1 The Various Effects of Insects on Ecosystem Functioning

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1.1 Summary

Insects represent a dominant component of biodiversity in most terrestrial ecosystems yet they have largely been neglected in studies on the role of biodiversity in nutrient cycling, or, more generally, the functioning of ecosystems. The scarcity of manipulative studies on the role of insects in ecosystem processes contrasts with the expert knowledge and large body of research already available, in particular in the field of insect herbivory. Insects are likely to play a key role in mediating the relationship between plants and ecosystem processes by influencing the physiology, activity and population dynamics of plants. The aim of this book is two-fold: (1) to summarize the effects that insects have on ecosystem functioning, focusing mainly, but not exclusively, on herbivorous insects. Authors with extensive experience in the field of plant–insect interactions will discuss the importance of insects in ecosystem functioning; and (2) to provide a detailed discussion of the advantages and disadvantages of various techniques of manipulating insect herbivory. Thus, the book aims to provide both a theoretical basis and practical advice for future manipulative studies on biodiversity–ecosystem functioning. This introductory chapter briefly summarizes the various effects of insects on ecosystem functioning and introduces the chapters in the various sections of this book.

1.2 Introduction

It appears to be obvious that the way matter flows through an ecosystem is influenced by the organisms within the system. Without autotrophic, chemotrophic or heterotrophic activity, matter fluxes through ecosystems would be very different. Nevertheless, research on the role of organisms in nutrient cycling or, more generally, the 'functioning' of ecosystems has had a

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mixed history. The reason is the traditional division of ecology into community ecology and ecosystem ecology (Odum 1953; Likens 1992; Jones and Lawton 1995). While community ecologists generally consider organisms to be the main drivers of ecosystem processes, they rarely measure nutrient cycling as a function of the constituent community. Conversely, systems ecologists quantify energy and element flux rates through ecosystems, but typically do so over large spatial scales (e.g. a watershed), and often with little reference to the role of organisms within the ecosystem. Classic ecosystem studies such as those performed within the framework of the International Biological Programme (IBP) in the 1960s and 1970s were very important in determining the contribution of various groups of organisms (plants, animals, etc.) to ecosystem productivity or energy flux (e.g. Bormann and Likens 1967; Golley et al. 1975; Likens et al. 1977). However, because of the different focus and because experimental community manipulations are difficult at the scale of hundreds of hectares, these ecosystem studies have generally not addressed the question of whether a particular change in the biotic community would lead to measurable changes in matter fluxes through the ecosystem. As a consequence of the division into systems and community ecology, we know a considerable amount about the structure and dynamics of natural communities, and about input/output relations of mineral nutrients for a variety of ecosystems, but we still know relatively little about the interaction between community dynamics and nutrient cycling (Mooney 1991; Loreau et al. 2001).

In the last decade, however, interest in the question of how important a diverse biotic community is for processes at the ecosystem level has greatly increased. Much of this work has been inspired by the realization that whilst global biodiversity is undergoing dramatic changes (Ehrlich and Ehrlich 1981; Wilson 1988), science has been unable to predict the effects of these changes on the ecosystems concerned (Schulze and Mooney 1993). Recent years have seen a dramatic increase in the number of manipulative experimental studies that have investigated the effects of particular components of diversity or of diversity per se for various aspects of ecosystem functioning (see reviews in Kinzig et al. 1991; Loreau et al. 2001, 2002; Wardle 2002). These studies have shown convincingly that changes in the diversity and composition of a community can have consequences at the ecosystem level that are sometimes drastic. A common result is that a decrease in diversity causes a loss in ecosystem function such as productivity or nutrient retention in the soil (e.g. Loreau et al. 2001, 2002). While in the first studies the term 'ecosystem functioning' was restricted to processes at the ecosystem level, some confusion has recently arisen from a rather loose use of this term. In the more recent literature, ecosystem functioning has been used to describe a variety of ecological processes not only at the level of the ecosystem, but also at the level of the community, populations or even individuals. As the focus of biodiversity–ecosystem functioning research is on ecosystem-level consequences of a loss of biodiversity, it is useful to define an ecosystem function or ecosystem process as any ecosystem-level attribute that can be measured in and compared between ecosystems. Thus, the state of a particular species or population cannot be an ecosystem function as this particular species or population will only occur in certain ecosystems and can hence only be measured in these ecosystems. In contrast, community-level attributes such as the stability of the community present in the ecosystem or the presence of a functional group of organisms such as pollinators can be measured in any ecosystem and therefore fall under this definition of ecosystem function. In a more narrow sense, the term ecosystem function is used for processes related to nutrient cycling at the ecosystem level (Schulze and Mooney 1993). This restricted definition is the one we would like to adopt for this book.

While the pioneering biodiversity–ecosystem functioning experiment was conducted using model communities composed of a variety of organisms (Naeem et al. 1994), most subsequent studies have focused on the manipulation of plant communities. This is true in particular for some of the most influential studies, which were carried out in grasslands (Tilman and Downing 1994; Tilman et al. 1996, 1997; Hooper and Vitousek 1997; Hector et al. 1999). In these studies as well as in later ones, plant species richness and/or plant functional group richness and composition were the main variables manipulated. Because producers are ultimately determining the amounts of carbon that enter an ecosystem in each food web, the manipulation at the plant level provided an obvious starting point in the analysis of the relationship between biodiversity and ecosystem functioning. However, an additional reason why plant communities have been the main object of a manipulative approach is that plant communities can be easily manipulated in climate chambers, greenhouses and field experiments. In other groups of organisms, manipulating organismic diversity is much more difficult, for example when the organisms are mobile, as is the case for most animals. Practical advantages may also have been responsible, at least in part, for the bias in more recent biodiversity–ecosystem function studies towards microcosm experiments with microbial communities (e.g. McGrady-Steed et al. 1997; Naeem and Li 1997). Only recently have organisms of other trophic levels been incorporated into experiments at spatial scales larger than a Petri dish. Pioneering mesocosm studies involving mycorrhizal fungi (van der Heijden et al. 1998), fresh-water insects (Wallace and Webster 1996; Cardinale et al. 2002), terrestrial insects (Cardinale et al. 2003; Schmitz 2003) and soil fauna (Wardle 2002) have brought a new impetus to biodiversity–ecosystem functioning research. However, because the diversity of invertebrates, vertebrates and microorganisms exceeds that of plant diversity by far, the existing manipulative studies of the heterotrophic component of ecosystems represent only a first step towards a more comprehensive understanding of the relationship between organismic diversity and ecosystem functioning.

With about 1 million described species, insect diversity is higher than that of any other animal or plant taxon (Stork 1988). In terrestrial ecosystems insects function as herbivores, pollinators, seed dispersers, predators, parasites, detritivores or ecosystem engineers. In the past decades, there have been several reviews of how insects, in particular herbivores, can affect ecosystem function (Mattson and Addy 1975; Gosz et al. 1978; Lee 1979; Hutchinson and King 1982; Seastedt and Crossley 1984; Lamb 1985; Detling 1988; Urbanek 1988; Hutson 1989; Whelan 1989; Huntly 1991; Curry 1994; Lerdau 1996; Lewinsohn and Price 1996; Wallace and Webster 1996; Price 1997; Coleman and Hendrix 2000; Schowalter 2000a; Feller 2002). Nevertheless, despite the many roles that insects fulfil in terrestrial ecosystems, their importance in nutrient cycling is not universally recognized. One reason for the skepticism is that the total biomass of insects (the standing crop) appears to be small compared to plant biomass or the biomass of other animals. For example, in an IBP study of a meadow-steppe in the V.V. Alkhin Central Chernozem Reserve in the Central Russian Upland, above- and belowground invertebrate biomass was equivalent to about 10 % of the yearly plant productivity of 11–14 tons dry weight ha^{-1} (Zlotin and Khodashova 1980). More than 90 % of the animal biomass was found below ground, and earthworms accounted for 94 % of soil animal biomass or 80–90 % of total animal biomass. The biomass of above- and belowground insects constituted less than 2 % of animal biomass, or 0.2 % of plant productivity. For some ecosystems these percentages may be higher, but in terms of contribution to total standing crop, biomass does not generally suggest a prominent role for insects in nutrient cycling (cf. Petrusewicz 1967; Schowalter 2000a). A second reason why insects are often not considered to be very important for nutrient cycling is that the average proportion of net primary productivity (NPP) consumed by herbivorous insects is 10 % or less, except in outbreak situations (e.g. Wiegert and Evans 1967; Detling 1988; Curry 1994; but see Coupe and Cahill 2003). In contrast, large mammalian herbivores such as the North American bison or African mammals are known to consume up to 90 % of prairie or savannah NPP (Detling 1988). The observation that insects generally affect an insignificant fraction of NPP was one of the reasons why Hairston et al. (1960) proposed their hypothesis that herbivores are regulated top-down rather than bottom-up.

The only instances where insects are unequivocally recognized to have a large effect on ecosystem functions are outbreaks of particular species such as the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) or *Epirrata autumnata* (Bkh.) (Lep., Geometridae). During outbreaks, the proportion of leaf area removed by the extremely high population densities of the outbreaking herbivore species can reach 100 %, which has immediate and large effects on nutrient fluxes (e.g. Lovett and Ruesink 1995; Kosola et al. 2001; Christenson et al. 2002). Because of their regular outbreaks, Schowalter proposed that herbivorous insects act as cybernetic regulators for ecosystem processes (Schowalter 2000a, b). In his interpretation, insect outbreaks are 'feedbacks that maintain ecosystem production within sustainable ranges' (Schowalter 2000b). While this hypothesis is based on the somewhat controversial view that there is a tendency for homeostasis at supraorganismal levels, it is true that outbreaks not only cause an immediate release of nutrients previously fixed in plants, but also have longer-lasting effects by changing a number of parameters that affect matter fluxes such as soil nutrient availability, the physiology of long-living plants such as trees, or plant species composition (e.g. Carson and Root 2000; Kosola et al. 2001; Christenson et al. 2002). Outbreaks are therefore one example of large insect effects on ecosystem processes.

The view that insects have only minute effects at the ecosystem level also contrasts with the results of studies on individual plant–insect interactions, which document large effects of insects on plant traits such as investment into secondary metabolites, plant architecture and seed number (e.g. Crawley 1983, 1986; Karban and Baldwin 1997). Why do insects, in particular herbivorous insects, have large effects on individual plants but apparently small effects at the ecosystem level? In our view, one important reason for this apparent discrepancy is the way in which insect effects on nutrient cycling have been measured in most ecosystem studies. The main variable quantified in studies at the ecosystem level has been the reduction of plant standing crop, but this is only one of the many ways in which herbivorous insects impact ecosystem functioning. First, insects modify the way in which nutrients are distributed within the ecosystem, but these effects have rarely been quantified (Stadler et al. 2001). There is a shortage of studies that quantify not only herbivory but also rates of mineralization, respiration, or the forms and availability of nitrogen or phosphorus. Second, many of the insect effects on plants such as shifts in phenology or changes in plant resource allocation do not result in immediate and obvious changes in matter fluxes, and their ecosystem-level effects can only be quantified in longer-term studies. For example, studies that employed insecticides over a longer time span have shown that above- and belowground insect herbivores affect plant community composition over a time-scale of several years (Brown 1990). Such a change in plant community composition will have consequences for nutrient cycling in the ecosystem, but this can only be assessed when nutrient fluxes are measured over an extended time period. Longer-term consequences for nutrient cycling can also be expected from the role of insects as pollinators, seed dispersers, predators, parasites, detritivores or ecosystem engineers, and these consequences need to be explored in more detail. Finally, the full extent to which insects influence nutrient cycling can only be unravelled through manipulative studies where the number of insects in the ecosystem is either augmented or reduced, yet such studies are still very rare (e.g. Mulder et al. 1999; Belovsky and Slade 2000; Cardinale et al. 2002; 2003; Mitchell 2003; Montoya et al. 2003; Schmitz 2003). This lamentable lack of studies is one of the main reasons why we started this book project. Before we outline the structure of this book, we briefly summarize the various effects of insects on ecosystem functioning. These effects are discussed in greater depths in the different chapters of the book.

1.3 A Brief Overview of Insect Effects on Ecosystem Function

Insects affect nutrient cycling both directly and indirectly. Direct effects include the reduction of NPP by herbivores and the breakdown of litter by detritivores, but there are other direct effects of insects on nutrient cycling, for example through their role as ecosystem engineers (Jones and Lawton 1995). Indirect effects of insects on ecosystem functioning include, for example, changes in matter fluxes due to changes in plant species composition that are mediated by insect herbivory. Insects affect ecosystem functions mainly through their interaction with plants. However, interactions of insects with other organisms also have bearings on matter flux in ecosystems. Table 1.1 provides a list of insect effects on ecosystem function.

1.3.1 Insect Effects on Ecosystem Function Via Interactions with Plants

Insects interact with plants in a number of ways. The main interactions that have consequences for ecosystem functioning are herbivory (i.e. antagonistic phytophagy, in contrast to mutualistic phytophagy, in the terminology of Lewinsohn and Price 1996) and mutualism, in particular pollination, seed dispersal and plant protection. Both of these interactions between plants and insects have direct and indirect effects on ecosystem function. Direct effects on carbon storage and element cycling, in particular NPP, are well documented for herbivory, but only to a lesser extent for mutualistic interactions. Indirect effects on ecosystem function involve effects on plant species composition including succession, on plant resource allocation and on food web interactions. While direct effects have received most attention, indirect effects may also greatly influence nutrient cycling, but quantification of these effects is still rudimentary.

1.3.1.1 Herbivory

Insect herbivores consume living material and therefore have a direct effect on NPP. This direct effect has been measured in a large number of studies (e.g. Petrusewicz 1967; Wiegert and Evans 1967; Golley et al. 1975; Mattson and

Table 1.1. Insect effects on nutrient cycling

(1) Plant–insect interactions that affect nutrient cycling

Interaction	Main mechanisms through which nutrient cycling is affected	Examples
(a) Herbivory		
Herbivory on roots, shoots, flowers, seeds	Direct change of carbon storage, element cycles	Reduction of standing crop
		Partial or complete defoliation during outbreak
		Induction of leaf fall
		Increasing nutrient leaching from foliage
		Production of honeydew
		Production of methane in guts (termites)
		Defaecation, respiration (CO_2)
	Effect on plant species composition	Change in direction of succession
		Recreation of early successional state by outbreak
		Effects on plant species diversity
		Recruitment limitation and species loss in case of seed predation
		Rank–abundance relationships altered
	Effect on plant resource allocation	Increase in foliage growth
		Increase in root exudation
		Root/shoot allocation modified
		Allocation of resources to chemical, physical defence with consequences for litter quality
		Release of VOC
		Other changes in allocation patterns
	Food web interactions altered	Stimulation/change of activity of decomposer organisms
		Effects on soil microbial community due to (root) herbivory
		Modification of plant–mycorrhiza interactions
		Modification of interaction between plants and pollinators, etc.

Table 1.1. (*Continued*)

(1) Plant–insect interactions that affect nutrient cycling

Interaction	Main mechanisms through which nutrient cycling is affected	Examples
(b) Mutualism		
Pollination, seed dispersal	Direct change of carbon storage, element cycles	Effects on standing crop and productivity Redistribution of nutrients
	Effect on plant species composition	Recruitment limitation and species loss
Protective mutualisms	Direct change of carbon storage, element cycles	Reduction of biomass loss
	Effect on plant species composition	Competitive interactions altered

(2) Other direct and indirect effects of insects on nutrient cycling

Functional role of insects	Main mechanisms through which nutrient cycling is affected	Examples
Detritivores	Direct change of carbon storage, element cycles	Reduction of standing crops of recalcitrant materials Increase in decomposition rate Shift from net immobilization to net mineralization Removal of dung and carrion

Breakdown of litter and wood

Table 1.1. (*Continued*)

(2) Other direct and indirect effects of insects on nutrient cycling

Functional role of insects	Main mechanisms through which nutrient cycling is affected	Examples
Ecosystem engineers	Direct change of carbon storage, element cycles	Moving of nutrients (e.g. termites)
	Modification of habitat conditions for other organisms	Substrate and microorganism mixing Reduction and abrasion of particles Modification of abiotic conditions for soil microfauna and other fauna Increase of plant growth by changing soil aeration, nutrient availability and water infiltration Creation of fungal gardens
Predators/parasitoids	Food web interactions altered	Effects on soil food web Trophic cascades
Microbial feeders	Direct change of carbon storage, element cycles	Change in decomposition rates
	Food web interactions altered	Grazing on fungal hyphae Effects on plant–mycorhiza interactions Effects on interactions between other soil organisms
Dispersal agents	Dispersal of other organisms	Distribution of arbuscular mycorrhizal spores

Addy 1975; Gosz et al. 1978; Lee 1979; Hutchinson and King 1982; Seastedt and Crossley 1984; Detling 1988; Curry 1994; Price 1997; Coleman and Hendrix 2000; Schowalter 2000a). Direct effects of flower and nectar feeders, and of seed predators, on NPP are relatively small, because reproductive organs make up only a small proportion of total plant biomass. Herbivory also increases nutrient leaching from foliage and the rate of fall of leaves (Mattson and Addy 1975), and insect faeces make nutrients available for mineralization that were previously fixed in plants (Seastedt and Crossley 1984). As with the consumption of biomass, these direct effects of insects on nutrient cycling are small for nominal herbivory but may be large in outbreak situations (Mattson and Addy 1975; Schowalter et al. 1986; Christenson et al. 2002). Outbreaks may result in leaching of nutrients out of the ecosystem, although some studies show that nutrients are redistributed within the ecosystem rather than lost (Lerdau 1996; Christenson et al. 2002; Lovett et al. 2002). As discussed above, it is in outbreak situations that direct effects of herbivorous insects on nutrient cycling become most visible. While outbreak situations clearly show the potential of herbivorous insects to directly affect nutrient cycling, the effects of continuous low-level herbivory do need to be investigated in more detail (Stadler et al. 2001).

An important indirect effect of herbivory on nutrient cycling is due to the role of herbivores in plant–plant competition. A large number of studies have shown that insect herbivores influence competitive interactions within the plant community and therefore affect plant species composition (Crawley 1983; Whelan 1989; Brown 1990; Louda et al. 1990; Brown and Gange 1992; Davidson 1993; Bach 2001; Blatt et al. 2001; Dyer and Shugart 2002). This holds not only for foliovores but also for seed predators and other root, shoot, flower or nectar feeders (Sallabanks and Courtney 1992; Davidson 1993; Brown 1997; Irwin et al. 2001). A number of studies employing insecticides have shown that the direction of succession depends on the presence of insect herbivores, both above- and below ground (Brown et al. 1987, 1988; Brown 1990). In the extreme case, herbivory causes plant death, for example in seedlings, with clear consequences for plant species composition (Crawley 1986; Khan and Tripathi 1991). Changes in plant species composition caused by insect herbivores may only be visible in long-term studies (Brown 1990; Cain et al. 1991; McCullough and Werner 1998; Bach 2001). Outbreaks of herbivores occur only infrequently, but they may play an important role in structuring plant communities (Danell and Ericson 1990; Carson and Root 2000), as they usually reduce the growth and resource acquisition of dominant plants and therefore delay or redirect succession (Davidson 1993; Carson and Root 2000; Blatt et al. 2001). One fascinating example in this respect are the interactions between insects and fire in northern and boreal forests in North America (McCullough and Werner 1998). Accumulation of fuels following insect outbreaks may determine extent and intensity of subsequent fires, or fire may predispose trees to subsequent attack by insects.

Both processes greatly affect forest species. Changes in plant species composition will result in changes in community productivity and nutrient cycling, but these indirect effects of insect herbivores in forests have not been quantified.

Another important effect of insects on plants which indirectly affects ecosystem function is a change in plant resource allocation. Allocation to root, shoot or to flowers and seeds changes after herbivore attack and these alterations may be long-lasting (e.g. Abrahamson and McCrea 1986; Dyer et al. 1991; Trumble et al. 1993; Marquis 1996; Honkanen and Haukioja 1998; Strauss et al. 1999; Stowe et al. 2000; Kosola et al. 2001). Plants often increase root exudation in response to herbivory and this has effects on soil fauna (Wardle 2002). Inducible plant defences also require changes in plant resource allocation (Karban and Baldwin 1997; Baldwin and Preston 1999). Inducible defences and other herbivore-induced changes in plant resource allocation are costly and affect plant competitive ability (Karban and Baldwin 1997; Baldwin 1998). Thus, an adjustment of plant resource allocation affects plant productivity and, in the longer term, plant species composition. In addition, it may affect nutrient cycling by changing the uptake and release of chemical compounds, and by changing litter quality. An example is the release of volatile organic compounds (VOCs) which play a role in attracting natural enemies of herbivores (Kessler and Baldwin 2001). The consequences of herbivore-induced changes in plant resource allocation for nutrient cycling have yet to be quantified for the ecosystem level. Most present studies focus on individual plants or, more rarely, plant populations.

Finally, insect herbivory can affect nutrient cycling by affecting food web interactions (Wardle 2002). For example, root herbivory impacts soil microbial communities with consequences for decomposition and nutrient release (Grayston et al. 2001). Other examples include a modification of plant–mycorrhiza interactions (Gehring and Whitham 2002) and the modification of interactions between plants and pollinators (Hambäck 2001). As in the case of herbivore impact on plant resource allocation, the consequences of herbivore-induced modifications of species interactions for nutrient cycling at the ecosystem level need to be investigated in more detail.

Two well-known and related hypotheses about the effects of herbivorous insects on nutrient cycling are the nutrient acceleration hypothesis and the grazing optimization hypothesis. The nutrient acceleration hypothesis states that herbivorous insects increase nutrient cycling by returning nutrients fixed in plants back to producers at a rate faster than the nutrients would otherwise flow through the processes of senescence, litter fall and decomposition (e.g. Chew 1974; Mattson and Addy 1975). Such increases in nutrient cycling have been documented, mostly in short-term studies (e.g. Lightfoot and Whitford 1990; Belovsky and Slade 2000). The controversial grazing optimization hypothesis states that low levels of herbivory actually increase plant productivity such that the relationship between productivity and herbivory intensity is hump-shaped (McNaughton 1993). Mathematical modelling shows that several mechanisms could account for a positive effect of herbivores on plant production, such as a stimulation of plant growth, an increase in cycling of a limiting nutrient or changes in plant species composition (De Mazancourt and Loreau 2000).

1.3.1.2 Plant–Insect Mutualisms

Pollination and seed dispersal are two services that insects provide for plants within the context of mutualistic interactions. In addition, there are a number of protective mutualisms between insects and plants, such as those between ants and ant–plant mutualisms (Fonseca 1994). Pollination and seed dispersal probably have little direct effects on nutrient cycling, even though energy expenditure on nectar rewards may be high, and the quantities of seeds moved by insect dispersers, in particular ants, can be large (Harder and Barrett 2002). The lack of pollinators or seed dispersers, and their choosiness, may, however, affect plant species composition (Howe and Smallwood 1982; Willson 1992; Corbet 1997), which will have consequences for nutrient cycling (see previous section).

Plants also employ insects to defend themselves against herbivores, for example by providing them with domatia or by attracting them with volatile emissions (Turlings et al. 1990; Grostal and O'Dowd 1994; Agrawal and Karban 1997; Kessler and Baldwin 2001). In the absence of the mutualists, plants suffer higher damage and may be displaced by stronger competitors. Thus, the different types of mutualisms between insects and plants are likely to affect nutrient cycling mainly via their effect on plant species composition.

1.3.2 Other Direct and Indirect Effects of Insects on Ecosystem Function

Insects also affect ecosystem functions directly without the involvement of living plant tissues. Insect detritivores such as cockroaches or springtails are an important component of soil macro- and mesofauna and hence the soil food web, and their presence is essential for litter breakdown and a fast return of nutrients to the primary producers (Wardle 2002). Soil insects also acts as ecosystem engineers by affecting soil conditions and creating physical structures which provide a modified habitat for soil microflora and other soil fauna. This affects nutrient cycling both directly and indirectly. Because the interactions in the belowground food web are complex, disentangling the effects of insects from those other soil fauna requires detailed studies (Wardle 2002). The most important insect ecosystem engineers globally are probably termites which move large amounts of soil and affect the soil's structure and fertility (Lee and Wood 1971). All insects, whether herbivore, detritivores or predators, affect nutrient cycling through processing of food and making organic matter available for mineralization.

In addition to the effects listed above, insects have a number of indirect effects on nutrient cycling. Predators and parasitoids affect interactions between plants and herbivores, pollinators or seed dispersers and can therefore modulate the effects of their prey on nutrient cycling. In tritrophic interactions between plants, herbivores, and predators and parasitoids, changes in carnivore abundance often affect plant biomass through trophic cascades (Schmitz et al. 2000; Cardinale et al. 2003; Schmitz 2003), although it has been argued that such food web dynamics are more important in water than on land (Polis 1999; Halaj and Wise 2001). Insect predators are an important part of the soil food web and have been shown to affect rates of decomposition although the exact mechanisms are far from clear (Wardle 2002). Because insects are an integral part of any terrestrial food web, they affect a great number of food web interactions which, at least in theory, could have consequences for nutrient cycling (Montoya et al. 2003). Insect ecosystem engineers among insects also affect food web interactions with possible consequences for ecosystem functioning (Johnson et al. 2002). So far, these interactions have rarely been studied with respect to their role in nutrient cycling.

1.4 The Aim and Structure of this Book

As illustrated in the previous sections, insects have a large number of effects on ecosystem functioning, yet little is known about the magnitude and relative importance of the various ways insects impact the matter fluxes in an ecosystem. What is underrepresented in the literature are manipulative studies that establish causal relationships between insects and ecosystem functioning, and that unravel the mechanisms underlying these relationships. Thus, studies are needed in which appropriate techniques are employed through which the action of insects in ecosystems can be reduced, augmented or simulated. Such techniques have been developed in the field of plant–insect interactions, and have been successfully employed to study the effects of insects at the level of individual plants, plant populations and plant communities. It is our view that research on the functional aspects of biodiversity can benefit from employing some of these approaches used in the studies of plant–insect interactions. The aim of this book is therefore two-fold. First, it aims to provide a summary of what is known about insect effects on ecosystem function, in particular on nutrient cycling. Particular attention is given to the role of herbivorous insects in terrestrial ecosystems, but effects of predators, parasitoids and detritivores are also touched upon. The second aim of this book is to provide a methodological guide to manipulative ecosystem studies of insect herbivory in the field. The techniques used to manipulate or simulate herbivory are critically reviewed, and their advantages and disadvantages are discussed in detail. We hope that by reviewing the known and suspected ecosystem-level effects of insects, and by providing methodological advice, this book will stimulate further research into the relationship between insects and ecosystem function.

Sections 2 and 3 of this book review what we know about the effects of herbivorous insects on ecosystem function. As belowground organisms have finally been recognized as being the main drivers of ecosystem processes (Wardle 2002), Section 2 focuses on the interactions between insects, the belowground community and ecosystem functioning. The belowground community represents a complex food web that consists of a large number of taxa including bacteria, protozoa, invertebrates and vertebrates. Insects involved in the belowground food web act as herbivores (e.g. the larvae of tipulids and a number of beetle families), detritivores (e.g. collembola) and predators (e.g. predatory beetle larvae). Because of the complexity of this food web, it is not always possible to isolate the effects of insects from those of other organisms. While emphasizing the particular role of insects, the chapters in the first section therefore also discuss the involvement of other belowground organisms in ecosystem functioning, if this is necessary for the understanding of the mechanisms underlying the cycling of nutrients. In the first chapter of this section, Hartley and Jones (Chap. 2) provide quantifications of direct and indirect effects of herbivorous insects on nutrient cycling, focusing on decomposition, mineralization and plant productivity. The chapter describes how stable isotope techniques and inventive uses of controlled environment studies have led to new insights into the role of soil biota in both below- and aboveground processes. In Chapter 3, Wardle and Bardgett review the indirect effects of aboveground herbivory on the decomposer community and identify four types of mechanisms through which herbivory affects the quantity and quality of plant-derived resources entering the soil. The authors argue that because decomposers affect plant-available nutrient supply, and therefore the quality and quantity of foliage available for invertebrate herbivores, herbivores function as important participants in feedbacks between the above- and belowground subsystems. In Chapter 4, Bonkowski and Scheu look at above- and belowground interactions from the opposite side and review the effects of interactions in the rhizosphere for aboveground processes. Bonkowski and Scheu discuss how aboveground herbivore–plant interactions and plant productivity are affected by the processes in a number of distinct belowground subsystems such as the bacterial loop and the fungal food chain. In Chapter 5, the final chapter of Section 2, Masters focuses on the role of belowground insect herbivores for nutrient cycling. In his chapter, Masters reviews the different effects of low, medium and high level of belowground herbivory for plant growth and nutrient cycling. The chapter also shows how belowground insect herbivory affects higher trophic levels such as seed predators and parasitoids with subsequent effects on nutrient cycling. Together, the chapters of the first sections provide a comprehensive review of the importance of above- and belowground interactions for ecosystem functioning, and they point out the approaches needed for a deeper understanding of the role of insects in influencing these interactions.

The chapters in Section 3 discuss aboveground interactions between plants, herbivorous insects and higher trophic levels, and the consequences of these interactions for nutrient cycling. In Chapter 6, Joshi and coauthors review results from the European BIODEPTH project and investigate the relationships between plant diversity, community productivity, and the diversity and abundance of insects in artificially assembled grassland plant communities. Joshi et al. show that a reasonable starting point in unravelling the complex relationship between producer diversity and whole-ecosystem consequences is to measure the effects of changing plant-species diversity on primary productivity, the basis of each food web, and to explore the potential consequences of these effects on higher trophic levels. The next two chapters use examples from biological control to illustrate the sometimes dramatic effects of insects on ecological processes. In Chapter 7, Zwölfer and Zimmermann use three case studies to show how insect–plant interactions may strongly affect plant community composition and all its dependent ecosystem properties. From successful biological weed control examples Zwölfer and Zimmermann deduce insect and plant properties that make a drastic insect-mediated change in vegetation cover more likely. Kruess and coauthors, in Chapter 8, show how the interactions between insects and plants and between insects and pathogens may be modified by the spatial context of the landscape in which these interactions take place. Such modifications affect matter fluxes both directly and indirectly, but these effects are far from being explored. In Chapter 9, the theme of food web interactions is taken a step further. Janssen and Sabelis review the effects of higher trophic levels on plant biomass, plant diversity and ecosystem processes. Navigating this virtually unexplored territory, one of the authors' sobering conclusions is that while food web interactions such as apparent competition, omnivory, intraguild predation or plant–plant interactions are important for ecosystem processes, generalizing rules relating food web interactions to ecosystem processes probably do not exist. In contrast to this view that it is very difficult to deduce generalizing mechanisms from the patterns observed, Carson et al., in Chapter 10, propose a general rule that predicts when insect herbivores will have very strong top-down effects on plant communities with subsequent effects on ecosystem functioning. The authors argue that outbreaks of specialist insects, traditionally seen as being of little importance for the long-term regulation of plant communities, are in fact both widespread and frequent enough to exert strong top-down effects on ecosystem functioning across multiple spatial scales. In Chapter 11, the final chapter of Section 3, Stadler et al. discuss the role of insects in forests and examine in detail the way in which the ecology of the insect herbivore influences nutrient cycling under chronic herbivory. The authors argue that in order to understand nutrient cycling in forests, it is important to appreciate the role of small herbivores such as aphids or adelgids as these excrete enormous amounts of honeydew and can change the flow of water and nutrients in the canopy.

The fourth section of this book concerns methodology. The chapters in this section review established and novel methods to manipulate the interaction between plants and insect herbivores. Particular emphasis is given to the advantages and disadvantages of the various methods to reduce, enhance or simulate the effects of herbivory on plant communities. The first two chapters by Hjältén and by Lehtilä and Boalt discuss the chances and pitfalls of simulated herbivory. In Chapter 12, Hjältén identifies the most obvious advantages and disadvantages of using simulated insect herbivory and suggests ways in which some of the problems can be avoided. He argues that except for some limited circumstances, the drawbacks of using artificial herbivory outweigh the main benefit of this method, which is the relative ease with which the degree, timing and distribution of damage can be controlled. In Chapter 13, Lehtilä and Boalt present the results of a literature survey in which authors have documented differences in effects when the same plant trait was analysed both using artificial herbivory and employing real herbivores. This literature survey reveals which traits are most sensitive to the way in which damage is applied in herbivory manipulations. Taken together, Chapters 12 and 13 should present a guide for the use of artificial herbivory in future studies on the effects of herbivorous insects on ecosystem function. In Chapter 14, another technique commonly used to elucidate the role of insects for ecological processes, the use of cages to exclude insect herbivores, or to assemble particular communities of insect herbivores and natural enemies, is reviewed critically. Using examples from his own work on a food web in a New England meadow ecosystem, Schmitz shows how enclosure cage experiments can be an effective tool in an endeavour to predict effects of perturbations on whole ecosystem function. In addition to discussing the requirements of cage design, Schmitz provides guidelines to show how predictive insights can be gained into complex trophic interactions by performing a series of cage experiments that examine successively how different ecosystem components fit together to determine function. Another method to exclude insects commonly employed in insect–plant studies is the use of insecticides, which allows experiments to be carried out in the field on a larger scale than cage experiments. Insecticide use too has a number of side effects that may confound the results of the experiment. In Chapter 15, Siemann and coauthors investigate the general principles that apply to the interpretation of insecticide experiments, and review the artefacts of the method that may masquerade as release from herbivory.

While the use of insecticides, cages or simulated herbivory all have their benefits, for many studies on the effects of insects on ecosystem function it may not be sufficient to concentrate on one of the established techniques only.

Chapter 16, by Rogers and coauthors, illustrates how a combination of cage, insecticide and simulated herbivory experiments can be used to unravel the role insects play in a particular ecosystem. Finally, in the last chapter of this section, Chapter 17, Voelckel and Baldwin go beyond a discussion of techniques that are already well established in the plant–insect literature, and develop a perspective for future manipulative studies employing the rapidly developing knowledge of molecular ecology. The authors describe the state of the art in research on herbivore-specific transcriptional responses and discuss their research potential for future ecosystem studies.

During the compilation of the literature review for this book, it became apparent to the editors that in addition to the lack of experimental studies little theory has been developed to investigate theoretically the effects of insect herbivory on ecosystem functioning (Bachelet et al. 1989; De Mazancourt and Loreau 2000; Blatt et al. 2001; Dyer and Shugart 2002). As a consequence, the last chapter of this book develops some simple theory to predict how the interaction between plant and insect herbivore diversity impacts plant productivity. This theory is intended to act as a starting point for further theoretical research into the effects of insect biodiversity on ecosystem functioning. In addition to this theoretical work, the last chapter uses the conclusions derived by the authors of the book chapters to attempt an outline of the areas where further research into insect effects on ecosystem functioning is needed. The editors hope that this outline along with the insights provided by the chapters of this book will stimulate entomologists, biogeochemists and other researchers to more closely investigate the role of the most speciose component of terrestrial biodiversity for ecosystem nutrient cycling.

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