiment also was performed to investigate the effects of previous plant infestation on the performance of *M. tanacetaria*.

MM and WWW conceived and designed the experiments. MM and SMM performed the experiments. MM analyzed the data. MM wrote the manuscript, which was edited by WWW.

1-8-4- Manuscript IV

Mehrparvar, M., Mahdavi Arab, N. & Weisser, W. W. Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing? Published in *Biological Control,* 65: 142-146.

In this manuscript, the effects of the three specialized tansy aphids as diet items on the survival and development of their two common and important predators, *Chrysoperla carnea* (Neuroptera: Chrysopidae) and *Coccinella septempunctata* (Coleoptera: Coccinellidae), were investigated. In these experiments, the predators were offered either each aphid species alone or a mixed diet of all three aphid species in order to determine whether the predators can successfully complete their development and survive when fed exclusively on only one of the three aphid species, also whether there is any benefit of dietary mixing.

MM and WWW conceived and designed the experiments. MM and NMA performed the experiments. MM analyzed the data. MM wrote the manuscript, which was edited by WWW.

1-8-5- Manuscript V

Balog, A., **Mehrparvar, M.** & Weisser, W. W. Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae). Published in *European Journal of Entomology,* 110(1): 153-157.

This study concerned investigation of whether aphids respond to the presence of polyphagous predators – rove beetles (Coleoptera: Staphylinidae)– by increasing the number of winged morphs among their offspring, and also if there are differences among the two predators species, *Drusilla canaliculata* and *Tachyporus hypnorum*, in their effects on aphid growth and winged morph production. In this experiment, the pea aphid, *Acyrthosiphon pisum*, the model aphid, was used since there are already results available from previous studies on production of dispersal morph in this aphid species, especially on wing induction caused by specialist predators.

AB and WWW conceived and designed the experiments. AB and MM performed the experiments. AB analyzed the data. AB wrote the manuscript, which was edited by MM and WWW.

CHAPTER II

2- Manuscript I

Multiple cues for winged morph production in an aphid metacommunity

Mohsen Mehrparvar, Sharon E. Zytynska & Wolfgang W. Weisser

Terrestrial Ecology, Department of Ecology and Ecosystem Management, Center for Life and Food Sciences Weihenstephan, Technische Universität München, 85354 Freising, Germany

Published in *PLoS ONE*
8(3): e58323

OPEN ACCESS Freely available online

PLOS | ONE

Multiple Cues for Winged Morph Production in an Aphid Metacommunity

Mohsen Mehrparvar*, Sharon E. Zytynska, Wolfgang W. Weisser

Terrestrial Ecology, Department of Ecology and Ecosystem Management, Center for Life and Food Sciences Weihenstephan, Technische Universität München, Freising, Germany

Abstract

Environmental factors can lead individuals down different developmental pathways giving rise to distinct phenotypes (phenotypic plasticity). The production of winged or unwinged morphs in aphids is an example of two alternative developmental pathways. Dispersal is paramount in aphids that often have a metapopulation structure, where local subpopulations frequently go extinct, such as the specialized aphids on tansy (*Tanacetum vulgare*). We conducted various experiments to further understand the cues involved in the production of winged dispersal morphs by the two dominant species of the tansy aphid metacommunity, *Metopeurum fuscoviride* and *Macrosiphoniella tanacetaria*. We found that the ant-tended *M. fuscoviride* produced winged individuals predominantly at the beginning of the season while the untended *M. tanacetaria* produced winged individuals throughout the season. Winged mothers of both species produced winged offspring, although in both species winged offspring were mainly produced by unwinged females. Crowding and the presence of predators, effects already known to influence wing production in other aphid species, increased the percentage of winged offspring in *M. tanacetaria,* but not in *M. fuscoviride*. We find there are also other factors (i.e. temporal effects) inducing the production of winged offspring for natural aphid populations. Our results show that the responses of each aphid species are due to multiple wing induction cues.

Citation: Mehrparvar M, Zytynska SE, Weisser WW (2013) Multiple Cues for Winged Morph Production in an Aphid Metacommunity. PLoS ONE 8(3): e58323. doi:10.1371/journal.pone.0058323

Editor: Nicolas Chaline, Université Paris 13, France

Received September 19, 2012; **Accepted** February 2, 2013; **Published** March 5, 2013

Funding: MM was supported financially by the Iranian Ministry of Science, Research and Technology (www.msrt.ir). This study was partly supported by grant WE 3081/2-3 of the Deutsche Forschungsgemeinschaft (DFG) to WWW. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: mohsen.mehrparvar@tum.de

Introduction

Phenotypic plasticity is the ability of a single genotype to produce more than one alternative phenotype in response to environmental conditions, or in other words the ability of a single genotype to express itself in different ways in different environments [1,2]. In some cases, phenotypic plasticity will be expressed as several highly morphologically distinct results and this is termed polyphenism [3]. The caste system in social insects such as Hymenoptera and Isoptera is one of the most striking examples for polyphenism with morphologically distinct, but most of the time genetically identical, workers and soldiers [3,4]. A wide variety of environmental stimuli can induce different phenotypes in organisms [1].

Aphids exhibit polyphenism, such that genetically identical individuals can potentially show different phenotypes, e.g. they can have wings or be unwinged [5]. Winged aphids are specialized for dispersal through flight, as they have a more developed sensory system, are more resistant to starvation and live longer [6,7]. These features are assumed beneficial for locating new habitats and host plants by winged aphids in a complex environment; each aphid species feeds on a restricted range of host plants and thus the locating, landing and quick initialisation of reproduction on suitable host plants is imperative to the fitness of the aphid [8]. Winged aphids have also been shown to have reduced fecundity and longer developmental times, which is likely due to the increased energy cost of having wings [6,9,10].

The production of winged disperser morphs in aphids can be influenced by both genetic and environmental factors [11]. The production of winged male aphids has been shown to be under genetic control [5,12,13,14]. However, the production of winged offspring from asexual mothers is likely influenced by a number of environmental factors rather than under genetic control [15,16,17]. In some aphid species, winged individuals are often produced at a certain times in the season; for example, winged dispersers are produced in early summer and then again at the end of the season, when winged individuals are mostly sexual morphs [18].

A considerable number of studies have addressed the environmental conditions that affect the production of winged individuals in aphids; crowding, interspecific interactions, host plant quality and abiotic factors induce winged morph production in aphids [5,11,13,19,20,21]. Increasing the population density of an aphid colony (i.e. crowding) creates greater tactile stimulation among individuals, which can trigger wing induction [22,23]. This increased production of winged dispersers regulates the population size of a colony on a plant, as the winged aphids move away to find new host plants. The degree of sensitivity to crowding is not the same across aphid species, and even varies between different genotypes within the same species [15,16,22,23,24]. The mere presence of natural enemies, including predators and parasitoids, is known to elicit wing induction in aphids [25,26,27,28,29,30,31], potentially through pseudo-crowding effects, through changes in aphid density as aphids are consumed/parasitized, or through the production of chemicals (e.g. aphid alarm pheromones) as the natural enemy moves among the plants [32,33,34]. It is advantageous for an aphid colony to quickly produce winged morphs when a predator is present, in order to leave a plant if the risk of predation is high. Furthermore, interspecific interactions among different aphid species that occupy the same host plant can also be a cue for enhancing production of winged morphs, likely through effects on aphid density [5,35].

Dispersal is important for aphids in order to find new host plants, or to escape sub-optimal conditions. Many aphids exhibit a metapopulation structure with frequent extinction of small local populations. A metapopulation is defined as a set of sub-populations connected by limited dispersal, with frequent extinctions and recolonization of sub-populations [36]. In a metapopulation setting, dispersal is even more important as each plant is an 'island of resource' separated by unsuitable habitat that the aphids have to navigate before reaching the next suitable plant. Two specialist aphid species (*Macrosiphoniella tanacetaria* and *Metopeurum fuscoviride* (Hemiptera: Aphididae)) on tansy (*Tanacetum vulgare* (Asteraceae)) exhibit classic metapopulation structuring [37,38,39]. *Metopeurum fuscoviride* is tended by ants, which can protect aphids from predators and may inhibit wing production [5]. *Macrosiphoniella tanacetaria* is not ant tended. Together, they form a metacommunity [40] where dispersal and local extinctions structure the composition of local communities. It is unknown which environmental factors induce the production of winged morphs in these species.

In this paper, we follow winged morph production in two tansy aphid species to investigate the environmental cues that cause dispersal in these aphids, which is important for the understanding of the metacommunity dynamics. We follow the aphids across generations, over the season, to show that wing production changes through time. It has previously been suggested that in a species with prenatal wing determination the winged offspring will not themselves produce winged individuals, regardless of the environmental conditions [13,18,41,42], and we consider maternal morph to see if this is true in our tansy-aphid system. Further, we tested the influence of increased crowding and the presence of a predator on the proportion of winged aphids.

Materials and Methods

Potted tansy plants were grown in a greenhouse until 20–25 cm in height prior to experimental use. The greenhouse conditions were ~25°C during the day and ~20°C at night with a 16h light 8h dark regime. As *M. fuscoviride* is an obligate myrmecophilous aphid, the ant species *Lasius niger* had access to its colonies during all experiments. Aphid wing-dimorphism phenotype identification was performed only on 4th instar nymphs or adults; winged 4th instar nymphs of aphids can easily be recognized from wingless ones by the presence of wing buds on their thorax. To exclude effects of genetic variation in the aphids, we used different genetic lines of aphids for each experimental replicate. Meteorological data were obtained from a weather station in the Jena Experiment (4 km away from the experimental site).

1. Seasonal Life Cycle and Time of Appearance of Winged Individuals of *M. tanacetaria* and *M. fuscoviride*

To follow the production of winged morphs over all generations throughout the season, colonies of tansy aphids were located early in the season, i.e. beginning of April when first-generation individuals (fundatrices) hatched from eggs. In 2010, second-generation aphids were collected from the field and used in the experiment. In 2011, fundatrices were collected and then placed on experimental plants.

In 2010, the generations of *M. tanacetaria* (MA) aphids were followed and the appearance of winged morphs was observed. On 12th May 2010, seven potted tansy plants were placed inside cages (28×28×120 cm), to prevent infestation by non-experimental aphids and natural enemies. The cages consisted of an aluminium frame, with thick polyethylene sheets forming the top and two sides of each cage, while the two other sides were covered by fine mesh to allow airflow. The open under-side was placed inside a plastic box that had its outer walls painted with Fluon (Fluoropolymer Dispersion, Whitford GmbH, Germany), a product which on drying creates a slick barrier, thus excluding ants and other arthropods. These cages were placed outside of the Institute of Ecology, Jena, Germany, and checked every two or three days for watering and counting aphids. Two apterous (unwinged) viviparous females of MA (2nd generation, collected from a field site) were placed on the plants and allowed to reproduce for two to three days. The adults were then removed. When the nymphs developed into 4th instar or adults (and before they started to produce offspring) the numbers of winged and unwinged individuals were counted. Then, all individuals except two unwinged adults were removed and these remaining two aphids were allowed to reproduce for two or three days, resulting in between 5 and 20 offspring. The two adults were removed and the offspring allowed to further develop on the plant. This was repeated until the end of the season, when all individuals were of the sexual morph. This procedure allowed a clear separation of generations and ensured that crowding was minimal.

In 2011, the generations of both *M. tanacetaria* (MA) and *M. fuscoviride* (ME), and the number of winged/unwinged aphids, were observed throughout the season until colonies were exclusively constituted of sexuals. Ten potted tansy plants were selected and placed inside aluminium-frame cages (as previously described). These cages were placed outside in the botanical garden of Jena, Germany. ME is obligatory ant-attended and therefore the bottom of each cage was not placed in a plastic tray to encourage natural ant attendance. There were numerous ant nests in the vicinity of experimental place, therefore aphid colonies were easily attended by ants. Two fundatrices were then placed on each plant, and allowed to reproduce for two to three days. The same method for generation separation was used as in 2010 and the presence of ants on plants in ME cages was checked every two days.

2. Winged Offspring Production by Winged and Unwinged Mothers

In order to determine if winged mothers of MA produce winged offspring, we collected 15 winged individuals, in June 2011, from different un-crowded natural colonies in Jena, Germany and put them individually on a freshly detached tansy leaf, which was placed upside down onto a plastic petri dish (15 cm in diameter) containing a thin layer of 0.7% Agar gel (experiment 2.1). The dishes were maintained in a climate chamber with temperature held at 20±2°C with 16h light, 8h dark regime. The winged aphids were allowed to reproduce for three days and then they were removed. The produced offspring were allowed to develop into either 4th instar or adult stage and then the numbers of winged and unwinged were counted.

Additional experiments were made with MA, to see whether unwinged mothers produce more winged offspring than winged mothers. Here, two experiments were performed, one in the climate chamber using petri dishes (experiment 2.2); and another in the greenhouse using potted plants (experiment 2.3). For the climate chamber experiment (2.2), 20 unwinged MA were used and this was run concurrently with the previous winged mother experiment (2.1), using the same experimental set-up in order to allow for comparison. For the greenhouse experiment (experiment 2.3), 15 unwinged MA were collected from different tansy plants in Jena, Germany. These adults were placed on 15 potted tansy plants (one aphid per plant, as 15 lines) in the greenhouse. In order to prevent the escape of aphids, each plant was placed in a Plexiglas cage (35×35×90 cm). These cages have three sides, plus the top and bottom, of Plexiglas, and the front covered in a fine mesh to allow airflow. The adults aphids were allowed to reproduce for three days, then all removed except five nymphs that remained on each plant. When the nymphs reached the adult stage, they were allowed to reproduce for three days and then they were removed. In this step the number of nymphs which remained on each plant was between 15–20 individuals, in order to maintain low densities of aphids. This rearing process was repeated until the nymphs of 4th generation molted to 4th nymphal instar. At this time, five unwinged and five winged nymphs from each plant were placed on two new plants separately and allowed to become adults and reproduce for three days. Afterwards, the adults were removed and nymphs were allowed to become 4th nymphal instar or adult in both winged and unwinged mother treatments, then they were collected and frozen for later counting and examining of the phenotype. This experiment was conducted in October 2010.

In 2012, another experiment was conducted (experiment 2.4) with 40 winged ME aphids in order to determine if winged mothers produce winged offspring. The experimental procedure was similar to experiment 2.1 with the exception that the ME winged aphids were collected from tansy around Freising, Germany and the aphids were maintained at room temperature (20–25°C) with natural light availability (June) and additional access from an ant colony.

3. Effect of Crowding

In 2012, 20 unwinged adults of each MA and ME were collected from different colonies in the field and reared individually on tansy plants (as 20 lines) in low colony densities for two generations. Nineteen lines of MA and 15 lines of ME were used for the experiment (experiment 3). There were two treatments for each line, crowding and control treatments. Two unwinged females from each line were randomly selected for the experiment (one per treatment). For the crowding treatment, one adult was placed together with another 30 aphids (4th nymphal instars and adults) from the same line in a small plastic vial (1.5 ml) to enhance crowding conditions and for the control treatment the single adult was placed in another vial. After 24 h, the adults from each of the control and crowded treatments were placed individually on a new tansy plant. The aphids were allowed to reproduce for three days, after which the adults were removed and offspring allowed to develop into 4th nymphal instar or adults. Then the numbers of winged and unwinged morphs were counted.

4. Effect of Predators on Wing Induction

In 2011, 15 unwinged adults from each MA and ME were collected on tansy plants in the botanical garden of Jena, Germany. Lacewing larvae, *Chrysoperla carnea* (Neuroptera: Chrysopidae) (obtained as eggs from a commercial supplier (Katz Biotech Services, Welzheim, Germany)), were used as the predator. Newly hatched larvae were reared in plastic vials (5 cm in diameter and 10 cm height) individually and were fed *ad libitum* with a mixed diet of MA and ME nymphs until they reached the 2nd larval stage when they were used for the experiment. The experiment (experiment 4) was conducted using Plexiglas cages in a greenhouse (see experiment 2.3), with access by ants for the ME aphids.

To minimize maternal effect, offspring from the same mother (clonal line) were exposed to different treatments. Fifteen adults of each aphid species were placed on 15 tansy plants as 15 lines (see Fig. S1). Then these 1st generation adults were allowed to give birth to offspring for two days and after that all but six nymphs were removed. These nymphs (2nd generation) were allowed to grow until they reached adulthood, then three of them were transferred to a new plant where they were allowed to reproduce for a further two days. Then, all but ten nymphs (3rd generation) were removed. When these nymphs developed to adults, five from each line were transferred to a new plant (i.e. five adults per plant). These adults were allowed to reproduce for two days and then they were removed from the plant together with all but 25 nymphs (4th generation) remaining per line. When the 4th generation nymphs reached the late 4th instar, 20 individuals from each plant were split into two groups of 10 and were transferred separately to two new plants (predator treatment and control treatment). In total, 15 different lines of each aphid species were established with one plant per line for each treatment (predator and control), after the 4th generation (30 plants total) (Fig. S1); each line was used as a replicate.

One 2nd instar lacewing larva was released on each predator-treatment plant and allowed to feed on the aphids for three days, after which it was removed. This represented the '*first three-day period*'. The remaining adult aphids were counted on both treatment and control plants and transferred to new plants to continue the experiment to the '*second three-day period*'. This second period was used since determination of offspring phenotype occurs some time before birth, which means that the production of winged morphs can be a delayed response. Here, another 2nd instar lacewing larva was released onto the predator-treatment plants, and left for three days. After the second three-day period the remaining adult aphids were counted and removed from all plants. Any offspring produced in both periods were allowed to develop to the 4th nymphal instar or adults, in the absence of predators, and the number of winged and unwinged aphids were counted.

Statistics

The results are presented as mean ± standard error. In all experiments, to compare the proportion of winged/unwinged offspring between different treatments the *cbind* function in R (R version 2.14.0, 2011) was used and binomial Generalized Linear Models (GLM) with log link function were performed.

In the crowding experiment (experiment 3), the numbers of winged individuals of MA for control treatment were all zero and therefore there was no variation in the data, so we used the non-parametric Wilcoxon Signed Ranks Test to compare the proportion of winged offspring in crowding and control treatments. For the ME crowding experiment, a GLM using binomial distribution with log link function was performed. To compare the number of produced offspring by MA and ME in crowding and control treatments, GLM using negative binomial distribution with log link function was used.

In the wing induction by predators experiment (experiment 4), to compare the number of surviving adults and total number of offspring at the end of each experimental period in control and predator treatments, a paired t-test was used. In the case that data were not normally distributed a square-root transformation was performed to normalize the data. If data were not normalized by transformation a non parametric test, Wilcoxon Signed Ranks

Test, was used. To compare the proportion of winged offspring in the predator and control treatments, a GLM using binomial or quasibinomial (when overdispersed) distribution with log link function was employed. A logistic regression, using the *cbind* function in R, was used to investigate the relationship between total number of offspring in the end of each experimental part and number of winged offspring. For all paired t-tests and Wilcoxon Signed Ranks Tests, the software package IBM SPSS Statistics version 19 was used.

Ethics Statement

No specific permits were required for the described field studies. All field locations belonged to either Friedrich-Schiller-University of Jena or Technische Universität München, and no special permission was required to work in these areas. We confirm that none of the species used were endangered or protected.

Results

1. Seasonal Life Cycle and Time of Appearance of Winged Individuals

Macrosiphoniella tanacetaria. On 30th April 2010, the first MA colonies were observed in the botanical garden of Jena, Germany. These colonies consisted of about 20 nymphs and one fundatrix (1st generation). In the experiment, there were no winged aphids observed until 26th May 2010 when the third generation had been produced. In the third generation, 85.6% of the aphids were winged dispersal morphs. The proportion of winged individuals declined through June and July (to 0% in the 8th generation) with a small peak during late July-August when 22.8–28.6% of offspring produced in generations 9–11 were winged (Fig. 1). The sexual individuals, apterous oviparous females, were observed in the first week of October (Fig. 1; Fig. S2). The experiment ended when all individuals were sexual females. No males were observed within the experimental populations. Fifteen generations of MA occurred in 2010.

In 2011, MA fundatrix adults were found on 5th April in the botanical garden of Jena, Germany. In the experiment, there were no winged individuals during the 1st and 2nd generations but, as in 2010, in the 3rd generation winged individuals formed the majority of the individuals (82.1%) (Fig. 1). Again, a decrease in percentage of winged individuals was observed and at the end of July (8th generation) there were no winged offspring. As in 2010, there was an increase in the number of winged individuals during generations 9–11 in mid-end August (Fig. 1). The first sexual forms appeared in the 15th generation, at the end of October, but asexual females were present until the 17th generation in the end of November when all individuals were sexual. Thus, while some 14th generation females already produced sexual offspring (7–10th October), others only produced sexual offspring in the 16th generation. In the 15th and 17th generations there was only one winged individual, which was male, while in the 16th generation there were two winged individuals, one male and one viviparous female. In 2011, 15–17 generations of MA occurred.

Metopeurum fuscoviride. Fundatrix individuals of ME were found on 17th April 2011 in a site near the Institute of Ecology, Jena, Germany. The winged individuals of ME occurred only in the 3rd to 5th generations (Fig. 1). The percentage of winged individuals in the 3rd and 4th generations was high (78.5 and 79.8% respectively) but in the 5th generation it was very low (2.5%) (Fig. 1). After the 5th generation there were no winged individuals produced with an exception of one winged individual that was found in one of the experimental populations at the end of September. The sexual forms occurred in the 13th and 14th generations (mid-October until early-November). As the sexual forms of ME (males and females) are wingless, there were no winged individuals in the end of season. ME had 13–14 generations in 2011.

2. Winged Offspring Production by Winged and Unwinged Mothers

Our experiments showed that winged mothers of both MA and ME are able to produce winged offspring. For MA, the mean percentage of winged offspring produced by winged mothers in the climate chamber (experiment 2.1) was low at 0.30±0.3% (overall 0.34% of offspring were winged, 1 out of 296). In the greenhouse (experiment 2.3) the percentage of winged offspring produced by winged mothers was higher 14.21±4.7% (overall 13.46% of offspring were winged, 63 out of 468); however, due to the different experimental design these results are not directly comparable. For ME in the laboratory (experiment 2.4) the proportion of winged offspring among winged mothers was 9.38±2.1% (overall 8.11% of offspring were winged, 27 out of 333). The percentages of MA and ME winged mothers which produced both morphs were 3.7% and 50% respectively, all others only produced unwinged offspring. No female produced only winged offspring.

In the climate chamber experiment (experiment 2.2), unwinged mothers of MA produced 3.72±1.8% winged offspring (overall 3.68% of offspring were winged, 12 out of 326). In comparison with the number of winged offspring produced by winged mothers (experiment 2.1, also in the climate chamber and conducted at the same time), unwinged mothers produced significantly more winged offspring (binomial GLM, $Z_{1,\ 33} = -2.32$, $P = 0.020$) (Fig. 2). The percentage of MA unwinged mothers that produced both morphs was 20.5%, compared to 3.7% by winged mothers.

In the greenhouse experiment (experiment 2.3), the percentage of winged offspring produced by MA unwinged mothers was significantly higher, 6.4 times, than the percentage of winged offspring produced by winged mothers (quasibinomial GLM, $t_{1,28} = -7.322$, $P < 0.001$) (Fig. 2). Here, 10 out of 15 plants with winged mothers had winged offspring.

3. Effect of Crowding

Macrosiphoniella tanacetaria. There was no winged offspring in the control (0.0%) while in the crowding treatment the mean percentage of winged offspring was 11.24±2.7% with 11 lines out of 19 producing winged morphs. Thus, crowding caused a statistically significant increase in production of winged morphs in MA (Wilcoxon Signed Ranks Test, $Z = -2.941$, $P = 0.003$). The number of produced offspring was affected by crowding treatment (negative binomial GLM, $\chi^2 = 6.778$, df = 1, $P = 0.009$) such that there were fewer aphids in the crowding treatment (363 offspring) than the control (539 offspring).

Metopeurum fuscoviride. The mean percentage of winged offspring produced in the control and crowding treatments were 2.38±1.1% and 2.71±1.2% respectively; crowding had no effect on the production of winged morphs (binomial GLM, $Z_{1,28} = 0.370$, $P = 0.711$). The number of produced offspring did not differ between crowding and control treatments (negative binomial GLM, $\chi^2 = 0.191$, df = 1, $P = 0.662$).

4. Effect of Predators on Wing Induction

Macrosiphoniella tanacetaria. In both experimental periods the number of surviving adults of MA was significantly lower in the predator treatment than the control (first three-day period: Wilcoxon Signed Ranks Test (data not normally distributed),

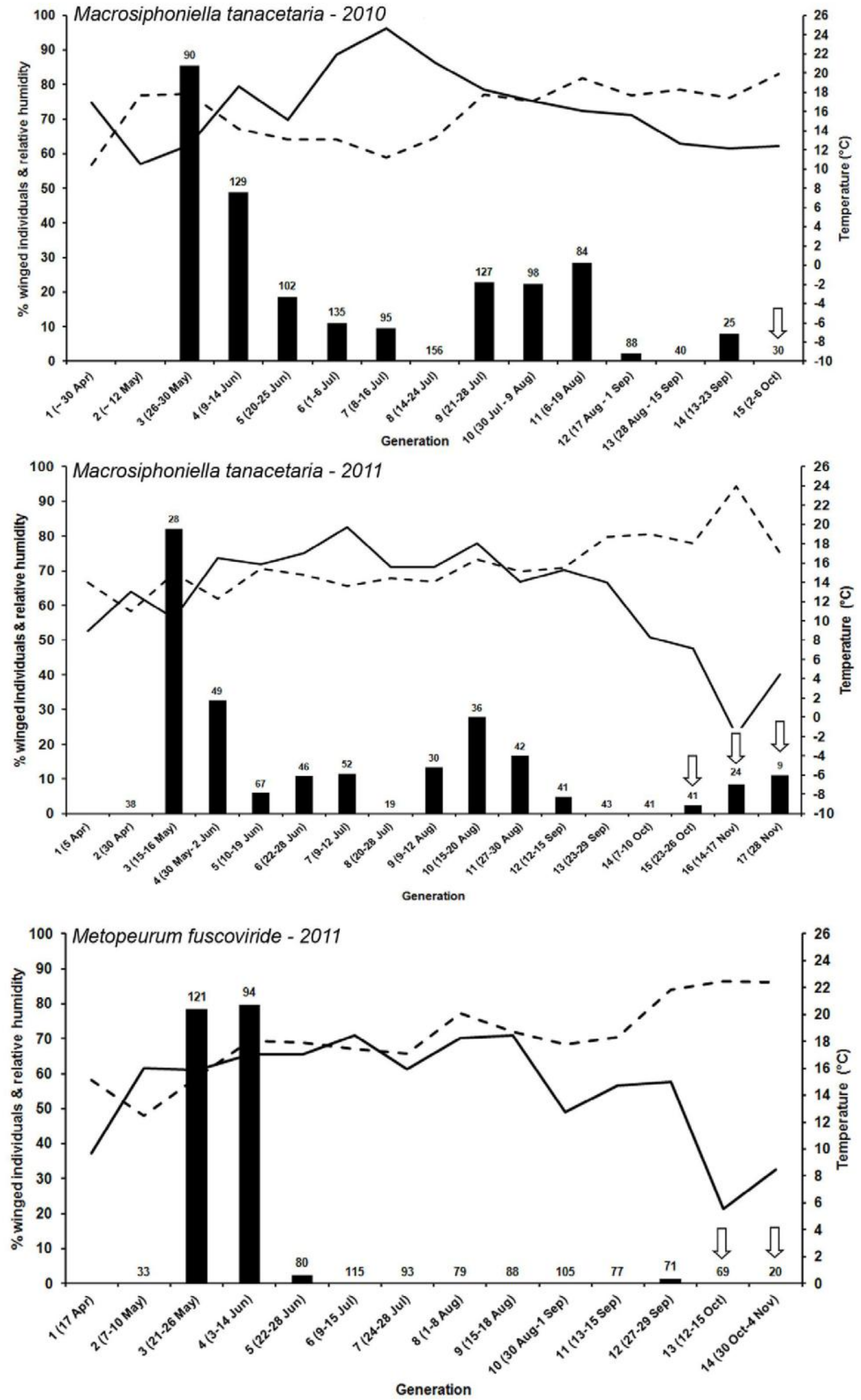

Macrosiphoniella tanacetaria - 2010
% winged individuals & relative humidity
Temperature (°C)
100
90
80
70
60
50
40
30
20
10
0
26
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
90
129
102
135
95
156
127
98
84
88
40
25
30
1 (~30 Apr)
2 (~12 May)
3 (26-30 May)
4 (9-14 Jun)
5 (20-25 Jun)
6 (1-6 Jul)
7 (8-16 Jul)
8 (14-24 Jul)
9 (21-28 Jul)
10 (30 Jul - 9 Aug)
11 (6-19 Aug)
12 (17 Aug - 1 Sep)
13 (28 Aug - 15 Sep)
14 (13-23 Sep)
15 (2-6 Oct)
Generation
Macrosiphoniella tanacetaria - 2011
% winged individuals & relative humidity
Temperature (°C)
38
28
49
67
46
52
19
30
36
42
41
43
41
41
24
9
1 (5 Apr)
2 (30 Apr)
3 (15-16 May)
4 (30 May-2 Jun)
5 (10-19 Jun)
6 (22-28 Jun)
7 (9-12 Jul)
8 (20-28 Jul)
9 (9-12 Aug)
10 (15-20 Aug)
11 (27-30 Aug)
12 (12-15 Sep)
13 (23-29 Sep)
14 (7-10 Oct)
15 (23-26 Oct)
16 (14-17 Nov)
17 (28 Nov)
Generation
Metopeurum fuscoviride - 2011
% winged individuals & relative humidity
Temperature (°C)
33
121
94
80
115
93
79
88
105
77
71
69
20
1 (17 Apr)
2 (7-10 May)
3 (21-26 May)
4 (3-14 Jun)
5 (22-28 Jun)
6 (9-15 Jul)
7 (24-28 Jul)
8 (1-8 Aug)
9 (15-18 Aug)
10 (30 Aug-1 Sep)
11 (13-15 Sep)
12 (27-29 Sep)
13 (12-15 Oct)
14 (30 Oct-4 Nov)
Generation

Figure 1. Percentage of winged individuals of *Macrosiphoniella tanacetaria* and *Metopeurum fuscoviride* in different generations. The production of winged individuals of *M. tanacetaria* (during the years 2010 and 2011) and *M. fuscoviride* (in the year 2011) during different generations was monitored and the time of appearance of sexual morphs were recorded. The arrows show generations where sexual forms were observed. The total numbers of offspring on which the winged individual percentage was based are shown on the top of each bar. The ambient temperature and humidity during the season is also showed on the graph. Solid lines show temperature and dashed lines show humidity.
doi:10.1371/journal.pone.0058323.g001

$Z = -2.981$, $P = 0.003$; second three-day period: paired t-test, $t_9 = 4.95$, $P < 0.001$) (Table 1). In the first three-day period 70% and in the second three-day period 53% of adults were eaten by predators. The number of offspring was lower in the predator treatment than in the control in both experimental periods (Table 1); this was significant in the first three-day period (paired t-test, $t_{14} = 2.628$, $P = 0.02$) but not in the second three-day period (paired t-test, $t_9 = 1.428$, $P = 0.187$). The reduction in adult and offspring number in the predator treatment shows that predators were actively preying on aphids in the respective replicates.

To consider the proportion of winged offspring produced we analysed the data together, with time period as a factor in the analysis. The presence of a predator significantly increased the percentage of winged individuals among the offspring (quasibinomial GLM, $F_{1,50} = 6.218$, $P = 0.016$) so that the percentage of winged offspring was higher in the predator treatment than control (Fig. 3A). The percentage of produced winged offspring in the second three-day period was significantly higher than the first three-day period (quasibinomial GLM, $F_{1,51} = 4.467$, $P = 0.039$). In the first three-day period, there was no significant relationship between the total number of offspring and the percentage of winged offspring (logistic regression, $t_{1,27} = 0.583$, $P = 0.564$). In the second three-day period the percentage of winged offspring was dependent on the number of offspring (logistic regression, $t_{1,22} = 2.362$, $P = 0.028$). This means that the number of offspring on the plant (crowding) possibly had an effect on the production of winged individuals.

Metopeurum fuscoviride. Contradictory with MA, predators had no effect on the number of surviving adults (first three-day period: Wilcoxon Signed Ranks Test, $Z = -1.656$, $P = 0.098$; second three-day period: Wilcoxon Signed Ranks Test, $Z = -0.998$, $P = 0.318$) (Table 1). In the first and second experimental periods 5.33% and 3.52% of the adults were eaten by predators, respectively. The total number of offspring in both experimental periods was similar between the predator and control treatments; however, there was a marginally significant effect of more offspring being produced in the control than the predator treatment in the first three-day period (first three-day period: paired t-test, $t_{14} = 2.067$, $P = 0.058$), with no effect in the second three-day period (paired t-test, $t_{14} = -0.648$, $P = 0.528$) (Table 1). These show that predators were active but because of the guarding action of the attending ants predators were not able to prey considerably on the ME.

The presence of predators had no effect on the production of winged individuals of ME in both experimental periods (binomial GLM, Predator: $Z_{1,57} = 0.455$, $P = 0.649$; Period: $Z_{1,57} = -0.227$,

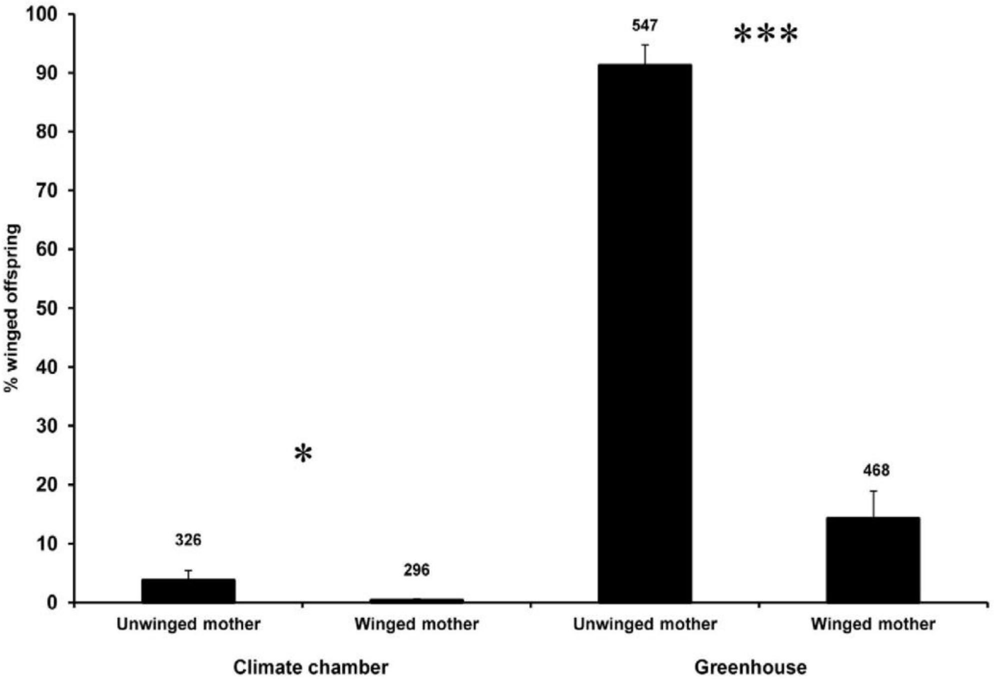


Figure 2. Percentage of produced winged offspring by unwinged and winged mothers of *Macrosiphoniella tanacetaria*. The percentage of winged morphs produced by unwinged and winged mothers of *M. tanacetaria* in the climate chamber (exp. 2.1 and 2.2) and greenhouse (exp. 2.3) experiments were compared. The total numbers of offspring on which the winged offspring percentage was based are shown on the top of each bar. The bars show mean±SE. *($P < 0.05$) and ***($P < 0.001$) indicate statistically significant difference between experimental treatments.
doi:10.1371/journal.pone.0058323.g002

Table 1. Number of surviving adults and number of offspring of *Macrosiphoniella tanacetaria* and *Metopeurum fuscoviride* in the first and second three-day period under control and predator treatments.

Species	First three-day period		Second three-day period	
	Control	Predator	Control	Predator
Macrosiphoniella tanacetaria				
Number of surviving adults	7.8±0.9	3.0±0.8	5.2±0.8	1.9±0.6
Number of offspring	50.9±6.2	29.9±5.2	41.3±8.5	25.4±5.0
Metopeurum fuscoviride				
Number of surviving adults	9.9±0.1	9.5±0.3	9.5±0.2	9.1±0.3
Number of offspring	51.2±1.8	45.5±2.4	42.7±1.4	43.9±1.0

Values are mean±SE.
The flow chart shows the experimental design for one aphid line and was the same for all aphid lines.
The sexual morphs of this aphid species, produced in the autumn, lay overwintering eggs after mating.
doi:10.1371/journal.pone.0058323.t001

$P = 0.821$) (Fig. 3B). There was a positive relationship between the total number of offspring and the percentage of winged morphs among the offspring produced in the first three-day period (logistic regression, $z_{1,28} = 2.207$, $P = 0.027$) while in the second three-day period there was not (logistic regression, $z_{1,28} = -0.202$, $P = 0.840$). This means that in the second three-day period the number of offspring on the plant (crowding) had no extra effect on the production of winged individuals.

Discussion

Our results revealed that these two specialized tansy aphids, MA and ME, differ in their responses to the environmental cues which normally trigger wing induction in aphids. In MA, seasonal/generational timing, mother morph, crowding and predators were found to have effects on the production of winged offspring. In the ant-tended species, ME, the production of winged morphs was affected by seasonal/generational timing but not by crowding or predators presence.

Seasonal Life Cycle and Time of Appearance of Winged Individuals

In 2010, we observed MA fundatrices (the stem mothers, which hatch from the overwintering eggs) at the end of April, suggesting that the eggs hatched before the middle of April. In 2011, MA fundatrices appeared two weeks earlier, in early April, suggesting that the eggs hatched in mid-March. Thus, the first appearance of MA differed in the two years of the study, and indicates that egg hatching and emergence of the first generation may be somewhat dependent on abiotic factors, e.g. temperature (see Fig. 1). Consistent with Hille Ris Lambers [13], we found no winged offspring in the first two generations.

The number of winged individuals for both MA and ME was high in the first half of the season, at the end of May and June. This coincides with an increase in vegetative growth of tansy plants, and as such would present the optimal time for aphid dispersal to new host plants. From following the seasonal pattern of wing production of MA, we found that this aphid species produced winged individuals throughout the whole season and therefore dispersal by flight is possible at any time. In both years, MA aphids did not produce any winged individuals in the 8th generation, which could be due to temporal effects on wing production; we found the proportion of winged offspring steadily fell from generation three to seven, but then increased again for generations nine through eleven for both study years (Fig. 1). In contrast, ME aphids produced the vast majority of winged morphs at the beginning of the season and this means their dispersal, followed by population expansion, occurs as one single major event. Therefore, for ME aphids, dispersal in the late season probably plays only a minor role in their population dynamics.

Variation in the production of winged individuals through the season is common across many aphid species but this has mostly been attributed to day length [18]. Here, we show that, consistently across the two study years, generation eight of the MA aphids produced no winged morphs whereas winged morphs were produced in the previous and the next generation. The difference in day length across these generations is minimal, especially as they occur across the summer solstice, and we suggest that this could indicate a temporal effect, i.e. the production of winged individuals influenced by both generational and seasonal (temperature and humidity) effects (see Fig. 1). Evolving a response (for winged offspring production) to the environmental factors such as temperature or day length could enable aphids to synchronize their development with the optimal dispersal time and maximize their chance of finding new host plants [18]. Tansy aphids are non host-alternating species, therefore the produced winged morphs during the 3rd to 5th generations are mainly for migration to, and colonization of, new host plants.

Winged Offspring Production by Winged and Unwinged Mothers

The production of winged individuals by winged mothers is uncommon, except during the last part of their reproductive lifespan [20]. We found that winged mothers in both aphid species produced winged offspring. In MA, the proportion of winged offspring was much higher for unwinged than winged mothers. The number of winged offspring produced by winged mothers was considerably larger in the greenhouse than the climate chamber experiment and may be due to the time in the season or plant quality. In contrast, approximately half of the winged ME mothers produced both winged and unwinged offspring. Thus, low production of winged offspring by winged mothers in MA is consistent with previous studies [16,42]; however, for the ant-tended ME production of winged offspring is higher.

Because of lower reproduction of winged morphs, aphid clonal growth is higher if only unwinged offspring are produced, thus production of winged morphs should be limited to necessary dispersal events [43,44]. MA aphids were found to produce winged offspring throughout the season, which may represent a

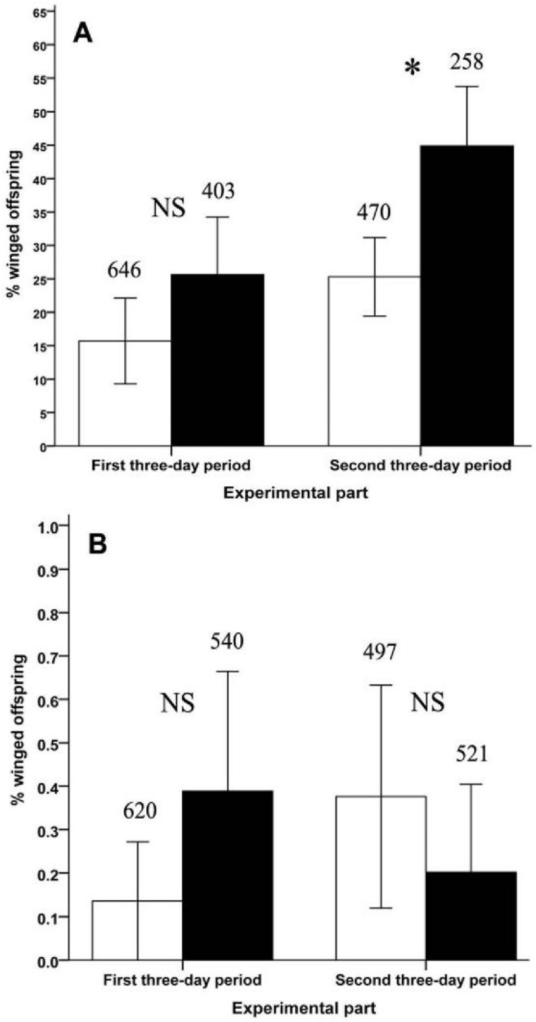


Figure 3. Percentage of produced winged offspring of *Macrosiphoniella tanacetaria* and *Metopeurum fuscoviride* in the presence of predators. Production of winged morphs in *M. tanacetaria* (A) and *M. fuscoviride* (B) as a function of the presence of a predator in the colony. White columns: control treatment, black columns: predator treatment. The total numbers of offspring produced in each treatment are shown on the top of each bar. The bars show mean±SE. *($P<0.05$) indicates statistically significant difference between experimental treatments.
doi:10.1371/journal.pone.0058323.g003

more stable reproductive strategy for these aphids as they are not protected by ants from predation. This also may be a result of the effect of crowding, which we showed to influence winged morph production in MA. Once a winged morph has located a new host plant then it produces mainly unwinged offspring, thus enhancing colony growth. On the other hand, the ME aphids generally produced winged offspring only at the beginning of the season and therefore it may be beneficial for winged mothers to also produce winged offspring to maximize dispersal during this unique event.

Effect of Crowding

Winged morph production and dispersal have both been considered as a driver of density regulation in aphids, and in many species the production of winged individuals is strongly density-dependent [15,16,19,23]. Production of winged individuals among aphid populations in a density-dependent fashion is possibly the best strategy for maximizing the number of migrants produced during the life of a colony and seasonal cycle of a clone [18]. In the present study, our results clearly showed that MA is responsive to crowding (tactile stimulation) and produced more winged offspring when surrounded by conspecifics than when alone. MA aphids also produced fewer offspring in the crowding treatment, which may indicate increased stress levels; however, it is also a general phenomenon that aphids produce fewer winged than unwinged offspring, as these need more resources. Despite the clear effect of crowding for MA, the effect size was small in comparison with pea aphid which produces a much higher proportion of winged morphs in response to crowding [16].

We found no effect of crowding for the ant-tended ME on wing production or offspring number. If an aphid often experiences high densities, it may seem reasonable to assume that they would have a weaker response to crowding. However, numerous empirical studies showed that the crowding has considerable effect on wing induction in gregarious aphid species (often found in tight groups) such as *Aphis craccivora* [22], *Megoura viciae* [23] and *Rhopalosiphum padi* [45] while it has less effect on non-gregarious species like *Myzus persicae* [46]. Non-gregarious aphids that do not often come into contact with other aphids, possibly exhibit little response to crowding stimuli since this effect is absent in their natural habitat and thus no adaptation to it has occurred [47]. The reason for our ME results is therefore more likely to be the presence of mutualistic ants. A number of studies show that the presence of attending ants inhibits the production of winged individuals in *Aphis fabae* [48,49,50] and *Lachnus allegheniensis* attended by *Formica obscuripes* [51].

Effect of Predators on Wing Induction

Our results clearly showed that for MA the presence of predators increased the production of winged offspring, which is consistent with studies on a number of other aphid species [25,26,28,32]. MA aphids produced a greater proportion of winged offspring in the second period, and this delayed response could be because determination of offspring phenotype occurs some time before birth; thus, the first offspring born in the first period are likely to be determined before the experiment started.

We again found contrary results for the ant-tended ME compared to MA aphids, with no effect of predators on the proportion of winged offspring produced. In our study, a small number of ME aphids were consumed showing that the predators did attempt to feed but were not very successful due to the protective role of attending ants. In a different aphid species, Dixon & Agarwala [25] also found that ant-tended colonies of *Aphis fabae* did not respond to the presence of the predator by producing more winged offspring. However, in *Aphis gossypii*, which it also attended by ants, the presence of natural enemies was found to lead to an increase in the percentage of winged offspring [29]. For ant-attended aphids, it may not be beneficial to produce winged morphs in response to predator presence; most of the time the ants will protect the aphid and furthermore, when the winged individual leaves the natal plant it loses the advantages of protection by ants.

Ecological Advantages of Winged Morph Production

The two main advantages of producing winged dispersal morphs in aphids are: 1) migration and dispersal between different host plants, and 2) escape from adverse environmental conditions. Dispersal between primary and secondary host plants during the season is fundamental for the survival of host-alternating aphid species (heteroecious). However, dispersal is also important for non host-alternating aphid species (autoecious), such as the tansy aphids studied here, because they allow aphids to disperse among several plants and enhance the reproductive chances. We generally found low proportions of winged offspring, which may be due to the tansy host species being a perennial plant. Previous work suggests that species feeding on perennial host plants, like tansy, exhibit a lower occurrence of winged morph production in comparison with those live on short persistence host plants, e.g. annual herbaceous plants [52]. Aphids can only exploit annual herbaceous plants, such as many crop species, for a short time period and therefore migration (by winged dispersal morphs) to new or more persistent hosts must take place at some point during the life cycle. Escape from adverse conditions such as decreasing plant quality, increasing interspecific competition caused by crowding and presence of natural enemies are important in order to maximize reproductive output [26,43,53].

The aphids we studied here exhibit classic metapopulation structuring in natural populations, and dispersal between plants is important for recolonization after the frequent extinction events that characterize such a system [37,54]. Weisser [37] argued that in the tansy system the main driver of local population extinction is from natural enemies (parasitoids and predators). In this paper, we showed that MA aphids produce winged individuals throughout the season and respond to predator attack by producing more winged individuals. This indicates they have evolved these traits to enable escape from areas of high predation pressure, and enhance recolonization over the whole season. The second aphid species we studied (ME) does not produce winged offspring throughout the season, neither does it respond to predation, and this is likely related to the aphid-ant mutualism they have evolved where the ant protects the aphids from predation and the aphid produces honeydew to feed the ants. These aphids are obligate mutualists and without ant-attendance they rarely survive [55], therefore any selective force for increased wing production due to predation pressure will be reduced.

In conclusion, aphids respond to various stimuli for the production of winged morphs, which will help them to track environmental conditions much more reliably [18]. We found that the cues that induced winged morph production varied among aphid species, likely due to whether they were ant-tended or not, and included temporal effects, maternal effects, crowding and presence of a predator. Understanding the role of environmental cues for wing induction in aphids in a metacommunity system will benefit the study of life-history evolution in spatially heterogeneous habitats.

Supporting Information

Figure S1 Illustration of the transferring of aphids to new plants in the effect of predators on wing induction experiment. The flow chart shows the experimental design for one aphid line and was the same for all aphid lines.
(TIF)

Figure S2 Photograph of *Macrosiphoniella tanacetaria* sexual female (Oviparae) with its egg. The sexual morphs of this aphid species, produced in the autumn, lay overwintering eggs after mating.
(TIF)

Acknowledgments

We wish to thank Sylvia Creutzburg and Stefanie Poser for their assistance, and Katz Biotech Services for the provision of lacewing eggs. We also thank two anonymous reviewers for their helpful comments.

Author Contributions

Conceived and designed the experiments: MM SZ WW. Performed the experiments: MM. Analyzed the data: MM SZ. Wrote the paper: MM SZ WW.

References

1. Whitman DA, Agrawal AA (2009) What is phenotypic plasticity and why is it important? In: Whitman DW, Ananthakrishnan TN, editors. Phenotypic plasticity of insects: mechanisms and consequences. University of Minnesota: Science Publishers. 1–63.
2. Begon M, Townsend CR, Harper JL (2006) Ecology: From individuals to ecosystems. Oxford, U.K.: Blackwell Publishing Ltd. 738 p.
3. Simpson SJ, Sword GA, Lo N (2011) Polyphenism in insects. Current Biology 21: R738–R749.
4. Miura T (2004) Proximate mechanisms and evolution of caste polyphenism in social insects: From sociality to genes. Ecological Research 19: 141–148.
5. Braendle C, Davis GK, Brisson JA, Stern DL (2006) Wing dimorphism in aphids. Heredity 97: 192–199.
6. Tsuji H, Kawada K (1987) Effects of starvation on life-span and embryo development of 4 morphs of pea aphid (*Acyrthosiphon pisum* (Harris)). Japanese Journal of Applied Entomology and Zoology 31: 36–40.
7. Hazell SP, Gwynn DM, Ceccarelli S, Fellowes MDE (2005) Competition and dispersal in the pea aphid: clonal variation and correlations across traits. Ecological Entomology 30: 293–298.
8. Powell G, Tosh CR, Hardie J (2006) Host plant selection by aphids: Behavioral, evolutionary, and applied perspectives. Annual Review of Entomology 51: 309–330.
9. Mackay PA, Wellington WG (1975) Comparison of reproductive patterns of apterous and alate virginoparous *Acyrthosiphon pisum* (Homoptera-Aphididae). Canadian Entomologist 107: 1161–1166.
10. Tsumuki H, Nagatsuka H, Kawada K, Kanehisa K (1990) Comparison of nutrient reservation in apterous and alate pea aphids, *Acyrthosiphon pisum* (Harris).1. Developmental time and sugar content. Applied Entomology and Zoology 25: 215–221.
11. Brisson JA (2010) Aphid wing dimorphisms: linking environmental and genetic control of trait variation. Philosophical Transactions of the Royal Society B-Biological Sciences 365: 605–616.
12. Braendle C, Caillaud MC, Stern DL (2005) Genetic mapping of aphicarus - a sex-linked locus controlling a wing polymorphism in the pea aphid (*Acyrthosiphon pisum*). Heredity 94: 435–442.
13. Hille Ris Lambers D (1966) Polymorphism in Aphididae. Annual Review of Entomology 11: 47–78.
14. Smith MAH, Mackay PA (1989) Genetic-variation in male alary dimorphism in populations of pea aphid, *Acyrthosiphon pisum*. Entomologia Experimentalis Et Applicata 51: 125–132.
15. Shaw MJP (1970) Effects of population density on alienicolae of *Aphis fabae* Scop. I. Effect of crowding on production of alatae in laboratory. Annals of Applied Biology 65: 191–196.
16. Sutherland ORW (1969) The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. Journal of Insect Physiology 15: 1385–1410.
17. Sutherland ORW (1969) The role of the host plant in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. Journal of Insect Physiology 15: 2179–2201.
18. Dixon AFG (1998) Aphid ecology: An optimization approach. London: Chapman & Hall. 300 p.
19. Müller CB, Williams IS, Hardie J (2001) The role of nutrition, crowding and interspecific interactions in the development of winged aphids. Ecological Entomology 26: 330–340.
20. Kawada K (1987) Polymorphism and morph determination In: Minks AK, Harrewijn P, editors. Aphids, their biology, natural enemies and control Amsterdam: Elsevier. 255–266.
21. Mittler TE, Sutherland ORW (1969) Dietary influences on aphid polymorphism. Entomologia Experimentalis Et Applicata 12: 703–713.
22. Johnson B (1965) Wing polymorphism in aphids II. Interaction between aphids. Entomologia Experimentalis Et Applicata 8: 49–64.

23. Lees AD (1967) The production of the apterous and alate forms in the aphid *Megoura viciae* Buckton, with special reference to the role of crowding. Journal of Insect Physiology 13: 289–318.
24. Braendle C, Weisser WW (2001) Variation in escape behavior of red and green clones of the pea aphid. Journal of Insect Behavior 14: 497–509.
25. Dixon AFG, Agarwala BK (1999) Ladybird-induced life-history changes in aphids. Proceedings of the Royal Society of London Series B-Biological Sciences 266: 1549–1553.
26. Weisser WW, Braendle C, Minoretti N (1999) Predator-induced morphological shift in the pea aphid. Proceedings of the Royal Society of London Series B-Biological Sciences 266: 1175–1181.
27. Sloggett JJ, Weisser WW (2002) Parasitoids induce production of the dispersal morph of the pea aphid, *Acyrthosiphon pisum*. Oikos 98: 323–333.
28. Kunert G, Weisser WW (2003) The interplay between density- and trait-mediated effects in predator-prey interactions: A case study in aphid wing polymorphism. Oecologia 135: 304–312.
29. Mondor EB, Rosenheim JA, Addicott JF (2005) Predator-induced transgenerational phenotypic plasticity in the cotton aphid. Oecologia 142: 104–108.
30. Poethke HJ, Weisser WW, Hovestadt T (2010) Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. American Naturalist 175: 577–586.
31. Balog A, Mehrparvar M, Weisser WW (2013) Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae). European Journal of Entomology 110: 153–157.
32. Kunert G, Weisser WW (2005) The importance of antennae for pea aphid wing induction in the presence of natural enemies. Bulletin of Entomological Research 95: 125–131.
33. Kunert G, Otto S, Rose USR, Gershenzon J, Weisser WW (2005) Alarm pheromone mediates production of winged dispersal morphs in aphids. Ecology Letters 8: 596–603.
34. Hatano E, Kunert G, Weisser WW (2010) Aphid wing induction and ecological costs of alarm pheromone emission under field conditions. PLoS ONE 5: e11188.
35. Lamb RJ, Mackay PA (1987) *Acyrthosiphon kondoi* influences alata production by the pea aphid, *Acyrthosiphon pisum*. Entomologia Experimentalis Et Applicata 45: 195–198.
36. Taylor AD (1990) Metapopulations, dispersal, and predator-prey dynamics: An overview. Ecology 71: 429–433.
37. Weisser WW (2000) Metapopulation dynamics in an aphid-parasitoid system. Entomologia Experimentalis Et Applicata 97: 83–92.
38. Massonnet B, Simon JC, Weisser WW (2002) Metapopulation structure of the specialized herbivore *Macrosiphoniella tanacetaria* (Homoptera, Aphididae). Mol Ecol 11: 2511–2521.
39. Loxdale HD, Schofl G, Wiesner KR, Nyabuga FN, Heckel DG, et al. (2011) Stay at home aphids: comparative spatial and seasonal metapopulation structure and dynamics of two specialist tansy aphid species studied using microsatellite markers. Biological Journal of the Linnean Society 104: 838–865.
40. Wilson DS (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73: 1984–2000.
41. Lees AD (1966) The control of polymorphism in aphids. Advances in Insect Physiology 3: 207–277.
42. Sutherland ORW (1970) An intrinsic factor influencing alate production by two strains of the pea aphid, *Acyrthosiphon pisum*. Journal of Insect Physiology 16: 1349–1354.
43. Weisser WW, Stadler B (1994) Phenotypic plasticity and fitness in aphids. European Journal of Entomology 91: 71–78.
44. Plantegenest M, Kindlmann P (1999) Evolutionarily stable strategies of migration in heterogeneous environments. Evolutionary Ecology 13: 229–244.
45. De Barro PJ (1992) The role of temperature, photoperiod, crowding and plant-quality on the production of alate viviparous females of the bird cherry-oat aphid, *Rhopalosiphum padi*. Entomologia Experimentalis Et Applicata 65: 205–214.
46. Williams IS, Dewar AM, Dixon AFG, Thornhill WA (2000) Alate production by aphids on sugar beet: how likely is the evolution of sugar beet-specific biotypes? Journal of Applied Ecology 37: 40–51.
47. Williams IS, Dixon AFG (2007) Life cycles and polymorphism. In: van Emden HF, Harrington R, editors. Aphids as crop pests. Wallingford: CAB International. 69–85.
48. El-Ziady S, Kennedy JS (1956) Beneficial effects of the common garden ant, *Lasius niger* L., on the black bean aphid, *Aphis fabae* Scopoli. Proceedings of the Royal Society London Series B 31: 61–65.
49. El-Ziady S (1960) Further effects of *Lasius niger* L. on *Aphis fabae* Scop. Proceedings of the Royal Society London Series B 35: 30–38.
50. Kleinjan JE, Mittler TE (1975) A chemical influence of ants on wing development in aphids. Entomologia Experimentalis Et Applicata 18: 384–388.
51. Seibert TF (1992) Mutualistic interactions of the aphid *Lachnus allegheniensis* (Homoptera: Aphididae) and its tending ant *Formica obscuripes* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 85: 173–178.
52. Groeters F (1989) Geographic and clonal variation in the milkweed-oleander aphid, *Aphis nerii* (Homoptera: Aphididae), for winged morph production, life history, and morphology in relation to host plant permanence. Evolutionary Ecology 3: 327–341.
53. Johnson B (1966) Wing polymorphism in aphids III. The influence of the host plant. Entomologia Experimentalis Et Applicata 9: 213–222.
54. Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601–613.
55. Flatt T, Weisser WW (2000) The effects of mutualistic ants on aphid life history traits. Ecology 81: 3522–3529.

Supporting Information

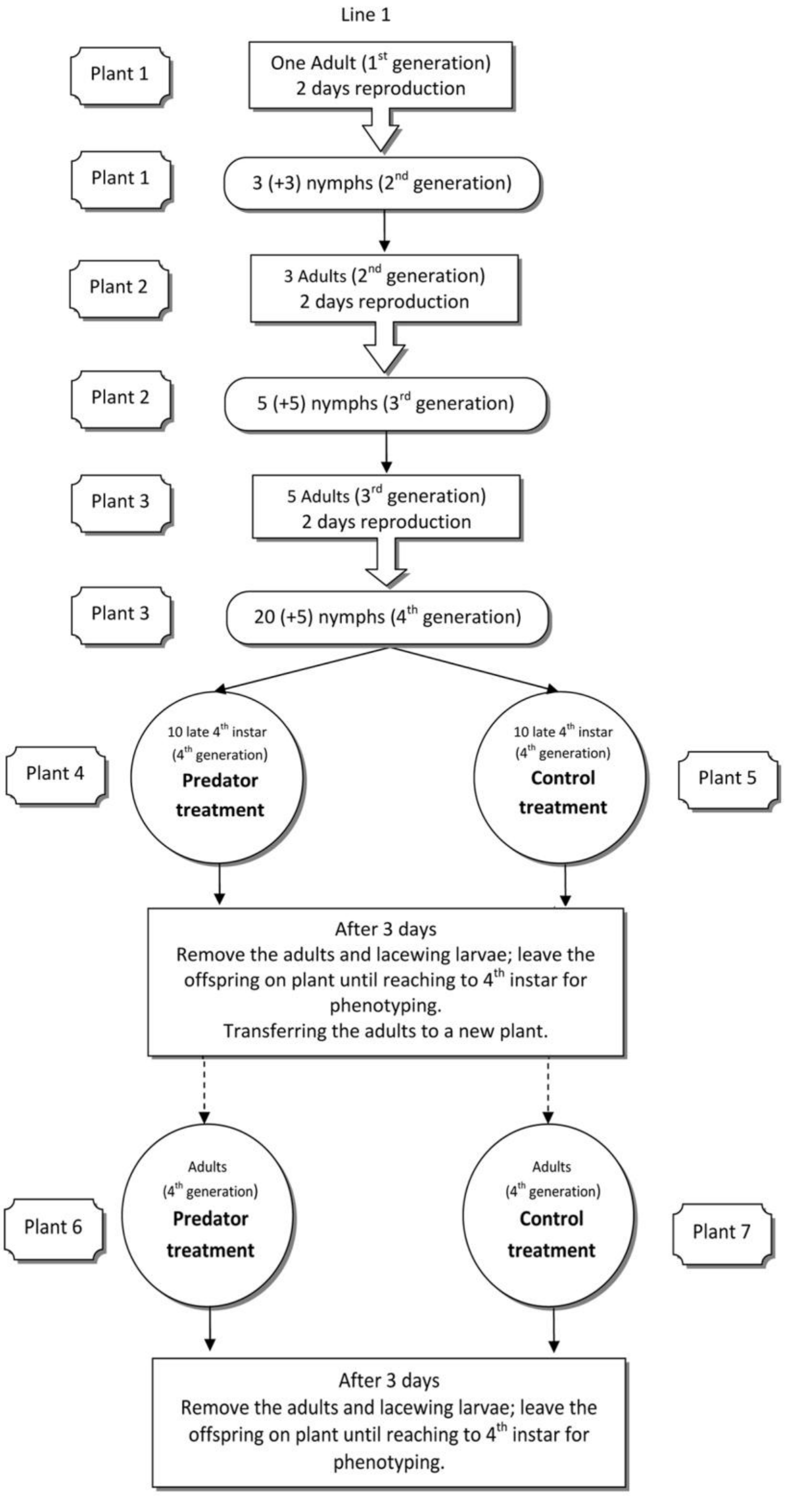


Figure S1: Illustration of the transferring of aphids to new plants in the effect of predators on wing induction experiment. The flow chart shows the experimental design for one aphid line and was the same for all aphid lines.

Figure S2: Photograph of *Macrosiphoniella tanacetaria* sexual female (Oviparae) with its egg. The sexual morphs of this aphid species, produced in the autumn, lay overwintering eggs after mating.

CHAPTER III

3- Manuscript II

Species–sorting by a mutualist in a herbivore metacommunity: Ant–mediated reversal of competitive hierarchies

Mohsen Mehrparvar*‡, Adalbert Balog*† & Wolfgang W. Weisser*‡

*Institute of Ecology, Friedrich–Schiller University Jena, Jena, Germany

† Department of Horticulture, Sapientia University, Sighisoara Str. 1C. Tirgu–Mures, Romania

‡ Present address: Terrestrial Ecology, Department of Ecology and Ecosystem management, Technische Universität München, Freising–Weihenstephan, Germany

In preparation for submission to *Ecology Letters*

Abstract

Differences in local habitat conditions underlie the species-sorting paradigm of metacommunity ecology, yet most emphasis has been on variability in environmental conditions. Using laboratory and field experiments, we showed that the presence of ants is decisive for community assembly in a metacommunity of three aphids on the tansy plant, *Tanacetum vulgare*. While the ant-tended aphid, *Metopeurum fuscoviride*, is competitively dominant in the presence of ants, due to preferential predation by ants on the other aphid species, the non-tended *Macrosiphoniella tanacetaria* is competitively superior in the absence of ants. For the non-tended aphid species, *Uroleucon tanaceti*, the net effect of ants presence is positive only in the presence of *M. fuscoviride* and other predators. The experimental results are consistent with the occupancy patterns found in the field. We conclude that in the aphid metacommunity, variability among habitats in the strengths of mutualism, predation and apparent competition drive the assembly of local communities.

Key words: Competition, aphid, mutualism, interspecific interactions, metacommunity structure

Introduction

Interspecific competition between two species can be modified by a third partner such as predators or parasitoids which may mediate the coexistence between two prey species by preventing competition (Slobodkin, 1964; Paine, 1966; Abrams, 1999; Vandermeer & Pascual, 2006; Gliwicz & Wrzosek, 2008). Classic examples come from intertidal communities where predation has been shown to alleviate the intensity of space competition by barnacles (Connell, 1961), or to maintain a high diversity of benthic invertebrates and algae (Paine, 1966). There are also evidences that show competitive interactions between plants are relaxed by herbivores via preferential consumption of competitively dominant plants or through indirect effects on plant competition (Berendse, 1985; Huntly, 1991; Belsky, 1992; Olff & Ritchie, 1998). Competitive interactions between phytophagous insects can also be altered by shared natural enemies (Holt & Lawton, 1994). These natural enemies can potentially keep populations of insect herbivores below competitive levels and consequently reduce competitive interactions, or change the outcome of competition through selective predation. Alternatively, shared natural enemies may also promote apparent competition, and it has been argued that this may affect many herbivorous insect communities (Lawton & Strong, 1981; Holt & Lawton, 1993, 1994; Denno *et al.*, 1995; van Veen *et al.*, 2006).

Positive interactions such as mutualisms also have the potential to alter known mechanisms of competitive exclusion or coexistence (Lee & Inouye, 2010). For example, the mutualistic Acacia ant, *Pseudomyrmex ferruginea* F. Smith protect small trees of bull's horn acacia (*Acacia cornigera* (L.) Willd.) from competitors by actively snipping off shoots of other plant species and also protect the plant from herbivores (Janzen, 1967). At a smaller scale of life, mutualistic rhizobial bacteria help their legume partners to win in competition with other plants which are potential competitors for nitrogen (De Wit *et al.*, 1966; Begon *et al.*, 2006).

For herbivorous insects, interspecific competition is considered by many to be one of the most important factors for species distribution, abundance and the structure of herbivore communities (e.g. Denno *et al.*, 1995; Stewart, 1996; Waltz & Whitham, 1997; Morin, 1999; Denno *et al.*, 2000; Fisher *et al.*, 2000; Tack *et al.*, 2009). Nevertheless, the importance of competition for the ecology and evolution of herbivorous insects has long been an issue of controversy (Schoener, 1982; Denno *et al.*, 1995; Stewart, 1996). In the early 1980s, based on results of several field experiments, it was argued that interspecific competition is too weak or infrequent to be a major factor to structuring phytophagous insect communities (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967; Wiens, 1977; Lawton & Strong, 1981; Denno *et al.*, 1995; Stewart, 1996).

A metacommunity can be defined as a community of ecological communities; more formally, a metacommunity is described as a set of local communities that are linked by dispersal of multiple, potentially interacting species (Leibold *et al.*, 2004; Holyoak *et al.*, 2005a). This ecological field of study is concerned with patterns of species distribution, abundance and interactions in patchy habitats which connected by dispersal. One of the metacommunity frameworks is species-sorting which describes variation in abundance and composition of species within the metacommunity due to individual species responses to environmental heterogeneity (Leibold *et al.*, 2004; Holyoak *et al.*, 2005a). Accordingly, local patches are viewed as heterogeneous in some factors, such as the presence or absence of natural enemies or mutualists, and the outcome of local species interactions and distributions are closely linked to aspects of local conditions and the environment. The key processes in a metacommunity are migration, population extinction and the establishment of new local populations (Hanski & Gilpin, 1991; Clobert *et al.*, 2004). Demographic and environment stochasticities can influence extinction locally; however, extinction can also be due to other factors, like habitat destruction, presence of natural enemies and mutualisms (Bengtsson, 1989; Hanski, 1998; Leibold *et al.*, 2004; Holyoak *et al.*, 2005a). Interspecific competition has a substantial role in a metacommunity context where local populations of potentially competing species are subject to frequent extinctions (Leibold *et al.*, 2004; Calcagno *et al.*, 2006; Hunt & Bonsall, 2009). In addition to the considerable role of interspecific competition on the colonization ability of species, it may also influence extinction rates (Bengtsson, 1991; Hunt & Bonsall, 2009).

In an attempt to analyze why there appears to be considerable variation in the importance of interspecific competition among herbivorous insects, Denno *et al.* (1995) discussed factors that contribute to a strong role for interspecific competitive interactions. They pointed out that competition occurs more frequently in sessile or less mobile insects such as Hemiptera; that it is likely to be more severe between closely related taxa or between species feeding on distinct resources, and that is more frequent among introduced species, in managed habitats and for concealed feeding niches – situations in which the activity of natural enemies is often reduced. Among the different feeding guilds of herbivorous insects, sap feeders (e.g. aphids) indeed show a much higher prevalence of competitive interactions (Stewart, 1996). However, in aphid communities, predators have an important effect on their prey, and mutualistic relationships like those with ants are also very common. The relationship between ants and ant-associated (myrmecophilous) aphids is a classic example of mutualistic interactions (Keller & Gordon, 2010). There are numerous studies regarding ant-aphid interactions, many of which indicate that ants are beneficial to aphids and protect them from both predation and parasitism (Renault *et al.*, 2005; Stadler & Dixon, 2008). Nevertheless, there are also examples that show ants to be both friends and enemies of aphids, hence, ants also meanwhile prey upon and reduce the agents of aphid predation (Billick *et al.*, 2007). Several lines of evidence show that ant-tending improves reproductive performance, and promotes developmental rates, or colony growth of aphids (Flatt & Weisser, 2000; Stadler & Dixon, 2008).

Often, several aphid species feeding on the same plant may be differentially affected by ants. In the present study system, involving tansy, *Tanacetum vulgare* L. (Asteraceae), more than 23 aphid species have been recorded on this plant globally (Blackman & Eastop, 2006; Holman, 2009). Fischer *et al.* (2001) suggested for three species studied, a hierarchy of associations with the black garden ant, *Lasius niger* (L.). In ant choice experiments, the authors found that the obligate myrmecophile aphid *Metopeurum fuscoviride* Stroyan is most preferred, followed by the facultative myrmecophiles *Brachycaudus cardui* (L.) and *Aphis fabae* Scopoli. Völkl *et al.* (1999) showed that this preference hierarchy correlated well with differences in the sugar composition and the quantity of honeydew produced by these aphids, with higher concentrations of trisaccharides and larger quantities of honeydew resulting in a more intimate association with ants; the more intimate relationship with *M. fuscoviride* results in longer colony persistence (Fischer *et al.*, 2001). Because aphids on tansy have been shown to have a metapopulation structure with frequent extinction of local populations (Weisser, 2000; Weisser & Härri, 2005), the interaction between ants and predators may therefore differentially affect not only the population ecology of these herbivores, but also competitive interactions among them and hence the metacommunity structure.

In this study, we used the tansy model system to study the role of ants and predators in affecting interspecific competition among the three dominant and specialized aphid herbivores and consequently their metacommunity structure. In particular, we addressed the following questions: 1) What is the effect of ants on population growth and colony persistence of the three aphid species?; 2) How do ants affect the outcome of competitive interactions among the three aphid species?; and 3) What are the consequences of ant presence on population size, colony persistence and outcomes of competitive interactions in the field, where predators are common?

Materials and Methods

Study system

Tansy is a perennial herbaceous composite from Europe and Asia (Mitich, 1992) which preferentially grows in disturbed, well-drained, poor soils. It often forms as isolated patches alongside river valleys, railway tracks and on wastelands. Single plants comprise a 'genetically identical' genet with up to 50 flowering ramets (shoots) (but usually much fewer). Plants propagate clonally underground via stolons. In Jena, Germany, eight aphid species have been found on tansy (Mehrparvar, pers. obs.) of which the three specialist species, i.e. *Macrosiphoniella tanacetaria* (Kaltenbach), *Metopeurum fuscoviride* Stroyan and *Uroleucon tanaceti* (L.) (Aphididae), are the most common. *Macrosiphoniella tanacetaria* is not ant-attended and feeds in loose colonies mainly on the tip of shoots. *Metopeurum fuscoviride* is an obligatory myrmecophilous aphid which is commonly attended by the black garden ant, *Lasius niger* (Mackauer & Völkl, 1993; Flatt & Weisser, 2000), but also by other species such as the common red ant, *Myrmica rubra* (L.). *Metopeurum fuscoviride* feeds in more compact colonies near the apex of ramets but can also occupy (at least to a certain extent) the same feeding niche as *M. tanacetaria.* Mixed colonies are very rarely observed in the field. Reduced survival and reproduction of *M. fuscoviride* has been shown when aphids are not ant-tended (Flatt & Weisser, 2000). The third species, *U. tanaceti*, feeds on the underside of lower leaves of its host plant and is also not ant-tended. Loxdale *et al.* (2011) discuss the life cycle of tansy aphids, *M. tanacetaria* and *M. fuscoviride*. Both species are monoecious and holocyclic on tansy, but whereas the males of the former species are winged, those of the latter are wingless (Blackman & Eastop, 2006).

The experimental system (comprising tansy plant, the three specialized aphid species and two ant species) was involved a greenhouse, maintained under normal prevailing summertime ambient conditions, and a field experiment performed in Jena, Germany, at the Jena experiment site on the northern outskirts of the city (50.95°N, 11.63°E).

I. Greenhouse experiment

Experimental plants and insects

Tansy stolons were collected from a wasteland near the Institute of Ecology in Jena and were planted in three-litre capacity pots filled with soil in May 2009. Plants were maintained under normal ambient conditions until the developed shoots had reached a height of 20 cm. Plants were then transferred to the greenhouse (T°C ~ 25°C during the day and ~ 20°C at night and with a 16h L: 8h D light regime).

Adult individuals (apterous viviparous females) of the three aphid species were collected from the field and transferred to the greenhouse for the experiment.

Colonies of the two ant species, *L. niger* and *M. rubra*, were collected from the same field as the tansy stolons and were thereafter maintained in the greenhouse. Each ant colony had several hundred workers, many ant larvae and pupae. The colonies were kept in 10-litre volume buckets, the inside of which was coated with Fluon (Fluoropolymer Dispersion, Whitford GmbH, Germany). The buckets were filled with humid soil and sprayed frequently with water to avoid desiccation.

Experimental design

As the aim of this experiment was to determine the competitive interactions among the three aphid species on tansy in the presence or absence of ants, it was performed in the absence of natural enemies in the greenhouse. This experiment involved the use of a randomized block design with 10 blocks. In total, 210 tansy plants were used. Each block had 21 plants: three ant treatments (with *L. niger*, with *M. rubra* and without ants) each one with seven aphid treatments, resulting in total 3 x 7 = 21 treatment combinations. The aphid treatments included each aphid species on its own, each aphid species with another aphid species, and all three aphid species together, i.e., *M. tanacetaria* alone; *M. fuscoviride* alone; *U. tanaceti* alone; *M. tanacetaria* + *M. fuscoviride*; *M. tanacetaria* + *U. tanaceti*; *M. fuscoviride* + *U. tanaceti*; and *M. tanacetaria* + *M. fuscoviride* + *U. tanaceti*. The experiment was started by placing two adult individuals of each aphid species on to each given experimental plant treatment, i.e. we used an additive design. After about four hours, subsequent to the plant infestation by aphids, the worker ants were allowed access to the aphid infested plants of the ant-tended treatments. For each block, two buckets containing the colonies of the two ant species were placed in the experimental arena, i.e. each ant colony attended the appropriate aphid treatments within a block. Plant pots were placed into water-filled plates to prevent the escape of worker ants as well as the access of vagrant workers in the greenhouse to non-ant treatments. The plants were irrigated gently every time they required water. Access of the appropriate ant species was regulated by a series of bamboos sticks (~ 5 mm. diam.). These connected the buckets housing the ant colonies to the plants. The plants in non-ant treatments were not connected to any ant colony.

Adult aphids were allowed to reproduce for 48 hours whereupon the numbers of adults were counted and the adults and all offsprings except three were removed from the plants. Following this, the number of aphids was counted each day for 20 days.

We used these variables for analysis: the number of adults initially put on the plant that survived until second day (*early adult survival*), the *cumulative number of individuals* (after 20 days), i.e. the sum of all daily aphid counts, as measure for population growth and productivity, and *colony persistence*, calculated as the number of days until no aphid was present any more on the plant, up to day 20.

II. Field experiment

Here tansy stolons were collected, cultivated and maintained as for the greenhouse experiment and involving the three tansy aphid species as before. Colonies of *L. niger* were searched for on the Jena experiment field site and marked with a flag about one week before to start the experiment.

Experimental design

The experiment involved a randomized block design with 30 blocks. Plants were divided randomly in to 30 subsets, each subset (block) including14 plants. Within a particular subset, plants of the approximate same height and number of leaves were used. There were two ant treatments (i.e. with and without access of workers of *L. niger*) in each block, and for each ant treatment there were, as before, seven plants with different combinations of aphids; each aphid species on its own, each aphid species with another aphid species, and all three aphid species together, resulting in total 2 x 7 = 14 treatment combinations per block. The 14 plants were placed randomly in four rows and four columns around an ant colony with a distance of about 1m between pots. Before placing the plant pots in the field, all weeds were re-mowed at ground level to exclude the access of ants to the experimental plants in without ant treatments via the aerial parts of nearby plants. For “without ant” treatments, each potted tansy plant was placed in another empty pot without holes in its base in order to exclude the ingress of ants. Insect glue was also daubed on the outside surface of the pots. The plants were irrigated gently as required.

The experiment was started by placing two unwinged adult female aphids and five 3rd and 4th instar nymphs, hence a total of seven aphids on the plant, for each of the three aphid species per experimental plant treatment. After one day of the experiment, aphids were checked and if the total number of aphids per species on each plant was less than five, numbers were suitably increased with a new individual/s. Thereafter, the numbers of aphids were counted each day in the morning for 21 days.

The following variables were used for analysis: the *cumulative number of individuals* after 21 days, i.e. the sum of all daily aphid counts, as measure for population growth and productivity, and *colony persistence*, calculated as the number of days until no aphid was present any more on the plant, up to day 21.

Statistical analysis

For the greenhouse experiment, generalized linear models using binomial distribution with logit link were used to analyse early adult survival of each aphid species.

For both greenhouse and field experiments, the cumulative numbers of individuals at the end of the experiment was transformed as (x + 1) and then for analysis, Generalized linear models using a Gamma distribution with log link function were used. For each aphid species, models included main effects for the competition (aphid combination) and ant treatment as well as interactions. Aphid competition treatments included the focal aphid species on its own, the combination of the focal with either of the two other aphid species combinations, and the three-species combination (4 levels). The ant treatment had three levels in the case of the greenhouse experiment (*L. niger*, *M. rubra*, no ant), and two levels in the case of the field experiment (with/without *L. niger*).

To analyze colony persistence of the greenhouse and field experiments, survival analysis (Kaplan-Meier) was employed. If the colony survived until the ends of experiment, then the time-point 20 or 21 entered in the survival analysis as censored data. For each ant treatment, a separate analysis was performed using the *log-rank* test (a test for comparing the equality of survival distributions which all time points are weighted equally) to compare colony persistence of each aphid species pairwise between different competition treatments. Pairwise comparisons between overall effects of each ant treatment on colony persistence of each aphid species was also performed using the *log-rank* test.

All analyses were conducted using SPSS version 16 (SPSS Inc, 2007).

Results

Greenhouse experiment

Macrosiphoniella tanacetaria

Early adult survival

The presence of ants strongly reduced early adult survival; in many cases no adults, and on average fewer than one adult survived until day two, while in the absence of ants, both individuals almost always survived (Fig. 1A, Table 1). Workers of both *L. niger* and *M. rubra* were often observed killing and carrying *M. tanacetaria* to their nest (Fig. S1). Competition did affect early adult survival (Table 1) so that the average number of adults when they were accompanied by other aphid species was smaller. The interaction between the competition and ant treatment was not significant (Table 1).

Table 1: The effect of ant presence and aphid-aphid competition on early adult survival and population growth (cumulative number of individuals) of specialized tansy aphids in the greenhouse and field experiments. Aphid competition treatments included the focal aphid species on its own, the combination of the focal with either of the two other aphids species combinations and the three-species combination. The ant treatment had three levels in the case of the greenhouse experiment (*L. niger*, *M. rubra*, without ant), and two levels in the case of the field experiment (with/without *L. niger*). All analyses were carried out in SPSS 16.0. For the analysis of early adult survival in the greenhouse, generalized linear models with a binomial error distribution and logit link were used. The cumulative numbers of individuals at the end of the experiments was transformed as (x+1) and analysed using generalized linear models with a Gamma error distribution and log link function. Significant results are indicated by **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

	Ant		**Competition**		**Ant × Competition**	
Source	**df**	χ^2	**df**	χ^2	**df**	χ^2
Greenhouse						
Early adult survival						
M. tanacetaria	2	43.96***	3	8.36*	6	3.65
M. fuscoviride	2	11.10**	3	1.13	6	6.99
U. tanaceti	2	18.77***	3	9.15*	6	7.49
Cumulative number of individuals						
M. tanacetaria	2	147.37***	3	42.21***	6	75.63***
M. fuscoviride	2	72.97***	3	11.02*	6	13.43*
U. tanaceti	2	17.35***	3	3.70	6	10.87
Field						
Cumulative number of individuals						
M. tanacetaria	1	100.19***	3	23.09***	3	16.55**
M. fuscoviride	1	732.97***	3	1.48	3	0.82
U. tanaceti	1	5.22*	3	9.14*	3	7.84*

Colony persistence and population growth

Both the presence of *L. niger* and *M. rubra* caused a drastic reduction in the colony persistence of *M. tanacetaria,* whereas in the absence of ants on the plant, colony persistence was on average about 2.5 times as long (Fig. 2A, Tables 2 & 3). Competition had no significant effect on colony persistence in the no-ant treatment (Table 2). In the presence of *L. niger,* the shortest colony persistence was observed when all the three aphid species were on the plant, while it was four times longer when *M. tanacetaria* was alone (Table 2). In the presence of *M. rubra*, the longest colony persistence was also in the 'no competition' treatment, whilst the presence of *M. fuscoviride* on the plant caused a significant decrease in the colony persistence (Table 2).

Considering cumulative number of individuals, the interaction between ant and competition treatments was significant (Table 1). The cumulative number of individuals of *M. tanacetaria* after 20 days was more than 12 and about eight fold in the no-ant treatment than in *M. rubra* and *L. niger* treatments respectively (Fig. 1D, Table 1). Competition reduced the cumulative number of *M. tanacetaria* individuals (Table 1) so that the number decreased to one third, half and one fifth in the presence of *M. fuscoviride*, *U. tanaceti* and in the combination of all the three species respectively.

Metopeurum fuscoviride

Early adult survival

In the presence of ants, early adult survival was generally better; in most cases both adults survived. In the absence of ants a very few adults survived in the first two days (Fig. 1B, Table 1). Competition had not significant effect on early adult survival (Table 1). There was also no significant difference for interaction between the ant and competition treatments (Table 1).

Colony persistence and population growth

In the presence of *L. niger*, *M. fuscoviride* colonies were more persistent than in the absence of ants, about four days on average, while the differences between no-ant and *M. rubra* treatments and, *L. niger* and *M. rubra* treatments were not significant (Table 3, Fig. 2B). In the absence of ants, colony persistence was longest in the no-competition treatment (*M. fuscoviride* on its own), but the presence of *M. tanacetaria* or *U. tanaceti* on the plant decreased colony persistence by about half and 0.8, respectively (Table 2). In the three-species treatment, colony persistence decreased also by about 0.6 in comparison with the no-competition treatment. Competition had no effect on the colony persistence of *M. fuscoviride* in the presence of ants, *L. niger* or *M. rubra* (Table 2).

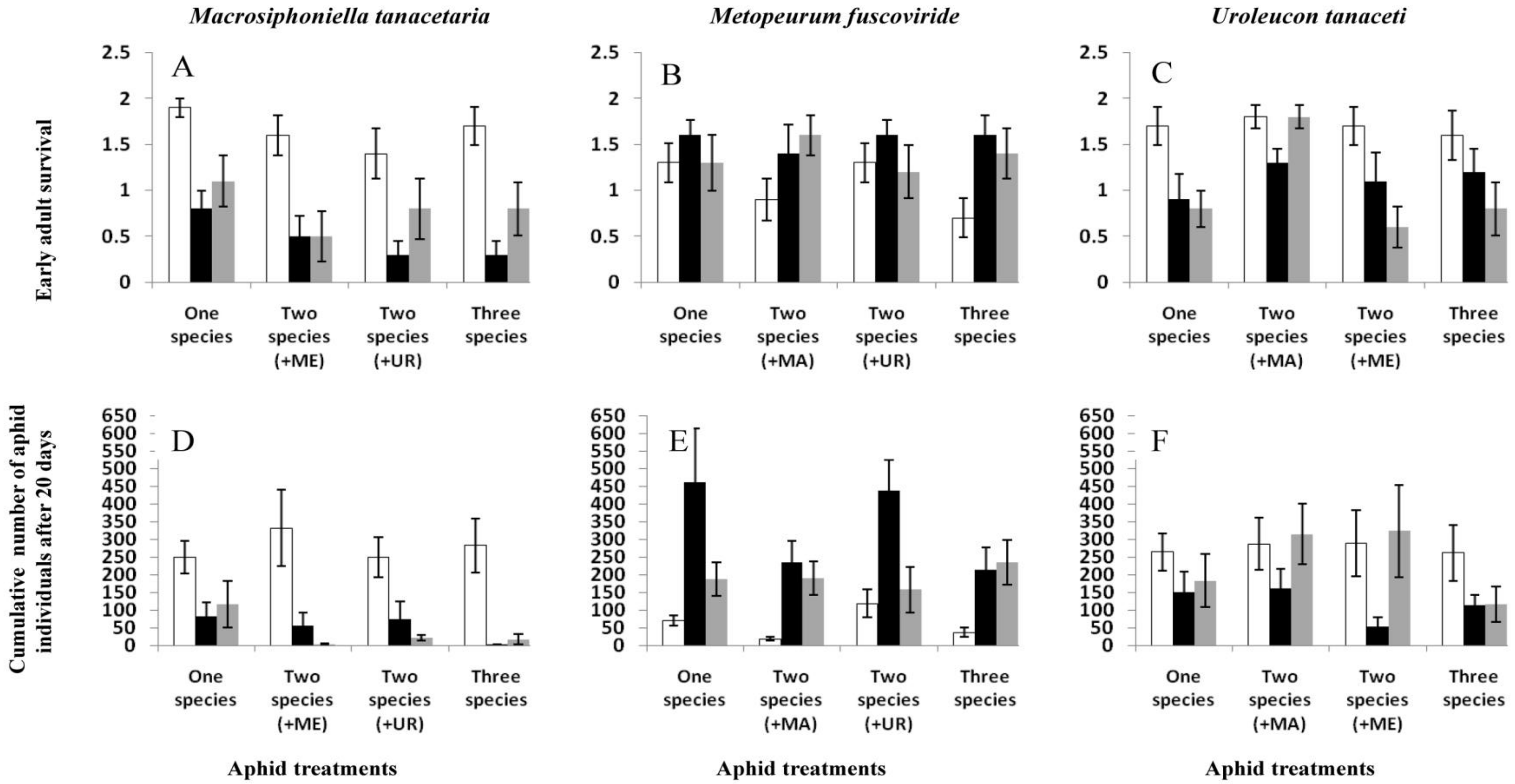


Figure 1: The effect of ant presence and aphid-aphid competition on early adult survival and population growth (cumulative number of individuals) of specialized tansy aphids in the greenhouse experiment. Aphid competition treatments included the focal aphid species alone, the combination of the focal with either of the two other aphids species combinations, and the three-species combination. The ant treatment had three levels (*L. niger*, *M. rubra*, without ant). Mean (±SE) numbers of *Macrosiphoniella tanacetaria* (A & D), *Metopeurum fuscoviride* (B & E) and *Uroleucon tanaceti* (C & F) early adult survival (A-C) and cumulative numbers of individuals after 20 experimental days (D-F) in different aphid (competition) treatments in the greenhouse experiment are shown. White columns: no ant, gray columns: *Myrmica rubra*, black columns: *Lasius niger* treatments. **MA**: *M. tanacetaria*; **ME**: *M. fuscoviride*; **UR**: *U. tanaceti*.

Table 2: The effect of the presence of ants and aphid-aphid competition on colony persistence of three specialized tansy aphids in the greenhouse and field experiments. Aphid competition treatments included the focal aphid species on its own, the combination of the focal with either of the two other aphids species combinations and the three-species combination. The ant treatment had three levels in the case of the greenhouse experiment (*L. niger*, *M. rubra*, without ant), and two levels in the case of the field experiment (with/without *L. niger*). All analyses were performed in SPSS 16.0. For the analysis of colony persistence a survival analysis (Kaplan-Meier) were used. Pairwise comparison between treatments was performed using the *log-rank* test. Mean (±SE) of colony persistence in different aphid (competition) treatments in the presence and absence of ants during the 20 days of greenhouse experiment and 21 days of field experiment are given. Means in rows with different letters are significantly different from one another ($P < 0.05$).

	One species	**Two species**			**Three species**
		(+MA)	**(+ME)**	**(+UR)**	
Greenhouse					
M. tanacetaria					
Without ants	19.80±0.20^{a}		15.10±2.59^{a}	18.00±2.00^{a}	16.40±2.11^{a}
Lasius niger	10.70±2.68^{a}		6.90±2.90^{ac}	8.10±2.72^{ad}	2.60±0.76^{bcd}
Myrmica rubra	11.50±2.46^{a}		3.60±0.62^{bd}	9.90±2.60^{ae}	4.50±1.84^{cde}
M. fuscoviride					
Without ants	20.00±0.00^{a}	10.60±2.41^{b}		15.90±2.28^{ab}	11.80±2.87^{b}
Lasius niger	18.20±1.80^{a}	17.10±2.10^{a}		20.00±0.00^{a}	19.20±0.80^{a}
Myrmica rubra	17.30±1.98^{a}	17.90±1.99^{a}		17.40±1.80^{a}	18.30±1.70^{a}
U. tanaceti					
Without ants	18.30±1.70^{a}	20.00±0.00^{a}	16.90±2.10^{a}		18.10±1.90^{a}
Lasius niger	15.20±2.61^{ab}	14.90±2.55^{ab}	10.50±2.54^{a}		17.10±2.10^{b}
Myrmica rubra	12.90±2.92^{a}	18.00±1.46^{a}	16.80±1.92^{a}		12.10±3.05^{a}
Field					
M. tanacetaria					
Without ants	16.53±0.66^{a}		16.17±0.67^{a}	12.57±0.78^{b}	11.57±0.75^{b}
With ants	11.10±0.52^{a}		5.70±0.74^{b}	6.37±0.58^{b}	5.70±0.9^{b}
M. fuscoviride					
Without ants	3.07±0.30^{a}	2.90±0.25^{a}		3.30±0.27^{a}	2.87±0.35^{a}
With ants	15.37±1.32^{a}	15.60±1.38^{a}		16.40±1.13^{a}	14.03±1.42^{a}
U. tanaceti					
Without ants	11.23±0.46^{a}	10.97±0.81^{a}	10.80±0.29^{a}		9.97±0.65^{a}
With ants	10.10±0.84^{a}	9.30±0.73^{a}	16.37±0.88^{b}		15.13±1.10^{b}

Considering cumulative number of individuals, the interaction between ant and competition treatments was significant (Table 1). The presence of ants significantly increased the cumulative number of *M. fuscoviride* individuals resulting in about six and four times more individuals in the presence of *L. niger* and *M. rubra* respectively, than in the no-ant treatment (Fig. 1E, Table 1). In the absence of ants, population growth of *M. fuscoviride* was very slow and even lower in the presence of *M. tanacetaria*, while *U. tanaceti* had no considerable effect. In the presence of ants, competition had no negative effect on cumulative number of *M. fuscoviride* individuals (Fig. 1E).

Uroleucon tanaceti

Early adult survival

In the absence of ants early adult survival of *U. tanaceti* was more than 1.5 times than in the presence of ants (Fig. 1C, Table 1). Competition affected early adult survival (Table 1), such that in the presence of ants and *M. tanacetaria* the early adult survival was higher than other treatments. The interaction between competition and ant treatment was not significant (Table 1).

Colony persistence and population growth

Colony persistence of *U. tanaceti* was significantly shorter in the presence of *L. niger* and *M. rubra* than in the absence of ants (Table 3, Fig. 2C). There was a tendency for lower colony persistence in competition with *M. fuscoviride* in the presence of *L. niger* (Table 2).

The presence of ants also had a negative effect on the cumulative number of *U. tanaceti* individuals and the effects of *L. niger* tended to be stronger than that of *M. rubra* (Fig. 1F). Competition had no significant effect on the cumulative number of *U. tanaceti* individuals and also the interaction between ant and competition treatment was not significant (Table 1). Patterns of population growth of *U. tanaceti* were, however, complicated (Fig. 1F). While populations of *U. tanaceti* grew well in the absence of ants; in the presence of *M. tanacetaria* or *M. fuscoviride* with *M. rubra*, the cumulative number of *U. tanaceti* individuals was the same as in the no-ants treatment (Fig. 1F).

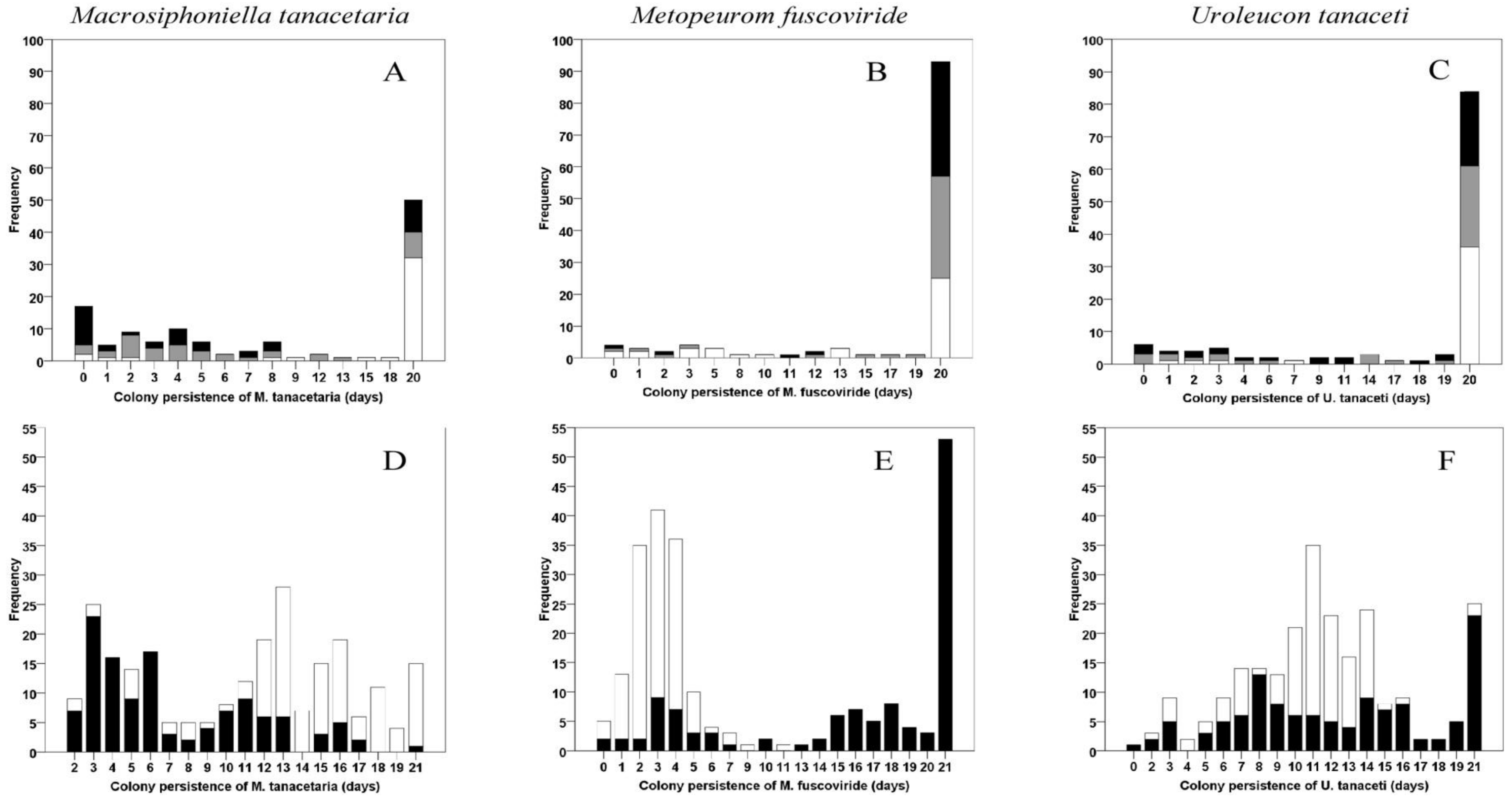


Figure 2: Frequency distribution of colony persistence of *Macrosiphoniella tanacetaria* (A & D), *Metopeurum fuscoviride* (B & E) and *Uroleucon tanaceti* (C & F) in the different ant treatments in the greenhouse experiment (A-C) and field experiment (D-F) are shown. The ant treatment had three levels in the case of the greenhouse experiment (*L. niger*, *M. rubra*, without ant), and two levels in the case of the field experiment (with/without *L. niger*). White areas: no ant, gray areas: *Myrmica rubra* and black areas: *Lasius niger* treatments.

Table 3: The overall effect of the presence of ants on colony persistence of three specialized tansy aphids in the greenhouse and field experiments. The ant treatment had three levels in the case of the greenhouse experiment (*L. niger*, *M. rubra*, without ant), and two levels in the case of the field experiment (with/without *L. niger*). For the analysis of colony persistence a survival analysis (Kaplan-Meier) were used. Pairwise comparison between ant treatments was performed using the *log-rank* test. Overall mean ± SE and Chi-Square (χ^2) are given and significant results are indicated by $^{**}P < 0.01$, $^{***}P < 0.001$. All analyses were carried out in SPSS 16.0.

	Mean ± SE	***Lasius niger*** χ^2	***Myrmica rubra*** χ^2
Greenhouse			
M. tanacetaria			
Without ants	17.33±0.97	27.38***	30.92***
Lasius niger	7.08±1.24		0.004
Myrmica rubra	7.38±1.10		
M. fuscoviride			
Without ants	14.58±1.19	8.15**	3.13
Lasius niger	18.63±0.70		1.47
Myrmica rubra	17.73±0.89		
U. tanaceti			
Without ants	18.33±0.80	10.4**	8.08**
Lasius niger	14.43±1.23		0.17
Myrmica rubra	14.95±1.22		
Field			
M. tanacetaria			
Without ants	14.21±0.40	100.13***	
Lasius niger	7.23±0.40		
M. fuscoviride			
Without ants	3.03±0.15	170.47***	
Lasius niger	15.35±0.65		
U. tanaceti			
Without ants	10.74±0.29	21.33***	
Lasius niger	12.73±0.52		

Field experiment

Macrosiphoniella tanacetaria colony persistence and population growth

The presence of ants, *L. niger*, halved colony persistence of *M. tanacetaria* (Fig. 2D, Tables 2 & 3). Competition had a negative effect on *M. tanacetaria* colony persistence in the absence of ants when it was accompanied by *U. tanaceti* (Table 2). In the presence of ants, competition, in all treatments, negatively affected the colony persistence of *M. tanacetaria* and decreased it so that this time was about half as long as when it was alone (Table 2).

The cumulative number of individuals after 21 days for *M. tanacetaria* was about 3.5 times larger without than with *L. niger* present (Fig. 3A). The interaction between ant and competition treatments was significant (Table 1). In the absence of ants, *M. fuscoviride* apparently had no effect on the population growth of *M. tanacetaria*, while the negative effect of *U. tanaceti* was found not to be negligible. In the presence of ants, competition decreased cumulative number of individuals in all competition treatments, more especially when *M. fuscoviride* was present, so that it was greater in the '*M. tanacetaria* alone' treatment compared with the other aphid combinations (Fig. 3A).

Metopeurum fuscoviride colony persistence and population growth

As with the greenhouse experiment, the ants had a positive effect on colony persistence of *M. fuscoviride* and colonies persisted on average about five times as long when they were not attended by ants (Tables 2 & 3). Competition had no discernible effect on the colony persistence of *M. fuscoviride* (Table 2). In the no-ant treatment, the colony persistence was very short independent of the competition treatment and the colonies went extinct almost in the first three days.

In the presence of *L. niger*, populations grew considerably and the cumulative number of individuals was high, about 33 fold, in all combinations with other aphids or when alone, while in the absence of ants, colonies became extinct in the first three or four days due to the action of predators in all aphid species combinations (Table 1, Figs. 2E & 3B). The main effect of competition and interaction between ant and competition were hence not significant (Table 1).

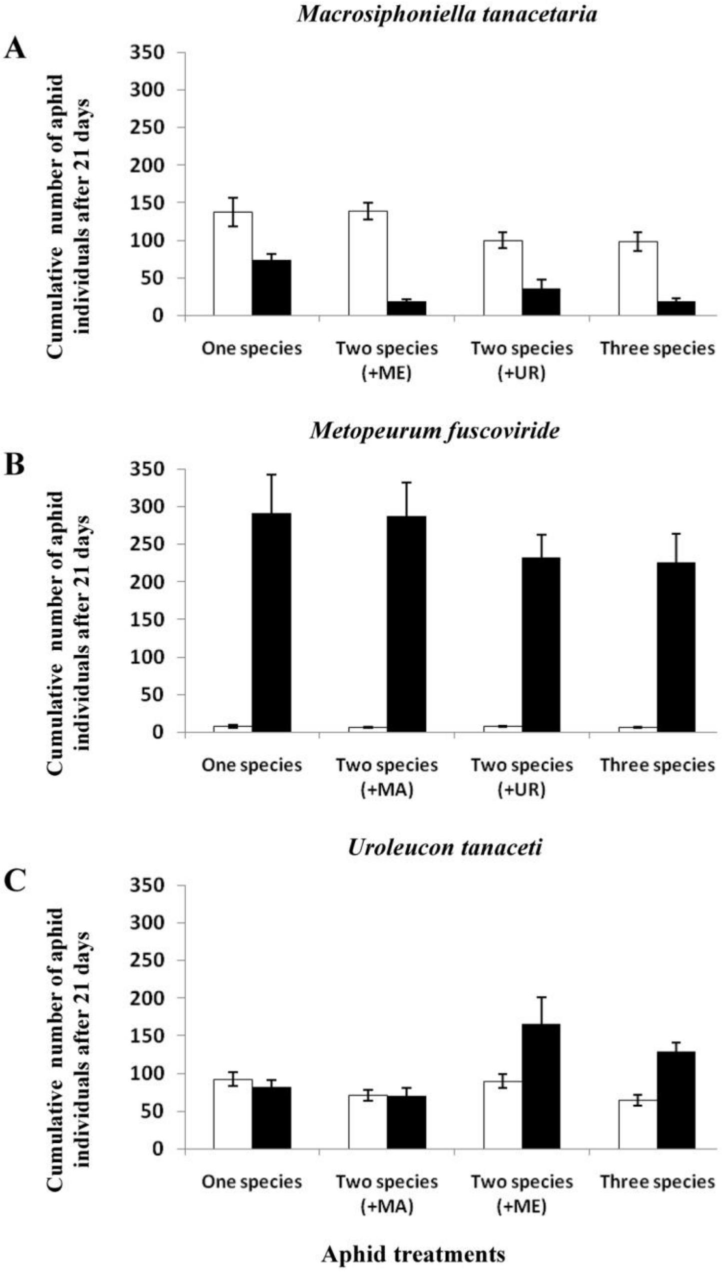


Figure 3: The effect of ant presence and aphid-aphid competition on population growth (cumulative number of individuals) of specialized tansy aphids in the field experiment. Aphid competition treatments included the focal aphid species on its own, the combination of the focal with either of the two other aphids species combinations and the three-species combination. The ant treatment had two levels (with/without *L. niger*). Mean (±SE) cumulative numbers of *Macrosiphoniella tanacetaria* (A), *Metopeurum fuscoviride* (B) and *Uroleucon tanaceti* (C) individuals during 21 experimental days in different aphid (competition) treatments in the field experiment are shown. White columns: no ant, black columns: with ant (*Lasius niger*) treatments. **MA**: *M. tanacetaria*; **ME**: *M. fuscoviride*; **UR**: *U. tanaceti*.

Uroleucon tanaceti colony persistence and population growth

In contrast to the greenhouse experiment, the presence of ants caused an overall increase in colony persistence of *U. tanaceti* (Table 2, Fig. 2F). Competition had no effect on the colony persistence of *U. tanaceti* in the absence of ants but the presence of *M. fuscoviride* and ants on the plant caused an increase in colony persistence of *U. tanaceti* (Table 2).

With regard to the cumulative number of *U. tanaceti* individuals, the interaction between ant and competition was marginally significant and patterns were complicated (Table 1, Fig. 3C). In the absence of ants, there was no effect of competition on the cumulative number of *U. tanaceti* individuals, whilst the presence of ants generally increased the number in comparison with no-ant treatments. *Uroleucon tanaceti* had the highest growth rate in the presence of *M. fuscoviride* and with access of ants while it was worse in the presence of *M. tanacetaria*, independent of ant presence (Fig. 3C).

Discussion

The present study is the first to follow the competition effects between three aphids in the presence of two ant species. The benefits of mutualism should ultimately be measured in terms of a direct or indirect competition effect between aphid species inhabiting the same host plant. *Tanacetum vulgare* and its three specialized aphids are an ideal model system for such studies.

Competition is not always straightforward, and can occur both directly and indirectly (Begon *et al.*, 2006). In the case of two aphid species, rather than occupy the same identical niche at the same time, it is better that each contending species occupies different parts of a plant, since they ultimately exploit the same resource, e.g. plant sap, and thereby by such means (resource partitioning) direct (interference) competition between them is reduced or eliminated. As shown by Moran & Whitham (1990), two different aphid species that feed on two different parts of a plant, root and leaf, can affect each other via competitive interactions. This is also the case as seen in the present study.

Macrosiphoniella tanacetaria lives on the top of the plant (new shoots), while *U. tanaceti* lives on the lower parts of the host plant, the underside of the leaves. The fitness of *M. tanacetaria* in the presence of *U. tanaceti* is reduced, indicating that even if the species inhabit different parts of the same host plant, there is an interspecific competition between them, probably via the reduction of available shared phloem nutrients, especially amino acids.

One of the findings of the present study is that the aggression level or protective level of the ant species tested are influenced by the aphid species involved, revealing that this multitrophic system of ant-tended aphid infested tansy plants and the ants themselves is much more complicated than was hitherto realized.

Ants had a drastic effect on decreasing colony persistence and population growth of *M. tanacetaria* in all combinations of aphid species, so that the number and survival of *M. tanacetaria* in the presence of ants was thereby significantly lower. There are two main reasons for this fact: firstly, ants when foraging on tansy plants preferentially prey upon *M. tanacetaria* and secondly, the ants disturb *M. tanacetaria* by walking through the colony which often makes them fall off the host plant and in this case, some of them fail to return and subsequently die. *U. tanaceti* colonies were often found to host a few individuals of *M. tanacetaria* (pers. obs.); this is probably because when *M. tanacetaria* individuals fall down from the top of the plant and climb up again to that particular plant or perhaps to another plant, they prefer to go throughout the *U. tanaceti* colony because of the presence of ants on the plant. This proves that not only is the relationship between *M. tanacetaria* and ants *not* a mutualistic one but it is also a *negative* (antagonistic) one. It has been repeatedly observed that ants prey upon *M. tanacetaria* and carry them to their nests (Fig. S1); hence, we would rather use the term 'predation' for this interaction. This phenomenon also reported for some other aphids (see Skinner, 1980; Sakata, 1994, 1995; Fischer *et al.*, 2001). When *M. fuscoviride* is present on plants, the aggression of ants increased and they showed highly invasive behaviour. This reveals that ants are more sensitive in terms of the protection of *M. fuscoviride*.

Metopeurum fuscoviride has a clear negative effect on *M. tanacetaria* in the presence of ants, probably because they are competitors for suitable positions on the host plant.

Population growth and colony persistence of *M. fuscoviride* in the presence of ants is much greater than in the absence of ants. The aphid species needs ants to protect them from natural enemies, including predators, parasitoids (one specialist in the case of *M. fuscoviride*, viz. *Lysiphlebus hirtocornis* Mackaeur) and fungal pathogens (Stadler & Dixon, 2008). *Metopeurum fuscoviride* benefit from ants in three main ways: firstly, by collecting honeydew and cleaning the environment which prevents *M. fuscoviride* sticking to the plant, perhaps also from being covered with honeydew, and also block growth of fumagine fungi; secondly, which is more important, by protecting *M. fuscoviride* against natural enemies. The third aspect, which is the most important in terms of direct competition between the aphid species, is that, as aforementioned, ants help their partners to win the competition by eliminating the competitor aphid species.

Although the benefits of ant attendance of aphid colonies are well documented, the selection pressures acting on aphids are as yet poorly understood (Flatt & Weisser, 2000). Previous studies have found that the main benefit for aphids is the protection of aphid colonies from natural enemies directly provided by ants (Tilles & Wood, 1982; Billick *et al.*, 2007). Our results suggest this protection can also be beneficial in terms of the other non-ant attended aphid species (competitors) on the same host plant. In other words, myrmecophilous aphids benefit from ants via the exclusion of competing aphids by their ant partners.

Even though *U. tanaceti* belongs to the same group of herbivores on the tansy plant, there is nevertheless a different and somehow complicated impact of ants on it. Ants occasionally visit the *U. tanaceti* colonies on the plant and maybe some predation happen but they are not attractive to the ants. Actually if the larvae of some common predators of the aphids such as *Coccinella* *septempunctata* and *Chrysoperla carnea* feed on *U. tanaceti,* they never become adults and die (Mehrparvar *et al.*, 2013).

In the two aphid species combination*, M. tanacetaria* with *M. fuscoviride,* and in the absence of ants, the cumulative number of *M. tanacetaria* individuals was the same as for the *M. tanacetaria* treatment alone. In this particular treatment, *M. fuscoviride* rapidly became extinct as when it was on its own. Therefore, there were no significant differences between treatments, i.e. *M. tanacetaria* alone and *M. tanacetaria* with *M. fuscoviride* in terms of cumulative number of individuals and colony persistence. However, in the presence of ants, the situation was reversed; here *M. tanacetaria* in contrast to the above situation, rapidly became extinct, mostly as a direct result of the action of ants, so that *M. tanacetaria* was eliminated by the ants in the early days of aphid population coexistence, and subsequently there were no *M. tanacetaria* individuals left to compete with *M. fuscoviride*. Meanwhile, *M. fuscoviride* grew well and its cumulative number of individuals and colony persistence were almost the same as when it was alone and indeed, there were no significant differences. *M. fuscoviride* wins the competition with *M. tanacetaria* when ants are present, but when ants are absent, *M. tanacetaria* wins.

In the absence of ants and in the two aphid species combination, *M. tanacetaria* with *U. tanaceti,* cumulative number of *M. tanacetaria* individuals was smaller than that of *M. tanacetaria* alone; this could be due to the negative effect of *U. tanaceti* on *M. tanacetaria* population growth. In addition, colony persistence of *M. tanacetaria* became significantly shorter than that of *M. tanacetaria* alone. *U. tanaceti* colonies grew but cumulative number of individuals was slightly smaller than *U. tanaceti* alone. In the presence of ants and in the combination of *M. tanacetaria* and *U. tanaceti*, the cumulative number of *M. tanacetaria* individuals was smaller than with *M. tanacetaria* alone, which means that *U. tanaceti* had a negative effect on *M. tanacetaria* growth. Generally, the presence of *U. tanaceti* on the plant has a negative effect on population growth and colony persistence of *M. tanacetaria*. Therefore, *U. tanaceti* is considered as a direct competitor of *M. tanacetaria*.

M. tanacetaria had a negative effect on the population growth of *U. tanaceti* but not its colony persistence per se. As populations of *U. tanaceti* and *M. tanacetaria* in the field did not increase much and were kept at low density due to predation, such competition had little discernable effect on the population growth.

In the *M. fuscoviride* with *U. tanaceti* treatment, *M. fuscoviride* soon became extinct in the absence of ants; thus here when aphids were reduced to one species, *U. tanaceti* did as well as if it were alone. In the presence of ants, the cumulative number of *M. fuscoviride* individuals was smaller than *M. fuscoviride* alone. There was no observed negative effect of *U. tanaceti* on *M. fuscoviride* colony persistence, but the population growth of *M. fuscoviride* in *M. fuscoviride* with *U. tanaceti* and three species treatments was smaller. This indicates that *U. tanaceti* had a negative effect on *M. fuscoviride* in competition point of view.

Apparently, ants had no discernable effect on population growth and colony persistence of *U. tanaceti*. On the other hand, the presence of *M. fuscoviride* on the plant in the field, which consequently attracted ants, had a clear *positive* effect on the population growth and colony persistence of *U. tanaceti*. The reason for this is seemingly that natural enemies cannot hold sway on the plant because of the ants, which are attending *M. fuscoviride*. Ants do not let natural enemies remain on the plant and eliminate them or chase them away. This in effect makes for an enemy-free environment which enhances *U. tanaceti* survival and population growth. Nevertheless, if the population of both or one of the species increases to high numbers, it could definitely create competition between these small herbivore species due a restriction of the available food source, phloem (Denno *et al.*, 1995).

As *M. fuscoviride* very soon became extinct in the *M. fuscoviride* with *U. tanaceti* treatment in the absence of ants, there was no significant differences between the cumulative number of individuals and colony persistence of *U. tanaceti* in *M. fuscoviride* with *U. tanaceti* treatment or *U. tanaceti* alone.

When all three aphid species were combined, *M. fuscoviride* soon became extinct due to the action of predators in the absence of ants; hence, aphids were reduced to two species to leave the situation as with *M. tanacetaria* with *U. tanaceti* together. In the presence of ants, *M. tanacetaria* population decreased drastically and the cumulative number of individuals was the same as with the *M. tanacetaria* with *M. fuscoviride* treatment. *M. fuscoviride* grew as well as in the *M. fuscoviride* with *U. tanaceti* treatment. *U. tanaceti* population growth was greater than *M. tanacetaria* with *U. tanaceti* and the *U. tanaceti* alone treatments.

In the three aphid species treatments and in the absence of ants, *M. tanacetaria* showed normal reproduction, whereas *M. fuscoviride* had lower reproduction and its growth rate was drastically reduced. In contrast, *U. tanaceti* showed normal reproduction; thus due to this competition effect, populations were seen to be reduced to two species, i.e. *U. tanaceti* with *M. tanacetaria.* In the presence of ants, the situation reduced eventually to *M. fuscoviride* with *U. tanaceti* because of the elimination of *M. tanacetaria* by the ants. The presence of *M. fuscoviride*, an obligatory myrmecophilous, on the plant along with *M. tanacetaria* had a very strong *indirect* effect on decreasing *M. tanacetaria* population size and colony persistence in the presence of ants. The reason was that ants, which attend *M. fuscoviride* on the plant, remove the other aphid species around the *M. fuscoviride* colony. As *M. tanacetaria* and *M. fuscoviride* can occupy the same place on the plant, more especially the yellow composite flower head, ants tend to eliminate *M. tanacetaria* in order to help their partners to win out in the ongoing interspecific competition between the aphid species. This could loosely be considered as apparent competition affect in which if ants are present on the plant, the winner will be *M. fuscoviride* and if ants are absent, it will rather be *M. tanacetaria*. Since *M. fuscoviride* would be eliminated by predators very soon in the no-ant treatments, it had little or no effect when directly competing with *M. tanacetaria*.

The interactions between aphid species and their mutualistic partners, ants, in the tansy aphid metacommunity were summarized as a conceptual graph in figure 4. Earlier, Denno *et al.* (1995) had assigned four factors which directly affect the direction of interspecific competition i.e. host plant, natural enemies, physical agents and intraspecific competition, and here in the present study we can add a new factor as mutualistic partnership which may strongly alter the straight of interspecific competition.

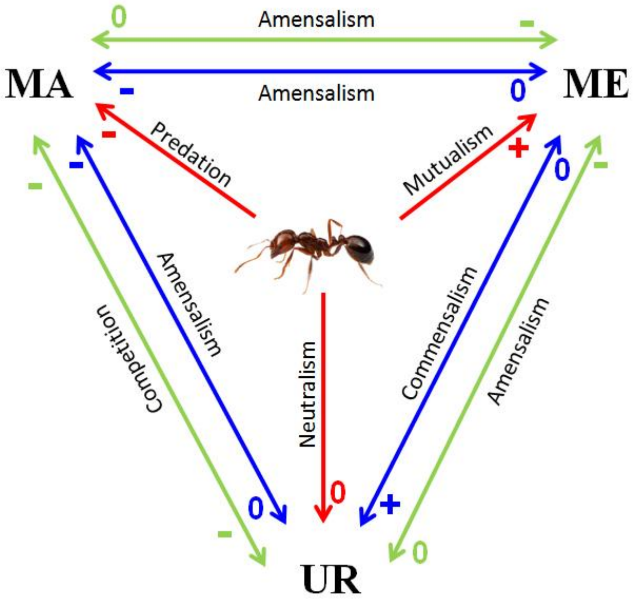


Figure 4: Community interaction web of tansy aphids and the mutualistic ants. Blue and green arrows show the direction of direct interactions between the aphids in the presence and absence of ants respectively. "+": positive effect; "-": negative effect, "**0**": neutral effect.

In conclusion, studies derived from experiments performed under specific environmental conditions clearly demonstrate a range of possible outcomes between plant-aphid and ants in this tritrophic system. The findings go some way to explain the coexistence of different species of aphids and their association with ants on a shared host plant at different spatial scales, an association sometime seen to involve competition by certain of the aphid players themselves, aided and abetted by the ants when the favoured *M. fuscoviride* is present. The association does not lead to a total mutualistic arrangement nor to a neutral coexistence between the competing aphids, but rather to some kind of apparent competition since the ants preferentially eliminate *M. tanacetaria.* We plan to continue further in depth studies in order to elucidate the factors that contribute in the metacommunity structure of tansy aphids.

Supporting Information

Figure S1: An ant worker (*Lasius niger*) is dragging down the leg of *Macrosiphoniella tanacetaria*. It has been frequently observed that *L. niger* prey upon *M. tanacetaria* and carry them to their nests.

CHAPTER IV

4- Manuscript III

Mechanisms of species–sorting: Do aphids choose plants to avoid future competitive interactions?

Mohsen Mehrparvar*†, Seyed Mozaffar Mansouri*‡ & Wolfgang W. Weisser*†

*Institute of Ecology, Friedrich–Schiller University Jena, Jena, Germany

†Present address: Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, Freising–Weihenstephan, Germany

‡Department of Ecology, Institute of Environmental Sciences, Graduate University of Advanced Technology, Kerman, Iran

Submitted to *Ecological Entomology*

Abstract

Interspecific interactions such as competition are important factors affecting insect herbivore fitness. Host choice in herbivorous insects including aphids has largely been studied with respect to host plant condition while the role of competition has received much less attention. Tansy (*Tanacetum vulgare* L.) hosts three specialized and competing aphids, *Macrosiphoniella tanacetaria* (Kaltenbach), *Metopeurum fuscoviride* Stroyan and *Uroleucon tanaceti* (L.) (Hemiptera: Aphididae). We performed a set of greenhouse and field experiments to investigate if aphid host plant choice reflects the outcome of competitive interactions with the other aphids. When winged individuals of each aphid species were given the choice between unoccupied plants or plants occupied by the same or another aphid species, choices broadly reflected the outcome of competitive interactions among aphids. Colonization of plants by winged individuals was influenced not only by the presence of other aphids on the host plant but also by previous infestation. The host choice of winged individuals largely reflected competitive hierarchies, i.e. aphids selected plants where future competition was less likely. In contrast, unwinged aphids did not show any host plant preference. For *M. tanacetaria* previously infested plants promoted the production of winged offspring. Our results show that competitive interactions have shaped host selection behaviour by aphids. In a metacommunity context, such preferences to colonise different habitats leads to species-sorting through habitat heterogeneity.

Key words: colonization, preference, performance, choice, competition, winged morph, aphid, species interactions

Introduction

Herbivorous insects that share a common host plant can affect each other directly or indirectly. In addition to direct competition for nutrient, feeding of these insects may induce host plant responses (Karban & Baldwin, 1997), that can promote competition between species even when they occur on different parts of the host plant or occupy the plant at different times (Denno *et al.*, 1995; Denno *et al.*, 2000). In the case of induced defence reactions, herbivore attack may also prime plants for a more efficient activation of defence responses in the case of subsequent herbivore attack (Bruinsma & Dicke, 2008). Host plant-mediated competitive interactions are considered to be important for the structuring of herbivorous insect communities (Kaplan & Denno, 2007). According to the preference–performance hypothesis (PPH), parental insect herbivores should select plants where competitive interactions are minimized, i.e. where performance of the offspring is maximal, and there are several examples that host plant choice is affected by interspecific competition (e.g. Clark *et al.*, 2011).

Aphids (Hemiptera: Aphididae) are phloem feeders and competitive interactions between them are likely to be frequent because of their reliance on the plant vascular system (Denno *et al.*, 1995; Karban & Baldwin, 1997; Denno *et al.*, 2000; Petersen & Sandstrom, 2001). For example, Messina *et al.* (2002) showed that previous infestation by conspecifics considerably reduced the performance of *Rhopalosiphum padi* (L.). Winged individuals of *R. padi* and *Diuraphis noxia* (Mordvilko) also preferentially settled on uninfested plants than on plants previously infested by *R. padi* (Messina *et al.*, 2002). In this case, dispersing aphids chose plants with a lower chance of future competitive interactions.

Tansy (*Tanacetum vulgare* L. (Asteraceae)) is a perennial herbaceous plant which hosts three specialist aphids: *Macrosiphoniella tanacetaria* (Kaltenbach), *Metopeurum fuscoviride* Stroyan and *Uroleucon tanaceti* (L.) (Aphididae). These three species are monoecious, remaining on the same host throughout their annual life cycle (Blackman & Eastop, 2006). Although tansy aphids share the same host plant, they are separated spatially on the different parts of the host plant. *Macrosiphoniella tanacetaria* is not ant-attended (Stadler, 2004) while *Metopeurum fuscoviride* is an obligatory myrmecophilous aphid commonly attended by ants such as the black garden ant, *Lasius niger* (L.) (Flatt & Weisser, 2000; Loxdale *et al.*, 2011). Both species feed on the apex of ramets but mixed colonies have not been observed. The third species, *U. tanaceti*, feeds on the underside of lower leaves of its host plant and is also a non-ant attended species (Loxdale *et al.*, 2011). All species have a classical metapopulation structure, and together, they form a metacommunity (Weisser, 2000; Massonnet *et al.*, 2002; Loxdale *et al.*, 2011). In a separate study, we show that there are strong interspecific competitive interactions among the three aphid species that are partly mediated by ants (Table 1). In the presence of ants, the ant-tended *M. fuscoviride* is competitively dominant, due to preferential predation by ants on the other aphid species, while the non-tended *M. tanacetaria* is competitively superior in the absence of ants. For the non-tended aphid species, *U. tanaceti*, the situation is slightly more complicated (Table 1): the net effect of ant presence is positive only in the presence of *M. fuscoviride* and predators because in this case ants are present on the plant that do not let natural enemies remain on the plant and eliminate them or chase them away. The competitive interactions may result in competitive exclusion of one or more species from a plant (Table 1), thus, it would be advantageous that winged mothers to choose the birth place of their offspring such that they avoid such competitive interactions.

In this study, we conducted several greenhouse and field experiments to understand: 1) whether host choice in tansy aphids is affected by the presence of conspecific or heterospecific aphids on the host plant, 2) if previous infestation of the host plant by conspecific or heterospecific individuals affects aphid host choice, 3) whether there is a difference in settling behaviour between winged and unwinged individuals, and 4) if tansy aphid host choice reflects the outcome of biological interactions with other aphids.

Table 1: Outcome of competitive interactions between tansy aphids in a greenhouse experiment (lasting 20 days, no predators) and a field experiment (lasting 21 days, in presence of natural enemies) (Mehrparvar *et al*. unpublished). For every species combination, five individuals of each species were placed on the plants initially and the survival and growth of the colonies were observed until end of the experiment. A species is considered competitively superior (winner) if colony persistence time and cumulative number of aphids was greater. MA: *Macrosiphoniella tanacetaria*, ME: *Metopeurum fuscoviride*, UR: *Uroleucon tanaceti*.

Species combination	**Winner**	**Remark**
MA+ME	With ants: ME	Ants tend ME and attack and kill MA.
	Without ants: MA	ME went extinct due to little reproduction (c.f. Flatt & Weisser, 2000) and/or predation (field experiment).
MA+UR	With ants: UR	Ants attack MA but not UR.
	Without ants: MA/UR	In the absence of ants in the field (in the presence of predators) MA was the superior competitor (based on cumulative number) but in the greenhouse (absence of predators) MA=UR.
ME+UR	With ants: ME	Ants tend ME and help it for population growth.
	Without ants: UR	ME extinct because of competition or/and predation.
MA+ME+UR	With ants: ME	Ants tend ME and help it for population growth and also meanwhile attack MA.
	Without ants: MA/UR	In the absence of ants in the field (in the presence of predators) MA was the superior competitor (based on cumulative number only) but in the greenhouse MA=UR.

Materials and Methods

Experimental plants and aphids

Tansy plant is native to Europe and Asia (Mitich, 1992). It can be found growing as isolated patches or stands of single plants on riverbanks and wastelands. Tansy hosts more than 23 aphid species globally (Blackman & Eastop, 2006; Holman, 2009).

At the end of March 2011, tansy plants were grown individually from seeds in one-litre pots (11 cm diameter). The plants were kept in a greenhouse at a temperature of about 25 °C during the day, 20 °C at night, and with a 16:8 h light: dark regime using artificial lighting. Plants were used for experiments when their height reached about 20 cm.

We used both winged and unwinged aphids for the experiments. In the beginning of May 2011, adult unwinged aphids of each of the three species, *Macrosiphoniella tanacetaria* (MA) *Metopeurum fuscoviride* (ME) and *Uroleucon tanaceti* (UR), were collected from the field and then separately reared in the greenhouse on potted tansy plants. Winged aphids used in choice experiments were collected 12 h before starting the experiments from the field and kept in 300 ml capacity empty plastic jars until required.

Colonization experiments

All experiments were performed in June 2011, at a time when the number of winged individuals in the field is large. Plexiglas cages (35L×35W×90H cm) were used in the greenhouse experiments in order to prevent the escape of aphids (Supporting Information: Fig. S1). To facilitate air ventilation, the front of the cages was covered by fine mesh.

Choice experiment I- Choice of occupied plants by winged aphids in the greenhouse

For this experiment, four potted tansy plants were placed inside each cage in the corners of an imaginary square of about 25 cm (Supporting Information: Figs. S2 & S3). There were four treatments: three plants were infested each with five third-instars of one of the aphid species (MA, ME or UR), whilst one plant was left uninfested as unoccupied plant. Nymphs were allowed to settle down for two hours and then their number was checked again, if the number had decreased by any reason, it was increased to five individuals using aphids from the stock culture. The position of each treatment within the cage was chosen randomly for each replicate. By using non-reproductive nymphs, offspring born to immigrants could be clearly identified on the plants.

At the start of the experiment, a small plastic vial (Eppendorf, 1.5 ml) containing a winged individual was hung by a thin wire in a central position from the ceiling of the cage above the plants and was then opened to allow the aphid to emerge from the vial. Thereafter, the winged aphid was allowed to choose a host plant. In some cases, the winged aphids climbed up the wire to walk to the bottom of the cage or fell down. In these cases, they were picked up carefully by a paint brush and put back on the plastic vial. All plants were checked hourly for six hours after the start of the experiment for the position of the winged aphid and production of nymphs. The first plant on which the aphid landed was noted. All aphids were observed to choose a host plant within six hours after release. The inspection was repeated after 24 hours. In total, 50 replicates using 50 different winged adults were run for each aphid species.

Choice experiment II- Choice of occupied plants by winged aphids in the field

This experiment was essentially the same as experiment I except that plants were placed in the field and were colonized by winged individuals that had emigrated from other plants in the region. Four plants were placed at the corner of a square with side length of 25 cm. In total, 30 groups of four plants were placed in a field in the botanical garden of Jena, Germany with a distance of 80 cm between groups. The experiment was carried out on 17-19 June 2011 [three-day average: temperature 15 °C (range 10.3 – 21.3 °C); relative humidity 66.3% (range 38.3 – 97.8%)]. Plants were placed in the field at 7 am and checked daily for three days for the presence of winged immigrants. The winged immigrants were identified to species and removed from the plant together with any offspring that was produced. If the number of third-instar nymphs on the plants was lower than five, nymphs from the stem culture were added to the plants.

Choice experiment III- Choice of previously infested plants by winged aphids in the greenhouse

At the start of this experiment, 200 potted tansy plants were randomly divided into four subsets of 50. Three subsets were used for infestation by the three aphid species and one subset was kept uninfested. In order to infest a plant, it was placed in a Plexiglas cage (cf. choice experiment I) and 15 newly moulted unwinged adults were placed on the plant and allowed to feed and reproduce for 15 days. Thereafter, all aphids and any visible traces of their presence (e.g. exuviae) were removed. We also cleaned the honeydew away (if any) using a wet paint brush. Control plants were also placed in Plexiglas cages. For the choice experiment, three plants, previously infested by MA, ME or UR, and one uninfested plant were placed inside a single cage as in choice experiment I. One winged aphid was released in the cage as described previously. Fifty replicates using 50 different winged adults were carried out for each of the three aphid species.

Choice experiment IV- Choice of previously infested plants by unwinged aphids in the greenhouse

This experiment was exactly the same as choice experiment III except that unwinged aphids were used instead of winged individuals and these were released in the center of the cage floor between the plants using a fine paint brush. The unwinged aphids were collected 12 h before starting the experiment from the field and kept in 300 ml capacity empty plastic jars until required. In total, there were 50 replicates using 50 different unwinged adults for each aphid species.

Performance experiment of *M. tanacetaria* on previously infested plants

The results of the colonization experiments prompted us to perform a performance experiment with MA on previously infested plants. This experiment assessed whether previous infestation influences a) offspring survival and the allocation of mothers into winged and unwinged offspring, and b) the number of offspring born to second generation unwinged mothers on the plants.

The experiment was conducted in the greenhouse using two treatments: plants previously infested by MA and control plants never exposed to infestation by aphids. Ten tansy plants grown from seeds as described above were placed in Plexiglas cages and each was infested with ten adult individuals of MA which were allowed to reproduce for ten days. Ten other plants were used as controls and were kept free of infestation and also placed in cages. After ten days, aphids including any offspring produced and exuviae were carefully removed from the infested plants using a paint brush. We also cleaned the honeydew away using a wet paint brush but some honeydew may have remained on the plants. There was no discernible damage to the infested plants. After three more days (days 11-13), three unwinged fourth instar nymphs of MA were placed on each of the 20 plants and allowed to develop into adults and to reproduce for three days. Then, the mothers and all nymphs except 10 were removed from the plant. The remaining nymphs were allowed to develop into adults. After adult moult, the number of survivors (of 10) was noted and their phenotype (winged/unwinged) was assessed. Five unwinged adults were allowed to remain on the plants, all others (including any offspring) were removed from the plants. Adults were allowed to reproduce for another ten days when the total number of offspring was assessed.

Statistical analysis

Choice experiments were analyzed using Chi-square tests implemented in the SPSS 16 software (SPSS Inc. 2007, procedures NPAR TEST, CHISQUARE).

For the performance experiment, we used a Generalized Linear Model (procedure glm) implemented in the statistical package R (R version 2.14.0, 2011) to compare the proportions of produced winged offspring between treatment and control. Since our count data was overdispersed, the cbind function and a quasibinomial distribution with logit link function were used. Offspring survival from birth to adult moult was analyzed using a t-test (procedure T-TEST) and the total number of aphids in the end of experiment was analyzed using a General Linear Model (procedure UNIANOVA) with the number of mothers as a covariate using the SPSS 16 software (SPSS Inc. 2007).

Results

Colonization experiments

All aphids were observed to choose a host plant within six hours after release. In all cases, aphids produced offspring on the plants where they were observed first. In the following, *aphid choice* therefore refers to both the first settling of an individual on a plant and subsequent production of offspring. As we only observed the aphids during first six hours and after 24 hours, we have no data on the timing of reproduction but it occurred between six to 24 hours.

Choice experiment I- Choice of occupied plants by winged aphids in the greenhouse

Most MA winged morphs chose plants occupied by UR followed by plants occupied by conspecifics (χ^2 = 25.2, df = 3, P< 0.001, N=50; Fig. 1a). Plants occupied by ME were very rarely chosen.

Winged individuals of ME preferred plants occupied by conspecific individuals, followed by plants occupied by MA or unoccupied plants, and plants occupied by UR (χ^2 = 19.92, df = 3, P< 0.001, N=50; Fig. 1a).

Winged individuals of UR did not show a clear preference (χ^2 = 4.08, df = 3, P = 0.25, N=50) even though a majority of individuals (36%) landed on plants occupied by MA (Fig. 1a).

Choice experiment II- Choice of occupied plants by winged aphids in the field

In 163 out of 168 cases, the winged individuals that landed on the experimental plants were UR. Thus, the results described here are only based on the 163 UR individuals. The distribution of winged individuals over plants was sometimes more than one individual on the same plant.

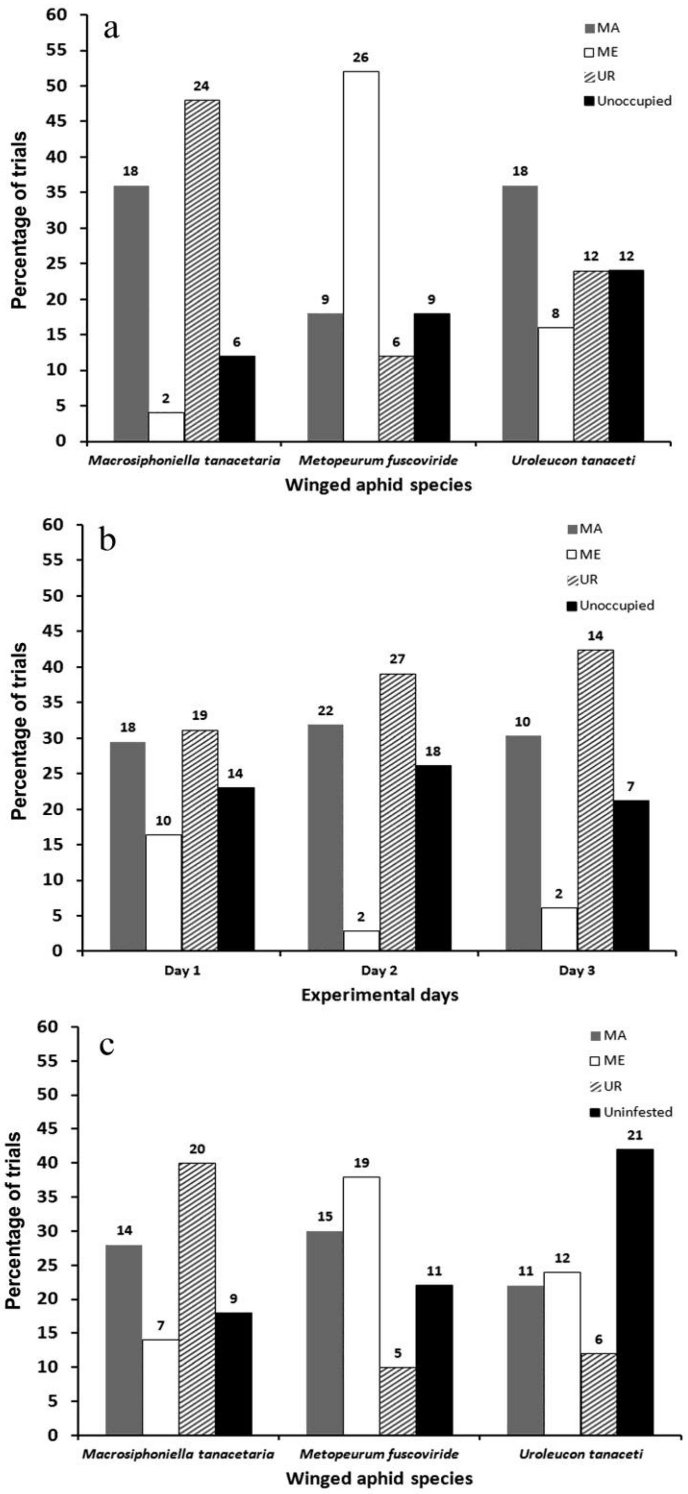


Figure 1: Host choice of aphids of three different species in host choice experiments, expressed as the percentage of replicates in which a particular plant was chosen. a) Choice among occupied plants by winged aphids in the greenhouse (choice experiment I) (N=50 for each species); b) Winged individuals of *U. tanaceti* in the field (choice experiment II); c) Choice among previously infested plants by winged individuals in the greenhouse (choice experiment III) (N=50 for each species). The numbers of individuals choosing a particular plant are shown on the top of each bar. MA: *Macrosiphoniella tanacetaria*, ME: *Metopeurum fuscoviride*, UR: *Uroleucon tanaceti*.

The distribution of UR winged individuals among the different plants on the first day of the experiment was not different from a random distribution ($\chi^2 = 3.33$, df = 3, $P = 0.34$, N=61 individuals; Fig. 1b). On the second ($\chi^2 = 20.33$, df = 3, $P < 0.001$, N=69 individuals) and third day ($\chi^2 = 9.3$, df = 3, $P < 0.05$, N=33 individuals) the distribution of new immigrant winged individuals among the plant treatments was non-random so that winged individuals were rarely found on plants occupied by ME (Fig. 1b). When plants with ME were excluded from the analysis, there was no significant difference anymore among the treatments (day 2: $\chi^2 = 1.82$, df = 2, $P = 0.4$, N=67 individuals; day 3: $\chi^2 = 2.39$, df = 2, $P = 0.3$, N=31 individuals).

Choice experiment III- Choice of previously infested plants by winged aphids in the greenhouse

For MA, a pattern similar to that of the choice experiment I was observed. Winged MA preferred plants which had previously been infested by UR followed by plants previously infested by MA ($\chi^2 = 8.08$, df = 3, $P < 0.05$, N= 50; Fig. 1c).

ME mostly (38% of choices) chose plants which had previously been infested by conspecific individuals. The second-most common choice was plants previously infested by MA and then uninfested plants. The plants previously infested by UR were chosen rarely ($\chi^2 = 8.56$, df = 3, $P < 0.05$, N= 50; Fig. 1c).

Winged individuals of UR preferred uninfested plants (42% of choices) over plants previously infested ($\chi^2 = 9.36$, df = 3, $P < 0.05$, N= 50; Fig. 1c). When the uninfested plants were excluded from the analysis, there was no significant preference for certain plants ($\chi^2 = 2.14$, df = 2, $P = 0.34$, N= 29).

Choice experiment IV- Choice of previously infested plants by unwinged aphids in the greenhouse

The host choice of unwinged individuals of MA and ME was not different from random (MA: $\chi^2 = 1.36$, df = 3, $P = 0.72$, N= 50; ME: $\chi^2 = 2.16$, df = 3, $P = 0.54$, N=

50; Fig. 2). For UR, there was a tendency that aphids avoid plants previously infested by MA or ME but this was not statistically significant ($\chi^2 = 5.2$, df = 3, $P = 0.16$, N= 50; Fig. 2).

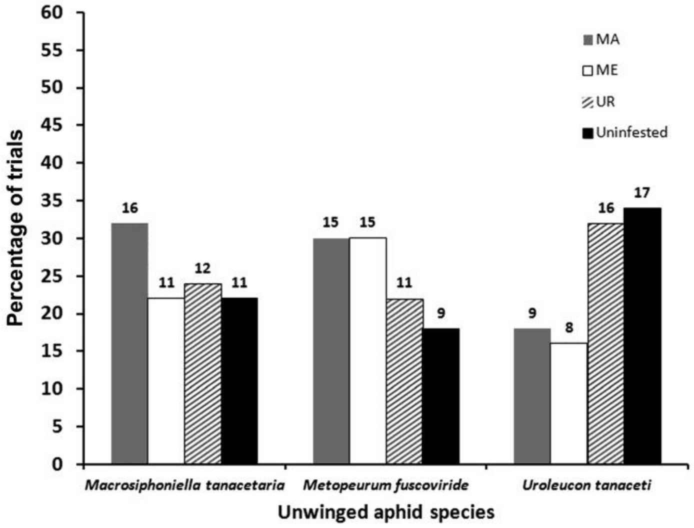


Figure 2: Host choice of unwinged aphids of three different species in host choice experiment, expressed as the percentage of replicates (N=50 for each species, choice experiment IV). The numbers of individuals choosing a particular plant are shown on the top of each bar. MA: *Macrosiphoniella tanacetaria*, ME: *Metopeurum fuscoviride*, UR: *Uroleucon tanaceti*.

Performance experiment of *M. tanacetaria* on previously infested plants

Previous infestation had no effect on offspring survival, i.e. the number of first instars out of 10 developing successfully into adults (mean=7.39 ± 0.77, t=-0.07, df=16, P=0.945). The percentage of winged morphs among these adults was significantly higher on previously infested plants than on uninfested plants (t=2.527, df=16, P<0.05; Fig. 3a).

Whenever there were fewer than five unwinged adults on the plants (min=3, N=8), all remaining unwinged adults were used in the reproduction trial. The number of offspring produced at the end of experiment was independent of the treatment (F=0.491, df=1, P=0.495; Fig. 3b). The initial number of MA mothers had no effect on the number of MA offspring produced at the end of experiment (F=2.773, df=1, P=0.118).

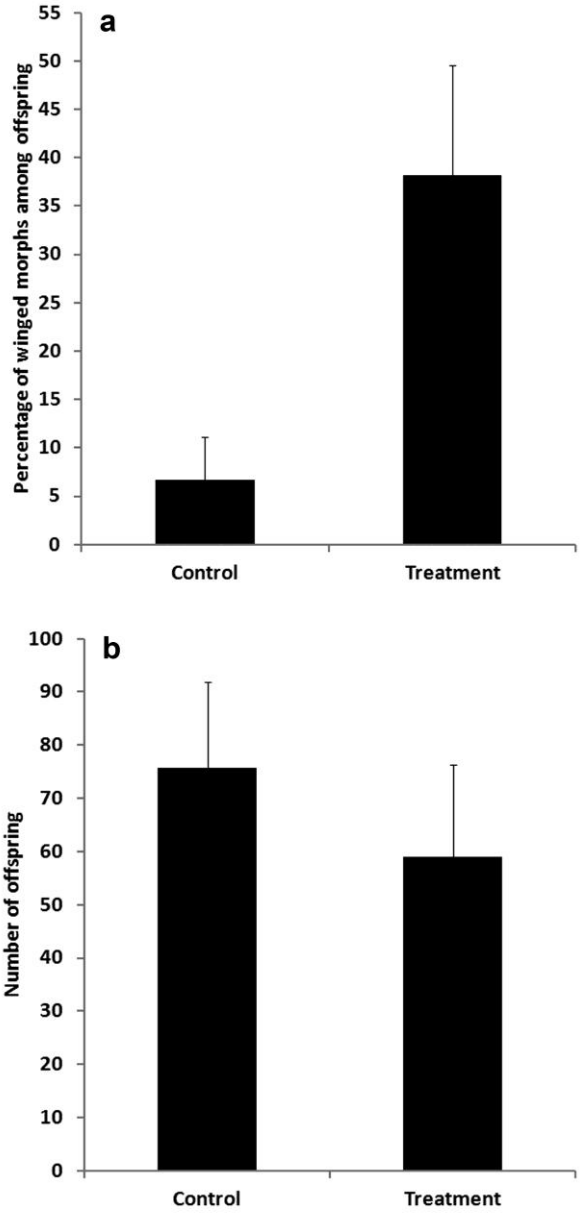


Figure 3: Results of performance experiment with *Macrosiphoniella tanacetaria* in greenhouse where aphids were placed on previously infested (treatment) and uninfested (control) plants. a) percentage of winged morphs among first-generation offspring, and b) number of offspring produced by five unwinged first-generation adults. (Mean ± SE).

Discussion

In this study, we tested how occupancy of plants affected host plant choice of winged and unwinged tansy aphids. We hypothesized that aphids select plants where the risk of future competition, for some species mediated by the aggression of mutualistic ants, is reduced (cf. Table 1). Our results show that colonization of plants by dispersing aphid individuals was in fact influenced by the presence of other aphids on the host plant. Importantly, we found that not only present occupation of aphids affected the colonization of plants but also previous occupation. Thus, aphids apparently detected that plants were occupied beforehand and this affected host choice. In contrast to winged individuals, unwinged females exhibited little host preference.

Avoiding competitive interactions is a strategy that may increase insect herbivore fitness. For example, the bark beetle *Pityogenes chalcographus* (L.) does not select trees that are already infested by another bark beetle infesting Norway spruce, *Ips typographus* (L.), avoiding interspecific competition (Byers, 1993). An effect of previous infestation on host choice by insect herbivores has also been shown in a number of other studies. For example, females of *Leptinotarsa juncta* (Germar) preferred to lay eggs on undamaged plants versus plants that had been infested by their competitor, *Epitrix fuscula* (Crotch) (Wise & Weinberg, 2002). Similarly, Agrawal (1999) showed that colonization of wild radish plants by leaf-mining flies, *Liriomyza* sp., was lower on plants that received previous damage by a lepidopteran larva, *Pieris rapae* (L.), compared to controls.

We found for the tansy-aphid system that winged aphid individuals avoided host plants where there was a high chance of competitive interactions. The avoidance of *M. fuscoviride*-infested plants by winged individuals of *M. tanacetaria* and *vice versa* reflects such a host choice, as *M. fuscoviride* is competitively dominant on plants with ants whereas *M. tanacetaria* is competitively dominant on plants without ants (Table 1, from here onward we used the full species names of aphids instead of using abbreviations for better reading). Because our aphid colonies were not ant-tended, our results suggest that winged individuals of *M. tanacetaria* base their choice on the presence of *M. fuscoviride* aphids, rather than on the presence of ants. In nature, it is in fact very rare to find both species together on a same host plant (Weisser & Härri, 2005).

In addition to these avoidance reactions, the preferences exhibited by winged individuals of *M. fuscoviride* and *M. tanacetaria* were also interesting. *M. fuscoviride* preferred plants that were occupied or previously infested with conspecifics. Since *M. fuscoviride* is an obligate myrmecophile (Fischer *et al.*, 2001) and needs mutualistic ants for survival and reproduction (Flatt & Weisser, 2000), aggregation may be beneficial as ants prefer attending larger *M. fuscoviride* colonies. Such behaviour has also been shown by Sauge *et al.* (2002; 2006) for peach plants where colonization by *Myzus persicae* (Sulzer) led to easier feeding and settlement for conspecific individuals on a susceptible cultivar. This does not, however, explain the preference for previously infested plants. Possibly plants where *M. fuscoviride* occurred have a higher chance of being attended by ants, i.e. aphids choosing those plants that will be more likely to be tended, but this remains to be tested.

Winged individuals of *M. tanacetaria* often chose plants occupied by *U. tanaceti*. While *M. tanacetaria* and *U. tanaceti* do compete, probably only when colonies have reached a large size (Table 1), this behaviour may also reflect facilitation. *Uroleucon tanaceti* induces leaf yellowing even at low densities and this may result in higher nutritional value of the host plant, at least in the short term. In the field, we frequently observed that tansy plants were colonized by both *M. tanacetaria* and *U. tanaceti* such that sometimes individuals of *M. tanacetaria* settled within *U. tanaceti* colonies on the underside of the lower leaves of the host plant. For another pair of aphid species, Brunissen *et al.* (2009) presented evidence that potato plants previously infested by *M. persicae* are more attractive for *Macrosiphum euphorbiae* Thomas winged individuals, than plants which were uninfested or previously infested by conspecifics. Such effects have also been reported in other plant-aphid systems (Prado & Tjallingii, 1997; Gonzales *et al.*, 2002).

The host plant selection scenario for *U. tanaceti* winged individuals was different and more complicated. In the greenhouse, the presence of other aphid species had no observable effect on selection behaviour (choice experiment I), while in the case of previous plant infestation (choice experiment III), winged individuals mostly chose plants that had previously been uninfested. Interestingly, in the field (choice experiment II), initial plant choice was as in greenhouse choice experiment I, i.e. a random choice of plants by immigrating winged *U. tanaceti* even though fewer individuals were found on plants with *M. fuscoviride* (Fig. 1b). Over the next two days the patterns indicated an increased avoidance of plants infested by *M. fuscoviride* (Fig. 1b). If plants with *M. fuscoviride* were excluded from the analysis, aphid choice was random in all three days. A likely explanation for the development of the avoidance patterns in the field is the presence of ants, which did not occur in the greenhouse experiments. In the first day of the experiment, plants were placed in the field, and at this point, plants were ant-free. From the second day onwards, ants explored the colonies of *M. fuscoviride* on the plants and starting to attend them. Thus, there are two possibilities: either winged *U. tanaceti* avoided plants with *M. fuscoviride* and ants on the second and third day, or ants attacked *U. tanaceti* individuals and killed them or forced them to leave the plant. Incidentally, in the field experiment, a considerable number of winged individuals of *U. tanaceti* (approx. 62%) landed on the plants occupied by conspecifics and settled down into an existing *U. tanaceti* colony. This may be indicative of an allee effect.

Phytophagous insects, including aphids use a combination of different pre- and post-feeding stimuli such as chemical and visual cues to detect a suitable host plant (Chapman *et al.*, 1981; Nottingham & Hardie, 1993; Bernays & Chapman, 1994; Powell *et al.*, 2006; Robert *et al.*, 2012). In the case of our experiments, winged aphids always remained on the plant where they alighted first, thus there was no preliminary probing that has been shown to be important for host choice in some species (Powell *et al.*, 2006; Pettersson *et al.*, 2007). There is growing evidence indicating that herbivore infection induces plant volatiles emissions which can be detected by other insects including aphids (e.g. Pickett *et al.*, 1992; Li *et al.*, 2002). Aphids have complex interactions with plants (Völkel & Baldwin, 2004) and feeding has been shown to induce volatile production in plants (e.g. Du *et al.*, 1998). Even though we do not know the exact cue that the winged aphids used in our experiments, it is likely that volatile, rather than visual cues affected host selection, as in the case of previously infested plants no trace of aphids should have been left on the plants. In fact, for *M. tanacetaria* and *M. fuscoviride* the observed patterns of host plant selection by winged individuals were the same when the plants were occupied or previously infested (see Figs. 1a & 1c). If this is true then the volatiles released by tansy plants must differ depending on the aphid that feeds or previously fed on them. The unwinged individuals of all the three aphid species did not exhibit preferences for particular plants. This indicates that unwinged individuals are not specialized for host plant selection.

In the performance experiment of *M. tanacetaria,* there were no fitness differences between aphids reared on uninfested and previously infested plants, yet interestingly the percentage of winged morphs among the offspring was higher on previously infested plants than on uninfested plants. In aphids, the production of winged morphs is a general response to adverse environmental conditions (Dixon, 1998; Weisser *et al.*, 1999; Braendle *et al.*, 2006; Balog *et al.*, 2013). In the present study, prior plant infestation was stimulus for wing induction in offspring and hence reflects the decision to leave the plant in the next generation. This was not consistent, however, with the decision of winged individuals to choose plants occupied by *M. tanacetaria* (choice experiment I). It is important to point out that while the proportion of winged morphs was increased not all offspring were destined to become winged morphs, hence it is conceivable that previous infestation prompts aphids to 'spread the risk' by colony growth on the current plant and colonization of few other plants.

The host selection behaviour shown by the tansy aphids may lead to different colony compositions in the field. Tansy aphids show a classical metapopulation structure (Weisser, 2000; Massonnet *et al.*, 2002; Loxdale *et al.*, 2011) where the extinction rates are high and as a result, a proportion of local habitats (plants) are always unoccupied. Based on the results obtained in this study it can be demonstrated that there could be several scenarios for colonization of these empty habitats. In the beginning of the season when most tansy plants are not occupied yet (Weisser, 2000), there is the same chance for each of the three specialized tansy aphids to occupy the plants. However, wherever ants are ready to attend the plants, the chances of successful occupation by *M. fuscoviride* are higher. After establishment of aphid colonies, the subsequent occupation and colonization will then be affected by the presence of or previous infestation by other aphid species on those plants. Based on field observations, a composition of *M. tanacetaria* and *M. fuscoviride* is very rare; however, a combination of *M. tanacetaria* and *U. tanaceti* or *M. fuscoviride* and *U. tanaceti* can be observed more frequently (Weisser & Härri, 2005).

In conclusion, we have shown that the tansy aphid metacommunity shows strong elements of species-sorting, i.e. different aphid species preferentially sort into different plants (=habitats), creating separate spatial niches through habitat heterogeneity. In other words, they chose or avoid specific host plant with or without conspecific or heterospecific aphid species, and therefore, these interactions have the potential to influence the structure and dynamics of the metacommunity via competition effects (*sensu* Stewart, 1996), and ultimately influence longer-term ecology and evolution.

Supporting Information

Figure S1: The Plexiglas cages (35L×35W×90H cm) which used for the experiments in the greenhouse in order to prevent the escape of aphids. To facilitate air ventilation, the front of the cages was covered by fine mesh.

Figure S2: Tansy pots inside the Plexiglas cages. For the greenhouse experiments, four potted tansy plants were placed inside each cage in the corners of an imaginary square of about 25 cm with the same distance from each other.

Figure S3: Final design of inside the cages for the experiments.

CHAPTER V

5- Manuscript IV

Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing?

Mohsen Mehrparvar*†, Nafiseh Mahdavi Arab*† & Wolfgang W. Weisser*†

*Institute of Ecology, Friedrich–Schiller University Jena, Jena, Germany
†Present address: Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, Freising, Germany

Published in ***Biological Control***
65: 142-146

Volume 65, Issue 1, April 2013

ISSN 1049-9644

ELSEVIER

Biological Control

Theory and Application in Pest Management

Editors

Jacques Brodeur Université de Montréal	**Edwin Lewis** University of California, Davis
Jenny Cory Simon Fraser University, Canada	**Paul J. Ode** Colorado State University
James D. Harwood University of Kentucky	**David TeBeest** University of Arkansas
John Hoffmann University of Cape Town	**S. Bradleigh Vinson** Texas A&M University
Barry Jacobsen Montana State University	

Editorial Board

Available online at www.sciencedirect.com

SciVerse ScienceDirect

Biological Control 65 (2013) 142–146

Contents lists available at SciVerse ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Diet-mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing?

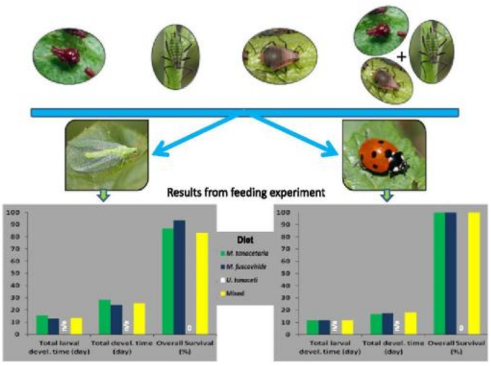
Mohsen Mehrparvar [*,1], Nafiseh Mahdavi Arab [1], Wolfgang W. Weisser [1]

Institute of Ecology, Friedrich–Schiller University Jena, Jena, Germany

HIGHLIGHTS

- ▶ We investigated the effects of diet mixing on generalist aphid predators.
- ▶ The aphids were *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanaceti*.
- ▶ The suitability of each aphid species is different and affects the fitness of its predator.
- ▶ The mixed diet was worse than the best single-aphid diet for *Coccinella septempunctata* and *Chrysoperla carnea*.
- ▶ The dietary mixing is not always beneficial for generalist predators.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 26 September 2012
Accepted 22 December 2012
Available online 3 January 2013

Keywords:
Aphid
Food suitability
Ladybird
Green lacewing
Nutritional ecology
Mixing diets benefits

ABSTRACT

Some predators have a broad prey range, but not all prey are equally suitable for a predator. We tested the suitability of three specialized tansy (*Tanacetum vulgare*) aphids, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanaceti*, on biological parameters of their major predators, *Coccinella septempunctata* and *Chrysoperla carnea*, when aphid species were offered either alone, or as a mixed diet of all the three aphid species. For the lacewing *C. carnea*, a diet consisting only of the generally ant-tended *M. fuscoviride* resulted in the shortest larval and total developmental time, in highest larval survival and pupation success. For the ladybird *C. septempunctata*, a pure diet of the non-tended *M. tanacetaria* was most suitable, resulting in the shortest total developmental time, heaviest fresh and dry weight. Larvae of both predator species had low survival and none of them developed to pupal stage when offered only *U. tanaceti* that has a bright red colour, is not ant-tended and feeds on the underside of lower leaves. The mixed diet of all three aphid species was worse than the best single-aphid diet for both predators, for almost all fitness parameters. Thus, while diet mixing may allow predators to avoid the negative impact of unsuitable prey, diet mixing does not necessarily result in the highest fitness of predators.

1. Introduction

The fitness of aphid predators varies distinctly according to the prey species that they fed on (Blackman, 1967; Kalushkov and Hodek, 2004; Khuhro et al., 2012; Omkar et al., 2009; Pappas et al., 2007; Phoofolo et al., 2007; Zhang et al., 2012). Certain aphid species can cause increased mortality, a prolonged developmental time or a decrease in larval survival rate in predators (Canard and

---

* Corresponding author. Address: Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising-Weihenstephan, Germany. Fax: +49 8161 71 4427.

E-mail addresses: mehrparvar@aphidology.com, mohsen.mehrparvar@tum.de (M. Mehrparvar), nafiseh.mahdavi@tum.de (N. Mahdavi Arab), wolfgang.weisser@tum.de (W.W. Weisser).

[1] Present address: Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, Freising, Germany.

1049-9644/$ - see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.biocontrol.2012.12.009

Principi, 1984). So far, several aphid species have been reported as being generally less suitable or even toxic for predators, among which are *Aphis sambuci* L. and *Macrosiphum albifrons* Essig for *Coccinella septempunctata* (L.) (Gruppe and Roemer, 1988; Nielsen et al., 2002), *Megoura viciae* Backton and *Aphis fabae* Scopoli for *Chrysopa perla* (L.) and *Adalia bipunctata* (L.) (Canard, 1970; Canard and Principi, 1984; Dixon and Agarwala, 1999), *Aphis nerii* Boyer de Fonscolombe for *Schizocosa* sp. (Toft and Wise, 1999).

The benefits of dietary mixing have been intensively investigated in generalist insect herbivores (Bernays et al., 1994; Unsicker et al., 2008; Waldbauer and Friedman, 1991) while less is known for generalist insect predators (Borg and Toft, 2000; Wallin et al., 1992). Diet mixing theory suggests that a generalist benefits from developing on a diversified diet, because (a) the different food items differ in their nutrient composition, thus satisfying better a varied nutrient demand (Evans et al., 1999; Hauge et al., 1998), or (b) the concentration of toxins in the diet is diluted (toxin dilution hypothesis) (Behmer et al., 2002). For aphid predators, there are some studies that focus on dietary mixing effects (Evans et al., 1999; Hauge et al., 1998; Hauge et al., 2011; Nielsen et al., 2002). The studies provided evidence that dietary mixing is not always beneficial. For example, Hauge et al. (1998) raised larvae of *C. septempunctata* on a mixed diet of three cereal aphid species, *Sitobion avenae* (Fabricius), *Rhopalosiphum padi* (L.) and *Metopolophium dirhodum* (Walker), and showed an intermediate performance for predators that fed on mixed diet in comparison with single-species diets.

While most studies on nutritional ecology of aphid predators have focused on economically important aphid species, these predators also feed on aphids of little economic importance that may have significant effects on the population dynamics of the predators. For economically relevant aphids, predators often encounter different aphid species only sequentially, often in different fields, e.g. when a single crop is only infested by a single aphid species, or when one species is strongly dominant. In contrast, in many natural systems a number of aphids of potentially different suitability occur on the same host plant or on different plants nearby. In our model system, there are three common aphid species that feed on tansy (*Tanacetum vulgare* L., Asteraceae): the ant-tended *Metopeurum fuscoviride* Stroyan and the untended *Macrosiphoniella tanacetaria* (Kaltenbach) and *Uroleucon tanaceti* (L.) (Aphididae) (Blackman and Eastop, 2006; Holman, 2009). *Macrosiphoniella tanacetaria* and *M. fuscoviride* feed on the apical part of the shoots while the third species, *U. tanaceti*, feeds on the underside of lower leaves of its host plant. These aphids hatch from overwintering eggs in March–April and go through parthenogenetic reproductive generations until late autumn (October). All three species may occur together in the same site or even on the same plant (pers. obs.).

In this study, we addressed two questions: (1) Do tansy aphids differ in their effects on survival and development of the common aphid predators *Chrysoperla carnea* (Stephens) and *C. septempunctata*? (2) Is a mixed diet of three tansy aphid species beneficial for the predators? To answer these questions the performance of two predators were investigated in the laboratory.

2. Materials and methods

2.1. Experimental insects

Predator insects, *Chrysoperla carnea* (Neuroptera: Chrysopidae) and *Coccinella septempunctata* (Coleoptera: Coccinellidae) were obtained as eggs from a commercial supplier (Katz Biotech Services, Welzheim, Germany). Upon arrival, the eggs were maintained in a climate chamber at 20 ± 2 °C, ~75% R.H. and a long day 16:8 h (L:D) photoperiod until emergence of larvae.

Three specialized tansy aphid species, *M. tanacetaria*, *M. fuscoviride* and *U. tanaceti* were collected in July 2010 from tansy plants in the botanical garden of Jena, Germany and were reared in a greenhouse on potted tansy plants. As *M. fuscoviride* is an obligatory myrmecophilous aphid, colonies of black garden ants, *Lasius niger* (L.), were collected in the field and used for rearing of this aphid species. Each ant colony had several hundred workers, many larvae and pupae. The colonies were kept in 10-litre volume buckets, half-filled with humid soil and coated on the inside with Fluon (Fluoropolymer Dispersion, Whitford GmbH, Germany). Access of the ants to plants was regulated by using bamboo (~5 mm. diam.) bridges.

2.2. Experimental design

The experiment was conducted in the climate chamber (see subsection 2.1). There were four different diet treatments: each of the three aphid species alone or a mixed diet of all the three aphid species (30 replicates per treatment). To evaluate larval performance in terms of development and survival, newly hatched predator larvae (±12 h old) were randomly allocated to the four diet treatments. The larvae were individually placed in plastic petri dishes (5.5 cm in diameter and 1.5 cm in depth) with moist filter paper in the bottom, and were fed with sufficient numbers of third and fourth nymphal instars until the larvae either pupated or died. In the mixed diet treatment, an equal number of individuals of each aphid species were offered to each larva. The larvae were checked daily and their survival, and any changes in the developmental stage (moults or pupation), were noted. At the time of checking, food remains were removed and new live aphids were added to the petri dishes. While the number of aphids eaten was not counted, we noted if in the mixed treatment the predators consumed aphids of all species, i.e. whether there was approximately the same number of each aphid species left. The pupal stage of *C. septempunctata* was considered to begin when the larva fixed its abdomen to the petri dish. The pupal duration time for *C. carnea* was measured from the day when a larva started to spin a cocoon until the day when the adult emerged. Adults were weighed (fresh weight) and dried in an oven at 60 °C for 48 h to determine the dry body weight.

From the raw data, the following variables were derived: larval survival for each larval instar, total survival, i.e. survival from birth to adulthood, pupal survival, developmental time for each larval instar, total larval developmental time, pupal duration time, total developmental time (from egg hatch to adult emergence) and percentage reaching the pupal stage $\left(\frac{\text{total no. pupae}}{\text{total no. first larval stage}} \times 100\right)$.

2.3. Statistics

The results are presented as mean ± standard error. To analyse developmental time for each larval instar, total larval developmental time, pupal duration time and total developmental time, survival analysis (Kaplan–Meier) was employed. For pairwise comparison between different diet treatments a separate analysis was performed for each dependent variable using the *log-rank* test (a test for the equality of survival distributions which all time points are weighted equally). A χ^2-test was used to see if there were significant differences between the numbers of individuals that successfully completed a particular larval instar. Fresh and dry weight of adults were analyzed using Generalized Linear Models. Where necessary, data was transformed as $\log_{10}(x + 1)$. As the larvae of predators which fed on *U. tanaceti* all died, this treatment was excluded for the analysis of adult fresh and dry weight. All analyses were conducted using SPSS version 19 (SPSS Inc, 2010).

3. Results

3.1. *Chrysoperla carnea*

The lacewing larvae readily consumed all aphid species, also in the mixed diet. Diet had considerable effects on the development and survival of *C. carnea* larvae. Larvae that fed on *U. tanaceti* did not survive until the end of third larval instar, so that overall survival was zero (Table 1). For the first instar, diet did not affect larval survival (Table 1), but for the second and third instar survival in the *U. tanaceti* treatment was significantly lower than in the other treatments (Table 1). In the other three diet treatments, there was no pupal mortality for those individuals who reached the pupal stage. The total survival was highest for the larvae that fed on *M. fuscoviride*, followed by *M. tanacetaria* and then the mixed aphid treatments (Table 1).

Larvae that fed on *U. tanaceti* took a very long time, about 19 days, to complete the first and second larval instar. Total developmental time was shortest for larvae fed on *M. fuscoviride*, followed by the mixed aphid treatment and then *M. tanacetaria* (Table 1).

Adult fresh weight was highest when larvae were offered a mixed diet; however, it was statistically the same as the *M. tanacetaria* treatment (Table 1). Adult fresh weight of individuals that fed on *M. fuscoviride* was lowest (Table 1). Adult dry weight was highest in the mixed diet (Table 1).

3.2. *Coccinella septempunctata*

The ladybird larvae also consumed all aphid species. In the mixed diet, the predators had eaten from all the three aphid species as evidenced by the low number of remaining aphids of each species at the daily checks. All individuals that fed on *M. tanacetaria*, *M. fuscoviride* and the mixed diet survived until they reached the pupal stage (Table 1). There was also no pupal mortality for those reaching the pupal stage.

Larvae that fed on *U. tanaceti* had long developmental times (approximately twice the other treatments) and none of them successfully completed the third larval instar. Pupal duration time was shortest in the *M. tanacetaria* diet, intermediate in the *M. fuscoviride* diet and longest in the mixed diet (Table 1).

Total larval developmental time did not differ among individuals that fed on *M. tanacetaria*, *M. fuscoviride* or the mixed aphid diet (Table 1). Total developmental time was the shortest for the *M. tanacetaria* diet, intermediate for the *M. fuscoviride* diet, and longest for the mixed diet (Table 1).

Larvae offered *M. tanacetaria* developed into heavier adults (both fresh and dry weight) than larvae offered other diets (Table 1). The lightest adult fresh and dry weight resulted from the mixed diet (Table 1).

4. Discussion

The results of this study showed that the three tansy aphid species differ in their effects on the survival and development of their predators. For both predator species, *U. tanaceti* was an unsuitable prey since the larvae that fed only on this species did not survive beyond the third instar. The reasons for this could be that *U. tanaceti* has not adequate nutrition content for development of the predators or that it contains substances that act as toxins or chemical defenses against predators. *Uroleucon tanaceti* has a bright red colour that can thus be considered aposematic. In the other single-aphid diet treatments, i.e. *M. tanacetaria* and *M. fuscoviride*, the predators could complete their development and at least some individuals emerged successfully as an adult.

The best prey for *C. carnea* in terms of shortest developmental time and highest survival rate was *M. fuscoviride*; however, heavier adult fresh and dry weights were achieved in the mixed diet treatment. For *C. septempunctata*, *M. tanacetaria* was the most suitable prey resulting in a faster developmental time, heavier adult fresh and dry weight. Thus, aphids varied in their suitability for the different predators as has also been previously found; for example, *Lipaphis erysimi* (Kaltenbach) was reported as a suitable prey for *C. septempunctata* (Omkar and Srivastava, 2003) while it was a less suitable prey for *C. carnea* (Liu and Chen, 2001) and *Anegleis cardoni* (Weise) (Omkar et al., 2009). Despite the differential effects on other predator fitness parameters, there were no significant differences in total larval developmental time between larvae of *C. septempunctata* fed on *M. tanacetaria* or *M. fuscoviride*, which this is consistent with the results of Kalushkov and Hodek (2004). They found no effect of 13 suitable aphid species on larval developmental time of *C. septempunctata*, but effects on other fitness parameters.

The mixed diet was worse than the best single-aphid diet for both predators in several fitness parameters. Thus, the predators did not obtain their highest fitness in a mixed diet. The lack of a mixing advantage may indicate a lack of nutritional complementary in relation to the requirements of the predators (Hauge et al., 2011). The lack of mixing benefit was also shown by Nielsen et al. (2002) when the mixed diet of two essential high quality aphid species, *M. dirhodum* and *S. avenae*, gained no advantage for larvae of *C. septempunctata*. Possibly a mixed diet of *M. tanacetaria* and *M. fuscoviride* may result in an even higher fitness but this remains to be tested. On the other hand, the lowered fitness in the mixed diet may be due to interference of ingested *U. tanaceti* with the utilization of the other two higher quality aphid species. However, the presence of the two high-quality aphids apparently alleviated the strongly negative effects of feeding solely on *U. tanaceti*, in accordance with the toxin dilution hypothesis (Behmer et al., 2002). Hauge et al. (1998) showed that the presence of a low quality aphid, *R. padi*, diminished the performance of *C. septempunctata*. In this and our study, the predators apparently were not able to avoid feeding on a low quality or toxic aphid species (Liu and Chen, 2001; Nielsen et al., 2002; Omkar and Srivastava, 2003). Hodek (1956), Blackman (1967) and Nedved and Salvucci (2008) also argued that *C. septempunctata* cannot distinguish and avoid unsuitable or toxic prey. It has been generally accepted that not all prey consumed is suitable food for predators. Food enabling development with high survival and oviposition is generally termed "essential prey" while food that is acceptable but less suitable and serves just for survival is termed "alternative prey" (Hodek and Honek, 1996). However, there may be different levels of suitability of essential prey (Hodek and Honek, 1996). For example, Liu and Chen (2001) reported that *Aphis gossypii* Glover and *Myzus persicae* (Sulzer) were more suitable for *C. carnea* while *L. erysimi* caused higher larval mortality and longer developmental time. Similarly, Omkar and Srivastava, (2003) found significant differences in the development and reproductive success of *C. septempunctata* larvae feeding on six different aphid species. Based on the results of our laboratory experiments and the distinction made by Hodek and Honek (1996), we can state that *M. tanacetaria* and *M. fuscoviride* are essential foods.

Both predators can be observed feeding on tansy aphids in the field. Our study shows that development and fitness of important aphid predators is increased when, in addition to the unsuitable *U. tanaceti*, one of the other aphid species is present on a tansy plant, while the presence of *U. tanaceti* itself decreases the fitness gain possible in a situation when only one of the two essential (*sensu* Hodek and Honek, 1996) aphids are on the plant. Due to the high turn-over of aphids on plants, such metacommunity dynamics are likely to have strong effects on predator development

Table 1
Survival (%), developmental time (day) and adult fresh and dry weight (mg) (mean ± se) of *Chrysoperla carnea* and *Coccinella septempunctata* fed on different aphid diets. MA: *Macrosiphoniella tanacetaria*, ME: *Metopeurum fuscoviride*, UR: *Uroleucon tanaceti*, MIX: Mixed diet. Within columns, the different letters indicate significant difference between treatments ($P < 0.05$).

	Diet	Survival [%][a]					Developmental time [days][b]							Adult fresh weight (mg)[c]	Adult dry weight (mg)[c]
		Larval				Total	Larval					Pupal	Total		
		1st	2nd	3rd	4th		1st	2nd	3rd	4th	Total				
Chrysoperla carnea	MA	93.3^{a}	92.9^{a}	100^{a}		86.7^{a}	3.7 ± 0.1^{a}	4.9 ± 0.2^{a}	6.7 ± 0.3^{a}		15.3 ± 0.5^{a}	12.9 ± 0.1^{a}	28.2 ± 0.5^{a}	6.94 ± 0.18^{a}	1.66 ± 0.04^{a}
	ME	96.7^{a}	96.6^{a}	100^{a}		93.3^{a}	3.6 ± 0.1^{a}	3.7 ± 0.1^{b}	5.1 ± 0.1^{b}		12.9 ± 0.2^{b}	11.7 ± 0.2^{b}	24.1 ± 0.2^{b}	6.44 ± 0.13^{b}	1.70 ± 0.04^{a}
	UR	93.3^{a}	32.1^{b}	0^{b}		0^{b}	4.6 ± 0.1^{b}	15.1 ± 0.1^{c}							
	MIX	93.3^{a}	89.3^{a}	100^{a}		83.3^{a}	3.7 ± 0.1^{a}	4.3 ± 0.1^{d}	5.6 ± 0.2^{c}		13.48 ± 0.3^{c}	12.2 ± 0.1^{b}	25.7 ± 0.3^{c}	7.09 ± 0.14^{a}	1.88 ± 0.03^{b}
	χ^2	0.46	45.62	88.00		77.76	37.87	102.17	52.48		101.09	29.07	54.56	12.89	22.68
	df	3	3	3		3	3	3	3		3	2	2	2	2
	P	0.93	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001		<0.001	<0.001	<0.001	<0.01	<0.001
Coccinella septempunctata	MA	100^{a}	100^{a}	100^{a}	100^{a}	100^{a}	2.1 ± 0.1^{a}	2.3 ± 0.1^{a}	2.2 ± 0.1^{a}	5.0 ± 0.0^{a}	11.6 ± 0.1^{a}	5.1 ± 0.1^{a}	16.7 ± 0.1^{a}	33.04 ± 0.76^{a}	7.38 ± 0.17^{a}
	ME	100^{a}	100^{a}	100^{a}	100^{a}	100^{a}	2.0 ± 0.0^{a}	2.1 ± 0.1^{ac}	2.6 ± 0.1^{b}	5.0 ± 0.0^{a}	11.7 ± 0.1^{a}	5.6 ± 0.1^{b}	17.3 ± 0.1^{b}	31.90 ± 0.58^{a}	6.80 ± 0.13^{b}
	UR	90.0^{b}	44.4^{b}	0^{b}		0^{b}	4.1 ± 0.1^{b}	4.9 ± 0.3^{b}							
	MIX	100^{a}	100^{a}	100^{a}	100^{a}	100^{a}	2.5 ± 0.1^{c}	1.9 ± 0.1^{c}	2.6 ± 0.1^{b}	4.6 ± 0.1^{b}	11.6 ± 0.1^{a}	6.6 ± 0.1^{c}	18.2 ± 0.2^{c}	29.60 ± 0.66^{b}	6.28 ± 0.17^{c}
	χ^2	9.23	57.35	102.00		120.00	109.36	88.47	61.04	27.07	0.46	58.75	41.23	13.21	22.25
	df	3	3	3		3	3	3	3	2	2	2	2	2	2
	P	0.026	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001	<0.001	0.794	<0.001	<0.001	0.001	<0.001

[a] Percentage of individuals that survived from the beginning to the end of each larval stage or from egg hatch until moulting into pupal stage; χ^2-test to compare the numbers of individuals that survived until the next stage.

[b] Developmental time for each larval stage, total larval developmental time, pupal duration time and total developmental time (from egg hatch to adult), survival analysis (Kaplan–Meier), pairwise comparison between diet treatments was performed using the log-rank test.

[c] Generalized linear model.

and fitness, at least early in predator development when larvae are not so mobile to exploit other plants. Field studies on predator behavior would further elucidate how predators respond to changes of aphid availability under natural conditions.

Acknowledgments

We would like to thank Sylvia Creutzburg for her help and S. Zytynska for comments on the manuscript. MM is thankful to the Iranian Ministry of Science, Research and Technology for financial support. WWW was supported by the DFG (WE 3081/2-3).

References

Behmer, S.T., Simpson, S.J., Raubenheimer, D., 2002. Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. Ecology 83, 2489–2501.

Bernays, E.A., Bright, K.L., Gonzalez, N., Angel, J., 1994. Dietary mixing in a generalist herbivore-tests of 2 hypotheses. Ecology 75, 1997–2006.

Blackman, R.L., 1967. Effects of different aphid foods on *Adalia bipunctata* L and *Coccinella 7-punctata* L. Annals of Applied Biology 59, 207–219.

Blackman, R.L., Eastop, V.F., 2006. Aphids on the World's Herbaceous Plants and Shrubs. John Wiley & Sons, London, UK.

Borg, C., Toft, S., 2000. Importance of insect prey quality for grey partridge chicks *Perdix perdix*: a self-selection experiment. Journal of Applied Ecology 37, 557–563.

Canard, M., 1970. The bearing of the nutritive value of various aphids (Homoptera, Aphididae) on the potential rate of increase of *Chrysopa perla* (L.) (Neuroptera, Chrysopidae). Annales de Zoologie Ecologie Animale 3, 345–355.

Canard, M., Principi, M.M., 1984. Life histories and behavior. In: Canard, M., Semeria, Y., New, T.R. (Eds.), Biology of Chrysopidae. Junk Publishers, The Hague, Dr W, pp. 57–149.

Dixon, A.F.G., Agarwala, B.K., 1999. Ladybird-induced life-history changes in aphids. Proceedings of the Royal Society of London Series B-Biological Sciences 266, 1549–1553.

Evans, E.W., Stevenson, A.T., Richards, D.R., 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. Oecologia 121, 107–112.

Gruppe, A., Roemer, P., 1988. The lupin aphid (*Macrosiphum albifrons* Essig, 1911) (Hom, Aphididae) in West-Germany: its occurrence, host plants and natural enemies. Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie 106, 135–143.

Hauge, M.S., Nielsen, F.H., Toft, S., 1998. The influence of three cereal aphid species and mixed diet on larval survival, development and adult weight of *Coccinella septempunctata*. Entomologia Experimentalis Et Applicata 89, 319–322.

Hauge, M.S., Nielsen, F.H., Toft, S., 2011. Weak responses to dietary enrichment in a specialized aphid predator. Physiological Entomology 36, 360–367.

Hodek, I., 1956. The influence of *Aphis sambuci* L. as prey of the ladybird beetle *Coccinella septempunctata* L.. Acta Societatis Zoologicae Bohemoslovacae 20, 62–74, In Czech, English abstract.

Hodek, I., Honek, A., 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht.

Holman, J., 2009. Host Plant Catalogue of Aphids: Palaearctic Region. Springer, Berlin.

Kalushkov, P., Hodek, I., 2004. The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. Biocontrol 49, 21–32.

Khuhro, N.H., Chen, H.Y., Zhang, Y., Zhang, L.S., Wang, M.Q., 2012. Effect of different prey species on the life history parameters of *Chrysoperla sinica* (Neuroptera: Chrysopidae). European Journal of Entomology 109, 175–180.

Liu, T.X., Chen, T.Y., 2001. Effects of three aphid species (Homoptera: Aphididae) on development, survival and predation of *Chrysoperla carnea* (Neuroptera: Chrysopidae). Applied Entomology and Zoology 36, 361–366.

Nedved, O., Salvucci, S., 2008. Ladybird *Coccinella septempunctata* (Coleoptera: Coccinellidae) prefers toxic prey in laboratory choice experiment. European Journal of Entomology 105, 431–436.

Nielsen, F.H., Hauge, M.S., Toft, S., 2002. The influence of mixed aphid diets on larval performance of *Coccinella septempunctata* (Col., Coccinellidae). Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie 126, 194–197.

Omkar, Kumar, G., Sahu, J., 2009. Performance of a predatory ladybird beetle, *Anegleis cardoni* (Coleoptera: Coccinellidae) on three aphid species. European Journal of Entomology 106, 565–572.

Omkar, Srivastava, S., 2003. Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. Biocontrol 48, 379–393.

Pappas, M.L., Broufas, G.D., Koveos, D.S., 2007. Effects of various prey species on development, survival and reproduction of the predatory lacewing *Dichochrysa prasina* (Neuroptera: Chrysopidae). Biological Control 43, 163–170.

Phoofolo, M.W., Giles, K.L., Elliott, N.C., 2007. Quantitative evaluation of suitability of the greenbug, *Schizaphis graminum*, and the bird cherry-oat aphid, *Rhopalosiphum padi*, as prey for *Hippodamia convergens* (Coleoptera: Coccinellidae). Biological Control 41, 25–32.

Toft, S., Wise, D.H., 1999. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. Oecologia 119, 191–197.

Unsicker, S.B., Oswald, A., Koehler, G., Weisser, W.W., 2008. Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. Oecologia 156, 313–324.

Waldbauer, G.P., Friedman, S., 1991. Self-selection of optimal diets by insects. Annual Review of Entomology 36, 43–63.

Wallin, H., Chiverton, P.A., Ekbom, B.S., Borg, A., 1992. Diet, fecundity and egg size in some polyphagous predatory carabid beetles. Entomologia Experimentalis Et Applicata 65, 129–140.

Zhang, S.-Z., Li, J.-J., Shan, H.-W., Zhang, F., Liu, T.-X., 2012. Influence of five aphid species on development and reproduction of *Propylaea japonica* (Coleoptera: Coccinellidae). Biological Control 62, 135–139.

ELSEVIER LICENSE TERMS AND CONDITIONS

Jun 09, 2013

This is a License Agreement between Mohsen Mehrparvar ("You") and Elsevier ("Elsevier") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by Elsevier, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

Supplier	Elsevier Limited The Boulevard,Langford Lane Kidlington,Oxford,OX5 1GB,UK
Registered Company Number	1982084
Customer name	Mohsen Mehrparvar
Customer address	Lehrstuhl für Terrestrische Ökologie Freising, 85354
License number	3164901466727
License date	Jun 09, 2013
Licensed content publisher	Elsevier
Licensed content publication	Biological Control
Licensed content title	Diet-mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing?
Licensed content author	Mohsen Mehrparvar,Nafiseh Mahdavi Arab,Wolfgang W. Weisser
Licensed content date	April 2013
Licensed content volume number	65
Licensed content issue number	1
Number of pages	5
Start Page	142
End Page	146
Type of Use	reuse in a manner not listed here
Requestor type	author of new work

Special requirements	This article is a part of my PhD study and I need to include that as a chapter in my thesis. My thesis, based on the rules of my university, will be published online with open access. So, I am writing to get specifically the permission for this issue.
Are you the author of this Elsevier article?	Yes
Order reference number	
Elsevier VAT number	GB 494 6272 12
Permissions price	0.00 EUR
VAT/Local Sales Tax	0.00 EUR
Total	0.00 EUR

CHAPTER VI

6- Manuscript V

Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae)

Adalbert Balog*†, Mohsen Mehrparvar*‡, Wolfgang W. Weisser*‡

***** Institute of Ecology, Friedrich–Schiller University, Dornburger Str. 159, Jena, Germany

† Department of Horticulture, Sapientia University, Sighisoara str. 1C. Tirgu–Mures, Romania

‡ Present address: Department of Ecology and Ecosystem Management, Terrestrial Ecology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

Published in ***European Journal of Entomology***

110(1): 153-157

Eur. J. Entomol. **110**(1): 153–157, 2013
http://www.eje.cz/pdfs/110/1/153
ISSN 1210-5759 (print), 1802-8829 (online)

Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae)

ADALBERT BALOG*, MOHSEN MEHRPARVAR** and WOLFGANG W. WEISSER**

Institute of Ecology, Friedrich-Schiller University, Dornburger Str. 159, Jena, Germany

Key words. Staphylinidae, *Drusilla canaliculata*, *Tachyporus hypnorum*, Aphididae, *Acyrthosiphon pisum*, aphid polyphenism, predator-prey interaction, rove beetles, maternal effects, induced defence

Abstract. A number of aphid species have been shown to produce winged dispersal morphs in the presence of natural enemies. Previous studies tested specialized aphid predators such as ladybirds or lacewing larvae. We confronted colonies of pea aphids with the polyphagous rove beetles, *Drusilla canaliculata* and *Tachyporus hypnorum*. For both predators we found that the percentage of winged morphs increased in predator-attacked pea aphid colonies compared to a control. The behaviour of the two rove beetles species was noticeably different. *D. canaliculata* mostly foraged on the ground and rarely on the plant, while *T. hypnorum* was almost exclusively observed on the plants, causing a higher number of aphids to drop to the ground, which resulted in a stronger increase in winged morph production. Our results clearly show that not only monophagous aphid predators but also more polyphagous insect predators, which include aphids in their diet, can induce aphids to produce winged morphs.

INTRODUCTION

Polyphenism is a general phenomenon in aphid species (Kawada, 1987; Dixon, 1998) and appears to be a case of phenotypic plasticity; environmental conditions are often perceived by the mother and result in maternal effects on the offspring (Dixon, 1998; Kunert & Weisser, 2003; Müller et al., 2001; Whitman & Agraval, 2009). Winged dispersal morphs (alate virginoparae) are reported to be produced in response to crowding and a declining host plant quality, in many aphid species (Kawada, 1987; Dixon, 1998). More recently, it has been shown that the presence of natural enemies also induces the production of winged offspring, e.g. in the pea aphid, *Acyrthosiphon pisum* (Harris) (Dixon & Agarwala, 1999; Weisser et al., 1999; Sloggett & Weisser, 2002; Kunert & Weisser, 2003) and the cotton-melon aphid, *Aphis gossypii* Glover (Mondor et al., 2005), but not in the black bean aphid, *Aphis fabae* (Scopoli) and the Vetch aphid, *Megoura viciae* Buckton (Kunert et al., 2008; Dixon & Agarwala, 1999). At least in the pea aphid, wing induction caused by natural enemies seems to be a general phenomenon since they react to important enemies such as ladybirds (adults and larvae), lacewing larvae, hoverfly larvae and hymenopterous parasitoids (Weisser et al., 1999; Sloggett & Weisser, 2002; Kunert & Weisser, 2003). All these predators, however, are specific aphid predators. In contrast, the effect of polyphagous predators that consume a range of prey (including aphids) on aphid wing polyphenism has not yet been investigated.

One group of polyphagous predators that is involved in aphid control, but has generally received little attention, are rove beetles (Coleoptera: Staphylinidae). Bryan & Wratten (1984) demonstrated that several species of rove beetles aggregate in patches of aphids and show a numerical response to increasing aphid densities. Under laboratory conditions, aphid predation accounted for more than 34% of rove beetle body weight (Bryan & Wratten, 1984). Many rove beetles are omnivorous and include both arthropods and other organisms, in particular fungi, in their diet. Sunderland et al. (1987) found aphids, 61 non-aphid arthropods, rust and non-rust fungi in the gut of *Tachyporus* spp. Other species of polyphagous rove beetles do not feed on fungi, e.g. *Drusilla canaliculata* and *Philonthus* spp., but on a wide range of arthropod prey, including aphids at an average rate of 20 /day (Good & Giller, 1991). Overall, rove beetles are significant predators of aphids and pose a mortality risk to aphid colonies.

In the present study, we exposed pea aphid colonies to individuals of both the arthropod and fungus feeding *Tachyporous hypnorum* (F.) and arthropod-feeding *Drusilla canaliculata* (F.) to ask the following questions: (1) does exposure to these predators result in a significant reduction in the growth of aphid colonies?; (2) do aphids respond to the presence of the predator by increasing the number of winged morphs among their offspring?; and (3) are there differences among the rove beetles species in their effect on aphid population growth and wing formation?

---

* Present and corresponding address: Department of Horticulture, Sapientia University, Sighisoara str. 1C, Tirgu-Mures, Romania; e-mail: adalbert.balog@gmail.com

** Present address: Department of Ecology and Ecosystem Management, Terrestrial Ecology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; e-mails: mehrparvar@aphidology.com, wolfgang.weisser@tum.de

TABLE 1. The average percentage of adult aphids that survived and average numbers of offspring present at the end of the first and second-three day periods (Wilcoxon Signed Ranks Test).

Percentage of adults surviving at the end of the first three-day period			Percentage of adults surviving at the end of the second three-day period	
D. canaliculata	Control	*T. hypnorum*	*D. canaliculata*	Control
56.4 ± 0.6%	77.6 ± 0.7%	58.6 ± 0.8%	54.6 ± 0.7%	74.3 ± 0.8%
$Z = -1.93$ $p < 0.05$		$Z = -0.98$ $p = 0.32$	$Z = -0.72$ $p = 0.46$	
Number of offspring at the end of the first three-day period			Number of offspring at the end of the second three-day period	
237.1 ± 10.82	275.0 ± 12.35	253.1 ± 18.71	124.4 ± 13.07	204.0 ± 12.29
$Z = -1.95$ $p < 0.05$		$Z = -0.29$ $p = 0.76$	$Z = -2.37$ $p = 0.01$	

MATERIAL AND METHODS

Experimental insects and plants

For the experiments, we used adults of two predatory species of rove beetles – *D. canaliculata* (F.) and *T. hypnorum,* and the red BP strain of the pea aphid *A. pisum* (Kunert et al., 2005). Rove beetles were collected in meadows in Jena, Germany, using dry pitfall traps, one week before the experiment started, and were kept in plastic tubes with sand in the bottom that was regularly watered to maintain high humidity, at 20°C. Beetles were fed ad libitum with mixed diets of *Aphis fabae*, *A. pisum*, fly larvae and fungus. Aphids were maintained on three week old plants of *Vicia faba* (variety "The Sutton", Nickerson-Zwaan, UK) in a walk-in climate chamber (Thermotec Germany) under long-day conditions (16L : 8D) at 20°C and about 75% relative humidity. Eighty five plants were covered with air-permeable cellophane bags. This transparent cover permitted the visual assessment of both the aphids and predators on the plants and ground without disturbing them.

Experimental design

To minimize maternal effects, a "split-brood-design" was used (Kunert et al., 2008). Thirty aphid lineages (n = 30) were established, each starting with a single adult asexual individual placed on a bean plant where it was allowed to reproduce for three days. The adult aphid was then removed. The offspring were reared until they reached the last (fourth) nymphal instar or the adult stage when they were transferred to new plants in groups of seven, where they reproduced for another three days and then removed from the plant. The second-generation offspring were reared until they reached the adult stage-after which they were used in the experiment. From each line, ten individuals were placed on each of three plants (ten adult aphids / plant with altogether 300 adult aphids on 30 plants). One of these plants served as a control (no predator), a second had a single adult of *D. canaliculata* placed on it and a third a single adult of *T. hypnorum*. By using individual aphids from one line in all the treatments, any confusion due to previous rearing conditions and treatment effects was avoided.

Aphids and predators were left on the plants for three days (first three-day period) after which the surviving adult aphids were counted and transferred to new plants. In the predator treatment, the beetles were also removed and new individuals placed on the new plants (one per plant). All aphid offspring remained on the plants where they were born until they reached the adult stage whereupon they were frozen for later counting and determination of the phenotype. The adult aphids and predators on the new plants remained for a further three days, representing the second three-day period. After this period, all adult aphids were removed from the plant and counted. Predators were also removed. The aphid offspring were again reared until adulthood and then frozen. Whilst there were 30 aphid lineages, only ten individuals of *T. hypnorum* were available initially. Thus, there were ten lines for all three treatments and another 20 lines for the control and *D. canaliculata* treatment. Because of the limited number of *T. hypnorum*, the experiment with this predator was only performed for one experimental period. Plants were inspected once every day during the experiment and the predators' position (on the plant or on the ground) and the number of aphids on the ground recorded. After the end of the experiment, the aphid offspring produced in both experimental periods were counted and examined for the presence of wings.

Statistical analysis

We compared the numbers of surviving adult aphids, numbers of offspring produced, the percentage of winged morphs among the offspring, and the percentage of aphids and predators on the ground in the predator treatments and control using a Wilcoxon Signed Ranks Test. This test takes into account the split-brood design. SPSS version 16.0 was used for this analysis. Predator activity on plant or ground was calculated by using the proportion of time they were observed on the ground (0, 0.33, 0.66, 1), and the means averaged over replicates. Because of the few replicates for *T. hypnorum*, the effects of this predator on aphids were analysed only after the first three-day period of assessment.

RESULTS

Aphid survival and reproduction

In the *D. canaliculata* treatment, the percentage of the initial number of adults transferred at the three-day period was lower than in the control. The average number of offspring produced during the first three-day period in the *D. canaliculata* treatment was significantly lower than in the control (Table 1). After six days, the percentage of adults remaining (from the initial number at the start of the experiment), did not differ between the *D. canaliculata* treatment and the control. The number of offspring produced in the second three-day period was lower in the *D. canaliculata* treatment than in the control (Table 1).

In the presence of *T. hypnorum,* adult aphid survival over the first three-day period was lower compared to the control but despite this trend, the apparent difference was not statistically significant. There was also no difference in the mean number of offspring counted after three days (Table 1).

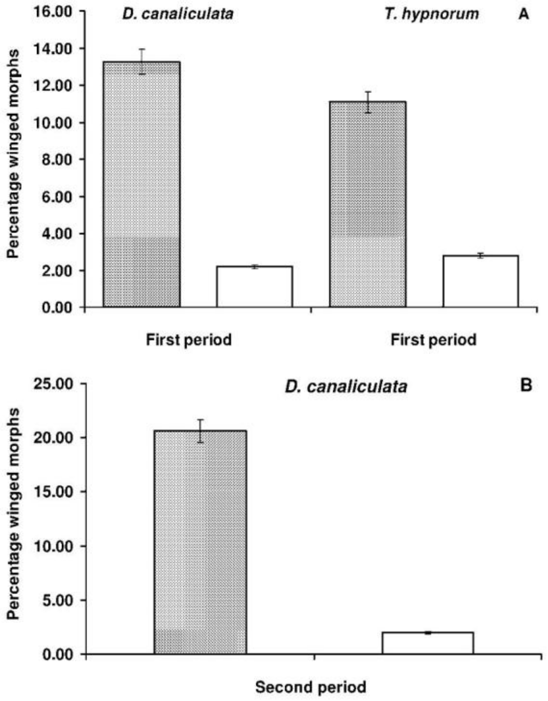


Fig 1. Percentage of winged morphs among offspring in the first (A) and second (B) three-day period in the experiment with the rove beetles *Drusilla canaliculata* (n = 30 lines) and *Tachyporus hypnorum* (n = 10 lines and first three-day period only). Full bars – predator treatment, open bars – control. Error bars refer to standard errors.

Occurrence of winged morphs

During both experimental periods, the percentage of winged offspring was higher in the *D. canaliculata* treatment than in the control (first three-day period 13.5 ± 0.69%, $Z = -4.38$, $p = 0.001$, $n = 30$, second three-day period 20.61 ± 2.26%, $Z = -4.37$, $p = 0.001$, $n = 30$, Fig. 1A, B). For the *T. hypnorum* treatment, despite the low number of replicates, the percentage of winged individuals was also higher than in the control (11 ± 1.48%, $Z = -2.02$, $p = 0.01$, $n = 10$; Fig. 1A).

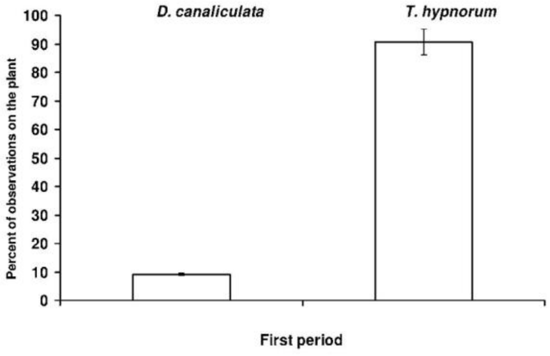


Fig 2. Percentage of *Drusilla canaliculata* and *Tachyporus hypnorum* on plants during the daily observations (average for three days). Error bars refer to standard errors.

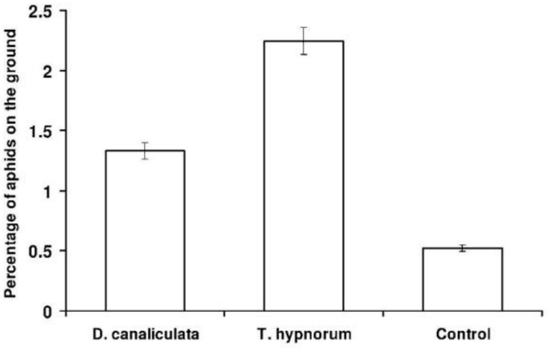


Fig 3. Percentage of aphids recorded on the ground (average for three days) in the *Drusilla canaliculata* and *Tachyporus hypnorum* treatments and the control. Error bar refers to standard errors.

Predator behaviour

The behaviour of the two predator species was noticeably different. In the three observations in the first three-day period, *D. canaliculata* spent less than 10% of the time on the plant (Fig. 2). Few aphids were observed on the ground during the daily checks (1.33 ± 0.31%). This, together with the short time spent on plants, shows that *D. canaliculata* mainly preys on aphids on the ground. In contrast, *T. hypnorum* was almost exclusively seen on the plants, either searching or feeding on aphids (Fig. 2), and the percentage of aphids that dropped from the plant on to the ground was higher (2.24 ± 0.53%) than in replicates with *D. canaliculata* (Fig. 3, $Z = -2.37$, $p = 0.01$, $n = 10$ lines with both predator treatments). The percentage of aphids on the ground in the control was very low (0.52 ± 0.09%) and much lower than in the predator treatments (comparison to *D. canaliculata* $Z = -1.97$, $p < 0.05$, $n = 30$, to *T. hypnorum* $Z = -2.19$, $p < 0.05$, $n = 10$, Fig. 3).

DISCUSSION

The results clearly demonstrate that the presence of rove beetles induces pea aphids to produce winged morphs. This is similar to other studies where predators have been found to increase wing induction in this aphid species (Kunert & Weisser, 2003). This trait modification increases the ability of aphids to disperse and to colonize new habitats, and hence has a bearing on the population dynamics of the prey, and one assumes, indirectly on the evolution of the aphids (Loxdale, 2010). Recent modelling has indeed suggested that such predator-induced dispersal can be adaptive if there is high mortality due to predation and a high correlation of the predation risk between two aphid generations (Poethke et al., 2010).

Despite the differences in feeding modes, both *D. canaliculata* and *T. hyphorum* significantly increased the number of winged morphs in the predator treatments; however, there was a difference in the percentages of winged morphs induced by the two predator species. *D.*

*canaliculat*a is frequently found in agricultural fields and is considered to be a polyphagous predator with a preference for ant larvae (Andersen, 1991, 2000). All the predators survived and caused a significant decrease in the percentage survival of adult aphids in the first three-day period but not in the second, which indicates the predator mainly fed on offspring in this period. The number of offspring left on the plant at the end of the period was lower in the predator treatment in both three-day periods. This lower number of offspring is most likely the result of some predation of offspring by the beetle as well as the reduced fecundity of the aphids due to the production of winged morphs, as observed in several aphid species (Dixon, 1998). Nevertheless, even though the percentage of adult aphids surviving until the end of the experiment was the same in the predator treatment and the control, differences in offspring production and the percentages of winged offspring were highly significant.

The rove beetle *T. hypnorum* has also been reported as a potentially important aphid control agent in cereal fields (Kennedy et al., 1986). Apart from preying on insects, *T. hypnorum* is also a fungivore with a preference for mildew (Dennis et al., 1991). The females of *T. hypnorum* especially are unlikely to feed exclusively on aphids for long periods. Although field experiments have indicated that *T. hypnorum* may be attracted to aggregations of aphids, they may feed there on insects attracted to honeydew, on mildew growing on honeydew and on the aphids themselves (Monsrud & Toft, 1999). The absence of mildew or other fungi on our experimental plants may be the reason why only two *T. hypnorum* out of ten individuals survived until the end of the first three-day period. Of special interest is the fact that despite this high mortality and the low rate of predation, there was a clear difference in the percentage of offspring produced.

In our experiments, *T. hypnorum* spent most of the time on plants (90%), possibly also searching for fungi. As a result it caused a greater number of aphids to fall to the ground than *D. canaliculata*. This predator thus preferentially fed on the ground after brief visits to the plants. The lower percentage of aphids found below the plants in the *D. canaliculata* treatments is therefore most likely to be a result of (a) a lower rate of disturbance of aphids on the plant, resulting in fewer individuals falling from the plant; and (b), a higher rate of predation of aphids on the ground. In our experiment, there were significant numbers of aphids on the ground, showing the disturbance caused in the predator treatments compared to the control, even though adult aphid survival was not affected by the predators.

Importantly, the low rate of predation on adult aphids by both *T. hypnorum* and *D. canaliculata* give support to the hypothesis of "pseudo-crowding" put forward by Sloggett & Weisser (2002), whereby aphid wing induction through natural enemies is mediated by the disturbance caused by predators in the aphid colony, leading to an increasing number of contacts among aphid individuals. These contacts have been shown to be responsible for wing induction also at high aphid densities (Sutherland, 1969). In predators that cause significant mortality of aphids, such as the seven-spot ladybird, a high fraction of unwinged individuals escape from this predator by falling to the ground below the plant (Minoretti & Weisser, 2000). Importantly, however, not all the insects that walk on plants disturb aphid colonies sufficiently to induce wing induction (Sloggett & Weisser, 2002).

In conclusion, in the present study we have shown that polyphagous rove beetles can affect wing polymorphism in the pea aphid despite only causing a moderate level of aphid mortality. Both predators differed in their feeding mode and site of activity, but the disturbance they caused in aphid colonies was sufficient to induce the same response in the aphid as monophagous aphid predators.

ACKNOWLEDGEMENTS. AB was supported by grant MTKD-CT-2005-029983 of the European Union Marie Curie Transfer of Knowledge fellowship, MM by grant of the Ministry of Science, Research and Technology of Iran, and WWW thanks the DFG for financial support (WE 3081/2-3). We thank S. Toft for valuable advice and providing *Tachyporus* individuals and S. Creutzburg for help with the experiments.

REFERENCES

ANDERSEN A. 1991: Carabidae and Staphylinidae (Col.) frequently found in Norwegian agricultural fields. New data and review. — *Fauna Norvergica (B)* **38**: 65–76.

ANDERSEN A. 2000: Long term developments in the Carabid and Staphylinid (Col., Carabidae and Staphylinidae) fauna during the conversion from conventional to biological farming. — *J. Appl. Entomol.* **124**: 51–56.

BRYAN K. & WRATTEN S.D. 1984: The responses of polyphagous predators to prey spatial heterogenity: aggregation by carabid and staphylinid beetles to their cereal aphid prey. — *Ecol. Entomol.* **9**: 251–259.

DENIS P., WRATTEN S.D. & SOTHERTON N.W. 1991: Mycophagy as a factor limiting predation of aphids (Hemiptera: Aphididae) by staphylinid beetles (Coleoptera: Staphylinidae) in cereals. — *Bull. Entomol. Res.* **81**: 25–31.

DIXON A.F.G. 1998: *Aphid Ecology*. Chapman & Hall, London, 300 pp.

DIXON A.F.G. & AGARWALA B.K. 1999: Ladybird-induced life-history changes in aphids. — *Proc. R. Soc. Lond. (B)* **266**: 1549–1553.

GOOD J.A. & GILLER P.S. 1991: The diet of predatory Staphylinid beetles – a review of records. — *Entomol. Mag.* **127**: 77–89.

KAWADA K. 1987: Polymorphism and morph determination. In Minks A.K. & Harrewijn P. (eds): *Aphids, Their Biology, Natural Enemies and Control. Vol. A.* Elsevier, Amsterdam, pp. 299–314.

KUNERT G. & WEISSER W.W. 2003: The interplay between density- and trait-mediated effects in predator-prey interactions: a case study in aphid wing polymorphism. — *Oecologia* **135**: 304–312.

KUNERT G., OTTO S., ROSE U.S.R., GERSHENZON J. & WEISSER W.W. 2005: Alarm pheromone mediates production of winged dispersal morphs in aphids. — *Ecol. Lett.* **8**: 596–603.

KUNERT G., SCHMOOCK-ORTLEPP K., REISSMANN U., CREUTZBURG S. & WEISSER W.W. 2008: The influence of natural enemies on wing induction in *Aphis fabae* and *Megoura viciae* (Hemiptera: Aphididae). — *Bull. Entomol. Res.* **98**: 57–62.

KENNEDY T.F., EVANS G.O. & FEENEY A.M. 1986: Studies on the biology of *Tachyporus hypnorum* F. (Col. Staphylinidae), associated with cereal fields in Ireland. — *Ir. J. Aagric. Res.* **25**: 81–95.

Loxdale H.D. 2010: Rapid genetic changes in natural insect populations. — *Ecol. Entomol. (Suppl. 1)* **35**: 155–164.

Minoretti N. & Weisser W.W. 2000: The impact of individual ladybirds (*Coccinella septempunctata*, Coleoptera: Coccinellidae) on aphid colonies. — *Eur. J. Entomol.* **97**: 475–479.

Mondor E.B., Rosenheim J.A. & Addicott J.F. 2005: Predator-induced transgenerational phenotypic plasticity in the cotton aphid. — *Oecologia* **142**: 104–108.

Monsrud C. & Toft S. 1999: The aggregative numerical response of polyphagous predators to aphids in cereal fields: attraction to what? — *Ann. Appl. Biol.* **134**: 265–270.

Müller C.B., Williams I.S. & Hardie J. 2001: The role of nutrition, crowding and interspecific interactions in the development of winged aphids. — *Ecol. Entomol.* **26**: 330–340.

Poethke H.J., Weisser W.W. & Hovestadt T. 2010: Predator induced dispersal and the evolution of dispersal in correlated environments. — *Am. Nat.* **175**: 577–586.

Sloggett J.J. & Weisser W.W. 2002: Parasitoids induce production of the dispersal morph in the pea aphid, *Acyrthosiphon pisum*. — *Oikos* **98**: 323–333.

Sunderland K.D., Crook N.E., Staccy D.L. & Fuller B.J. 1987: Study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. — *J. Appl. Ecol.* **24**: 907–933.

Sutherland O.R.W. 1969: The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. — *J. Insect Physiol.* **15**: 1385–1410.

Weisser W.W., Braendle C. & Minoretti N. 1999: Predator-induced morphological shift in the pea aphid. — *Proc. R. Soc. Lond. (B)* **266**: 1175–1182.

Whitman D.W. & Agrawal A. 2009: What is phenotypic plasticity and why is it important? In Whitman D.W. & Ananthakrishnan T.N. (eds): *Phenotypic Plasticity of Insects: Mechanisms and Consequences*. Science Publishers, Enfield, New Hampshire, pp. 1–63.

Received June 25, 2012; revised and accepted August 27, 2012

CHAPTER VII

7- GENERAL DISCUSSION

In this thesis, specialized tansy aphid species were used as model organisms to investigate the effects of biological interactions and environmental factors on metapopulation and metacommunity core processes that ultimately shape the metacommunity structure.

7-1- Species interactions and their effects on metacommunity processes

The current interest in the field of metacommunity ecology is mostly concerned with exploring which kinds of ecological interactions occur at different spatial scales and ascertaining the relative importance of such interactions between species and dispersal in structuring natural communities. Interestingly, in the tansy–aphid metacommunity, the different aphid species feed on the same host plant species and this characteristic allows comparisons of aphid dynamics and factors influencing local processes. From the point of view of species interactions, two types of interactions in the tansy–aphid metacommunity may be considered: *intra*guild interactions which include interactions between aphids, and *inter*guild interactions consisting of the interactions between aphids and other organisms in the metacommunity. In the following, the effects of these interactions on metacommunity processes and eventually their effects on the metacommunity structure and assembly are discussed.

7-1-1- Dispersal

Dispersal in a metacommunity is a key process which affects local community composition (Leibold, 2009). It has two main consequences in metacommunities: firstly, dispersal allows new species to colonize local communities from which they were previously absent. Secondly, differences among local communities become homogenized by the effect of dispersal (Hanski, 1999; Leibold, 2009). Interaction between these two consequences of dispersal can happen if different species have very different dispersal abilities and rates (Leibold, 2009).

Aphids are among the organisms that are capable of producing special morphs for dispersal, namely winged morphs. Winged individuals are able to fly and colonize new habitats; therefore they facilitate dispersal between habitat patches (Loxdale *et al.*, 1993). The results of this study showed that the production of winged individuals and therefore the ability of dispersal is completely different between *M. tanacetaria* and *M. fuscoviride*. Two questions therefore arise as to why these two aphid species have different winged morph production during the season and why their responses to the crowding and presence of predators are different?

At the beginning of the season, surviving overwintering tansy aphid eggs hatch and then the new asexual generations of aphids attempt to expand their populations. In order to disperse successfully, they have to produce large enough numbers of dispersal morphs; hence during the first two generations they produce only unwinged parthenogenetic morphs, which have higher reproduction potential. After this time when the host plants vegetation growth is suitable to sustain population growth, aphids produce winged morphs to expand their populations and spread to new host plant resources and occupy as many such new habitats as possible by initiating new colonies. Production of dispersal morph in *M. fuscoviride* is limited to the third to fifth generations; therefore this aphid, in comparison with *M. tanacetaria* which produces winged morphs during the entire growing season, has limited dispersal and can disperse between patches only during the early part of the season. Furthermore, *M. fuscoviride*, in contrast with *M. tanacetaria*, did not respond to the crowding and presence of predators. These differences could have an adaptive evolutionary basis.

Winged morph production and dispersal of *M. fuscoviride* is considerably affected by its mutualistic partners. In the beginning of the growing season, mutualistic ants explore the new established colonies of *M. fuscoviride* and a connection between them is established. From this time onwards, the trade–off between costs and benefits of this relationship are deterministic for the production of winged morphs in *M. fuscoviride*. Logically, *M. fuscoviride* should not produce winged individuals because if it does so, the winged individuals that leave the colony lose the benefits gained by ant attendance. In addition, ants prefer to attend bigger colonies of *M. fuscoviride* than smaller ones (Stadler & Dixon, 2005). Hence there is a competition between aphid colonies gaining benefits of attending ants, whilst at the same time there is a concomitant reduced chance for small colonies of obligatory myrmecophilous *M. fuscoviride* to be attended by such guard ants. Based on these factors, *M. fuscoviride* needs to aggregate and live in bigger colonies i.e. crowded colonies. As a result, this species appears not to be sensitive to crowding and does not respond to it by production of winged morphs. Accordingly, the results of chapter IV show that winged individuals of *M. fuscoviride* prefer to choose plants that were occupied/previously infested by their conspecifics. Another benefit that aphids gain from attendance by ants is protection against predators and also competitors (chapter III). Therefore, production of winged morphs in response to predator presence in ant–tended aphids may not be beneficial, as most of the time the ants protect the aphid and furthermore, when the winged individual aphid leaves the natal plant it loses the advantages of protection by ants. In addition to these aspects, ants can also directly regulate the production of winged individuals. It has been shown by several studies that ants inhibit the production of winged morphs among attended aphids (El-Ziady & Kennedy, 1956; El-Ziady, 1960; Kleinjan & Mittler, 1975; Seibert, 1992; Braendle *et al.*, 2006). Therefore, any selective force for increased wing production due to predation pressure will be reduced.

On the other hand, as *M. tanacetaria* is not an ant–tended aphid, so it needs to evolve some other strategies in order to escape adverse environmental conditions. This aphid is clearly adapted in terms of its sensitivity to environmental stimuli and other cues such as crowding, presence of predators and competitors in order to be able to respond to them at appropriate times by producing winged morphs. In a community the relationships between species is very important for their dispersal strategies and this could be altered by such interactions. The observed differences between dispersal urge and ability are assumed to strongly affect the population dynamics of each species and change the metacommunity structure.

The role of individual dispersing aphids is to emigrate from their natal habitat and locate a suitable new habitat for colonization and following immigration, build a new colony there. In order to flourish, a newly established colony needs to grow rapidly. In the tansy–aphid system, the winged aphids mostly produce unwinged nymphs, which have greater reproduction ability. However, there is also a small fraction of winged nymphs that could be considered as reserves for dispersal in the case of sudden changes in environmental conditions and as such, could save the colony from extinction via dispersal to new habitats.

The factors mediating dispersal probably interact and it is possible that after a while, various factors are involved in decision making in terms of whether an aphid should produce winged offspring, whether a winged aphid should depart from a patch or not, how far it will move, and eventually where it should settle (Loxdale *et al.*, 1993). Here, in the context of evolutionary ecology, it is important to understand how such multiple factors interact to shape the overall dispersal patterns in a metacommunity (Clobert *et al.*, 2004).

It would be interesting to know how far the tansy aphids disperse. However, molecular marker studies suggest not very far, perhaps less than half a kilometer in the case of *M. fuscoviride* and probably not much farther in *M. tanacetaria* (Loxdale *et al.*, 2011); but a set of experimental studies could establish, using marked (physically or molecularly) winged morphs, to explore how far individuals can disperse from the source population and how much this distance may differ during the season. It is also worth testing the effect of inter- and intraspecific competition on production of winged offspring. A modeling approach is required to analyze the long–term fitness consequences of this or alternative dispersal strategies. Understanding the role of environmental cues for wing induction in aphids in a metacommunity system will undoubtedly benefit the study of life–history evolution in spatially heterogeneous habitats.

7-1-2- Colonization

Colonization is also a very important process in metacommunities (Gaggiotti *et al.*, 2002), since a successful colonization may lead to the establishment of a population in a habitat patch. In aphids, as discussed above, colonization is normally brought about via the dispersal morphs. In the tansy–aphid metacommunity, each aphid species has its own strategies for colonization, which is related to its ecological requirements. In colonization and establishment of a new colony in a new habitat, competitive and mutualistic interactions play very important roles. The presence or absence of other aphid members (same or different species) of this metacommunity and the presence or absence of mutualistic ants have a very critical impact on the colonization of a particular species in a habitat patch. In host plant choice, winged aphids try to select plants that support their requirements and avoid competitive interactions. For example, winged individuals of *M. tanacetaria* mostly choose plants occupied/previously infested by *U. tanaceti*. This could be because *U. tanaceti* induces ramet senescence and thus such tansy genets may be of higher nutritional value. Contrastingly, *M. tanacetaria* rarely establishes its colony in the presence of *M. fuscoviride*, since tending ants could, and probably would, predate *M. tanacetaria*. *Metopeurum fuscoviride* prefers plants that have been occupied/previously infested by conspecifics which reflects the fact that this aphid prefers to aggregate and land where there is a high chance of protection by ants. This behavior by *M. fuscoviride* may also be considered to have effective impact as a rescue effect, i.e. could rescue colonies that may be going towards extinction, an important factor in terms of population persistence and metapopulation dynamics. The presence of mutualistic ants could also prohibit other aphid species from colonising the same plants when their mutualistic aphid partners are present. For example, the presence of ants that attend *M. fuscoviride* cause *U. tanaceti* to avoid landing on plants with *M. fuscoviride*. *Uroleucon tanaceti* prefers plants without other aphids, which may well mean that this species does so to avoid competitive interactions. In a metacommunity, colonization of one species may cause the extinction of another (Case, 1991). So in light of this fact, if *M. fuscoviride* colonizes a habitat patch that is already occupied by *M. tanacetaria*, it may leads to exclusion of *M. tanacetaria*, more especially if the mutualistic ants find the new established colony of *M. fuscoviride* and start to farm it. However, the probability of colonization success for *M. fuscoviride* decreases with residence number and the strength and disparity of interspecific interactions and also the presence of predators (chapters III & IV).

7-1-3- Extinction

Extinction of a population in a metacommunity can happen as a result of different drivers such as natural enemies, competitive interactions which lead to competitive exclusion, and stochastic events (Addicott, 1978c; Bengtsson, 1989; Harrison, 1991; Hanski, 1998). Predators could have effective impact on the extinction of tansy aphid populations. Among the predators of tansy aphids, ladybirds (coccinellids), lacewings (chrysopids) and hoverflies (syrphids) are the most common, as observed frequently in the field. As shown in chapter III, some tansy aphid colonies became extinct due to predators in the field experiment. For example, colonies of *M. fuscoviride* in the absence of ants quickly went extinct as a result of the action of predators. Extinction of an aphid population could be due to the abundance and the nature of natural enemies; here the suitability and the effect of aphids as prey is important because it could support the growth and population increase of predators (chapter V) which finally increase the predation pressure. Another role of predators in population extinction, when they do not cause direct extinction, is that they can decrease the population size and then the extinction probability by other factors increases by decreasing population size. Müller & Godfray (1999) evaluated the effects of predators and mutualistic ants on exclusion of two aphid species, *Aphis jacobaeae* Schrank and *Brachycaudus cardui* (L.), in a community. They reported that when aphid colonies were exposed to predators, they disappeared very quickly, whilst colonies that were unavailable to predators survived longer. In addition, they showed that colonies of *B. cardui* attended by ants persisted much more than un-attended colonies. Furthermore, aphid parasitoids (Hymenoptera: Braconidae) could also cause extinction in tansy aphid populations. Weisser and his colleagues have shown that the main driver for extinction of *M. fuscoviride* populations is its specialized parasitoid wasps, *Lysiphlebus hirticornis* Mackauer (Braconidae: Aphidiinae), which sometimes causes 100% parasitism (Weisser, 2000; Nyabuga *et al.*, 2010).

Another cause of population extinction of a species could be competition (*sensu* Stewart, 1996). Competitive interactions between aphid species may lead to extinction of inferior aphid species (in terms of fitness on a given habitat patch). However, as was shown in chapter III, the position of superior and inferior competitors in competitive hierarchies could be altered by the presence of mutualists such that this element helps its partner to win the competition. Whereas in *M. fuscoviride*, the presence of ants are critical for a longer survival time and population growth in a habitat patch, as mentioned above, this could lead to the extinction of *M. tanacetaria* colonies. Addicott (1978c; 1978b) in his studies on metapopulation dynamics of aphids on fireweed (*Epilobium angustifolium* L.) reported that the extinction rate of *Aphis varians* Patch is higher when it occurs with *Macrosiphum valerianae* (Clarke), which apparently occurred through exploitative rather than interference competition. Further evidence for the effect of competitive interaction on population extinction comes from a study by Bengtsson (1989) in three *Daphnia* species which live in small rock–pools. He used a long–term field experiment with artificial rock–pools and observational data of the distributional dynamics of the species, and revealed that interspecific competition between the three species led to increased local extinction rates. However such biological interactions can lead to population extinction locally, but in metacommunity point of view they can coexist regionally. For example, Slatkin (1974) and Hanski (1983) in their models, both demonstrate how two similar competitors, which cannot coexist locally, may nevertheless coexist as competing metapopulations.

Here it may be concluded that the extinction or persistence of species in a metacommunity is influenced strongly by the resident predator community, the strength of competitive interaction between them, and of course, by the availability of mutualistic partners.

7-2- Application of metacommunity ecology

Study of metacommunity ecology and understanding impacts of its involving processes help us to manage natural resources in more rational ways. Metacommunity ecology provides useful knowledge on how to manage ecological interactions and biological resources, more especially in the context of managing biodiversity and ecosystem services in human–dominated landscapes (Holt *et al.*, 2005; Verhoef & Morin, 2010). Metacommunity theories offer insights into how local and regional processes can affect diversity, species composition and ecosystem services in our complex and multiscale natural world (Leibold *et al.*, 2004; Bengtsson, 2010). The most important application of metacommunity theories could be in conservation ecology, crop protection and biological control (Holt *et al.*, 2005; Bengtsson, 2010).

Today in the ever fast changing world, the destruction and fragmentation of natural habitats happen frequently, which may lead (and often does) to reduce connectivity among patches of the original habitats and decrease the regional species pool (e.g. Kruess & Tscharntke, 1994; Vitousek *et al.*, 1997; Benton *et al.*, 2003). In such fragmented habitats, metacommunity processes are crucial in determining the maintenance of local and regional species richness (Holt *et al.*, 2005). Therefore, maintenance of biological diversity requires a rigorous understanding of processes operating at multiple scales, i.e. both local and regional processes, which are meanwhile important for diversity and ecosystem functioning.

In the agricultural landscape, fragmentation of habitats causes significant effects on biological diversity so that it decrease the numbers of species and also reduces the effects of natural enemies (Kruess & Tscharntke, 1994; Letourneau *et al.*, 2012). In these habitats, the lack of habitat connectivity release pest insects from the control of predators and parasitoids (Kruess & Tscharntke, 1994). For example, Stutz & Entling (2011) showed that densities of aphid predators on cherry trees can be enhanced and consequently aphid damage be reduced by increasing the connectivity between fruit trees and other woody habitats. In agriculture, a considerable number of pest problems and their control involves into metacommunity dynamics (Holt *et al.*, 2005). In biological control of pests, metacommunity theories often concern species interactions in spatially structured habitats (Bengtsson, 2010), and indeed it has been shown that the success of applying a biological control agent is strictly depended to the structure of the landscape in which the control is being attempted (Thies & Tscharntke, 1999; Holt *et al.*, 2005).

Another important application of metacommunity ecology is in wildlife conservation (Holt *et al.*, 2005; Bengtsson, 2010; Economo, 2011). Non-native invasive species when entering or artificially/accidentally introduced into a new habitat, can potentially impact metacommunity processes in a variety of ways (Holt *et al.*, 2005); hence, they are able to change the community structure and assembly. For instance, they can cause the extinction of native species in the habitat if they are superior to these as competitor. Here metacommunity theories could greatly help in the management of the invasive species concerned.

7-3- Conclusion

The findings of this thesis contribute to the understanding of the biological interactions between species, species which exhibit classical metapopulation structure, and how this could influence the metacommunity structure and assembly by affecting the core processes in metacommunity dynamics. This study supports the hypothesis that metapopulation processes are important in determining regional metacommunity structure and assembly. The dynamics of each population can be influenced by a combination of various biological interactions such as competition, mutualism and predation. The present work reveals that the three tansy aphid species studied experience various interactions that determine their local distribution and abundance. These aphids coexist regionally but not all of them in a single patch (plant), a finding in agreement with immigration–extinction models for coexistence of similar competitors in patchy habitat systems. It was found that the tansy aphids metacommunity shows strong elements of species–sorting, i.e. different aphid species eventually sort into different habitats which in turn creating separate spatial niches through habitat heterogeneity. The species–sorting paradigm describes variation in abundance and composition within the metacommunity due to individual species responses to environmental heterogeneity, such that certain local conditions may favour certain species and not others (*sensu* Leibold *et al.*, 2004). In such a tansy aphid metacommunity, individual plants (resource patches) showed strong habitat heterogeneity, at least related to the presence and absence of mutualistic ants, other aphid competitors and predators.

Presence or absence of each of these elements changes the patch conditions toward suitability for a particular aphid species. This is the first time, as far as I am aware, that such a dynamic has been demonstrated in detail for these particular tansy-feeding species in the context of metacommunity ecology, and indeed aphids in general, which are of course, amongst the major insect pests of agriculture, horticulture and forestry (Van Emden & Harrington, 2007). Hence, the present work has considerable potential in applied approaches to combat aphid pests, as well as being of fundamental scientific interest in its own right.

LIST OF REFERENCES

Abrams, P. A. (1999) Is predator-mediated coexistence possible inunstable systems? *Ecology*, 80: 608-621.

Addicott, J. F. (1978a) Competition for mutualists: aphids and ants. *Canadian Journal of Zoology*, 56: 2093-2096.

Addicott, J. F. (1978b) Niche relationships among species of aphids feeding on fireweed. *Canadian Journal of Zoology*, 56: 1837-1841.

Addicott, J. F. (1978c) The population dynamics of aphids on fireweed: a comparison of local populations and metapopulations. *Canadian Journal of Zoology*, 56: 2554-2564.

Agrawal, A. A. (1999) Induced responses to herbivory in wild radish: Effects on several herbivores and plant fitness. *Ecology*, 80: 1713-1723.

Amarasekare, P. (1998) Allee effects in metapopulation dynamics. *The American Naturalist*, 152: 298-302.

Andersen, A. (1991) Carabidae and Staphylinidae (Col.) frequently found in Norwegian agricultural fields. New data and review. *Fauna Norvergica (B)*, 38: 65-76.

Andersen, A. & Eltun, R. (2000) Long-term developments in the carabid and staphylinid (Col., Carabidae and Staphylinidae) fauna during conversion from conventional to bilogical farming. *Journal of Applied Entomology*, 124: 51-56.

Andrewartha, H. G. & Birch, L. C. (1954) *The distribution and abundance of animals*. University of Chicago Press, Chicago.

Balog, A., Mehrparvar, M. & Weisser, W. W. (2013) Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae). *European Journal of Entomology*, 110: 153-157.

Bates, A. J., Sadler, J. P. & Fowles, A. P. (2006) Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. *Oecologia*, 150: 50-60.

Begon, M., Townsend, C. R. & Harper, J. L. (2006) *Ecology: From Individuals to Ecosystems*. Fourth edn. Blackwell Publishing Ltd, Oxford, U.K.

Behmer, S. T., Simpson, S. J. & Raubenheimer, D. (2002) Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. *Ecology*, 83: 2489-2501.

Belsky, J. A. (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, 3: 187-200.

Bengtsson, J. (1989) Interspecific competition increases local extinction rate in a metapopulation system. *Nature*, 340: 713-715.

Bengtsson, J. (1991) Interspecific competition in metapopulations. *Biological Journal of the Linnean Society*, 42: 219-237.

Bengtsson, J. (2010) Applied (meta)community ecology: diversity and ecosystem services at the intersection of local and regional processes. In: *Community ecology: processes, models, and applications* (eds. Verhoef, H. A. & Morin, P. J.). Oxford University Press Oxford, pp. 115-130.

Benton, T. G., Vickery, J. A. & Wilson, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, 18: 182-188.

Berendse, F. (1985) The effect of grazing on the outcome of competition between plant-species with different nutrient-requirements. *Oikos*, 44: 35-39.

Bernays, E. A., Bright, K. L., Gonzalez, N. & Angel, J. (1994) Dietary mixing in a generalist herbivore - tests of 2 hypotheses. *Ecology*, 75: 1997-2006.

Bernays, E. A. & Chapman, R. F. (1994) *Host-plant selection by phytophagous insects*. Chapman & Hall, New York.

Billick, I., Hammer, S., Reithel, J. S. & Abbot, P. (2007) Ant-aphid interactions: Are ants friends, enemies, or both? *Annals of the Entomological Society of America*, 100: 887-892.

Blackman, R. L. (1967) Effects of different aphid foods on *Adalia bipunctata* L and *Coccinella 7-punctata* L. *Annals of Applied Biology*, 59: 207-219.

Blackman, R. L. (1987) Reproduction, cytogenetics and development. In: *Aphids, their biology, natural enemies and control* (eds. Minks, A. K. & Harrewijn, P.). Elsevier Amsterdam, pp. 163-195.

Blackman, R. L. & Eastop, V. F. (2000) *Aphids on the world's crops (An identification and information guide)*. Second edn. John Wiley & Sons, London, UK.

Blackman, R. L. & Eastop, V. F. (2006) *Aphids on the world’s herbaceous plants and shrubs*. John Wiley & Sons, London, UK.

Borg, C. & Toft, S. (2000) Importance of insect prey quality for grey partridge chicks *Perdix perdix*: a self-selection experiment. *Journal of Applied Ecology*, 37: 557-563.

Braendle, C., Caillaud, M. C. & Stern, D. L. (2005) Genetic mapping of aphicarus - a sex-linked locus controlling a wing polymorphism in the pea aphid (*Acyrthosiphon pisum*). *Heredity*, 94: 435-442.

Braendle, C., Davis, G. K., Brisson, J. A. & Stern, D. L. (2006) Wing dimorphism in aphids. *Heredity*, 97: 192-199.

Braendle, C. & Weisser, W. W. (2001) Variation in escape behavior of red and green clones of the pea aphid. *Journal of Insect Behavior*, 14: 497-509.

Brisson, J. A. (2010) Aphid wing dimorphisms: linking environmental and genetic control of trait variation. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365: 605-616.

Bruinsma, M. & Dicke, M. (2008) Herbivore-induced indirect defense: From induction mechanisms to community ecology. In: *Induced plant resistance to herbivory* (ed. Schaller, A.). Springer, pp. 31-60.

Brunissen, L., Cherqui, A., Pelletier, Y., Vincent, C. & Giordanengo, P. (2009) Host-plant mediated interactions between two aphid species. *Entomologia Experimentalis Et Applicata*, 132: 30-38.

Bryan, K. M. & Wratten, S. D. (1984) The responses of polyphagous predators to prey spatial heterogeneity: aggregation by carabid and staphylinid beetles to their cereal aphid prey. *Ecological Entomology*, 9: 251-259.

Byers, J. A. (1993) Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. *Experientia*, 49: 272-275.

Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006) Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecology Letters*, 9: 897-907.

Canard, M. (1970) The bearing of the nutritive value of various aphids (Homoptera, Aphididae) on the potential rate of increase of *Chrysopa perla* (L.) (Neuroptera, Chrysopidae). *Annales de Zoologie Ecologie Animale*, 3: 345-355.

Canard, M. & Principi, M. M. (1984) Life histories and behavior. In: *Biology of Chrysopidae* (eds. Canard, M., Semeria, Y. & New, T. R.). Dr W. Junk Publishers, The Hague, pp. 57-149.

Case, T. J. (1991) Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society*, 42: 239-266.

Chapman, R. F., Bernays, E. A. & Simpson, S. J. (1981) Attraction and repulsion of the aphid, *Cavariella aegopodii,* by plant odors. *Journal of Chemical Ecology*, 7: 881-888.

Clark, K. E., Hartley, S. E. & Johnson, S. N. (2011) Does mother know best? The preference–performance hypothesis and parent–offspring conflict in aboveground–belowground herbivore life cycles. *Ecological Entomology,* 36: 117-124.

Clobert, J., Ims, R. A. & Rousset, F. (2004) Causes, mechanisms and consequences of dispersal. In: *Ecology, genetics, and evolution of metapopulations* (eds. Hanski, I. & Gaggiotti, O. E.). Elsevier Academic Press, pp. 307-335.

Cole, B. J. (1983) Assembly of mangrove ant communities: patterns of geographical-distribution. *Journal of Animal Ecology*, 52: 339-347.

Connell, J. H. (1961) Influence of interspecific competition and other factors on distribution of barnacle *Chthamalus stellatus*. *Ecology*, 42: 710-&.

De Barro, P. J. (1992) The role of temperature, photoperiod, crowding and plant-quality on the production of alate viviparous females of the bird cherry-oat aphid, *Rhopalosiphum padi*. *Entomologia Experimentalis Et Applicata*, 65: 205-214.

De Wit, C. T., Tow, P. G. & Ennik, G. C. (1966) Competition between legumes and grasses. *Verslagen van landbouwkundige Onderzoekingen*, 112: 1017-1045.

Dennis, P., Wratten, S. D. & Sotherton, N. W. (1991) Mycophagy as a factor limiting predation of aphids (Hemiptera: Aphididae) by staphylinid beetles (Coleoptera: Staphylinidae) in cereals. *Bulletin of Entomological Research*, 81: 25-31.

Denno, R. F., McClure, M. S. & Ott, J. R. (1995) Interspecific interactions in phytophagous insects - competition reexamined and resurrected. *Annual Review of Entomology*, 40: 297-331.

Denno, R. F., Peterson, M. A., Gratton, C., Cheng, J. A., Langellotto, G. A., Huberty, A. F. & Finke, D. L. (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology*, 81: 1814-1827.

Dixon, A. F. G. (1998) *Aphid ecology: An optimization approach*. 2 edn. Chapman & Hall, London.

Dixon, A. F. G. & Agarwala, B. K. (1999) Ladybird-induced life-history changes in aphids. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 266: 1549-1553.

Du, Y., Poppy, G. M., Powell, W., Pickett, J. A., Wadhams, L. J. & Woodcock, C. M. (1998) Identification of semiochemicals released during aphid feeding that attract parasitoid *Aphidius ervi*. *Journal of Chemical Ecology*, 24: 1355-1368.

Ebenhard, T. (1991) Colonization in metapopulations: a review of theory and observations. *Biological Journal of the Linnean Society*, 42: 105-121.

Economo, E. P. (2011) Biodiversity conservation in metacommunity networks: Linking pattern and persistence. *The American Naturalist*, 177: E167-E180.

El-Ziady, S. (1960) Further effects of *Lasius niger* L. on *Aphis fabae S*cop. *Proceedings of the Royal Society London Series B*, 35: 30-38.

El-Ziady, S. & Kennedy, J. S. (1956) Beneficial effects of the common garden ant, *Lasius niger* L., on the black bean aphid, *Aphis fabae* Scopoli. *Proceedings of the Royal Society London Series B*, 31: 61-65.

Evans, E. W., Stevenson, A. T. & Richards, D. R. (1999) Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia*, 121: 107-112.

Fischer, M. K., Hoffmann, K. H. & Völkl, W. (2001) Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance. *Oikos*, 92: 531-541.

Fisher, A. E. I., Hartley, S. E. & Young, M. (2000) Direct and indirect competitive effects of foliage feeding guilds on the performance of the birch leaf-miner *Eriocrania*. *Journal of Animal Ecology*, 69: 165-176.

Flatt, T. & Weisser, W. W. (2000) The effects of mutualistic ants on aphid life history traits. *Ecology*, 81: 3522-3529.

Gaggiotti, O. E. & Hanski, I. (2004) Mechanisms of population extinction. In: *Ecology, genetics, and evolution of metapopulations* (eds. Hanski, I. & Gaggiotti, O. E.). Elsevier Academic Press, pp. 337-366.

Gaggiotti, O. E., Jones, F., Lee, W. M., Amos, W., Harwood, J. & Nichols, R. A. (2002) Patterns of colonization in a metapopulation of grey seals. *Nature*, 416: 424-427.

Gliwicz, Z. M. & Wrzosek, D. (2008) Predation-mediated coexistence of large- and small-bodied *Daphnia* at different food levels. *The American naturalist*, 172: 358-374.

Gonzales, W. L., Ramirez, C. C., Olea, N. & Niemeyer, H. M. (2002) Host plant changes produced by the aphid *Sipha flava*: consequences for aphid feeding behaviour and growth. *Entomologia Experimentalis Et Applicata*, 103: 107-113.

Good, J. A. & Giller, P. S. (1991) The diet of predatory staphylinid beetles - a review of records. *Entomologists Monthly Magazine*, 127: 77-89.

Gotelli, N. J. (1991) Metapopulation models - The rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist*, 138: 768-776.

Groeters, F. (1989) Geographic and clonal variation in the milkweed-oleander aphid, *Aphis nerii* (Homoptera: Aphididae), for winged morph production, life history, and morphology in relation to host plant permanence. *Evolutionary Ecology*, 3: 327-341.

Gruppe, A. & Roemer, P. (1988) The lupin aphid (*Macrosiphum albifrons* Essig, 1911) (Hom, Aphididae) in West-Germany: Its occurrence, host plants and natural enemies. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 106: 135-143.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960) Community structure, population control, and competition. *American Naturalist*, 94: 421-425.

Hanski, I. (1983) Coexistence of competitors in patchy environment. *Ecology*, 64: 493-500.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, 396: 41-49.

Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.

Hanski, I. & Gaggiotti, O. E. (2004a) *Ecology, genetics, and evolution of metapopulations* Elsevier Academic Press, USA.

Hanski, I. & Gaggiotti, O. E. (2004b) Metapopulation biology: Past, present, and future. In: *Ecology, genetics, and evolution of metapopulations* (eds. Hanski, I. & Gaggiotti, O. E.). Elsevier Academic Press, pp. 3-22.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42: 3-16.

Hanski, I. & Gilpin, M. E. (1997) *Metapopulation biology: Ecology, genetics, and evolution*. Academic Press, London.

Harrison, P. J., Hanski, I. & Ovaskainen, O. (2011) Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. *Ecological Monographs*, 81: 581-598.

Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, 42: 73-88.

Hatano, E., Kunert, G. & Weisser, W. W. (2010) Aphid wing induction and ecological costs of alarm pheromone emission under field conditions. *PLoS One*, 5: e11188.

Hauge, M. S., Nielsen, F. H. & Toft, S. (1998) The influence of three cereal aphid species and mixed diet on larval survival, development and adult weight of *Coccinella septempunctata*. *Entomologia Experimentalis Et Applicata*, 89: 319-322.

Hauge, M. S., Nielsen, F. H. & Toft, S. (2011) Weak responses to dietary enrichment in a specialized aphid predator. *Physiological Entomology*, 36: 360-367.

Hazell, S. P., Gwynn, D. M., Ceccarelli, S. & Fellowes, M. D. E. (2005) Competition and dispersal in the pea aphid: clonal variation and correlations across traits. *Ecological Entomology*, 30: 293-298.

Hille Ris Lambers, D. (1966) Polymorphism in Aphididae. *Annual Review of Entomology*, 11: 47-78.

Hodek, I. (1956) The influence of *Aphis sambuci* L. as prey of the ladybird beetle *Coccinella septempunctata* L. *Acta Societatis Zoologicae Bohemoslovacae*, 20: 62-74 (In Czech, English abstract).

Hodek, I. & Honek, A. (1996) *Ecology of Coccinellidae*. Kluwer Academic Publishers, Dordrecht.

Holman, J. (2009) *Host plant catalogue of aphids: Palaearctic region*. Springer, Berlin.

Holt, R. D., Holyoak, M. & Leibold, M. A. (2005) Future directions in metacommunity ecology. In: *Metacommunities: spatial dynamics and ecological communities* (eds. Holyoak, M., Leibold, M. A. & Holt, R. D.). The University of Chicago Press Chicago, pp. 465-489.

Holt, R. D. & Lawton, J. H. (1993) Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist*, 142: 623-645.

Holt, R. D. & Lawton, J. H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, 25: 495-520.

Holyoak, M., Leibold, M. A. & Holt, R. D. (2005a) *Metacommunities: spatial dynamics and ecological communities*. The University of Chicago Press, Chicago.

Holyoak, M., Leibold, M. A., Mouquet, N., Holt, R. D. & Hoopes, M. F. (2005b) Metacomminities: A framework for large-scale community ecology. In: *Metacommunities: spatial dynamics and ecological communities* (eds. Holyoak, M., Leibold, M. A. & Holt, R. D.). The University of Chicago Press Chicago, pp. 1-31.

Hoopes, M. F., Holt, R. D. & Holyoak, M. (2005) The effects of spatial processes on two species interactions. In: *Metacommunities: spatial dynamics and ecological communities* (eds. Holyoak, M., Leibold, M. A. & Holt, R. D.). The University of Chicago Press Chicago, pp. 35-67.

Hunt, J. & Bonsall, M. B. (2009) The effects of colonization, extinction and competition on co-existence in metacommunities. *Journal of Animal Ecology*, 78: 866-879.

Huntly, N. (1991) Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*, 22: 477-503.

Janzen, D. H. (1967) Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *University of Kansas Science Bulletin*, 47: 315-558.

Johnson, B. (1965) Wing polymorphism in aphids II. Interaction between aphids. *Entomologia Experimentalis Et Applicata*, 8: 49-64.

Johnson, B. (1966) Wing polymorphism in aphids III. The influence of the host plant. *Entomologia Experimentalis Et Applicata*, 9: 213-222.

Kalushkov, P. & Hodek, I. (2004) The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. *Biocontrol*, 49: 21-32.

Kaplan, I. & Denno, R. F. (2007) Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters*, 10: 977-994.

Karban, R. & Baldwin, I. T. (1997) *Induced responses to herbivory*. University of Chicago Press, Chicago.

Kawada, K. (1987) Polymorphism and morph determination In: *Aphids, their biology, natural enemies and control* (eds. Minks, A. K. & Harrewijn, P.). Elsevier Amsterdam, pp. 255-266.

Keller, L. & Gordon, E. (2010) *The lives of ants*. Oxford University Press, Oxford, U.K.

Kennedy, T. F., Evans, G. O. & Feeney, A. M. (1986) Studies on the biology of *Tachyporus hypnorum* F. (Col. Staphylinidae), associated with cereal fields in Ireland. *Irish Journal of Agricultural Research*, 25: 81-95.

Khuhro, N. H., Chen, H. Y., Zhang, Y., Zhang, L. S. & Wang, M. Q. (2012) Effect of different prey species on the life history parameters of *Chrysoperla sinica* (Neuroptera: Chrysopidae). *European Journal of Entomology*, 109: 175-180.

Kleinjan, J. E. & Mittler, T. E. (1975) A chemical influence of ants on wing development in aphids. *Entomologia Experimentalis Et Applicata*, 18: 384-388.

Kokko, H., Sutherland, W. J. & Johnstone, R. A. (2001) The logic of territory choice: Implications for conservation and source-sink dynamics. *American Naturalist*, 157: 459-463.

Kruess, A. & Tscharntke, T. (1994) Habitat fragmentation, species loss, and biological-control. *Science*, 264: 1581-1584.

Kunert, G., Otto, S., Rose, U. S. R., Gershenzon, J. & Weisser, W. W. (2005) Alarm pheromone mediates production of winged dispersal morphs in aphids. *Ecology Letters*, 8: 596-603.

Kunert, G., Schmoock-Ortlepp, K., Reissmann, U., Creutzburg, S. & Weisser, W. W. (2008) The influence of natural enemies on wing induction in *Aphis fabae* and *Megoura viciae* (Hemiptera: Aphididae). *Bulletin of Entomological Research*, 98: 59-62.

Kunert, G. & Weisser, W. W. (2003) The interplay between density- and trait-mediated effects in predator-prey interactions: a case study in aphid wing polymorphism. *Oecologia*, 135: 304-312.

Kunert, G. & Weisser, W. W. (2005) The importance of antennae for pea aphid wing induction in the presence of natural enemies. *Bulletin of Entomological Research*, 95: 125-131.

Lamb, R. J. & Mackay, P. A. (1987) *Acyrthosiphon kondoi* influences alata production by the pea aphid, *Acyrthosiphon pisum*. *Entomologia Experimentalis Et Applicata*, 45: 195-198.

Lawton, J. H. & Strong, D. R. (1981) Community patterns and competition in folivorous insects. *American Naturalist*, 118: 317-338.

Lee, C. T. & Inouye, B. D. (2010) Mutualism between consumers and their shared resource can promote competitive coexistence. *American Naturalist*, 175: 277-288.

Lees, A. D. (1966) The control of polymorphism in aphids. *Advances in Insect Physiology*, 3: 207-277.

Lees, A. D. (1967) The production of the apterous and alate forms in the aphid *Megoura viciae* Buckton, with special reference to the role of crowding. *Journal of Insect Physiology*, 13: 289-318.

Leibold, M. A. (2009) Spatial and metacommunity dynamics in biodiversity. In: *The Princeton guide to ecology* (ed. Levin, S. A.). Princeton University Press Princeton, pp. 312-319.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7: 601-613.

Letourneau, D. K., Allen, S. G. B. & Stireman, J. O. (2012) Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops. *Journal of Applied Ecology*, 49: 1405-1416.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15: 237-240.

Li, X. C., Schuler, M. A. & Berenbaum, M. R. (2002) Jasmonate and salicylate induce expression of herbivore cytochrome P450 genes. *Nature*, 419: 712-715.

Liu, T. X. & Chen, T. Y. (2001) Effects of three aphid species (Homoptera: Aphididae) on development, survival and predation of *Chrysoperla carnea* (Neuroptera : Chrysopidae). *Applied Entomology and Zoology*, 36: 361-366.

Loxdale, H. D. (2010) Rapid genetic changes in natural insect populations. *Ecological Entomology*, 35: 155-164.

Loxdale, H. D., Hardie, J., Halbert, S., Foottit, R., Kidd, N. A. C. & Carter, C. I. (1993) The relative importance of short-range and long-range movement of flying aphids. *Biological Reviews*, 68: 291-311.

Loxdale, H. D., Schöfl, G., Wiesner, K. R., Nyabuga, F. N., Heckel, D. G. & Weisser, W. W. (2011) Stay at home aphids: comparative spatial and seasonal metapopulation structure and dynamics of two specialist tansy aphid species studied using microsatellite markers. *Biological Journal of the Linnean Society*, 104: 838-865.

Macarthur, R. H. & Wilson, E. O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton

Mackauer, M. & Völkl, W. (1993) Regulation of aphid populations by aphidiid wasps - does parasitoid foraging behavior or hyperparasitism limit impact. *Oecologia*, 94: 339-350.

Mackay, P. & Wellington, W. (1977) Maternal age as a source of variation in the ability of an aphid to produce dispersing forms. *Researches on Population Ecology*, 18: 195-209.

Mackay, P. A. & Wellington, W. G. (1975) Comparison of reproductive patterns of apterous and alate virginoparous *Acyrthosiphon pisum* (Homoptera-Aphididae). *Canadian Entomologist*, 107: 1161-1166.

Massonnet, B., Simon, J. C. & Weisser, W. W. (2002) Metapopulation structure of the specialized herbivore *Macrosiphoniella tanacetaria* (Homoptera, Aphididae). *Molecular Ecology*, 11: 2511-2521.

Mehrparvar, M., Mahdavi Arab, N. & Weisser, W. W. (2013) Diet-mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing? *Biological Control*, 65: 142-146.

Messina, F. J., Taylor, R. & Karren, M. E. (2002) Divergent responses of two cereal aphids to previous infestation of their host plant. *Entomologia Experimentalis Et Applicata*, 103: 43-50.

Minoretti, N. & Weisser, W. W. (2000) The impact of individual ladybirds (*Coccinella septempunctata*, Coleoptera : Coccinellidae) on aphid colonies. *European Journal of Entomology*, 97: 475-479.

Mitich, L. W. (1992) Intriguing world of weeds .35. Tansy. *Weed Technology*, 6: 242-244.

Mittler, T. E. & Sutherland, O. R. W. (1969) Dietary influences on aphid polymorphism. *Entomologia Experimentalis Et Applicata*, 12: 703-713.

Miura, T. (2004) Proximate mechanisms and evolution of caste polyphenism in social insects: From sociality to genes. *Ecological Research*, 19: 141-148.

Miyazaki, M. (1987a) Forms and morphs of aphids. In: *Aphids, their biology, natural enemies and control* (eds. Minks, A. K. & Harrewijn, P.). Elsevier Amsterdam, pp. 27-50.

Miyazaki, M. (1987b) Morphology of aphids. In: *Aphids, their biology, natural enemies and control* (eds. Minks, A. K. & Harrewijn, P.). Elsevier Amsterdam, pp. 1-25.

Mondor, E. B., Rosenheim, J. A. & Addicott, J. F. (2005) Predator-induced transgenerational phenotypic plasticity in the cotton aphid. *Oecologia*, 142: 104-108.

Monsrud, C. & Toft, S. (1999) The aggregative numerical response of polyphagous predators to aphids in cereal fields: attraction to what? *Annals of Applied Biology*, 134: 265-270.

Moran, N. A. & Whitham, T. G. (1990) Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. *Ecology*, 71: 1050-1058.

Morin, P. J. (1999) *Community ecology*. Blackwell, Massachusetts.

Müller, C. B. & Godfray, H. C. J. (1999) Predators and mutualists influence the exclusion of aphid species from natural communities. *Oecologia*, 119: 120-125.

Müller, C. B., Williams, I. S. & Hardie, J. (2001) The role of nutrition, crowding and interspecific interactions in the development of winged aphids. *Ecological Entomology*, 26: 330-340.

Nedved, O. & Salvucci, S. (2008) Ladybird *Coccinella septempunctata* (Coleoptera : Coccinellidae) prefers toxic prey in laboratory choice experiment. *European Journal of Entomology*, 105: 431-436.

Nielsen, F. H., Hauge, M. S. & Toft, S. (2002) The influence of mixed aphid diets on larval performance of *Coccinella septempunctata* (Col., Coccinellidae). *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 126: 194-197.

Nottingham, S. F. & Hardie, J. (1993) Flight behavior of the black bean aphid, *Aphis fabae*, and the cabbage aphid, *Brevicoryne brassicae*, in host and nonhost plant odor. *Physiological Entomology*, 18: 389-394.

Nowak, H. & Komor, E. (2010) How aphids decide what is good for them: experiments to test aphid feeding behaviour on *Tanacetum vulgare* (L.) using different nitrogen regimes. *Oecologia*, 163: 973-984.

Nowicki, P. & Vrabec, V. (2011) Evidence for positive density-dependent emigration in butterfly metapopulations. *Oecologia*, 167: 657-665.

Nyabuga, F. N., Loxdale, H. D., Heckel, D. G. & Weisser, W. W. (2010) Spatial population dynamics of a specialist aphid parasitoid, *Lysiphlebus hirticornis* Mackauer (Hymenoptera: Braconidae: Aphidiinae): evidence for philopatry and restricted dispersal. *Heredity*, 105: 433-442.

Olff, H. & Ritchie, M. E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, 13: 261-265.

Omkar, Kumar, G. & Sahu, J. (2009) Performance of a predatory ladybird beetle, *Anegleis cardoni* (Coleoptera: Coccinellidae) on three aphid species. *European Journal of Entomology*, 106: 565-572.

Omkar & Srivastava, S. (2003) Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. *Biocontrol*, 48: 379-393.

Paine, R. T. (1966) Food web complexity and species diversity. *American Naturalist*, 100: 65-75.

Pappas, M. L., Broufas, G. D. & Koveos, D. S. (2007) Effects of various prey species on development, survival and reproduction of the predatory lacewing *Dichochrysa prasina* (Neuroptera : Chrysopidae). *Biological Control*, 43: 163-170.

Petersen, M. K. & Sandstrom, J. P. (2001) Outcome of indirect competition between two aphid species mediated by responses in their common host plant. *Functional Ecology*, 15: 525-534.

Pettersson, J., Tjallingii, W. F. & Hardie, J. (2007) Host-plant selection and feeding. In: *Aphids as Crop Pests* (eds. van Emden, H. F. & Harrington, R.). CAB International Wallingford, pp. 87-113.

Phoofolo, M. W., Giles, K. L. & Elliott, N. C. (2007) Quantitative evaluation of suitability of the greenbug, *Schizaphis graminum*, and the bird cherry-oat aphid, *Rhopalosiphum padi*, as prey for *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biological Control*, 41: 25-32.

Pickett, J. A., Wadhams, L. J., Woodcock, C. M. & Hardie, J. (1992) The chemical ecology of aphids. *Annual Review of Entomology*, 37: 67-90.

Plantegenest, M. & Kindlmann, P. (1999) Evolutionarily stable strategies of migration in heterogeneous environments. *Evolutionary Ecology*, 13: 229-244.

Poethke, H. J., Weisser, W. W. & Hovestadt, T. (2010) Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. *American Naturalist*, 175: 577-586.

Powell, G., Tosh, C. R. & Hardie, J. (2006) Host plant selection by aphids: Behavioral, evolutionary, and applied perspectives. *Annual Review of Entomology*, 51: 309-330.

Prado, E. & Tjallingii, W. F. (1997) Effects of previous plant infestation on sieve element acceptance by two aphids. *Entomologia Experimentalis Et Applicata*, 82: 189-200.

Renault, C. K., Buffa, L. M. & Delfino, M. A. (2005) An aphid-ant interaction: effects on different trophic levels. *Ecological Research*, 20: 71-74.

Robert, C. A. M., Erb, M., Duployer, M., Zwahlen, C., Doyen, G. R. & Turlings, T. C. J. (2012) Herbivore-induced plant volatiles mediate host selection by a root herbivore. *New Phytologist*, 194: 1061-1069.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature*, 392: 491-494.

Sakata, H. (1994) How an ant decides to prey on or to attend aphids. *Researches on Population Ecology*, 36: 45-51.

Sakata, H. (1995) Density-dependent predation of the ant *Lasius niger* (Hymenoptera: Formicidae) on two attended aphids *Lachnus tropicalis* and *Myzocallis kuricola* (Homoptera: Aphididae). *Researches on Population Ecology*, 37: 159-164.

Sauge, M. H., Lacroze, J. P., Poessel, J. L., Pascal, T. & Kervella, J. (2002) Induced resistance by *Myzus persicae* in the peach cultivar 'Rubira'. *Entomologia Experimentalis Et Applicata*, 102: 29-37.

Sauge, M. H., Mus, F., Lacroze, J. P., Pascal, T., Kervella, J. & Poessel, J. L. (2006) Genotypic variation in induced resistance and induced susceptibility in the peach - *Myzus persicae* aphid system. *Oikos*, 113: 305-313.

Schoener, T. W. (1982) The controversy over interspecific competition. *American Scientist*, 70: 586-595.

Seibert, T. F. (1992) Mutualistic interactions of the aphid *Lachnus allegheniensis* (Homoptera: Aphididae) and its tending ant *Formica obscuripes* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, 85: 173-178.

Seymour, A. S., Gutierrez, D. & Jordano, D. (2003) Dispersal of the lycaenid *Plebejus argus* in response to patches of its mutualist ant *Lasius niger*. *Oikos,* 103: 162-174.

Shaw, M. J. P. (1970) Effects of population density on alienicolae of *Aphis fabae* Scop. I. Effect of crowding on production of alatae in laboratory. *Annals of Applied Biology*, 65: 191-196.

Simon, J. C., Rispe, C. & Sunnucks, P. (2002) Ecology and evolution of sex in aphids. *Trends in Ecology & Evolution*, 17: 34-39.

Simpson, S. J., Sword, G. A. & Lo, N. (2011) Polyphenism in insects. *Current Biology,* 21: R738-R749.

Skinner, G. J. (1980) The feeding habits of the wood-ant, *Formica rufa* (Hymenoptera: Formicidae), in limestone woodland in north-west England. *Journal of Animal Ecology*, 49: 417-433.

Slatkin, M. (1974) Competition and regional coexistence. *Ecology,* 55: 128-134.

Slobodkin, L. B. (1964) Experimental populations of *Hydrida*. *Journal of Animal Ecology*, 33: 131-148.

Slobodkin, L. B., Smith, F. E. & Hairston, N. G. (1967) Regulation in terrestrial ecosystems and implied balance of nature. *American Naturalist*, 101: 109-&.

Sloggett, J. J. & Weisser, W. W. (2002) Parasitoids induce production of the dispersal morph of the pea aphid, *Acyrthosiphon pisum*. *Oikos*, 98: 323-333.

Smith, M. A. H. & Mackay, P. A. (1989) Genetic-variation in male alary dimorphism in populations of pea aphid, *Acyrthosiphon pisum*. *Entomologia Experimentalis Et Applicata,* 51: 125-132.

Stadler, B. (2004) Wedged between bottom-up and top-down processes: aphids on tansy. *Ecological Entomology,* 29: 106-116.

Stadler, B. & Dixon, A. F. G. (1999) Ant attendance in aphids: why different degrees of myrmecophily? *Ecological Entomology,* 24: 363-369.

Stadler, B. & Dixon, A. F. G. (2005) Ecology and evolution of aphid-ant interactions. *Annual Review of Ecology, Evolution, and Systematics,* 36: 345-372.

Stadler, B. & Dixon, A. F. G. (2008) *Mutualism: ants and their insect partners*. Cambridge University Press, New York.

Stephens, P. A., Sutherland, W. J. & Freckleton, R. P. (1999) What is the Allee effect? *Oikos*, 87: 185-190.

Stewart, A. J. A. (1996) Interspecific competition reinstated as an important force structuring insect herbivore communities. *Trends in Ecology & Evolution*, 11: 233-234.

Stutz, S. & Entling, M. H. (2011) Effects of the landscape context on aphid-ant-predator interactions on cherry trees. *Biological Control*, 57: 37-43.

Sudd, J. H. (1987) Ant aphid mutualism. In: *Aphids, their biology, natural enemies and control* (eds. Minks, A. K. & Harrewijn, P.). Elsevier Amsterdam, pp. 355-365.

Sunderland, K. D., Crook, N. E., Stacey, D. L. & Fuller, B. J. (1987) A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology*, 24: 907-933.

Sutherland, O. R. W. (1969a) The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. *Journal of Insect Physiology*, 15: 1385-1410.

Sutherland, O. R. W. (1969b) The role of the host plant in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. *Journal of Insect Physiology*, 15: 2179-2201.

Sutherland, O. R. W. (1970) An intrinsic factor influencing alate production by two strains of the pea aphid, *Acyrthosiphon pisum*. *Journal of Insect Physiology*, 16: 1349-1354.

Tack, A. J. M., Ovaskainen, O., Harrison, P. J. & Roslin, T. (2009) Competition as a structuring force in leaf miner communities. *Oikos*, 118: 809-818.

Taylor, A. D. (1990) Metapopulations, dispersal, and predator-prey dynamics: An overview. *Ecology*, 71: 429-433.

Thies, C. & Tscharntke, T. (1999) Landscape structure and biological control in agroecosystems. *Science*, 285: 893-895.

Thomas, C. D. & Hanski, I. (1997) Butterfly metapopulations. In: *Metapopulation biology: Ecology, genetics and evolution* (eds. Hanski, I. & Gilpin, M. E.). Academic Press San Diego, pp. 359-386.

Tilles, D. A. & Wood, D. L. (1982) The influence of carpenter ant (*Camponotus modoc*) (Hymenoptera: Formicidae) attendance on the development and survival of aphids (*Cinara* spp.) (Homoptera: Aphididae) in a giant sequoia forest. *The Canadian Entomologist*, 114: 1133-1142.

Toft, S. & Wise, D. H. (1999) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia*, 119: 191-197.

Tsuji, H. & Kawada, K. (1987) Effects of starvation on life-span and embryo development of 4 morphs of pea aphid (*Acyrthosiphon pisum* (Harris)). *Japanese Journal of Applied Entomology and Zoology*, 31: 36-40.

Tsumuki, H., Nagatsuka, H., Kawada, K. & Kanehisa, K. (1990) Comparison of nutrient reservation in apterous and alate pea aphids, *Acyrthosiphon pisum* (Harris) .1. Developmental time and sugar content. *Applied Entomology and Zoology*, 25: 215-221.

Unsicker, S. B., Oswald, A., Koehler, G. & Weisser, W. W. (2008) Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia*, 156: 313-324.

Van Emden, H. F. & Harrington, R. (2007) *Aphids As Crop Pests*. CABI, Wallingford.

van Veen, F. J. F., Morris, R. J. & Godfray, H. C. J. (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, 51: 187-208.

Vandermeer, J. & Pascual, M. (2006) Competitive coexistence through intermediate polyphagy. *Ecological Complexity*, 3: 37-43.

Verhoef, H. A. & Morin, P. J. (2010) *Community ecology: processes, models, and applications*. Oxford University Press, Oxford.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) Human domination of earth's ecosystems. *Science*, 277: 494-499.

Völkel, C. & Baldwin, I. T. (2004) Herbivore-specific transcriptional responses and their research potential for ecosystem studies. In: *Insects and ecosystem function* (eds. Weisser, W. & Siemann, E.). Springer-Verlag Berlin.

Völkl, W., Woodring, J., Fischer, M., Lorenz, M. W. & Hoffmann, K. H. (1999) Ant-aphid mutualisms: the impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia*, 118: 483-491.

Waldbauer, G. P. & Friedman, S. (1991) Self-selection of optimal diets by insects. *Annual Review of Entomology*, 36: 43-63.

Wallin, H., Chiverton, P. A., Ekbom, B. S. & Borg, A. (1992) Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomologia Experimentalis Et Applicata*, 65: 129-140.

Waltz, A. M. & Whitham, T. G. (1997) Plant development affects arthropod communities: Opposing impacts of species removal. *Ecology*, 78: 2133-2144.

Weisser, W. W. (2000) Metapopulation dynamics in an aphid-parasitoid system. *Entomologia Experimentalis et Applicata*, 97: 83-92.

Weisser, W. W. (2001) Predation and the evolution of dispersal. In: *Insect movement: mechanisms and consequences* (eds. Woiwod, I. P., Reynolds, D. R. & Thomas, C. D.). CAB International Oxon, pp. 261-280.

Weisser, W. W., Braendle, C. & Minoretti, N. (1999) Predator-induced morphological shift in the pea aphid. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 266: 1175-1181.

Weisser, W. W. & Härri, S. A. (2005) Colonisations and extinctions at multiple spatial scales: a case study in monophagous herbivores. *Annales Zoologici Fennici*, 42: 363-377.

Weisser, W. W. & Stadler, B. (1994) Phenotypic plasticity and fitness in aphids. *European Journal of Entomology*, 91: 71-78.

Whitman, D. A. & Agrawal, A. A. (2009) What is phenotypic plasticity and why is it important? In: *Phenotypic plasticity of insects: mechanisms and consequences* (eds. Whitman, D. W. & Ananthakrishnan, T. N.). Science Publishers University of Minnesota, pp. 1-63.

Wiens, J. A. (1977) On competition and variable environments: Populations may experience "ecological crunches" in variable climates, nullifying the assumptions of competition theory and limiting the usefulness of short-term studies of population patterns. *American Scientist*, 65: 590-597.

Williams, I. S., Dewar, A. M., Dixon, A. F. G. & Thornhill, W. A. (2000) Alate production by aphids on sugar beet: how likely is the evolution of sugar beet-specific biotypes? *Journal of Applied Ecology*, 37: 40-51.

Williams, I. S. & Dixon, A. F. G. (2007) Life cycles and polymorphism. In: *Aphids as crop pests* (eds. van Emden, H. F. & Harrington, R.). CAB International Wallingford, pp. 69-85.

Wilson, D. S. (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, 73: 1984-2000.

Wise, M. J. & Weinberg, A. M. (2002) Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology*, 27: 115-122.

Wright, S. (1940) Breeding structure of populations in relation to speciation. *The American Naturalist*, 74: 232-248.

Yee, D. A., Taylor, S. & Vamosi, S. M. (2009) Beetle and plant density as cues initiating dispersal in two species of adult predaceous diving beetles. *Oecologia*, 160: 25-36.

Zera, A. J. & Denno, R. F. (1997) Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology*, 42: 207-230.

Zhang, S.-Z., Li, J.-J., Shan, H.-W., Zhang, F. & Liu, T.-X. (2012) Influence of five aphid species on development and reproduction of *Propylaea japonica* (Coleoptera: Coccinellidae). *Biological Control*, 62: 135-139.

Zheng, C. Z., Weisser, W. W., Harri, S. A. & Ovaskainen, O. (2009) Hierarchical metapopulation dynamics of two aphid species on a shared host plant. *American Naturalist*, 174: 331-341.

ACKNOWLEDGMENTS

At the outset, my thanks to GOD, the beneficent and the merciful, for granting me the wisdom, health and strength to undertake this research task and for providing me with the opportunity to step into the fascinating and rewarding world of scientific research.

I would like to express my gratitude to my supervisor, Prof. Dr. Wolfgang W. Weisser, who gave me the opportunity to work in his group in Jena and later in Freising and complete my doctoral studies. His expertise, knowledge, understanding and patience added considerably to my graduate experience. He is the one who truly made a difference in my life. It was under his sponsorship that I developed a focus and became more interested in ecology. He provided me with direction, technical support and became more of a mentor and friend than a supervisor. His constant encouragement, support, and invaluable suggestions made this work possible, and indeed successful.

Special thanks also to Prof. Dr. Hugh D. Loxdale, who enthused me during the time. I am much indebted for his valuable advice on my work, and for spending his precious time reading and editing my manuscripts, more especially in providing me with helpful comments and advice. I doubt that I will ever be able to express my appreciation fully, but I owe him my eternal gratitude.

It is my further great fortune to acknowledge the support of two special individuals. Words fail me to express my gratitude to Drs. Sharon Zytynska and Sebastian Meyer for their generous support, encouragement, understanding and precious friendship. Thanks are also due for kindly providing me with statistical advice at critical times during the analysis of the data and for helping me in structuring this thesis.

I would like to thank Prof. Boris Schröder, Prof. Christoph Vorburger and PD. Dr. Thomas Hovestadt for their time and effort in reviewing this work.

Thanks also to Sylvia Creutzburg for her support, technical help and for providing greenhouse and lab facilities for my experiments; and to Mrs. Brigitte Grimm and Mrs. Maria Heilmeier for their help and support.

Moving to Freising was a major event of my doctoral study. I would like to thank all the people that help me make this transition as smooth as it actually turned out. In my new home, I made many new friends who helped me and my family in every step of my scientific progress and life. I am indebted to them all.

I just have a limited space to express my gratitude to all the many other people who helped and supported me and exchanged their knowledge, skills and invaluable assistance during my stay in Germany. Alas, I am unable to name everyone individually and thank them for everything that they did for me, but nevertheless I would like to take the opportunity to express my special thanks to Christoph, Claudia, Holger, Iris, Katja, Manfred, Marco, Martin, Nadja, Nicola, Petra, Werner and to the famous and highly prized Jena group, Anja, Denise, Franklin, Gerlinde, Ilka, Juliane, Kerstin, Lars, Rose & Silke. We had nice times together, including lots of stories and much humour, which will be always remain in my memory.

I would like to thank my best friends, Drs. Seyed Massoud Madjdzadeh and Adalbert Balog for their constant support and valuable advice.

My doctoral study was supported by the Iranian Ministry of Science, Research and Technology. This research would undoubtedly not have been possible without this financial support.

I wish to express my love and gratitude to my wife, Nafiseh, and my beloved family for their understanding and endless love. I am deeply and forever indebted to my parents and my grandmother for their love, support and encouragement throughout my entire life. I am also very grateful to my brothers Mojtaba, Moein and Mohammad Mahdi. I doubt that I will ever be able to express my appreciation fully, but I owe them my eternal gratitude.

Last, but by no means least, thanks to my beautiful, wondrous, lovely daughter, Zahra, for giving me unlimited happiness and pleasure. I offer my immense gratitude for her unconditional love and her delightful diversions. Thank you my darling for your patient during this period and making it all worthwhile.

CURRICULUM VITAE

First Name: Mohsen

Surname: Mehrparvar

Date of Birth: 22 September 1979

Place of Birth: Kerman, IRAN

Sex: Male

Marital Status: Married, One child

Nationality: Iranian

Address: Department of Ecology, Institute of Science and High Technology & Environmental Sciences, Graduate University of Advanced Technology, Kerman, Iran.

Postal code: 7631133131 P.O.Box: 76315-117

E-mails: *mehrparvar@aphidology.com*
mohsen.mehrparvar@tum.de

Education

- 2009- Present Ph.D. Student in Ecology, Technische Universität München, Germany.
- 2002-2005 M.Sc. in Agricultural Entomology, Isfahan University of Technology, Iran. Thesis: Bioecology of *Macrosiphum rosae* and rose aphid fauna in Isfahan, Iran.
- 1997-2002 B.Sc. in Plant Protection, Shahid Bahonar University of Kerman, Iran. Senior Project: Preparation of pictorial software of Iranian agricultural pests.

Titles & positions

- November 2009 – Present

  Subject Editor, North-Western Journal of Zoology. Oradea, Romania.

- September 2005 – April 2009

  Academic staff, Department of Ecology, International Center for Science, High Technology & Environmental Sciences. Kerman, Iran.

October 2008 – April 2009

  Assistant of Research Institute of Environmental Sciences. Kerman, Iran.

- November 2007 – October 2008

  Director of Research and Technology administration, International Center for Science, High Technology & Environmental Sciences. Kerman, Iran.

- February 2005 – July 2008

  Lecturer, Department of Plant Protection, College of Agriculture, Shahid Bahonar University of Kerman. Kerman, Iran.

Honors & awards

- Receiving a scholarship by the Ministry of Science, Research and Technology of Iran for doctoral study in foregin countries in 2008.
- The best researcher of International Center for Science, High Technology & Environmental Sciences in 2007.
- The first–best student graduated in Agricultural Entomology, Isfahan University of Technology (IUT) (in M.Sc. degree, 2005).
- Receiving a fellowship by Isfahan University of Technology (IUT) in 2003.

Research experiences

- Morphometric analysis of populations of black legume aphid , *Aphis craccivora* (Hemiptera: Aphididae) on different host plants (2008).
- Morphological analysis of populations of *Macrosiphoniella sanborni* (Homoptera: Aphididae) in Iran (2007-2008).

- Investigation of biodiversity and geographical distribution of aphid species of rangelands and wild plants in the North of Kerman province (2006-2008).
- Collection and identification of pests (aphids) of ornamental plants and their natural enemies in Isfahan landscape (2004-2006).
- Collection and identification of insects of wild pistachio forests in Kerman Province (2000-2002).

Graduate student's thesis advisor

- Goodarzifar, Z. (2010) Study of aphid fauna (Hem.: Aphididae) associated with wild plants family Asteraceae in North-West of Fars province. Shahid Bahonar University of Kerman, Iran.
- Ganjalikhani, S. (2009) The study of population fluctuations of the wheat aphids (Homoptera: Aphididae) and bioecology of their important parasitoids (Hymenoptera: Aphidiinae) in Kerman. Zaboul University, Iran.
- Barahoei, G. H. (2009) A study of biodiversity of aphid parasitoids (Hymenoptera: Braconidae) in Kerman province. Shahid Bahonar University of Kerman, Iran.

Teaching experience

Teaching courses for undergratuate students in: Entomology, Technology of chemical control, Pests of garden plants, Pests of agricultural crops and Pests of stored products. In Shahid Bahonar University of Kerman, Iran.

Membership in professional societies

- 1999-Present: Member of Entomological Society of Iran.
- 2006-Present: Member of Iranian Society of Biology.

Research interests

- Aphid ecology especially community ecology of aphids and their interactions with other insects such as natural enemies and mutualistic ants.
- Systematics and biodiversity of aphids (traditional and molecular systematic).

LIST OF PUBLICATIONS

Journal publications

- **Mehrparvar, M.**, Zytynska, S. E. & Weisser, W. W. (2013) Multiple cues for winged morph production in an aphid metacommunity. *PLoS ONE*. **8(3):** e58323.
- **Mehrparvar, M.**, Mahdavi Arab, N. & Weisser, W. W. 2013. Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing? *Biological Control*. **65:** 142-146.
- Balog, A., **Mehrparvar, M.** & Weisser, W. W. 2013. Polyphagous predatory rove beetles (Coleoptera: Staphylinidae) induce winged morphs in the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae). *European Journal of Entomology*. **110(1):** 153-157.
- Barahoei, H., Madjdzadeh, S. M. & **Mehrparvar, M.** (2012) Aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) and their tritrophic relationships in Kerman province, Southeastern Iran. *Iranian Journal of Animal Biosystematics*. **8(1):** 1-14.
- **Mehrparvar, M.,** Madjdzadeh, S. M., Mahdavi Arab, N., Esmaeilbeygi, M. & Ebrahimpour, E. 2012. Morphometric discrimination of Black Legume Aphid, *Aphis craccivora* Koch (Hemiptera: Aphididae), populations associated with different host plants. *North-Western Journal of Zoology*. **8(1):** 172-180.
- Barahoei, H., Madjdzadeh, S. M. & **Mehrparvar, M.** 2011. Morphometric differentiation of five biotypes of *Lysiphlebus fabarum* (Marshall) (Hymenoptera: Braconidae: Aphidiinae) in Iran. *Zootaxa*. **2745:** 43-52.
- Barahoei, H., Madjdzadeh, S. M. **Mehrparvar, M.** & Stary, P. 2010. A study of *Praon* Haliday (Hymenoptera: Braconidae: Aphidiinae) in south-east Iran with two new records. *Acta Entomologica Serbica*. **15(1)**: 107-120.
- Madjdzadeh, S. M. & **Mehrparvar, M.** 2009. Morphological discrimination of geographical populations of *Macrosiphoniella sanborni* (Gillette, 1908) (Hem.: Aphididae) in Iran. *North-Western Journal of Zoology*. **5(2):** 338 – 348.
- Madjdzadeh, S. M., **Mehrparvar, M.** & Abolhasanzadeh, F. 2009. Morphometric discrimination of host–adapted populations of *Brachycaudus helichrysi* (Kaltenbach) (Hemiptera Aphididae). REDIA. XCII: 143-145.

- **Mehrparvar, M.**, Mobli, M. & Hatami, B. 2008. Seasonal population fluctuations of the rose aphid, *Macrosiphum rosae* (L.) (Hemiptera: Aphididae), on different cultivars of roses and nastaran. *Journal of Science and Technology of Agriculture and Natural Resources*. **12(45)**:711 – 719. [in Persian with English Abstract]

- **Mehrparvar, M.** & Rezwani, A. 2007. A new species of *Macrosiphoniella* and redescription of *Coloradoa heinzei* (Hemiptera: Sternorrhyncha: Aphididae) as a new record in Iran. *Zootaxa*.**1634**: 61 – 68.

- **Mehrparvar, M.** & Hatami, B. 2007. Effect of temperature on some biological parameters of an Iranian population of the Rose Aphid, *Macrosiphum rosae* (Hemiptera: Aphididae). *European Journal of Entomology*. **104**: 631–634.

- **Mehrparvar, M.**, Hatami, B. & Stary, P. 2005. Report of *Aphidius rosae* (Hym.: Braconidae), a parasitoid of rose aphid, *Macrosiphum rosae* (Hom.: Aphididae) from Iran. *Journal of Entomological Scociety of Iran*. **25(1)**: 63 – 64.

Conference contributions

- **Mehrparvar, M.**, Balog, A. & Weisser, W. W. 2011. Interspecific competition in a specialized aphid community. The 41st annual conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ). Oldenburg, Germany. pp 116-117.

- **Mehrparvar, M.**, Mahdavi Arab, N. & Weisser, W. W. 2011. The influence of three specialized tansy aphids on some biological parameters and survival of seven–spotted ladybird and green lacewing. Proceedings of the 2nd Iranian Pest Management Conference (IPMC). Kerman, Iran. pp 20.

- Goodarzifar, Z., Madjdzadeh, S. M. & **Mehrparvar, M.** 2010. Study of aphid fauna (Hem.: Aphididae) associated with Asteraceae in rangelands and deserts of Fars province. Proceedings of the 16th National and 4th International Conference of Biology. Mashhad, Iran. pp 594.

- Barahoei, H., Madjdzadeh, S. M. & **Mehrparvar, M.** 2010. Aphid parasitoid fauna (Hym.: Braconidae) of Kerman Province. Proceedings of the 16th National and 4th International Conference of Biology. Mashhad, Iran. pp 589.

- Ganjalikhani, S., Rakhshani, E., Zamani, A.A. & **Mehrparvar, M.** 2010. Functional response of *Aphidius rhopalosiphi* De Stefani-Perez (Hym., Braconidae) on grain aphid, *Sitobion avenae* (F.) (Hem., Aphididae) under laboratory condition. Proceedings of the 19th Iranian Plant Protection Congress. Tehran, Iran. pp 75.

- Madjdzadeh, S. M., **Mehrparvar, M.** & Abolhasanzadeh, F. 2009. Morphometric discrimination of host–adapted populations of *Brachycaudus helichrysi* (Kaltenbach) (Hem.: Aphididae). 8th International Symposium on Aphids. Catania, Italy. pp 87.

- **Mehrparvar, M.**, Madjdzadeh, S. M., Ebrahimpour, E. & Esmaeil Beygi, M. 2008. Morphometric study of the pea aphid, *Acyrthosiphon pisum* (Hem.: Aphididae) populations feeding on alfalfa in Iran. Proceedings of the 18th Iranian Plant Protection Congress. Hamedan, Iran. pp 66.

- Madjdzadeh, S. M. & **Mehrparvar, M.** 2008. Investigation of morphological variation among the *Macrosiphoniella sanborni* populations induced by geographic and climatic conditions of Iran. Proceedings of the 18th Iranian Plant Protection Congress. Hamedan, Iran. pp 65.

- Mansouri, S. M. & **Mehrparvar, M.** 2008. Host preference of alate individuals of the wheat green aphid, *Sitobion avenae* (Hem.: Aphididae) on different cereals. Proceedings of the 18th Iranian Plant Protection Congress. Hamedan, Iran. pp 416.

- **Mehrparvar, M.**, Madjdzadeh, S. M. & Mahdavi Arab, N. 2008. Morphological variation among the black legume aphid, *Aphis craccivora* (Hem.: Aphididae) populations feeding on different host plants. Proceedings of the 18th Iranian Plant Protection Congress. Hamedan, Iran. pp 67.

- Ganjalikhani, S., Zamani, A. A., **Mehrparvar, M.** & Rakhshani, E. 2008. Study on development, longevity and fecundity of English grain aphid, *Sitobion avenae* (Hem., Aphididae). Proceedings of the 18th Iranian Plant Protection Congress. Hamedan, Iran. pp 455.

- **Mehrparvar, M.** & Hatami, B. 2008. Biodiversity of natural enemies of the rose aphid, *Macrosiphum rosae* (Aphididae), in Isfahan, Iran. Proceedings of the 15th National & 3rd International Conference of Biology. Tehran, Iran. pp 127.

- **Mehrparvar, M.** & Madjdzadeh, S. M. 2008. Intraspecific variation in the black legume aphid, *Aphis craccivora* (Hem.: Aphididae) induced by different host plants (Leguminosae) using morphometric analysis. Proceedings of the 15th National & 3rd International Conference of Biology. Tehran, Iran. pp 126.

- **Mehrparvar, M.,** Mehrparvar, M., Sayahi, S. & Mahdavi Arab, N. 2008. Population fluctuation of the pine aphid, *Eulachnus tuberculostommata*

(Hemiptera: Lachnidae) in Kerman, Iran. Proceedings of the 15th National & 3rd International Conference of Biology. Tehran, Iran. pp 126-127.

- **Mehrparvar, M.**, Madjdzadeh, S.M. & Mahdavi Arab, N. 2007. A survey of aphid fauna on plant family Lamiaceae in Northern half of Kerman province and a new record, *Ovatus mentharius* (Hom.: Aphididae) for Iran. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 139-140.

- **Mehrparvar, M.**, Madjdzadeh, S.M. & Mahdavi Arab, N. 2007. *Aphis pseudopulchella* Blanchard (Hom.: Aphididae): A new record for Iran. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 199-200.

- Madjdzadeh, S.M. & **Mehrparvar, M.** 2007. Organisation of the parasitoid communities associated with *Tetramesa leucospae* (Hym.: Eurytomidae) in Iran. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 245-246.

- **Mehrparvar, M.**, Hatami, B. & Khajehali, J. 2007. Preliminary study of Urban aphid fauna of Isfahan. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 147-148.

- **Mehrparvar, M.**, Rezwani, A. & Naseri, F. 2007. Study of *Artemisia* aphid fauna in northern half of Kerman province and reports of a new species and a new record for Iran. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 197-198.

- Falahati, E., Takkaloozadeh, H.M. & **Mehrparvar, M.** 2007. A survey of aphid fauna of Willow (*Salix* spp.) and Poplar (*Populus* spp.) in Kerman. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 155-156.

- **Mehrparvar, M.** & Hatami, B. 2006. Seasonal fluctuation of the Rose Aphid, *Macrosiphum rosae* (Hom.; Aphididae) population in Isfahan, Iran. 1st Iranian congress of ecology. Tehran, Iran.

- **Mehrparvar, M.** & Hatami, B. 2006. Effect of temperature on some biological parameters of the rose aphid, *Macrosiphom rosae* (Homoptera: Aphididae). Proceedings of the 17th Iranian Plant Protection Congress. Karaj, Iran. pp 282.

- **Mehrparvar, M.**, Mobli, M. & Hatami, B. 2005. Comparison of four varieties of rose according to infestation to the rose aphid (*Macrosiphum rosae*). Proceedings of the 4th Iranian Horticultural sciences congress. Mashhad, Iran. pp 362.

- **Mehrparvar, M.** & Hatami, B. 2005. Seasonal occurrence of the *Aphidus rosae* Haliday (Hym.: Braconidae) parasitoid of *Macrosiphum rosae* L. (Hom.: Aphididae) in Isfahan, Iran. Proceedings of the 2nd International Symposium on Biological Control of Arthropods. Switzerland. pp 118.

- **Mehrparvar, M.**, Iranmanesh, M., Shahidi, G.H. & Kheyrandish, M. 2004. Preparation of a pictorial software about pests of agricultural crops in Iran. Proceedings of the 16th Iranian Plant Protection Congress. Tabriz, Iran. pp 327.