CHAPTER 8

Summary

The intensification of human land use by agriculture and settlements causes a serious reduction in plant and animal species diversity. How these environmental changes functionally influence biotic interactions is hardly known yet. Even though the effects of plant odours and plant structures on herbivore-parasitoid interactions receive growing attention, there are still knowledge gaps to fill concerning the impact of chemical and structural diversity of whole habitat patches on the performance of herbivorous insects and their natural enemies.

This thesis investigated as **general hypothesis** that diverse and complex vegetation within habitats protects herbivores, but impairs the foraging success of parasitoids. The main objective was to determine how plant species diversity and associated volatile blends as well as plant structural complexity affect the oviposition site selection of the leaf beetle, *Galeruca tanaceti* L. (Coleoptera: Chrysomelidae), and the parasitism success of its egg parasitoid, *Oomyzus galerucivorus* Hedqvist (Hymenoptera: Eulophidae).

Egg deposition within high plant species diversity might represent an 'infochemical shelter' for leaf beetle eggs and result in reduced egg parasitism, because a potentially complex volatile blend can negatively affect the host location ability of parasitoids. However, the future food plant availability for the larvae might be more important for oviposition site selection than escape into enemy-free space. In the field, leaf beetle egg clutch occurrence was positively related to the presence and quantity of two major Asteraceae host plants, *Achillea millefolium* (yarrow) and *Centaurea jacea*. Moreover, egg clutches were found significantly more often in patches with high plant species diversity. Two-choice olfactometer tests elucidated that the female beetles respond to released plant volatiles during oviposition. Leaf beetle females preferred the odours of a diverse plant species mixture (including food plants) for oviposition, when tested against the odours of grass plants, which they mostly use as an oviposition substrate. Despite that, when an odour blend originating from a diverse plant species composition was offered against an odour blend emanating from the host plant yarrow

only, no significant difference in egg depositions was detected. In a static four-arm olfactometer the response of the parasitoids to host and non-host plant odours was tested. Individuals were either naïve or experienced with yarrow. The bioassays revealed that experienced parasitoids were attracted to yarrow odours, but naïve ones were not. However, experienced wasps were not attracted to yarrow anymore, when yarrow odours were offered in a mixture together with odours of thyme (*Thymus vulgaris*, Lamiaceae), a non-host plant of the leaf beetle. In conclusion, it could be shown in laboratory bioassays that the parasitoid responds only to pure host plant odours, but not to odour mixtures derived from host and non-host plants. In the field, the herbivore preferred to oviposit within patches offering diverse plant species compositions and high host plant availability. In spite of that, the laboratory experiments point to a higher importance of host plant presence for the oviposition decision of the leaf beetle in comparison to plant diversity. But regardless whether oviposition site selection in *G. tanaceti* is an active choice of oviposition sites within high plant diversity or rather a passive consequence of ovipositing close to host plants, this oviposition behaviour still offers crucial selective advantages for the leaf beetle. It could solve an herbivorous insect's dilemma to reduce egg parasitism and provide the larvae with food at the same time (***chapter 2***).

Besides a diverse plant species composition, tall and structurally complex plants or vegetation might also represent an enemy-free space for the herbivore by turning host search for the parasitoid more difficult. In the field, the influence of plant architecture, regarding plants chosen as egg deposition sites, and the structural complexity of the surrounding vegetation on oviposition site selection of the leaf beetle and the parasitism success of the egg parasitoid was examined. On the scale of individual plants, plant height had a positive influence on herbivore oviposition site selection and egg clutch height a negative impact on parasitism. Additionally, probability of oviposition of the beetle was higher on simple plants than on plants with ramifications, while the parasitoid remained unaffected by the degree of ramification. On the microhabitat scale ($r = 0.1$ m around a plant with egg clutch), both increasing height and density of the vegetation enhanced leaf beetle egg deposition, whereas egg parasitism was reduced. Therefore, the herbivore and its egg parasitoid were influenced in opposite ways by habitat structure on both spatial scales investigated, suggesting the existence of an enemy-free space for the herbivores' eggs on tall plant individuals as well as in tall and complex vegetation (***chapter 3***).

Oviposition height could be a crucial factor for the fitness of overwintering leaf beetle eggs with respect to various biotic and abiotic mortality risks. Therefore, the height at which egg clutches were attached to plants was examined in different habitats and at different times of the season. Oviposition height was compared to general occurring vegetation height within habitats and its impact on winter mortality and parasitism risk of the egg clutches was analysed. Oviposition height of the leaf beetle was not uniform, but changed significantly with the structure of the habitat and during the season. Mean oviposition height per site (70.2 ± 4.9 cm) was significantly higher than mean vegetation height (28.4 ± 2.4 cm). Height of plants with egg clutches attached and oviposition height were significantly positively correlated. The results suggest that females try to oviposit as high as possible in the vegetation and on the plants selected. In accordance with this, the probability of egg parasitism and of winter egg clutch mortality significantly declined with increasing oviposition height. A preference of *G. tanaceti* for oviposition sites high up in the vegetation might therefore have evolved due to selection pressures by parasitoids and winter mortality (***chapter 4***).

It was previously shown that the leaf beetle can reduce the risk of egg parasitism by depositing egg clutches in structurally complex vegetation (see chapter 3). This could imply that beetle females should prefer, and actively select, patches with dense vegetation as oviposition sites to increase their own reproductive success. To investigate the importance of vegetation structure for herbivore oviposition, field data were analysed statistically with null models and the obtained results were evaluated in a laboratory bioassay. Particularly, the following two hypotheses were tested: (A) Leaf beetle females encounter grass stems used for oviposition by chance. Thus, within the habitat the number of egg clutches in patches with different plant stem densities is directly proportional to the number of stems in these patches. (B) Leaf beetle females actively select oviposition sites within high stem density and avoid ovipositing within low stem density. Hence, the number of egg clutches in patches with high stem density is disproportionately higher than in low stem density areas. The statistical analysis of the field data revealed that stem density and vegetation height are significantly positively correlated with egg clutch presence. Moreover, in the field a disproportionately high presence of egg clutches was determined in patches with high stem densities. However, in a laboratory two-choice arena assay females did not deposit a disproportionately higher number of egg clutches in the high-density areas, but the results indicated that stem encounter rate has an influence on oviposition site selection. However, according to the field results both stem density and vegetation height trigger oviposition site selection of the herbivore (***chapter 5***).

Preceding fieldwork verified that both tall and dense vegetation and leaf beetle egg deposition close to the tips of tall plants reduces parasitism success (see chapter 3 and 4). To elucidate the mechanisms underlying the low parasitism efficiency in complex structured vegetation, the searching behaviour of the egg parasitoid was analysed in the laboratory. In bioassay arenas dried grass stems were arranged according to the natural situation in different setups with low and high vegetation density, height and connectivity (number of connections between plants). The experiments should determine whether a high degree of structural complexity constricts the movement of the egg parasitoid, and thus, decreases the searching activity. Furthermore, the aim was to single out a possible key factor which shows the strongest influence on the parasitoids' movement patterns. The laboratory assays revealed that high stem density decreased the walking time of the parasitoids on the ground, but increased the propensity to fly between stems. Tall stems increased the time spent walking on them and walking time was almost proportional to grass stem length. No difference was observed in the number of contacts with grass stems in all investigated setups, in contrast to the likelihood of reaching the upper part of the stems. Fewer wasps reached the middle and upper part of grass stems in the high connectivity setup. Thus, laying eggs at the tip of long grass stems in dense vegetation is an adaptive strategy for the leaf beetle, because this type of vegetation structure is the one, which maximises the number of connection points between plant parts. The connection points disorient wasps, which lose time, reverse their direction or fly away (***chapter 6***).

Diverse habitats, where host plants are intermingled with non-host plants, can have profound consequences for the orientation behaviour, and along with it, for the performance and survival of herbivores and natural enemies. The spatial structure of plants may influence the visual orientation and can further physically affect the movement behaviour of arthropods. Moreover, plant species diversity may influence the composition of the volatile bouquet within habitats, since different plant species are known to release various volatile compounds. Therefore, plant species composition may affect the olfactory orientation of arthropods. So far, experimental studies produced contradicting results regarding the effects of vegetational complexity on arthropod individuals and populations. Several hypotheses have been developed and evidence has been gathered for each of the proposed theories, nevertheless they are still under heavy debate. When considering the available knowledge on the impact of vegetational complexity on arthropods, it appears that some possible interactions have been neglected so far. ***Chapter*** *7* addresses this issue and summarises at first the current knowledge on the effects and mechanisms of vegetational complexity regarding herbivorous and carnivorous arthropods, including the results gained in this thesis. Subsequently, on the basis of the available information, attention is drawn to possible relationships between plant species/chemical diversity and structural complexity concerning arthropod orientation which have been scarcely explored up to now. It is taken into account that volatile chemical diversity might change with both plant species composition and structural complexity, which might have profound effects on the perception of chemical diversity by herbivores and higher trophic levels.