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

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