Part I INTRODUCTION

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Indirect interaction webs: an introduction

TAKAYUKI OHGUSHI, TIMOTHY P. CRAIG, AND PETER W. PRICE

The modification of plant traits by species utilizing a plant can be of crucial importance in determining the ecological and evolutionary interactions among community members centered on the plant. The authors in this volume review studies that integrate direct and indirect effects of plant-mediated traits on the ecology and evolution of plant–herbivore and other plant-mediated interactions. They synthesize these data to provide a more complete understanding of plant-based ecological community structure, which will provide a new perspective on the organization of these communities. Also, they suggest directions for future study. The richness of plant-trait-mediated effects results in the production of far more linkages among species than food web interactions alone. This richness also strengthens the argument that insect species on plants constitute real communities rather than noninteracting assemblages of individual species. Herbivore modification of plant traits is very common and widespread in terrestrial plants, and this initiates indirect interactions between species utilizing the same host plant. These interactions can be mediated by herbivore-induced changes in plant defensive chemicals, nutritional status, and the subsequent growth of plants attacked. Modification of plants in ways other than the simple removal of tissue can have complex impacts on other herbivores, and produce effects that cascade upward to higher trophic levels including predators and parasitoids. Thus, the structure and biodiversity of plant-based terrestrial communities can be strongly influenced by interaction linkages initiated by herbivory.

Indirect effects occur when the impacts of one species on another are influenced by one or more intermediate species. Indirect effects are important

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because they are common in biological systems, and may change outcomes of interactions among species. Indirect effects are diverse, but they can be classified as either (1) density-mediated or (2) trait-mediated (Abrams *et al.* 1996). Density-mediated indirect effects result in a numerical response of the induced species, while trait-mediated indirect effects influence traits such as behavior, morphology, and life histories of the induced species. Density-mediated indirect effects, such as apparent competition and top–down trophic cascades, have been studied much more thoroughly than trait-mediated indirect effects (Holt and Lawton 1994, Pace *et al.* 1999). Recently there has been an increased appreciation of the importance of trait-mediated indirect effects on community organization (Werner and Peacor 2003). For example, a special feature section on "Linking individual-scale trait plasticity to community dynamics" in the journal *Ecology* (volume 84:1081–1157 in 2003) focused on this issue. However, the authors focused on trait-mediated indirect effects in prey–predator interactions, such as changes in prey behavior to avoid predation risk, and they paid little attention to the plant-mediated indirect effects on community composition and structure. We argue that density-mediated indirect effects predominate in herbivore–predator interactions, while trait-mediated indirect effects are of primary importance in plant–herbivore interactions. This is because predators usually kill individuals in lower trophic levels while herbivores predominately alter traits of plants attacked, without killing them. Our emphasis is on the importance of herbivore modification of terrestrial plant traits in producing indirect effects that link multiple interactions and shape community structure.

"Indirect interaction webs" (Ohgushi 2005) is a new concept used in this book to evaluate the functioning of nontrophic, indirect links in ecological communities. Food webs that measure only direct and trophic interactions are the traditional tool used to evaluate the forces structuring ecological communities. We argue that food webs by themselves are inadequate models for understanding ecological communities because they ignore important indirect, nontrophic links. On the other hand, indirect interaction webs contrast them from traditional food webs that fail to capture the frequency and importance of trait-mediated effects. This novel approach of incorporating indirect, nontrophic links into the web of biotic interactions offers a new perspective on how species interactions evolve in communities, and how biodiversity originates, and is maintained, in terrestrial systems. Plants, as primary producers, are at the base of interaction webs as well as food webs so it is logical to develop our understanding of these systems from the "bottom up." The importance of bottom–up forces on community structure has recently gained extensive empirical and theoretical support that challenges the traditional view that plant-centered communities are structured from the top down by the influence of natural

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enemies (Hunter and Price 1992, Whitham *et al.* 2003). The inclusion of non-trophic and indirect interactions provides a new perspective on plant–herbivore interactions that is not found in earlier reviews on this subject. The book, therefore, provides a comprehensive overview of the impact of herbivore-induced indirect effects on the ecology and evolution of plant–herbivore interactions, community organization, and biodiversity. This volume is the first to integrate information on how trait-mediated indirect effects influence the structure of plant-based ecological communities.

This book comprises an introduction and 15 chapters by international experts in the rapidly developing field of indirect effects produced by plant-mediated interactions. The authors focus on four questions of fundamental importance in research on the indirect effects of plant-mediated interactions: (1) What novel interaction linkages are produced by plant-mediated indirect effects? (2) What complex interactions are generated by plant-mediated indirect effects in multi-trophic systems? (3) What are the effects of plant-mediated indirect effects on community structure and biodiversity? and (4) What are the evolutionary consequences of plant-mediated indirect effects?

What novel interaction linkages are produced by plant-mediated indirect effects?

Interaction linkages among organisms produced by plant-mediated effects have important, but poorly understood, roles in structuring ecological communities. The effect of one organism can be propagated through a community to other organisms as the result of changes in plants that we term plant-mediated indirect effects. Ecological research has long focused on studies of how single, direct interactions shape ecological communities. Recent research, however, indicates that complex interactions among multiple species are often more important than interactions among pairs of species (Tscharntke and Hawkins 2002, Stanton 2003). Indirect effects frequently structure these multispecies interactions, but only recently have studies been conducted that can evaluate these effects in terrestrial communities. Density-mediated indirect effects, such as trophic cascades and apparent competition, are one kind of indirect interaction that has been recognized to be much more common than previously thought (Holt and Lawton 1994, Pace *et al.* 1999).

Trait-mediated indirect effects are another, potentially very important, kind of indirect interaction that has been studied less frequently than density-mediated indirect effects. Research on plant–herbivore systems has provided increasing evidence of the importance of these plant-trait-mediated interactions. Substantial, indirect interactions caused by herbivore-induced changes in terrestrial plants occur frequently among temporally separated, spatially separated, and taxonomically distinct species (Ohgushi 2005). The importance of such interactions has not been previously recognized, because of the traditional view that interactions usually occur only among closely related species or among species that simultaneously use the same plant resources. Herbivory on terrestrial plants is usually nonlethal, and it can induce a wide variety of changes in plant traits that can influence interactions among very different species. Measuring these changes provides a mechanistic understanding of how plants mediate indirect interactions among herbivores, and other members of an ecological community. An understanding of plant-mediated indirect interactions among herbivores will allow us to establish linkages between previously isolated areas of inquiry such as: above- and belowground ecology, herbivory and pollination ecology, and insect and microbial ecology. This will result in a much more complete picture of how multiple species are connected in ecological communities through plant-mediated indirect effects. We believe that the indirect interactions are ubiquitous in plant–herbivore interactions in terrestrial systems and that inadequate knowledge of such interactions has impeded progress in understanding how ecological communities function.

There is increasing evidence of plant-mediated indirect interactions among insect herbivores. In particular, feeding-induced plant resistance is a well-documented phenomenon for both sap-feeding and leaf-chewing insects. Denno and Kaplan (Chapter 2) provide a thorough overview on plant-mediated indirect interactions between herbivorous insects, and they identify possible underlying mechanisms responsible for them. Plant-mediated indirect interactions are highly asymmetric, and they occur among temporally and spatially separated insects, and among phylogenetically distinct herbivores. They also explore the life-history traits of herbivorous insects that contribute to competitive superiority in plant-mediated interactions. They demonstrate that studying plant-mediated indirect interactions among insect herbivores provides novel conclusions that challenge the traditional paradigms of community organization that have been based on competition theory.

Hartley *et al.* (Chapter 3) focus on the asymmetric interactions between aphids and other organisms that exploit the plant vascular system. First, they examine the indirect interactions between phloem-feeding aphids and leaf miners that physically disrupt the flow of nutrients within the vascular system. The leaf miners significantly decreased aphid survival, but the aphids did not affect the leaf miners. Second, they address how plants mediate interactions between taxonomically separated organisms: phloem-feeding aphids and hemi-parasites that obtain nutrients from the xylem of the host plant roots. The aphids improved performance of the parasite because the aphids increased root biomass, and provided more opportunities for the parasite to connect to its host. In contrast, the parasite had a negative effect on the aphid performance. Hartley *et al.* stress that the indirect interactions can result in the physical alteration of the structures within plants, and that such interactions have been poorly studied.

Studies of plant–herbivore and plant–pollinator interactions have long developed in isolation. Bronstein *et al.* (Chapter 4) explore how herbivory indirectly affects pollination through changes in reproductive traits of shared plants. Herbivore damage can alter flower appearance, reduce flower numbers and size, affect both nectar quantity and chemistry, alter flowering phenologies, and restrict potential resource allocation to seeds. Each of these phenomena, in turn, can deter pollinators, and/or alter the efficacy of individual pollinator visits. To develop a predictive framework, they propose a new physiologically based graphical model designed to explore how plant resources are apportioned to pollinator attraction/reward and to herbivore deterrence, and how allocation schedules are altered by both activities. Bronstein *et al.* apply this model to a pollination system in which a major pollinator (a hawkmoth, *Manduca sexta*) is also a damaging herbivore of the same plant (*Datura wrightii*) while in the larval stage.

Plant-mediated indirect effects can produce interactions between phylogenetically distant herbivores. Mammalian herbivores are ubiquitous and important plant consumers in most terrestrial communities, and they can affect plants by modifying their life history, overall architecture, leaf morphology, chemistry, and spatial distribution. Gómez and González-Megías (Chapter 5) provide a variety of examples of how mammalian herbivores influence directly and indirectly performance or population size of herbivorous insects. Specifically, they assess the importance of the trait-mediated indirect effects that influence the interaction between these two kinds of herbivores. They stress that plant-trait-mediated indirect effects are crucial for insects since the main effect of ungulates is not a change in plant density but a modification of the chemical, physiological, morphological, and architectural traits of plants. Thus, future research needs to consider jointly the effects of both herbivorous vertebrates and invertebrates to draw a more accurate picture of the dynamics of terrestrial communities.

Plant-mediated indirect interactions extend to microorganisms. The use of a common host plant indirectly links insects and mycorrhizal fungi, because both require carbon from the host. Gange (Chapter 6) reviews examples of how indirect interactions between insects and mycorrhizal fungi link below- and aboveground processes. In general, insect herbivory reduces mycorrhizal colonization of plants, through competition for carbon. The most important effect of herbivory is on the mycorrhizal species diversity. Insect host plant choice is unaffected by the mycorrhizal status of a plant, but mycorrhizae can dramatically increase or decrease herbivorous insect growth. Ectomycorrhizal fungi seem to have fewer effects than do arbuscular mycorrhizae. Positive effects of mycorrhizae on insects are caused by alterations in plant morphology or nutritional quality, while negative effects are the result of the modification of plant defenses. Gange also explores the potential role of these interactions in structuring the insect and mycorrhizal communities.

What complex interactions are generated by plant-mediated indirect effects in multitrophic systems?

Plant-mediated indirect effects can affect not only herbivores, but also their natural enemies as the result of bottom–up cascades through trophic levels (Price *et al.* 1980, Hunter *et al.* 1992). Indirect effects can influence the relative importance of top–down effects (control exerted by predators on lower trophic levels) and bottom–up effects (control exerted by resources available to each trophic level). In the past top–down effects have often been considered to be more important than bottom–up effects in multitrophic interactions (cf. Berryman 2002). We believe this is primarily due to the use of food webs to analyze community structure. Food web analysis focuses on the top–down effects of predators, and thus does not reveal effects exerted by lower trophic levels on higher trophic levels. The importance of indirect effects in structuring complex systems has been indicated by recent work on interactions that include more than three trophic levels (Gange and Brown 1997, Tscharntke and Hawkins 2002). Trophic cascades from higher to lower trophic levels are well-known indirect effects in aquatic multitrophic systems (Carpenter *et al.* 1985, Carpenter and Kitchell 1988), in which predators decrease herbivore abundance, and the decreased herbivory in turn increases primary production. Thus, trophic cascades initiated by predators have chiefly density-mediated indirect effects (but see Schmitz *et al.* 2004). In contrast, herbivore-induced changes in plant traits cascade upwards from plants to predators via herbivores. These are indirect effects because plants do not respond numerically, but instead change traits in response to herbivory. Interaction linkages of herbivores through plant-mediated indirect effects have the potential to influence the third trophic level, which enhances the bottom–up cascades in multitrophic systems. Thus, interactions between trophic levels can be bidirectional, with each trophic level exerting influences on the other. Bidirectionality creates feedback loops from terrestrial plants that receive herbivory to higher trophic levels. We argue that plant-mediated indirect effects have great impacts not only on herbivores, but also on their natural enemies. These bottom–up effects from plants may alter the patterns and intensity of top–down effects on lower trophic levels. Thus, to understand the relative importance of bottom–up and top–down forces in plant-based multitrophic systems, we need to know much more about how feedbacks induced by changes in plant quality and architecture in response to herbivory influence higher trophic levels.

Recent studies of multitrophic interactions including plants, herbivores, and their natural enemies have highlighted the relative importance of top–down and bottom–up forces and that of direct and indirect effects in forming ecological communities. Thus, the multitrophic level approach addresses the complexity of ecological communities much more realistically than we have recognized from the study of pair-wise interactions alone. Traditionally, above- and belowground communities have been investigated separately even though both systems are highly interdependent. Poveda *et al.* (Chapter 7) review the evidence of interactions between above- and belowground components. They argue that the relative importances, and the combined effects, of belowground and aboveground herbivores on plant performance and on plant–herbivore, herbivore–parasitoid, and plant–pollinator interactions are almost unknown. They describe a system consisting of multitrophic interactions with organisms including root herbivores and soil decomposers underground, and aphids and their parasitoids and flower visitors aboveground. There are two positive plant-mediated indirect interactions between below- and aboveground processes: the positive effect of root herbivores on flower visitors, and the positive impact of root herbivores and decomposers on aphid densities that indirectly affect the number of parasitized aphids.

Endophytic fungi cause morphological, physiological, and chemical changes in their host plants, including the synthesis of alkaloids that may confer protection against herbivores and pathogens. Thus, they may indirectly affect insect herbivores and natural enemies through changes in these plant traits. Chaneton and Omacini (Chapter 8) provide an overview of indirect effects of fungal endophytes on herbivorous insects and their natural enemies to illustrate the role of mutualistic fungal endophytes as elicitors of bottom–up indirect effects transmitted to higher trophic levels. They describe direct and indirect effects involved in a system consisting of Italian ryegrass, *Neotyphodium* endophyte, aphids, and their primary and secondary parasitoids. They illustrate how the symbiotic interactions result in the propagation of bottom–up cascades to higher trophic levels in multitrophic interaction webs.

Plant secondary chemical compounds, those that apparently lack primary roles in basic functions such as growth and reproduction, are thought to play a role in direct defense against herbivores. These may be produced constitutively or induced by wounding or herbivory. These secondary compounds may also have indirect effects at the second or higher trophic levels. Sabelis *et al.* (Chapter 9) review how secondary plant compounds from plants under herbivore attack indirectly affect other herbivores, predators, hyperpredators, and omnivores. Such indirect effects are of fundamental importance in understanding the structure of arthropod communities on plants.

What are the effects of plant-mediated indirect effects on community structure and biodiversity?

The role of herbivore-induced changes in plant traits in shaping arthropod communities and in maintaining biodiversity on terrestrial plants has only recently been appreciated (Waltz and Whitham 1997, Martinsen *et al.* 2000). Adaptations and counter-adaptations in plant–herbivore interactions produce temporal and spatial resource heterogeneity that increases species richness and interaction diversity. Most of the earth's biodiversity is in its interaction diversity: the tremendous variety of ways in which species are linked together into constantly interacting networks (Thompson 1996). Plant-mediated interaction linkages strongly influence interaction diversity and shape the network structure of interacting species in ecological communities. Knowledge of both the trophic and nontrophic interaction linkages produced by herbivore-induced effects is critical if we are to understand how the network of species interactions alters biodiversity components in arthropod communities. Herbivory changes plant quality and architecture, and it increases the food and habitat heterogeneity provided by terrestrial plants. Herbivore-induced changes can generate bottom–up cascading effects that influence entire arthropod communities, thereby altering both species richness and abundance. Moreover, positive indirect interactions often increase arthropod biodiversity. For example, one herbivore can facilitate the success of other herbivores by inducing compensatory regrowth that increases the nutritional status and/or plant biomass. This may, in turn, result in an increase of species and interaction diversity. Ecosystem engineers create physical structures and they initiate a web of nontrophic interactions (Lill and Marquis 2003). They can also increase species and interaction diversity by creating habitats for other arthropods.

Herbivorous insects rarely kill terrestrial plants, but they frequently induce changes in a range of plant traits. Therefore herbivore-induced indirect interactions are common and widespread in plant–insect interactions. Ohgushi (Chapter 10) illustrates how herbivore-induced indirect interactions create multiple plant–insect linkages mediated by plant- and ant-mediated effects in willow and goldenrod. He proposes the use of indirect interaction webs, which include nontrophic and indirect links, to depict interaction linkages. He demonstrates that these indirect interaction webs revealed more than three times the number of direct and indirect interactions in these systems than would have been detected using traditional plant-based food webs. Recognizing the importance of the indirect interaction linkages produced by herbivore-induced changes in plant traits will alter our understanding of the organization of arthropod community structure on terrestrial plants.

Numerous insect herbivore species act as physical ecosystem engineers by modifying plant architecture to create shelters. Plant manipulation by these engineers through leaf-shelter building, galling, or stem-boring, provides habitat for other species, and has a positive effect on organism abundance and species diversity in arthropod communities. Marquis and Lill (Chapter 11) provide a number of examples of how insect ecosystem engineers are widespread on terrestrial plants, and identify several pathways through which ecosystem engineers interact with other herbivorous and predatory arthropods, thereby altering trophic structure of the associated arthropod fauna of the host plant. One example of ecosystem engineering is insects that build leaf shelters. They not only create habitats for other organisms but they can also modify leaf quality by reducing the production of secondary compounds and lignin that are positively correlated with light availability. Thus the leaf-shelter builder has an indirect positive effect on habitat quality for herbivores inhabiting the shelter. To fully understand the impact of insect ecosystem engineers on the entire arthropod community, future research needs to focus on both the interactions within the shelters and on the impact of the engineer outside of the shelter.

The role of mutualism in broader levels of community organization is poorly understood because much of the study of mutualisms has focused on just a few species. Wimp and Whitham (Chapter 12) explore how plant traits determine the distribution and intensity of ant–aphid mutualisms, which in turn affect arthropod community structure. Ant–aphid mutualisms negatively impact other herbivores, generalist predators, and sub-dominant species of tending ants, but they attract a specialist community of parasites and predators that have unique adaptations for evading ant defenses. In addition to their effects on species richness and the relative abundance of community members, ant–aphid mutualisms can also enhance community stability in terms of species turnover rate and spatial heterogeneity of species diversity. Wimp and Whitham propose that future studies should: (1) consider the important role of bottom–up effects of host plants in determining the distribution of the mutualists, (2) examine interactions between the mutualism and the surrounding community on a variety of different scales, (3) encompass multiple trophic levels, and (4) explore the effects of mutualisms on species composition as well as diversity.

Bailey and Whitham (Chapter 13) examine how herbivores can indirectly impact biodiversity through plant-mediated impacts on dependent community