

# Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect, and facilitative interactions

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Accepted: 5 March 2008

*Key words:* trait-mediated, plant trait, ecosystem engineer, honeydew, mutualism, community structure, bottom-up trophic cascade, complex interactions

## Abstract

One of the most important issues in ecology is understanding the causal mechanisms that shape the structure of ecological communities through trophic interactions. The focus on direct, trophic interactions in much of the research to date means that the potential significance of non-trophic, indirect, and facilitative interactions has been largely ignored in traditional food webs. There is a growing appreciation of the community consequences of such non-trophic effects, and the need to start including them in food web research. This review highlights how non-trophic, indirect, and facilitative interactions play an important role in organizing the structure of plant-centered arthropod communities. I argue that herbivore-induced plant responses, insect ecosystem engineers, and mutualisms involving ant-honeydew-producing insects all generate interaction linkages among insect herbivores, thereby producing complex indirect interaction webs on terrestrial plants. These interactions are all very common and widespread on terrestrial plants, in fact they are almost ubiquitous, but these interactions have rarely been included in traditional food webs. Finally, I will emphasize that because the important community consequences of these non-trophic and indirect interactions have been largely unexplored, it is critical that indirect interaction webs should be the focus of future research.

## Introduction

One of the most important issues in ecology is understanding the causal mechanisms that shape the structure of ecological communities through trophic interactions (Paine, 1980; Hunter et al., 1992; Polis, 1999; Berlow et al., 2004; Borer et al., 2005). Food webs that depict the structure of ecological communities through direct trophic (feeding) interactions have been a basic tool used to understand how ecological communities are structurally organized (Polis & Winemiller, 1996).

The focus on direct, trophic prey-predator interactions in much of the research to date means that the potential significance of non-trophic, indirect, and facilitative interactions has been largely ignored in traditional food webs. It is critical to consider the impact of these less-explored interactions in constructing interaction webs, because they are very common in a wide variety of ecosystems and they play an important role in structuring ecological communities,

thus influencing interaction and species biodiversity (Bruno et al., 2003; Strauss & Irwin, 2004; Ohgushi, 2005; Thompson, 2005; Bascompte et al., 2006). In this context, community ecologists have started to explore interaction networks that include non-trophic, mutualistic, and indirect interactions such as plant-pollinator (Jordano et al., 2006), ant-plant (Guimarães et al., 2006), parasite-host (Lafferty et al., 2006), and plant-herbivore (Ohgushi, 2005, 2007) systems.

I will highlight how non-trophic, indirect, and facilitative interactions play an important role in organizing the structure of plant-centered arthropod communities. Specifically, I will argue that herbivore-induced plant responses, insect ecosystem engineers, and mutualisms involving ant-honeydew-producing insects all generate interaction linkages among insect herbivores, resulting in complex indirect interaction webs on terrestrial plants. Finally, I will emphasize that because the important community consequences of these non-trophic interactions have been largely unexplored, it is critical that indirect interaction webs should be the focus of future research.

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### Trait-mediated indirect effects in ecological communities

Because organisms interact not only directly, but also indirectly with other organisms in nature, indirect effects are important forces in forming ecological communities (Strauss, 1991; Wootton, 1994). There is rapidly growing evidence of trait-mediated indirect effects in prey–predator interactions when prey avoid predation risk through behavioral changes (Werner & Peacor, 2003; Schmitz et al., 2004; Preisser et al., 2005; Prasad & Snyder, 2006; Thaler & Griffin, 2008) and in plant communities when herbivory alters the outcomes of competitive interactions among plants (Callaway et al., 2003; Russell & Louda, 2005). However, community consequences of trait-mediated indirect effects in insect–plant interactions have received little attention relative to those in prey–predator interactions (Ohgushi, 2005).

Terrestrial plants are usually not killed when they are attacked by herbivores, but instead herbivory alters various plant traits. Recent studies of interactions between plants and herbivores have revealed that there are many herbivore-induced plant responses (Karban & Baldwin, 1997). Plants respond to herbivore damage by changes in allelochemistry, cell structure and growth, physiology, morphology, and phenology. As herbivores are the most common components in an ecosystem and produce non-lethal effects on terrestrial plants, this ensures that most plants have traits altered by herbivory. Because these plants provide food and habitat resources to other herbivores, the herbivore-induced alteration of plant traits is undoubtedly the mechanistic basis of trait-mediated indirect effects (Ohgushi, 2005). Hairston et al. (1960) argued that because herbivores rarely deplete green plants, they are not limited by bottom-up forces. Thus, it has been concluded that interspecific competition among herbivorous insects is unlikely to occur (Lawton & Strong, 1981; Strong et al., 1984). However, unlike direct interspecific competition, the indirect interactions mediated by plant traits commonly occur at low levels of herbivory, when green plant material, undamaged by herbivores, remains plentiful (Ohgushi, 2005; Denno & Kaplan, 2007). Hence, the traditional view that interspecific competition occurs only under conditions when resources are highly limiting has failed to recognize the ubiquity of interspecific interactions between herbivorous insects mediated through herbivore-induced changes in plant traits.

### Plant-centered indirect interaction webs

Interaction linkages caused by plant-mediated indirect effects have the potential to strongly influence the

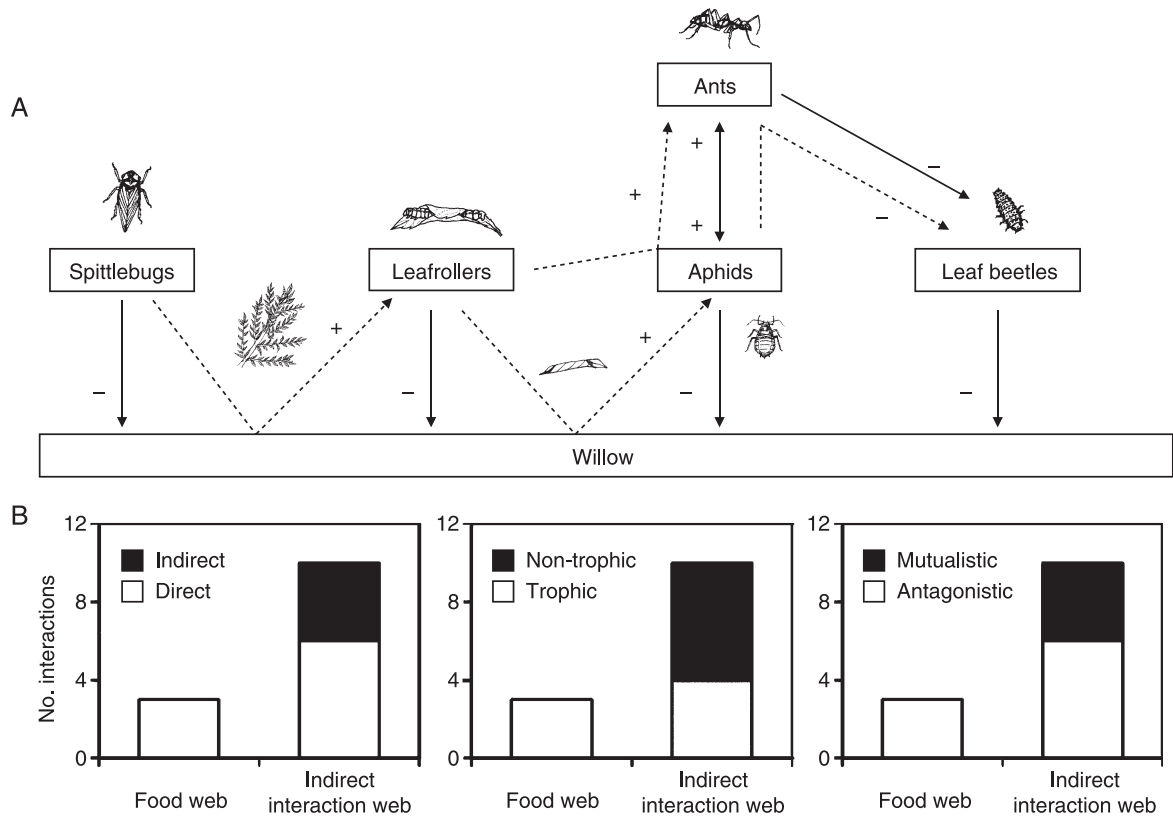
biodiversity of ecological communities by shaping the structure of the network of species interactions (Ohgushi et al., 2007). Feeding relationships are a crucial part of community structure, but food webs provide an incomplete picture of the forces structuring insect communities, because they ignore indirect plant-mediated effects. ‘Indirect interaction webs’ that include non-trophic, indirect links should therefore be used to improve our understanding of the complexity of connections in a plant-based ecological community (Ohgushi, 2005). Because interaction webs include critical information about non-trophic interactions, they provide a more complete understanding of community structure than can be provided by food webs alone.

### Indirect interaction webs on willow and goldenrod

To demonstrate how plant-based indirect interaction webs differ from traditional food webs in depicting herbivore communities, I will give three examples of indirect interaction webs of herbivorous insects associated with willow and goldenrod. As detailed descriptions of these interaction webs have been provided elsewhere (Ohgushi, 2007), here I will emphasize how insect herbivores in these webs are connected to each other by non-trophic, indirect links, and facilitation.

#### Willow and spittlebug

The willow *Salix miyabeana* Seemen (Salicaceae) is distributed in the northern part of Japan, and it is a common woody plant growing along riversides. In flood plains of the Ishikari River in Hokkaido, the spittlebug, *Aphrophora pectoralis* Matsumura (Homoptera: Aphrophoridae), 23 species of leaf-rolling lepidopteran caterpillars, and the leaf beetle, *Plagioderia versicolora* Laicharting (Coleoptera: Chrysomelidae), are the most common insects that feed on *S. miyabeana*. In late summer into autumn, spittlebug females lay eggs into the distal part of new shoots. This kills the terminal shoot, but enhances proximal shoot growth in the following year, resulting in longer shoots with a greater number of leaves (Nozawa & Ohgushi, 2002). This enhanced shoot growth, in turn, increases the density of leafrollers, probably because of an increase in the number of new leaves that provide suitable materials for caterpillars to make leaf shelters. After the caterpillars have pupated and emerged from leaf shelters as adults, the leaf shelters be colonized by the aphid, *Chaitophorus saliniger* Shinji (Homoptera: Aphididae) (sometimes up to 70%: Nakamura & Ohgushi, 2003). This aphid is highly specialized in colonizing leafrolls, and it is rarely observed outside them. Once the aphids become established in the leafrolls, the aphid colonies are tended by



**Figure 1** (A) Indirect interaction web of herbivorous insects on *Salix miyabeana*. Solid and dashed lines show direct and indirect links, respectively. (B) Number and types of interactions detected in the food web and in the indirect interaction web.

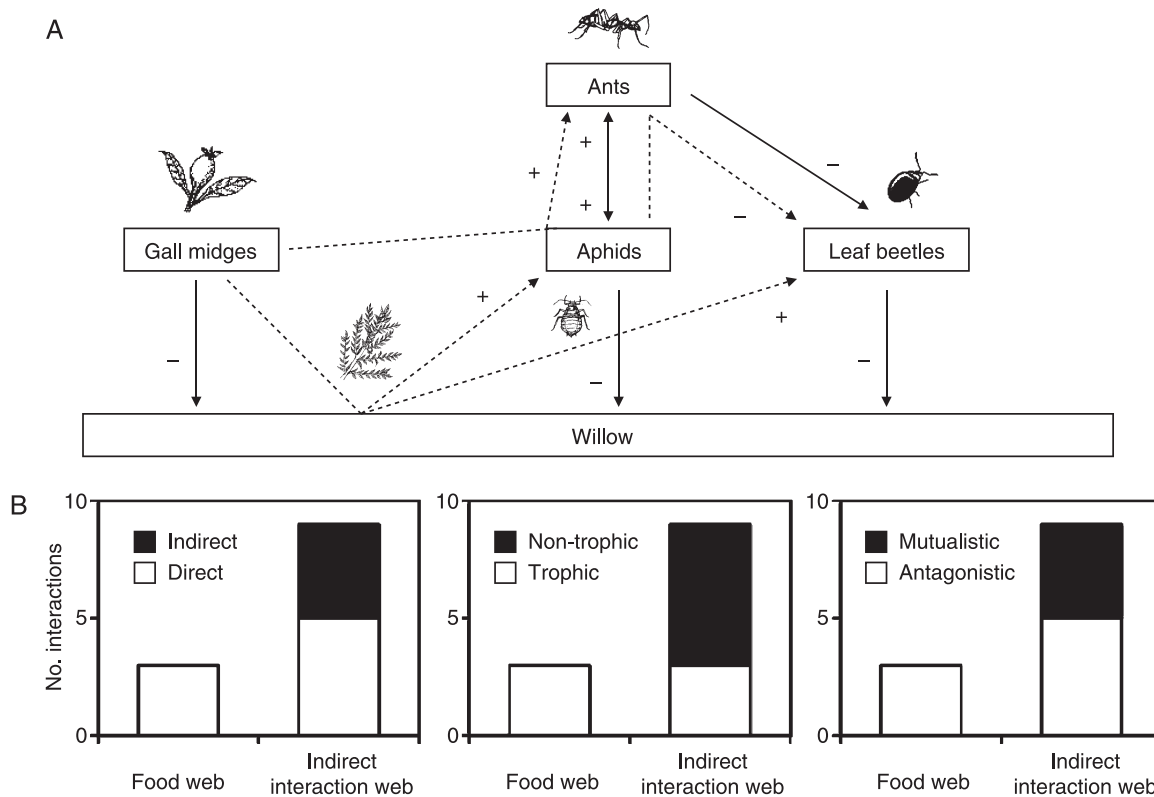
ants, *Camponotus japonicus* Mayr, *Lasius hayashi* Yamauchi et Hayashida, and *Myrmica jessensis* Forel (all Hymenoptera: Formicidae). The number of aphids and associated ants significantly increased with increasing numbers of leafrollers, and the increased number of ants, in turn, negatively influenced the larval survival of the leaf beetle, *P. versicolora* (Nakamura & Ohgushi, 2003). The presence of leafrollers reduced the daily survival rate of the leaf beetle larvae by 60%, and the number of ants on shoots with leafrollers was significantly greater than that on shoots lacking leafrollers.

In this case, the food web was composed of three independent insect–plant interactions: the interactions consisting of spittlebugs, leafrollers, and leaf beetles that all feed on *S. miyabeana* (Figure 1). In the interaction web, the following indirect interactions were added: the positive interaction between spittlebugs and leafrollers resulting from enhanced shoot growth, the positive interaction between leafrollers and aphids resulting from the construction of leaf shelters, the positive interaction between leafrollers and three ant species through aphid colonies within leaf shelters, and the negative interaction between

aphids and leaf beetles mediated by ants tending aphids to obtain honeydew. From the moment that the aphids were included in this web because leaf shelters were available, three direct interactions were newly established: the negative interaction between aphids and willow, the positive interaction between aphids and three species of ants, and the negative interaction between ants and leaf beetles. Thus, the indirect interaction web consisted of six direct and four indirect interactions, including four positive interactions, while the food web consisted of only three negative, direct interactions. The indirect interaction web on willow shows that indirect, non-trophic, and facilitative interactions are 40, 60, and 40% of all interactions, respectively, in contrast to the lack of such interactions in the food web.

#### Willow and gall midge

Our studies revealed another interaction linkage (Figure 2), which is propagated through gall initiation by the gall midge, *Rabdophaga rigidae* Shinji (Diptera: Cecidomyiidae), on *Salix eriocarpa* Franch. et Savat. (Salicaceae) in central Japan (Nakamura et al., 2003). The gall midge is a



**Figure 2** (A) Indirect interaction web of herbivorous insects on *Salix eriocarpa*. Solid and dashed lines show direct and indirect links, respectively. (B) Number and types of interactions detected in the food web and in the indirect interaction web.

common insect herbivore on *S. eriocarpa*, and initiates stem galls on the apical regions of current-year shoots in mid-May. In response to gall initiation, *S. eriocarpa* rapidly develops vigorous lateral shoots, resulting in a secondary leaf flush. The colonization rate of the aphid *Aphis farinose* Gmelin (Homoptera: Aphididae), a common sap-feeder, was four times greater on galled shoots than on ungalled shoots (Nakamura et al., 2003). Similarly, the numbers of adults of two leaf beetles, *P. versicolora* and *Smaragdina semiaurantiaca* Fairmaire (Coleoptera: Chrysomelidae), were 3–10 times greater on galled than on ungalled shoots. The increased densities of aphids and leaf beetles were not only due to increased numbers of newly emerged shoots and leaves, but also due to improved leaf and stem quality. Nitrogen and water content was significantly increased, but toughness was decreased in the apical stems and the upper leaves of galled shoots. Furthermore, we frequently observed that increased ant tending for honeydew in aphid colonies resulted in the removal of leaf beetles from adjacent shoots.

In this case, three independent trophic interactions were involved in the food web on willow: the interactions

consisting of gall midges, aphids, and leaf beetles (Figure 2). These herbivorous insects are unlikely to compete with each other directly, because they are in different feeding guilds, being stem-gallers, sap-suckers, and leaf chewers, respectively. In the indirect interaction web, the following four indirect interactions were added: the positive interaction between gall midges and aphids through increased quantity and quality of food resource, the positive interaction between gall midges and two leaf beetle species through increased quantity and quality of the food resource, the positive interaction between gall midges and ants through increased density of the aphids, and the negative interaction between aphids and leaf beetles through tending ants for aphid honeydew. Furthermore, two direct interactions were established: the positive interaction between the aphids and the ants, and the negative interaction between the ants and the leaf beetles. Thus, the indirect interaction web revealed five direct and four indirect interactions, including four positive interactions, contrasting to three negative, direct interactions in the food web. The indirect interaction web on the willow has revealed that indirect, non-trophic, and mutualistic

interactions are 44, 67, and 44% of all interactions, respectively.

#### Goldenrod and aphids

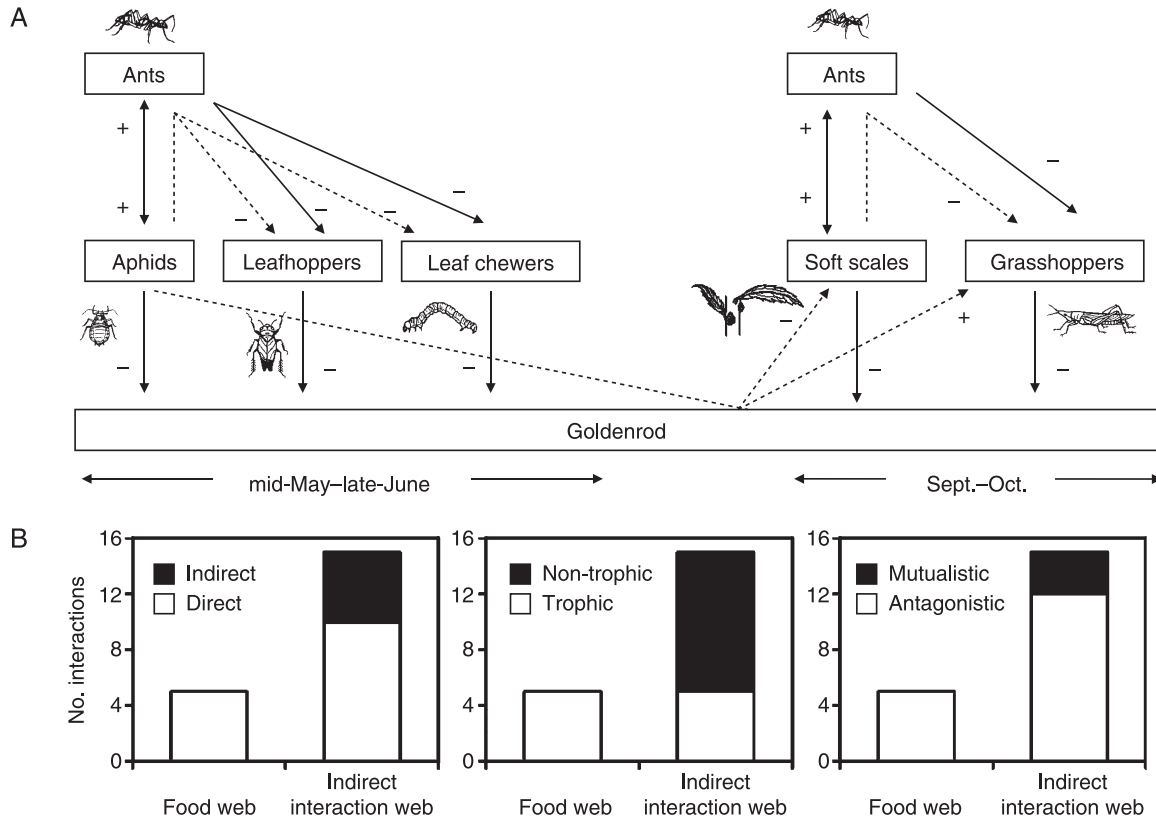
Plant-based indirect interaction webs occur not only on woody plants but also on herbaceous plants, such as the goldenrod, *Solidago altissima* L. (Asteraceae) (Y Ando & T Ohgushi, unpubl.). The goldenrod was introduced from the USA 100 years ago, and it has become widely distributed across Japan. Its common insect herbivores are aphids, leafhoppers, and leaf-chewing geometrid caterpillars in spring and early summer, and grasshoppers and soft scales in autumn. The aphid *Uroleucon nigrotuberculatum* Olive (Homoptera: Aphididae), which is present from late June to late July, is the most common insect early in the growing season. The native ant *Formica japonica* Motschoulsky (Hymenoptera: Formicidae) was frequently observed feeding on scattered aphid honeydew on adjacent leaves (Y Ando & T Ohgushi, unpubl.). Aphid removal resulted in an eight times greater abundance of the leafhopper, *Nephotettix cincticeps* Uhler (Homoptera: Cicadellidae), and of the geometrid caterpillars, which was due to a decreased number of ants on aphid-free plants. However, aphid feeding changed neither nitrogen nor water content of the leaves in early season. The impacts of aphid infestation were evidently transmitted to the soft scale *Parasaissetia nigra* Nietner (Homoptera: Coccidae), and to the leaf-feeding grasshopper *Atractomorpha lata* Motschulsky (Orthoptera: Pyrgomorphidae) in late September when the aphids were absent. Aphid infestation in spring and early summer increased leaf nitrogen and stimulated lateral shoots in autumn. Aphid removal resulted in a 4-fold increase of soft scales on plants. This is probably because decreased phloem quality in aphid-exposed plants reduced colonization by the soft scales. As the soft scales are tended by *F. japonica*, the number of ants was significantly greater on aphid-free plants than on aphid-exposed plants. Conversely, feeding damage by grasshoppers on aphid-exposed plants was twice that on aphid-free plants. Grasshopper density probably increased on aphid-exposed plants because of increased leaf nitrogen and decreased impact of ants tending scale insects. Thus, aphids early in the season negatively affected soft scales by decreasing food quality but positively influenced grasshoppers through increased leaf quality and decreased ant tending on the soft scales late in the season.

The goldenrod food web had five independent plant–insect interactions: feeding interactions consisting of aphids, leafhoppers, and geometrid leaf chewers in spring and early summer, and soft scales and grasshoppers in autumn (Figure 3). As early feeders are temporally separated from autumn feeders, there cannot be direct

competition between them for food resources. In the indirect interaction web, the following indirect interactions were detected: the negative interaction between aphids and leafhoppers through ants tending aphids for honeydew, and the negative interaction between aphids and leaf chewers through tending actions of ants early in the season, and the negative interaction between aphids and soft scales through changes in sap quality, the positive interaction between aphids and grasshoppers through increased leaf nitrogen, and the negative interaction between soft scales and grasshoppers through tending ants for soft scale honeydew late in the season. In addition, five direct interactions were newly established: the positive interaction between aphids and ants, the negative interaction between ants and leafhoppers, and the negative interaction between ants and leaf chewers in spring and early summer, and the positive interaction between soft scales and ants, and the negative interaction between ants and grasshoppers in autumn. Thus, the indirect interaction web revealed 10 direct and five indirect interactions, including three positive interactions, while the food web approach encompassed only five negative, direct interactions. The indirect interaction web on goldenrod has revealed that indirect, non-trophic, and mutualistic interactions are 33, 67, and 20% of total interactions, respectively, in contrast to the lack of such interactions in the food web.

As we can see in the three examples of indirect interaction webs, the interaction linkage has the potential to form a complex network structure of indirectly interacting herbivorous insects. In these three cases, the link densities are three times higher in the indirect interaction webs than in the food webs (Figure 4), suggesting that the network of interactions among insect herbivores is much richer than previously thought due to the large number of non-trophic, indirect, and facilitative links. Comparisons between food webs and indirect interaction webs of the three case studies clearly illustrate that we have long overlooked important components that link interactions in insect herbivore communities. It is now widely appreciated that multi-trophic interactions are important forces in structuring terrestrial communities (Gange & Brown, 1997; Tschardt & Hawkins, 2002). Thus, the inclusion of non-trophic, indirect interactions connecting multiple trophic interactions should enrich the theory of multitrophic community dynamics.

In the indirect interaction webs mentioned above, herbivore-induced plant changes such as secondary regrowth and plant quality, ecosystem engineers such as leaf-rolling caterpillars, and ant-homopteran mutualisms can provide mediators linking insect herbivores involved in different food chains. In the following sections, I will review how herbivore-induced plant changes have a



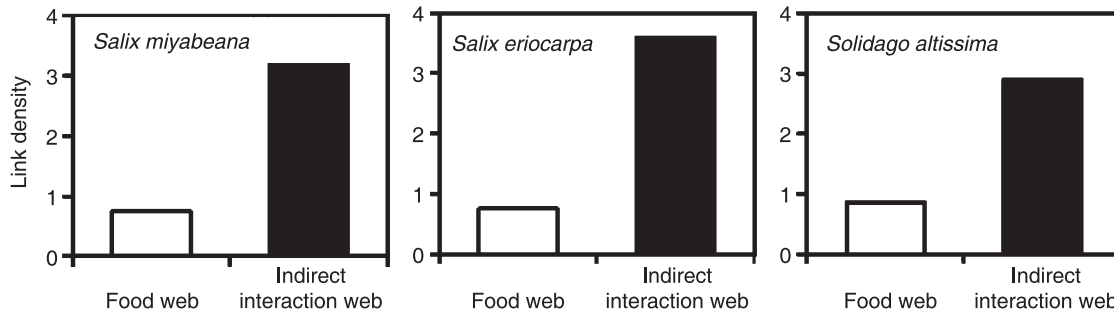
**Figure 3** (A) Indirect interaction web of herbivorous insects on the goldenrod, *Solidago altissima*. Solid and dashed lines show direct and indirect links, respectively. (B) Number and types of interactions detected in food web and indirect interaction web.

community-wide impact on arthropods associated with the plant.

### Community consequences of herbivore-induced changes in plant quality

Herbivore-induced plant responses as indicated by changes in nutrients, allelochemistry, physical structure

and growth, physiology, morphology, and phenology are common and widespread in plants following herbivory (Karban & Baldwin, 1997). Although there is increasing evidence of indirect interactions between insect herbivores that are separated in time and space through herbivore-induced changes in plant quality (Ohgushi, 2005, 2007; Kaplan & Denno, 2007), there are still few studies on partial or entire community-wide effects of herbivore-induced



**Figure 4** Comparison of link densities between food webs and indirect interaction webs on *Salix miyabeana*, *Salix eriocarpa*, and *Solidago altissima*.

changes in plant quality. Using jasmonic acid, Thaler et al. (2001) examined the effects of induced resistance of tomato on performance of insect herbivores. Application of jasmonic acid induced proteinase inhibitors and polyphenol oxidase, which caused resistance to herbivores. The numbers of major insect herbivores, including armyworms, flower thrips, flea beetles, and aphids, were reduced by 50–75% on the jasmonic acid-treated plants relative to control plants in the field. Furthermore, survival and larval mass of beet armyworms and cabbage loopers were reduced by 50–80% on the jasmonic acid-treated plants. Likewise, Kessler et al. (2004) found that genetically modified (lipoxygenase-deficient) tobacco that lacks induced resistance received greater herbivory than wild tobacco with induced resistance. Also, two new species, a leafhopper and a cucumber beetle, attacked non-defended plants, suggesting that induced defenses changed the species composition of the herbivore community. González-Megías & Gómez (2003) removed the leaf beetle *Timarcha lugens* Rosenhauer (Coleoptera: Chrysomelidae), which feeds on flowers, fruits, and vegetative tissues of the shrub *Hormathophylla spinosa* (L.) P. K pfer (Brassicaceae), and demonstrated that the beetle has a great impact on the structure of the arthropod community. Leaf beetle removal increased the abundance of sap-suckers, flower-feeders, folivores, and predators, resulting in an altered community composition and an increase in species diversity in the community. They suggested that this large impact of the leaf beetle on community structure is caused not only by direct consumption of plant tissues but also by changes in nutritional quality and/or secondary compounds through beetle feeding. On the other hand, the removal of the gall-forming aphid, *Pemphigus betae* Doane (Homoptera: Aphididae), from susceptible cottonwood plants decreased both species richness and the relative abundance of arthropods (Dickson & Whitham, 1996). They suggested that the positive effects of aphids on arthropod communities are due to changes in host plant quality, probably because gall formation altered the sink-source transportation patterns of cottonwoods.

### Community consequences of herbivore-induced secondary growth

Secondary growth in response to herbivory can indirectly influence preference and performance and the abundance of late-emerging insects (Ohgushi, 2005). In the indirect interaction webs mentioned earlier, secondary growth that was enhanced by spittlebug oviposition in the previous year increased the density of leafrolling caterpillars, which indirectly increased aphid–ant mutualisms later in the season (Figure 1). Also, regrowth of *S. eriocarpa* following

gall initiation increased the number of aphids and leaf beetles through the provision of high quality resources (Figure 2). Goldenrods that were colonized by aphids early in the growing season enhanced subsequent branching and this enhanced the production of new leaves with high nutritional value, which may have indirectly and positively influenced grasshopper density (Figure 3). It should be noted that secondary growth often produces rapidly growing tissues that are high in nutritional value for herbivores (Price, 1991). In fact, lateral shoot production of willows in response to gall initiation was followed by the production of a number of newly emerged leaves, which had higher nitrogen and water content and were less tough than older leaves (Nakamura et al., 2003).

Tscharntke (1999) studied the community-wide effects of lateral shoot production, which was induced by caterpillars of the stem boring moth *Archanara geminipuncta* Haworth (Lepidoptera: Noctuidae), attacking the common reed, *Phragmites australis* (Cav.) Trin. ex Steud. Syn. (Poaceae), on subsequent insect herbivores. Production of new lateral shoots significantly affected the community structure of gall-making insects, increasing the abundance of six species of gall midges and decreasing the abundance of one species. Likewise, lateral shoot production of willows in response to stem-boring caterpillars of the swift moth, *Endoclita excrescens* Butler (Lepidoptera: Hepialidae), significantly increased both the relative abundance and the species richness of insect herbivores (S Utsumi & T Ohgushi, unpubl.). Secondary growth of plants can affect not only herbivores but also predators. We found that the secondary growth of willows following artificial pruning can greatly influence the structure of the arthropod community (Nakamura et al., 2006). Shortly after cutting the tree at the base of the trunk, a number of lateral shoots developed, and this was followed by a large flush of new leaves that had increased leaf nitrogen and water content, and reduced leaf toughness. The shoot regrowth had 5.8 times more herbivorous insect species, and 2.6 times more total herbivorous insects, compared to the herbivores on uncut willows. Moreover, this bottom-up effect extended to predators. The number of species and the abundance of predators on cut willows were 11 and 3.5 times greater than those on uncut willows, respectively.

### Community consequences of habitat construction by ecosystem engineers

Another common form of herbivore-induced changes in plants is generated by a wide variety of ecosystem engineering effects on terrestrial plants. Ecosystem engineering occurs not because of direct responses of plants to herbivory, but instead as the result of structural

alteration of plants manipulated by insects. It is important to note that ecosystem engineering is ubiquitous on terrestrial plants. The structures produced by common insect herbivore guilds, including gall makers, leaf rollers, case bearers, stem borers, and leaf miners provide new habitats for other herbivores and/or their natural enemies (Marquis & Lill, 2007). Recent studies have emphasized that insect ecosystem engineers have the potential to greatly affect the species richness, abundance, and trophic interactions of arthropod communities by providing new habitats for secondary users. Martinsen et al. (2000) demonstrated that arthropod species richness increased in response to increased leaf shelters on cottonwoods. Leafroll removal caused a 5-fold decline in species richness and a 7-fold decline in abundance, while leafroll addition resulted in a 2.5-fold increase in species richness and a 6-fold increase in abundance. Likewise, Lill & Marquis (2003) showed that the availability of leaf shelters is an important determinant of species richness for insect herbivores on white oak, *Quercus alba* L. (Fagaceae). The removal of leaf shelters made by leaf-tying caterpillars reduced species richness of insect herbivores by 14–38%. Marquis & Lill (2007) reviewed thoroughly how insect ecosystem engineers directly and indirectly influence plant-based community structure of arthropods.

### Community consequences of mutualisms of ant and honeydew-producing insects

Ant-mediated indirect effects are important links to other herbivorous insects and ant-tended insects. In indirect interaction webs, aphids within leafrolls on willow trees indirectly reduced the survival of leaf beetle larvae through the removal behavior of tending ants (Figure 1). Also, ants that harvested scattered aphid honeydew on goldenrod leaves reduced the number of leafhoppers and geometrid caterpillars in spring, and ants that tended scale insects reduced the number of grasshoppers in autumn (Figure 3).

Ants that tend aphids have strong indirect effects on the structure, diversity, and stability of arthropod communities due to their removal behavior (Wimp & Whitham, 2007). Nevertheless, only a few studies have analyzed how this mutualism affects the arthropod community as a whole. Wimp & Whitham (2001) found that ant–aphid mutualisms had a large impact on the species composition of arthropod communities on cottonwoods. When they examined the number of species associated with trees having aphid–ant associations and those without, they found that of the 90 species examined, 56% were found only on trees without aphid–ant mutualisms, 12% were found only on trees with aphid–ant mutualisms, and 32% were common on both. Kaplan & Eubanks (2005) illustrated that the mutualistic

association between cotton aphids, *Aphis gossypii* Glover (Homoptera: Aphididae), and red fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), on cotton plants negatively influenced 27% of herbivore and 54% of predator taxa. They concluded that the relationships between fire ants and aphids serve as a key interaction that greatly alters the structure of cotton arthropod communities.

It is important to note that ant-mediated indirect effects on other insects and/or communities would be largely dependent on the herbivore-induced changes in plant quality (Nakamura & Ohgushi, 2003; Nakamura et al., 2003; Wimp & Whitham, 2007). For example, spring colonization by aphids on goldenrods negatively affected the density of scale insects in autumn through changes in plant quality, which in turn decreased scale insect–ant mutualisms (Figure 3). Furthermore, aphid–ant mutualisms were rarely established when the leaf shelters constructed by leafrolling caterpillars were not available on willow trees (Figure 1).

### Why are plant-centered indirect interaction webs so common?

Herbivore-induced changes in plant traits, habitat construction by insect herbivores, and mutualisms between ant and honeydew-producing insects can provide a mechanistic basis for indirect interaction webs by adding indirect and non-trophic links. I argue that indirect interaction webs of herbivorous insects are ubiquitous on terrestrial plants, and thus their effects must be taken into consideration when studying arthropod community structure. Why are herbivore-induced changes that provide a mechanistic base for indirect interaction webs so common and widespread in terrestrial plants? There are several factors that contribute to their ubiquity.

#### Plants are large and long lived

First, plants are large relative to most insect herbivores, so damage is much more common than death from herbivory. Second, plants are long lived relative to many insect herbivores, so defense is an important strategy. Third, plants are rooted in the ground and cannot escape attack by behavioral means so they evolve to either defend themselves against, tolerate, or to compensate for damage by insects. Thus, these plant characteristics combine to result in plants usually surviving attacks by herbivores, but having a high likelihood of being altered by herbivory.

#### Inducible defenses

Many chemical and physical defensive traits of plants against herbivores are inducible rather than constitutive (Karban & Baldwin, 1997). The theory of plant-induced



defense predicts that plants should immediately induce defenses at low levels of herbivory, because it is too late to initiate induced defenses when plants are heavily damaged (Karban & Baldwin, 1997; Sabelis et al., 1999). Current evidence indicates that plant-mediated indirect interactions between herbivorous insects through herbivore-induced plant resistance can indeed occur at low levels of herbivory (Agrawal, 2005; Kaplan & Denno, 2007).

#### **Compensatory growth**

Secondary growth compensating for damaged parts requires the utilization of resources stored in undamaged tissues, and an increased acquisition of resources derived from enhanced photosynthesis and increased nutrient uptake from the soil. Because these responses are very costly for plants, heavy herbivory largely prevents plants from compensating for damaged parts (Whitham et al., 1991; Huhta et al., 2000). In fact, overcompensation occurs only at low levels of herbivory, and plants that are completely defoliated can no longer compensate for tissue loss (Stowe et al., 2000).

#### **Ecosystem engineers**

Insect ecosystem engineering is unlikely to occur at high levels of herbivory, because young and vigorous plant tissues that are easily manipulated are not available to insect ecosystem engineers on heavily damaged plants.

Herbivore-induced changes are most likely to occur at low or moderate levels of herbivory, and they will decrease with increasing level of herbivory. Therefore, we can predict that indirect interactions caused by herbivore-induced plant changes will frequently occur in terrestrial systems because of low levels of herbivory (4–18% of plant biomass: Cyr & Pace, 1993; Polis, 1999).

#### **Ecological consequences of plant-centered indirect interaction webs**

This review has highlighted how non-trophic interactions among insect herbivores produce indirect interaction webs of insect herbivores through several types of indirect effects. They strongly affect the community structure of both herbivorous and predacious insects. Trophic links remain an important factor in structuring insect communities, but, to develop a more complete understanding of how interaction networks structure insect communities, we need to include non-trophic and indirect links. Here, I summarize the ecological consequences of the plant-centered indirect interaction webs.

Although interspecific interactions between herbivorous insects have long been considered unimportant, because they do not result in the depletion of plant

resources (Hairston et al., 1960; Lawton & Strong, 1981), recent reviews have argued that interspecific competition between insect herbivores frequently occurs as a result of herbivore-induced changes in plant resistance (Denno & Kaplan, 2007; Kaplan & Denno, 2007). In Figures 1–3, the indirect interaction webs, which consist of various types of non-trophic and indirect interactions, comprise 60–67% and 33–44% of the total interactions, respectively, which are much greater than the 33–40% of total interactions that are trophic interactions. Also, facilitative interactions that are not included in food webs are much more common in plant-based insect communities than previously thought. In the indirect interaction webs, 20–44% of the total interactions are facilitative (Figures 1–3). The frequently observed positive interactions occur, because ecosystem engineers provide new habitats for secondary users, and herbivores induce secondary growth of plants that enhance the quantity and quality of resources available to other insect herbivores. Thus, the real interaction networks of interacting insect herbivores on terrestrial plants are much more complex than previously thought (Figure 4).

There is an emerging appreciation of the integration of trait evolution and community and/or ecosystem ecology (Whitham et al., 2003; Crutsinger et al., 2006). Recent studies have demonstrated that genetic variation in plants can have significant effects on arthropod communities (Johnson & Agrawal, 2005; Wimp et al., 2005; Johnson et al., 2006; Shuster et al., 2006). Variation in plant phenotypes and/or genotypes also has the potential to greatly influence ecosystem functions through direct and indirect interactions (Madritch & Hunter, 2002; Schweitzer et al., 2005). Recent reviews have emphasized the importance of linking phenotypic plasticity and/or trait evolution with the organization of the ecological community in order to bridge the large gap between evolutionary biology and community ecology (Miner et al., 2005; Fordyce, 2006; Johnson & Stinchcombe, 2007). Therefore, an understanding of the community consequences of herbivore-induced changes in plants provides profound insights into the emerging view of how phenotypic plasticity of plants influences the community structure of arthropods associated with the plant.

Herbivore-induced changes in plants can greatly increase the bottom-up effects of plant genotypic or phenotypic variation on the preference/performance relationships and the abundance of herbivores and predators, as effects move upwards through trophic levels, because they enhance the spatial and temporal resource heterogeneity of terrestrial plants. One of the important predictions based on this view of plant-centered indirect interaction webs is that herbivore-induced bottom-up trophic cascades will frequently occur in terrestrial systems (Ohgushi et al.,

2007). Insect herbivores induce a wide variety of trait changes in plants, which can greatly affect the relative abundance, species richness, and composition of insect herbivore communities. This bottom-up effect from plants will extend to the third trophic level, and alter the abundance and/or species richness of natural enemies. This is an outcome of feedback loops of non-lethal effects of herbivores on terrestrial plants, which in turn influences higher trophic levels. Indeed, current evidence demonstrates the bottom-up trophic cascades initiated by herbivore-induced changes in plant traits (Dickson & Whitham, 1996; Kagata et al., 2005; Rodriguez-Saona et al., 2005; Nakamura et al., 2006; Kaplan et al., 2007).

Because most herbivorous insects are more or less specialized for using particular tissues of a plant, an increase in the heterogeneity of food and habitat resources within a plant can offer wider niches to herbivorous insects. The resource quality of host plants for herbivorous insects is highly variable both within and among host plants. Within-plant resource heterogeneity can have large effects on the preference and performance of insect herbivores, and it therefore alters their distribution and abundance (Orians & Jones, 2001; Roslin et al., 2006). Changes caused by herbivores and ecosystem engineers in small parts of a plant can greatly increase the overall heterogeneity in food and habitat resources in a plant. Increased biomass and improved plant quality due to compensatory regrowth may increase the spatial variation of resource availability to insect herbivores, because the development of vigorous shoots in response to herbivory does not occur evenly throughout the plant. The creation of new habitats by ecosystem engineers may also enhance the within-plant heterogeneity of food and habitat resources by increasing the spatial complexity of plants (Marquis & Lill, 2007). This is because young and vigorous plant tissues available to insect ecosystem engineers are spatially limited. In addition, increased numbers of prey species and enhanced prey abundance resulting from the increase in within-plant heterogeneity may influence species richness and abundance of predators and result in bottom-up trophic cascades. The positive feedback loop that results in increased species richness will create new species interactions, providing new niches available to other community members. Current evidence suggests that herbivore-induced changes in plant traits increase the range of resources available to new species, resulting in an increase in species richness (Martinsen et al., 2000; González-Megías & Gómez, 2003; Lill & Marquis, 2003; Nakamura et al., 2006).

There is a growing appreciation that trait-mediated indirect effects are a key factor in structuring ecological communities in various systems (Werner & Peacor, 2003;

Callaway et al., 2003; Schmitz et al., 2003; Ohgushi, 2005; van Veen et al., 2005a; Prasad & Snyder, 2006; Ohgushi et al., 2007). In terrestrial systems, there is a major difference in the ways in which plants and herbivores respond to being fed upon: induced plant responses are common outcomes of non-lethal herbivory on plants, but herbivores lack induced responses following predation (Ohgushi, 2005). Hence, arthropod communities on terrestrial plants are more likely to be organized by trait-mediated indirect effects, compared to communities in other ecological systems in which non-lethal effects of consumers are not prevalent.

Finally, it should be noted that studies of indirect interaction webs will offer a better understanding of the maintenance and creation of biodiversity of terrestrial arthropods and plants, both of which are the groups that provide the majority of biodiversity on the Earth. Biodiversity consists both of the number of species and the interactions among species (Thompson, 1996; Price, 2002), and the long-term maintenance of biodiversity requires conserving both species and interaction diversity (Gilbert, 1980; Vázquez & Simberloff, 2003; Ebenman & Jonsson, 2005). However, conservation research has primarily focused on species diversity, and it has largely ignored the importance of interaction diversity in ecological communities. It is critical that we gain a clearer understanding of how all kinds of species interactions organize ecological communities in order to develop strategies to conserve biodiversity. Indirect effects, facilitation, and habitat modification are likely to play an important role in promoting community stability and resistance and ecosystem functioning (Bonsall & Hassell, 1997; McCann et al., 1998; Cardinale et al., 2002; Neutel et al., 2002; van Veen et al., 2005b; Bascompte et al., 2006). Indirect interaction webs include more of these interactions that structure plant-centered arthropod communities than food webs. Therefore, the indirect interaction web approach will offer important insights into how interaction networks structure ecological communities, and this knowledge will aid efforts to conserve interaction biodiversity in nature.

### Acknowledgements

I am grateful to Stig Larrson, Barbara Ekbom, and Christer Björkman for the invitation to speak at SIP13. I thank Tim Craig and Peter Price for reviewing an earlier version of the manuscript. This research was partly supported by the Ministry of Education, Culture, Sports, Science and Technology Grant-in-Aid for Scientific Research (A-15207003) to Takayuki Ohgushi and the Global COE Program A06 to Kyoto University.

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