HERBIVORY IN RIPARIAN BUFFERS OF AGRICULTURAL LANDSCAPES IN SW FINLAND

by

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This thesis is based on the following publications and manuscripts, referred to in the text by their Roman numerals:

I   Gilbert, S., K. Norrdahl, J. Martel & T. Klemola (2013). Vole damage to woody plants reflects cumulative rather than peak herbivory pressure. – *Annales Zoologici Fennici*, 50, 189-199.

II   Gilbert, S., J. Martel, T. Klemola & K. Norrdahl (2013). Increasing vole numbers cause more lethal damage to saplings in tree monocultures than in mixed stands. – *Basic and Applied Ecology*, 14, 12-19.

III   Yletyinen, S. & K. Norrdahl (2008). Habitat use of voles (*Microtus agrestis*) in wide and narrow buffer zones. – *Agriculture, Ecosystems & Environment*, 123, 194-200.

IV   Gilbert, S., K. Norrdahl, H. Tuomisto, G. Söderman, V. Rinne & E. Huusela-Veistola. Reverse influence of riparian buffer width on herbivorous and predatory Heteropteran assemblages. – *Manuscript*

CONTENTS

1. INTRODUCTION

Food webs underlie the functioning of both natural and human-modified ecosystems, and understanding food web dynamics is therefore pivotal for both theoretical and applied ecology. Since the 1960s research on food webs has revolved to a great extent around a single question: "Why is the world green?" Conventionally the greenness of the world has been explained by trophic interactions that are controlled either by consumers (the top-down model) (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981) or by resources (the bottom-up model) (Murdoch 1966; White 1978). According to the top-down view, the world is green because predators, parasites or parasitoids suppress herbivore numbers to the extent that they are unable to reach densities sufficient to decimate all plant material. In contrast, the bottom-up view posits that the world is green because the low nutritional quality or anti-herbivory defences of many plants render them resistant to herbivory. This divided view of trophic dynamics has been subject to vigorous debate for decades. More recently, however, ecologists have reached a consensus that both forces act synergistically in shaping reticulate food webs (e.g. Gruner et al. 2008; Garibaldi et al. 2010; Estes et al. 2011). Accordingly, research has shifted towards exploring the relative strengths of bottom-up and top-down forces.

Top-down and bottom-up control may be interactions between producer and consumer such as plant-herbivore, plant-detrivore interactions or between consumers at different trophic levels, such as herbivore-carnivore, carnivore-carnivore or host-parasite interactions. Thus herbivores, and consequently their impact on plants, are influenced by both producers and consumers at higher trophic levels. Herbivores shape plant communities by exerting selective pressure on their preferred food plant (e.g. Leibold 1989; Schmitz 1993; 1994; Norrdahl et al. 2002; Hambäck et al. 2004) and by accelerating nutrient cycling by making nutrients available to plants through their excrements (Van Andel 1999; Schmitz 2008 and references therein). By these means herbivores may alter competitive interactions among plants, subsequently affecting successional processes (e.g. Kuijper & Bakker 2005; Ostfeld & Canham 1993; Norrdahl et al. 2002; Howe et al. 2006), and plant species diversity (Olff & Ritchie 1998).

Plants, on the other hand, are not defenceless against herbivores. They possess an array of defensive armour, including chemical compounds, physical features and spatial or temporal escape from herbivores. These affect both the susceptibility of plants to herbivores and the intensity of herbivory. The vulnerability of a plant to herbivory also depends on the quality of its neighbours. Thus plant species diversity and composition influence grazing pressure by herbivores (e.g. Tahvanainen & Root 1972; Atsatt & O'Dowd 1976; Siemann et al. 1998; Koricheva et al. 2000; Jactel et al. 2005). Crop diversification has therefore been suggested in agricultural and silvicultural plantations as a method of reducing herbivory damage

to economically valuable plants (Andow 1991; Johansson 2003). Moreover, herbivore abundance and distribution, and the consequent grazing pressure, may be assumed to be related to habitat selection by herbivores (Williams et al. 2012).

In ecosystems modified by humans for production, such as agro-ecosystems, herbivores represent a dilemma. On the one hand, they are potential crop pests; on the other, at densities not exceeding the economic threshold – defined as "the (pest) density at which control measures should be initiated to prevent an increasing pest population from reaching the economic injury level" (Stern et al. 1959) – herbivores are necessary for ecosystem services and for ecosystem functioning through trophic interactions: adequate herbivore numbers can maintain viable natural enemy (predators and parasites) populations, which regulate herbivore populations. This top-down predator force has sometimes been successfully applied in the biological control of crop pest populations (Landis et al. 2000; Perdikis et al. 2011). In this thesis, herbivory is addressed in terms of ecological theory and application to a specific study system: riparian buffers in the agricultural landscape.

1.1   Herbivory in productive environments

In a seminal paper, Hairston, Smith and Slobodkin (1960) postulated that predators limit herbivore densities to such a degree that they are unable to decimate all available plant material (the HSS hypothesis); this is why the world is green – or, more specifically, why herbivores seldom overexploit their plant resources. Later it was pointed out that the HSS is not ubiquitous but depends on the primary productivity of the environment (Fretwell 1977). This idea was further formulated into the ecosystem exploitation hypothesis (EEH hypothesis; Oksanen et al. 1981). The convergence of the EEH with the original HSS is limited to productive environments, such as forests, that can support sufficient prey densities for the maintenance of predators (Oksanen et al. 1981).

1.1.1. Herbivory pressure in boreal ecosystems

Consistently with the predictions of the classic trophic exploitation models, some studies have suggested that mammalian herbivory pressure on productive temperate and boreal vegetation is trivial (Crawley 1983; Oksanen 1988; Moen & Oksanen 1998). On the other hand, abundant herbivores can have a dramatic effect on plants at the species level in boreal, temperate and tropical systems (Batzli & Pitelka 1970; Ostfeld & Canham 1993; Terborgh et al. 2001; Norrdahl et al. 2002; Hambäck et al. 2004; Howe et al. 2006; Huitu et al. 2009; Estes et al. 2011). It has been suggested that the nature or characteristics of predator-prey dynamics may influence the outcome of plant-herbivore interactions (Oksanen & Oksanen 2000): In stable systems, where predators drive herbivore numbers towards low or medium equilibrium points (Hanski et al. 1991), the grazing pressure

of for instance voles on grassland vegetation may be negligible (Crawley 1983). On the other hand, cyclic or chaotic predator-prey dynamics may lead to more pronounced herbivore pressure on plants (Abrams 1999; Oksanen & Oksanen 2000).

A further factor contributing to the potential impact of herbivores on plants is the relative palatability of a plant. According to the edibility hypothesis, herbivores can create a plant community dominated by unpalatable plants by selectively grazing on preferred food plants while leaving less palatable ones intact (Leibold 1989; Schmitz 1994; Schmitz 2000; Chase 2000; Howe et al. 2006). Studies in boreal ecosystems have demonstrated that strong seasonality may reduce the herbivory on herbaceous vegetation: During the summers, *Microtus* voles reduced only the quantity of their preferred food plants. In wintertime, on the other hand, the preferred plants escaped herbivory through temporal refuges (wilting or freezing), thereby forcing the herbivores to attack less palatable plants, i.e. woody ones (Norrdahl et al. 2002; Hambäck et al. 2004).

Norrdahl et al. (2002) have postulated that the top-down effect of vole herbivory may be a step-function with a critical threshold density, whereby voles expand their diet from high quality food (grasses and forbs) to poorer quality food such as tree seedlings only above the threshold density. In predator-driven cyclic vole populations, where herbivore densities surpass the critical threshold more or less regularly but only for a short period, most damage to the saplings of woody plants should thus occur at the short vole peaks. In cyclic vole populations the height of density peaks varies more than their duration (e.g. Norrdahl 1995), suggesting that the height of the density peak correlates with the extent of herbivory pressure above the assumed threshold line. Hence the damage to woody plants should be more strongly associated with peak abundances than with the cumulative impact of herbivory throughout the vole oscillation cycle.

1.1.2. Herbivory pressure and plant species diversity and composition

The impact of herbivores on plants is influenced by the plant diversity of the community. According to the associational resistance hypothesis, plants in polycultures are less prone to herbivory than monocultures (Pimentel 1961) because less palatable plants mask palatable ones (Tahvanainen & Root 1972). The contrary phenomenon, in which higher plant diversity results in increased herbivory as compared to monocultures, is called associational susceptibility (White & Whitman 2000).

Diverse plant communities have been shown to experience less insect pest damage or have lower insect herbivore abundances in various ecosystems, including agro-ecosystems (Andow 1991), grasslands (Siemann et al. 1998; Koricheva et al. 2000) and forests (Jactel et al. 2005). It has also been suggested that rather than plant diversity *per se*, the key characteristic of vegetation that determines the level of insect herbivore damage, at

least in forest ecosystems, is plant species composition (Jactel et al. 2005; Koricheva et al. 2006; Vehviläinen et al. 2007). Some studies have also provided evidence for tree species diversity effects on mammalian herbivory (e.g. Hjälten et al. 1993; White & Whitman 2000; Edenius et al. 2002; Bergvall et al. 2006; 2007; Vehviläinen & Koricheva 2006) but the results have been inconsistent. Palatability to herbivores varies greatly among woody plant species, affecting the damage experienced by the species (Hjältén et al. 1993) The level of damage caused by mammalian herbivores also depends on the type of herbivore, its level of specialization and the scale at which herbivores select their food (Hjältén et al. 1993; White & Whitman 2000; Muzika & Liebhold 2000; Hjältén et al. 2004; Koricheva et al. 2006; Vehviläinen & Koricheva 2006; Vehviläinen et al. 2006; Vehviläinen et al. 2007). Moreover, mammalian herbivores at high densities can have dramatic effects on woody plants, decimating a majority of the seedlings at the early establishment phase, irrespective of their palatability (Hambäck et al 2004; Dahlgren et al. 2009). Thus herbivore abundance may be expected to influence the direction of the neighbour association effect, in particular in the case of plants that are less palatable than their neighbours. If herbivores avoid unpalatable plants until the quantity of preferred plants drops below the level needed to sustain all individuals, the relationship between herbivore abundance and damage may be linear in preferred plants but is likely to be non-linear in unpalatable ones (Norrdahl et al. 2002).

1.1.3. Herbivory pressure and habitat quality

Grazing pressure on plants can be assumed to be tightly linked to the habitat selection of herbivores (Williams et al. 2012). Theories of habitat selection predict that the fitness of an individual will be associated with habitat quality (Morris 2003), which in turn is affected by resource abundance (e.g. Morris 1994), foraging efficiency (Morris 1988), and the risks associated with foraging (Brown 1988), and is reflected in the spatial distribution of individuals. Thus the provision of supplementary food should change habitat selectivity (Morris 2005), and according to patch use theory the use of enriched habitats should increase (Brown 1988).

For herbivores vegetation is a key constituent of habitat quality, providing resources and shelter. Small mammals generally prefer protective vegetation cover over either high-quality food (such as newly developed, highly nutritious grass sward) (Kotler & Blaustein 1995; Korpimäki et al. 1996; Koivunen et al. 1998; Pusenius & Schmidt 2002) or open areas (Morris 2005), because of the lower (perceived or real) risk of predation. Contrary to the prediction of the patch use theory, the provision of supplementary food did not increase the use of the enriched patch; instead, it increased the exploitation of another habitat patch, one with natural cover (Morris 2005). Morris (2005) has suggested that the voles' avoidance of the enriched habitats was due to the increased risk of predation by an omnivorous bear, which was attracted to the food supplementation.

A thorough understanding of the relative roles of supplementary food and protective cover may help in habitat management in and around cultivations to divert herbivory pressure away from economically valuable plants.

1.1.4. Herbivory pressure and natural enemies

The impact of herbivores can be reduced by increasing the efficiency of their natural enemies. One approach to this goal is conservation biological control. This involves habitat manipulation to favour the natural enemies (predators or parasitoids) of the pest that naturally occur in the area. This approach is linked to the ecology of the specific pest and of its natural enemies, and the quality of the habitat in which they occur (Landis et al. 2000). In agro-ecosystems it involves the protection of natural enemies against the adverse effects of pesticides and of incompatible cultivation practices, and the enhancement of their populations by the provision of food supplements such as nectar and pollen (Perdikis et al 2011). Nectar- or pollen-feeding is important for the reproductive success of several predatory insects (Wäckers & Rijn 2005; as cited in Olson & Wäckers 2007). Numerous studies have indeed focused on the effects of vegetation on natural enemies (e.g. Gurr et al. 2003 and references therein). But the physical attributes of the habitat may also influence herbivores directly or indirectly through natural enemies. For instance the size of non-crop areas in the mosaic of the agricultural landscape has been reported as the main factor contributing to the efficiency of the natural enemy (the parasitoid *Tersilochus heterocerus*), which controls the crop damage caused by the rape pollen beetle *Meligethes aeneus* (Thies & Tscharntke 1999).

1.2. Agricultural ecosystems

In an ecological context agricultural landscape comprises a natural ecosystem, which, although modified by cultivation practices, interacts closely with the surrounding nature and its biodiversity (Tiainen et al. 2004). Since the Second World War, however, agricultural modernization, with both extensive and intensive land use harnessed for crop production, has led to landscape fragmentation, with only small and isolated semi-natural habitats (Kleijn & Sutherland 2003; Bianchi et al. 2006). These, coupled with the monocultures typical of intensive farming have disrupted the close interplay between ecology and agriculture (Altieri & Nicholls 2005), and have contributed to the rapid decline of biological diversity and the associated ecosystem services, such as biological pest control and pollination (Wilby & Thomas 2002; Kleijn & Sutherland 2003). The majority of the remaining biodiversity is found in the semi-natural features of agricultural landscapes (Kleijn et al. 2001), which include several types of landscape elements that are not harnessed for agricultural production (e.g. field margins).

1.2.1. Agri-environment schemes

In 1992 the European Union introduced agri-environment schemes (AES) in response to concern over the negative environmental and biodiversity impacts of intensive farming practices. An AES is based on paying farmers to modify their farming practices so as to provide environmental benefits (Kleijn & Sutherland 2003; Merckx et al. 2009). All EU member states are obligated to implement such schemes according to environmental needs and potential, but the content of the schemes vary widely among countries (Kleijn & Sutherland 2003). In Finland the AES programme was adopted in 1995 in conjunction with accession to the EU. Typical schemes involve field margins, i.e. non-crop areas bordering crop fields; these have permanent herbaceous vegetation with grass dominance. The definition of field margins varies between countries and according to their location in relation to other landscape features; broadly, however, their environmental and conservational roles include the prevention or reduction of eutrophication, agrochemical drift, nutrient flow along with melting snow and water, and siltation; the provision of resources (species refuges, foraging and breeding habitats, ecological corridors); and the promotion of biodiversity (Marshall & Moonen 2002).

Riparian buffers are one type of field margin situated between crop field and water bodies. In Finland, basic environmental support is granted for the establishment and maintenance of a narrow filter strip at least 3 m wide between arable land and the bank of a watercourse. An additional, voluntary special support scheme encourages the construction of buffer zones at least 15 m wide. As a grassland management measure, recipients of special support are obligated to mow the grass and to remove the cut vegetation from the buffer zone once a year (Ministry of Agriculture and Forestry in Finland 2006). While the basic scheme covers most of the agricultural land in Finland, the additional, optional scheme is expected to benefit the maintenance of biodiversity more efficiently than basic measures such as narrow filter strips (Ministry of Agriculture and Forestry in Finland 2004).

Riparian buffers are principally aimed at water quality protection: They prevent the flow of nutrients and agro-chemicals from crop-fields to water courses (Reichenberger et al. 2007; Uusi-Kämppä et al. 2010) but they can also enhance biodiversity (e.g. Marshall & Moonen 2002), and function as ecological corridors for wildlife (Marshall & Moonen 2002). In addition, they may increase the efficacy of biological pest control (Landis et al. 2000; Duelli & Obrist 2003).

According to some studies, the AES have not mitigated the loss of biodiversity (Kleijn et al. 2006; Blomqvist et al. 2009). Some farmers have also voiced their concern about non-crop habitats, such as riparian buffers becoming sources of weeds, pests and plant diseases (Marshall & Arnold 1995; Deschênes et al. 2003). Current environmental and biodiversity loss in agro-ecosystems, coupled with pressure to limit economic investment in the AES, foregrounds the importance of further investigation of the pros and cons of

management practices. Non-crop habitats, such as different types of field margins, can provide a multitude of ecological services, but they are often constructed with one principal goal in mind (Olson & Wäckers 2007). For example, although riparian buffer zones can provide a range of ecological services, they are mainly established to reduce diffuse pollution (Ministry of Agriculture and Forestry in Finland 2007). The optimal width of a buffer zone to reduce diffuse pollution depends on a number of factors, including hill slope, the physical attributes of the soil, stocking density and the nature and application mode of agro-chemicals. The width recommended for the promotion of biodiversity is usually much greater than that prescribed for pollution control (Fischer & Fischenich 2000, as cited in Cole et al. 2008). The main applied purpose of this thesis is to investigate some of the potential risks and benefits associated with riparian buffer width and the abundance of the woody plant cover, with particular regard to herbivory pressure.

1.2.2. *Role of woody plants in riparian buffers*

Trees and shrubs increase the structural complexity of habitats, which may be beneficial for rural fauna and flora (Söderström et al. 2001 and references therein; Merckx et al. 2009), and support local biodiversity better than structurally more homogenous habitats (Luoto et al. 2002). Due to their deep roots, woody plants generally prevent erosion, leaching and cave-ins more efficiently than herbaceous plants (Finnish Ministry of Agriculture and Forestry in Finland 2007). Additionally, some studies have indicated that riparian buffers with woody plants may be more efficient in nutrient uptake and retention than buffers with only herbaceous vegetation (Osborne & Kovacic 1993; 2006; Mander et al. 1996; Søvik & Syversen 2008), as they reduce the sediment-carrying capacity of the water entering the buffer (Søvik & Syversen 2008) and improve the infiltration capacity of the soils (Lyons et al. 2000). Consequently, woody plants in general tend to increase the environmental and biodiversity benefits of the riparian buffers. Optimally riparian buffers with woody plants can provide additional income for farmers (e.g. berry-producing species). On the other hand, planting young saplings in riparian buffers may incur costs due to vertebrate herbivores. *Microtus* voles, which abound in boreal grasslands such as riparian buffers, can cause considerable damage to young seedlings and saplings (e.g. Gill & Marks 1991; Ostfeld & Canham 1993; Huitu et al. 2003, 2009).

1.3. Aims of the thesis

The principal purpose of this thesis is to investigate the factors affecting trophic interactions in riparian buffers of agro-ecosystems. For the most part, the focus is on factors affecting vole herbivory (**I-III**); the exception is one article (**IV**), which is more concerned with the factors determining Hemipteran insect assemblages and their possible implications for biological control. Articles **I** and **II** deal with the experimental

testing of the impact of voles on woody sapling establishment in productive semi-natural grasslands; in articles **III** and **IV** the purpose is to determine the relationship between the characteristics of riparian buffers and vole habitat selection (**III**) and Hemipteran species composition as well as the abundance and species richness of herbivorous and predatory Heteroptera (true bugs) (**IV**)**.**

In article **I** the threshold herbivory hypothesis, based on Norrdahl et al. (2002), was tested. This hypothesis predicts that the top-down impact of vole herbivory on sapling survival will be more strongly associated with vole peaks than with the cumulative impact of herbivory at all abundances. The height of the vole peak was used as an index of the degree of herbivory pressure above the assumed threshold density. A further question was whether the expansion of vole herbivory from preferred herbaceous plants to woody plants is step-wise or occurs gradually as vole densities increase. A final question was whether the level of herbivory damage is better explained by the absolute vole density or by the density relative to the carrying capacity of the vegetation.

In article **II** survival of unpalatable woody plant saplings as a function of increasing vole abundance in monocultures versus mixed stands was investigated. The hypothesis put forward was that sapling survival would be negatively related to vole abundance both in monocultures of black alder (*Alnus glutinosa*) (poor quality forage for voles) and in mixed stands of black alder and five other, more palatable woody species, but that the threshold herbivore density would be lower in the monocultures than in the mixed stands because the mixed stands provide more food alternatives, of varying palatability.

In article **III**, habitat use by voles was compared in narrow and wide field buffers, to evaluate whether increasing the width of the buffer adds to the risk of voles entering the crop field. Emphasis was on differences in the size of the home range and space use of field voles in narrow vs. wide buffers as well as on seasonal differences in the use of field buffers vs. adjacent cultivated fields?

In article **IV** the main purpose was to determine the degree to which hemipteran assemblage structure and variation therein can be explained by the biotic and abiotic attributes of riparian buffers (woody plant cover, degree of dominance by grasses, plant species composition; riparian buffer width), taking spatial autocorrelation into account. A particular focus was on patterns in herbivorous pests (such as *Lygus*) and beneficial predatory groups (such as *Nabis*).

2. MATERIALS AND METHODS

2.1. Study area

All the studies included in this thesis were carried out on riparian buffers in the municipalities of Aura (60ºN, 22ºE) and Jokioinen (60ºN, 23ºE) in southwest Finland. The region is characterized by intensive farming practices, including conventional tilling after harvest in September–October, harrowing and sowing (with fertilizers) in May, and harvesting in August–September. Herbicides are used irregularly in crop fields with weed problems. The use of both fertilizers and herbicides has declined over the last two decades because of changes in administrative guidelines and the increasing prices of chemicals (Hyvönen et al. 2003). The sampling sites for the study investigating Hemipteran assemblages (**IV**) were spread out across both municipalities. The experimental study, for which habitat quality was manipulated (**III**) was conducted at four sites (two narrow riparian buffers and two wide ones) in Jokioinen. For the purposes of studies **I** and **II**, six experimental fields, three in Aura and three in Jokioinen, were constructed. The study sites in Aura and Jokioinen were treated as identical replicates although there were disparities in their farming histories. The major difference was in the abundance of herbaceous vegetation during the construction of the experimental fields. This caused some difficulties in maintaining vole abundances at the desired level, while simultaneously constructing an opportunity to determine whether the level of herbivore damage was more closely related to actual vole abundance (given as the vole abundance index based on live trapping) or the abundance (index) adjusted to the quantity of vegetation (assumed to indicate carrying capacity). Detailed descriptions of the sites are given in the manuscripts and published articles.

2.1.1. Riparian buffers

The riparian buffers selected for the studies in this thesis varied in width and in their woody plant cover. In **III** and **IV** the particular interest was in the association between on the one hand riparian buffer quality, on the other field vole habitat use (**III**) or Hemipteran assemblages (**IV**). Although studies **I** and **II** were also situated in riparian buffers, the focus was not on the buffer *per se* but on the effect of *Microtus* voles on the establishment and survival of woody plant species in the buffers.

2.2. Study species

2.2.1. Woody plants

The combination of criteria for the selection of woody plant species followed the national regulations for riparian buffer construction: their nativity to Finland and their

natural occurrence in riparian buffers, growth form (tree or shrub), diversity of plant genera, their presumed ability to grow and become established in these nutrient-rich environments, and their availability in Finnish tree nurseries. The species selected for the sapling establishment experiments (**I** and **II**) were the black alder *Alnus glutinosa* L., the downy birch *Betula pubescens* Ehrh., the tea-leaved willow *S. phylicifolia* L., the aspen *Populus tremula* L. and the aspen hybrid *P. tremula* × *P. tremuloides* Michx (the last two hereafter referred to collectively as *Populus*), the dark-leaved willow *Salix myrsinifolia* Salisb., and the Saskatoon serviceberry *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem. The phenotype of *S. myrsinifolia* indicated introgression by some other *Salix* species, possibly *S. phylicifolia*. Although these willows may have been hybrids rather than pure *S. myrsinifolia*, they are referred to as *S. myrsinifolia*. These species met the selection criteria and also occurred naturally at the sampling sites for article **(IV)**, with the exception of the Saskatoon serviceberry. This species was chosen to replace the intended *Ribes alpinum* due to the unavailability of native options. Like *R. alpinum*, the Saskatoon serviceberry is a deciduous berry-producing shrub. *A. glutinosa* was selected for monocultures because of its nitrogen-fixing capacity, which may increase its capacity to reduce the phosphorus load in riparian habitats (Mander et al. 1996). The black alder is also a common tree species in riparian habitats in southern Finland.

2.2.2. Invertebrate herbivores

Heteroptera (true bugs) and Auchenorrhyncha (free-living hemipterans) were inventoried at each site. True bugs occupy a wide range of habitats (e.g. Lundgren 2011) and have variable foraging regimes. Many true bug species are omnivores, but predominantly any one species is either predatory or herbivorous (Morris 1979; Lundgren 2011). True bugs have been regarded as a suitable group for biodiversity evaluations (Duelli & Obrist 1998; Di Giulio et al. 2001; Zurbrügg & Frank 2006), as their species richness reflects total arthropod richness in cultivated landscapes (Duelli & Obrist 1998; Fauvel 1999). Free-living hemipterans are a potential indicator group of habitat quality for conservation purposes (Hollier et al. 2005), since they have been found to be sensitive to the vertical structure of the vegetation and consequently respond readily to cutting regimes (Andrzejewska 1965).

2.3.1. Vertebrate herbivore

Microtus voles, the field vole (*M. agrestis* Linnaeus, 1761) and the sibling vole (*M. levis* Miller, 1908, syn. *M. rossiaemeridionalis*) are the principal vertebrate herbivores of boreal grassland habitats such as riparian buffers (Crawley 1983; Norrdahl 1995); their population oscillations seem to be mainly driven by predation (Norrdahl 1995; Klemola et al. 2000). Both species are folivorous and use similar although not identical food

resources (Myllymäki 1977). As they coexisted in the control plots of the experimental fields and could not be excluded there (**I** and **II**), they are collectively regarded as voles throughout this thesis.

2.3. Experimental and observational procedures

2.3.1. *Effect of voles on woody plant saplings*

Six experimental fields were constructed, each consisting of one open area (control) and three enclosures of 450 m² each. In each control area/enclosure one plot consisted of a monoculture of black alder, the other of a mixture of six species (see 2.3.2). Sixty saplings of black alder were planted in each monoculture, and a total of sixty woody plant saplings (ten of each woody plant species) in each mixed stand. The experiments testing the relative impact of cumulative vs. peak herbivore pressure (**I**) and the effect of herbivore abundance on sapling survival in monocultures vs. mixed stands (**II**) were conducted concurrently, within the same enclosures. For the purposes of study **I**, only mixed stands were used. All the saplings (both in monocultures and in mixed stands) were exposed to different vole herbivory pressures; in each of the six experimental fields, the open area was used as a control area, representing natural vole density of the study site. One pair of voles was introduced in one of the enclosures ('stable density') and two pairs in another ('variable density'). One enclosure ('vole exclosure') was left empty and access by voles was disabled by fences. The main purpose was to maintain low vole numbers in the stable density enclosures and otherwise low vole numbers, but with one peak in the variable density. The crucial point was that the average density throughout the experiment should be the same in both treatment groups. Unfortunately, maintenance of vole abundances at the intended levels proved problematic, as indicated by the repeated live-trapping occasions. Some of the 'vole exclosures' were not absolutely vole-proof throughout the experiment, as indicated by the signs of vole browsing observed on some saplings. Yet not a single vole was caught in these exclosures during the trapping periods. Moreover, the mean vole numbers in the stable and variable density enclosures were not comparable (stable: mean ± SE: 50.3 ± 59.1 voles ha^{-1} and variable: 90.6 ± 130.3).

The statistical models were therefore built based on calculated indices of the mean and maximum numbers of voles caught during recurring live-trapping occasions, rather than on treatment effect. In article **I** these indices were used to assess whether cumulative (mean) or peak (maximum) vole abundance had a greater impact on the level of damage to the saplings. The peak vole abundance index was also used to compare black alder sapling survival in monocultures and in mixed stands of alder and five other, more palatable species (**II**).

2.3.2. Vole habitat selection

Vole home range size and habitat use in relation to the habitats available were studied by radio-tracking (III). Radiotelemetry is a method commonly used in field studies of vertebrate populations to collect information on population mechanisms such as home range use and habitat preferences (White & Garrott 1990). The information obtained can be used to implement management strategies. A general assumption is that the behaviour of individuals with transmitters represents that of the population as a whole (Moorhouse & MacDonald 2005). The data collected were analysed with compositional analysis, a method recommended for quantifying habitat use as the experimental unit is the radio-collared animal rather than individual radio-locations (Aebischer et al. 1993).

Prior to fitting the radio-collars, four riparian buffers adjacent to cultivated fields – two narrow filter strips (≤ 5 m) and two wide buffer zones (> 15 m) – were manipulated by mowing and the provision of supplemental food (pellets for laboratory rodents) and artificial cover (plywood plates raised 10 cm above ground) in a multifactorial design. The treatments (food, cover, food + cover and control – no food or cover) were randomly assigned to each study site and were applied to both mowed and unmowed patches.

2.3.3. Hemipteran assemblages in riparian buffers

Window traps were chosen as an insect sampling method. These are functionally 'passive' (i.e. they do not attract insects) and perform well in diversity evaluations because they sample a wide range of insects (Duelli & Obrist 1998). The traps were set in a total of forty sampling sites, selected on the basis of visual impression of the woody plant cover and assigned accordingly to three categories: 1 = Open buffers (n = 13): either no woody plants at all or single trees/shrubs, but dominated by open view; 2 = Patches of woody plants (n = 13): clusters of trees/shrubs, clearly separated by open gaps; 3 = Continuous belt of woody plants (n = 14): view dominated by trees/shrubs. Most of the woody plants belonged to the genus *Salix*, but *Alnus*, *Populus*, *Betula*, *Picea*, *Pinus*, *Sorbus* and *Prunus* species also occurred at some sites.

The main focus in this study was on buffer width and woody plant cover, but other biotic and abiotic factors were also recorded. Biotic factors included floristic composition, grass coverage, and crop species in the adjoining field; abiotic factors included landscape characteristics of the riparian buffer that might be relevant for true bugs and free-living hemipterans, such as watercourse width and the distance from the insect trap to various landmarks – the edge of the crop field, the water channel, the nearest woody plant, and the nearest forest edge. Geographical coordinates were recorded to test spatial autocorrelation.

Insects were collected at nineteen sites in the municipalities of Aura and Jokioinen in July–August 2003 and June 2004. Sampling was continued at 21 different sites (in Aura) during June and July–August of 2005. Heteroptera (true bugs) and Auchenorrhyncha (free-living hemipterans) were separated from the samples and identified to species level; true bugs were further divided into trophic guilds (herbivores and predators) according to their primary diet, as described in the literature (e.g. Rinne & Rintala 2009). Many true bugs are omnivores, but the feeding ecology is predominantly either herbivorous or predatory (Morris 1979; Lundgren 2011).

3.   RESULTS AND DISCUSSION

3.1.   Threshold herbivory

Contrary to the prediction of the threshold herbivory hypothesis, vole browsing at low vole abundances was not limited to the most palatable species. *Alnus glutinosa*, which is perceived as poor forage for voles (Hjältén & Palo 1992; Hjältén *et al*. 1993; Hjältén *et al*. 2004), suffered some damage even at low vole abundances. The most considerable damage, however, (over 60% saplings per species damaged) was observed in species more palatable than *A. glutinosa*. Thus, while there seems to be no clear threshold, the level of damage appeared to vary according to the relative palatability of the plant species in the community. Furthermore, cumulative herbivory (mean vole abundance) explained the fate of the saplings as well or better than the peak herbivory (peak vole abundance). These findings suggest that there is no sharp threshold density at which voles expand their diet from the most palatable plant species to woody species, or that such a threshold lies at a very low vole numbers.

The results were more consistent with studies highlighting the importance of learning in the food choices of mammalian herbivores (e.g. Bryant et al. 1991; Bergvall & Leimar 2005), and with the detoxification limitation hypothesis (Marsh et al. 2006). If voles have to learn the suitability of alternative food sources by tasting, vole damage to poor quality saplings should reflect the cumulative number of individuals, as was the case in our study.

Interestingly, the impact of vole browsing on saplings was better explained by the indices of actual abundance than by the index adjusted to the presumed carrying capacity of the herbaceous vegetation.

The fate of a sapling thus depended more on vole numbers than on the amount of herbaceous vegetation around the sapling. This is in agreement with previous observations that protective vegetation cover around a sapling increases rather than decreases the risk of sapling damage (Gill & Marks 1991; Ostfeld & Canham 1993; Pusenius & Ostfeld 2000; Pusenius *et al*. 2000).

3.2.   Vole herbivory in tree monocultures and mixed stands

Although the average probability of vole damage or sapling survival of the black alder saplings did not differ between monocultures and mixed stands, an increasing vole abundance reduced sapling survival in monocultures significantly more than in mixed stands. Our results thus suggest that the effect of stand diversity on herbivory depends on herbivore abundance. The benefits of stand diversity are elevated by increasing

herbivore abundance. Many commercially cultivated tree species are relatively poor-quality food for vertebrate herbivores. For these saplings, mixed stands may be viewed as insurance against occasional peaks in herbivore density. Herbivores are likely to taste the poor-quality saplings in mixed stands, but the impact of herbivore activity, as shown by our experimental results, should be less destructive in the presence of more palatable species.

3.3. Habitat selection by voles on narrow and wide riparian buffers

Vole habitat use differed in narrow and wide riparian buffers. Firstly, voles moved longer distances in the narrow filter strips than in the wide buffer zones, indicating the superior quality of the latter as a vole habitat. In a more linear habitat, such as the filter strips, the animals were forced to extend their foraging trips. Secondly, removal of the herbaceous cover (mowing) led to disparities in vole habitat use between the narrow riparian buffers as compared to their wider counterparts. In the narrow buffers habitat use did not differ between mowed and unmowed patches, while in the wide buffers voles were only encountered in patches with abundant herbaceous cover. Furthermore, in the narrow riparian buffers voles entered the crop fields more frequently than in the wide ones. In agreement with a previous study (Morris 2005), the natural cover provided by unmowed herbaceous vegetation was preferred over enriched habitats (with supplemental food provided) or artificial cover. Thirdly, there were no seasonal differences in vole habitat use between narrow and wide riparian buffers. These results agree with previous conclusions that for small mammalian herbivores such as voles cover is the primary determinant of habitat quality (Kotler & Blaustein 1995; Korpimäki et al. 1996; Koivunen et al. 1998; Pusenius & Schmidt 2002; Morris 2005). Our findings also suggest that wide riparian buffer zones do not pose a higher risk of voles entering the crop field as compared to narrow filter strips.

3.4. Hemipteran assemblages in relation to riparian buffer characteristics

In article IV I examined the degree to which riparian buffer characteristics explain Hemipterans species assemblages, focusing in particular on herbivorous pests (such as *Lygus*) and on beneficial predatory groups (such as *Nabis*) (**IV**). Grass cover and floristic composition were the most important determinants of Hemipteran species turnover, coinciding with earlier suggestions that vegetation is the major determinant of insect assemblages (e.g. Frank & Künzle 2006; Schaffers et al. 2008; Kőrösi et al. 2012), while true bug abundance was related to the riparian buffer width and woody plant cover. The abundance of herbivorous and predatory true bugs showed reverse patterns in relation to buffer width; this suggests that increasing the width of a riparian buffer will lead to

a higher predator-to-prey ratio in true bug assemblages, thereby potentially reducing pest problems. However, the two herbivorous Hemipteran groups, herbivorous true bugs and free-living hemipterans, showed opposite abundance patterns in relation to both riparian buffer width and woody plant cover. In addition, true bug abundance and species richness was higher in the riparian buffers with woody plants, with the exception of the crop pest *Lugus ruglipennis*, which was more abundant in the narrow buffers with no woody plants.

Such findings call for caution in generalizing from results. Responses to land use management may differ among taxonomic groups or trophic guilds within insect assemblages.

4. CONCLUSIONS

In the first article, all woody plants irrespective of their palatability experienced damage even at low vole abundances. Even though no clear threshold was found, the level of damage varied according to the relative palatability of the plant species in the community. In the second article, vole herbivory at increasing abundance was more lethal to unpalatable *A. glutinosa* in monocultures than in mixed stands. Both studies (**I, II**) confirmed previous suggestions as to the importance of learning in the food choices of mammalian herbivores (e.g. Bryant et al. 1991; Bergvall & Leimar 2005). If voles have to learn the suitability of alternative food sources by tasting, vole damage to poor quality saplings should reflect the cumulative number of individuals, as was the case in our study (**I**). However, in monocultures of unpalatable plant species herbivores do not have alternatives; thus they accept a low-quality food rather than starve to death. (**II**). Saplings recovered well from minor vole damage, suggesting that woody plant saplings have relatively good establishment opportunities even in the presence of voles.

In the third article, I found that vole activity in the wide buffers was concentrated on patches with high grass, while in the narrow buffers open areas were readily crossed. Voles also used crop fields in the narrow filter strips more frequently than in the wide buffer zones. In accordance with previous findings (Morris 2005), food-enriched habitat patches were avoided by voles.

In the fourth article, I found reverse patterns in *Lygus rugulipennis* (a common crop pest) and *Nabis* species (a potential biological control agent) in relation to riparian buffer width and woody plants. This finding suggests that increasing riparian buffer width and including woody plants may lead to a higher predator-to-prey ratio in true bug assemblages, thereby potentially reducing pest problems. The opposite patterns found in two herbivorous Hemipteran groups, herbivorous true bugs and free-living hemipterans, in relation to both riparian buffer width and woody plant cover nevertheless call for caution in generalizing from the results.

4.1. Management implications

The main implications of this thesis for riparian buffer management are the following:

1) Increasing the width of the riparian buffer does not pose a pest hazard to adjacent cultivation by vertebrate (vole) or invertebrate (true bugs) herbivores (**III**, **IV** respectively). However, in contrast to true bugs, the abundance of free-living hemipterans may increase with increasing buffer width. These findings indicate that responses to riparian buffer width are likely to differ among taxonomic groups

or trophic guilds within insect assemblages. Thus a general directive concerning riparian buffer width for biological pest control may lead to different outcomes in different cultivated areas, depending on the identity of both potential pests and natural enemies present in them.

2)   Woody plant cover was related to higher true bug abundance and species richness, as opposed to open buffers without woody plants. Thus woody plants may increase the biodiversity value of riparian buffers, although the patterns may be specific to any taxonomic group or trophic guild. Indeed, an increasing pattern in relation to woody plants was observed in both herbivorous and predatory true bugs species.

3)   The establishment and survival prospects of woody plant saplings in riparian buffers are relatively good, but sapling survival may be reduced at increasing vole densities (**I, II**). The impact of vole browsing can be reduced by diverting vole activity away from the saplings. In the summer, removing herbaceous vegetation from a sufficiently large area around the plantation can render the saplings unattractive (**III**). Yet the greater part of seedling and sapling damage occurs during the winter. Some safeguards against winter damage, at least in the case of unpalatable woody species, may be provided by neighbour effects. Even though voles are likely to taste saplings of all species in mixed stands, the impact of herbivore activity on the unpalatable species should be less severe in the presence of more palatable species (**II**).

The main aspect calling for future work is the full potential of riparian buffers in supporting efficient biological control. Learning to enhance biological pest control would increase the multi-functionality and cost-efficiency of these non-crop areas.

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