



Turun yliopisto
University of Turku



TRITROPHIC INTERACTIONS AMONG PLANTS, HERBIVORES AND PLANT MUTUALISTS

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ABSTRACT

Plants form the first trophic level in terrestrial ecosystems and provide energy and nutrients to higher trophic levels. Herbivores, frugivores or fungal endophytes use plants directly, while predators consume plants indirectly by consuming herbivores. However, species are often simultaneously interacting with antagonistic and mutualistic partners at various trophic levels. For this reason, the outcomes of species interactions can indirectly affect other species in the community. The aim of my thesis was to study tritrophic interactions between plants, their antagonists, such as insect or avian herbivores, and mutualists such as insectivorous or frugivorous birds and symbiotic endophyte fungus.

In **Chapters I-III** I concentrated on the interactions among plants, herbivores and protective plant mutualists. In the first two Chapters, I investigated whether birds use volatile organic compounds or changes in visual properties of leaves from herbivore-damaged trees as foraging cues. I found that trees respond to herbivore damage both locally and systemically, but the olfactory foraging cue hypothesis was not supported. Instead, herbivory affected visual properties of leaves viewed by birds, although these changes may be in the limit of detection to them. In addition, my results indicate that cryptically coloured herbivores may have slightly better camouflage when on herbivore-damaged trees, although the herbivores are discriminable to birds against the leaves of the host plant regardless of the treatment (**Chapter II**). In **Chapter III** I studied the relationship between plants and protective fungal symbiont by testing whether systemic endophyte fungi can protect grasses against wild avian grazers. In this study I used two grass species, red fescues and tall fescues, which differ in texture. Both species have naturally both endophytic and non-endophytic individuals. I found that softer red fescue was preferred over coarse tall fescue, regardless of the endophyte status.

In **Chapter IV** I studied the interaction between plants, herbivores and seed-dispersing mutualists. I tested whether insect herbivory causes allocation cost to fleshy fruiting plants by affecting ripening or chemical composition of berries. I also investigated potential ecological cost of herbivory measured as probability for ripe berries to be removed by frugivorous birds. I found that berries in undamaged ramets neighbouring herbivore-damaged conspecifics had lower probability to be removed by frugivores, although herbivory did not affect ripening or chemical composition of berries. This indicates that in clonal plants, herbivore damage may cause priming effect on neighbouring ramets, which can affect plant mutualists.

The results of this thesis extend current knowledge about plant responses to herbivory, and also how these responses affect plant mutualists. In addition, my thesis provides information about the foraging behaviour of herbivores and plant mutualists. This kind of knowledge is essential for biological control and agricultural procedures, as well as on the planning of urban grass areas.

TIIVISTELMÄ

Kasvit muodostavat ensimmäisen ravintoketjun tason eli trofiatason maaekosysteemeissä, ja näin ollen toimivat ravinnon ja energianlähteinä ylemmille trofiatasoille. Kasvinsyöjät eli herbivorit, hedelmänsyöjät eli frugivorit ja symbionttiset endofyyttisienet ovat suoraan riippuvaisia kasveista, kun taas herbivoreja syövien petojen riippuvuus kasveista on epäsuoraa. Eri trofiatasoilla olevat lajit ovatkin jatkuvassa vuorovaikutuksessa keskenään, minkä vuoksi kahden lajin väliset vuorovaikutussuhteet voivat vaikuttaa myös muihin lajeihin. Väitöskirjassani olen tarkastellut usean trofiatason välisiä yhteyksiä kasvien ja niille haitallisten ja hyödyllisten eliöiden, eli antagonistien ja mutualistien, välillä. Esimerkkeinä antagonisteista käytin hyönteis- ja lintuherbivoreja, kun taas mutualisteina käytin hyönteissyöjälintuja, endofyyttisiä ja siementenlevittäjälintuja.

Tutkimuksissa **I-II** tutkin herbivorian aiheuttamien kasvista haihtuvien yhdisteiden, ja lehdissä tapahtuvien visuaalisten muutosten vaikutusta hyönteissyöjälintujen ravinnonhankintakäyttäytymiseen. Kasvit reagoivat sekä paikallisesti että kokonaisvaltaisesti herbivorian aiheuttamiin vaurioihin. En kuitenkaan löytänyt selvää tukea sille, että haihtuvat yhdisteet toimisivat hajuvihjeinä linnuille. Sen sijaan sain selville, että kasvinsyöjien aiheuttamat vauriot voivat vaikuttaa kasvin vahingoittumattomien lehtien ulkonäköön, joskin nämä muutokset voivat olla lintujen visuaalisen erotuskyvyn rajoilla. Herbivorian aiheuttamat muutokset kasvissa voivat lisäksi tehdä kryptisestä herbivorista vähemmän näkyvän linnuille, vaikka linnut todennäköisesti erottavatkin herbivorin lehtiä vasten riippumatta siitä onko kasvia vahingoitettu vai ei (**II**). Tutkimuksessa **III** tutkin voivatko endofyyttisienet suojella heiniä hanhien laidunnukselta. Tässä tutkimuksessa käytin kahta heinälajia, jotka eroat karkeudeltaan. Molemmilla lajeilla osa yksilöistä oli luontaisesti endofyyttisiä ja osa endofyyttömiä. Tulokseni osoittavat, että hanhet suosivat pehmeämpää ruoholajia karkean ruohon sijaan riippumatta endofyyttisienen läsnäolosta.

Tutkimuksessa **IV** testasin aiheuttaako hyönteisherbivoria allokaatiokustannuksia kasville vaikuttamalla marjojen kypsymiseen tai biokemialliseen koostumukseen. Tutkin myös mahdollisia herbivorian aiheuttamia ekologisia kustannuksia kasville, joita mittasin marjojen todennäköisyytenä tulla siementenlevittäjien syömiksi. Tulokseni osoittavat, että marjoilla, jotka kasvoivat varvuissa lähellä herbivorien vaurioittamia varpuja, oli pienempi todennäköisyys tulla siementenlevittäjien syömiksi. Herbivoria ei vaikuttanut marjojen kypsymiseen tai biokemialliseen koostumukseen. Tämä viittaa siihen, että klonaalilla kasveilla herbivoria voi aiheuttaa puolustusreaktion vahingoittumattomissa naapurikasveissa, mikä voi vaikuttaa myös kasvien mutualisteihin.

Tämän väitöskirjan tutkimukset syventävät ymmärrystämme siitä, miten kasvit reagoivat herbivoriaan, ja miten nämä reaktiot vaikuttavat kasvien mutualisteihin. Tutkimukseni lisäävät myös tietoa herbivorien ja kasvien mutualistien ravinnonhankintakäyttäytymisestä. Tällainen tieto on oleellista niin biologisen torjunnan kuin maataloudenkin kannalta, ja sitä voidaan soveltaa myös viheralueiden suunnittelussa.

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LIST OF ORIGINAL PUBLICATIONS

- I** Koski T-M, Laaksonen T, Mäntylä E, Ruuskanen S, Li T, Girón-Calva PS, Huttunen L, Blande JD, Holopainen JK, Klemola T (2015) Do insectivorous birds use volatile organic compounds from plants as olfactory foraging cues? Three experimental tests. *Ethology*, 121: 1131–1144, doi:10.1111/eth.12426
- II** Koski T-M, Lindstedt C, Klemola T, Troscianko J, Mäntylä E, Tyystjärvi E, Stevens M, Helander M, Laaksonen T (2017) Insect herbivory may cause changes in the visual properties of leaves and affect the camouflage of herbivores to avian predators. *Behavioral Ecology and Sociobiology*, 71: 97, doi:10.1007/s00265-017-2326-0
- III** Koski T-M, Saikkonen K, Klemola T, Helander M. Can fungal endophyte protect grasses against avian grazers? Experiments with tall- and red fescues. *Manuscript*
- IV** Koski T-M, Kalpio M, Laaksonen T, Sirkiä PM, Kallio HP, Yang B, Linderborg KM, Klemola T (2017) Effects of insect herbivory on bilberry production and removal of berries by frugivores. *Journal of Chemical Ecology*, 43: 422–432, doi:10.1007/s10886-017-0838-8

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1. INTRODUCTION

As primary producers, plants form the first trophic level in terrestrial ecosystems, providing energy and nutrients to higher trophic levels. Herbivores, frugivores or symbiotic fungal endophytes, *i.e.* the second level, are directly dependent on plants as they consume leaves, fruits or absorb nutrients from plant tissues. Predators, *i.e.* the third level, are indirectly dependent on plants because predators feed on the herbivores. These feeding relationships are referred as food chains (Elton 1927).

The relationships existing among species can also be described based on the outcome of the interactions. The two of the most intuitive types of interactions are likely antagonism and mutualism. In antagonism, one species benefits by causing negative effects on the other, while in mutualism both partners benefit from the interaction (Herrera and Pellmyr 2002). Good examples of antagonism are plant–herbivore and predator–prey interactions where one species is consumed by the other. Likewise, a classical example of mutualism can be found in a symbiotic relationship between plants and systemic micro-organisms, such as vertically (via seeds) transmitted endophytic fungus (Saikkonen *et al.* 2010). In this relationship, the fungus lives intercellularly inside the plant and repels herbivores by producing secondary chemicals (Clay and Schardl 2002; Saikkonen *et al.* 2013). Another good example of mutualism is the plant–frugivore relationship where the plant’s seeds are dispersed by fruit-consuming animals. In addition, predators can indirectly benefit plants by consuming the herbivores.

Species are often interacting simultaneously with antagonistic and mutualistic partners at various trophic levels. For example, plants can be under an antagonist interaction from leaf-feeding herbivores while being in a mutualistic interaction with seed dispersers, the natural enemies of the herbivores or symbiotic micro-organisms. Due to this complexity, the outcomes of between-species interactions can indirectly affect other species in the community. For example, insect herbivory may affect plant fitness due to investments in defence, which can result in allocation or ecological costs (Heil 2002; Strauss *et al.* 2002; Bronstein *et al.* 2007). This can occur if herbivory causes allocation costs to plants due to resource limitation, or if the defence or tolerance response of the plant physiologically compete with processes related to the attraction of mutualists. For example, plants may have fewer resources to invest in the number and nutritional quality of fruits, or the defence response can affect their palatability due to pleiotropy (Eriksson and Ehrlén 1998; Adler 2000; Adler *et al.* 2006; Irwin and Adler 2006; Treadwell and Cuda 2007; Whitehead and Poveda 2011). This can further affect foraging choices of frugivores. On the other hand, antagonistic interactions between two species can have a positive effect on the third interactive partner. For example, the predator-prey relationship between natural enemies and herbivores can benefit plants via reduced herbivore abundance. In the case of plant-fungus symbiosis, the negative effects of fungal alkaloids on herbivores benefit both the plant and the symbiotic fungus via reduced grazing damage.

These complex relationships existing among plants and species at higher trophic levels, especially between plants and insects, are one of the major forces that have

driven the diversification of life we see today (Herrera and Pellmyr 2002). Because the between-species interactions determine dynamics among trophic levels, food webs, and ultimately ecological networks, it is important to investigate the relationships existing among multiple trophic levels. In my thesis I have examined tritrophic interactions by studying antagonistic interactions between plants and herbivorous insect- or avian grazers, as well as mutualistic interactions between plants and protective or seed-dispersing organisms.

1.1. Tritrophic interactions among plants, herbivores and protective plant mutualists

Because herbivory can drastically decrease plant performance and reproduction (*e.g.* Louda 1984; Marquis 1984; Puentes and Ågren 2012), plants have evolved several mechanisms to tolerate herbivory. For example, grasses have good regrowth capacity, underground storages and silicon-based physical defence (Vicari and Bazely 1993; Huitu *et al.* 2014; Rudall *et al.* 2014), which make them tolerant to herbivory. Plants can also reduce herbivore damage via constantly present constitutive defences, and/or by induced defences that are activated when needed (Herrera and Pellmyr 2002; War *et al.* 2012). These defence strategies can also be categorized to direct and indirect ones based on whether the plant is actively defending itself or whether it is relying on mutualists (Howe and Jander 2008). Direct defences generally affect herbivore performance, such as in the case of structural defences (trichomes, hairs, etc.) and production of lethal or development-disturbing secondary chemicals (reviewed in War *et al.* 2012). Indirect defences can also vary from harmful to lethal from a herbivore perspective, as this line of defence includes the attraction of natural enemies of the herbivores as well as production of toxic or unpalatable secondary chemicals by plant symbionts. Consequently, studying the defence response of plants and their protective mutualist not only gives valuable knowledge about trophic interactions but also about biological pest control.

1.1.1. Natural enemies of herbivores

The attraction of natural enemies of herbivores is considered as an indirect and induced defence of plants, and there are many examples of this plant-predator mutualism. For example, the lima bean plant (*Phaseolus lunatus* L.) can benefit from predatory mites that reduce herbivore mite infestation (Dicke 1986), and *Arabidopsis thaliana* (L) Heynh. benefits from *Cotesia rubecula* Marshall parasitoid which reduces the damage caused by *Pieris rapae* L (Lepidoptera: Pieridae) caterpillars (van Loon *et al.* 2000). Although natural enemies of herbivores may use direct cues, *e.g.* chewing damage in leaves to locate their prey, it is well known that herbivore-mediated systemic changes in plant metabolism attract these carnivores. For example, volatile organic compounds, VOCs from herbivore-damaged plants attract invertebrate predators and parasitoids (Turlings *et al.* 1990; Takabayashi and Dicke 1996; Hilker *et al.* 2002; van Wijk *et al.* 2008). Herbivory also inflicts systemic changes in the photosynthetic activity and/or

light reflectance of plants (Oleksyn *et al.* 1998; Zangerl *et al.* 2002; Retuerto *et al.* 2004; Mäntylä *et al.* 2008a, b; 2017; Amo *et al.* 2013; Hussain *et al.* 2014), which may also serve as visual foraging cues to predators.

The attraction of natural enemies to herbivore-damaged plants is largely studied in invertebrates, but little is known how vertebrate predators respond to herbivore-mediated changes in plants. It has been shown that insectivorous birds can detect systemic changes in plants (Mäntylä *et al.* 2004; 2008a, b; 2014; Amo *et al.* 2013), but the cues used are still unclear. Consequently, there is an urgent need for further studies that investigate the indirect defence of plants via vertebrate predators. For example, knowledge about the exact mechanism behind the attraction of birds to herbivore-damaged trees can have applications on biological pest management, because birds improve plant performance both in natural and agricultural environments (Marquis and Whelan 1994; Mols and Visser 2007; Van Bael *et al.* 2008; Mäntylä *et al.* 2011).

1.1.2. Plant symbionts

Many organisms from plants to vertebrates have mutualistic micro-organisms, which help, *e.g.* in nutrient acquisition, digestion and tolerance against abiotic stress. In return, these symbionts rely on the host for energy, shelter and even reproduction. For example, the above-ground parts of many temperate grasses are inhabited by systemic, vertically transmitted endophytic *Epichloë* fungi (Clay and Schardl 2002; Saikkonen *et al.* 2013; Helander *et al.* 2016), which can increase hardiness, growth, drought resistance and the competitive ability of the plants (Arachevaleta *et al.* 1989; Clay 1990; West *et al.* 1993; Clay and Holah 1999). The systemic fungal endophytes are often obligatory, *i.e.* they do not survive without the host. Plants also harbour facultative fungal symbionts, such as horizontally (via sexual spores) transmitted endophytes, to which the host is not necessary (Isaac 1992; Sapp 1994; Saikkonen *et al.* 2010). However, I concentrate on the systemic fungal endophytes, as these are more likely to act as plant mutualists (Saikkonen *et al.* 2006).

Symbiotic micro-organisms can also protect the host against antagonists. For example, the facultative bacterial symbiont *Hamiltonella defensa* increases the resistance of pea aphids (*Acyrtosiphon pisum* Harris) against parasitoid wasps (Oliver *et al.* 2005). In grasses, the *Epichloë* fungus protects the plant by producing secondary chemicals, which repel both invertebrate and vertebrate herbivores (reviewed in Schardl *et al.* 2013). These negative effects of endophytic grasses on herbivores have been demonstrated in numerous studies (Porter and Thompson 1992; Clement *et al.* 1997; Saikkonen *et al.* 2006; 2010; Huitu *et al.* 2014), but the focus has mainly been on agricultural species and mammalian livestock. Consequently, not much is known about the repellent effects of endophytes on other vertebrate herbivores. However, fungal endophytes have been detected in all plant species studied today (Cambell *et al.* 2008) and can thus affect a wide range of herbivores. Negative effects of endophytes on wild herbivores could also be considered in the planning of urban areas, because geese and other grazers decrease the aesthetics of the areas due to defecations, and because they also can cause safety hazards at airports (Conover and Chasko 1985; Dolbeer *et al.* 2000; Dolbeer 2009; Little and Sutton 2013).

1.2. Tritrophic interactions among plants, herbivores and frugivores

Seed dispersal by animals has evolved independently in many seed plant lineages. In general, most of the seed dispersal is mediated by vertebrates, and thus it is not surprising that frugivory and associated seed dispersal have evolved several times in vertebrate phylogeny (Herrera and Pellmyr 2002). Foraging choices of especially frugivorous birds and mammals have great impact on plants, because they are the most common seed-dispersers (Herrera and Pellmyr 2002).

Herbivory can negatively affect plant reproduction due to allocation costs (Heil 2002; Strauss *et al.* 2002; Bronstein *et al.* 2007), because damaged plants allocate resources to defence or compensatory growth leaving less resources for other functions. Investments in defence can also result in ecological costs (Heil 2002; Strauss *et al.* 2002; Bronstein *et al.* 2007) by affecting plant mutualists, such as frugivores. This can occur, for example, if induced defence against herbivory in vegetative tissues results in the accumulation of secondary metabolites also to reproductive tissues (Eriksson and Ehrlén 1998; Adler 2000; Adler *et al.* 2006; Irwin and Adler 2006; McArt *et al.* 2013). For example, in *Hamelia patens* Jacq. (Rubiaceae) insect herbivory negatively affects foraging choices of seed-dispersing birds by altering the palatability and developmental time of fruits (Whitehead and Poveda 2011). Many avian frugivores are sensitive to changes in the biochemical composition of fruits: some birds are able to discriminate between varying anthocyanin or lipid concentrations based on the colour of the fruit (Catoni *et al.* 2008; Schaefer *et al.* 2008; 2014; Alan *et al.* 2013; Bolser *et al.* 2013), while some birds detect very small differences in sugar concentration of the fruits (Levey 1987; Schaefer *et al.* 2003). Because the differences in plant characteristics and frugivore preferences likely lead to differences in seed dispersal success, it is important to understand factors affecting fruit production and attractiveness of plants to frugivores.

2. AIMS OF THE THESIS

In **Chapters I-II** I examined the mutualistic relationships between plants and insectivorous birds as a particular group of natural enemies of herbivores. In these chapters, I investigated the mechanism how birds detect herbivore-mediated systemic changes in plants. Although birds are traditionally considered anosmics, they can use olfaction in different contexts, such as foraging (Kelly and Marples 2004; Nevitt and Bonadonna 2005; Cunningham *et al.* 2009). It has been suggested that similarly to many invertebrate carnivores, birds may also use VOCs as olfactory foraging cues to detect herbivore-damaged plants (Mäntylä *et al.* 2008a; 2014; 2017; Amo *et al.* 2013). This is referred to as the olfactory cue hypothesis. On the other hand, herbivory also inflicts systemic changes in the photosynthetic activity and/or light reflectance of plants (Oleksyn *et al.* 1998; Zangerl *et al.* 2002; Retuerto *et al.* 2004; Mäntylä *et al.* 2008a, b; 2017; Amo *et al.* 2013; 2016; Hussain *et al.* 2014), which may also serve as visual foraging cues to predators. Birds likely see far more shades of colour than humans, because they have four cone types dedicated to colour vision (UV sensitive: UVS, short wave sensitive: SWS, medium wave sensitive: MWS and long wave sensitive: LWS). In comparison, mammals are mono- or dichromatic (apart from primates that are trichromatic). Furthermore, the cone spectral sensitivities of birds are further tuned by oil droplets that filter light before it enters the visual pigment, and luminance (lightness) vision of birds is based on double cones (Endler and Mielke 2005; Cuthill 2006; Stevens 2013). Thus, the attraction of birds to herbivore-damaged trees may also be due to changes in light reflectance of leaves, as the results from Mäntylä *et al.* (2008b) suggest. In **Chapter I**, I examined the olfactory cue hypothesis by using three experimental tests. In **Chapter II** I tested how birds see the herbivore-mediated changes in leaves by using experimental herbivore manipulation and avian vision modelling. In addition, in **Chapter II** I also tested how these changes in the visual properties of leaves affect the camouflage of a cryptic herbivore. This was based on a new ‘disruption of camouflage’ hypothesis, which predicts that changes in the visual properties of the background (*i.e.* leaves) can potentially reduce the effectiveness of the camouflage of the herbivores.

In **Chapter III** I focused on another type of protective mutualist of plants, by using a systemic endophyte fungus. I tested the grazing preferences of freely foraging geese between endophytic and non-endophytic grasses by using two grass species: red fescue and tall fescue. Both endophytic and non-endophytic individuals are common in natural populations of the grass species studied. These grass species were also known to differ due to their alkaloid content and texture with the tall fescue being coarser than softer red fescue. I was also interested in whether endophytic grasses or selected grass species would be less attractive to the geese, because such plants could be sown in recreational areas to reduce human-geese conflict (Conover and Chasko 1985; Conover 1991; Niemi *et al.* 2007; Washburn *et al.* 2007; Pennell *et al.* 2010; Washburn and Seamans 2012).

In **Chapter IV** I tested how herbivore damage affects plant reproduction measured as the ripening and chemical composition of bird dispersed berries of

bilberry (*Vaccinium myrtillus* L). I also studied how this plant-herbivore interaction affects plant mutualists measured as the probability of the berries to be foraged by birds. Although the purpose of potentially unpalatable secondary metabolites in fleshy fruits and their possible effects on seed dispersers has long been of interest (reviewed in Herrera 1982; Cipollini and Levey 1997; Eriksson and Ehrlén 1998), the effects of herbivory on other biochemical characteristics, such as sugar or anthocyanin concentrations, are poorly known. However, because removal of leaf tissue can negatively affect anthocyanin and sugar concentration as well as the pH of fruits (Casierra-Posada *et al.* 2013; Pastore *et al.* 2013), I expected the herbivore damage to affect berry quality, and thus the probability of berries to become foraged by frugivores. However, because the study plant is clonal, herbivory may induce systemic resistance in other interconnected ramets (*i.e.* functionally autonomous clones) (Gómez and Stuefer 2006; Gómez *et al.* 2007; 2010; Chen *et al.* 2011). Consequently, I surveyed the development and removal of berries not only from herbivore-damaged and control ramets but also from undamaged ramets neighbouring herbivore-damaged conspecifics.

The research questions were:

- 1) Can insectivorous birds use volatile organic compounds from herbivore-damaged plants as olfactory foraging cues? (**Chapter I**)
- 2) Does herbivore damage cause changes in the visual properties of leaves and act as visual foraging cues to insectivorous birds? Can these changes in leaves reduce the camouflage of a background matching herbivore, making it more visible to birds? (**Chapter II**)
- 3) Can systemic fungal endophyte fungus protect plants against avian grazers? Are there differences in geese preference between two grass species that differ in texture and alkaloid content? (**Chapter III**)
- 4) Can insect herbivory cause: a) allocation costs to bilberry by the affecting the ripening and chemical composition of berries and b) an ecological cost by affecting the probability of ripe berries to be removed by frugivorous birds? (**Chapter IV**)

The tritrophic interactions investigated in this thesis are presented in Figure 1.

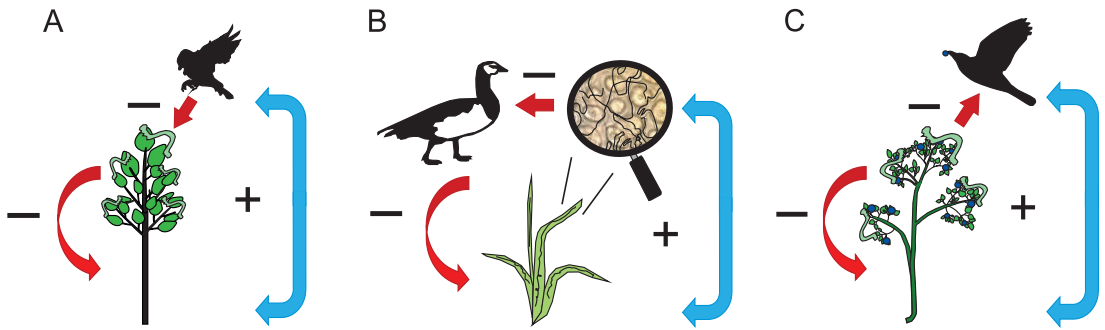


Figure 1. Tritrophic interactions. Blue double-ended arrows represent mutualistic interactions, red curved arrows represent a negative effect of herbivores on plants, and red straight arrows represent negative interactions between herbivores and plant mutualists. **A)** Insectivorous birds can be considered plant mutualists as they reduce herbivore damage via predation (**Chapters I-II**). **B)** Fungal endophytes can protect the host grass from herbivore grazing by causing negative effects on herbivores (**Chapter III**). **C)** Frugivorous animals benefit plants by dispersing seeds. However, herbivory may negatively affect fruit production or attractiveness of fruits to seed dispersers and thus affect the plants and their mutualists (**Chapter IV**).

3. METHODS

3.1. Study species and areas

In all chapters, the Botanical Garden of the University of Turku, Finland or the forests in Ruissalo Island, Finland were used as study areas. These sites were selected because of the availability of birds or trees for the experiments (**Chapter I-III**), a high abundance of bilberries (**Chapter IV**), and the availability of greenhouses or other facilities (**Chapters I and III**). Part of the experiments conducted in **Chapter III** took place also in the Helsinki Zoo due to high abundance of barnacle geese (*Branta leucopsis* Bechstein). Some of the experiments in **Chapter I** were conducted in Kevo, in northernmost Finnish Lapland (69°45'0"N, 27°01'0"E) and in Maaria, Turku in south-western Finland (60°27'0"N, 22°16'0"E). These two sites were compared to control for possible background herbivory, because natural herbivory in birch trees increases along a latitudinal gradient from north to south in Fennoscandia (Kozlov 2008).

In **Chapters I-II**, I used mountain birches (*Betula pubescens* ssp. *czerepanovii* N. I. Orlova), silver birch (*B. pendula* Roth) or European white birch (*B. pubescens* Ehrh), because they are the most common deciduous trees in Finland and are hosts to several insect species (Koponen 1983; Heimonen *et al.* 2015). The autumnal moth larvae (*Epirrita autumnata* Borkhausen) were used as defoliators in all the experiments where manipulation of herbivore damage was used (**Chapters I, II and IV**), because this species feeds on the used tree species and bilberry (Silvonon *et al.* 2014). In addition, autumnal moth larvae have been used as defoliators in previous studies (Mäntylä *et al.* 2008a, b; 2014). In **Chapter III** I used red fescue (*Festuca rubra* L) and tall fescue (*Schedonorus phoenix* Scop) as plant species. These grasses grow naturally in Finland (seeds collected from Kevo and Åland Island in **Chapter III**) and often harbour systemic fungal *Epichloë* endophytes. These grasses are also commercially used in several countries, *e.g.* as pasture or turf grasses (Hoveland 1993; Kvalbein and Aamlid 2012). Red fescue and tall fescue also differ in texture, with red fescue being a soft and likely more attractive species for grazers compared to coarse tall fescue. In **Chapter IV**, I used bilberry as a model plant, because it produces sweet-tasting, animal dispersed berries with high concentrations of anthocyanins (Ritchie 1956; Kalt *et al.* 1999; Honkavaara *et al.* 2007; Riihinen *et al.* 2008; Laaksonen *et al.* 2010; Pato and Obeso 2012).

In **Chapters I-II** I used three of the most common insectivorous species: pied flycatcher (*Ficedula hypoleuca* Pallas), great tit (*Parus major* L) and blue tit (*Cyanistes caeruleus* L) to study the mechanisms behind the attraction of birds to herbivore-damaged trees. These species also nest in the nest boxes (60°26' N, 22°10' E) on the island of Ruissalo, which makes them easy to capture (**Chapter I**). The foraging behaviour of freely foraging wild birds was observed indirectly from peck marks in plasticine larvae in **Chapter I**, from grazing damage of grasses in **Chapter III**, and from the disappearance of bilberries in **Chapter IV**. In **Chapter III** the barnacle goose was selected as avian grazer, because due to its increased population

size (Väisänen *et al.* 1998; Väänänen *et al.* 2010; 2011) it causes littering problems in many recreational areas of Finland (Niemi *et al.* 2007; Vuorisalo 2016). Although the barnacle goose does not nest on the main island of Ruissalo (study area in **Chapter III**), but in the small islets around it, it causes littering problems also in Ruissalo (Vuorisalo 2016; Emma Kosonen, City of Turku, Environmental protection, personal communication). However, the grazing pressure and littering are less intense in the Botanical Garden of University of Turku compared to the Helsinki Zoo (the other study area in **Chapter III**), where ca. 150–200 pairs breed in the Zoo's 22 ha area or in its vicinity (Ville Vepsäläinen, Helsinki Zoo, personal communication).

3.2. Attraction of natural enemies of herbivores: VOCs as olfactory foraging cues for birds

Chapter I consists of three experimental tests where birds were allowed to choose between VOC blends of herbivore-damaged trees and undamaged control trees in an aviary and in the wild. In the first and second experiment, I used data where the laboratory made VOC blends: a) terpene blend (diluted in hexane) partially mimicked the blend of volatiles released by herbivore-damaged mountain birches, b) a green leaf volatile (GLV) blend or c) a control solution (100 % hexane) were used. In the first experiment, the VOC blends were applied to artificial trees in aviaries, where the responses of adult pied flycatchers (10 males and 10 females were used in total with each aviary having a male-female pair with their juveniles) were tested for two one-hour trials over 2 days. The terpene blend vs control was tested on the first day, and the terpene blend vs GLV blend was tested on the following day. The preference of birds was measured as the first choice (the first landing site) and number of visits in trees.

In the second experiment, the same VOC blends were applied to living natural trees in wild, in Kevo (northern location) and in Turku (southern location). In addition, dead trees (cut tree branches which were left to dry) were used to control VOC natural emissions, because plants release VOCs as a by-product of their metabolism. In addition to VOC blends, artificial larvae (plasticine) were attached to trees to monitor foraging behaviour of wild birds from the pecking marks on larvae.

In the third experiment, I defoliated 20 silver birch saplings with autumnal moth larvae and used 20 undamaged saplings as controls. Before the behavioural experiment, defoliated branches and corresponding number of branches from control trees were removed to minimise visual cues (*e.g.* chewing damage, droppings). The trees were covered with black mesh bags, and placed on the opposite ends of a large plywood aviary (ca. 3 × 2.5 m). Plastic trees were placed next to real ones to provide perches for the birds. Great tits and blue tits (123 individuals in total) were captured from their nest boxes and released individually into a small booth (height 18.5 cm, depth 28 cm, width 18.5 cm) from which the bird had free access to the experimental aviary. An individual test took 10 min, starting from when the bird was released into the booth. Each landing was counted as a choice, and the preference of birds was observed as the first choice (*i.e.* first landing) and by the number of visits. In addition to behavioural tests, locally induced VOCs were collected with a headspace sampling

system (Mäntylä *et al.* 2008a; 2014; Girón-Calva *et al.* 2014). These measurements were taken from the defoliated branches and corresponding control branches from seven tree pairs. The measurements were conducted four–eight days after the onset of defoliation and ca. two–twenty hours before the trees were used in the aviary experiment.

3.3. Attraction of natural enemies of the herbivores: changes in the visual properties of plants as foraging cues for birds

In **Chapter II** I studied how herbivore-mediated changes in plant metabolism affect the visual properties of leaves, and how these changes are perceived in an avian visual system. In addition, I tested whether herbivore-mediated changes affect the background matching of the cryptically coloured insect herbivores. The idea behind this was a new ‘reduction in camouflage’ hypothesis predicting that herbivore-mediated changes in the visual properties of leaves would reduce the background matching of the herbivore. To answer these questions, I used data where herbivore-manipulation (*i.e.* autumnal moth larvae) was used to induce systemic changes in 16 silver birch trees, while 16 trees were left as controls. The herbivore-mediated changes were measured from chlorophyll and leaf water content, photosynthetic activity and light transmission of leaves from undamaged leaves of both treatments. To enable the conversion of the leaves and larvae to avian vision, two photographs were taken from every leaf and larvae: a ‘UV photograph’ was taken with UV-pass filter (Baader U; 310–400 nm transmittance) and a ‘human visible’ photo was taken with a filter blocking UV and infrared lens (Baader UV/IR Cut; 400–700 nm transmittance). The camera was also equipped with an UV transmitting lens (Coastal Optical Systems) as well as an image sensor sensitive to UV and ‘human-visible light’ (ca. 400–700 nm). The photographs were taken under a light bulb emitting visible and UV wavelengths (Arcadia Fluorescent Bird Compact Lamp). A grey standard (Labsphere Spectralon diffuse reflectance standard), which reflected 50 % of all light across the avian visual spectrum, was included in every photo.

3.3.1. Avian vision models

I used Image Calibration and Analysis Toolbox (Troscianko and Stevens 2015) in ImageJ (Schneider *et al.* 2012) to combine corresponding ‘human visible’ and UV photographs for leaves and larvae. With this Toolbox, I also normalized and linearized the photographs against the grey standard. After this, I selected a ca. 3 mm × 3 mm patch (region of interest, hereafter referred as ROI) from an area where the leaf appeared dark green in the ‘human vision’ photograph (in visible wavelengths) or dark in a UV photograph ($n = 122$ leaves). This was done in order to avoid areas where light reflected brightly back from the wax layer of the leaf. From the larvae photographs ($n = 45$), I took the ROI (2–3 segments long) from the dorsal side of the lateral line of each larva. This section of the larvae is green with thin yellow stripes in ‘human-visible’ photograph and appears dark in UV photograph. I did not include yellow lateral line of a larva in the ROI, but the thinner yellow lines could not be excluded.

I also used the Image Calibration and Analysis Toolbox to convert ROIs to the predicted photoreceptor responses of single and double cone types of a blue tit (Hart *et al.* 2000; Hart 2001; Troscianko and Stevens 2015). The Toolbox contains a mapping function which converts the image data from camera colour space to the predicted cone response data of a focal visual system, *i.e.* to a cone catch data. From this cone catch data, I wanted to describe the colour properties of the leaves by calculating the hue of leaves by deriving a colour channel that best explained variation in colour (*e.g.* Komdeur *et al.* 2005; Evans *et al.* 2010; Spottiswoode and Stevens 2011; Stevens *et al.* 2014). For this, I used principal component analysis on a covariance matrix of the standardised (transformed to proportions) single cone catch values of blue tit (*e.g.* Spottiswoode and Stevens 2011). The extracted principal component scores provided a calculation of hue of leaves by using the formula $(MWS+LWS) / (UVS+SWS)$. This is broadly based on the idea that colour perception in animals stems from antagonistic opponent colour channels that are frequently represented by a ratio (*e.g.* in humans, the red-green colour channel is LWS / MWS) (Lovell *et al.* 2005). In this hue formula, an increase in score values above 1 means that leaves have a shift to longer wavelengths, *i.e.* are more green or yellow, whereas values smaller than one suggest a shift towards more blue-UV colours. In addition, to allow comparison of achromatic properties of leaves among treatments and to compare the leaves to larvae, I calculated standardised contrast from the double cone values for each leaf and larvae. For this I used the formula: $\text{contrast} = \text{luminance standard deviation (SD)} / \text{luminance mean}$ (Troscianko *et al.* 2016). The difference in contrast between larvae and leaves was calculated with a formula [*i.e.* $(\text{luminance SD}/\text{luminance mean of a larva}) - (\text{luminance SD}/\text{luminance mean of a leaf})$].

To test how well blue tits may discriminate (1) between the leaves of control and herbivore-damaged silver birch trees and (2) between autumnal moth larvae and leaves, I used colour and luminance discrimination models (Vorobyev and Osorio 1998) for the cone-catch data. The discrimination model is based on the idea that receptor noise limits discrimination, and the model uses units of ‘just noticeable differences’ (hereafter, JNDs). Values <1 to 3 indicate that the two colours are likely indistinguishable by the given visual system under optimal light conditions and values >3 indicate that two objects are likely discriminable (Siddiqi *et al.* 2004). By using these models, I compared all control leaves against all leaves from defoliated trees, and every leaf against every larva to test whether they are discriminable in avian vision based on chromatic or achromatic differences.

3.3.2. Chlorophyll concertation, fluorescence, leaf water content and light transmission of leaves

I analysed herbivore-mediated changes from leaves by using concentrations of chlorophyll *a* and *b*, photosynthetic activity, water content and light transmission measurements. The chlorophyll concentration was measured from dark-adapted leaves following the method of Inskeep and Bloom (1985). Chlorophyll *a* fluorescence induction curves were measured from the same leaves with a PAM-101 fluorometer (Heinz Walz, Effeltrich, Germany). These results were used to calculate the

photosynthetic activity of leaves, indicating general health and lack of significant stress of the photosynthesis machinery of the plant (Krause and Weis 1991; Takahashi and Murata 2008; Tyystjärvi 2008). The relative water content (*i.e.* mass of water divided by fresh weight) of 15-20 leaves per tree was determined by weighing the fresh leaves, and weighing them again after 48 hours of freeze-drying. In addition, one or two leaves per tree (28 trees in total) were placed on top of a light source for transillumination and photographed from above. The same grey standard as used in the photographs of leaves and larvae for avian vision models was also included in every photo, and the photos were converted to black and white images. The mean grey value of each leaf and the grey standard were recorded in the ImageJ program. Based on these, I calculated the standardised light transmission by subtracting the average grey value of a tree (calculated from one or two leaves) from the mean value of the grey standard.

3.4. Protective plant symbionts: fungal endophytes in grasses and herbivorous geese

In this experiment, I investigated how fungal endophytes affect freely foraging barnacle geese at two sites differing in the grazing pressure by the geese. I used red fescues and tall fescues at the high grazing pressure site of the Helsinki Zoo (referred as Helsinki experiment), while only tall fescue was used in the low grazing pressure site in the Botanical Garden of University of Turku (referred as Turku experiment). The grasses used in the Helsinki experiment were first grown in pots in a greenhouse, cut to 3-4 cm tall to attract geese (Summers and Critchley 1990; Hassall *et al.* 2001; Durant *et al.* 2003), and then the pots were dug at ground level in eight areas. The grasses were regularly cut if they exceeded this height. In each area, there were two tall fescue and red fescue patches: ten E+ pots or E- tall fescue pots formed a patch (ca. 20 × 50 cm), while six E+ or E- red fescue pots formed a 10 x 24 cm patch. The distance between conspecific patches was 3 meters, while the distance between closest tall fescue and red fescue patch was 5 m within an area.

In the Turku experiment, I sowed tall fescue seeds (E+ or E-) into ten 1 m × 1.2 m plots. The distance between the plots was 2.5 m, and the plots formed an alignment close to a pond where ca. 40 barnacle geese were observed foraging earlier in the spring. Before the experiment, the grass was cut to 6-7 cm height and kept at this height during the experiment. In both experiments, I measured the preference of geese as proportion of area eaten, length of eaten grass and number of goose droppings. To exclude the effect of cutting and growth of new tillers, the grass was considered eaten when the height was under threshold value (2.8 cm in Helsinki experiment and 5.8 cm in Turku experiment). The length of eaten grass was calculated by subtracting the measured grass height from the threshold value.

3.5. Plants, herbivores and frugivores: effects of herbivory on berry production and seed-dispersing mutualists

In this study I manipulated the herbivore damage in bilberries to test how it effects chemical composition and ripening of berries as well as the foraging behaviour of frugivorous birds. I used 20 forest blocks in Ruissalo Island (in 2013 and 2014) and in each block I had three control plots and three herbivore plots (each *ca.* 1–3 m²). In herbivore plots, two bilberry ramets were defoliated by autumnal moth larvae by covering *ca.* 25 % of a ramet with mesh bags containing the larvae. However, I expected that undamaged ramets in the herbivore plots had rhizome or root connections to defoliated ramets, because ramets belonging to the same clone tend to be closely associated (Ritchie 1956; Albert *et al.* 2003). Furthermore, because clonal plants can induce resistance in the neighbouring ramets (Gómez *et al.* 2007; 2010; Gómez and Stuefer 2006; Chen *et al.* 2011), I considered two undamaged ramets in herbivore plots as the ‘rhizome signalling’ treatment. Similarly, in control plots, I applied empty mesh bags to two ramets (referred as methodological control ramets) to control the possible effect of the bag (*e.g.* due to shading or reduced evaporation), while two ramets within the plot were left as non-bagged controls. After 7 to 21 days the mesh bags were removed. I calculated the number of flowers and raw berries at the beginning of the experiment and surveyed the ramets 11–12 times to calculate the number of ripened berries and how many of them disappeared (interpreted as eaten by frugivorous birds).

I also collected berries from one bagged and one non-bagged ramet per plot for analyses of anthocyanins, sugars and organic acids. The total content of anthocyanins (mg/g of dry weight, DW) was determined by spectrophotometer ascyanidin-3-*O*-galactoside (Extrasynthese, Genay, France) equivalents at 530 nm. In addition, the anthocyanin profiles were determined with ultra-high performance liquid chromatograph with a diode array detector (UHPLC-DAD). The most common anthocyanins of bilberries were identified based on the UV-Vis spectra and literature (Laaksonen *et al.* 2010), and the proportions of individual anthocyanins in each sample were defined by their shares in the HPLC chromatograms. Based on this information, the contents of each anthocyanin in all samples were calculated. Concentrations of sugars and organic acids were analysed as Trimethylsilyl (TMS) derivatives by using gas chromatograph with a flame ionization detector (GC/FID). The peaks of the TMS derivatives of sugars and acids were identified by comparing their retention times with the retention times of external standards (for acids: ascorbic, citric acid malic and quinic acids, and for sugars: sucrose, glucose, fructose, myo-inositol and xylose). Quantifications (mg/g DW) were made in relation to the area of the internal standards (which were sorbitol for sugars and tartaric acid for acids).

3.6. Statistical analyses

For all statistical analyses, I applied linear (LMM) and generalized linear mixed models (GLMM) with the specific error distribution and link function chosen according to the dependent variable in question. To test hypotheses provided in Aims 2 in the Aims of the Thesis in the previous chapter, experimental manipulations formed

the most interesting fixed explanatory factors in the models. Other fixed factors were selected based on their biological relevance for the question studied. In all models, the dependency structures among the observations were taken into account as random factors. All models were run using the SAS statistical software, primarily using the procedure GLIMMIX (Stroup 2013). However, in **Chapter I** the locally induced VOCs from control and herbivore-damaged trees were analysed with a nonparametric Mann–Whitney U-test due to large variation and skewed distribution of the data. In addition, the association between the average hue of a tree (calculated from hue values of individual leaves) and the average chlorophyll concentration of a tree (calculated from chlorophyll *a* and *b* values of individual leaves) were analysed with Pearson’s product-moment correlation coefficients in **Chapter II**. More detailed descriptions about the statistical methods are described in my original publications used for this thesis (**Chapters I-IV**).

4. RESULTS AND DISCUSSION

4.1. VOCs as olfactory foraging cues for birds

In **Chapter I**, I studied tritrophic interaction among plants, insect herbivores and protective plant mutualists by testing the mechanism behind the attraction of birds to insect-damaged trees. In the third experiment I found that the silver birches were responding to herbivore-damage by increasing local VOC production, as 22 compounds out of 39 had higher emission rates in defoliated trees compared to control trees. However, I did not find supporting evidence for the olfactory cue hypothesis in the three experiments conducted, as there was no clear difference in the first choice, number of visits of birds or predation rate on plasticine larvae. Although in the first experiment birds visited terpene scented trees more often than GLV trees, this difference was likely due to two very active individuals in the aviary experiment, and this observed preference was not found when the same VOC blends were applied in wild conditions.

From the bird's point of view, it would likely be beneficial to be able to smell herbivore-induced VOCs, because they are considered to be reliable signals of the presence and identity of herbivores (Vet *et al.* 1991; Vet and Dicke 1992; Dicke 1999; Halitschke *et al.* 2001; Hilker *et al.* 2002; Gosset *et al.* 2009). However, the odour and volatility of VOCs may change shortly after plants have released them due to some VOCs diffusing very quickly in the atmosphere, while others may become less volatile when reacting with other compounds (Kroll and Seinfeld 2008; Holopainen and Blande 2013). It is important to note that although the compounds of the laboratory made VOC blends were partly mimicking the blend of volatiles released by defoliated mountain birches, artificial VOC blends cannot fully mimic the complexity of natural VOC blends. In addition, the birds in my aviary experiments were not habituated to forage in an aviary or trained to associate olfactory cues to food. By contrast, in the experiment by Amo *et al.* (2013) where support for the olfactory cue hypothesis was found, the hand-reared birds were habituated to foraging in an aviary on several occasions. However, wild and non-trained birds were also used by Mäntylä *et al.* (2004; 2008b), where birds showed preference for herbivore-damaged trees. My results from these three experiments indicate that for prey-searching insectivorous passerines VOC-based olfactory foraging cues may not be completely necessary or the only foraging cues.

4.2. Changes in the visual properties of plants as foraging cues for birds

In **Chapter II** I further studied the mechanism behind the attraction of insectivorous birds to insect-damaged trees. I found that silver birches had a systemic response to herbivore damage as the intact leaves of herbivore-damaged trees had a significantly lower concentration of chlorophyll *a*. In addition, the hue of leaves of herbivore-damaged trees was shifted to longer wavelengths, and they also had higher achromatic

contrast. I also found a negative correlation between concentrations of chlorophyll *a* and the hue of the leaves of both undamaged and damaged trees. Because both hue and contrast calculations were based on spectral sensitivities of the blue tit, my results indicate that herbivore-damaged trees may appear ‘greener or more yellowish’ to birds, and that changes in chromatic and achromatic properties of the leaves may act as visual foraging cues to birds. However, based on the discrimination models, these changes in the chromatic and achromatic properties of leaves are not obvious, and may offer limited detection to insectivorous birds.

In **Chapter II**, I also investigated the relationship among plants, herbivores and insectivorous birds from the herbivore’s perspective. I did not find support for the ‘reduction in camouflage’ hypothesis, as herbivore-mediated changes in leaves did not reduce the background matching of the cryptic herbivore. Instead, the colour JND values and difference in contrast between larvae and leaves were higher when larvae were tested against control trees. This indicates that larvae may be less conspicuous when on damaged trees, although these perceptual differences are likely small. Nevertheless, although to human eyes the autumnal moth larvae closely resemble the colour of leaves, the larvae should be detectable for birds on leaves on both control and herbivore-damaged trees. This is in accordance with findings by Stobbe *et al.* (2009) that insectivorous birds can use both chromatic and achromatic cues in detection of cryptic prey.

4.3. Fungal endophytes in grasses and herbivorous geese

In **Chapter III** I studied the tritrophic interactions among plants, herbivores and protective mutualists, using a grass-endophyte-avian grazer system. I found only minor differences between E+ and E- grasses in high grazing intensity site (in the Helsinki experiment) indicating a slight avoidance of E+ grasses. Nevertheless, I do not relate these subtle differences to be caused by fungal alkaloids, but rather to be explained by better recovering capacity of E+ grasses and/or their higher silicon content (Arachevaleta *et al.* 1989; Clay 1990; West *et al.* 1993; Clay and Holah 1999). In accordance to my predictions, I found that barnacle geese preferred red fescues over tall fescues when the two grass species were simultaneously available for birds. This result is consistent with previous studies showing that tall fescue is not preferred foraging species to herbivorous geese (Smith *et al.* 1999; Pennell *et al.* 2010; Washburn and Seamans 2012). The reason for this is likely the fact that tall fescue is coarse and has a high tensile strength making it more difficult to forage (Owen *et al.* 1977; Conover 1991). In low grazing intensity site (in the Turku experiment) where only tall fescue was used, I found that the tiller density at the beginning of the experiment negatively affected the foraging activity of the geese. In addition, the proportion of area eaten in the low grazing intensity, tall fescue plots declined after beginning of the experiment. Because previous studies have shown that increasing standing crop and the cover of forage can limit the foraging efficiency of herbivores (van de Koppel *et al.* 1996; van der Wal *et al.* 1998), my results support the idea that

when the tall fescue plots grew denser during the experiment, they likely became more difficult or less attractive for the geese to forage.

4.4. Effects of insect herbivory on berry production and seed-dispersing mutualists

In **Chapter IV** I investigated the interactions among plants, insect herbivores and seed-dispersing plant mutualists. My results indicate that the herbivory treatment indirectly affected the probability for berries to be foraged, because the undamaged ramets in herbivore plots were least-favoured by seed-dispersers. I suspect that herbivore-damage likely caused priming effect in these ramets, because they were rhizome or root connected to the herbivore-damaged ramets (Ritchie 1956; Albert *et al.* 2003) and because interconnected ramets are likely able to induce systemic resistance upon insect herbivory (Gómez and Stuefer 2006; Gómez *et al.* 2007; 2010; Chen *et al.* 2011). In addition, VOC mediated plant-plant signalling has been identified in several plant species (*e.g.* Karban *et al.* 2003; Engelberth *et al.* 2004; Gómez and Stuefer 2006; Ton *et al.* 2007; Gómez *et al.* 2007; 2010; Chen *et al.* 2011). This potential priming effect may have affected the attractiveness of berries by affecting their contrasts against leaves, because in some plants systemic defence induction affects light reflectance and/or photosynthetic activity of leaves (Zangerl *et al.* 2002; Mäntylä *et al.* 2008a, b; Amo *et al.* 2013). In addition, induced defence response may affect attractiveness of the plants by affecting the palatability of fruits (Whitehead and Poveda 2011).

I also found that berries in ramets with a high fruit yield had higher probability to be foraged compared to berries in ramets with lower fruit yield, which is in accordance with previous studies (Sallabanks 1993; Ortiz-Pulido *et al.* 2007; Blendinger *et al.* 2008). The likely reason for this is that by favouring plants with high fruit yield frugivores likely maximize their foraging efficiency or minimize search and travel time (Martin 1985; Sallabanks 1993). In addition, the large fruit display is likely more conspicuous (Howe and Estabrook 1977; Denslow *et al.* 1986; Sallabanks 1993). However, in contrast with some previous studies (Obeso 1993; Koptur *et al.* 1996; Thalmann *et al.* 2003), I did not find an allocation cost between defence and reproduction, as herbivory did not affect the ripening or the concentrations of anthocyanin, sugar or acid of bilberries. However, my findings are similar to Primack and Hall (1990), as they found that pink lady's slipper orchids (*Cypripedium acaule* Aiton) were able to mature their fruits despite defoliation. In addition, Obeso and Grubb (1993) did not find an effect of defoliation on fruit production during the year of damage. Storages, for example carbohydrates and nitrogen in roots or rhizomes, are the most obvious reason for the lack of effect of herbivore damage, and some clonal plants also transport resources among interconnected ramets (Loescher *et al.* 1990; Lähdesmäki *et al.* 1990; Alpert 1991; Evans 1992; Kaur *et al.* 2012). It is also possible that plants may have increased their photosynthetic capacity, or that bilberry is moderately tolerant to vegetative damage (Tolvanen 1994; Tolvanen *et al.* 1994; Tolvanen and Laine 1997).

5. CONCLUSIONS

In this thesis I investigated tritrophic interactions among plants, herbivores and protective or seed-dispersing plant mutualists. My results provide information about plant responses to herbivory, as they demonstrate that plants can respond to herbivore damage both locally (*i.e.* increased VOC emissions from damaged site found in **Chapter I**) and systemically (*i.e.* decreased chlorophyll *a*, changes in hue and contrasts found in **Chapter II**). I also found that these plant responses to herbivore damage can affect natural enemies of herbivores via changes in visual properties of leaves, because herbivore-mediated systemic changes in leaves may be visible, although likely not obvious to birds (**Chapter II**). In addition, these changes may make cryptic herbivores slightly less detectable to birds when on herbivore-damaged plants, although herbivores can still be discriminable to birds against the leaves of both the undamaged and damaged host plant (**Chapter II**). However, I did not find that VOCs released due to herbivore damage would attract insectivorous birds (**Chapter I**). Whether changes in visual properties of leaves affect foraging behaviour of birds and whether birds can combine olfactory and visual cues during foraging require further studies involving behavioural tests and visual modelling.

Herbivore-mediated changes in plants may also have an ecological cost to plants by affecting seed-dispersing mutualists, because I found that herbivore damage in clonal plants may lower the probability for berries to be foraged from undamaged neighbouring plants (**Chapter IV**). Foraging behaviour of animals can also be affected by the abundance of resources and by how much effort is required to obtain these resources. For example, a high abundance of plant-provided resources, such as berries (**Chapter IV**), can attract plant mutualists. In addition, the coarseness of the plant can make it more difficult for plant antagonists to forage, and thus, coarse species such as tall fescues should be used to reduce the attractiveness of recreational areas to wild geese (**Chapter III**).

In summary, the results of this thesis advance our understanding about the effects of antagonist and mutualist relationships among plants and species at other trophic levels. These results also provide knowledge about plant responses to herbivory, indirect defences as well as of the foraging behaviour of frugivores and grazers. The results from tritrophic interactions among plants, herbivores and protective mutualists also provide information relevant for biological pest management as well as for planning urban grass areas.

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