Omnivore Population Dynamics and Trophic Behavior

Applications for Sustainable Willow Short Rotation Coppice

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Abstract

Plant traits can mediate the interactions between plant feeding trophic omnivores and their herbivore prey via density effects and by altering the omnivore's trophic behavior (plant vs. prey feeding). These bottom-up effects can be important for our mechanistic understanding of omnivory as a stabilizing feature of food-webs, but can also be applied in management for conservation biological control.

This thesis investigates how plant nutrient status influence heteropteran omnivore population dynamics and trophic behavior and explores management solutions for conservation biological control that can reduce the risk of leaf beetle outbreaks in willow short rotation coppice. The results provide novel empirical support for the established assumption that plant feeding can decouple omnivores from fluctuations in their prey populations. Plant feeding stabilizes omnivore population dynamics, which may explain why omnivore populations show no numeric response to fluctuations in leaf beetle population densities. The potentially strong omnivore-plant coupling suggests that omnivores can function effectively at low prey densities (contrary to specialist predators) to provide what has been referred to as 'background level' control of insect pests.

The applied part of the thesis demonstrates that retaining willow refuges to reduce omnivore mortality and stabilize population densities across harvests increase rather than decrease the risk of leaf beetle outbreaks. The results also reveal that willow stands surrounded by landscapes with high proportion open land cover are less likely to experience leaf beetle outbreaks. This outcome was expected partly because of the recorded high and stable densities of heteropteran omnivores on high nutrient status host plants in agriculture dominated landscapes. In addition, the results illustrate that landscape-moderated recolonization after disturbance can change over time and that considering the temporal dynamics of populations may be crucial when designing and evaluating studies at landscape level. In conclusion, this thesis highlights the importance of basic ecological knowledge of predator trophic behavior for developing successful conservation biological control.

Keywords: trophic omnivore, population dynamics, stability, trophic behavior, time series, recolonization, landscape, leaf beetle, willow short rotation coppice

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Liman, A-S., Dalin, P. & Björkman, C. Variability in omnivore population density stabilized by leaf nitrogen status (manuscript).

II Liman, A-S., Dalin, P. & Björkman, C. Detectability of landscape effects on recolonization increases with regional population density (accepted for publication in Ecology and Evolution).

III Liman, A-S. & Björkman, C. Predator refuges for conservation biological control in intermediately disturbed systems – the rise and fall of a simple solution (manuscript).

IV Liman, A-S., Dalin, P., Bylund, H. & Björkman, C. Omnivore-prey population dynamics. Are plant-feeding omnivore populations decoupled from prey fluctuations? (manuscript).

The contribution of Anna-Sara Liman to the papers included in this thesis was as follows:

- I Main author and analysis. Performed experiments. Field data collected with Peter Dalin. Study idea and design with Peter Dalin and Christer Björkman.
- II Study idea and design, main author and analysis.
- III Main author and analysis.
- IV Study idea and design, main author and analysis.

Abbreviations

CBC	Conservation Biological Control
GLMM	Generalized Linear Mixed Models
SRC	Short Rotation Coppice

1 Introduction

1.1 The trophic level concept

The trophic level concept is commonly used to position organisms hierarchically in a food chain (Lindeman, 1942). An organism's trophic position represents its sequential order from the base of the chain. Primary producers (plants) occupy trophic position one, primary consumers (herbivores) occupy position two and secondary consumers (predators) occupy position three and beyond. This system to group organisms into discrete, homogenous trophic levels can be useful for explaining many ecological relationships, but it is often described as an abstraction that does not capture the complexity of real systems (Polis et al. 1989; Polis & Strong 1996).

The main critique to the trophic level concept can be related to the occurrence of species that are omnivorous, i.e. feed on more than one trophic level (Polis *et al.*, 1989; Polis & Strong, 1996). Omnivory was in the early days of ecology thought to be rare (Pimm & Lawton, 1977, 1978), but later studies has shown that omnivory is prevalent across ecosystems and taxa (Polis *et al.*, 1989; Arim & Marquet, 2004; Bascompte & Melián, 2005). In an analysis of 58 real food webs, Thompson et al. (2007) showed that above the herbivore trophic level, food webs were better described as a web of omnivores. In terrestrial insects, omnivory is represented in at least 40 families and 12 orders (Coll & Guershon, 2002).

1.2 Trophic omnivory and food web stability

The prevalence of trophic omnivory has shown to be important for our understanding of food-web dynamics and the persistence and stability of ecosystems (Vandermeer, 2006). Omnivory, per definition, introduce a multitude of 'weak' direct interactions between species in a food web. Much of the classic work on omnivory suggested, perhaps counter intuitively, that systems with omnivory were less stable than those without (Pimm & Lawton, 1978). Recent theoretical studies have revealed that food-web models with omnivory, tend to be relatively stable (Holyoak & Sachdev, 1998; Emmerson & Yearsley, 2004; Kratina *et al.*, 2012). Despite the predicted importance of omnivores, empirical studies on the role of omnivory for population and community stability are rare - with a few exceptions (Fagan, 1997; Eubanks & Denno, 1999, 2000). We know little about the basic population ecology and behavior of trophic omnivores and their role in both natural and managed systems (Eubanks, 2005).

1.3 Definitions of trophic omnivory

The term trophic omnivore is broad because it covers all species that utilize resources at more than one trophic level (Pimm & Lawton, 1978). By this definition, the term includes e.g. species that alternate between plant-feeding and predation as well as intra-guild predators (predators that share the same prey and consume each other) and predators that consume herbivores as well as detritus-feeders. The term trophic omnivore is used similarly for life-long omnivores and for temporary omnivores, i.e. species that are only omnivorous in certain life stages (Coll & Guershon, 2002).

This thesis only include studies on life-long trophic omnivores, i.e. permanent trophic omnivores that are primarily predators and secondarily plant feeders i.e. zoophytophagous. In the rest of the thesis, trophic omnivore (or just omnivore) follows this more narrow definition.

1.4 Population dynamics of trophic omnivores

The primary topic for this thesis is trophic omnivore population dynamics, i.e. to understand why populations of omnivores (alternating between plant and prey) vary in space and change over time. Trophic omnivores differ from strict herbivores and predators since they track resources at two different trophic levels. Understanding the relative role of plant and prey as potential ‘drivers’ of omnivore population dynamics is key for understanding the ultimate effect of plant feeding on prey suppression (Eubanks, 2005). Paper I and IV, therefore, deal exclusively with bottom-up effects (supply of resources from the first and second trophic level) on omnivore populations. There are naturally other factors that alone and in interaction shape variations in omnivore abundance, such as top-down effects (e.g. predators and parasitoids), horizontal interactions (e.g. competition and intraguild predation) and abiotic conditions (e.g. weather conditions) (Hunter & Price, 1992; Matson & Hunter, 1992; Denno *et al.*, 1995, 2005). Except for abiotic conditions, these other factors have not been considered in this thesis.

Nitrogen concentration is a characteristic of plant quality with a potentially strong direct effect on trophic omnivore survival (in early nymphal stages) and for performance in absence of prey. Nitrogen is also relevant for comparing the relative importance of resources at different trophic levels (Eubanks & Denno, 1999, 2000; Denno & Fagan, 2003; Matsumura *et al.*, 2004). It is generally recognized that herbivore population density increases on nitrogen enriched plants (Mattson, 1980; Awmack & Leather, 2002) and that sap-feeding insects (i.e. many heteropteran omnivores) may be especially responsive to enhanced plant nitrogen, since they feed selectively and on tissue that does not contain nitrogen based allelochemicals (toxic secondary metabolites) (Holopainen *et al.*, 1992; Wheeler, 2001; Huberty & Denno, 2004). Nitrogen concentration is substantially lower in plant than in herbivore biomass and the relative abundance of nitrogen in relation to growth conditions is, by orders of magnitude, more variable in plants than in herbivores (Mattson, 1980; Sterner & Elser, 2002; Andersen *et al.*, 2004). The mismatch in nitrogen across trophic levels has also been critical for the evolution of omnivory in heteropteran insects (Eubanks *et al.*, 2003).

Previous studies indicate that omnivore population dynamics may be more similar to herbivore than predator population dynamics, i.e. bottom-up effects related to plant nutrient status seem to be more important than those related to prey resources (Eubanks & Denno, 1999, 2000). One aim of this thesis has been to continue to explore the relative role of plant and prey resources for omnivore population dynamics.

1.5 Trophic behavior and omnivore-prey interactions

The functional response of an insect describes how variability in food resources influences consumption rates (Solomon, 1949; Holling, 1959). Omnivores utilize both plant and prey resources and can, therefore, theoretically show functional responses to both plant and prey. If omnivores show functional responses to resources at one trophic level (e.g. plant quality) this will influence consumption of the resources at the alternate trophic level (prey). This could be thought of as an omnivore's trophic behavior.

Mechanistically, we still have a poor understanding of omnivore feeding decisions. Food mixing across trophic levels is likely to be complex and highly species specific (Agrawal *et al.*, 1999; Coll & Guershon, 2002). Food mixing could primarily be a way to fit nutritional needs, or it could be driven by the resource of highest abundance and quality (Coll & Guershon, 2002). Feeding preferences are also affected by evolutionary history, i.e. omnivores that have evolved from ancestrally herbivorous or predatory lineages may as a result have different preferences (Eubanks *et al.*, 2003). Therefore, alternative food resources play very different roles for different groups of omnivores. For example will the role of plant feeding probably differ depending on if the omnivore eat pollen (very rich in nitrogen), plant sap (less rich in nitrogen) or just utilize the plant as a water resource (Gillespie & McGregor, 2000; Eubanks & Styrsky, 2005). The relative role of resources will ultimately influence the degree of flexibility associated with trophic omnivory (Eubanks & Denno, 1999). If the resources are interchangeable, the omnivores would benefit from higher flexibility than herbivores or predators with only one resource, but if they are not equivalent this would make them more sensitive to rapid spatial and temporal changes in resources.

In summary, plant traits can mediate the interaction between omnivores and their prey through density effects and changes in trophic behavior. Plant quality can thus have implications for the strength of (i) the omnivore-plant interaction, (ii) the omnivore-herbivore interaction, and therefore also for (iii) the herbivore-plant interaction (Coll & Guershon, 2002). Increased omnivore plant feeding can in a tri trophic system potentially cause a trophic cascade and relax the top-down control of the herbivore, whereas increased predation indirectly will relax herbivory.

1.6 Stability and the risk of insect outbreaks

Stability (roughly synonymous with ‘unchanging’) is a broad concept that can have very different meaning when looking at populations, communities and food-webs (Snyder & Tylianakis, 2012). The three definitions identified by Pimm (1984); variability, resilience and resistance all have implications for understanding and avoiding pest outbreaks, especially in systems where disturbances such as harvests influence the population dynamics of both predators and herbivores (Snyder & Tylianakis, 2012). High variability in herbivore pest population densities is the most central meaning of stability, for management in forestry and agriculture, since it is associated with the risk of insect outbreaks.

Highly fluctuating populations have a greater risk to reach outbreak densities. Even quite short periods of high population densities can cause significant damage and economic loss, which make reducing insect herbivore population density and variability the primary focus of insect pest control (Björkman *et al.*, 2000b; Dalin *et al.*, 2009). The insect outbreak phenomenon is well studied and there are many possible explanations for why and when herbivore pest populations fluctuate to reach outbreak levels in both managed and unmanaged systems (Barbosa *et al.*, 2012). Herbivore escape from predators and parasitoids is an aspects of insect outbreak risk with special relevance for understanding differences in outbreak occurrence between systems with different disturbance frequency (natural vs. managed and perennial vs. annual systems) (Letourneau *et al.*, 2009; Letourneau, 2012). Disturbance from harvest and other management can interrupt the predator-prey relationship and thereby allow for fast herbivore population growth rates - which increase the risk of an outbreak.

1.7 Conservation biological control

Conservation Biological Control (CBC) seeks to preserve and enhance predator and parasitoid numbers and facilitate their ability to suppress prey populations (Landis *et al.*, 2000). Two of the primary aims of CBC are to provide alternative food and shelter for predators and parasitoids. Supplementary or complementary food can improve the abundance and fitness of predators and parasitoids, whereas sheltered areas can provide a refuge from disturbance and/-or suitable overwintering habitats (Jonsson *et al.*, 2008). Well known examples of these two types of management are ‘flower strips’ providing complementary resources such as nectar and pollen for e.g. parasitoids and ‘beetle banks’ providing shelter for predatory beetles (Thomas *et al.*, 1992; Gurr *et al.*, 2005).

CBC could be managed through actions at several scales, from the local patch to the landscape (Landis *et al.*, 2000). Habitat management and diversification is a form of CBC that focuses on the local patch and its immediate surroundings (Landis *et al.*, 2000). Extensive literature is available to show that this form of CBC has been successful in a variety of agro-ecosystems (Landis *et al.*, 2000). Examples of management for CBC at larger spatial scales include for example landscape diversification and landscape level site selection (Tscharntke *et al.*, 2007). Developing management practices for CBC often require in depth knowledge of the ecology and behavior of the organisms in the system (Jonsson *et al.*, 2008).

The CBC initiative fits well with an increased interest in assemblages of generalist and omnivorous predators for pest suppression and what has been referred to as the ‘back-ground level control’ or the ‘early-season control’

(Symondson *et al.*, 2002; Welch *et al.*, 2012). Diversification and management to improve habitat continuity and availability of alternative resources correspond with the needs of many omnivorous predators and other generalist predators (Symondson *et al.*, 2002). One aim of this thesis has been to explore different management alternatives to improve the conservation biological control of herbivore pests by omnivorous predators in systems with intermediate harvest regimes in general and in willow short rotation coppice in particular. Paper II and III focus on management actions that aim to facilitate recolonization and population build-up and stabilize omnivore-plant associations across harvests.

2 Thesis aims

I. To increase our knowledge about the relative role of bottom-up effects at different trophic levels for shaping abundance and trophic behavior of omnivores and to discuss how these effects translate into omnivore-prey population dynamics and influence the risk of insect herbivore outbreaks.

More specifically

- to explore how leaf nitrogen status of the host plant influence omnivore population dynamics and trophic behavior (Paper I)
- to explore the degree of coupling between omnivore and prey population dynamics (Paper IV)

II. To understand how omnivore-prey dynamics is affected by disturbance (i.e. repeated stem harvest) and explore methods to increase the resilience of the conservation biological control in intermediately harvested systems, using willow short rotation coppice as a model system

More specifically

- to explore how landscape composition and temporal variation in population size interactively determine recolonization/community assembly (Paper II)
- to test the theoretical prediction that saving predator refuges decreases the risk of willow leaf beetle outbreaks (Paper III)

3 Study system

I have used two different willow study systems in this thesis that are chemically similar and host similar insect communities (Volf *et al.*, 2015) but differ in disturbance regimes. The natural grey willow system (*Salix cinerea*-unmanaged) was used for studies on omnivore population dynamics and trophic behavior (Paper I and IV) whereas the short rotation coppice system (*Salix viminalis*-managed) was used for recolonization and CBC studies (Paper II and III).

Grey willow

The grey willow (*Salix cinerea* L.) is native to Sweden, growing in wet, and moderately nutrient-rich soils, often forming dense stands along small streams, ditches and pastures and at forest edges (Jonsell, 2000). The size of stands range from a few square meters to hectares, although small stands are more common. Individual stands are often of the same clone, which make willows advantageous model systems, since 'genotypes' can be replicated across different treatments using cuttings from the same clone. Thereby the results can be more broadly generalized and potential variation associated with genotype can be evaluated. Hybridization is, however, common and can be troublesome since it may make field identification of stands uncertain (Jonsell, 2000).

Willow Short Rotation Coppice

In a Short Rotation Coppice (SRC) system, fast growing tree species are repeatedly cut back (coppiced) and harvested at regular intervals, through the crops life span of 15-25 years. The most commonly used willow species in northern Europe include genetic varieties of *Salix viminalis* L. The current standard in Sweden is to plant cuttings in a double-row system, with distances between rows of 0.75-1.5 m and spacing of 0.6 m within the rows (Mola-Yudego, 2010).

Willows are grown in Sweden primarily as a biomass crop for energy production, but with additional potential for biofiltration of waste water and sewage sludge. Commercialization of willow SRC started in Sweden in the early 1990s and this is where much of the breeding and technology has developed. Currently, Sweden has the largest cover of willow SRC in Europe (~16 000 ha, which translates into about 0.5% of the total arable land) (Mola-Yudego, 2010) and the Swedish Board of Agriculture predicts a short term increase of SRC by 30 000 ha (SOU 2007:36). The commercial extent in the rest of Europe is still quite small, although there is a potential for an increase (Mola-Yudego, 2010). For example, the UK Biomass Strategy predicts an increase in perennial energy crops up to 350 000 ha (Defra, 2007). It is, however, difficult to predict the future of willow SRC in northern Europe, since it is determined by a diversity of socio-political factors such as Energy policy, Agriculture policy, market development and attitudes among farmers (Weih, 2004).

Leaf beetles herbivores on willow

Three leaf feeding willow beetles *Phratora vulgatissima* L., *Galerucella lineola* F. and *Lochmea caprea* L. (Coleoptera Chrysomelidae) commonly occur at high densities in grey willow stands and willow SRC in northern Europe (Sage *et al.*, 1999; Björkman *et al.*, 2004; Dalin, 2006). The by far most abundant species is *P. vulgatissima* (Björkman *et al.*, 2004). Both adults and larvae feed on willow foliage. Adult feeding cause small holes in the leaf surface, while larvae feeding skeletonize the leaves. Partial defoliation can, during an outbreak of leaf beetles in SRC, reduce willow stem biomass up to 40% (Björkman et al. 2000) and can in some cases even cause shoot death (Bell *et al.*, 2006).

The willow leaf beetles are all univoltine in Sweden, overwinter as adults and emerge in mid May (Sage *et al.*, 1999; Björkman & Eklund, 2006). Females of *P. vulgatissima* oviposit at the base of the willow shoots and larvae' feeding is initially gregarious whereas *G. lineola* females oviposit at all levels of the shoot and larvae disperse before feeding. Female *L. caprea* oviposits in the soil below willow shoots and their larvae feed solitary at all levels of the shoot. Leaf beetle females oviposit from late May to mid June. Larvae pass through three instars and then pupate in the soil below the willow shoots. The next generation of adult beetles emerges in August and leave the willows to hibernate in under the bark of old trees, or in similar structures (Björkman & Eklund, 2006).

Trophic omnivores on willow

Mirids (Heteroptera Miridae) are among the most numerous phytophagous insects on grey willow both in terms of species and individuals (Strong *et al.*, 1984). Two mirid species occur at high densities in both willow systems, in late May to early July; *Orthotylus marginalis* Reut. and *Closterotomus fulvomaculatus* De Geer (Miridae) (Björkman *et al.*, 2004; Dalin, 2006). The most abundant species is the mirid *O. marginalis*, whereas the mirid *C. fulvomaculatus* generally occur at lower densities (Björkman *et al.*, 2003). Another omnivorous bug found in the same system is *Anthocoris nemorum* L. (Heteroptera Anthocoridae) (Björkman *et al.*, 2004).

All the three heteropteran species are trophic omnivores, i.e. they rely to a large extent on resources from the willow host plant, but are also frequent predators of e.g. eggs of *P. vulgatissima* and young larvae of *P. vulgatissima*, *G. lineola* and *L. caprea* (Björkman et al. 2000; Björkman et al. 2004). All species are univoltine in northern Europe (Sage *et al.*, 1999; Björkman & Eklund, 2006). Both mirid species overwinter as eggs inserted into crevices in the bark associated with leaf buds on current years shoot. Nymphs emerge in late May and adults in early July. *Anthocoris nemorum* overwinter as adults, insert their eggs into leaf tissue mainly at leaf margins (Sigsgaard, 2004). Nymphs and a new generation of adults emerge in late May and early July respectively.

Mirids and many other heteropterans use a solid-to-liquid feeding method, i.e. use salivary enzyme complexes to liquify plant or prey tissues before eating it (Wheeler, 2001). The presence and absence of salivary and digestive enzyme combinations, are highly correlated with the feeding habits of mirids and other heteropterans (Torres & Boyd, 2009). These adaptation are thought to allow mirids to have a very broad diet, make use of relatively large prey and to evaluate and access plant tissues of various quality (Wheeler, 2001). We still have limited knowledge of mirid plant feeding behavior, partly because plant feeding does not necessarily leave scars (Wheeler, 2001 and references therein). The two mirid species studied here mainly seem to be utilizing the leaf veins that run through the mesophyll. Intense feeding on veins of immature leaves can lead to leaf deformations (authors´pers. obs).

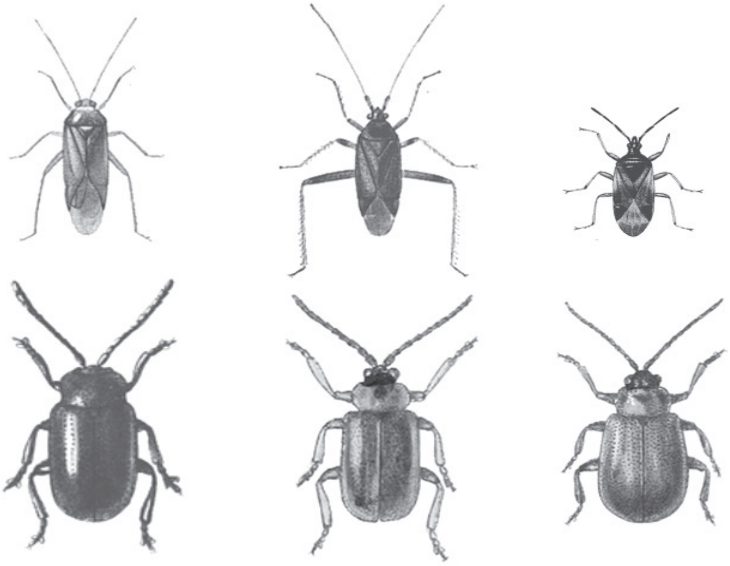

Figure 1. The six species studied in this thesis. From left to right: *Orthotylus marginalis* Reuter and *Closterotomus fulvomaculatus* De Geer (Heteroptera: Miridae) and *Anthocoris nemorum* L. (Heteroptera: Anthocoridae), *Phratora vulgatissima* L., *Galerucella lineola* F. and *Lochmea caprea* L. (Coleoptera: Chrysomelidae).Original illustrations: Watson, L. and Dallwitz, M.J. 2003 onwards. British insects. http://delta-intkey.com

4 Methods

4.1 Multivariate time series data

The papers in this thesis all rely on multivariate time series on population densities of omnivores and herbivores collected in a natural and a managed willow system 1999-2012. Annual estimates were achieved by ‘knock-down’ sampling in early June, conducted every 15 meter along transects through the willow stands (Björkman *et al.*, 2004; Dalin, 2006). The number of samples differed between stands but was proportional to stand size. These quite simple and straight forward sampling techniques give good estimates of population densities of all species that are of interest within the papers of this thesis.

Time series data is, throughout all papers, modeled using generalized linear mixed models (GLMM). Counts of individuals are usually modeled assuming a Poisson distribution, which assumes by definition, that the variance is equal to the mean. However, count data is often overdispersed, i.e. the variance is larger than the mean, and this can lead to inappropriate inference if not accounted for (Zuur *et al.*, 2009). A common reason for overdispersion in ecological count data is zero-inflated data which means the response variable contains more zeros than expected based on the Poisson distribution. In all papers utilizing count data, this was accounted for by either using a quasi-likelihood model where the dispersion parameter is estimated from the data, or by incorporating a random effect at the individual sample level (Hinde, 1982; Zuur *et al.*, 2009). Another option to deal with overdispersion in count data, caused solely by an excessive number of zero observations, is to use zero-inflated models (Zuur *et al.*, 2009). Zero-inflated Poisson models are also called mixture models, where the count process and the binomial process (presence-absence) are modeled separately. This type of model was used for a data set in Paper III where overdispersion was mainly caused by zero observations.

Using time series data from spatially related locations introduces two factors that, if not compensated for, violates the assumption of independence between sampling points (Zuur *et al.*, 2009). The temporal dependence structure, i.e. correlation in observations between years, was accounted for by incorporating a temporal correlation structure between the observations (or residuals) in the model. Similarly, observations (or residuals) in spatial locations close to each other are, for several reasons, likely to be correlated. The spatial dependence was accounted for by formulating models with sampling location as a random effect.

There are several advantages of using time series data in ecological research. Repeated measures over time e.g. allows for incorporation of abiotic heterogeneity (Paper II). Time series data also allow for dynamic response variables, population growth rates or population variability, which often is more informative than population density snap shots (Paper I & IV). An apparent disadvantage of time series data is that it is often collected with the aim to address a different question. The time series used in this thesis was primarily collected with the aim to address population variability in willow leaf beetles. This has limited the number of explanatory variables and/or limited the amount of temporal variation in explanatory variables that could be included in the analyses.

4.2 Leaf nitrogen gradients

The grey willow stands used in Paper I occupied two different habitat types: open habitats (agricultural landscapes) and forest edge habitat (coniferous dominated mixed forest landscapes). These two habitat types were assumed to differ in soil nitrogen due to different land use in the surrounding landscapes (agriculture vs. forestry). The willow stands were, therefore, ordered along a measured leaf nitrogen gradient (Fig. 2). The nitrogen gradient was recreated in the greenhouse using cuttings from the willow clones used in the field study (Fig. 2). The nitrogen gradient in the field was used as an explanatory variable for omnivore population density and variability, whereas the greenhouse gradient was used to test how leaf nitrogen status influenced omnivore performance and trophic behavior.

Leaf nitrogen status was estimated using an optical chlorophyll meter (Model, SPAD-502, Konica Minolta Sensing Inc. 2009). This is a non-destructive alternative to analytical methods to estimate leaf nitrogen which is extensively evaluated for a number of hardwood species, including *Salix* and *Populus* species (Chang & Robison, 2003; Bonneville & Fyles, 2006; Weih & Rönnberg-Wästjung, 2007). The relationship between SPAD values and mass based leaf nitrogen concentrations in grey willow was determined using leaf samples from 15 different clones, using both leaves collected in the field and in the greenhouse (Fig. 2). SPAD meters are, given the sometimes mid-range correlations between them and leaf nitrogen status, mainly useful for assessing leaf nitrogen status for relative comparisons of leaves under similar environmental conditions (Chang & Robison, 2003). The validation curve obtained in this study explained 67% of the variation suggesting that SPAD values provide adequate indicators of leaf nitrogen concentrations, for our purpose.

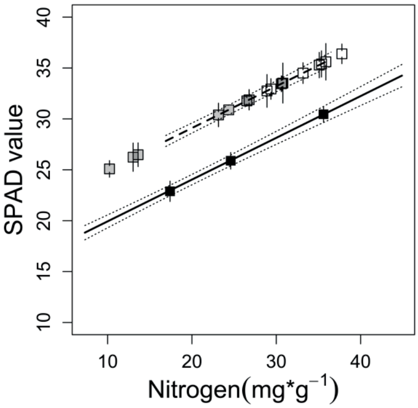

Figure 2. SPAD-leaf nitrogen validation models plotted with field- and greenhouse-recorded leaf nitrogen gradients. Predictions were based on linear models describing the relationship between SPAD-values and leaf nitrogen concentrations (mg*g-^{1}) in grey willow leaves (R^2=0.67) collected in the greenhouse (solid line) and the field (dotted line). Fine dotted grey lines are standard errors of prediction estimates. Open squares show mean SPAD values recorded in June in 17 grey willow stands in forest and open habitats (squares with white and grey background). Solid back squares show mean SPAD values recorded in the greenhouse under different nitrogen treatments (1.4, 8.4 and 15.4 mg N*week^{-1}). Bars show standard errors.

4.3 Landscape analysis

Geographic information systems were used in Paper II to describe the landscape surrounding the willow stands. Land-cover data and aerial photography, sourced from the Swedish mapping, cadastral and land registration authority was used to determine the relative proportions of open and forest land-cover in the landscape and to delineate stands geographically. More detailed spatial data on agricultural land use sourced from the Integrated Administration and Control System (IACS) was used to map potential trends in land-use.

4.4 Field experiments

In Paper III we used a full-scale field experiment in willow SRC to explore the effect of retaining refuges, i.e. preserving parts of the field during harvest, for the risk of leaf beetle outbreaks. Approximately 50% of the willow SRC stands were retained as predator refuges at eight coppiced sites, while no refuges were provided at eight control sites (100% of the stems were coppiced). Population densities of omnivores and leaf beetles were monitored in the re-growing part of the stands over the four years after stem coppicing. Predation pressure on leaf beetle eggs was measured in years three and four.

Field experiments, such as this refuge experiment, that cover spatial and temporal scales relevant for management are often preferable compared to small scale experiments. Field experiments can, however, be practically challenging. We were, in this experiment, not able to collect a complete control data-set until year two after coppicing. Therefore, we could not study the effect of retaining refuges on harvest-associated omnivore mortality or leaf beetle and omnivore recolonization the first year. This was, however, partly compensated for by a more detailed monitoring of refuge treated stands the first year.

5 Results and discussions

5.1 Population dynamics and trophic behavior

5.1.1 Population density and variability, Paper I and IV

The results presented in Paper I show that both spatial and temporal variation in omnivore population density is associated with plant quality (nitrogen status). *Orthotylus marginalis* populations exhibited lower variability and achieved higher densities with increasing leaf nitrogen content of the host plant (Fig. 3). Predicted average population densities increased by 50% per 10 unit increase in SPAD value, which corresponds to an average increase in leaf nitrogen from 10 to 35 $mgN*g^{-1}$. Superior performance on high leaf nitrogen plants, under rapid spatial and temporal declines in prey density, can mechanistically explain the observed high density and stability of *O. marginalis* populations in high leaf nitrogen stands. Our results are among the first to support the notion that omnivore population stability is associated with host plant nitrogen status.

The results presented in Paper IV showed no indications of asynchronously fluctuating omnivore-prey population dynamics in any of the three omnivore species (*O. marginalis, C. fulvomaculatus, A. nemorum*). None of the 105 (0%) studied bivariate time series were significantly cross correlated, despite fluctuating dynamics in all three prey species (Fig. 4). It should be noted that the cross correlation approach that was used to analyze this data can only reveal if there is a correlation between two time series. Additional life table and/or experimental studies are needed to explore the omnivore-prey dynamics in more detail. We could also show strong and consistent negative density dependent population growth rates in all omnivore species. This pattern could partly be explained by variation in shoot-length mediated inter- and intraspecific competition for stem tissue suitable for mirid egg deposition. For a future more detailed understanding of omnivore population dynamics in this system we also need to consider other factors as drivers of short-term population change, including top down control and intra-guild predation among omnivores.

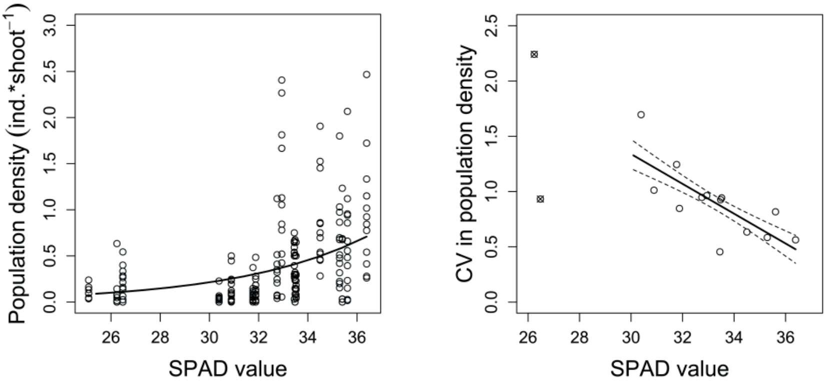

Figure 3. Left panel show population density and right panel show population variability in *Orthotylus marginalis* (Het.Miridae) in 17 grey willow (*Salix cinerea*) stands 1999-2011 in relation to SPAD value, which is well correlated to leaf nitrogen status. Solid and dotted lines show average model predictions and estimate standard errors. Open circles show individual data points. Data points that were not included in the variability analysis are indicated with a cross.

The results in Paper I and IV combined suggest that high quality plant feeding may decouple omnivore performance from prey density and buffer against spatial and temporal changes in prey availability. Our results are consistent with accumulating evidence that relate the distribution, dispersal, performance and oviposition preference of omnivorous insects to intraspecific variation in plant nutrient status (Eubanks & Denno, 1999, 2000b; Eubanks & Styrsky, 2005; Groenteman *et al.*, 2006; Jiménez *et al.*, 2012). The population dynamics of zoophytophagous species, such as the mirids studied here could, therefore, in many ways be more similar to herbivores than to both specialist and generalist predators.

5.1.2 Trophic behavior, Paper I

Intraspecific variation in host plant nitrogen status was also shown to alter omnivore trophic behavior (plant vs. prey feeding). Mirids on high nitrogen status host plants consumed fewer eggs than mirids on plants with lower nitrogen status (Fig. 5). In Paper I, we included results for one of the mirids (*O. marginalis*) but an almost identical (but stronger) response was also recorded for the other mirid species (*C. fulvomaculatus*) in the same experiment (Liman et al. unpublished data).

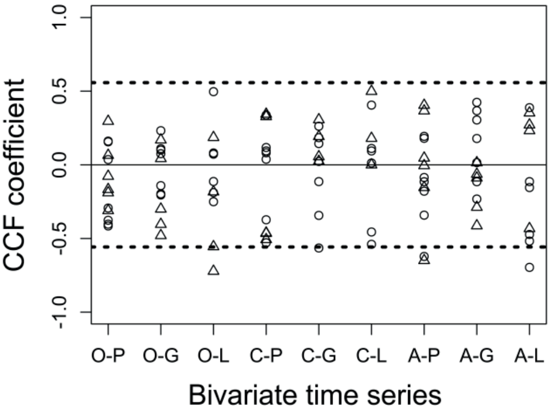

Figure 4. Sample Cross Correlation Function (CCF) coefficients for bivariate time series with a time lag of -1 (y_t=omnivore population growth and x_{t-1}=prey population growth). The analysis was based on data collected in 13 natural grey willow stands, in forest (circles and open (triangles) habitats. Dotted horizontal lines are critical values for a significant cross correlation at the 95% level (±2/√n) (n=14 equals a critical values of 0.532. Significantly positive CCF coefficients (above the dotted line) would have indicated a numerical response in omnivore populations to prey populations. Omnivorous predators: O=*Orthotylus marginalis*, C= *Closterotomus fulvomaculatus*, A=*Anthocoris nemorum* and Prey: P=*Phratora vulgatissima*, G=*Galerucella lineola*, L=*Lochmea caprea*.

The population level effect and the behaviorsal effect (plant vs. prey feeding) of leaf nitrogen status differed in their consequence for prey suppression. The different environmental conditions (field vs. greenhouse) and spatial and temporal scales make it impossible to fully integrate the effects. Other aspects that may influence the strength of omnivore-prey interactions such as omnivore-prey ratio, omnivore prey searching behavior, inter- and intraspecific interactions, can also change with leaf nitrogen status, which make it difficult to predict how the observed per capita effects translate into the population level. Others, e.g. Eubanks & Denno (2000b) have found that the density effect of plant nutrient status is generally stronger than the per capita changes in trophic behavior, especially when longer time scales are considered.

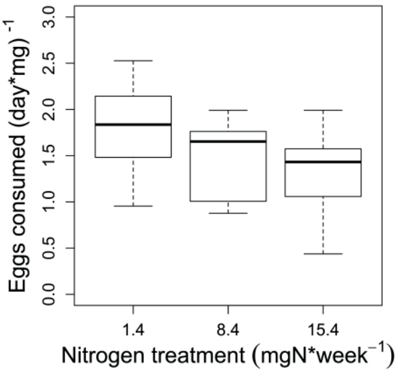

Figure 5. Omnivore predation rate as a function of plant nitrogen treatment in a greenhouse experiment using three nitrogen treatments (1.4, 8.4 and 15.4 mgN*week^{-1}). The omnivore species used was *Orthotylus marginalis* (Het. Miridae) and the prey used were eggs of *Phratora vulgatissima* (Col. Chrysomelidae).

5.1.3 Omnivore-Prey interactions, Paper I and IV

The degree of coupling between predator and prey populations will have consequences for per capita predation rates and for when predators are ‘functionally effective’ (Straub *et al.*, 2008). Omnivorous predators are distracted by alternative resources and can, therefore, have lower per capita predation rates, but can on the other hand persist in the habitat. High predator-to-prey ratios will allow them to function effectively at low prey densities. Theoretically this would allow predation by omnivores (and other generalist predators) to have a disproportionate effect on final prey density, i.e. they prey on small populations when the per capita effect on the prey population is higher (Piñol *et al.*, 2009). Omnivore predation even has the potential to drive prey populations to local extinction as plant feeding allows them to persist to track prey items remaining in spatial refuges. Omnivores could, therefore, be particularly suitable agents for conservation biological control in perennial systems with management that allow for continuous omnivore-plant and omnivore-prey relationships.

5.2 Conservation Biological Control

5.2.1 Landscape moderated recolonization, Paper II

Recolonization of willow SRC after coppicing was landscape moderated in three of four species, suggesting that landscape scale site selection may be one possible way to minimize the risk of willow leaf beetle outbreaks (Fig. 6). Average predicted population densities of the omnivore *O. marginalis* were 270% higher after recolonization in open landscapes (100% open habitat) compared to landscapes with only 30% open habitat (Fig. 6). Within the same range of open habitat proportions we found that average willow leaf beetle densities decreased by 78% (*P. vulgatissima*) and 89% (*G. lineola*) (Fig. 6).

This pattern was expected because population density of omnivorous mirids (and thereby leaf beetle predation pressure) is higher and more stable over time in natural grey willow stands growing in nitrogen-rich environments (open agriculture-dominated landscapes) (Paper I). Willow leaf beetle population densities are lower in natural grey willow stands in open habitats partly due to high predation pressure from omnivorous mirids (Dalin, 2006). There was, however, no detectable effect of landscape composition on the less common mirid omnivore *C. fulvomaculatus* (Fig. 6).

Important to notice is that this landscape moderated effect was variable over time, i.e. it was only detectable in high density years. In years when density was regionally low, there was no detectable effect of landscape composition. This result was consistent across species. Such interaction effect are predicted by hierarchy theory (Wiens, 1989), since e.g., weather acting on a broader regional scale is expected to constrain differences at landscape scale. This result is an example of why we need to consider the dynamics of populations and communities in landscape scale studies. The importance of patch context for willow leaf beetle outbreaks thus differ between years. Recolonization and the risk of outbreaks is similar in all types of landscapes in years when population densities are low, but the risk of an outbreak may be more pronounced in sites established in forest dominated landscapes in high density years.

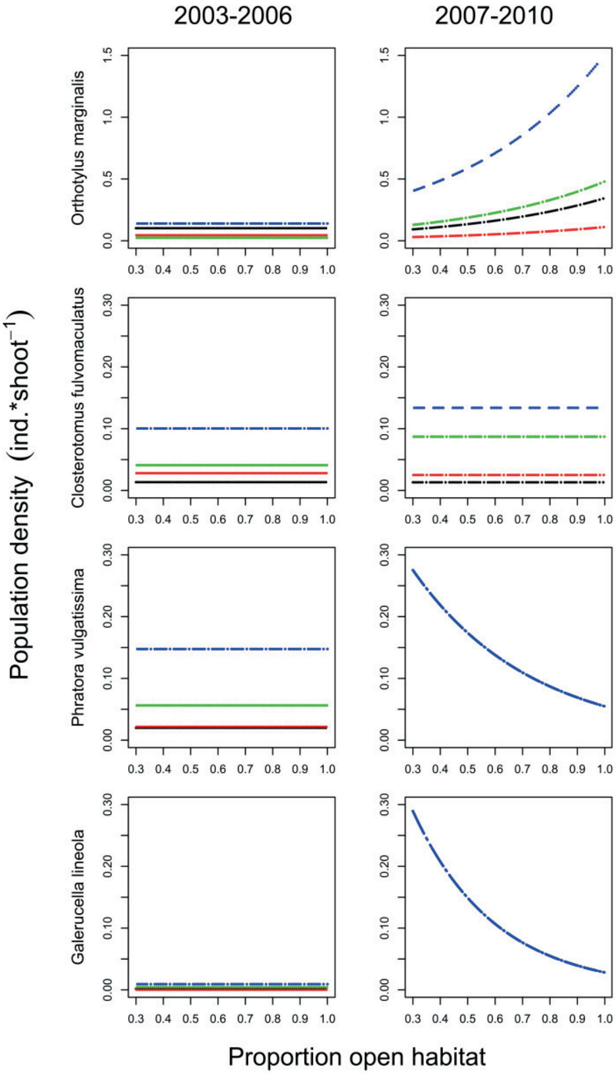

Figure 6. Model predicted population densities of two mirid and two leaf beetle species based on annual field surveys in 10 willow short rotation coppice stands, in relation to proportion open habitat in the landscape surrounding the stands under two subsequent coppice cycles. The left panel illustrates the effect of landscape when population densities were low (2003-2006) and the right panel shows the same sites under higher population densities (2007-2010). Non-significant terms were excluded from the models. The line color indicate year since harvest (red= year 1, black= year 2, green=year 3 and blue=year 4). Single blue lines indicate that there was no difference between years.

5.2.2 Refuges for CBC in perennial crops, Paper III

Contrary to theoretical predictions, saving predator refuges increased rather than decreased the risk of willow leaf beetle outbreaks (Fig. 7). Average densities of willow leaf beetles were 85% (*P. vulgatissima*), 77 % (*G. lineola*) and 98% (*L. caprea)* higher the fourth year after coppicing in the stands with refuges compared to the control stands. Predator densities were higher in stands without refuges the second and third year after coppicing, but negative population growth in control stands between year three and four inverted this difference the fourth year. The model results were consistent across all predator and all leaf beetle species respectively. We also found that local population densities of both trophic levels were higher in the refuges compared to the coppiced part of the stand, the first year after coppicing. The preference for refuges was stronger for leaf beetles than for predators.

These unexpected results of retaining refuges of willow to promote predators could be a result of strong effects of e.g. an interaction between dispersal and patch age. Coppicing during the dormant season removes the generative buds from the stools and modifies the phenology of the stems, so that leaves unfold later and grow smaller. Patch age may thus indirectly have prevented dispersal of omnivorous predators into the re-sprouting part of the stand in refuge treated stands and caused lower leaf beetle return frequencies in stands without refuges.

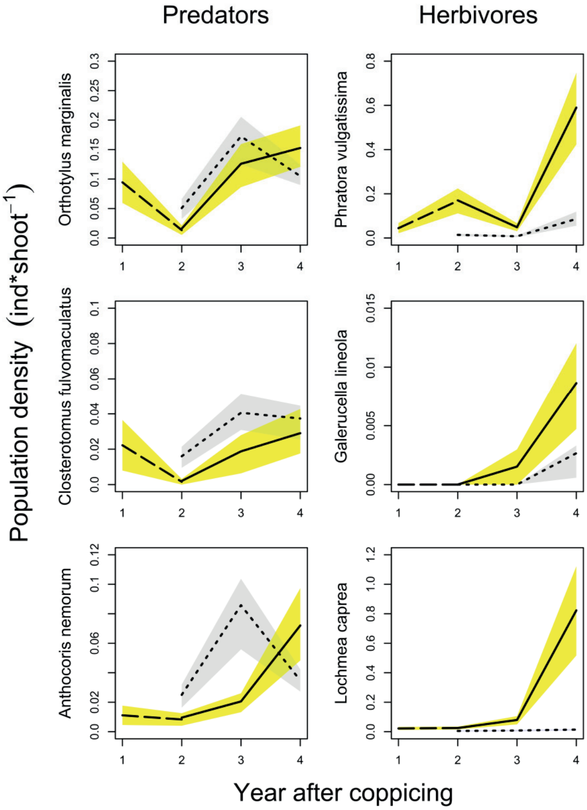

Figure 7. Population densities of omnivorous predators (left column) and herbivores (right column) in willow short rotation coppice stands, four years after coppicing. Solid lines are model predicted mean effects in stands without refuges (n=8) and dotted lines are predicted mean effects in stands without refuges (n=8). Standard error was calculated from the raw data. Dashed lines illustrate mean values for stands with refuges, the first year after coppicing, Non-significant terms were removed from the final models. All pair-wise comparisons between treatments, years and species were significantly different at p<0.01, except two: there was no difference in population density between the predator species *A. nemorum* and *C. fulvomaculatus* or between herbivore densities the second and third year after coppicing. Note the different scales on the y-axis.

6 Conclusions

The results presented this thesis provide novel empirical support for the established assumption that plant feeding can decouple omnivores from fluctuations in their prey populations. Omnivore performance increased and populations exhibited more stable long-term dynamics at higher densities on willows with higher leaf nitrogen status. In addition, omnivore populations showed no numeric response to fluctuations in leaf beetle population densities. One consequence of the strong association with plant nutrient status is that omnivores can be 'functionally effective' at low prey densities (when omnivore-to-prey ratios are high). Omnivores could, therefore, play an important role for controlling herbivore pests at an initial phase of an increase and management for conservation biological control targeting omnivores should focus on promoting continuous omnivore-plant relationships.

The results from a full-scale field experiment demonstrated that retaining willow refuges to stabilize omnivore population densities across harvests increase rather than decrease the risk of leaf beetle outbreaks. The result of an eight year long study revealed that willow stands surrounded by landscapes with high proportion open land cover were less likely to experience leaf beetle outbreaks. Landscape level site selection could thus be used to improve the conservation biological control of willow short rotation coppice.

The results presented in Paper II were also used to illustrate that considering the temporal dynamics of populations may be crucial when designing and evaluating studies at landscape level. Landscape-moderated differences in recolonization of willow after harvest were only detectable when regional densities of the four species were relatively high. Today most studies in landscape ecology represent snap shots in time, which as a consequence may not allow for generalization over time.

6.1 Future perspectives

Trophic omnivores can show a diversity of trophic behaviors i.e. they can be predominantly herbivorous or predatory (phytozoophagous vs. zoophytophagous). One challenge for the future would be to explore if/how the importance of plant nutrient status change along a gradient in trophic behavior. Theoretically, one might expect strongly phytophagous species to respond stronger both functionally and numerically to plant nutrient status and host plant mediated effects on trophic interactions may vary in strength depending on the omnivores position on this gradient in omnivory (Lalonde *et al.*, 1999; Coll & Guershon, 2002). The more detailed differences in trophic behavior between omnivores can also be important for understanding functional diversity.

Food webs of arboreal mirids has been shown to include closely related species exhibiting the full range of trophic behaviors, from strictly phytophagous to zoophagous, with the majority of species being omnivorous (phytozoophagous and zoophytophagous) (Wheeler, 2001). It has also been shown that these species tend to hatch in a phenological sequence, with the most phytophagous species in early spring (when the quality of many plants is at its peak) and the more zoophagous species later in the summer (when more prey is available and plant quality is less good) (Dempster, 1964; Jonsson, 1985). This indicates that the relative importance of plant and prey resources may indeed change from phytozoophagous to zoophytophagous species. Species specific combinations of salivary enzymatic complexes and/or stable isotope analysis could be used to provide a greater resolution of trophic position and behavior and group species on a continuous scale from phyto- to zoophagous (Wheeler, 2001; Torres & Boyd, 2009). A challenge for this approach would be to replicate the different trophic behaviors.

References

Agrawal, A. A., Kobayashi, C. & Thaler, J. S. (1999). Influence of prey availability and induced host resistance on omnivory by western flower thrips. *Ecology*, 80(2), pp 518–523.

Andersen, T., Elser, J. J. & Hessen, D. O. (2004). Stoichiometry and population dynamics. *Ecology Letters*, 7(9), pp 884–900.

Arim, M. & Marquet, P. A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecology Letters*, 7(7), pp 557–564.

Awmack, C. & Leather, S. (2002). Host plant quality and fecundity in herbivorous insects. *Annual review of entomology*, 47, pp 817–844.

Barbosa, P., Letourneau, D. K. & Agrawal, A. A. (Eds) (2012). *Insect Outbreaks Revisited*. Chichester, UK: Wiley-Blackwell.

Bascompte, J. & Melián, C. J. (2005). Simple Trophic Modules for Complex Food Webs. *Ecology*, 86(11), pp 2868–2873.

Bell, A. C., Clawson, S. & Watson, S. (2006). The long-term effect of partial defoliation on the yield of short-rotation coppice willow. *Annals of Applied Biology*, 148(2), pp 97–103.

Björkman, C., Bengtsson, B. & Häggström, H. (2000a). Localized outbreak of a willow leaf beetle: plant vigor or natural enemies? *Population Ecology*, 42, pp 91–96.

Björkman, C., Bommarco, R., Eklund, K. & Höglund, S. (2004). Harvesting disrupts biological control of herbivores in a short-rotation coppice system. *Ecological Applications*, 14(6), pp 1624–1633.

Björkman, C., Dalin, P. & Eklund, K. (2003). Generalist natural enemies of a willow leaf beetle (*Phratora vulgatissima*): abundance and feeding habits. *Journal of Insect Behavior*, 16(6), pp 747–764.

Björkman, C. & Eklund, K. (2006). Factors affecting willow leaf beetles (*Phratora vulgatissima*) when selecting overwintering sites. *Agricultural and Forest Entomology*, 8(2), pp 97–101.

Björkman, C., Höglund, S., Eklund, K. & Larsson, S. (2000b). Effects of leaf beetle damage on stem wood production in coppicing willow. *Agricultural and Forest Entomology*, 2, pp 131–139.

Bonneville, M. & Fyles, J. W. (2006). Assessing variations in SPAD 502 chlorophyll meter measurements and their relationships with nutrient content of trembling aspen foliage. *Communications in Soil Science and Plant Analysis*, 37(3-4), pp 525–539.

Chang, S. X. & Robison, D. J. (2003). Nondestructive and rapid estimation of hardwood foliar nitrogen status using the SPAD-502 chlorophyll meter. *Forest Ecology and Management*, 181(3), pp 331–338.

Coll, M. & Guershon, M. (2002). Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology*, 47, pp 267–97.

Dalin, P. (2006). Habitat difference in abundance of willow leaf beetle *Phratora vulgatissima* (Coleoptera: Chrysomelidae): plant quality or natural enemies? *Bulletin of Entomological Research*, 96(6), pp 629–635.

Dalin, P., Kindvall, O. & Björkman, C. (2009). Reduced population control of an insect pest in managed willow monocultures. *PLoS ONE*, 4(5), p e5487.

Defra (2007). UK Biomass Strategy. [online],. Available from: http://www.biomassenergycentre.org.uk/

Dempster, J. P. (1964). The feeding habits of the Miridae (Heeroptera) living on broom (*Sarothamnus scoparius* (L.) WIMM.). *Entomologia Experimentalis et Applicata*, 7, pp 149–154.

Denno, R. & Fagan, W. (2003). Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, 84(10), pp 2522–2531.

Denno, R., Lewis, D. & Gratton, C. (2005). Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici*, (August), pp 295–311.

Denno, R., McClure, M. & Ott, J. (1995). Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual review of entomology*, 40, pp 297–331.

Diehl, S. (2003). The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. *Ecology*, 84(10), pp 2557–2567.

Emmerson, M. & Yearsley, J. M. (2004). Weak interactions, omnivory and emergent food-web properties. *Proceedings. Biological sciences / The Royal Society*, 271(1537), pp 397–405.

Eubanks, M. D. (2005). Predaceous herbivores and herbivorous predators: the biology of omnivores and the ecology of omnivore–prey interactions. *Ecology of predator-prey interactions*. pp 3–16. Oxford University Press.

Eubanks, M. D. & Denno, R. F. (1999). The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology*, 80(4), pp 1253–1266.

Eubanks, M. D. & Denno, R. F. (2000). Host plants mediate omnivore-herbivore interactions and influence prey suppression. *Ecology*, 81(4), pp 936–947.

Eubanks, M. D. & Styrsky, J. D. (2005). Effects of plant feeding on the performance of omnivorous ”predators”. In: Wäckers, F. L., van Rijn, P. C. J., & Bruin, J. (Eds) *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. pp 148–177. Cambridge University Press.

Eubanks, M. D., Styrsky, J. D. & Denno, R. F. (2003). The evolution of omnivory in heteropteran insects. *Ecology*, 84(10), pp 2549–2556.

Fagan, W. (1997). Omnivory as a stabilizing feature of natural communities. *The American Naturalist*, 150(5), pp 554–567.

Gillespie, D. R. & McGregor, R. R. (2000). The functions of plant feeding in the omnivorous predator *Dicyphus hesperus*: water places limits on predation. *Ecological Entomology*, 25(4), pp 380–386.

Goeriz Pearson, R. E. (2009). *Nutrient regulation by an omnivore and the effects on performance and distribution. PhD diss.* College Park, Univ. Maryland.

Groenteman, R., Guershon, M. & Coll, M. (2006). Effects of leaf nitrogen content on oviposition site selection, offspring performance, and intraspecific interactions in an omnivorous bug. *Ecological Entomology*, 31(2), pp 155–161.

Gurr, G. M., Wratten, S. D., Tylianakis, J., Kean, J. & Keller, M. (2005). Providing plant foods for natural enemies in farming systems: balancing practicalities and theory. In: Wäckers, F.L., van Rijn, P.C.J., Bruin, J. (Ed) *Plant-provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. pp 267–304. Cambridge, UK: Cambridge University Press.

Hinde, J. (1982). Compound Poisson Regression Models. In: Gilchrist, R. (Ed), 1982. pp 109–121. Springer-Verlag New York Inc.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, 91, pp 385–398.

Holopainen, J. K., Tuhkalainen, J., Kainulainen, P. & Satka, H. (1992). Resource partitioning to growth, storage and defence in nitrogen fertilized Scots pine and susceptibility of the seedlings to the tarnished plant bug *Lygus rugulipennis*. *Canadian Journal of forest Research*, 22, pp 588–592.

Holyoak, M. & Sachdev, S. (1998). Omnivory and the stability of simple food webs. *Oecologia*, (June), pp 413–419.

Huberty, A. & Denno, R. (2004). Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, 85(5), pp 1383–1398.

Hunter, M. & Price, P. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73(3), pp 724–732.

Jiménez, J. M., Wieski, K., Marczak, L. B., Ho, C. K. & Pennings, S. C. (2012). Effects of an Omnivorous Katydid, Salinity, and Nutrients on a Planthopper-Spartina Food Web. *Estuaries and Coasts*, 35(2), pp 475–485.

Jonsell, B. (ed) (2000). *Flora Nordica*. Bergius Foundation, Stockholm.

Jonsson, M., Wratten, S. D., Landis, D. A. & Gurr, G. M. (2008). Recent advances in conservation biological control of arthropods by arthropods. *Biological Control*, 45(2), pp 172–175.

Jonsson, N. (1985). Ecological segregation of sympatric heteropterans on apple trees. *Norwegian Journal of Entomology*, 32, pp 7–11.

Konica Minolta Sensing Inc. (2009). Chlorophyll Meter SPAD-502 Plus Instruction Manual.

Kratina, P., LeCraw, R., Ingram, T. & Anholt, B. (2012). Stability and persistence of food webs with omnivory: Is there a general pattern? *Ecosphere*, 3(June), pp 1–18.

Lalonde, R. G., Mcgregor, R. R., Gillespie, D. R. & Roitberg, B. D. (1999). Plant-feeding by arthropod predators contributes to the stability of predator-prey population dynamics. *Oikos*, 87(3), pp 603–608.

Landis, D. A., Wratten, S. D. & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45, pp 175–201.

Letourneau, D. K. (2012). Integrated Pest Management - Outbreaks Prevented, Delayed, or Facilitated? In: Barbosa, P., Letourneau, D. K., & Agrawal, A. A. (Eds) *Insect Outbreaks Revisited*. pp 371–394. Chichester, UK: Wiley-Blackwell.

Letourneau, D. K., Jedlicka, J. a., Bothwell, S. G. & Moreno, C. R. (2009). Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 40, pp 573–592.

Lindeman, R. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23(4), pp 399–417.

Matson, P. & Hunter, M. (1992). Special feature: the relative contributions to top-down and bottom-up forces in population and community ecology. *Ecology*, 73(3), pp 49–50.

Matsumura, M., Trafelet-Smith, G. & Gratton, C. (2004). Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology*, 85(9), pp 2601–2615.

Mattson, W. J. J. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, 11, pp 119–161.

Mola-Yudego, B. (2010). Regional potential yields of short rotation willow plantations on agricultural land in northern Europe. *Silva Fennica*, 44(July 2009), pp 63–76.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, 307, pp 321–326.

Pimm, S. L. & Lawton, J. H. (1977). Number of trophic levels in ecological communities. *Nature*, 268(5618), pp 329–331.

Pimm, S. L. & Lawton, J. H. (1978). On feeding on more than one trophic level. *Nature*, 275(5680), pp 542–544 Nature Publishing Group.

Piñol, J., Espadaler, X., Pérez, N. & Beven, K. (2009). Testing a new model of aphid abundance with sedentary and non-sedentary predators. *Ecological Modelling*, 220, pp 2469–2480.

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20(1989), pp 297–330.

Polis, G. & Strong, D. (1996). Food web complexity and community dynamics. *American Naturalist*, 147(5), pp 813–846.

Sage, R. B., Fell, D., Tucker, K. & Sotherton, Nicolas, W. (1999). Post hibernation dispersal of three leaf eating beetles (Coleoptera: Chrysomelidae) colonising cultivated willows and poplars. *Agricultural and Forest Entomology*, 1, pp 61–70.

Sigsgaard, L. (2004). Oviposition preference of *Anthocoris nemorum* and *A. nemoralis* for apple and pear. *Entomologia Experimentalis et Applicata*, 111(3), pp 215–223.

Snyder, W. E. & Tylianakis, J. M. (2012). The Ecology of Biodiversity- Biocontrol Relationships. In: Gurr, G. M., Wratten, S. D., Snyder, W. E., & Read, D. M. Y. (Eds) *Biodiversity and Insect Pests. Key Issues for Sustainable Management*. pp 23–40. Oxford, UK: Wiley-Blackwell.

Solomon, M. E. (1949). The natural control of animal populations. *The Journal of Animal Ecology*, 18(1), p 1.

SOU 2007:36Bioenergi från jordbruket – en växande resurs. Betänkande av Utredningen om jordbruket som bioenergiproducent. Stockholm.

Sterner, R. & Elser, J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton University Press.

Straub, C. S., Finke, D. L. & Snyder, W. E. (2008). Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, 45, pp 225–237.

Strong, D. R., Lawton, J. H. & Southwood, T. R. E. (1984). *Insects on Plants: Community Patterns and Mechanisms*. Oxford, UK: Blackwell Scientific.

Symondson, W. O. C., Sunderland, K. D. & Grennstone, M. K. (2002). Can Generalist Predators be Effective Biocontrol Agents. *Annual Review of Entomology*, 47, pp 561–594.

Thomas, M. B., Wratten, S. D. & Sotherton, N. W. (1992). Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *Journal of Applied Ecology*, 29(2), pp 524–531.

Thompson, R. M., Hemberg, M., Starzomski, B. M. & Shurin, J. B. (2007). Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, 88(3), pp 612–7.

Torres, J. B. & Boyd, D. W. (2009). Zoophytophagy in Predatory Hemiptera. *Brazilian Archives of Biology and Technology*, 52(October), pp 1199–1208.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., Tylianakis, J. M., Nouhuys, S. Van & Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, 43(3), pp 294–309.

Vandermeer, J. (2006). Omnivory and the stability of food webs. *Journal of theoretical biology*, 238(3), pp 497–504.

Weih, M. (2004). Intensive short rotation forestry in boreal climates: present and future perspectives. *Canadian Journal of Forest Research*, 34, pp 1369–1378.

Weih, M. & Rönnberg-Wästjung, A.-C. (2007). Shoot biomass growth is related to the vertical leaf nitrogen gradient in *Salix* canopies. *Tree physiology*, 27(11), pp 1551–9.

Welch, K. D., Pfannenstiel, R. S. & Harwood, J. D. (2012). The Role of Generalist Predators in Terresterial Food Webs: Lessons for Agricultural Pest Management. In: Gurr, G. M., Wratten, S. D., Snyder, W. E., & Read, D. M. Y. (Eds) *Biodiversity and Insect Pests. Key Issues for Sustainable Management*. pp 41–56. Oxford, UK: Wiley-Blackwell.

Wheeler, A. G. (2001). *Biology of the Plant Bugs (Hemiptera: Miridae): Pests, Predators, Opportunists*. Ithaca, New York: Comstock Publishing Associates.

Wiens, J. (1989). Spatial scaling in ecology. *Functional Ecology*, 3(4), pp 385–397.

Volf, M., Hrcek, J., Julkunen-Tiitto, R. & Novotny, V. (2015). To each its own: differential response of specialist and generalist herbivores to plant defence in willows. *Journal of Animal Ecology*,.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

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