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Eco-evolutionary dynamics of plant–herbivore communities: incorporating plant phenotypic plasticity

Takayuki Ohgushi

The interplay between evolution and ecological communities is critical for the integration of different levels of biological organization. Recent work has begun to unveil the importance of plant phenotypic plasticity and plant–herbivore (co)evolution to link plant evolution and associated insect communities. Specifically, herbivore-induced plant traits (i.e., plastic phenotypes) have significant effects on the structure and diversity of herbivore communities, which can in turn promote the evolution of not only the focal plant but also insect community members. Here, I will provide a conceptual framework on the eco-evolutionary dynamics of plant–herbivore communities to understand how biological organizations are integrated in plant–insect interactions. Research on eco-evolutionary dynamics of plant–herbivore communities will undoubtedly enrich understanding of a wide range of plant–insect interactions.

Address

Center for Ecological Research, Kyoto University, Otsu, Japan

Corresponding author: Ohgushi, Takayuki
(ohgushi@ecology.kyoto-u.ac.jp)**Current Opinion in Insect Science** 2016, **14**:40–45This review comes from a themed issue on **Ecology/Parasites/Parasitoids/Biological control**Edited by **Sergio Rasmann** and **Kailen Mooney**<http://dx.doi.org/10.1016/j.cois.2016.01.006>

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Introduction

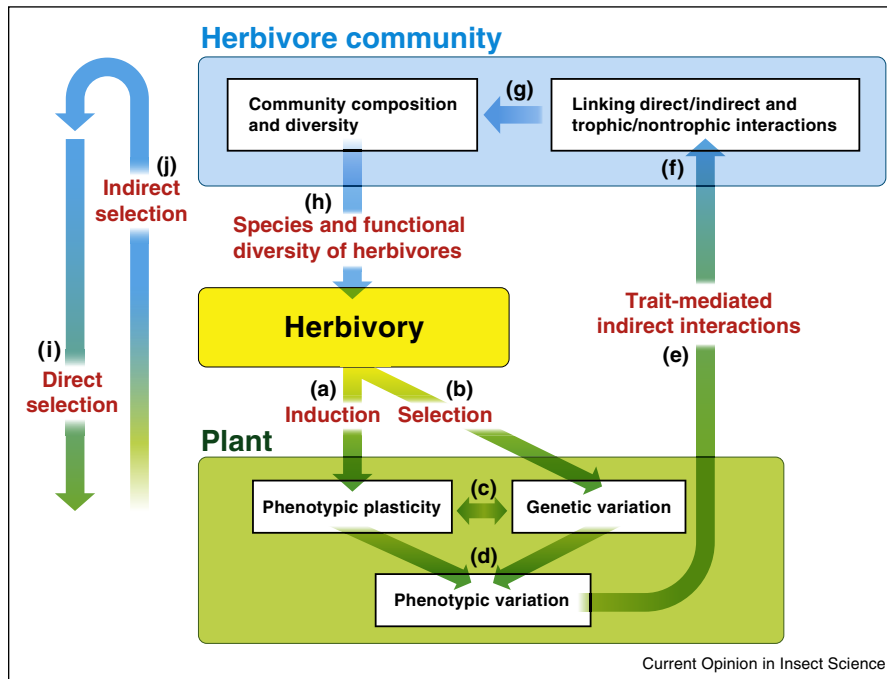
Since there are multiple scales of biological organization from genes to ecosystems, ecologists have long recognized the importance of integrating across scales. Eco-evolutionary dynamics, the interplay of evolution and ecological processes, is critical for understanding the evolution of biological diversity, community structure, and ecosystem functions [1,2]. In this context, recent studies on plant–insect interactions have highlighted that genetic diversity in plant populations can be a driver of associated insect communities [3,4], based on the idea that plant genotypes produce phenotypic variation affecting the preference and performance of multiple coexisting insect herbivores. However, the phenotypic variation

in plants is also generated by ubiquitous changes in phenotypes induced by herbivory (i.e., phenotypic plasticity) [5]. Although it is increasing evidence that plant genetic variation can shape insect communities, how this interacts with phenotypic plasticity is poorly understood [6,7,8,9]. Although it is widely accepted that how the phenotypic and genetic variation among individuals influences population and community dynamics is critical for understanding the interplay of ecology and evolution [10–12], current eco-evolutionary dynamics research generally lacks explicit consideration of phenotypic plasticity as a source of ample phenotypic variation. To date, there are no studies documenting the consequences of phenotypic plasticity in the eco-evolutionary dynamics, except for one in a predator–prey system [13]. Phenotypic plasticity is the property of a genotype that produces different phenotypes in response to different environments, and phenotypic variation plays an important role in creating the conditions to facilitate the process of adaptive evolution [14]. Here, I highlight the importance of herbivore-induced plant phenotypes for understanding the eco-evolutionary dynamics of plant–herbivore communities. A body of theoretical and empirical work on herbivore-induced plant phenotypes has mainly explored plant anti-herbivore defenses, with secondary metabolites involved in resistance [5] and regrowth as a mechanism of tolerance [15]. Also, there is an increasing appreciation of indirect defense; plants induce volatiles or other means (e.g., extrafloral nectaries or food bodies) when attacked by herbivores to attract natural enemies of insect herbivores [16]. Thus, I will primarily focus on the eco-evolutionary dynamics in plant–herbivore interactions based on our current understanding of inducible plant defensive traits.

Conceptual framework of eco-evolutionary dynamics of plant–herbivore communities

Plant phenotypes have significant bottom-up impacts on associated arthropod communities [17,18]. Thus, plant–insect interactions offer an ideal system to test whether induced plant phenotypes link plant evolution and insect communities. Here, I outline a conceptual framework of eco-evolutionary dynamics (feedbacks) in plant-based insect communities (Figure 1). There are two sources of the phenotypic variation in plants: genetic variation and phenotypic plasticity, both of which can be influenced by herbivory. Herbivory imposes selection on defensive genotypes and it also induces plastic trait changes. For example, rabbit grazing exerts selection on herbivore-induced tolerance traits, such as compensatory regrowth and photosynthetic rates in red fescue [19]. As induced

Figure 1



Conceptual framework of eco-evolutionary dynamics of plant-herbivore communities. Herbivory causes phenotypic plasticity through induction (a) and genetic variation through selection (b). As induced phenotypic plasticity has a genetic base, trait evolution may affect the likelihood and intensity of its phenotypic plasticity as a trait. On the other hand, phenotypic plasticity in turn affects the mode of adaptive evolution (c). Both are important sources of phenotypic variation in plants (d). Increased phenotypic variation enhances trait-mediated indirect interactions among herbivore community members by affecting their preference and performance (e), thereby linking direct/indirect and trophic/nontrophic interactions in the herbivore community (f), and altering community composition and diversity of herbivores (g). As for a feedback, community composition and diversity of herbivores can increase or decrease herbivory. Herbivore species identity and functional diversity influence the intensity of herbivory differently, with enhancement by synergism or reduction by antagonism among herbivores (h). There are two pathways — direct and indirect — of selection of insect communities on plant trait evolution. Direct selection will occur when herbivore community properties, such as species or functional diversity, exert selection on plant traits (i). By contrast, indirect selection will occur when herbivore communities induce plant phenotypes, these induced phenotypes feed back to directly exert selection on herbivore traits, and these changes in turn lead to further selection on plant traits (j).

plant phenotypes have a genetic basis [20–22], trait evolution may affect the likelihood and intensity of phenotypic plasticity as a trait. On the other hand, phenotypic plasticity in turn affects the mode of adaptive evolution [14,23,24]. Increased phenotypic variation through phenotypic plasticity enhances trait-mediated indirect interactions among herbivore community members [25,26] by affecting their preference and performance, and thus links direct/indirect and trophic/nontrophic interactions [25–28]. This can alter community composition and species diversity of herbivores [29].

As for a feedback, composition and diversity of herbivore communities can increase or decrease herbivory, depending on species identity and synergism/antagonism of inducers. This is because species and functional diversity of inducers increase or decrease abundances of subsequent herbivores via herbivore-induced plant changes, resulting in different intensity of overall herbivory [25,27]. Species characteristics (e.g., foundation, keystone, and dominant

species) and function (e.g., feeding modes and specialization) of inducers can influence the intensity of herbivory differently. These changes in herbivore community determine not only the strength of selection on plant traits, but also the expression of induced phenotypes. Note that there are two pathways — direct and indirect — of selection by insect communities on plant traits. Direct selection will occur when herbivore community properties, such as species or functional diversity, exert selection on plant traits. By contrast, indirect selection will occur when herbivore communities induce plant phenotypes, these induced phenotypes feed back to directly exert selection on herbivore traits, and these changes in turn lead to further selection on plant traits.

From herbivore-induced plant phenotypes to insect communities

Plant induced responses to herbivory, which increase phenotypic variation, offer a mechanistic basis for trait-mediated indirect interactions among associated

herbivores affecting communities [25,26,30,31,32*]. There is an increasing appreciation of how insect herbivores indirectly affect herbivore communities through induced plant phenotypes, showing effects of induced phenotypes on abundance of individual herbivore species. Yet we know little about such effects on herbivore species diversity and community composition.

Plants use secondary metabolites for defense and many of them are inducible by herbivory. Induced metabolites affect insect communities by changing resistance or susceptibility to individual herbivores. We expect less herbivore abundance on more defended plants with induced metabolites, and there are several supporting studies [33–35], depending on feeding specialization [36–38]. For example, early-season insect herbivory on white oak saplings increased foliar tannin and decreased nitrogen content, which resulted in decreased herbivore abundance [39]. However, induced resistance does not always negatively influence insect abundance, as when white cabbages with induced glucosinolates were colonized preferentially by specialist herbivores [38]. Induced defenses also shape herbivore diversity and community composition. Genetically modified tobacco without induced resistance received colonization of two new generalist herbivores [35]. Also, species diversity of herbivorous insects on milkweed plants was significantly affected by initial herbivore damage that alters plant quality by increasing defensive chemicals [34]. It should be noted that the strength and direction of herbivore-induced phenotype effects on the higher trophic levels can be altered by plant genotypes. In a milkweed-herbivorous insect–ant system [40,41], plant genotypes differ in their induced defense in response to feeding damage by monarch caterpillars, with some having induced susceptibility to aphids and thus having more ants that collect honeydew, and others having induced resistance to aphids and thus having fewer ants. I am not aware of field studies documenting that herbivore-induced volatiles as a mean of the plant indirect defense determine herbivore diversity or community composition under natural conditions.

Plants have the ability to regrow when damaged by herbivores. Despite the ubiquity of such plant tolerance, little attention has been paid to its community consequences [15]. Induced regrowth affects insect communities in two ways: improvement of nutrition and habitat diversification. First, induced regrowth produces rapidly growing tissues that provide a highly nutritional resource [42], which in turn increases abundance [43–45] and diversity [43,46,47], and changes herbivore community composition [43,47]. For example, willow regrowth following damage by stem-boring swift moth caterpillars influences insect communities [29]. Here, boring damage induced the growth of lateral shoots with leaves having higher nitrogen and water content and, as a result, the moths indirectly increased the diversity and abundance of herbivores and predators.

Herbivore-induced regrowth also occurs in herbaceous plants. Shoot damage of common reed by a stem-boring moth altered herbivore community composition via shoot regrowth [46], and aphid colonization on tall goldenrods enhanced shoot regrowth in late season, which altered herbivore and predator communities [45]. Herbivore-induced regrowth can also cause increased complexity of plant architecture, thereby creating more diverse habitats that allow more species to coexist. For example, the modification of tree branches by larval feeding of a long-horn beetle increased abundance and diversity of the community of secondary users [48], with accounting for 95% increase in abundance and 82% increase in diversity. This positive effect was due to increased egg deposition by secondary users, suggesting that a main effect from induced morphology is increased structural diversity.

In conclusion, induced regrowth with improved nutritional quality or complex structure can increase species diversity and abundance of insect herbivores. On the other hand, induced secondary metabolites are expected to decrease diversity and abundance of generalist herbivores, and increase diversity and abundance of specialist herbivores, due to the latter's adaptation to plant secondary metabolites [49,50]. I predict that induced regrowth may have larger and more widespread community-level effects than induced chemical defenses. This is because induced regrowth can change multiple plant traits including physical structure, growth pattern, quality in terms of nutrition and defensive chemicals, biomass, and phenology, whereas induced chemicals influence plant quality alone, which is supported by a recent meta-analysis [51].

Feedback from herbivore community to trait evolution in the focal plant and associated herbivores

Since selection on traits of organisms often reflects the actions of many community members, the selective regimes caused by multiple interacting species cannot be understood by selection resulting from pairwise interactions [52,53**]. To date, a few studies have revealed diffuse selection on plant resistance through interactions with multiple herbivores [54–57], and recent field experiments have illustrated the rapid evolution of plant defenses under selection by multiple herbivores (i.e., direct selection of herbivore communities on plant traits in Figure 1(i)) [58,59]. However, most cases have focused on the selection exerted by multiple herbivores as a whole, but not on how species or functional diversity and community composition of herbivores impose selection on plant traits highlighted in Figure 1. Therefore, no studies have demonstrated evolution of plants driven by these properties of plant-associated herbivore communities. Note that community properties promote induced plant phenotypes, which impose selection on plant-use traits of herbivores, and such traits may affect plant defenses via

changes in herbivory intensity (i.e., indirect selection of herbivore communities on plant traits in [Figure 1\(j\)](#)).

I am unaware of such studies except for our work, demonstrating herbivore community composition promoting trait evolution of a leaf beetle, a dominant herbivore in the willow-based insect community [60,61*,62**]. This leaf beetle exhibits large among-population variation in preference for host leaf-age. We also detected significant additive genetic variance for the preference for new versus old leaves. The preference was largely dependent on new leaf production in regrowth plants, which is responsible for the geographic variation in plant populations. In addition, a common garden experiment showed that such variation of regrowth no longer existed among plant populations, suggesting that the geographic variation in regrowth intensity was not due to plant genetic variation. We found that local community composition and species diversity of herbivores determined the intensity of willow regrowth, which in turn promoted evolution of the feeding preference in the beetle, from exclusive preference for new leaves in plants with induced regrowth to non-preference in plants without induced regrowth. Therefore, the herbivore community properties shape the selective regime for the beetle evolution mediated by induced leaf regrowth. This in turn leads to the question: does the feeding preference feed back to affect insect communities? Experiments manipulating the composition of beetle feeding types showed that dominance of beetles with strong new leaf preference led to lower subsequent abundance of the beetle larvae, but increased abundance of aphids. Aphid-attending ants increased with aphid abundance, which decreased herbivore diversity due to ants' removal or predation. By contrast, dominance of the non-preference type has the reverse pattern, with decreasing aphids thereby increasing herbivore species diversity. Therefore, this study strongly supports the idea outlined in [Figure 1](#) by illustrating the importance of herbivore-induced plant phenotypes (i.e., insect community-specific plant regrowth) as a driving force for selection on herbivores. Since the feeding evolution of herbivores commonly occurs in a plant-based community, eco-evolutionary feedback loop in short-lived herbivores through the phenotypic plasticity of long-lived plants may be widespread in nature.

Our studies suggest that the evolutionary changes in feeding preference lead to an eco-evolutionary interplay by altering the diversity and composition of the associated herbivore communities, which may subsequently impose different selective regimes on plant defense (i.e., indirect selection of herbivore communities on plant traits in [Figure 1\(j\)](#)).

Conclusions and future directions

We are recognizing how induced plant phenotypes determine structure and diversity of herbivore communities,

which in turn promotes trait evolution of plants and/or associated insect herbivores. Research on plant–insect interactions may offer the most promising prospects stimulating the eco-evolutionary dynamics research by incorporating induced plant phenotypes for following reasons. First, herbivore-induced phenotypic plasticity in plants is very common and widespread in nature, and is an essential source of plant phenotypic variation [5,25]. Second, induced plant phenotypes can strongly influence composition and biodiversity of the plant-based herbivore community [27], as well as plant genotypes. Third, plants usually support a wide range of herbivorous insects with different guilds, feeding specializations, and functions, which induce plant phenotypes differently, as when some herbivores disproportionately enhance an opportunity to impose selection on insects and plants than others. Such knowledge is very informative when we consider which plant trait evolution form diversity and community composition, or which traits evolve and how they do so in response to diversity and composition of associated herbivore community.

There are several critical points to further develop the eco-evolutionary perspectives in plant–insect communities. (1) Since community and ecosystem consequences of plant genetic diversity have recently been well documented, understanding the importance of induced phenotypes relative to the genetic diversity effect, and their interactive effects on community structure and trait evolution are essential [11,13**,41]. Specifically, we should recognize the importance of combined effects of phenotypic plasticity and genetic diversity on community dynamics of associated insects. Also, the distinct difference in community-level effects of induced phenotypic plasticity and genotypic diversity is that the former travels in space via induced volatiles and allelopathy, and, as a result, transmit to neighbor plants [50]. In this context, we need field experiments in which genetic diversity and induced phenotypic diversity are manipulated independently. I predict that the induced phenotypic diversity may be more important in perennial plants with longer lifetime than annual plants, because longer generation time decreases the chance of trait evolution. (2) As the overall selection pressure imposed by multiple herbivores may be non-additive, it is unlikely to be a sum of selection pressures by individual herbivore species. Thus, we should focus on species and functional diversity, and community composition of herbivores, to understand selective regimes on not only plant resistance but also insect host-use traits via induced plant phenotypes. This approach will provide profound insights into how species and functional diversity of herbivore communities promote the evolution of the focal plant and associated insect community members. (3) We should appreciate the indirect selection from the herbivore community to plant evolution via evolution of host-use traits of herbivores in response to plant phenotypic plasticity caused by

herbivore community composition, because the indirect selection via other community members has been largely ignored in research on the eco-evolutionary dynamics in a multi-species context. (4) Since the structure of plant-associated insect communities varies across different spatial scales, we need to understand how the geographic structure of plant-based communities shapes the interplay of ecological and evolutionary dynamics in insect-plant interactions [53^{••}].

It is generally accepted that phenotypic plasticity is widespread in nature and can affect all levels of ecological organization [63]. However, the community consequences of phenotypic plasticity remain largely unknown. An exciting new avenue for future research is to understand how phenotypic plasticity plays an important role in eco-evolutionary feedbacks in a wide variety of plant-insect systems. Research on eco-evolutionary dynamics of plant-herbivore communities will undoubtedly enrich understanding of a wide aspect of plant-insect interactions in multiple biological organizations.

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