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Response of Native Insect Communities to Invasive Plants

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enemy release, exotic plant, metapopulation, natural enemy, parasitoid, pollinator, population dynamics

Abstract

Invasive plants can disrupt a range of trophic interactions in native communities. As a novel resource they can affect the performance of native insect herbivores and their natural enemies such as parasitoids and predators, and this can lead to host shifts of these herbivores and natural enemies. Through the release of volatile compounds, and by changing the chemical complexity of the habitat, invasive plants can also affect the behavior of native insects such as herbivores, parasitoids, and pollinators. Studies that compare insects on related native and invasive plants in invaded habitats show that the abundance of insect herbivores is often lower on invasive plants, but that damage levels are similar. The impact of invasive plants on the population dynamics of resident insect species has been rarely examined, but invasive plants can influence the spatial and temporal dynamics of native insect (meta)populations and communities, ultimately leading to changes at the landscape level.

INTRODUCTION

The introduction and establishment of invasive plants into new habitats in which they have not coevolved with the native biota are identified as a major threat to biodiversity and ecosystem structure and function (97, 145). Invasive plants can affect native communities by competing with and excluding other plants, and also by disrupting a wide range of trophic interactions that are associated with them. The success of invasive plant species in their new range, in turn, also depends on the interactions with native plants and herbivores (99). Hence, predicting the interactions between invasive plants and native food webs and communities and their consequences for ecosystem functioning is one of the greatest contemporary challenges in ecology (15). As primary producers, plants fuel most terrestrial food webs, and as a new resource, invasive plants can affect native insect herbivores and their natural enemies directly. However, invasive plants can also indirectly alter the abundance or performance of native insects on native plants, via their effects on the quality, abundance, or diversity of native plants or on the structure of their habitat. Interactions between invasive plants and native insects have long been studied in ecology (41). However, particularly during the past decade, interest in this topic has risen, in line with the rapidly increasing number of plants that invade new habitats and concerns about the ecological and economic costs of invasions worldwide.

In this review we examine the direct and indirect effects of invasive plants on native insect communities. Although the consequences of these effects to the functioning of invaded ecosystems represents an exciting and fertile area of research (133), this subject is beyond the scope of our review. The review is divided into two sections. In the first section, we provide an overview of the effects of invasive plants on the performance and behavior of insect herbivores and their natural enemies (predators and parasitoids). Invasive plants may contain novel secondary compounds that are toxic to native herbivores and their natural enemies, or may produce odors that are attractive to native insects and consequently interfere with interactions of these native insects with native plants. These effects can lead to altered performance but also to adaptive responses in native insects. In the second section, we discuss effects of invasive plants on native insect populations and communities. We discuss how insect communities in native and invaded plant communities differ and review the literature to examine whether insect herbivory and herbivore and predator communities differ on invasive and native congeneric plant species. We also describe how invasive plants can affect pollinator communities. Subsequently, we describe how invasive plants can affect insect communities at larger temporal and spatial scales. Finally, we suggest a number of future directions for research on the impact of invasive plants on native insects.

DEFINING DIFFERENT TYPES OF PLANT INVASIONS

A common interpretation of an invasive plant is a species of intercontinental origin that is introduced into a nonnative habitat. A distinction is often made between plant species that spread broadly within their newly occupied regions (invasive species) and those that do not (naturalized species). Many plant species also expand their ranges within continents due to indirect anthropogenic processes such as land use changes and climate warming. In this review we do not distinguish between these types of invaders and range expanders but consider all plant species that enter a new habitat as “invasive” plants. However, we realize that for plant species involved in intra-continental range expansion, the identity and genetic composition of the insect community (e.g., herbivores, predators, pollinators) encountered by the plants in their new habitat are not as different as for plant species that have traversed a substantial barrier (e.g., oceans for transcontinental invaders).

EFFECTS OF INVASIVE PLANTS ON THE PERFORMANCE AND BEHAVIOR OF NATIVE INSECTS

Performance of Herbivores, Parasitoids, and Predators on Invasive Plants

In nature, insect herbivores must discriminate between suitable and unsuitable plants for their own nutrition and/or that of their progeny. The recognition of suitable oviposition and feeding cues in native plant–insect food webs has been studied over many years and a wealth of data has been generated (4, 19). Moreover, it has long been established that the nutritional quality of plant tissues, as mediated by concentrations of primary and secondary plant metabolites, as well as by morphological characteristics, may significantly affect the feeding behavior and development of native herbivores (4).

Based on a growing number of studies, there is no clear consensus regarding how well native herbivores perform on invasive plant species. In some studies, invasive plants are highly suitable as hosts and insects achieve high potential fitness (61, 71), whereas in other studies the invasive plants are toxic to native herbivores (38, 88, 135). In some instances, survival of insect herbivores is low on invasive plants (38, 61, 88, 107), whereas in others survival is high but development time is extended and/or adult body mass is reduced (18, 148).

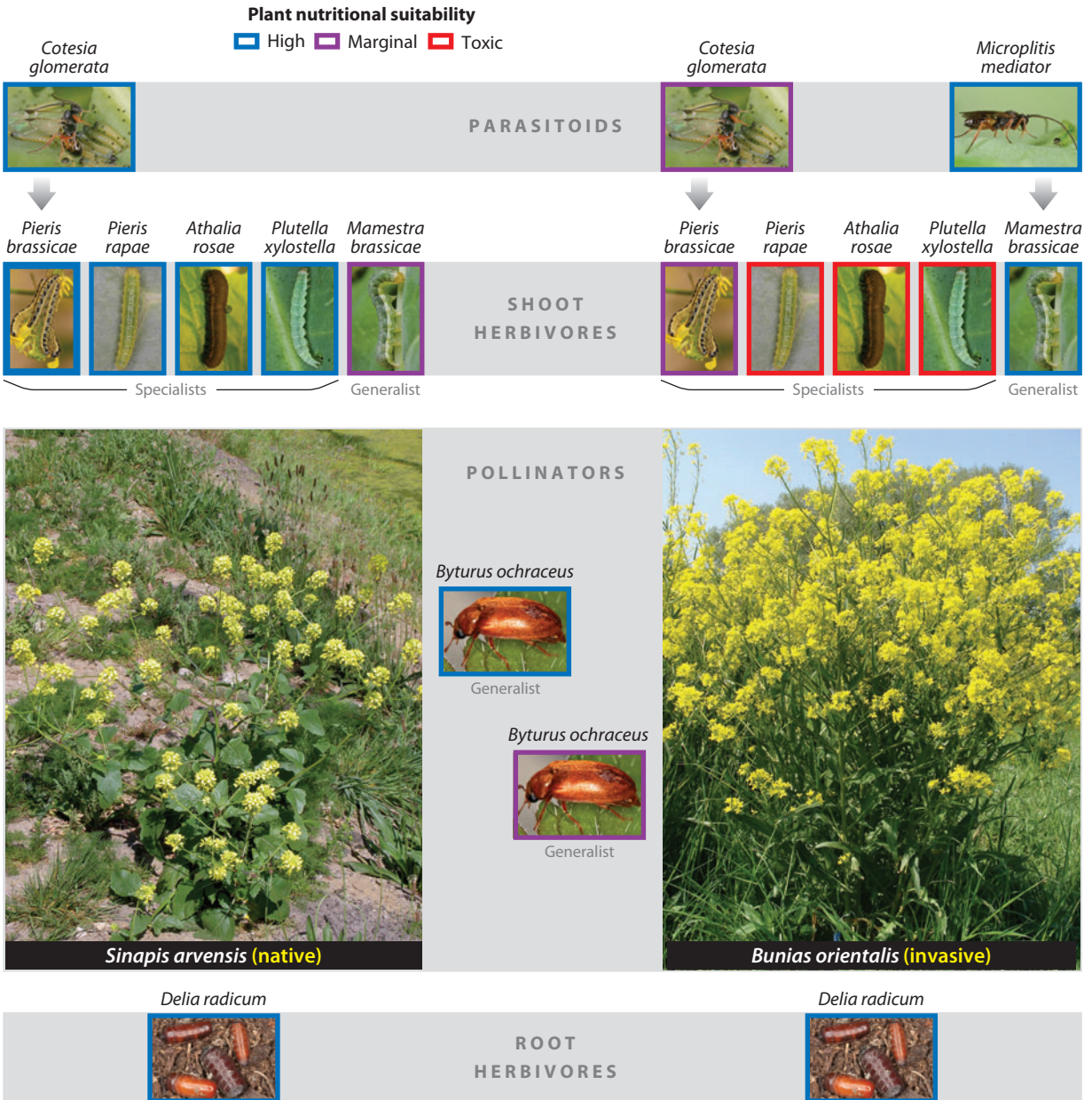
The ability of native herbivores to exploit invasive plants also often differs between specialists and generalists. For example, the generalists *Mamestra brassicae* and *Spodoptera littoralis* developed well on the invasive crucifer *Bunias orientalis*, whereas several crucifer specialists either perished or had very low fitness on this plant species (47, 61, 107). In a study in the United States, several generalist herbivores grew faster and survived better on native black cherry than on 16 invasive tree or forb species (135). In contrast, generalist and specialist chrysomelid beetles exhibited similar life-history responses when feeding on invasive plants in the order Zingiberales (50).

Host plants can also affect the development of predators and parasitoids via their impact on the nutritional quality of their herbivore prey or host (109). In particular, primary and secondary metabolites—nutrients and allelochemicals, respectively—ingested by the herbivore host can directly or indirectly affect the feeding or oviposition preference of predators and parasitoids (109). Moreover, the development of parasitoids, in particular those that develop inside of their hosts (i.e., endoparasitoids), is often closely associated with host-related attributes such as size, growth rate, and diet (60). In spite of the fact that parasitoids and predators have long been recognized as critical to the structure and function of ecological communities (117), little research has been conducted on the effects of invasive plants on the development of higher trophic levels (62, 63). The few studies that are available suggest that the effects of invasive plants on parasitoid development are highly trait dependent. For instance, the development of the pupal parasitoid *Pteromalus puparum* is less affected by plant origin (native *Brassica nigra* versus invasive *Bunias orientalis*) than the development of the larval endoparasitoid *Cotesia glomerata* on their shared host *Pieris brassicae* (47) (**Figure 1**). This difference could be because the suitability of a host for an endoparasitoid is determined largely by host growth and survival after parasitism, whereas host suitability for a pupal parasitoid is determined by a host's previous nutritional history (60). Although the pupae of surviving *P. brassicae* were smaller on the invasive plant than on the native plant, the size of the pupal parasitoid was unaffected because the female wasps adjusted their clutch size in accordance with host size, laying fewer eggs on pupae from *P. brassicae* reared on the invasive host plant (47). Invasive plants may also differ in nutritional quality in different parts of their invasive ranges. The development of a generalist herbivore and its specialized endoparasitoid, for example, differs considerably on two populations of the invasive weed *B. orientalis* (64).

Allelochemical:
a chemical produced by a living organism that exerts a negative physiological effect on individuals of another species when released into the environment

Host Shifts of Native Insects to Invasive Plants

Invasive plants may possess certain unique chemical or morphological traits that are absent in native food plants. Consequently, they may not be recognized as suitable oviposition sites by local populations of herbivore species. However, invasive plants can also be important substitutes as food plants. Several studies have reported shifts from native host plants to invasive plants by native generalist and specialist herbivores. For instance, larvae of the southern cabbageworm, *Pontia protodice*, which is native to the southeastern United States, feed on a range of well-established



invasive cruciferous plants (Brassicaceae) that originate from Eurasia (89). Similarly, *Pieris oleracea*, which occurs over much of the United States and southern Canada, oviposits and feeds on several invasive crucifers including *Brassica rapa*, *Sisymbrium altissimum*, and *Raphanus raphanistrum* (21). In California, 34% of the native specialist butterfly species feed on invasive plants (53). Several species of butterflies in California are even dependent on invasive plants for their survival in urban environments because the native food plants were eliminated (127). The specialist herbivore, the Baltimore checkerspot butterfly, *Euphydryas phaeton*, has recently expanded its dietary breadth from feeding exclusively on turtlehead, *Chelone glabra*, to also feeding on the introduced weed, ribwort plantain, *Plantago lanceolata*, in eastern North America (10). However, herbivores performed less well on the invasive plant, in terms of reduced pupal mass and relative growth rate on plantain, suggesting that there may be a trade-off between plant quality and accessibility. Generalist herbivores, such as banded woollybear caterpillars, *Pyrrharctia isabella*, also feed on a wide variety of abundant invasive plants in North America, including ribwort plantain, *P. lanceolata*, and dandelion, *Taraxacum officinale* (34).

The ability of native herbivores to switch to invasive plants has recently been debated (13, 25, 73). Certainly many plants escape from their coevolved specialist herbivores when they establish in new habitats, but this is dependent to a large extent on the allelochemistry of the invasive plant relative to native plants. As some of the abovementioned studies show, invasive plants that establish in habitats where there are related native plants may also be attacked by native specialists (and may even become preferred host plants for them) provided they produce allelochemicals that are also found in related native plants. Thus phylogeny, based on physiological equivalence, can often explain why particular invasive plants are nutritionally suitable for (and possibly even preferred by) native insects (1, 65). For instance, native pierid butterflies in North America develop very successfully on Eurasian crucifers that are closely related with native plants (21), but they do poorly on crucifers, such as garlic mustard (*Alliaria petiolata*), that produce novel allelochemicals (88). Insects feeding on native thistles, such as *Cirsium altissimum*, also readily switch to the closely related invasive *C. vulgare*, effectively suppressing the ability of the latter species to establish and spread (134).

Natural enemies may or may not associate with their herbivore prey or hosts on novel, invasive plants. The ability of predators and parasitoids to adapt to novel plants and to enjoy realized fitness on them is dependent on the completion of several hierarchical steps involving the location of suitable habitat, plant location, prey/host acceptance, and palatability (144). Although these processes have been well studied with insect herbivores and their natural enemies in native communities, little is known about shifts from native to invasive plants involving several trophic levels. A recent study showed that whereas the herbivore *Pieris brassicae* preferred the native crucifer *Sinapis arvensis* to the invasive *Bunias orientalis*, its parasitoid *Cotesia glomerata* did not discriminate between the

Figure 1

Example of the complexity of interactions involving native and invasive plants, native herbivores, their natural enemies, and pollinators. The picture shows several specialist herbivores and a generalist insect herbivore, two endoparasitoids, and a pollinator associated with the native wild brassicaceous plant *Sinapis arvensis* and the invasive related species *Bunias orientalis* in western Europe. Both plants produce aromatic glucosinolates (= sinalbin). For *Pieris brassicae* and its endoparasitoid *Cotesia glomerata*, *Pieris rapae*, *Athalia rosae*, and *Plutella xylostella*, survival and fitness on the native plant is high, whereas few *P. brassicae* and none of the other species survive to pupation on the invader. The root specialist *Delia radicum* survives well on both plants. By contrast, the generalist herbivore *Mamestra brassicae* performs better on the invasive plant than on the native plant; its solitary endoparasitoid, *Microplitis mediator*, also develops successfully on *B. orientalis*. The pollinating beetle *Byturus ochraceus* prefers the native over the invasive species when they grow together. Figure based on studies by Müller (107), Harvey et al. (61), Hochkirch et al. (74), and Fortuna et al. (48). Photo credits: *B. ochraceus*, Hedwig Storch; *A. rosae*, Caroline Müller; all other insect photos courtesy of Tibor Bukovinszky, Hans Smid, and Bugs-in-the-Picture (<http://www.bugsinthepicture.com/>).

Associational effect:

influence of a plant on another plant in close proximity that increases or decreases the likelihood of detection by or vulnerability to herbivores on that plant

Allelopathy:

a biological phenomenon by which an organism releases chemicals into the environment that influence the growth or survival of another organism; usually refers to plants or microbes

Symbiont:

an organism that has a close interaction with an organism of another species that is beneficial to both species

two host plants (48) (**Figure 1**). Moreover, the buckeye butterfly, *Junonia coenia*, and several of its predators are now intimately associated with the invasive plant *P. lanceolata* in western North America (129). However, the timescales over which shifts occur, and how the degree of success of these shifts changes up the food chain, have been little studied. These shifts are dependent on the natural enemy recognizing suitable visual and chemical cues emitted by the invasive plant that provide reliable information about the presence of prey or hosts (142). If the cues are recognized, then the natural enemy will potentially exploit its prey or host on the novel plant. At this point the interaction switches from a behavioral process to a more intimate physiological one (60).

Evolutionary Responses of Native Insects to Invasive Plants

Because invasive plants can act as resources for native insect herbivores, and insects can rapidly adapt to these new resources, invasive plants can drive selection in native insects resulting in morphological changes (17, 132). Invasive plants may function as “evolutionary traps” if herbivores are attracted to or readily accept an invasive plant species as a food source but have lower fitness on the invasive species than on native host species (88, 126). Such traps can exert selection against the use of invasive plants by native insects (46). Selection on native insects can also occur when invasive plant species are beneficial to native herbivore species, for example, because they provide high-quality resources. In such cases, the herbivore may adapt to the novel host, and host shifts from native insects onto invasive plants can occur (17, 132). This can ultimately lead to morphological or physiological adaptations of the insects. The soapberry bug, *Jadera haematoloma*, is a good example of an insect species that exhibits genetic adaptation to invasive plants. In Florida, the native host plant *Cardiospermum corindum* has fruits with a much larger radius than the invasive host plant *Koeleria elegans* and *J. haematoloma* has much shorter mouthparts on invasive hosts than on native hosts. In contrast, in the southcentral United States, fruits of invasive plants are larger than those of the native host plant *Serjania brachycarpa*, and here mouthparts of beetle “races” on the invasive plant are larger (16, 17). Several studies have shown that levels of herbivory on invasive plants increase with time since introduction of the invasive species (66, 128, 151).

Effects of Invasive Plants on Associational Effects

A different mechanism by which invasive plants can affect native insects is via associational effects on native plants. Several studies have shown that the presence of neighboring plants can affect host plant selection of insects associated with native plants. Invasive plants can attract insect herbivores, resulting in increased attack on native plants by these herbivores (124), or can deter insects from native plants, resulting in reduced levels of attack (67). Moreover, invasive plants compete with native plants for nutrients and light and thereby affect the growth and chemistry of native plants, which can lead to altered performance of insects on those native plants (90, 124). Invasive plants can also affect plant defenses of native plants via emissions of plant volatiles. Plant-emitted volatiles can induce defense responses in neighboring plants of different species (85), but whether volatiles of invasive plants can cause such effects in native co-occurring plants remains to be tested. Invasive plants can also affect insect-plant interactions on native plants via the release of chemicals by the invasive plant into the soil (allelopathy; 6, 72). A large number of chemicals released by plant roots affect the growth as well as the chemistry of other plants (7), and this can potentially affect the performance of insects on these other plants. For example, *Centaurea maculosa* exudes catechin, which is toxic to native plant species in North America where it is invasive (6). A number of studies have shown that invasive plants in their new range interact with native soil-borne pathogens and symbionts (3, 98). Via their effects on soil biota, invasive plants can indirectly affect current or

future native plants that grow in the vicinity of the invasive plant. Because soil pathogens, symbionts, or even nonpathogenic bacteria can induce belowground and aboveground plant defense responses (9), via their effects on soil biota, invasive plants can influence the growth and nutritional quality of native plants and hence the aboveground plant-insect interactions that occur on these plants.

Effects of Invasive Plants on Native Insects via Apparent Competition

When native and invasive plant species share one or more of the same herbivore species, a negative indirect interaction known as apparent competition may occur between them (75, 149). In apparent competition, the presence or increase in abundance of one plant species (e.g., the invasive species) causes the shared herbivores to have an increased negative effect on the biomass, population growth rate, abundance, or local persistence of the other species (e.g., the native species). Explanations for this herbivore-mediated interaction between native and invasive species include (a) differential attack rates, often involving higher preference or performance on the native plant species; (b) differential tolerance to herbivory, allowing the buildup of herbivore populations that have a more detrimental effect on the less tolerant plant species; (c) one species provides a refuge for shared herbivores, resulting in greater herbivore impact on the other species; and (d) one species provides a necessary resource at a particular time or stage of the herbivore's life cycle, allowing for increased herbivore pressure on the other plant species (149).

Apparent competition, in which shared herbivores are more detrimental to the invasive plant species, could represent an important mechanism promoting biotic resistance to invasion (110, 134). Alternatively, invasion success may be promoted in cases in which the native plant species suffer disproportionately from herbivory. In fact, this latter result is reported in the vast majority of cases (31, 120). For example, the invasive plant *Medicago polymorpha* promotes increased herbivory by the alfalfa weevil *Hypera brunneipennis* on native *Lotus wrangelianus* (90). If Holt & Lawton's view (75) is correct, invasive and native plant species may interact more strongly through apparent competition than through interference or exploitative competition.

Effects of Invasive Plants on Native Insect Behavior

A number of studies have examined the impact of invasive plants on feeding or oviposition preferences of native herbivore insects. The results of these studies are mixed. Several studies show that insect herbivores prefer native plants over invasive ones (12, 148); however, others report that native insect herbivores prefer invasive plants (45, 113). Host plant preferences can be a plastic trait, influenced by the presence or relative abundance of invasive plants. In an oviposition preference study in which several populations of the butterfly *Pieris oleracea* were tested, butterflies from areas where garlic mustard, *Alliaria petiolata*, was present strongly preferred to oviposit on this invasive species over the native host, *Cardamine diphylla*. In comparison, females from uninvaded areas showed no preference for one plant species or the other (88). Interestingly, offspring of the females from the invaded area also performed better on the invasive plant than did offspring of females originating from uninvaded areas (88). Although largely overlooked, invasive plants can also affect the behavior of native insects via their impact on native insect performance. The butterfly *Lycæides melissa*, for example, performs poorly on the invasive plant *Medicago sativa*, resulting in smaller adult females. The reduction in body size, in turn, negatively affects mating success because males are less likely to mate with smaller females (46).

Invasive plants affect the behavior of native insects through the release of volatile compounds (odors) and by changing the chemical complexity of the invaded habitat. Plants release volatile

Apparent competition:

a negative interaction between two species in the same trophic level that is mediated through the action of shared natural enemies

compounds that are used by arthropods within communities and constitute infochemical webs and networks (35). Volatile blends change in quantitative and qualitative properties in response to biotic and abiotic forces, such as pathogen or herbivore damage and/or microclimate and soil quality. Concentrations of volatiles often increase markedly after herbivore damage, and these odors are attractive to natural enemies of herbivores, including parasitoids and predators (35). The distance over which volatiles are bioactive is poorly known but probably depends to some extent on the local structure and species diversity of the plant community as well as on microclimate (11). The empirical literature is replete with studies that have examined the effects of chemical complexity of the plant community on the biology and ecology of herbivores and their natural enemies (e.g., 55, 101). However, thus far, the potential community-related effects of volatiles of invasive plants have rarely been explored.

If the plant species complex within a habitat is generally stable over time, insects may evolve responses that enable them to target suitable resource-containing patches or sites and to avoid patches that do not contain suitable resources. However, once an invasive plant enters a habitat, it can interfere with the chemical properties of the native plant community and thereby affect the behavior of native insects in the habitat (29, 48, 63, 68). Odor plumes emitted from a novel plant may confuse native insects by masking the odors of native plants, particularly if the invader has a volatile profile that is similar to that of native species in the community. Assuming that an invasive plant might be initially less susceptible to herbivore attack than its native neighbors, we might predict that host preference behavior of herbivores and parasitoids might change on the basis of qualitative and quantitative differences in the chemical induction of the invader compared with the more heavily damaged native plants. Moreover, natural enemies often must choose between plants containing hosts/prey and plants infested with only nonhost/nonprey species. Parasitoids respond to complex volatile blends (142), and the establishment of an invasive plant in a native community may disrupt this process, with negative effects on the ability of the parasitoid female to locate hosts.

EFFECTS OF INVASIVE PLANTS ON NATIVE INSECT POPULATIONS AND COMMUNITIES

Native Insect Communities in Invaded and Noninvaded Plant Communities

Invasive plants can greatly affect native insect communities by competing with or displacing native host plants (106, 146). Hence, invasions by exotic plants can negatively influence the diversity or abundance of native insects. Stands of the invasive alien vine *Vincetoxicum rossicum* in old fields in Canada, for example, support much lower numbers of arthropods than native plants do (43). Similarly, in Chile, arthropod abundance and species richness are lower in invaded forests than in native forests (54). Other studies have shown that the removal of invasive plants leads to an increase in native insect abundance and diversity (58) or even to a full recovery of the native insect community (52).

Comparison of Insect Communities on Invasive Plants and Native Congeners

A rapidly increasing number of studies have evaluated the impact of invasive plants on native insects by comparing insect damage on invasive and co-occurring native congener or conspecific plant species. These studies typically have compared these damage levels to examine the enemy release hypothesis (41, 86). This hypothesis explains the successful establishment and spread of exotic species by release from specialized herbivores and other natural enemies in the invaded area. Several meta-analyses that compared the level of damage (caused by native insects but also

by vertebrate herbivores) on native and exotic plants concluded that invasive plant species experience less herbivore damage from native herbivores than co-occurring native species do (92, 112). However, other meta-analyses concluded that overall herbivore damage does not differ between invasive plants and native congeners (23, 25, 66). Clearly, the effects greatly depend on the invasive and native plant species studied, but also on the multitrophic composition of the native community within which the native and invasive plants co-occur.

Many case studies have compared insect damage on one or two invasive and congeneric native plant or tree species, but studies in which a larger number of native and exotic plant pairs are compared may be particularly interesting, as these comparisons enable a broader interpretation of the results. In a study in which leaf damage by insects for 39 invasive and 30 native plant species was examined, invasive plants experienced significantly less leaf damage than native plants did (15). Similar results were reported in other large studies (56, 111). In contrast, in a common garden experiment with 15 plant pairs of invasive and native old-field species, the invasive plants experienced similar or even higher levels of herbivore damage compared with native species (2). However, over the following season, when overall levels of herbivore damage were higher, invasive plant species experienced significantly lower damage than native plant species did (3). A comparison of nine congeneric pairs of naturally growing native and invasive grassland species in Europe showed that invasive and native species incurred similar damage levels (39). These studies clearly exemplify the variation in results reported in comparisons of damage on native and exotic plants. From these studies, we can only conclude that there is no empirical support for the hypothesis that release from insect herbivory in the introduced area is a general pattern for invasive plants. It is also plausible that the degree of invasiveness may be explained by the extent to which the invasive species is released from herbivory. A number of studies have examined herbivore damage on invasive and noninvasive exotic plants or have compared plants that differ in invasiveness. Indeed several studies show that highly invasive plants generally experience less damage than noninvasive plants (14, 79), but others report that this is not the case (93, 111).

Important questions remaining include, (a) Are similar levels of damage on invasive and native plants caused by different densities of herbivores? and (b) Is the damage caused by the same or by different species of insect herbivores (92)? Hence, it is important to examine whether densities of insects and the composition of the insects on native and invasive plants differ. We conducted a literature search and identified 16 studies that provide information on insect herbivore composition, abundance, or richness on a range of invasive and related native plant and tree species. These studies are shown in **Supplemental Table 1** (follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). In roughly half of these studies, the abundance of insect herbivores was lower on invasive plants than on native plants, in two studies herbivore densities were higher, and the other studies report that herbivore densities were similar on invasive and native plants. Similar results were reported for herbivore richness. Overall, the results suggest that invasive plants may indeed support fewer insects than native plants do. Several studies measured the composition of the herbivore communities on native and invasive plants. In some studies the composition did not differ (24, 49), whereas some experiments also show that particular native herbivore species occur only on the invasive plant species (94), or that herbivore communities distinctly differ between native and invasive plants (59). As insect damage patterns do not differ between native and invasive plants, the results suggest that native herbivorous insects may have a greater per capita impact on invasive plants than on native plants. Whether this is true awaits further research.

Although the overall pattern indicates that herbivore densities may be lower on invasive plants, there are large differences between comparisons of individual native and invasive plants. For example, in a comprehensive study with 45 woody species, of which 30 were invasive, native species



Supplemental Material

overall had greater insect biomass than invasive species but had similar richness (154). However, a closer inspection of the data shows that in roughly one-third of the significant native-invasive comparisons, herbivore biomass was higher on the invasive species (154). A study of lepidopteran caterpillar assemblages reported greater herbivore diversity on two invasive plants (*Piper aduncum* and *P. umbellatum*) in a rainforest in Papua New Guinea (108). The species richness of caterpillars was higher on both invasive plant species than on the native *P. macropiper*, and even higher than the median richness on 69 other native plant species that were hosts to the caterpillars. Remarkably, the composition of caterpillar species on *P. aduncum*, which is an aggressive invader, was indistinguishable from that on the native hosts (108). These results emphasize that certain species of invasive plants can support native insect communities comparable to those found on native plants. In contrast, a comparative study of 511 native and 214 invasive plant genera in North America showed that native plants supported threefold more lepidopteran species than invasive plants did (136).

We identified five studies that have compared the abundance and richness of predators and parasitoids on native and exotic congeneric plants (**Supplemental Table 1**). Most of these studies report that carnivore abundance and richness do not differ between native and exotic plants (e.g., 42, 118). However, one study, conducted in Texas, reported that predators were more abundant and higher in richness on invasive Chinese tallow trees (*Triadica sebifera*) than on the native tree species *Acer saccharinum*, *Platanus occidentalis*, and *Liquidambar styraciflua* (59).

Effects of Invasive Plants on Native Pollinators and Plant-Pollinator Interactions

Pollinators are important for the reproduction of most plant species and they are keystone species in many ecosystems (87). Similar to their interactions with herbivores, invasive plants can potentially affect the interactions between native plants and their pollinators, but they can also have direct effects on the native community of pollinators. Invasive plants can negatively affect pollination of native plants by competing for pollinators or by increasing heterospecific pollen deposition (36, 96). However, invasive plants can also positively affect pollination of native plants, for example, due to attraction of pollinators that subsequently also pollinate native plants (80). Many studies have examined the effects of a wide range of invasive plants on flower visitation of native co-occurring plants. These studies confirm that invasive plants can have both positive and negative effects on flower visitation of native co-occurring plants. However, two recent meta-analyses concluded that invasive plants, on average, have a negative effect on the visitation rates of pollinators and reproductive success of native coflowering plants (104, 105). It appears from these analyses that invasive plants may lure pollinators away from native plants because the invasive plants possess characteristics that make them more attractive competitors for pollinators (105). Many invasive plants have more colorful or bigger flowers or produce more flowers per plant than native species do (22, 119). Several studies have compared flower visitation on native and invasive congener species. These studies also generally show that visitation rates are higher on invasive congeners (116, 141), although some studies reported no differences or the opposite effect (74, 84). Visitation rates by pollinators were higher on flowers of the native crucifer *Simaps arvensis*, for example, than on the invasive crucifer *Bunias orientalis*, and in this case the invasive plant does not distract visitors from native plants (74) (**Figure 1**). The impact of invasive plants on native plant-pollinator interactions also depends on the local density of the invasive plant (83). In habitats in Ireland, for example, flower visitation of the native plant *Digitalis purpurea* is negatively correlated with the local density of the invasive shrub *Rhododendron ponticum* (36).

Far fewer studies have examined the direct effects of invasive plants on native pollinator communities. Invasive plants have been viewed as one of the major threats to native pollinator communities (87). However, many studies report that invasive plants are readily visited by generalized native

pollinators (22, 96, 102). These studies suggest that at least for generalist pollinators, the effects of plant invasions may be limited. Interestingly, an analysis of a large database of invasive plants in the Czech Republic shows that the diversity of pollinator species associated with an invasive plant increases with its residence time in the invaded area. This finding indicates that invasive plants, over time, become even more integrated into native pollinator communities (119). The amount of overlap in the pollinator visitation of native and invasive plants greatly depends on the similarity in floral traits between the invasive and native plants (51). A cross-European study of plant-pollinator networks that were invaded (or not) by invasive plants showed that, on average, invasive species were visited by about half of all pollinator species present, which was much higher than visitation rates for native plants, and that total visitation rates for native and invasive species combined were higher in the invaded networks (143). Moreover, although the invasive species readily integrated into these pollinator networks, they did not affect the structure of the network (143). In contrast, studies that have examined entire pollinator communities in invaded and uninvaded areas or in areas where the invasive plant has been removed typically show that the diversity and abundance of pollinators are higher in the uninvaded areas or increase after the invasive plants have been removed (58, 138). Areas invaded by goldenrod *Solidago canadensis* in Poland, for example, have far fewer and a much lower diversity of wild pollinators even though goldenrods produce large amounts of nectar and pollen (106). Researchers have argued that invasive plants indirectly affect pollinators via their negative impact on the diversity of the native floral community (131). The abovementioned effects of invasive plants on pollinators are driven largely by behavioral decisions of pollinators. Whether invasive plants also directly affect pollinators via nutritional effects is less well known. Nectar or pollen of invasive plants may be toxic to insects (e.g., *R. ponticum*; 131) but can also be a high-quality resource available in high quantities. As many pollinators can move over large distances and may frequently visit both invaded and noninvaded plant communities, disentangling the impact of invasive plants on pollinator community dynamics remains a challenge.

Effects of Invasive Plants on the Population Dynamics of Insects

Whereas studies on the spatial and temporal population dynamics of invasive plant species are numerous (e.g., 100, 115), studies regarding the impact that invasive plant species have on the population dynamics of resident arthropod species are surprisingly rare. Here, we consider how invasive plants and their consequent change to landscape structure affect the spatial and temporal dynamics of insects in invaded habitats. Our approach is to scale up in system complexity from metapopulations to metacommunities, then to landscapes, and finally to invasions at continent-wide scales.

Metapopulation Dynamics

One of the obvious consequences of the successful invasion of an invasive plant species is that the structure of the landscape can be drastically altered (e.g., 37, 40). For insects that do not utilize the invasive plant, the availability of suitable host plants for herbivores or pollinators may decrease or become increasingly more fragmented over time. Changes in the geography, abundance, and quality of plant patches, and whether those patches are composed of native or invasive species, can greatly affect herbivore population persistence, interactions with natural enemies, and community diversity and composition (20, 57, 67). For both metapopulation and metacommunity theory, connectivity among habitat patches is often a key parameter associated with these population or community characters (20, 57, 77). High connectivity among patches can promote synchronous dynamics among patches and reduce population persistence, reduced connectivity can lead to greater asynchrony among patches and promote increased persistence at the metapopulation level, and too little connectivity may cause each patch to function as independent unit (20, 57, 77).

Metapopulation: a group of spatially separated populations of the same species which interact at some level

Connectivity: a measure for the frequency of movement of individuals between patches

Metacommunity: a set of interacting communities which are linked by the dispersal of multiple, potentially interacting species

Matrix: unsuitable intervening habitat that surrounds patches of suitable habitat

Although there is a plethora of theory linking connectivity to temporal population dynamics (and population persistence), experimental studies in nature, at appropriate spatial scales, are quite scarce (but see, e.g., 28, 29, 33, 70).

Connectivity is dependent not only on the linear distance among patches or the abundance and dispersion of patches (i.e., structural connectivity) but also on the behavioral responses of organisms to the various elements that compose a landscape (i.e., functional connectivity; 5, 28). The composition of the matrix is quite important in determining patch occupancy or abundance (44, 147). Because invasive plants are often associated with disturbed matrix habitats and fragment edges (97, 104), these plant species have the potential to be very important to the connectivity of arthropod species among fragmented native plant populations.

Despite the fact that invasive plant species have the potential to greatly affect metapopulation structure, there are surprisingly few studies on this subject. However, Cronin and colleagues (e.g., 28, 29, 67, 68, 121, 122) provide the most extensive body of work on the effects of invasive plant species on the dispersal and spatial population dynamics of animal populations. The study system involves a planthopper (*Prokelisia crocea*) and its facultative specialist egg parasitoid (*Anagrus columbi*), which are distributed among patches of a native grass (prairie cordgrass, *Spartina pectinata*) in tall-grass prairie fragments. In North Dakota, the matrix within which prairie cordgrass patches are embedded consists of either mudflat, a mixture of native grasses, or the invasive grass smooth brome, *Bromus inermis* (67). Smooth brome invasion is associated with significantly reduced growth rates and increased extinction rates of cordgrass patches and a significantly decreased rate of establishment of new cordgrass patches (37). These results suggest that the spatial population dynamics of the planthopper and parasitoid are unlikely to be in equilibrium. For ongoing plant invasions, population or community dynamics are likely to be transient or nonequilibrium. This is an important issue because predictions from most metapopulation/metacommunity theories are based on the assumption that the system is in equilibrium.

Dispersal of the planthopper and parasitoid among cordgrass patches was strongly influenced by matrix composition. Connectivity for both species was substantially higher when the matrix was smooth brome than when it was mudflat (29, 67). For the planthopper, the underlying mechanism involved a greater propensity to cross a cordgrass–smooth brome boundary than a cordgrass–mudflat boundary, and more tortuous movement pathways in smooth brome than in mudflat (68, 122). The latter behavior can be more effective for discovering a new patch if patches are clumped (153), as is the case in this study system. The mechanisms promoting higher connectivity for the parasitoid when the matrix is smooth brome are not well understood. Based on mark-recapture experiments, there is no evidence of a difference in response to the matrix type at the patch boundary or in the diffusion rate in different matrix habitats (121). This finding illustrates that interacting species may respond very differently to variation in landscape structure (30).

Invasive smooth brome affected not only planthopper and parasitoid dispersal, but also their spatial and temporal population dynamics. Both species exhibit mainland-island metapopulation dynamics—the numerous small cordgrass patches are prone to extinction but the few larger patches exhibit long-term persistence (27). Local patch extinction rates were substantially higher when the matrix was smooth brome than when it was mudflat or a mixture of native grasses. To understand the consequences of the invasion of smooth brome on the temporal dynamics of the metapopulation, researchers replicated large-scale cordgrass networks and embedded them in a matrix composed of either smooth brome or mudflat (28, 29). At the metapopulation scale, planthoppers and parasitoids in the mudflat networks had high and relatively stable densities over time, and persistence was 100%. In contrast, populations in the smooth brome networks had densities that averaged 50% lower and were spatially 50–90% more variable, and the metapopulation went extinct in 4–5 generations (28).

An interesting contrast to the above planthopper-parasitoid system is a study on flea beetles (*Aphthona nigricutis*) as potential biological control agents of invasive leafy spurge *Euphorbia esula* (81). The authors found that female beetles are more likely to immigrate to leafy spurge patches embedded in a grass matrix than a shrub matrix. Similarly, colonization of invasive purple loosestrife (*Lythrum salicaria*) by leaf beetles (*Galerucella* spp.) is greater when the surrounding habitat is meadow rather than forest (32). The studies with leafy spurge, purple loosestrife, and prairie cordgrass support the notion that the matrix matters greatly to connectivity (147). Moreover, these studies with invasive weeds suggest that release strategies involving biocontrol agents should consider the structure of the landscape into which releases are planned. Unfortunately, at this point, we do not know whether the efficacy of leafy spurge control by *Aphthona* beetles or loosestrife control by *Galerucella* spp. is affected by landscape structure.

Metacommunity Dynamics

Whereas metapopulation theory emphasizes extinction-colonization dynamics of one or two species (e.g., predator-prey, host-parasite), metacommunity dynamics extends these ideas to ensembles of local communities of organisms linked together by migration (91). Metacommunity studies emphasize the interdependence of local, within-patch interactions (within species, between species, between species and the environment) and regional processes (i.e., dispersal). Patterns of diversity (α , i.e., the local diversity within a habitat; β , i.e., the between-habitat diversity; and γ , i.e., the diversity at a larger geographical scale), and the mechanisms of local community assembly (neutrality, species sorting, colonization-competition trade-offs, source-sink dynamics), are the typical empirical pursuits (95).

Metacommunity studies are typically observational (69%), are conducted in aquatic habitats, and involve passively dispersed organisms, and experimental studies are most often very small in scale (e.g., laboratory mesocosms, small pools) and focus on microbes (95). Moreover, studies in nature invariably focus on relatively simplified systems involving permanent patches with distinct boundaries and relatively homogeneous matrix habitats. In contrast, invasive plants and the herbivore assemblages associated with these invaded habitats represent much more dynamic and complex systems. In addition, wide-ranging invasive plants, in which separate communities vary in the coverage of the invasive species, represent a natural experiment ideal for testing how landscape change affects local community assembly.

Although invasive and native plant species and their assemblage of herbivores are ideally suited for metacommunity-level studies, such studies are almost nonexistent. A Web of Knowledge search (September 18, 2013) involving the keywords “metacommunity” and “invas*” yielded only 48 hits. Of those studies, only one empirical study has considered invasive plant species in a metacommunity context—a study on the plant-bee pollinator community associated with the sub-Andean zone of central Chile (140). Fourteen of the 77 plant species in this pollinator network were invasive species. Using a stochastic metacommunity model, the authors concluded that the removal of the invasive plant species decreased the likelihood of persistence of native plants and bees and caused significant changes to community structure. This study provides only a glimpse of the fruitful avenues of research that can be pursued with invasive plant species.

Landscape Dynamics

The field of landscape ecology eschews the simple dichotomous view of the world as envisioned by metapopulation and metacommunity theory (i.e., discrete habitat patches embedded in an inhospitable matrix). Instead, real landscapes are composed of patches of varying quality that may have indistinct boundaries, their geometry and occurrence may be transient, and the matrix

may be quite heterogeneous (150). One aspect of landscape ecology focuses on how changes in the arrangement or composition of the various landscape elements (i.e., landscape context) influence within-patch dynamics, boundary or edge responses, spillover among adjacent elements, functional connectivity, and distribution of organisms (139). Successful plant invaders are an obvious instigator of landscape change and are consequently an ideal group of species to advance this relatively young field of study.

Invasive plant species change landscape context for resident arthropod species by altering the regional coverage or abundance of native plant species, the quality of host plants (by representing a lesser or higher quality host, or by indirectly affecting native host plant quality), or the permeability of landscape elements to the movement of these species. Research by landscape ecologists often focuses on the relative contributions of landscape context (usually considered across a range of spatial scales), regional processes (e.g., structural connectivity), and local processes (e.g., habitat quality) to population densities or community structure. Most studies of landscape context effects have focused on how arthropod abundance or community structure in native or agricultural habitats (generally a nonnative plant) is affected by the proportional abundance of the other habitat in increasingly larger areas surrounding the focal habitat (e.g., 82, 137). Not surprisingly, few studies have actually examined how changes in landscape context, as brought about by an invasive plant species, affect arthropod populations and community structure. One exception is a study that focused on the invasion of *Impatiens glandulifera* into riparian habitats and its effect on pollinator communities, mainly bumble bees (8). Visitation rates to plants by bumble bees were higher in areas with intensive agriculture than in areas with more natural land cover. However, in sites invaded by *I. glandulifera*, this landscape-context effect was masked by bumble bees being highly attracted to flowers of the invasive plant. Other studies have shown that an increase in abundance of native plants within an agricultural landscape can increase pollinator services and biocontrol of pests in crop systems (e.g., 123, 137). Promoting native plants within the agricultural landscape is thought to be key to increasing ecosystem services brought about by pollinators, predators, and parasitoids (78).

Studies of landscape-context effects are often dependent on relatively high-resolution aerial or satellite images to construct maps of the distribution of different landscape elements. Crop and noncrop, forested and nonforested, or urbanized and seminatural habitats are relatively easy to discern, even with low-resolution imagery. However, discerning individual plant species, or distinguishing native from invasive plant species, can be challenging. In recent years, technological advances in the field of remote sensing and increased availability of imagery have greatly expanded our capabilities to develop not only maps of the distribution of individual plant species, but also maps that provide levels of herbivory or plant nutritional or developmental conditions (69, 130, 152). With these new tools, we expect a bright future with regard to understanding the landscape-level effects of invasive plant species on insect communities. However, the development of distribution maps is only a precursor to meeting our greatest needs in this field—the collection of quantitative data on insect movement and appropriate-scale experimental manipulations of the landscape.

Continent-Wide Invasions

The most notable plant invasions have occurred, or are occurring, at continent-wide scales, spreading relatively quickly across continents along a long latitudinal or longitudinal gradient [e.g., giant cane (*Arundo donax*), water hyacinth (*Eichhornia crassipes*), Japanese knotweed (*Polygonum cuspidatum*), common prickly pear (*Opuntia stricta*)]. At these spatial scales, biogeographic phenomena and evolutionary processes will affect invasive plant–insect interactions. In particular, geographic or clinal variation (including latitudinal or longitudinal gradients) in biotic or abiotic conditions, and local adaptation by native and invasive plants, potentially can be important drivers

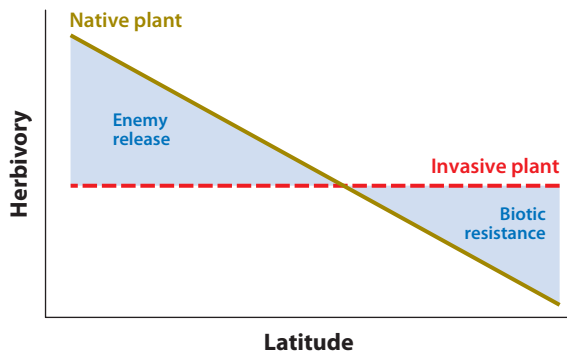


Figure 2

Hypothetical relationship between latitude and herbivory for a native and an invasive plant species. The native plant species exhibits a latitudinal gradient in herbivory but the invasive species does not. At lower latitudes, herbivory is much greater on the native plant species than on the invasive plant species, supporting the enemy release hypothesis (88). At higher latitudes, the greater herbivory of the invasive species relative to native species would suggest a case for biotic resistance (112, 136). On the basis of this relationship, invasion success is predicted to be greater at lower latitudes.

of community structure. Here, we illustrate an emergent property that arises from large-scale studies of invasive plant–insect interactions by focusing on one topic: latitudinal gradients in herbivory and plant defenses of native and invasive plant species.

During the past decades various theories have suggested that the strength of species interactions should be greater at lower latitudes than at higher latitudes (for review, see 125). For plant–herbivore interactions, rates of herbivory are generally higher in the tropics than in temperate regions (26, 114). Coley & Aide (26) argue that this herbivory gradient is consistent with the idea that more favorable climatic conditions or longer-lived plant parts in the tropics allow herbivores to feed longer and more consistently throughout the year. Increased consumer pressure at low latitudes should select for increased plant defense or reduced palatability at low latitudes than at high latitudes (103). For invasive plant species, latitudinal variation in interaction strength between native plants and their herbivores can generate latitudinal variation in invader success.

Invasive species that invade at a continent-wide scale may not arrive preadapted to their novel environment and, unlike co-occurring native plant species, may not initially exhibit a latitudinal gradient in plant defense or palatability to herbivores. During this establishment period, significant differences may occur between native and invasive species with regard to latitudinal variation in defense and palatability to shared herbivores (**Figure 2**). Large-scale geographic (clinal) variation in plant defense or palatability to herbivores may explain why invasion success is larger in low than in high latitudes and may help explain the equivocal support for the enemy release hypothesis (23). It seems logical that clines in plant–herbivore traits are likely to differ between native and invasive species, particularly soon after invasion, and that these differences can generate important large-scale variability in enemy escape and apparent competition, two factors that may be key to the successful colonization or spread of invasive species. However, in light of the rapidity with which exotic species can form clines and evolve (76), these differences are likely to be transient. At present, we are only beginning to explore the interplay of biogeography and evolution in the interactions between native and invasive plants and their shared herbivores. The affect that these larger-scale phenomena have on higher trophic levels or community structure is almost entirely unexplored (62).

CONCLUSIONS AND FUTURE DIRECTIONS

One important conclusion from our review is that invasive plants can have severe negative impacts on native insects and that they can interfere with the interactions between insects and native plants. However, our review also emphasizes that invasive plants can be beneficial to native insects and that they can act as important resources for these insects. This latter aspect often is overlooked or ignored.

A pervasive theme in many of the topics discussed here is that the underlying theory is well developed and often well supported or evaluated by empirical data using native species, but scarcely broached using invasive species. Clearly, because invasive plants are important and often dominant components of most ecological communities, an understanding of their impact on native plants and associated food webs is essential. We argue that studies of invasive plants have the potential to contribute substantially to the advancement of ecology and evolutionary biology. Advantages of invasive plant species derive from the potential naïveté of the invaded community; the seminatural experiment carried out during the invasion process, often at large spatial scales; and the often dramatic alterations to communities that are created by a successful plant invasion. For example, invasive plant species represent a novel resource in a community and are ideal for examining questions about cascading effects of host shifts. Host shifts of herbivores may promote host shifts at higher trophic levels, a possibility that has not been well studied. For many invasive plant species the history of introductions is well known; hence invasive plants offer a unique opportunity to determine timescales of host shifts and responses by higher trophic levels.

As native insects are potentially naïve to allelochemicals and volatiles of invasive plants, indirect effects between native and invasive plants (e.g., associational effects mediated through soil biota, apparent competition) may be quite strong and have impacts that reverberate throughout the food web. The study of the indirect effects of invasive plants on native insects via their effects on native plants is still wide open and awaits further research.

So far, most studies that have addressed the enemy release hypothesis have focused on levels of herbivory and have paid little attention to the density of herbivores. Investigating per capita damage to native and invasive plants should yield clearer data on the impact that herbivores have on each plant species and help researchers better resolve the mechanisms driving differences or similarities in herbivory among plant species. Our review shows that herbivore densities are lower on invasive plants than on native plants but that predator densities do not differ. Future studies should examine whether herbivores indeed experience more top-down control on invasive plants than on native plants (42).

Metapopulation and metacommunity theories implicitly assume that populations or communities are in equilibrium, but invaded communities are often distinctly transient or nonequilibrium. Invasive plant species and their associated insects are potentially great systems for testing ideas about transient or nonequilibrium dynamics. It is especially important that these studies span multiple insect generations. Currently, there are almost no studies on the effects of invasive plants on the temporal population dynamics of insect metapopulations or metacommunities. In the field of landscape ecology, areas invaded to different degrees by an invasive plant species allow for seminatural experiments to test for the effects of landscape change on population or community parameters. The scale of these types of invasions often exceeds, by orders of magnitude, the generally small scale of metacommunity and landscape experiments.

Most ecologists define the term enemies as organisms at the third trophic level or even higher; however, in invasion ecology the term thus far has been used almost exclusively to describe plant enemies, such as herbivores and pathogens. Given the potentially important role played by predators and parasitoids in mediating community-level processes and dynamics, future studies need

to explore the effects of invasive plants on carnivorous insects and arthropods as well as take a tritrophic or food web-level approach to studying invasive species (62).

SUMMARY POINTS

1. Invasive plants generate novel interactions with native insects. They can be toxic to native insects or serve as highly suitable hosts. This can ultimately lead to host plant shifts.
2. Through associational effects, invasive plants can influence interactions between insects and native plants.
3. Through their effects on the development and nutritional quality of the herbivores, invasive plants can affect the development and fitness of native parasitoids and predators.
4. Changes in the chemical and structural complexity in native habitats caused by invasive plants can alter the foraging behavior and dispersal abilities of native insects.
5. Herbivore densities are lower on invasive plants than on native plants, but there is no evidence that invasive plants overall suffer from less damage inflicted by native herbivores.
6. Invasive plants often are visited more frequently by native pollinators than native plants are, and invasive plants are well integrated into native pollinator webs.
7. Because invasive plants can drastically change landscape structure, they have the potential to alter connectivity among suitable habitat patches; local and regional population dynamics; and extinction risk of native herbivores, pollinators, and their natural enemies.
8. For plant invasions occurring at continent-wide scales, clinal or geographic variation in native plant–herbivore interactions can promote variation in invasion success.

DISCLOSURE STATEMENT

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1. Invokes the term ecological fitting to describe the ability of native herbivores to exploit novel resources, such as those represented by an invasive plant.

3. First study to show that invasive plants suffer less from aboveground and belowground enemies than native congener plants do.

8. Demonstrates how a plant invasion and landscape structure can interact to affect plant-pollinator interactions.

13. Shows that in North America many invasive plants produce novel phytotoxins that are absent from native plant taxa.

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143. Reports that invasive plants in Europe are incorporated into native pollinator webs.



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