

## **General introduction and thesis outline**

Diverse habitats have multiple direct and indirect effects on the individual behaviour and the population dynamics of phytophagous insects. Plant species diversity may have a strong impact on the composition of the odour bouquet prevailing in the environment and the structural complexity of the vegetation. Hence, plant species diversity can directly affect the orientation and host plant location process of herbivores. Indirectly, the vegetational complexity of habitats affects herbivores *via* carnivores, because the presence of host and non-host plants within diverse habitats also influences the prey and host location process of predators and parasitoids. Therefore, habitat vegetational complexity can play a crucial role in oviposition site selection of herbivorous insects and the interaction with their natural enemies such as parasitoids.

### **Host plant location and selection in herbivorous insects**

For the majority of herbivores host plant selection is closely linked with oviposition site selection, since most phytophagous insects feed and deposit their eggs on the same plant species. In general, the host plant selection behaviour of insects has been divided into several sequential steps comprising habitat finding, host plant finding, host plant recognition and acceptance which is in turn connected to host plant suitability (Prokopy and Owens 1983, Jones 1991). Herbivores use both chemical and visual cues to locate host plants and to discriminate host from non-host plants in diverse habitats (for reviews see Jones 1991, Bernays and Chapman 1994, Schoonhoven *et al.* 2005, Fernandez and Hilker 2007). It is assumed that phytophagous insects employ during host plant location a specific ‘host plant search image’ which is based on representative chemical and visual characteristics of their host plants (Städler 2002). Many examples show that typical volatile compounds emitted by host plants guide herbivores while searching and play an important role in host plant recognition (for reviews see Visser 1986, Honda 1995, Bruce *et al.* 2005). For instance, it has been reported that host plant odour signals attract herbivores over distances of up to 100

metres (see Schoonhoven *et al.* 2005). The decision to select a host plant for oviposition and/or feeding may further be affected by other types of infochemicals derived from competitors or natural enemies (reviewed in Kats and Dill 1998, Dicke 2000). Besides chemical host plant properties, visual plant attributes such as growth form, leave shape or colour can also influence the host location process of herbivorous insects (reviewed in Prokopy and Owens 1983). Visual host plant cues were observed to elicit positive responses in herbivores over a distance of up to 10 metres (see Schoonhoven *et al.* 2005). However, within habitats olfactory and visual plant cues always occur in combination and the relative importance of either cue for herbivores during host location is sometimes difficult to assess. The relevance of different types of host plant cues seems to depend largely on the investigated species (e.g. Finch *et al.* 2003, Couty *et al.* 2006). Finally, for host plant recognition and acceptance contact cues such as non-volatile chemicals or mechanical stimuli may be decisive factors. For example, leaf epicuticular waxes and other non-volatile secondary compounds or plant trichomes on the plant surface are known to trigger the acceptance or rejection of host plants for oviposition and/or feeding (e.g. reviewed in Dethier 1982, Honda 1995, Städler 2002, Müller and Riederer 2005).

### **Host and prey location in carnivorous insects**

Like herbivores, foraging carnivores also have to locate hosts or prey on different spatial scales, starting with the location of the habitat of hosts or prey, then finding plants harbouring hosts or prey and finally recognise and accept suitable targets (for reviews see Hassell and Southwood 1978, Vinson 1998). To find their way to their victims carnivorous insects can use both olfactory and visual plant cues (e.g. Hattingh and Samways 1995, Freund and Olmstead 2000, Henneman *et al.* 2002). The shape and pattern of plants may be important to find habitats and patches with hosts or prey (Hattingh and Samways 1995, Wäckers and Lewis 1999, Freund and Olmstead 2000). Furthermore, plant colour may provide parasitoids and predators with valuable information during foraging (Wäckers and Lewis 1999, Henneman *et al.* 2002, Fischer *et al.* 2004, Goyer *et al.* 2004). However, chemical cues may constitute more specific and reliable signals indicating the presence of hosts or prey within the habitat. Extensive research has elucidated that foraging natural enemies rely on various kinds of infochemical cues, which may originate either directly from host or prey

individuals, for example pheromones, or indirectly from the food plants of their victims, for example volatile secondary plant compounds (for reviews see Vet and Dicke 1992, Steidle and van Loon 2003, de Boer and Dicke 2005, Hilker and Meiners 2006). Carnivorous insects are known to be attracted by plant volatiles from intact (Takabayashi *et al.* 1991, Reddy 2002, Bukovinszky *et al.* 2005) and infested food plants of their victims. However, food plants that are damaged by herbivore feeding or oviposition produce specific volatile compounds, which allow the natural enemies to locate and select their targets very precisely (e.g. reviewed in Hilker and Meiners 2002). Thereby, carnivorous insects often combine the use of direct and indirect cues during foraging and are attracted to infochemicals derived from the whole complex of host/prey and associated food plants (e.g. Erbilgin and Raffa 2001, reviewed in Reddy and Guerrero 2004). Whether carnivores respond to very specific signals or to signals, which are generally present in multiple host/prey-plant complexes, depends on the dietary specialisation of the carnivore species and on the diet breadth of their victims (Vet and Dicke 1992, Steidle and van Loon 2003). The response to the occurring signals may be either innate or acquired through associative learning when hosts or prey are encountered in their presence (Steidle and van Loon 2003, de Boer and Dicke 2006).

### **Driving factors in oviposition strategies of herbivores**

Oviposition site selection is a demanding task for herbivorous arthropods, because herbivore females have to integrate a variety of factors to optimise their reproductive success (Jaenike 1978, Thompson 1988, Janz 2002, Scheirs *et al.* 2004). These factors include, for example, host plant availability and suitability, mortality risks of the mother and the larvae as well as larval mobility and host finding capability (e.g. Tammaru and Javoiš 2005, Tschanz *et al.* 2005, Moravie *et al.* 2006, Pöykkö 2006, Jervis *et al.* 2007). The egg deposition site chosen by the female determines to a large extent the future feeding site of the larvae, since herbivore larvae often have limited dispersal abilities (Jones 1991). Therefore, female herbivores gain maximal fitness, when their oviposition preference coincides with the performance of the larvae, provided that the most suitable feeding site ensures maximal larval fitness as assumed by the ‘preference-performance hypothesis’ (Jaenike 1978, Thompson 1988, Janz 2002). In this context, Janz (2002) classified different ‘internal’ and ‘external’ factors,

which may affect oviposition site selection and thus, plant-herbivore interactions as well. According to Janz (2002), internal factors represent factors that derive directly from the plant or the herbivore, for instance plant chemistry and architecture or the age and egg load of the female. External factors, in contrast, constitute abiotic influences, intra- and interspecific competitors or natural enemies of herbivores. However, in the past the quality and the quantity of host plants received much emphasis and were considered as crucial factors that predominantly determine host plant choice of ovipositing females (e.g. Kareiva 1983, Awmack and Leather 2002, Rhainds and English-Loeb 2003, Stiling and Moon 2005). Particularly, high nutritional quality of host plants is often related to fast growth rates and short developmental periods during the larval stage (Lill and Marquis 2001, Kessler and Baldwin 2002, Pöykkö 2006, Müller and Arand 2007). Although the preference of the female and the performance of the offspring should closely match from an evolutionary standpoint, it has been quite frequently observed that this is not always the case. Several reasons account for that finding, for instance herbivores may have limited discrimination abilities to distinguish hosts from non-host plants leading to suboptimal oviposition decisions (Janz and Nylin 1997, Bernays 1999) or constraints in searching time may demand to accept low quality host plants (Courtney *et al.* 1989, Tammaru and Javoš 2005). Moreover, the risk of predation for either adults or the larvae might be more decisive than host plant quality. The reduced predation or parasitism rate at specific oviposition sites may compensate for low nutritional quality or otherwise inferior properties of the selected host plant (Fox and Eisenbach 1992, Ohsaki 1994, Gratton and Welter 1999, Ballabeni *et al.* 2001). However, a trade-off between reduced mortality risk and high host plant quality does not necessarily have to exist (Yamaga and Ohgushi 1999, Kessler and Baldwin 2002).

### **Enemy-free space and oviposition site selection**

Natural enemies can directly affect the oviposition site selection of herbivores and are important factors that shape herbivore-plant interactions. Jeffries and Lawton (1984) defined the term ‘enemy-free space’ as ‘ways of living that reduce or eliminate a species’ vulnerability to one or more species of natural enemies’. Generally, animals may gain enemy-free space through different modalities, which are either related to the species itself or to the biotic and abiotic environment (for reviews see Jeffries and

Lawton 1984, Fryer 1986, Berdegue *et al.* 1996). For example the size or morphology of a species may determine the degree of exposure to carnivorous insects (see Rashed *et al.* 2005). Furthermore, biotic interactions can affect the mortality risk of an organism, for instance when several herbivores share a natural enemy (Holt and Lawton 1993, 1994). Most of all, the position a herbivore occupies within the habitat on a temporal and spatial scale may determine its vulnerability to predators and parasitoids (Price *et al.* 1980, Novotny *et al.* 1999, Heard *et al.* 2006). This may be especially true for herbivore eggs, since they are immobile and constitute a relatively defenceless stage in insect development (but see Blum and Hilker 2002). Herbivores and their offspring may escape from predators or parasitoids through adapting their activity patterns or time of occurrence on a daily or seasonal time scale (Clancy and Price 1986, Novotny *et al.* 1999, Nomikou *et al.* 2003). On a spatial scale different properties of the vegetation offer possibilities for structural or infochemical refuges which may protect herbivores against natural enemy attack (e.g. Vos *et al.* 2001, Bukovinszky *et al.* 2007). Plant species diversity and composition as well as the structural complexity of the vegetation play a key role in herbivore-carnivore interactions. Therefore, the following section deals with the influence of diverse vegetation on foraging herbivores and natural enemies.

### **Vegetational complexity and its impact on the orientation of herbivores and natural enemies**

The vegetational complexity of habitats is determined by plant species diversity and the three-dimensional spatial structure of these plant species. Moreover, plant species diversity may affect the composition of the volatile bouquet prevailing within habitats, since different plant species are known to produce and release various plant secondary compounds (e.g. reviewed in Dudareva *et al.* 2006, Knudsen *et al.* 2006). A diverse plant species composition in natural habitats, where host plants are intermingled with non-host plants, can have profound positive and negative consequences for the orientation behaviour of herbivores and natural enemies. Chemical and physical non-host plant characteristics can negatively influence searching behaviour and the host plant location process of herbivores. For example, non-host plants may emit repellent volatile compounds (e.g. Uvah and Coaker 1984, Mauchline *et al.* 2005) or volatiles that mask the odours of the host plant (e.g. Thiery and Visser 1986, Nottingham *et al.*

1991, Amarawardana *et al.* 2007). Physically non-host plants may mask visual cues of the host plant (Feeny 1976, Rausher 1981, Finch and Collier 2000, Hambäck 2003) or they may hinder the herbivore to access the host plant (Perrin and Phillips 1978, Litsinger *et al.* 1991, Coll and Bottrell 1994). Furthermore, non-host plants may indirectly affect herbivores *via* natural enemies, which they may provide with shelter or alternative food sources and thus, increase the mortality risk for herbivores (e.g. reviewed in Russell 1989, Landis 2000, Langellotto and Denno 2004, Romeis *et al.* 2005).

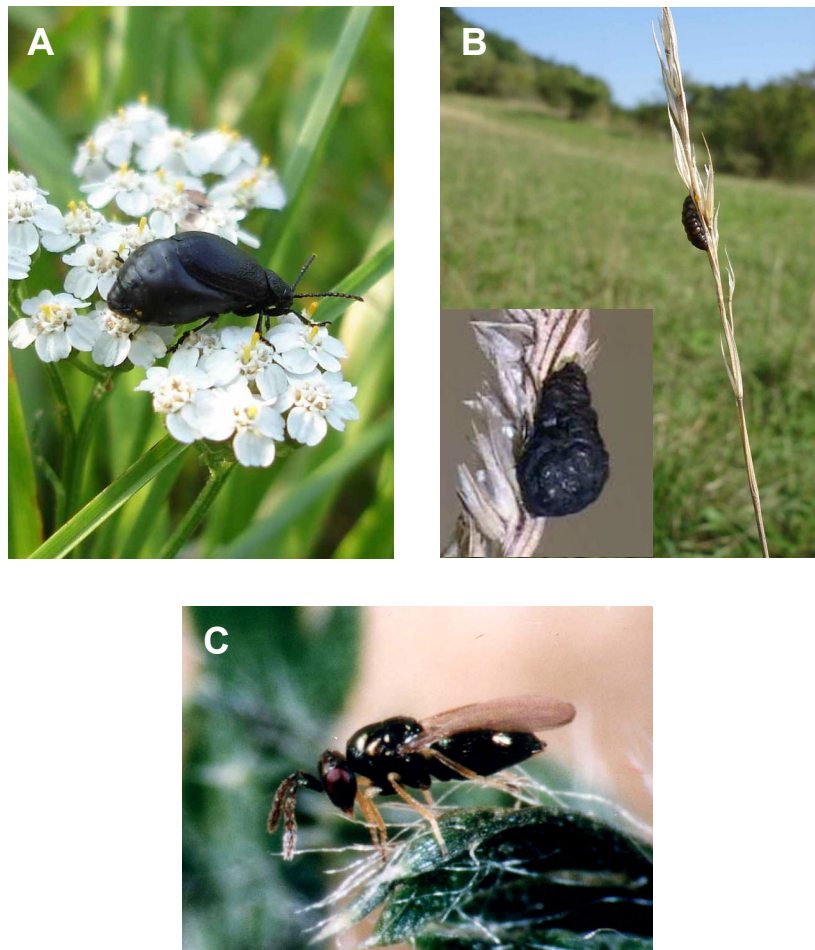
Nevertheless, diverse vegetation may also be beneficial for herbivores, particularly for generalists, in terms of greater resource availability and dietary mixing (Bernays and Minkenberg 1997). Furthermore, non-host plants may also constitute important so-called non-consumable resources for herbivores. Structural features of the vegetation can be crucial for survival, when certain non-consumable substrates are needed, e.g. for roosting, mate location, overwintering or as pupation sites (Wiklund 1984, Bernays and Chapman 1994, Dennis 2004, Veldtman *et al.* 2007). Several insect species are known to oviposit on non-host plants, which might not only allow successful overwintering, but may also be a strategy to provide eggs with enemy-free space (Obermaier *et al.* 2006, Veldtman *et al.* 2007). Moreover, non-host plant species, as part of diverse vegetation, can interfere with the host and prey location process of predators and parasitoids. The structure of the neighbouring vegetation surrounding host plants chosen for oviposition can reduce the predation and parasitism success of natural enemies, because access to prey or hosts is hampered through visual or physical interference (Tschanz *et al.* 2005, Obermaier *et al.* in press). On a smaller spatial scale, plant architecture can provide phytophagous arthropods with enemy-free space, because the searching efficiency of natural enemies can vary tremendously between different plant species or plant parts (Grevstad and Klepetka 1992, Hopkins and Dixon 1997, Legrand and Barbosa 2003). Several investigations showed that complex plant architecture negatively affects the movement ability and the searching time of parasitoids, which reduces their foraging success (Andow and Prokrym 1990, Lukianchuk and Smith 1997, Cloyd and Sadof 2000, Gingras *et al.* 2003). Moreover, differences in plant architecture can simply make the accessibility of prey impossible, because herbivores occupy well concealed locations on host plants, which are out of reach for natural enemies (Freese 1995, Clark and Messina 1998a, b, Stone and Schönrogge 2003, Chen and Welter 2007, Rouault *et al.* 2007). Besides spatial refuges

vegetation may also offer chemical refuges for herbivores, because volatiles released by non-host plants may disrupt the prey or host location process of natural enemies, which try to follow volatiles cues associated with prey or hosts (Vos *et al.* 2001). Non-host plants may emit odorants that have a repellent effect on natural enemies (Gohole *et al.* 2003, Wäckers 2004, Sanon *et al.* 2006) or they release volatiles which mask the odour of the host plants (Monteith 1960). In addition, odours released by non-host plants might even be more attractive for natural enemies than odours of host-infested plants (Perfecto and Vet 2003, Gols *et al.* 2005, Bukovinszky *et al.* 2007).

The overwhelming majority of studies, concerning the influence of non-host plants on the performance and survival of phytophagous insects, have been conducted in agroecosystems (e.g. reviewed in Trenbath 1993, Tonhasca and Byrne 1994, Landis *et al.* 2000, Hooks and Johnson 2003, Norris and Kogan 2005). So far, these investigations revealed mixed results regarding the responses of herbivores towards habitat diversification. Generally, research work in this area wanted to assess the value of increased plant species diversity, for example achieved through intercropping or maintenance of weedy vegetation, as management tool for pest suppression. Therefore, mostly negative effects on phytophagous insects were expected in those studies. In contrast, it has seldom been investigated how diverse vegetation might support herbivores and enhance their performance, while potentially hampering natural enemies.

### **Study organisms**

The leaf beetle, *Galeruca tanacetii* L. (Coleoptera: Chrysomelidae), and its egg parasitoid, *Oomyzus galerucivorus* Hedqvist (Hymenoptera: Eulophidae), were used as model organisms to elucidate the influence of vegetational complexity in a naturally evolved herbivore-parasitoid system. The impact of structural and chemical plant characteristics on the herbivore-parasitoid interaction was investigated in the field, with semi-field experiments in the greenhouse and in the laboratory. The fieldwork was conducted on extensively managed meadows and mesoxerophytic grassland sites at the 'Hohe Wann' nature reserve (Northern Bavaria, Germany).



**Fig. 1.** The investigated herbivore-parasitoid system. (A) Gravid *Galeruca tanacetii* female on *Achillea millefolium* flower in the field (photo: B. Randlkofer). (B) Leaf beetle egg clutches on the tip of dried grass stems (photos: B. Randlkofer). (C) The egg parasitoid *Oomyzus galerucivorus* (photo: T. Meiners).

### **The herbivore – *Galeruca tanacetii***

The tansy leaf beetle, *G. tanacetii*, is polyphagous and in the literature it is mentioned that beetles feed on plant species of the families Asteraceae, Brassicaceae, Caryophyllaceae, Dipsacaceae, Liliaceae, Lamiaceae, Polygonaceae and Solanaceae (Lühmann 1939, Pevett 1953, Obermaier and Zwölfer 1999) (Fig. 1A). In the study area, one of the main host plants of *G. tanacetii* is yarrow, *Achillea millefolium* L. (Asteraceae), but larvae can also be found feeding on *Centaurea jacea* L. (Asteraceae) and *Salvia pratensis* L. (Lamiaceae) (E. Obermaier, personal observation). *G. tanacetii*



can occur as pest on potato, cabbage, beans, dahlia and other cultural plants (Lühmann 1939, Heinze 1974, Roditakis and Roditakis 2006). The leaf beetle is a univoltine species distributed throughout Europe and in the East Palaearctic region, Near East and North Africa (Fauna Europaea Web Service 2004, version 1.1, <http://www.faunaeur.org>). The leaf beetle females oviposit on dry plant stems, mostly non-host plants such as grasses, during autumn from September to early December (Siew 1966, Meiners *et al.* 2006). The eggs are laid in clutches which contain on average about 65 eggs (Obermaier unpublished data). The eggs are usually arranged in a drop shaped or globular form and are protected by a dark and solid extrachorion (Scherf 1966, Messner 1983) (Fig. 1B). As the gravid females are unable to fly, they have to walk up the plant structures for egg deposition. The species overwinters in the egg stage and egg clutches stay on the plants for up to 7 months until hatching of the larvae in April (Obermaier and Zwölfer 1999). After hatching in April-May, the larvae have to find suitable host plants in the surrounding of the oviposition site where they feed for about three weeks until pupation (Obermaier and Zwölfer 1999). After pupation, the adults can be found from early June onwards before they enter a reproductive diapause in mid-summer.

### **The egg parasitoid – *Oomyzus galerucivorus***

Throughout Europe *O. galerucivorus* parasitises different *Galeruca* species (Sinacori and Mineo 1993), however, its main host in Germany is the leaf beetle *G. tanaceti* (Fig. 1C). The eulophid wasp is a solitary parasitoid, i.e. usually only one egg per host egg is deposited by the females, which parasitise the egg clutches of its host shortly after beetle oviposition in autumn. The parasitoid larvae hibernate in the host eggs and adults emerge next spring (Meiners *et al.* 2006). The host egg clutches are protected with defensive chemical compounds (Hilker and Schulz 1991, Pankewitz and Hilker 2006), but as a specialist the egg parasitoid overcomes the host's defence *via* complete excretion of these chemicals (Meiners *et al.* 1997). Due to their minute body size (ca. 1.5 mm) the egg parasitoids search for host egg clutches at close range by walking up and down vertical structures within the vegetation (Meiners unpublished data). Regarding the orientation to chemical and optical cues, so far, it is known that naïve parasitoids do not respond to odours from the host, host eggs, plant leaves (intact/damaged) from different host plant species and oviposition substrate (dried

grass stems) (Meiners *et al.* 1997, Hilker and Meiners 1999). Experienced parasitoids however are attracted by the odours of yarrow leaves and naïve wasps respond to a mix of three terpenes (camphor, alpha-pinene, beta-caryophyllene) contained in yarrow (Meiners unpublished data). In the field it has been revealed that the presence of the major leaf beetle host plant *A. millefolium* affects parasitism positively (Meiners and Obermaier 2004). Furthermore, it is known that the contact to host faeces elicits arrestment in the parasitoids, but odours of faeces is unattractive (Hilker and Meiners 1999). Host eggs in close range of about 2 cm are not recognised, but chemical compounds contained in the egg clutch extrachorion are involved in host recognition behaviour (Meiners *et al.* 1997, Hilker and Meiners 1999).

### **Thesis outline**

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 *G. tanaceti* and the parasitism success of its egg parasitoid *O. gallerucivorus*. Particularly, the following questions were examined:

- (1) Do leaf beetle females select oviposition sites within enhanced plant species diversity?
- (2) Do leaf beetle females differentiate between high and low plant diversity by olfaction?
- (3) Does a diverse odour bouquet, as a consequence of high plant species diversity within the habitat, influence the egg parasitoid negatively?
- (4) Do leaf beetle females select oviposition sites within complex structured vegetation to minimise the parasitism risk of the eggs?
- (5) Does a complex vegetation structure impair the egg parasitoid's host finding ability?

**Chapter 2** addresses the question whether a diverse plant species composition might represent an 'infochemical shelter' for the eggs of *G. tanaceti* and whether a trade-off

exists between food plant availability and escape into enemy-free space. Therefore, the egg-laying response of the generalist leaf beetle was examined in relation to host plant availability and plant species diversity in the field. Furthermore, the effect of mixed odour bouquets derived from host and non-host plant species on leaf beetle oviposition site selection and on the orientation of its egg parasitoid was determined in semi-field and laboratory experiments.

**Chapter 3** elucidates whether tall and structurally complex plants or vegetation 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 and 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 a small spatial scale.

**Chapter 4** deals with the influence of oviposition height on the mortality risk of leaf beetle eggs. 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 vegetation height within habitats and its impact on winter mortality and parasitism risk of the egg clutches was analysed.

**Chapter 5** investigates whether beetle females prefer to oviposit in patches with dense vegetation and whether plant stem density is a key factor in triggering oviposition site choice. Previous investigations (see chapter 3) revealed that the leaf beetle is able to reduce the risk of egg parasitism by depositing egg clutches in dense vegetation. The influence of plant stem density on herbivore oviposition was examined by analysing field data with null models and evaluating the results in a laboratory bioassay.

In **chapter 6** the movement behaviour of the egg parasitoid in differentially complex vegetation structures was investigated. In the laboratory it was analysed how low and high vegetation density, height and connectivity influence the searching behaviour of the parasitoid. The experiments should determine whether a high degree of structural complexity constricts the movement of the egg parasitoid, and thus, decreases the searching activity within structures of high complexity or on plant parts relevant for host encounter. Furthermore, the aim was to single out a possible key factor which shows the strongest influence on the movement patterns.

**Chapter 7** summarises and discusses the available knowledge on the effects and mechanisms elucidated so far concerning the impact of vegetational complexity on the responses of herbivorous and carnivorous arthropods, including the results gained in this study. This chapter surveys how plant species diversity affects herbivores and higher trophic levels, particularly with regard to the implications of plant species composition on olfactory orientation of arthropods. Further, it is highlighted how vegetation structure *per se* can influence herbivores and their natural enemies. Finally, on the basis of the available information, attention is drawn to relationships between plant species/chemical diversity and structural complexity concerning arthropod orientation which have been scarcely explored up to now.

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