

Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt
Lehrstuhl für Terrestrische Ökologie

The fragrance to rule them all - Insect community dynamics on tansy

Matthias Senft

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To my beloved family.



"The Aphid", painted by my son, Paul - January 2019

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Table of Contents

Summary.....	ix
Zusammenfassung.....	xi
1 Introduction	1
1.1 Community ecology	2
1.1.1 Population and community dynamics.....	2
1.1.2 Species interactions	4
1.1.3 Indirect interactions	5
1.2 Chemical ecology.....	6
1.2.1 Plant volatile organic compounds (VOCs)	6
1.2.2 Plant VOCs and insects.....	7
1.3 Aphid ecology	8
1.3.1 Aphid biology	8
1.3.2 Aphid-plant interactions	9
1.3.3 Aphids and natural enemies	10
1.3.4 Aphids and mutualistic ants	11
1.4 Overall aims and structure of this thesis (<i>thesis rationale</i>).....	12
2 The study system and methods.....	15
2.1 Introduction to case organisms	16
2.1.1 Tansy (<i>Tanacetum vulgare L.</i>)	16
2.1.2 The pink tansy aphid (<i>Metopeurum fuscoviride</i> Stroyan)	17
2.1.3 Mutualistic ants.....	18
2.1.4 Aphidophagous predators.....	19
2.2 Methods	20
2.2.1 Plant chemotype characterization.....	20
2.2.2 Field observational study	21
2.2.3 Performance and preference experiments	22
2.2.4 Exclusion experiment	25
3 Manuscript overview.....	27
Manuscript 1 Habitat variation, mutualism and predation shape the spatio-temporal dynamics of tansy aphids.....	28
Manuscript 2 Plant chemotype mediates herbivore-mutualist interactions via differential host-plant preferences	30
Manuscript 3 Additive effects of plant chemotype, mutualistic ants and predators on aphid performance and survival.....	32
4 Discussion.....	34
4.1 Main findings.....	35

4.2 Seasonal dynamics.....	36
4.3 Aphid dispersal and population development	37
4.4 Species interactions and community dynamics	38
4.4.1 Aphids and their host plant tansy.....	38
4.4.2 Aphids and mutualistic ants	40
4.4.3 Aphids and natural enemies	42
4.5 Aphid metapopulation and community dynamics.....	43
4.6 Conclusion.....	44
5 References.....	45
Appendix A. <i>Curriculum Vitae</i>	61
Appendix B. Included manuscripts.....	64
B.1 “Spatio-temporal dynamics of tansy aphids”	64
B.2 “Preference Experiment”	84
B.3 “Exclusion Experiment”	119

Summary

An ecological community is an assemblage of organisms that interact with each other in space and time. Mechanisms structuring such communities are usually complex because often a myriad of interacting factors affect species composition and abundance simultaneously. Direct and indirect interactions among and within species make it even more complex. However, it is precisely this complexity that makes such community systems so interesting to study. Therefore, the main goal of this thesis was to understand how biotic and abiotic factors and processes influence the community structure and dynamics of aphids, mutualistic ants and their natural enemies on their host plant. Here, a special focus was on the impact of direct and indirect species interactions and how these cascade across different trophic levels (bottom-up and top-down processes).

To do so, an aphid-plant model system was used that consists of a specialized aphid (*Metopeurum fuscoviride* Stroyan) with a classical metapopulation structure on its patchily growing and aromatic host plant tansy (*Tanacetum vulgare* L.). This aphid species is further associated with mutualistic ants (Formicidae) as well as aphidophagous predators (Arthropoda).

The first manuscript shows results of an observational study that evaluates how abiotic and biotic factors affected aphid population dynamics under natural conditions in a population of around 200 tansy plants. Overall, seasonality and precipitation events had a strong influence on the number of aphid colonisation and extinction events, and thus aphid colony development. Differences among host plants regarding size and within-field location affected the spatio-temporal distribution of aphid colonies, *inter alia* through aphid dispersal limitations. Among the most remarkable results are the effects of mutualistic ants on aphid dynamics in this system, especially the increased chance to establish an aphid colony on a plant, where ants were already patrolling beforehand. Another interesting result of this study is that predation was not exclusively driving aphid metapopulation dynamics, as was previously assumed for this system. Thus, predators were only able to drive an aphid colony extinct if the colony was already small.

Tansy is known for its highly diverse chemical phenotype. Based on the similarity of chemotypic profiles regarding 22 terpenoids putatively emitted from specialized glandular trichomes on the plant surfaces, plants can be clustered into four main volatile chemotype classes. It has been shown previously that these are able to affect the tansy insect community. However, so far potential tansy chemotype effects on aphids (e.g. colonisation probability) and the associated insect community dynamics (e.g. presence of mutualistic ants or predators) are mostly shown by correlational studies without controlling for extraneous variables. Therefore, a series of experimental approaches was carried out.

In the second manuscript the reproductive performance and preference of *M. fuscoviride* aphids as well as the preference of their mutualistic ant partner (*Lasius niger* L.) towards twelve different tansy chemotypes representing the four main chemotype classes were tested. The results confirm that aphids and ants exhibit host preferences for different plant chemotypes. While ants showed a strong preference pattern across chemotype classes, aphid preference was not always consistent across chemotypes belonging to the same chemotype class and also did not correlate with aphid performance on the respective chemotype. Although the main chemotype class, and thus the overall similarity of chemical profiles is an important predictor of aphid and ant preferences, small differences among individual compounds will define the outcome of the species composition. However, the effect of plant chemotype is not strong enough to completely inhibit aphid colonisation and ant-tending on less preferred plants in this experimental approach. Nevertheless, when

transferring these results to the field, where aphids and ants are confronted with larger dimensions (e.g. distances and plant sizes), such preferences can structure the plant-aphid-ant community at a very local scale with individual communities forming at the level of the plant.

The third manuscript describes a semi-natural field experiment designed to disentangle bottom-up chemotype effects (i.e. four different tansy chemotypes representing two main chemotype classes) and top-down effects of mutualistic ants and naturally-occurring predators on aphid population dynamics. Different tansy chemotypes directly affected aphid population development, but not colony survival, and indirectly the abundances of mutualistic ants and predators. While more ants were tending aphids on a particular chemotype, this did not alter the effect of ants on aphid population development. In contrast, a higher number of predators indeed had a stronger negative impact on aphid numbers.

In conclusion, the results presented in this thesis emphasize the importance of spatio-temporal constraints and dispersal limitations as well as aphid, ant and predator preferences and population growth in affecting aphid metapopulation structure and dynamics. In addition to aphid preferences, the preference of mutualists and predators further highlights the importance of intra-specific host-plant variation, especially plant chemical diversity, in shaping the whole insect community on tansy in small-scale field sites. Different preferences can affect the spatial distribution of different species in a diverse field of tansy plants, and thus influence the outcome of species interactions and in consequence the success of aphid colonisations and aphid population development. Therefore, the results show that insect species specialized on patchily-distributed host plants and their associated insect community can be structured at the level of the plant, which could lead to metacommunity dynamics across a divers plant population. A better understanding of the dynamics of this non-pest species not only can help to close the gap between theoretical and empirical metacommunity ecology, it might also provide insights into related crop pests, and thus help to develop strategies for pest control.

Zusammenfassung

Eine ökologische Gemeinschaft ist eine Ansammlung von Organismen, die in Raum und Zeit miteinander interagieren. Oftmals beeinflusst eine Vielzahl von Faktoren die Zusammensetzung und die Häufigkeit der verschiedenen Arten einer Gemeinschaft. Darüber hinaus tragen direkte und indirekte Interaktionen innerhalb einer Art und zwischen verschiedenen Arten zur Komplexität solcher Systeme bei. Genau diese Komplexität macht solche Systeme so interessant.

Das Hauptziel dieser Arbeit war es, zu verstehen, wie biotische und abiotische Faktoren und Prozesse die Struktur von Gemeinschaften aus Blattläusen, mutualistischen Ameisen und natürlichen Blattlausgegenspielern auf ihrer Wirtspflanze beeinflussen. Ein besonderer Fokus lag dabei auf den Auswirkungen direkter und indirekter Interaktionen der verschiedenen Arten dieser Gemeinschaft (*Bottom-Up-* und *Top-Down-Prozesse*).

Als Modellsystem diente eine spezialisierte Blattlaus (*Metopeurum fuscoviride* Stroyan) mit einer klassischen Metapopulationsstruktur auf ihrer Wirtspflanze, dem Rainfarn (*Tanacetum vulgare* L.), einschließlich mutualistischer Ameisen (Formicidae) und natürlicher Blattlausgegenspieler (Arthropoda).

Im ersten Manuskript wird gezeigt, wie abiotische und biotische Faktoren die Blattlauspopulationsdynamiken unter natürlichen Bedingungen auf rund 200 Rainfarnpflanzen beeinflussen. Im Allgemeinen hatten Saisonalität und Niederschlag einen starken Einfluss auf die Blattlausdynamiken im Feld. Sie beeinflussten nicht nur die Anzahl der Besiedlungsergebnisse, sondern auch die Auslöschung von Blattlauskolonien auf verschiedenen Pflanzen. Unterschiede zwischen Rainfarnpflanzen hinsichtlich ihrer Größe und Lage innerhalb des Feldes nahmen zusätzlich Einfluss auf die räumliche und zeitliche Verteilung der Blattlauskolonien. Hier spielen mögliche Limitierungen in der Ausbreitungsfähigkeit dieser Blattlausart eine wichtige Rolle. Zu den bemerkenswertesten Ergebnissen dieser Studie zählt der Effekt mutualistischer Ameisen auf die Blattlausdynamik. So erhöhten Ameisen die Besiedlungswahrscheinlichkeit durch Blattläuse auf Pflanzen, auf denen Ameisen bereits im Vorfeld patrouillierten. Ein weiteres interessantes Ergebnis dieser Studie ist, dass der Fraßdruck durch Blattlausgegenspieler nicht ausschließlich die Dynamik der Blattlausmetapopulation bestimmt, wie dies zuvor angenommen wurde. So waren natürliche Fressfeinde nur dann in der Lage eine Blattlauskolonie zu vernichten, wenn die Kolonie bereits klein war.

Der Rainfarn ist bekannt für seinen stark ausgeprägten und vielfältigen chemischen Phänotyp (sog. Chemotypen). In einer vorangegangen Studie konnten die im ersten Manuskript beschriebenen Rainfarnpflanzen in vier Hauptchemotypklassen eingeteilt werden. Diese Einteilung erfolgte auf der Grundlage der Zusammensetzung 22 flüchtiger Duftstoffe (Terpenoide), die von spezialisierten Drüsentrichomen auf der Pflanzenoberfläche abgegeben werden. Es wurde gezeigt, dass diese einen Einfluss auf die assoziierte Insektengemeinschaft (z.B. Blattlausbesiedlung und das Auftreten mutualistischer Ameisen) haben.

Da diese Ergebnisse bislang aber ausschließlich auf Korrelationsstudien beruhen, wurde im Rahmen dieser Arbeit eine Reihe von Experimenten durchgeführt, um die Effekte des Rainfarn-Chemotypes auf die Populationsdynamiken der Blattläuse und der assoziierten Insektengemeinschaft unter Ausschluss externer Faktoren zu untersuchen.

Im zweiten Manuskript wird die Fortpflanzungsleistung und Präferenz von *M. fuscoviride*-Blattläusen sowie die Präferenz ihres mutualistischen Ameisen-Partners (*Lasius niger* L.) auf beziehungsweise gegenüber zwölf verschiedenen Rainfarn-Chemotypen untersucht. Die zwölf Chemotypen repräsentierten dabei die vier Hauptchemotypklassen. Die Ergebnisse

dieser Experimente bestätigen, dass Blattläuse und Ameisen in der Tat bestimmte Chemotypen bevorzugen. Ameisen zeigten dabei ein konsistentes Präferenzmuster gegenüber Pflanzen der verschiedenen Chemotypklassen. Wohingegen die Vorlieben der Blattläuse teilweise gegenüber verschiedener Pflanzen einer Chemotypklasse variierte. Während die Hauptchemotypklasse und somit die Ähnlichkeit des Duftprofils im Großen und Ganzen bei der Wahl einer Pflanze eine wichtige Rolle spielt, entscheiden am Ende quantitative Unterschiede in einzelnen Duftstoffen über das Ergebnis der Spezieszusammensetzung auf einer Pflanze. Obwohl Blattläuse bestimmte Chemotypen favorisieren, zeigt diese Studie auch, dass dies nicht direkt mit der Fortpflanzungsleistung auf dem entsprechenden Chemotyp zusammenhängt. Des Weiteren waren in diesem experimentellen Ansatz die Effekte des Chemotypes nicht stark genug, um eine Blattlauskolonisierung auf weniger bevorzugten Chemotypen vollständig zu verhindern und Ameisen kümmerten sich ("melken") auch um Blattläuse auf weniger bevorzugten Chemotypen. Überträgt man diese Ergebnisse jedoch in die Natur, wo Blattläuse und Ameisen mit größeren Dimensionen konfrontiert sind (z.B. Entfernung und Pflanzengrößen), können unterschiedliche Vorlieben die Insektengemeinschaft durchaus auf der Ebene individueller Pflanzen strukturieren.

Im dritten Manuskript wird ein halbnaturliches Feldexperiment beschrieben, welches die Stärke von *Bottom-up*- und *Top-down*-Effekten auf die Populationsdynamik der Blattläuse untersucht. Die Entwicklung von Blattlauspopulationen wurde hierbei auf vier verschiedenen Rainfarn-Chemotypen (*Bottom-up*), die zwei verschiedenen Hauptchemotypklassen angehörten, beobachtet. Dabei wurde die Anwesenheit von mutualistischen Ameisen und natürlich vorkommenden Blattlausgegenspielern kontrolliert (*Top-down*). Der Chemotyp beeinflusste direkt die Entwicklung der Blattlauspopulation, nicht jedoch das Überleben der Kolonien. Zudem beeinflusste er indirekt die Anzahl der mutualistischen Ameisen, die sich um eine Kolonie kümmerten, sowie die Anzahl der Blattlausgegenspieler. Obwohl sich mehr Ameisen um die Blattläuse auf einem bestimmten Chemotyp kümmerten, hatte dies keinen zusätzlichen positiven Effekt auf die Entwicklung dieser Blattlauspopulationen. Im Gegensatz dazu konnte eine gesteigerte Anzahl von Fressfeinden durchaus einen stärkeren Fraßdruck auf die Blattlauskolonie ausüben, was schließlich zu einer stärkeren Reduzierung der Blattlauskolonie führte.

Zusammenfassend zeigt diese Arbeit, dass die Verteilung von Blattlauskolonien sowohl von räumlichen und zeitlichen Einschränkungen, als auch von der Entwicklung der Blattlauskolonien und der Ausbreitungsfähigkeit dieser Art abhängt. Diese Arbeit hebt zudem die Bedeutung der innerartlichen chemischen Variation der Wirtspflanze hervor. Hierbei spielen vor allem unterschiedliche Präferenzen von Blattläusen, Ameisen und Blattlausgegenspielern eine wichtige Rolle. Diese beeinflussen die Verteilung einzelner Arten in diesem System und somit die Artenzusammensetzung und Interaktionen innerhalb der Gemeinschaft und dadurch auch den Erfolg und die Entwicklung einer Blattlausbesiedlung. Die Ergebnisse zeigen, dass Insektenarten, welche auf heterogene und räumlich getrennte Wirtspflanzen spezialisiert sind, auf Pflanzenebene strukturiert sein können. Dies kann zur Ausbildung einer Metagemeinschaftsstruktur führen. Ein besseres Verständnis der Dynamik dieser Nichtschädlingsart kann nicht nur dazu beitragen, die Lücke zwischen theoretischer und empirischer Forschung zu schließen, sondern kann auch Aufschluss über verwandte Pflanzen-Herbivoren-Systeme geben und so dazu beitragen, Strategien zur Schädlingsbekämpfung zu entwickeln.

1 Introduction

This chapter gives an introduction to ecological communities and how these are shaped by species interactions. It highlights relevant aspects of chemical ecology which plays an important role in plant-insect interactions. Further, it introduces aphid-plant systems as a suitable model for studying mechanism structuring terrestrial insect communities. Finally, this chapter concludes with an overview of the aims and the structure of this thesis.

1.1 Community ecology

What is community ecology? Community ecology – as J.H. Lawton (1999) pointed out with very good reason – is a mess. But let us start at the beginning. It is a discipline in ecology focusing on sets of organisms that interact with each other in a given area (Krebs 1972, Whittaker 1975, Price 1984, Morin 2011). Such ecological communities can be defined in many ways, for instance by physical (i.e. distinct habitat boundaries, e.g. ponds), taxonomic (i.e. indicator species), interactive (i.e. existence of strong interactions), and statistical definitions (i.e. patterns of association; Morin 2011). An important question in community ecology is how different processes and factors influence abundances and the identity of members within and between communities (Morin 2011). These different processes and factors can act on different temporal and spatial scales and can be of an abiotic as well as biotic nature. P. J. Morin (2011) illustrated nicely the hierarchical way in which different factors interact to form a local community: according to that, a local ecological community depends on what the regional species pool has to offer. The latter, in turn, is influenced by evolutionary processes, physiological constraints and historical events. Dispersal ability and habitat selection further determines which species from the regional species pool enters the local community. Intra- and inter-specific interactions among species finally define the outcome of the community composition (Morin 2011). Here, I will focus on the last two hierarchical levels: dispersal, habitat selection and interactions among species in terrestrial communities, or rather plant-herbivore-predator systems.

1.1.1 Population and community dynamics

Potential habitats (i.e. resources) often are patchily distributed (e.g. ponds, islands or fragmented woodlands; Gyllenberg and Hanski 1997, Hanski 1998). In terrestrial systems with herbivores (i.e. small insect herbivores) feeding on a restricted number of plants (i.e. specialists), patchily growing host plants can be considered as islands of suitable habitat surrounded by largely unsuitable habitat (Price et al. 1980, Gripenberg and Roslin 2005). Individuals of a species inhabiting such patchily distributed habitats also often are able to migrate between such habitats (i.e. immigration and emigration), for instance to optimize resource availability (Charnov 1976, Morin 2011). Such species then might show characteristics of a metapopulation (Levins 1969, Hanski and Gilpin 1991, Hanski 1998): a classical metapopulation consists of separated local subpopulations, inhabiting different habitat patches. Occasional migration between separated habitat patches allows colonisation of empty patches (i.e. establishing new subpopulations) while other local subpopulations go

extinct. Therefore, a metapopulation exists in a stable equilibrium between colonisations and extinctions, "a population of unstable populations" so to say (Levins 1969, Hanski 1998).

The classical metapopulation concept assumes that all habitat patches are identical and migration is not affecting local population dynamics (i.e. local subpopulations are largely independent) within a metapopulation (Levins 1969, Gyllenberg and Hanski 1997, Hanski 1998). However, this barely meets the standard of real metapopulations (Gyllenberg and Hanski 1997). Thus, migration can indeed affect local dynamics of metapopulations for instance through rescue effects (i.e. lower risk of extinction of smaller subpopulations due to migration effects; Gotelli 1991), as shown for one of the most intensively studied terrestrial metapopulation species, the Glanville fritillary butterfly (*Melitaea cinxia* L.; Hanski et al. 1994). Furthermore, patch heterogeneity, especially intraspecific trait variation in host-plant species (i.e. resource) could have a significant ecological impact on population and community dynamics (Bolnick et al. 2011). Thus, habitat patches (e.g. plant patches) may differ in a number of traits, comprising abiotic and biotic factors, including patch size and quality, but also competing, predatory and mutualistic species (Hanski and Gilpin 1991). This led to the development of so called structured metapopulations models, that also consider patch heterogeneity and migration effects (Hanski et al. 1994, Gyllenberg and Hanski 1997).

The metacommunity concept expands this view by including sets of interacting species ("a community of metapopulations"; Hanski and Gilpin 1991). Here, infrequent dispersal of individuals of a set of interacting species between habitat patches occurs, and different members of the community go sporadically extinct on some habitat patches and (re-) colonise others (Leibold and Miller 2004, Leibold et al. 2004, Holyoak et al. 2005). So far, research on metacommunities is based on four non-mutually exclusive paradigms based on different levels of species movement and habitat patch diversity ("patch-dynamics", "species-sorting", "mass-effects" and "neutral effects" paradigms; Leibold et al. 2004). However, especially in terrestrial communities different species are often subjected to different dispersal rates, home-ranges and degrees of patch connectivity (Stroud et al. 2015), and thus it is often difficult to scale-up from metapopulations to metacommunities (Leibold and Miller 2004). Therefore, metacommunity research is still an ongoing field of debate and theoretical work needs still to be empirically confirmed (Leibold et al. 2004). To be able to understand metapopulation and metacommunity dynamics it is crucial to understand what biotic and abiotic factors influence colonisation and local extinction events of community members on individual patches.

1.1.2 Species interactions

Alongside environmental (e.g. disturbances) and spatio-temporal factors, intra- and interspecific interactions are drivers of population and community dynamics (Hunter and Price 1992, Leibold and Miller 2004, Holyoak et al. 2005, Mutshinda et al. 2009). Once individuals of different species inhabit the same patch, species within such an ecological community can directly interact in various ways, including competitively, predatorily, herbivorously or parasitically, commensalistically or mutualistically (Morin 2011). Here, I will focus on predation, parasitism and herbivory (Fig. 1a), which are interactions between species where one partner benefits (consumer) and the other is harmed (prey or plant), as well as mutualism (Fig. 1b), an interaction from which both partners mostly benefit. These direct interactions are by no means only unidirectional or always bring the same advantage/disadvantage. While, for instance, herbivory in most cases negatively affects a plant and benefits the consumer herbivore, the plant effect on the consumer herbivore itself can vary. As herbivores directly depend on plants, plant-derived differences (i.e. resource-based) can have large impacts on herbivores and affect herbivore population dynamics or structure. One example would be that the consumer herbivore has a lower performance when feeding on a certain plant, compared to when feeding on another one (e.g. different species, variety, genotype, phenotype, chemical variability, quantity or quality; Awmack et al. 1997, Awmack and Leather 2002, Johnson 2008).

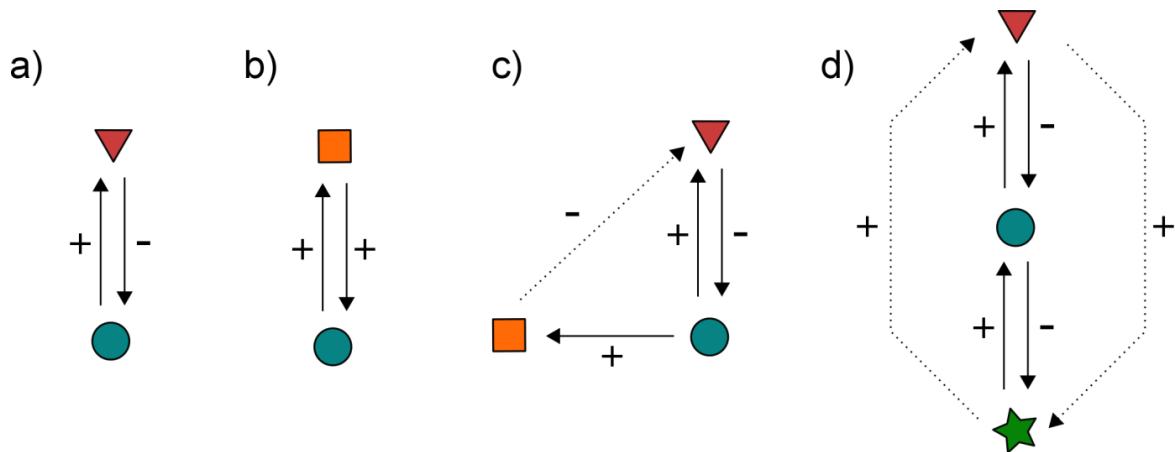


Fig. 1. Examples of direct and indirect interactions in ecological communities. Stars represent primary producers (e.g. plants), circles herbivores, triangles predators or parasitoids and squares mutualists. Direct interactions are represented by solid lines and indirect interactions are indicated with dashed lines. a) Predation, parasitism and herbivory. b) Direct positive effects in mutualistic relationships. c) Potential indirect effects in a species combination containing herbivores, predators and a mutualistic. d) Indirect effects in trophic cascades.

In addition to such bottom-up processes, herbivore populations are also confronted with regulating top-down forces arising from predation, parasitism or mutualism (Schmitz et al. 2000, Weisser 2000, Winder et al. 2001, Pillai et al. 2012). It is assumed that predators play

a major role in regulating herbivore populations, either directly through affecting herbivore population growth, decreasing abundances, potentially leading to local extinctions or indirectly by affecting the herbivore behavior, and thus altering herbivore distribution (e.g. herbivores colonizing enemy-free space; Nomikou et al. 2003).

In many systems it is still under debate whether bottom-up, top-down or both forces control abundances and the distribution of herbivores in terrestrial systems (Walker and Jones 2001). Often, it depends on the developmental stage of the focal herbivore (Walker and Jones 2001). However, researchers likely approach such tritrophic interactions affecting population development and community composition from a single perspective only or favor one of the two forces (i.e. bottom-up or top-down acting forces; Hunter and Price 1992, Walker and Jones 2001). As it is more likely that rather both forces act in concert in natural terrestrial systems leading to the observed pattern of species distribution and dynamics, a more holistic approach is needed (Hunter and Price 1992, Walker and Jones 2001). In consequence, we should consider both forces (i.e. bottom-up and top-down) simultaneously (e.g. assessing their relative importance), and also taking into account that forces may act directly or indirectly across trophic levels (e.g. plant affecting herbivore-predator interactions; Mooney and Singer 2012).

1.1.3 Indirect interactions

Alongside direct pairwise interactions among species within an ecological community, also indirect, cascading interactions can influence the outcome of the community composition. Such indirect interactions can be of an abiotic (e.g. change in environmental conditions affect species abundances in an interacting community; Tylianakis et al. 2008, Walther 2010) or biotic nature. The latter occur when one species (donor) influences another species (receiver) via a third, intermediate species (transmitter; Abrams 1987). These indirect effects possibly exist in every complex community with more than two species, and can have impacts on abundances, dynamics, behavior and genetics of the receiver species (Fig. 1c-d; Morin 2011). Wootton (1994) defined two types of indirect interactions: "interaction chain indirect effects" where the donor species (e.g. plant) leads to a change in the abundance of the transmitter species (e.g. herbivore) which in consequence affects the receiver species (e.g. predator; also described as "density-mediated indirect effects"; see Mooney and Agrawal 2008, Mooney and Singer 2012, Moreira and Mooney 2013); and "interaction modification indirect effects" where the donor indirectly affects the receiver species without changing transmitter abundances, e.g. through behavior or trait modifications leading to a change in the per capita effect of the transmitter on the receiver species ("trait-mediated indirect effect"; also see Mooney and Agrawal 2008, Mooney and Singer 2012, Moreira and

Mooney 2013). Thus, plants (donor) can affect herbivore traits (transmitter) leading to an altered predator (receiver) susceptibility. This can be negative for herbivores (i.e. increased predator susceptibility; Fig. 1d) or positive, for instance when herbivores sequester plant secondary compounds (Brower et al. 1967, Mooney and Singer 2012). Another example would be when plants (donor) affect predator traits (transmitter), for example by providing extrafloral nectaries and in doing so, increasing the predators longevity and searching efficiency which in consequence negatively affects the prey (receiver; Siekmann et al. 2001).

In summary, bottom-up effects arising from host-plants variation can affect herbivore populations in various direct and indirect ways, and thus are able to change species interactions, population and community dynamics (Karban 1992). Here, variability in host-plant chemistry is a key factor.

1.2 Chemical ecology

Chemical ecology deals with chemical interactions between organisms and their environment, mostly focusing on chemical compounds involved in the interaction within and between different species (e.g. communication; Harborne 1993). Remarkably, plants produce around 80% of all known natural chemical compounds, so called secondary plant compounds. (Harborne 1993).

1.2.1 Plant volatile organic compounds (VOCs)

The myriad variety of secondary plant compounds arises from basically only a few main metabolic pathways (Paiva 2000, Moore et al. 2014). Among nitrogen-containing, phenolic or acetylenic secondary plant compounds; the largest and most diverse group of secondary plant compounds comprises terpenes (syn. terpenoids, isoprenoids; Dudareva et al. 2004, Schoonhoven et al. 2005, Moore et al. 2014). The latter can be classified based on the number of subunits: monoterpenes, sesquiterpenes, diterpenes, triterpenes, *et cetera* (Schoonhoven et al. 2005). Monoterpenes and sesquiterpenes are often part of plant essential oils and contribute to a plants' characteristic odor profile (Dudareva et al. 2004, Schoonhoven et al. 2005). However, many monoterpenes and sesquiterpenes are toxic, and therefore need to be stored in special cavities, like glandular trichomes on the plant surface to prevent autotoxicity (Schoonhoven et al. 2005). Some of these constantly emit secretions, and thus VOCs; others only after wounding or induction (e.g. stress-induced active biosynthesis and emission; Turlings et al. 1990, Turlings and Tumlinson 1992, Holopainen and Gershenzon 2010, Loreto and Schnitzler 2010).

A plants' characteristic odor profile can be composed of up to several hundred ubiquitous (e.g. green leaf volatiles; Visser and Avé 1978) and species-specific VOCs (Pichersky and Gang 2000). Quantitatively, often only a few VOCs dominate a plants' odor profile, nevertheless, also minor compounds ("satellite compounds", i.e. less abundant; Kleine and Müller 2011) contribute to the overall odor profile (Buttery and Ling 1984). Interestingly, the quantity and combination of VOCs contributing to the overall chemical odor profile of a plant can differ among closely related taxa and even between individuals within one species (Henderson 1986, Holopainen et al. 1987b, Storer et al. 1993, Raguso and Pichersky 1995), leading to the definition of so called different plant chemotypes (Forsén and Von Schantz 1973).

Therefore, VOCs provide a good basis for differentiation between host and non-host plants (Visser and Avé 1978, Nottingham et al. 1991) and can *inter alia* serve as indicator for host plant quality (e.g. infestation) in insect-plant interactions (Myers 1985, Fitt 1989, Blaakmeer et al. 1994, Takabayashi et al. 1994).

1.2.2 Plant VOCs and insects

As plants maintain a relatively sessile lifestyle, they were in the need of developing a vast array of direct and indirect defense mechanisms, for instance against pathogens and herbivory. Here, the myriad variety of secondary plant compounds, like VOCs, offers a wide range of possibilities. Plants have, for instance, toxic compounds as well as compounds with a deterrence or anti-feedant activity at their disposal (Bennett and Wallsgrove 1994, Martin and Bohlmann 2005). In addition to such direct defense mechanisms, plants also use VOCs for indirect defense, for instance, for communicating within the same plant (i.e. internal) and between neighboring plants (intraspecific communication) in response to an attack to induce systemic resistance (Riedlmeier et al. 2017), or to communicate with higher trophic levels (i.e. inter-specific communication using infochemicals) to attract for example natural enemies of herbivores (Paré and Tumlinson 1999, Ninkovic et al. 2001, Linhart et al. 2005, de Vos and Jander 2010, Holopainen and Blande 2012).

However, some herbivores do not only avoid toxic or unfavorable secondary plant compounds, like VOCs, they also have evolved mechanisms to exploit them, for instance by using them as nutrients, incorporating them into their own defense mechanism or using them to locate their host plant (Gauld et al. 1992, Bennett and Wallsgrove 1994, Dyer 1995). Because, in addition to visual cues, insects highly depend on chemoreception in order to find food sources or oviposition sites or during communication (e.g. detection of mating partners; Schoonhoven et al. 2005). Ecological relevant compounds in insect host location are

probably the ones constantly emitted, as they provide a more reliable VOC profile (i.e. not depending on induction; Clancy et al. 2016). Furthermore, the identification of a suitable host plant by (phytophagous) insects is most often based on the composition and quantity of ubiquitous compounds within the VOC profile and only rarely based on species-specific VOCs (Bruce et al. 2005, Bruce and Pickett 2011).

In summary, different plant chemotypes (volatile secondary plant compounds), but also different metabotypes (non-volatile secondary plant compounds) play an important role in plant-insect interactions, e.g. by affecting herbivore health, growth, behavior or population dynamics ("allelochemicals"; Whittaker 1970, Clancy et al. 2016, Clancy et al. 2018). Their effect can not only be restricted to herbivores directly feeding on them, but also on the associated insect community (e.g. higher trophic levels), including predators or mutualistic helpers. In so doing, variation in host-plants chemistry could affect herbivores, which further indirectly affect predators or mutualists via density- and trait-mediated effects (see chapter 1.1.3) or variation in host-plant chemistry could affect the third trophic level directly which in consequence feeds back on aphids via density- and trait-mediated effects (see chapter 1.1.3). Due to its nature, plant-aphid-predator systems are ideal to study such complicated bottom-up and top-down mechanisms.

1.3 Aphid ecology

Aphids are ideal to study direct and indirect effects, arising from bottom-up and top-down forces that influence population and community dynamics in terrestrial environments (e.g. Dixon 1998, Müller and Godfray 1999, Weisser 2000, Kaplan and Eubanks 2005, Zytynska and Weisser 2016). Furthermore, many aphids show evidence of being structured as a classical metapopulation with local extinction and colonisation events, as well as limited dispersal (Addicott 1978b, Weisser 2000, Massonnet et al. 2002, Zheng et al. 2009, Loxdale et al. 2011, Mehrparvar et al. 2014). Therefore, the next sections deal with aphid biology and the biotic interactions with its host plants and the associated insect community aphids are subjected to.

1.3.1 Aphid biology

Aphids are small, soft-bodied and phloem-sucking insects belonging to the superfamily of Aphidoidea (Hemiptera; Blackman and Eastop 1994, Dixon 1998, Stern 2008). They achieved attention mostly for being major agricultural crop pests (van Emden and Harrington 2007). Their success as crop pests is generally due to their way of propagation: most aphids

undergo a cyclical parthenogenetic pathway, with several asexual generations (i.e. parthenogenetic and viviparous) between each sexual generation (Dixon 1977, Kindlmann et al. 2007). This nearly doubles the reproduction rate compared to solely sexual reproduction (Dixon 1992, Powell et al. 2006).

Some aphids species have unwinged (aptera) and winged (alatae) asexual morphs (Dixon 1977). These different morphs are produced for instance in response to seasonality, overcrowding or predator presence and serve dispersal (Dixon 1977, Mehrparvar et al. 2013b).

Aphids produce mostly large amounts of honeydew, as a waste product incurring by their way of feeding: to be able to concentrate essential nutrients (e.g. amino acids) from indigested nutritionally unbalanced phloem sap, aphids need to process a vast amount of phloem sap and excrete the surplus of not needed phloem compounds via the “production” of honeydew (Auclair 1963). Honeydew is a sugar-rich waste product, also containing free amino acids, amides, proteins, alcohols, auxins, salts, and vitamins (reviewed in Auclair 1963, Way 1963). Honeydew has a huge impact on members of the community associated with honeydew-producing aphids: it is used as food source by mutualistic ants (Way 1963), parasitoids (Wäckers et al. 2008, Tena et al. 2016) and soil organisms (Seeger and Filser 2008) and may attract aphidophagous predators (Raymond et al. 2000). Honeydew composition and quality as food source depends not only on the aphid or the host plant species (Fischer and Shingleton 2001, Pringle et al. 2014, Tena et al. 2018), but also may vary between host plants of the same species (i.e. different genotypes; Mooney and Agrawal 2008). Here, plant-derived differences in phloem chemistry can affect aphid honeydew chemistry (Merritt 1996, Taylor et al. 2012, Pringle et al. 2014).

1.3.2 Aphid-plant interactions

Despite a short phase of dispersal during their life cycle, aphid populations maintain a relatively sessile feeding behavior, and thus directly depend on the quality and nutrients offered by the chosen host plant (Karley et al. 2002). Thus, even small variation in plant traits, genotype or differences in chemical plant characteristics can have impacts on aphids performance (Linhart et al. 2005, Krauss et al. 2007, Johnson 2008, Utsumi et al. 2011, Williams and Avakian 2015, Jakobs and Müller 2017).

The host-plant selection process of aphids is a complex concatenation of different behaviors and a result of interpreting different physical and chemical cues (e.g. VOCs). Powell et al. (2006) structured this selection process in his review into six behavioral stages: first, during flying, a combination of optical and olfactory cues are used for orientation (Pickett et al.

1992); second, after landing on a potential host-plant, the detection of volatiles on the immediate plant surface, gustatory cues (e.g. epicuticular waxes, trichome exudates) but also substrate texture, topology and color can affect an aphids' decision prior to stylet insertion; third, aphids probe epidermal cells by a few quick stylet penetrations; fourth, if the potential host is not rejected yet, a number of deeper stylet penetrations of mesophyll and parenchyma tissues follows; fifth, a phloem sieve element cell is punctuated and a watery saliva is injected to prevent sieve-element occlusion mechanisms (Will and van Bel 2006); and sixth, it follows the acceptance of the phloem sap, extended feeding and further reproduction, or the rejection of the current plant, initiating the search for another potentially more suitable host plant (Powell et al. 2006).

Ninety percent of aphids are monophagous (i.e. no alternating between host plants; Eastop 1972). However, host-plant variation can also arise between individuals of the same species (i.e. intra-specific variation). At least since the 80', variation in natural plant populations is considered in aphid ecology (reviewed in Moran 1981, Whitham 1983, Service 1984, Maddox and Root 1987, Karban 1992). This implicates that aphids potentially visit multiple plants (i.e. all belonging to the same species) in a diverse population before accepting a host, leading to structured aphid populations based on their preferences and the resulting performance on the chosen host plant. In insect-plant systems host-plant preference and performance are often positively linked (Gripenberg et al. 2010). However, this may not apply for every system. Thus, Hemipteran species (including aphids) often only show a weak or no host-plant preference and performance link at all (Leddy et al. 1993, Shishehbor and Brennan 1996, Gripenberg et al. 2010, Zytynska and Preziosi 2011, Zytynska and Weisser 2016). This could be especially the case if a third species, which is able to affect aphid performance (e.g. predator or mutualist), is involved (Lima and Dill 1990, Nomikou et al. 2003, Heisswolf et al. 2005, Van Mele et al. 2009, Gripenberg et al. 2010, Mehrparvar et al. 2018), even more if these show preferences for different host-plants themselves (Clancy et al. 2016).

Although host plant selection and dispersal is mainly attributed to winged aphid individuals, also unwinged aphids can contribute to within-field dispersal (Ben-Ari et al. 2015). For instance, after dropping from a plant (e.g. in response to predator presence; Roitberg et al. 1979), apterous aphids need to be able to effectively locate a host-plant, e.g. discriminate between host and non-host plants or less suitable plants (Gish and Inbar 2006).

1.3.3 Aphids and natural enemies

Aphids are prey to a vast number of aphidophagous predators, including ladybirds (Coleoptera, Coccinellidae) and parasitoids (Hymenoptera, Braconidae, Aphidiinae) as the

most prominent ones (e.g. used in biological control of aphids; Dixon 1977, Dixon 1998). In general, the top-down effect of predators is assumed to play an important role in regulating aphid populations (Weisser 2000, Costamagna and Landis 2006). Here, predators negatively affect aphid densities, and thus contribute to extinctions of local aphid colonies, and thus affecting the aphid metapopulation dynamics (Helenius 1990, Dixon 1998, Weisser 2000). Further, the presence of predators could also affect aphid distribution, e.g. by affecting dispersal (i.e. induction of winged morph production to avoid predation by escape; Dixon and Agarwala 1999, Weisser et al. 1999, Mehrparvar et al. 2013b) or when aphids preferably colonise enemy-free space (Lima and Dill 1990, Fréchette et al. 2012, Vosteen et al. 2016). Interestingly, it has already been shown that predators of aphids might be affected (directly or indirectly) by chemical variation of the host-plant, with predators being associated with different plant chemotypes (Benedek et al. 2015, Bálint et al. 2016).

1.3.4 Aphids and mutualistic ants

Furthermore, aphids are often associated with mutualistic ants (e.g. Herzig 1938, Nixon 1951, Way 1963, Buckley 1987, Flatt and Weisser 2000). In exchange for honeydew, ants protect aphids against natural enemies (i.e. ants attack or carry predators away) and improve the hygienic situation of the tended colony (i.e. by removing sugar-rich honeydew; reviewed in Way 1963). This increases the fitness of aphids by supporting aphid development and fecundity (Way 1963, Stadler et al. 2001, Stadler et al. 2002, Stadler and Dixon 2005). For some aphids this relationship is crucial (i.e. obligatory) and the availability of ants sets limits to the distribution of aphids (i.e. only a fraction of the potential habitat is colonised by aphids; Wimp and Whitham 2001, Mehrparvar et al. 2018). Thus, the presence of ants can positively influence aphid occurrence and performance directly and indirectly by affecting aphid-natural enemy interactions, and thus ants can have a crucial impact on metapopulation and community dynamics in such systems (Nixon 1951, Addicott 1978b, 1979, Buckley 1987, Flatt and Weisser 2000, Stadler and Dixon 2005). However, the presence of ants can also have a negative impact on aphids, once mutualistic turns into antagonistic ant behavior (i.e. ants predate on aphids; Billick et al. 2007, Singh et al. 2016). As already mentioned above, the relationship between ants and aphids can be, for instance, influenced by the quality and quantity of the excreted honeydew (e.g. altered sugar composition; Sakata 1995, Völkl et al. 1999, Fischer et al. 2002, Woodring et al. 2004, Detrain et al. 2010, Pringle et al. 2014), but also by genetic (Johnson 2008) or chemical traits of respective host-plants (i.e. plant secondary compounds; Clancy et al. 2016, Züst and Agrawal 2017). Here, both direct and indirect effects (i.e. mediated through density and or trait-mediated mechanisms) of host-

plant-derived secondary compounds (e.g. volatiles) on mutualistic ants might play important roles (Junker et al. 2011, Moreira and Mooney 2013).

1.4 Overall aims and structure of this thesis (*thesis rationale*)

In summary, plant-aphid-ant-predator community ecology is not a "mess", it is rather a complex combination of multispecies interactions. And while many studies about metapopulation or metacommunity dynamics focus on landscape-scales, specialized aphid-plant systems might offer a suitable model system to study terrestrial metacommunities at a much finer scale (van Nouhuys and Hanski 2002, Zheng et al. 2015): here, individual plant patches can be considered as individual habitat patches surrounded by unsuitable habitat, allowing the study of factors and mechanisms, including patch heterogeneity and biotic interactions. Therefore, this thesis aims to disentangle certain identifiable and ecologically important interactions to elucidate mechanisms structuring aphid populations (*Metopeurum fuscoviride* Stroyan) and the associated insect community on the patchily growing host plant tansy (*Tanacetum vulgare* L.). Here, the focus was on species interactions, especially the role of plant chemical diversity combined with mutualistic ants (*Lasius niger* L.) but also aphidophagous predators in affecting aphid population dynamics; population measures were *inter alia* aphid colonisation events, colony development (e.g. growth) and colony survival.

To unravel the underlying mechanisms structuring aphids, ants and natural enemies on tansy, We first used observational field surveys of naturally occurring aphids in a small-scale field side. This approach helped to get some ideas of the mechanisms involved, but as these results are all correlational, I also carried out controlled experimental approaches to focus on the most interesting mechanisms involved. A detailed description of the study system and the methods used can be found in chapter 2.

Overall, this thesis addresses three main questions (see below) that are answered in the scope of three manuscripts (Fig. 2). A full summary of each included manuscript, as well as the publication status and the authors' contribution can be found in chapter 3. Included manuscripts are attached in the appendix of this thesis (Appendix B1-3). This thesis only contains first author manuscripts (two published and one in revision) to meet the requirements for a publication-based dissertation in accordance with the regulations for the Award of Doctoral Degrees at the Technische Universität München (Promotionsordnung; Appendix 6 [ad § 6 (9)]). However, within the scope of this project further publications have been written in which I was involved as a co-author and which form the basis for publications presented in this thesis or treat further aspects of this model system (Clancy et al. 2016; Ztynska et al. 2019).

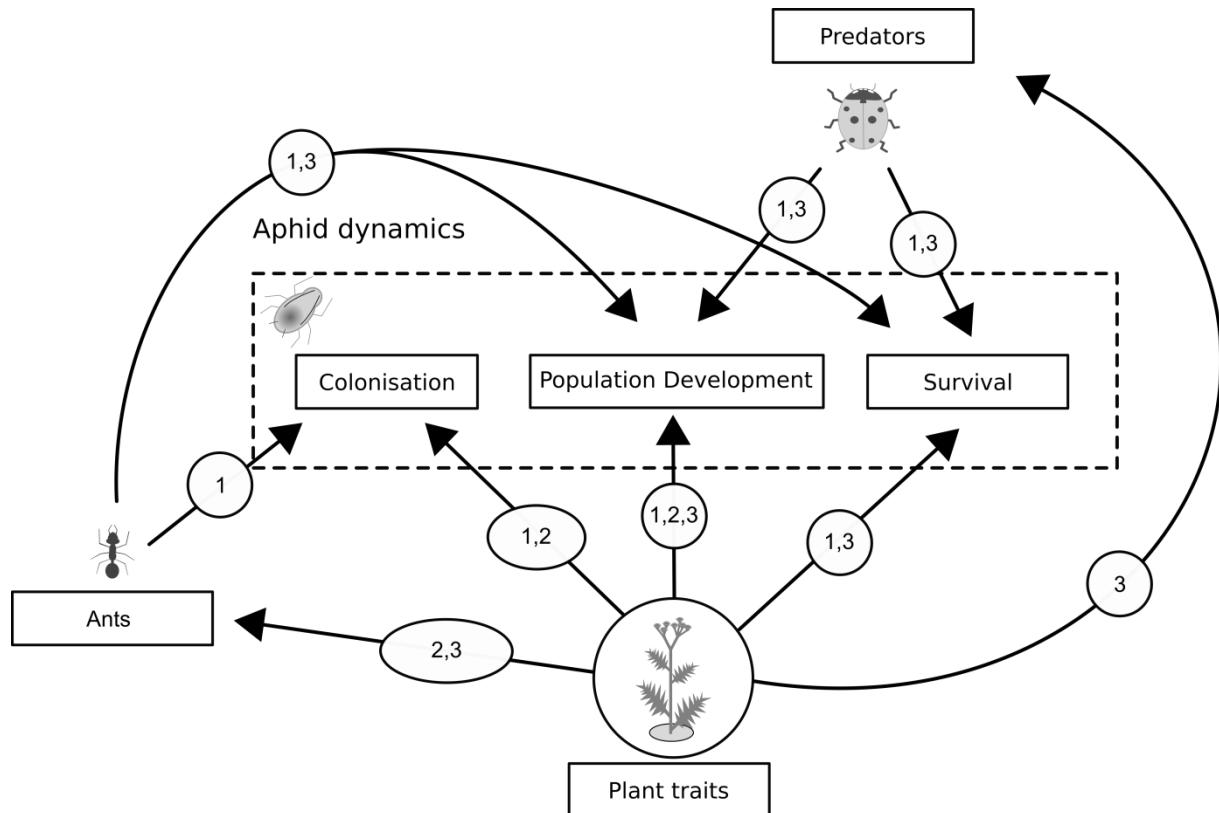


Fig. 2. Manuscript overview. Mechanisms structuring aphid population dynamics and the dynamics of the associated insect community are diverse. This scheme shows which processes are in the scope of each manuscript 1-3 (Appendix B1-3). The main question of each manuscript can be found below and a full summary of each manuscript, including the publication status and the authors' contribution can be found in chapter 3.

Question 1: How do abiotic and biotic factors influence the spatio-temporal dynamics of tansy aphids during the season?

The first manuscript (Appendix B1) shows the direct effects of seasonal timing and precipitation, as well as habitat differences (i.e. plant traits), mutualistic ants and predators on aphid population dynamics. Weekly survey data of insect communities on 178 individual tansy plants on a small-scale field site located in Southern Germany during the season 2014 was analyzed. Four different models were established that describe the seasonal dynamics of tansy aphids on the level of individual plants based on colonisation and extinction events, colony peak population sizes and persistence.

Question 2) Do aphids and their mutualistic ant partner show a distinct preference pattern towards different plant chemotypes?

In a previous study (not included in this thesis), we analyzed plant chemotype diversity in a single small-scale field site (e.g. differences in stored and emitted volatiles) and described effects of plant chemotype on aphid colonization probability and ant encounters under natural conditions (Clancy et al. 2016). This study combined data from the first manuscript (Appendix

B1) on insect communities and data of chemotype profiles of the 176 individual tansy plants and forms the basis for the second manuscript (Appendix B2). As all findings on potential aphid and ant chemotype preferences were so far based on observational surveys and many factors play a role in the field, the second manuscript (Appendix B2) deals with an experimental approach testing the preference of aphids and ants towards different tansy chemotypes and the performance of aphids on different chemotypes. Here, I used four-way choice experiments and as well as performance experiments.

Question 3) How does the plant chemotype affect aphid population development, predator-aphid as well as ant-aphid interactions?

In the third manuscript (Appendix B3), I present results from a semi-natural field experiment to test the relative effects of bottom-up and top-down effects in this plant-aphid-predator system. I tested bottom-up effects of plant chemical variation and top-down effects of the associated arthropod community by controlling the presence/absence of mutualistic ants and presence/absence of naturally-occurring predators on aphid population dynamics.

In chapter 4 I will discuss the main findings presented in this thesis and look at individual results in their entirety and place them in the context of current literature. The findings presented in this thesis have implications for research on patchily-distributed plants hosting specialized insect species, where local insect communities are structured at the level of the plant. This possibly leads to metacommunity dynamics across a plant population. A good understanding of this non-pest species might provide insights to related crop pests and a better understanding of their dynamics.

2 The study system and methods

This chapter gives an overview about the study system and its characteristic features, as well as a general overview of the applied methods. A detailed description of the relevant methods can be found in each manuscript (Appendix B).

2.1 Introduction to case organisms

To find out more about the mechanisms affecting aphid population dynamics and the associated insect community, I used a model system, consisting of the plant tansy (*Tanacetum vulgare* L.), the highly specialized aphid *Metopeurum fuscoviride* Stroyan and its mutualistic ant partners as well as aphidophagous predators and parasitoids. In the following sections I will introduce the key species of this thesis.

2.1.1 Tansy (*Tanacetum vulgare* L.)

Common tansy (*Tanacetum vulgare* L. syn. *Chrysanthemum vulgare* (L.) Bernh.) is a perennial herbaceous plant that belongs to the family of Asteraceae (Fig. 3). It occurs throughout temperate Europe and Asia and is invasive in Northern America (Mitich 1992). It grows in sandy and well-drained soils, often in agricultural landscapes along roadsides, rivers and wastelands (Halliday and Tutin 1989). Tansy propagates by either seed dispersal (sexual) or tussock-forming rhizome growth (asexual) forming clusters (genets) of genetically identical shoots (ramets) of about 30-150 cm (Halliday and Tutin 1989, Weisser and Härtig 2005). These different plant clusters can be easily distinguished in the field (hereafter referred to as “plant”). Plants in this study either belonged to a natural population of tansy plants within an agricultural landscape in Southern Germany at N 48°25'1.51", E 11°46'1.19" (manuscript 1) or were derived from seeds collected in 2013 from the foreaid field site for experimental purpose (manuscripts 2 and 3).



Fig. 3. Tansy illustration in Thomé (1885).

Tansy has a long history in medicinal, insect repellent and chemical research (Mitich 1992). Interest in tansy chemical research started in the 1950s and was driven by its high amount and diverse spectrum of essential oils (Guenther 1952, Rudloff 1963, Von Rudloff and Underhill 1965). The diverse composition of volatile compounds found in tansy led to the classification of different tansy chemotypes (Forsén and Von Schantz 1973). Very early on, the heritability of different chemotypes was investigated, with that the genetic predisposition regarding chemotypes was fathomed (Forsén and Von Schantz 1973, Lokki et al. 1973, Holopainen et al. 1987a). In a previous study (Clancy et al. 2016), we could show that the chemotype profile remains stable, when splitting mother plants into multiple repotted daughter plants (i.e. clones through vegetative multiplication). This chemotype stability allows this plant to be used for several experimental approaches with multiple replicates.

Despite its repellent characteristics, tansy is a food source or habitat for up to 143 different phytophagous insect species (Schmitz 1998, Klausnitzer 2008). Among them, there are several highly specialized aphid species.

2.1.2 The pink tansy aphid (*Metopeurum fuscoviride* Stroyan)

In the focus of this thesis was the pink tansy aphid (*Metopeurum fuscoviride* Stroyan; Fig. 4). It is a holocyclic and monoecious aphid species feeding on tansy and belonging to the family of Aphididae (order: Hemiptera). It is widely distributed in Europe (Heie 1995). After hatching from overwintering eggs in spring (April), fundatrices produce one or two generations of mostly apterous (i.e. unwinged) viviparous females (Mehrparvar et al. 2013b). Then the number of alate (i.e. winged) viviparous females increases abruptly in early summer for a short period of time (around June). Subsequent to this dispersal stage population growth occurs (Mehrparvar et al. 2013b). In late autumn (October and November), oviparous females and apterous males (i.e. sexual morphs) are produced. After mating and laying overwintering eggs the cycle is completed (Mehrparvar et al. 2013b).



Fig. 4. *Metopeurum fuscoviride* feeding on tansy.

2 The study system and methods

Metopeurum fuscoviride is an obligate myrmecophilous aphid species and typically tended by mutualistic ants. Among those, the black garden ant, *Lasius niger* L. (Formicidae) and the common red ant, *Myrmica rubra* L. (Formicidae) are the most common ones (Flatt and Weisser 2000, Fischer et al. 2001, Klausnitzer 2008, Senft et al. 2017). In return for honeydew, ants provide aphids with hygienic and protective services and therefore increase their fitness (Nixon 1951, Addicott 1978a, Buckley 1987, Flatt and Weisser 2000, Stadler and Dixon 2005).

Metopeurum fuscoviride aphid populations have a metapopulation structure on tansy (Weisser 2000, Weisser and Härr 2005, Loxdale et al. 2011). Weisser (2000) showed that both aphids and associated parasitoid populations are subjected to frequent extinctions and colonisation events. Furthermore, aphids are genetically structured more at individual plant level than on site level due to limited dispersal rates (i.e. low inter-population gene flow) and parthenogenetic life cycle (Loxdale et al. 2011).

Furthermore, we could show in a previous study (Clancy et al. 2016) that the tansy chemotype pattern of volatile compounds (i.e. terpenes) that are potentially released into the headspace from storage glands on the surface of the plant (i.e. "compounds likely emitted from storage") affects the early aphid colonisation probability of *M. fuscoviride*. Here, especially minor compounds (i.e. not the main dominant compounds) had stronger effects (Clancy et al. 2016).

Aphids used in this study either belonged to a local population naturally colonizing tansy plants within an agricultural landscape in Southern Germany at N 48°25'1.51", E 11°46'1.19" (manuscript 1) or were collected for experimental purpose around the Weihenstephan Campus of the Technical University of Munich, Freising, Germany, and reared under greenhouse conditions at Dürnast Experimental Station, Technical University Munich, Freising, Germany (manuscripts 2 and 3).

2.1.3 Mutualistic ants

The black garden ant, *Lasius niger* L., belongs to the family of Formicidae and has a holarctic distribution. It is the most common ant species in Europe (Wilson 1955, Collingwood 1979). *Lasius niger* forms single-queened (monogyny) nests with up to 10,000 workers, often in human disturbed areas, woodlands and pastures (Collingwood 1979). It builds earthen mounds or it nests under stones, in rotting wood or walls (Wilson 1955). *Lasius niger* is an aggressive ant species and outcompetes other ant species (Binz et al. 2014). This ant species feeds on insect remains, floral nectar, fruits and homopteran excretions (i.e. honeydew; Wilson 1955, Collingwood 1979).

2 The study system and methods

The European fire ant, *Myrmica rubra* L., also belongs to the family of Formicidae and has a holarctic distribution. However, in northern areas it can only be found in warm sheltered zones (Collingwood 1979). In contrast to *L. niger* colonies, *M. rubra* builds polygynous colonies (i.e. multiple queens) with up to a few thousand workers (Collingwood 1979). Nests can be found under stones or in the ground, near riversides and coasts as well as sheltered valleys (Collingwood 1979). This ant has the same food habits as *L. niger* (Collingwood 1979).

For both ant species, we could previously show that their presence on different plants is potentially also affected by the volatile chemotype (i.e. "compounds likely emitted from storage") of tansy plants (Clancy et al. 2016).

Either natural occurring ants (*L. niger* and *M. rubra*) within an agricultural landscape in Southern Germany at N 48°25'1.51", E 11°46'1.19" (manuscript 1) were observed or ant colonies (*L. niger*) were collected around the Weihenstephan Campus of the Technical University of Munich or around Dürnast Experimental Station, Technical University Munich, Freising, Germany for experimental purpose (manuscripts 2 and 3).

2.1.4 Aphidophagous predators

Metopeurum fuscoviride is attacked by common aphidophagous predators, such as ladybirds (e.g. *Coccinella septempunctata* L., Coccinellidae), lacewing (*Chrysoperla carnea* Stephens, Chrysopidae), syrphid larvae (Syrphidae, Fig. 5) and spiders (Araneae) as well as parasitoids, like *Lysiphlebus hirticornis* Mackauer or *Aphidius tanacetarius* Mackauer (Aphidiidae; Starý 1966, Mackauer and Starý 1967, Mackauer and Völkl 1993, Weisser 2000, Klausnitzer 2008, Mehrparvar et al. 2013a, Benedek et al. 2015). There is evidence that the tansy chemotype might affect the whole food web structure on tansy with different predators preferring different plant chemotypes (Benedek et al. 2015, Bálint et al. 2016).

For this study natural occurring aphidophagous predators within an agricultural landscape in southern Germany at N 48°25'1.51", E 11°46'1.19" (manuscript 1) and around Dürnast Experimental Station at N 48°24'32", E 11°43'20" (manuscript 3) were used.



Fig. 5. Syrphid larvae (Syrphidae) attacking a *Metopeurum fuscoviride* aphid.

2.2 Methods

To answer the various research questions regarding mechanisms affecting aphid population dynamics and the associated insect community in the tansy system, a field observational study, semi-natural and fully controlled experimental approaches were carried out. The following paragraph gives a general introduction to the main methods used in this thesis. A detailed description of the methods with all specifications are given in the respective manuscripts (Appendix B).

2.2.1 Plant chemotype characterization

As already mentioned tansy has a diverse set of volatile organic compounds (VOCs). Based on their abundances more than thirty different chemotypes have been already defined (Forsén and Von Schantz 1973, Tetenyi et al. 1975, Abad et al. 1995, Rohloff et al. 2004, Dragland et al. 2005, Kleine and Müller 2011). However, this classification was mostly based on one or few dominant compounds. Non-dominant compounds, so-called satellite compounds, are often neglected and not further considered, especially when it comes to plant-insect interactions (Kleine and Müller 2011, Benedek et al. 2015, Bálint et al. 2016, Jakobs and Müller 2017).

Therefore, in the scope of this thesis, the effect of the whole set of VOCs of tansy, including satellite compounds on aphids, ants and predators was analyzed. The chemotypic analysis of tansy plants was designed and performed by Mary V. Clancy, Jörg-Peter Schnitzler and colleagues at the Helmholtz Zentrum München GmbH, Research Unit Environmental Simulations (EUS), Institute of Biochemical Plant Pathology, Neuherberg, Germany (Clancy

2 The study system and methods

et al., 2016). As the characterization of tansy plants is a central part of this thesis (manuscripts 2 and 3) and the respective paper, which I co-authored, describing this method is not included in this thesis, I will briefly introduce their method:

In a first approach, VOCs were collected from the headspace of undamaged leaves from plants in a field in southern Germany ($N\ 48^{\circ}\ 25'\ 1.51''$, $E\ 11^{\circ}\ 46'\ 1.19''$). The stir bar sorptive extraction method (SBSE) was used (Sandra et al. 2000). Undamaged leaves were individually bagged with polyethylene terephthalate (PET) foil bags and non-polar polydimethylsiloxane coated stir bars (TWISTER; Gerstel, Mülheim an der Ruhr, Germany) were placed within the bag. Emitted VOCs were collected for three hours during the day and further analyzed using gas chromatography mass-spectrometry (GC-MS). The collected VOCs were identified and quantified using their mass spectra and comparing them with available standards, mass spectral and Kovats retention index libraries. A detailed description of sample handling, extraction method, temperature program, and equipment specification can be found in Clancy et al. (2016).

In a second approach, VOCs were directly extracted with hexane from frozen samples of fresh leaves, also collected from plants of the same field site. Collected VOCs were identified and quantified using the same GC-MS approach as described for the SBSE approach (Clancy et al. 2016).

By comparing both VOC collection methods, a differentiation of volatiles that are stored (i.e. not found in the headspace of plants), volatiles that are potentially released into the headspace from storage (i.e. “compounds likely emitted from storage”) and potentially stress-induced volatiles, was possible, as described in Clancy et al. (2016). Based on the relative abundances of the 22 identified compounds “likely emitted from storage”, plants were clustered into chemotype classes by using the *pvcust* function in R (R Development Core Team, 2017). Four main chemotype classes could be identified (Class 1-4; Clancy et al. 2016).

The chemotype characterizations of experimental plants in my experiments were done using compounds, likely emitted from storage, identified by hexane extracted leaf samples and subsequent GC-MS only (manuscripts 2 and 3).

2.2.2 Field observational study

To identify factors affecting natural dynamics of tansy aphids and their associated insect community I followed aphid populations, ants and aphidophagous predators on tansy plants over the whole season in 2014 on a small-scale field site in southern Germany

2 The study system and methods

(N 48°25'1.51"; E 11°46'1.19"). The field site was approximately 1400 m² in size. 178 tansy plants could be clearly distinguished from each other and were marked. Plant vegetation data, such as plant location, plant size, C/N ratio, a measure for plant accessibility (in respect to surrounding tansy plants: a plant surrounded by other tansy plants has a lower accessibility than a plant less blocked by other tansy plants) and plant exposure (in respect to vegetation other than tansy plants that was blocking tansy plants), were assessed. Further, for each marked plant the chemotype was determined by our collaboration partner (see chapter 2.2.1).

Individual plants were followed on a weekly basis from May until October. Here, aphid abundances on the level of the plant, presence of ant species and abundances of aphidophagous predators (identified to family level) were recorded. Data for weekly precipitation events were obtained from a publicly available data base (weather station at N 48°24'32", E 11°43'20"; Bavarian State Research Centre for Agriculture).

The data obtained in this field study were incorporated in manuscript 1 (Appendix B1) and Clancy et al. (2016). A summary of manuscript 1 can be found in chapter 3, including publication status and detailed author contributions.

Manuscript 1 (Spatio-temporal dynamics of tansy aphids; Appendix B1)

In manuscript 1 (Appendix B1) I focus on factors, like seasonal timing, precipitation, as well as habitat differences (plant size, C/N ratio, location and surrounding vegetation), mutualistic ants and aphidophagous predators affecting aphid dynamics. As response variables for modelling aphid dynamics, I used colonisation and extinction events (binomial data) of aphid colonies on the level of the plant as well as their peak population size and persistence (count data). I established generalized linear mixed effect model fits (GLMER) with a binomial error distribution (binomial data) with individual plant as random factor due to repeated measures. For count data I used generalized linear model (GLM) with a quasi-Poisson error distribution. In both cases, I used time, precipitation, plant volume and C/N ratio, accessibility and exposure as well as aphid natural enemies, conspecifics on surrounding plants and the presence of mutualistic ants as explanatory variables. More details regarding the data collection and analysis can be found in manuscript 1 (Appendix B1).

2.2.3 Performance and preference experiments

As many factors influence aphid population dynamics in the field, I tested for differences regarding the performance and the preference of pink tansy aphids and the preference of

their mutualistic ant partner (*L. niger*) towards different tansy chemotypes (see chapter 2.2.1 and Appendix B2 for information about plant chemotype characterization) in a series of controlled performance and four-way choice experiments presented in manuscript 2 (Appendix B2). Twelve different chemotypes belonging to four different chemotype classes (two from class 1; six from class 2; three from class 3 and two from class 4) were used in the experiments described below. These experiments were carried out in May and June 2016 at Dürnast Experimental Station, Technical University Munich, Freising, Germany. In the following sections, I will give a brief overview about the experimental design and the analyses used. A detailed description can be found in manuscript 2 (Appendix B2).

Preference experiment - 4-way choice experiment

In several four-way choice experiments, I tested the preference towards uninfested tansy chemotypes of aphids and ants as well as the tending preference of ants towards aphids on different chemotypes when offering four different chemotypes simultaneously.

Four shoots of different chemotypes were installed in the corners of a quadratic arena (24 x 24cm) surrounded by acrylic walls covered with white cardboard to reduce optical disturbance from the surrounding (Fig. 6). Three different chemotype assemblies (i.e. combinations) were tested: two assemblies that contained four different chemotypes, each belonging to one of the four main tansy chemotype classes, also found in the field study (Clancy et al. 2016) in order to maximize chemotype differences and to test for consistent preferences across chemotype classes; and one assembly that contained three different chemotypes of class 2 and one chemotype of class 3, to test for consistencies among chemotypes across one chemotype class.

To test the preference of aphids, I put thirty aphids (ten adults, ten 4th instar and ten 3rd instar aphids; all reared on a chemotype not used in the experiment) in the middle of the arena and recorded their chemotype choice after 24 hours (i.e. number of feeding aphids on each chemotype). To test the preference of ants, I connected a small colony to the arenas (ants were able to enter the arena in the center of the cage). After settling overnight, I recorded two times for ten minutes (75 minutes between surveys) different ant behaviors to assess their preference towards uninfested chemotypes: I used a point system to quantify ant-plant interactions (walking closer than one centimeter to the plant: one point; touching the plant: two points; climbing up the plant: three points). When I tested the tending preference of ants, I counted the number of tending ants three times between 12 p.m. and 4 p.m. with at least 30 minutes between two surveys. After each preference experiment the biomass of each chemotype within the cage was measured. All preference experiments were repeated

2 The study system and methods

eight to ten times. The data was analyzed using a GLM with a quasi-binomial error distribution (overdispersed data). As response served the number of aphids that chose a plant (or points given for ant-plant interactions or number of tending ants) in combination with the total number or points given within a cage using the cbind function in R. Chemotype class or individual chemotypes and the assembly tested were used as explanatory variables. As covariates I used the measure for biomass, position within the cage, and only when testing ant tending preference, number of offspring.

The influence of each individual volatile (22 compounds) "likely emitted from storage pools" affecting preferences in the 4-way experiments, was analyzed using generalized linear mixed-effect models (GLMERs) with a binomial error distribution ("lme4" package in R; Bates et al. 2015). As response variables I used the same as described in the previous section for the GLMs and as explanatory variables served the relative concentration of each individual volatile and chemotype nested within assembly as random effect. I applied model comparison through likelihood ratio tests to calculate significance levels.

Further details of the experimental design and analysis can be found in manuscript 2 (Appendix B2).



Fig. 6. Experimental setup of the aphid/ant four-way choice experiments.

Performance experiment

In a performance experiment, I tested for differences in the performance (i.e. reproduction) of aphids on different tansy chemotypes. For this purpose three 4th instar (clonal line; previously reared on a non-tested chemotype) were transferred to experimental plants. To disentangle any ant effect, the performance assay was performed without tending ants. Twelve different chemotypes belonging to four different chemotype classes (two from class 1; six from class 2; three from class 3 and two from class 4) were used in this assay and repeated five times

2 The study system and methods

(if not mentioned otherwise). The abundance of aphids on each plant was assessed after ten days. The data was analyzed with a GLM using a quasi-Poisson error distribution with either chemotype class or chemotype as explanatory variable.

I tested whether the mean preference in the 4-way choice (see above) is correlated with the performance of aphids (log-transformed) by using linear mixed effect models (LME) with assembly of chemotypes in the 4-way choice experiment (i.e. different combinations) as a random factor.

Further details of the experimental design and analysis can be found in manuscript 2 (Appendix B2).

2.2.4 Exclusion experiment

To disentangle and evaluate direct and indirect effects of plant chemotype, mutualistic ants and predators on the performance of tansy aphid populations, I carried out an exclusion experiment under semi-natural field conditions presented in manuscript 3 (Appendix B3). I used a fully-factorial randomized block design with aphid populations (starting colony sizes of 25 aphids with a mixed age structure) on four different chemotypes from two chemotype classes (two from chemotype class 2 and two from chemotype class 4; also see Clancy et al. (2016) for more information about main chemotype classes), subjected to two different ant treatments (presence/absence) and predator treatments (presence/absence). Tube-like cages surrounding each plant were designed in the way to give ants access over PVC-tubes connected to an ant colony in the “ants present” treatments and to allow predators to enter the cages via the top of the cages for the “predators present” treatments (see Appendix B3 for details). While ant colonies were actively moved to the experimental site and connected to the “ants present” treatments, aphidophagous predators were allowed to naturally colonize plants in the “predators present” treatments from the surrounding environment (a rectangular meadow with grass and a variety of flowering plants at N 48°24'32", E 11°43'20"). I repeated the 16 different treatments (4 chemotype treatments x 2 ant treatments x 2 predator treatments) five times (five blocks with one ant colony and one repeat of each treatment in randomized order; $N_{total}=80$; Fig. 7).

The experiment was conducted from mid-June until mid-July in 2015. After settling, aphids, ants and predators were counted in each cage on the days 0, 2, 4, 6, 8, 11, 14, 17 and 20 from 9 a.m. to 4 p.m. in a randomized order. The aboveground biomass (dry weight) of each tansy plant was measured at the end of the experiment.



Fig. 7. Experimental setup of the predator/ant exclusion experiment.

I used three different measures for quantifying aphid population performance: initial population growth rate (subtraction of the natural log of the aphid abundance on day eight and the log of the initial aphid abundance, divided by the number of days passed; Agrawal et al. 2004), reflecting the reproduction potential of a colony; final abundance (i.e. log of the difference between the final and the initial aphid abundance), which reflects the overall success; and survival, a measure for colony persistence. The initial population growth rate and the final aphid abundance were analyzed using linear models with either chemotype class or individual chemotypes, ant treatment (P/A) and predator treatment (P/A) as explanatory variables and experimental block (1-5) and plant biomass as covariates.

Aphid colony survival was analyzed using estimates of the different survival curves based on the Kaplan-Meier method. I used the “survfit” function (package “survival”; Therneau, 2015) in R and analyzed the effect of different treatments (chemotypes, ants and predators) on aphid colony survival with a cox proportional hazard model.

Additionally, ant and predator abundances were analyzed using a GLMER with a Poisson error distribution. Here, plant identity was used as random factor due to repeated observations. Predator or ant treatment and chemotype or chemotype class were used as explanatory variables. I established two models, one where I included aphid abundance (during the day of observation) as covariate and one without aphid abundance to be able to differentiate between density- and trait-mediated effects of chemotypes (i.e. effects of chemotypes could be potentially mediated by different aphid abundances; Mooney and Singer 2012, Moreira and Mooney 2013). As fixed effects and covariates, I included experimental block, plant biomass and day of observation in both models.

Further details of the experimental design and analysis can be found in manuscript 3 (Appendix B3).

3 Manuscript overview

This thesis contains three first author manuscripts (Appendix B1-3). For each manuscript the publication status, a short summary and a detailed description of each authors' contribution is given.

Manuscript 1

Habitat variation, mutualism and predation shape the spatio-temporal dynamics of tansy aphids

Matthias Senft, Wolfgang W. Weisser and Sharon E. Zytnyska

Published 2017 in Ecological Entomology, 42, 389-401, DOI: 10.1111/een.12396

Summary

Different factors and mechanisms may affect population dynamics of aphids on patchily distributed host plants. Frequently, local aphid populations go extinct on some patches and aphids also may colonize new patches throughout the season, leading to metapopulation dynamics.

In this manuscript the direct effects of seasonal timing and precipitation, as well as habitat differences and effects of the associated insect community on aphid (meta-) population dynamics were investigated. As a model system, the specialized aphid (*Metopeurum fuscoviride* Stroyan), its host plant (*Tanacetum vulgare* L.) as well as mutualistic ants and aphidophagous predators naturally occurring on a small-scale field site located in Southern Germany in 2014 were used.

178 individual tansy plants were marked and the following plant characteristics were taken: plant size, C/N ratio, location and surrounding vegetation. Individual plants were followed on a weekly basis from May till October by assessing the number of aphids and aphidophagous predators as well as the presence of mutualistic ants.

On the basis of this data covering the whole season in 2014 four different models were established that described the seasonal dynamics of tansy aphids on the level of individual plants based on colonisation and extinction events, aphid colony peak population sizes and persistence.

The results show that seasonal timing and precipitation both had effects on aphid colonisation as well as extinction events and aphid colony persistence. While colonisation events decreased over time and after strong rain events, the number of extinction events increased. Furthermore, plant size and within-field location play important roles in determining the spatio-temporal distribution of aphid colonies. Interestingly, we also found that the presence of both mutualistic ants, *Lasius niger* and *Myrmica rubra*, increased aphid colonisation probability. However, *M. rubra* was not as beneficial for aphids, as aphid colonies tended by this ant species had a reduced colony persistence. We also found that a higher colony size reduced the probability of extinction by predation.

This manuscript points out the importance of dispersal limitation, population growth and the presence of mutualists ants affecting the spatio-temporal dynamics even on a small scale field site in this system.

Author contributions

SEZ designed the field study. MS and SEZ collected the data on plant characteristics. The plant sample preparation for the C/N analysis was done by MS. MS did the weekly surveys of insect communities. Data preparation and initial analysis was done by MS, commented on by SEZ and WWW. Data interpretation was done by MS, SEZ and WWW. MS prepared all figures. All contributed to the first draft, completed by MS and commented on by SEZ and WWW. All authors read and approved the final manuscript.

Manuscript 2

Plant chemotype mediates herbivore-mutualist interactions via differential host-plant preferences

Matthias Senft, Mary V. Clancy, Wolfgang W. Weisser, Jörg-Peter Schnitzler
and Sharon E. Zytynska

Rejected (with option to resubmit) by Oecologia. In revision.

Summary

Intra-specific variation of host-plants can have decisive effects on specialized consumer herbivores, for instance, due to differences in quality as food source or other plant traits affecting herbivore population development (e.g. performance). Herbivores, like aphids, use olfactory cues for orientation during host plant finding and often chose plants that infer a higher herbivore performance. However, herbivores are not only subjected to bottom-up forces, but also to top-down forces arising from natural enemies or mutualistic ants potentially affecting aphid preference and performance.

In this manuscript I analyzed the preference and performance (i.e. reproduction) of the specialized tansy aphid *Metopeurum fuscoviride* Stroyan and the preference of their mutualistic ant partner (*Lasius niger* L.) for twelve different tansy (*Tanacetum vulgare* L.) chemical phenotypes (i.e. chemotypes, defined by the relative abundance of their volatile terpenoids) by using performance as well as 4-way choice experiments.

The results show that aphids differentially prefer different chemotypes and chemotype classes. Here, especially, isomers of terpinenes affect the preference of aphids. This preference is not consistent across overall similar chemotypes and not correlated with aphid performance. Further, the effect of plant chemotype is not strong enough to completely inhibit the colonisation of less preferred plants.

In contrast to aphids, ants showed a more consistent preference pattern towards certain chemotypes that are not occupied by aphids (also across similar chemotypes, i.e. plants of chemotype class 3). This only partly overlaps with aphid preference. However, when aphids were present on different plant chemotypes, ants still show a similar preference pattern, but also will tend aphids on almost all other plants, except for reduced tending on class 4 chemotypes.

This manuscript indicates that while the main chemotype class is overall important, each individual chemotype profile will finally determine the outcome of these plant-insect interactions. It further shows that the plant chemotype directly affects aphid preference and reveals the importance of mutualistic ants in the tansy system, as ants not only respond to aphid colonisation, but also are directly affected by the host-plant chemotype. Transferring these results to a natural environment, where aphids and its mutualistic ants have to deal with larger distances between plants (i.e. beyond a few centimeters), such preferences can structure communities associated with tansy in a chemotypic diverse field at a very local scale. Here, the plant chemotype affects aphids directly and indirectly via the availability of ants on ant preferred and non-preferred plants, as their availability enhances the chance of subsequent and successful aphid colonisation.

Author contributions

This study was designed by MS, SZ, JPS and WWW. The cage design and the experimental implementation was done by MS. Data regarding the performance and preference experiments, as well as data on plant biomass were collected and prepared by MS. Plant samples for chemotype analysis were taken by MVC and MS. MVC performed the GC-MS identification and quantification. MS analyzed the data, prepared all figures and wrote the first draft, commented on by SEZ, WWW and JPS. All authors contributed to the revisions.

Manuscript 3

Additive effects of plant chemotype, mutualistic ants and predators on aphid performance and survival

Matthias Senft, Mary V. Clancy, Wolfgang W. Weisser, Jörg-Peter Schnitzler
and Sharon E. Zytynska

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Summary

Herbivores, like aphids, are subjected to a number of forces affecting their population dynamics. While natural enemies control aphids in a top-down manner, differences in host-plant traits shape aphid populations from the bottom-up. Both forces act simultaneously and often affect each other directly or indirectly across trophic levels leading to cascading effects in tri-trophic interactions.

In this manuscript I used a semi-natural field experiment to disentangle bottom-up effects of different tansy (*Tanacetum vulgare* L.) plant chemical phenotypes (i.e. chemotypes, defined by the relative abundance of their volatile terpenoids) and top-down effects of mutualistic ants and naturally-occurring predators on the population dynamics of the specialized tansy aphid *Metopeurum fuscoviride* Stroyan (i.e. population growth rate, final aphid abundance and colony survival). Further, effects of tansy chemotypes on the third trophic level (mutualistic ants and predators) and their mechanistic were explored. To do so, I used four distinct plant chemotypes and manipulated the presence/absence of mutualistic ants and presence/absence of naturally-occurring predators on these chemotypes and followed abundances of aphids, ants and predators in the different treatments for three weeks.

The results show, that different tansy chemotypes directly affected aphid population dynamics, namely colony growth rates and final aphid abundances but not colony survival. Plant chemotype also affected the abundances of mutualistic ants and predators, indirectly mediated through aphid density (mutualistic ants) and through potential changes in aphid traits (mutualistic ants and predators). While more ants were tending aphids on a particular chemotype (higher ant-aphid ratio), this did not change the overall beneficial effect of ants on aphid population development (higher ant abundance did not increase positive effect on aphids). However, it showed that ants had a preference towards aphids on certain chemotypes. In contrast to ants, predators had an overall negative effect on final aphid abundance and colony survival, and higher abundances were indeed able to affect aphids more strongly (higher aphid reduction when more predators were present).

These results support findings from field observations and confirm the important role of the plant chemotype shaping aphid population dynamics by affecting many species in arthropod communities. Thus, aphid populations can be structured at the level of individual plants leading to spatial effects at very local scales (within field-sites containing a diverse set of different chemotypes).

Author contributions

This study was designed by MS, SZ, JPS and WWW. The cage design and the experimental implementation was done by MS. Data on aphid, ant and predator abundances during the experiments, as well as data on plant biomass were collected and prepared by MS. Plant samples for chemotype analysis were taken by MVC and MS. MVC performed the GC-MS identification and quantification. MS analyzed the data, prepared the figures and wrote the first draft, commented on by SEZ and WWW. All authors contributed to the revisions.

4 Discussion

This chapter summarizes and discusses the main findings of this study and places them in the context of current literature. The results help to better understand metapopulation and community dynamics in terrestrial insect communities inhabiting patchily distributed host plants or habitats, and might provide insights into related pest species.

4.1 Main findings

In this thesis, I used a terrestrial insect model system, consisting of the aromatic and patchily growing host plant tansy, a highly specialized aphid species with a classical metapopulation structure and the associated insect community (mutualistic ants and natural enemies) to explore the effects of environmental factors and biological interactions on its metapopulation and community structure. The focus of this work was in particular on the influence of the plant chemotype in shaping the insect community and affecting aphid population dynamics.

With a series of observational and experimental approaches (Appendix B1-3) I show that the metapopulation structure and dynamics of *Metopeurum fuscoviride* aphids and the dynamics of their associated insect community are shaped by multiple interacting factors and mechanisms. I demonstrate that it is crucial to be aware of them all if we aim to understand the mechanisms of metapopulation and community dynamics in terrestrial insect communities. This implies seasonal and spatial constraints (Appendix B1), intra-specific host-plant variation (Appendix B2-3) and species interactions (Appendix B2-3), of which mutualistic interactions play a very special role.

While seasonal timing and precipitation set general limits to aphid distribution development (Appendix B1), the within-field distribution of aphids was affected not only by the spatial arrangement and patch size of individual plants but also by dispersal limitations of aphids (Appendix B1). Furthermore, inter-specific interactions among species of the tansy community influenced aphid distribution and population development (Appendix B1-3). On the one hand mutualistic ants benefited aphid populations, on the other hand predators negatively affected aphid abundances. Furthermore, intra-specific variation in the terpene volatile profile of tansy plants (i.e. chemotypes) played a pivotal role in shaping aphid populations through directly affecting their performance and host-plant preferences. In addition, the tansy chemotype influenced the occurrence of mutualists and natural enemies via direct and/or indirect effects (Appendix B2-3). Thus, the intrinsic preference of their mutualistic ant partners towards different plant chemotypes (i.e. direct chemotype effect) and aphids feeding on them (i.e. indirect chemotype effect) could finally affect aphid distribution and population development (Appendix B2-3): an ant chemotype preference implicated more ant-plant interactions on certain chemotypes (i.e. presence of ants on certain plant patches) which then enhanced the chance for this obligate myrmecophile aphid species to establish viable colonies on such plant patches where ants were already present (Appendix B1). In contrast to this beneficial effect, the indirect chemotype effect on natural enemies (i.e. preference for aphids on certain chemotypes) led to aphids on certain plants being exposed to a higher predation pressure (Appendix B3). When the aphid colony size was low, then predators were able to drive a colony to extinction (Appendix B1).

4.2 Seasonal dynamics

The results described in manuscript 1 and 3 (Appendix B1 and B3) indicate that aphid metapopulation development on tansy is potentially subjected to various seasonal restrictions. Thus, seasonal timing and precipitation set general limits to aphid dispersal and distribution by limiting aphid colonisation events and by affecting colony persistence and extinctions under natural conditions: as time progressed and after rain the number of colonisation events was reduced and the number of local colony extinctions increased. An important factor regarding the seasonal restrictions of colonisation events in the field is the short timeframe when winged individuals are produced by this aphid species during the early part of the season (Mehrparvar et al. 2013b). Although, the results suggest, that plants also could be colonised in the absence of winged individuals over short distances (discussed later), the number of winged individuals observed in the field was correlated with the number of colonisation events on previously unoccupied plant patches. An early colonization certainly has benefits for aphids, as it allowed aphid colonies to persist for a longer time. As seasonality and rain often go hand in hand, and dispersal (i.e. new colonisation events) happened mostly during a dry spell, the causality between the association between rain and aphid metapopulation dynamics might mostly be due to the rains' effect on colony extinction. As shown for another aphid species, the disturbance caused by rain is a factor not to be underestimated in aphid metapopulation dynamics (Mann et al. 1995).

Another important aspect regarding seasonal dynamics of aphid populations is the seasonal availability of mutualistic ants accompanied by the appearance of predators. As *M. fuscoviride* is an obligate myrmecophilous aphid species, the availability of ants is crucial for viable colonies (e.g. Stadler 2004). Both the observational field study of natural tansy communities (Appendix B1) and the experimental approach exploring plant-aphid-mutualist-predator interactions (Appendix B3) indicated that ants are not always available. Thus, the number of ant encounters in the field under natural conditions and the number of ants tending aphid colonies under experimental conditions decreased between June and July. This change in ant behavior might be due to a change in nutritional needs of ant colonies, as a result of mating flights of ants (Hart et al. 2018) implying that a substantial number of winged ant individuals abandon their nests. This possibly leads to a decrease in the need for sugar-rich resources (Edwards 1951), like aphid honeydew. Similar patterns of aphid colony abandonment and reduced protection by ants are also described elsewhere (Addicott 1979, Stadler 2004, Rico-Gray and Oliveira 2007), where ants were not able to respond to increasing aphid abundances, possibly due to a surplus of sugar-rich sources (Addicott 1979, Rico-Gray and Oliveira 2007). In consequence, aphids are left to themselves increasing their susceptibility to natural enemies. However, such an association between ant colony

development (i.e. mating flights) and aphid colony abandonment needs to be further investigated as I did not explicitly tested for that.

4.3 Aphid dispersal and population development

In addition to seasonal parameters affecting the overall temporal distribution potential (e.g. availability of winged individuals or mutualistic ants), I could show that the spatial within-field distribution pattern of aphids is subjected to a number of structural field characteristics and associated dispersal limitations (Appendix B1). Thus, the location of a plant patch within the field site plays an important role in structuring aphid populations on tansy and allows conclusions about a potential colonisation by aphids to be drawn. Thus, in the beginning of the season it was more likely that more accessible plants (i.e. less blocked by other tansy plants) were colonised (e.g. plants located at the edge of the field). This observation supports the assumption that the described natural aphid metapopulation is a sink-population with winged individuals potentially immigrating from other sites at the regional scale in the beginning of the season, firstly colonizing the most accessible plants (Winder et al. 1999, Fievet et al. 2007). This is further supported by the fact that sexual morphs at the end of the season were scarce and only one colony contributed to the next years' aphid population by potentially producing overwintering eggs.

Furthermore, while more isolated plants, in terms of distance to other occupied plant patches, were predominately colonised by winged aphids (i.e. presence of winged individuals during colonisation), unwinged aphids might also contribute to colonisations of plants patches (i.e. absence of winged individuals during colonisation) in close vicinity of already occupied patches (Zheng et al. 2009, Ben-Ari et al. 2015), especially late in the season. However, it remains unclear whether the absence of winged individuals is due to active (Ben-Ari et al. 2015) or passive (by ants; reviewed in Buckley 1987) migration of unwinged aphids or by winged aphids moving from one plant to another leaving a bunch of offspring on each plant behind. In consequence of short distance migration, new aphid colonies on plant patches more likely established and already existing colonies less likely went extinct when other aphid colonies were close. This not only supports the assumptions that rescue effects contribute to aphid population development (Brown and Kodric-Brown 1977, Gotelli 1991), but also reveals that dispersal limitations and source–sink dynamics in this system potentially influence the within-field distribution of aphids and their metapopulation structure (Utsumi et al. 2011).

Another structural feature which is important for the distribution potential and performance of aphid colonies is the size of a plant patch. I could show that larger plant patches not only

increased the chance of aphid colonisation, such patches also supported larger colonies and lowered the risk of colony extinction (see Holyoak et al. 2005). However, it remained unclear whether it is simple stochastic (i.e. more likely to find a larger plant) or whether larger plants have other beneficial characteristics (e.g. nutrient-wise or less chance for predators to find them on larger plants). Patch size and isolation are both aspects covered by the classical theory about island geography proposed by MacArthur and Wilson (2001), known to affect for instance species abundance in fragmented habitats.

4.4 Species interactions and community dynamics

Relevant drivers of populations and community dynamics besides environmental and spatio-temporal factors are intra- as well as to a certain degree interspecific interactions among members forming these communities (Leibold et al. 2004, Holyoak et al. 2005, Mutshinda et al. 2009). In the following paragraphs interactions among members of the insect community on tansy as well as bottom-up and top-down cascading direct and indirect effects (Mooney and Agrawal 2008, Mooney and Singer 2012, Moreira and Mooney 2013), with a special focus on plant chemotype effects, will be discussed.

4.4.1 Aphids and their host plant tansy

Due to the intimate nature of the aphid-plant relationship, small differences among host-plant individuals (e.g. quality, genotype, chemotype) can have substantial consequences for the aphids' performance on the chosen plant (Linhart et al. 2005, Krauss et al. 2007, Johnson 2008, Utsumi et al. 2011). While the results suggest that differences among tansy plants regarding basic plant chemistry, here the leaf ratio of carbon to nitrogen, did not have a measurable effect on aphid population dynamics or performance under natural conditions (also see Karley et al. 2002, Williams and Avakian 2015, Jakobs and Müller 2017), this study emphasizes the importance of volatile secondary plant compounds in shaping the insect community on tansy.

Previous chemical analyses of tansy field plants, presented in Clancy et al. (2016), a paper I co-authored but did not include in this thesis, led to the identification of 121 volatile organic compounds (VOCs). 22 compounds of them are constitutively and "likely emitted from storage glands" on the plant surface (i.e. compounds not only stored or induced; Clancy et al. 2016). During the host-plant selection process aphids depend on chemical cues (Van Emden 1972, Pickett et al. 1992), therefore it is plausible that such constantly emitted compounds provide aphids with reliable information about the potential host plant (i.e. in contrast to stored or induced compounds; Clancy et al. 2016). Based on the similarity of chemotypic

profiles regarding the 22 VOCs "likely emitted from storage glands", field (Clancy et al. 2016) and also experimental plants (Appendix B2 and B3) could be grouped into four main tansy chemotype classes (class 1-4).

The results in Clancy et al. (2016) further suggest that especially early in the season (i.e. when aphid dispersal was high, due to the presence of winged individuals) aphid colonisation probability was influenced by the plant chemotype: aphids preferably colonized chemotype class 1 and 2 plants under natural conditions. Interestingly, when looking at individual VOCs, especially minor compounds had stronger effects on the aphid colonisation probability compared to main dominant compounds (Clancy et al. 2016). Therefore, it is important for further research to not only consider the main compounds or a subset of compounds when assessing aphid or insect dynamics like it was done in previous studies on this system (e.g. Benedek et al. 2015, Jakobs and Müller 2017):

In line with this presumption, the results I show in the second manuscript (Appendix B2) confirmed experimentally that aphids indeed differentiate between different tansy chemotypes belonging to one of the four main chemotype classes described in Clancy et al (2016). While aphids consistently preferred chemotype class 1 plants and least preferred chemotype class 4 plants (as in the field; Clancy et al. 2016), the preference for chemotype class 2 and 3 plants was inconsistent (between high and low). Interestingly, due to the moderate effect size, aphid preference towards certain plants was not strong enough to completely inhibit the colonisation of less preferred chemotypes. Although contributing, aphid chemotype preference alone does not exclusively explain distribution patterns found in the field (Clancy et al. 2016).

Interestingly, the results further suggest, that, while the main chemotype class is a predictor for aphid preference, the individual chemotype profile, and thus, a few volatile organic compounds will determine the outcome of this interaction. Here, the amount of isomers of two chemical related compounds, terpinenes and terpineols, within the chemotype profile might take over a key role. Thus, aphid colonisation probability under natural conditions (Clancy et al. 2016) and aphid preference in this experiment (Appendix B2) were negatively associated with them, and also might explain inconsistencies among chemotypes of the same chemotype class. Such a negative effect could be due to an insecticidal or insect repellent potential (Choi et al. 2002, Sampson et al. 2005).

Although tansy chemotype profiles play a role during the aphids' decision to colonise a certain plant and aphid colonies perform better on some individual chemotypes (Appendix B3), I found no direct preference-performance relationship (Appendix B2). As found recently by Clancy et al. (2018), while the VOC profile of tansy plants was important in the beginning of the season (during dispersal), other non-volatile metabolites (as identified by untargeted metabolomics) were found to be more important in respect to aphid performance (i.e. colony

growth rates) and thus late-season aphid population dynamics. However, as plant chemotype effects are not only restricted to aphids, directly feeding on them, but also on the associated insect community (e.g. higher trophic levels), including mutualistic helpers and natural enemies, further species-interactions might lead to different performances on individual chemotypes and thus might explain aphid preferences (e.g. enemy-free space, also see chapter 4.4.3; Jeffries and Lawton 1984) and also patterns seen under natural conditions (Clancy et al. 2016).

4.4.2 Aphids and mutualistic ants

Ants are omnipresent and run most terrestrial ecosystems due to their mere abundance and diversity, function as ecosystem engineers and dominance within the insect fauna (Hölldobler and Wilson 1990, Folgarait 1998). Thus, species interactions with ants are common between members of terrestrial communities (Folgarait 1998). Among the most remarkable results of this thesis were the effects of mutualistic ants and their composition on shaping the metapopulation structure of aphids in this system and how this can be influenced by different tansy plant chemotypes. Thus, in addition to the overall seasonal availability of ants (discussed above), the availability of mutualistic ants (*Lasius niger* and *Myrmica rubra*) on different plant patches could have a significant impact on aphid population distribution and development: the presence of scouting ants on a plant patch, not yet occupied by aphids, promoted a subsequent colonisation by aphids on that very plant patch (Appendix B1). The simple presence of ants on not yet colonised plants, probably increases the chance for newly arrived aphids to be discovered fast. Such a fast establishment of this mutualistic relationship should increase the aphids' fitness by reducing predation pressure, increasing fecundity and benefitting development right from the start which then enhances the chance of establishing a viable colony (Stadler et al. 2001, Stadler et al. 2002, Stadler and Dixon 2005). Although potentially tending *L. niger* ants were not in general spatially limited to certain plants or parts of the field site, an ant encounter was more likely (i.e. more often frequented) if an *L. niger* nest was close by, suggesting dispersal limitations for this species as well (plants further away from a ant nest are less frequented by ants). This could further limit the aphid within-field distribution and thus impact their metapopulation structure, as aphid colonisation probability and success highly depend on the availability of ants (also see Wimp and Whitham 2001, Fischer et al. 2015).

The results of the observational study described in Clancy et al (2016) further suggest that the presence of scouting, not yet tending, ants on tansy plants can be influenced by individual volatiles emitted from tansy plants (i.e. VOCs "likely emitted from storage glands"). However, these observations only present a snapshot of the actual situation, especially, as ants are highly mobile and might be missed quite often. Therefore, I also carried out an

experimental approach (Appendix B2) testing the chemotype preferences of *L. niger* ants. These results indeed confirmed an intrinsic preference of these mutualists for different tansy chemotypes (i.e. without aphids). Compared to aphids, ants even showed a more consistent preference pattern towards unoccupied tansy chemotypes with plants of chemotype class 3 being most preferred implicating more plant-ant interactions. In this ant-plant interaction the volatile eucaliptol (dominating class 3 chemotypes) might play a crucial role and might serve as attractant, as shown for other insect species (e.g. ambrosia beetle, *Xyleborus glabratus*; Kuhns et al. 2014). As already mentioned above, more ant-plant interactions can benefit aphids (also see Wimp and Whitham 2001).

Interestingly, when aphids were available on all tested chemotypes, ants showed a weaker, less consistent preference pattern for aphids on different chemotypes and chemotype classes. Although ants still preferred tending aphids on class 3 chemotypes, they will tend aphids on most chemotype classes, with one exception: ants showed reduced tending willingness on class 4 chemotypes. Such a softened preference pattern can arise when aphids on less preferred plants overcome the ants' preference by, for example, offering similar or better honeydew quality or quantity (Cushman 1991, Fischer and Shingleton 2001, Stadler et al. 2002, Vantaux et al. 2011). However, in the field, where ants are confronted with larger scales (i.e. e.g. plant size and distance between individual plant patches) such preferences can lead to differences in the structure of associated communities at a very local scale with different local communities on individual plants.

The results in manuscript 3 (Appendix B3) further confirmed the reduced tending willingness of *L. niger* ants for aphids on class 4 chemotypes and revealed potential mechanism leading to such a pattern. In this semi-natural experimental approach I examined tansy plant chemotype effects of plants belonging to chemotype class 2 and 4 on aphid population development (bottom-up effects), predator-aphid as well as ant-aphid interactions (top-down effects) simultaneously. Ants preferably tended aphids on one class 2 chemotype while having the choice between aphid colonies on two chemotype class 2 and two chemotype class 4 plants. The analysis revealed that both density-mediated and trait-mediated indirect effects of the plant chemotype affect ant tending (i.e. ant abundance). While density-mediated indirect effects mean that the chemotype directly affects aphid abundances which then leads to more ants tending aphids, trait-mediated indirect effects suggest that the plant chemotype alters aphid traits which then had an effect on the number of ants tending (Mooney and Agrawal 2008, Mooney and Singer 2012, Moreira and Mooney 2013). Here the honeydew quality or quantity could differ among chemotypes either being beneficial or unfavorable in respect to ant recruiting (Brower et al. 1967, Fischer and Shingleton 2001, Vantaux et al. 2011, Pringle et al. 2014, Züst and Agrawal 2017). Although more ants were tending aphid colonies on one of the chemotype class 2 plants, higher ant abundances did

not increase the general beneficial effect of ants on aphids in this system (Stadler 2004, Mehrparvar et al. 2014). Thus, aphid colonies tended by *L. niger* ants had in general an increased growth rate and were able to build up higher numbers on every chemotype (Appendix B3).

However, I also found that not every mutualistic ant species brings the same advantage for aphids which can be crucial for aphid population development. Thus, aphid colonies tended by *Myrmica rubra* had a shorter persistence on plants compared to colonies tended by *L. niger* under natural conditions (Appendix B1). It remains unclear what led to this observation. Potential mechanisms could be lower willingness to defend aphid colonies due to higher costs (Stadler and Dixon 2005), competition with other ant species (e.g. *L. niger*, Binz et al. 2014) leading to a disturbance of tending behaviour or *M. rubra* ants simply might shift from tending to predatory behaviour due to nutritional needs (Edwards 1951, Singh et al. 2016).

4.4.3 Aphids and natural enemies

Top-down effects of predators were assumed to play an important role in regulating aphid populations, as in this system (Weisser 2000, Costamagna and Landis 2006, Diehl et al. 2013). Predators negatively affect aphid densities leading to extinctions of local aphid colonies, in consequence affecting metapopulation dynamics (Helenius 1990, Dixon 1998, Weisser 2000). With the results presented here, I could demonstrate that natural enemies are not exclusively driving aphid dynamics in this system (see chapters 4.1-4.4.2). Thus, predators were only able to drive a local colony extinct, when its aphid abundance was already low, which can be the result of a number of reasons shown to affect aphid populations in this and other systems, like dispersal and dispersal limitation (high emigration or low rescue effect; Carter and Dixon 1981, Gotelli 1991, Karley et al. 2004) ant availability (Way 1963), low aphid performance on certain plants (Zytynska and Preziosi 2011), but also repeated predator visits (Meyhöfer 2001).

I also could show that aphid colonies exhibiting higher predator pressure in the field (i.e. higher predator-prey ratios, Appendix B1) or were subjected to higher abundances of visiting predators under experimental conditions (Appendix B3) were not able to establish high aphid abundances. Here again, the potential of the plant chemotype becomes apparent. As shown previously (Benedek et al. 2015, Bálint et al. 2016), I also found an association between aphid natural enemies and chemotypes. Thus, the semi-natural experimental approach presented in manuscript 3 (Appendix B3) revealed that predators were more abundant on class 4 chemotypes in comparison to class 2 chemotypes. The analysis showed that this association could not be explained by density-mediated indirect effects arising through the preference of predators for colonies with higher abundances (Mooney and Singer 2012). The

analysis rather showed that this is caused by trait-mediated indirect effects, e.g. direct effects of plant chemotype on aphid susceptibility to predatory attacks, leading indirectly to higher predator abundances (Mooney and Singer 2012). As the experimental design did not allow to test for direct effects of plant chemotypes on the abundance of predators, this remains to be elucidated by further experiments. Anyway, the found predator-plant association might explain *inter alia* the reduced colonisation probability of chemotype class 4 plants in the field (Clancy et al. 2016). As aphids either chose to colonise enemy-free plants or their colonisation success was reduced due to immediate predation.

4.5 Aphid metapopulation and community dynamics

All populations and communities fluctuate to a certain degree in space and time (Lande et al. 2003). The metapopulation and metacommunity concept links ecological processes to such variations in space and time (Hanski 1998, Leibold et al. 2004, Alexander et al. 2012). When there is a metapopulations or metacommunity structure, then there is an equilibrium between colonisations and extinctions of suitable habitat patches; here infrequent dispersal between habitat patches allows new patches to be colonised by e.g. potential members of a community (Levins 1969, Hanski 1998). This leaves a fraction of suitable habitat patches unoccupied, at least for a certain amount of time. Besides such fluctuations, also dispersal limitations might contribute to unoccupied patches, although being theoretically available and *prima facie* suitable (Ehrlen and Eriksson 2000). However, differences between habitat patches not immediately apparent, like intra-specific trait variation in host plants or the presence of other species, can lead to differences in the suitability as resource for consumer species, leaving habitat patches unoccupied or affect the outcome of species interactions within its associated community. An important question is how and to what degree different processes and factors influence the abundances and the identity of members within and between communities leading to different assemblages and spatial distribution patterns (Morin 2011). In terrestrial systems it is often difficult to scale up from metapopulation to a metacommunity, mostly due to different spatial limitations (e.g. different dispersal abilities) of community members (in this case: aphids, ants and natural enemies; Leibold and Miller 2004, Leibold et al. 2004). So far, most research on metapopulation or community dynamics in terrestrial systems has focused on competitive models (e.g. competing aphid species) or predator-prey interactions (Hastings 1980, Tilman 1994, Winder et al. 2001, Leibold et al. 2004, Pillai et al. 2012), also in the tansy system (Weisser 2000, Loxdale et al. 2011, Mehrparvar et al. 2014).

By conducting a combination of observational and controlled experimental approaches, I was able to present insights into potential mechanisms driving metapopulation dynamics of

M. fuscoviride aphids and dynamics of the associated insect community (ants and natural enemies) in the tansy system. The results presented in this thesis emphasize the importance of spatio-temporal constraints, dispersal limitations, aphid preference and population growth as well as the preference of mutualists and predators in shaping the community on tansy; it highlights especially the importance of incorporating within-species variation of host plants when studying the dynamics of aphids and their associated insect community in small-scale field sites. While direct effects between two species in this system had the strongest effect on structuring this community, plant chemotypes variation could also affect aphid population indirectly through a chain of direct interactions passing through higher trophic levels. Since plant chemical variation, especially in non-dominant compounds, can not only directly affect aphids but also mediate interactions between aphids and their associated insect community affecting aphid colony growth rates, and thus local aphid colony survival. Low colony growth rates and small colony sizes make aphid colonies prone to extinction by predators at the level of an individual host-plants. Furthermore, the findings of this study also point out that mutualistic ants not only affect interactions with competitors (Mehrparvar et al. 2018) or natural enemies (Stadler 2004), these mutualists build up aphid population structure and affect the whole community right from the bottom.

4.6 Conclusion

Although the tansy system does not represent a classical metacommunity (Leibold and Miller 2004, Leibold et al. 2004), because the different community members act on different spatial scales and patch boundaries are less distinct for certain members, it shows that its insect community can be structured at the level of individual plants. This can lead to individual plant-specific community dynamics. As shown in this study, such potential metacommunity dynamics can happen on much smaller scales (i.e. individual plants), than often described in current literature which focuses on regional scale dynamics.

Furthermore, it is crucial to consider within-species host plant variation in future studies about metacommunity dynamics, especially focusing on sessile plant-specialist herbivores. Neglecting such important interactions could limit our understanding of ecological communities. The results presented here help to better understand mechanism important in other spatially structured habitats that may not fall under the classic idea of a metacommunity and might provide insights to related crop pests and thus, help to better understand their dynamics.

5 References

This chapter contains all references used in the main text. References used in included manuscripts are listed in the Appendix.

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