Alien plants versus alien herbivores: does it matter who is non-native in a novel trophic interaction?
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Introductions of both plants and herbivorous insects have had tremendous impacts on the world’s ecosystems. Novel herbivorous insect–plant interactions are important consequences of introductions of either plants or herbivorous insects. We contrast novel herbivorous insect–plant interactions that arise due to plant versus insect introductions with the aim of understanding whether the causes and consequences of the interaction depend on which party is non-native. The biotic context of the herbivore–plant interaction, in terms of mutualists, predators, and competitors can limit the prevalence of that interaction and varies between native and introduced ranges. Introduced plants can have a large, direct impact on their environment, whereas the impact of introduced herbivorous insects is often mediated through the plants that they consume.

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Numerous plants and herbivorous insects have invaded biogeographic regions in which they were previously absent. The ecological consequences of both plant and insect invasions can be tremendous for invaded communities. In recent years, substantial effort has been made to understand the consequences of plant introductions and the novel herbivore–plant interactions that arise from plant introductions. However, situations where novel trophic interactions form between non-native insect herbivores and native plants are also common, but have received different types of attention. As such, we perceive a bias in studies of herbivorous insect versus plant invasions. Non-native herbivorous insects receive attention when they colonize plants of economic value, and non-native plants receive attention when they invade natural communities. This bias could be overcome by considering the fundamental similarities and differences between herbivorous insect versus plant introductions and the interactions that result from them.

It is important to know whether the context of the trophic interaction (i.e. whether it is in the plant’s or insect’s native range) affects the prevalence and consequences of that interaction. For example, if the trophic interaction does not depend on the ‘nativeness’ context of the interacting organisms, then programs that screen native herbivore interactions with non-native plants may inform predictions about the potential for those herbivores to invade the native range of those plants. Here, we review recent advances in our understanding of invasions by plants and herbivorous insects with particular reference to the novel insect herbivore–plant interactions that arise. We highlight some key differences between novel interactions that form due to the introduction of non-native herbivorous insects versus the introduction of non-native plants.

The arrival and establishment of non-native plants and herbivores
Novel interactions between plants and herbivorous insects are constrained by the arrival and establishment of introduced plants or herbivores, which is not a random process. At the very beginning of an introduction, propagule pressure, the frequency of introduction of a given non-native species, is the most consistent predictor of invasion status [1,2]. However, the modes of arrival of non-native plants and herbivores vary markedly (Table 1). For example, roughly 75% of plants in the Global Invasive Species Database were introduced deliberately as agricultural, forage, and ornamental plants, whereas only 12% of invasive insects were introduced deliberately (mostly as biological control agents), whereas the rest were introduced unintentionally, often associated with introduced plant material [3]. As such, it is possible that many introduced plants may have been selected for vigor and agricultural output, whereas introduced insect herbivores have been disproportionately selected for their elusiveness.

At the establishment phase of an introduction, both non-native plants and herbivores must deal with the consequences of small population sizes, though when introductions are intentional, populations may be large from the outset. It is currently unclear whether there are
fundamental differences with how herbivores and plants deal with the consequences of small population sizes such as increased inbreeding, Allee effects and stochasticity. However, differences may be expected based on reproductive strategies of plants and insect herbivores. Specifically, plants may be able to overcome reproductive-based Allee effects by reproducing vegetatively, apomictically, or via self-fertilization. Similar reproductive strategies are present, but less common in insects.

### Table 1

<table>
<thead>
<tr>
<th>Potential differences between plant and herbivorous insect invasions.</th>
<th>Invasive plant</th>
<th>Invasive herbivorous insect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary mode of introduction</td>
<td>Intentional; escape from cultivation, forage, plantings [3,7]</td>
<td>Accidental; hitchhikers on plant material, soil, wood products [3,7]</td>
</tr>
<tr>
<td>Likelihood to find resources</td>
<td>High (but non-directed dispersal may limit ability to find adequate habitats)</td>
<td>Variable (depends on host range: generalist–specialist)</td>
</tr>
<tr>
<td>Antagonistic interactions with consumers/enemies</td>
<td>Herbivores (fitness consequences variable based on herbivore pressure and tolerance of herbivory)</td>
<td>Predators, parasitoids (fitness consequences variable based on toxicity, concealment, and presence of related species)</td>
</tr>
<tr>
<td>Mutualist interactions</td>
<td>Resource acquisition: mycorrhizae, rhizobia; reproduction: pollinators; protection from herbivores: predators and parasitoids [27]</td>
<td>Protection for resource mutualisms with ants [29]; digestive mutualisms with gut microbes [30]</td>
</tr>
<tr>
<td>Long term consequences of novel interaction at the community level</td>
<td>Direct consequences (new resource — potentially inducing host shifts at second and third trophic level) [28,30]</td>
<td>Primarily indirect consequences via host plants [24,34]</td>
</tr>
<tr>
<td>Interplay with the ‘other’ exotic type</td>
<td>Facilitation by exotic herbivores [47]; Antagonism with specialist exotic herbivores such as biological control agents</td>
<td>Facilitation due to lack of natural enemies in degraded environments [50]; facilitation when exotic plant is host [49]</td>
</tr>
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### Plant and insect herbivore traits promoting invasions

Which traits make non-native organisms successful invaders? Since early descriptions of the ‘perfect weed’ [4], considerable efforts have been made to uncover general plant traits associated with invasiveness. Recent meta-analyses, however, show contradicting results and, even though results of individual studies sometimes document clear effects of specific traits, predicting which plant species are likely to become invasive based on traits alone remains unfeasible [5]. In comparison, investigations of traits associated with insect invasiveness have typically been made by examining individual invasions, and such case studies often test single-factor hypotheses too narrow in scope to have predictive value on the general traits of successful invaders [6]. In general, attempts to anticipate plant invasiveness focus on aspects of its ecology beyond its potential interactions with native herbivores, but anticipating the potential for an herbivore invasion typically involves understanding which plants it could potentially consume [7].

For insect herbivores, traits facilitating establishment and traits promoting invasiveness do not necessarily overlap. For example, a broad host range is regarded as a trait increasing the chances of establishment in a new environment. However, some of the most destructive invasive herbivorous insects are dietary specialists (e.g. emerald ash borer, hemlock woolly adelgids) that have found the right dietary niche [8], while others (e.g. Japanese beetle, gypsy moth) are broad generalists. So, host breadth may promote establishment but be unrelated to invasiveness once established.

### Consequences of novel herbivore–plant interactions with introduced plants or herbivorous insects for the invader

Novel interactions commonly form between introduced plants and native herbivorous insects and also between introduced herbivorous insects and native plants. There is evidence that, in both of these scenarios, the novel interaction is important (Table 1).

With introduced plants, the interaction or lack of interaction with herbivores form cornerstones of theories of enemy release [9] and biotic resistance [10], which seek to predict the success of non-native plants. Enemy release suggests that introduced organisms escape top-down limiting factors, such as herbivores, in their introduced range. Review and meta-analysis suggests that enemy release contributes to the success of many invasive plants, but not others [11]. Biotic resistance suggests that biotic interactions in the native community, such as herbivory, can limit the establishment or invasiveness of introduced organisms. Again, herbivores likely play a role in mediating the biotic resistance of native communities in many cases, but effect of herbivores varies considerably between systems [12].

With introduced herbivorous insects, finding a suitable host (i.e. forming a novel interaction) is a critical step in
their establishment and invasion (Table 1). If suitable hosts are often lacking, one expectation might be that a great number of herbivore introductions fail. Currently, information on potential introductions that never established is limited, so it is difficult to assess causes of non-establishment of introduced herbivores [49]. One interesting case of ‘non-invasion’ is the introduction of herbivores along with their non-native hosts. In some of these cases, those herbivores colonize native plants and become invasive. In other cases, those herbivores never expand their host range onto local natives. For example, the cork oak twig gall, Plagiotrochus amenti Cynipidae, was introduced to North America presumably on ornamental cork oak (Quercus suber) material. It was first mentioned in North America in 1926 (as P. suberi), and, since then, it has never been observed on a host plant native to North America [13]. By contrasting these ‘non-invasions’ to situations where herbivores do expand their host range onto native plants, it may be possible to better understand herbivore traits that allow the formation of novel host interactions.

Ecological fitting as a predictor of novel herbivore–plant interactions with introduced plants or herbivorous insects

Ecological fitting has emerged as a key framework for understanding which novel interactions will form between plants and insect herbivores [8,14,15]. In its simplest form, ecological fitting attributes an interaction between a plant and herbivorous insect to a match between herbivore and plant traits — without reference to the biotic or abiotic context of that interaction. In this case, the nativeness of plant and herbivore is immaterial; however, this is an assumption that we challenge in the next section.

The concept of evolutionary naïveté is closely linked to ecological fitting. In the context of novel plant–herbivore interactions, the question is whether naïveté disproportionately benefits the novel plant or the novel herbivore [16]. There is substantial evidence that naïveté benefits plants at the detriment of their herbivores in many cases. Many exotic plant species contain toxins that native herbivores cannot cope with [17], benefiting the plant by making the new environment an ‘enemy-free space’. Because relatives tend to share similar defensive traits, phylogenetic dissimilarity between native and novel hosts is a common predictor of non-native plant escape from native herbivores [18,19,20*].

Conversely, there is also evidence that naïveté can benefit herbivores by promoting a novel interaction to the detriment of the plant [21*,22]. For example, aggregative oviposition in the invasive viburnum leaf beetle has evolved to overcome egg-crushing defenses of viburnum hosts in its native range [23]. In its introduced range, the efficiency of this ‘offensive’ behavior is increased due to reduced egg-crushing defense in novel host plants, providing a coevolutionary mismatch facilitating the herbivore’s invasion [21*]. This scenario is likely prevalent in the case of herbivores that exert strong selection on their hosts, such as herbivores that often kill their host [24]. For example, many trunk-boring herbivores such as emerald ash borer perform better on novel hosts than on native hosts, regardless whether those hosts or the herbivore were introduced [25].

Factors that affect non-native herbivore or plant establishment outside of plant–herbivore interactions

Introduced plants and insect herbivores must cope with their novel environment, new resources, new antagonists, and new mutualists. Each of these factors has the potential to alter the formation and outcome of novel herbivore–plant interactions. We suggest that, because there are key differences in how plants and insects interact with their novel environment, these factors can alter the outcome of novel herbivore–plant interactions depending on which party is introduced.

The abiotic environment can alter novel herbivorous insect–plant interactions. For example, the outcome of Manduca sexta interactions with a novel host depended on the climate in which those interactions occurred [26*]. Currently, it is unclear whether there are predictable trends in how the abiotic environment affects novel herbivore–plant interactions (e.g. whether higher temperatures tend to allow herbivores to colonize less palatable hosts or higher precipitation allows plants to better tolerate novel herbivores).

Biotic interactions can also affect the outcome of novel herbivore plant interactions. In particular, while herbivores must contend with and potentially evolve to utilize plants with novel traits, they must also cope with novel predators and pathogens. In contrast, ignoring soil communities, novel plants contend primarily with top-down trophic interactions. Competition with native flora or fauna may additionally shape the outcome of a novel herbivore–plant interaction.

One likely difference between introductions of non-native plants versus non-native herbivores is the type of mutualisms that those organisms enter (Table 1). During the introduction and establishment processes, alien plants are likely to interact with new mutualists, such as native pollinators and soil mycorrhizae, upon which their survival may depend. On the one hand, depending on specialized mutualists may be a barrier to the establishment and spread of exotic plants [27]. On the other hand, ‘diffuse’ mutualisms that can be easily re-established in the introduced range (such as associations with generalist pollinators or seed dispersers) can help establishment and promote invasiveness [28*]. Invasive insect herbivores may also depend on novel mutualists to
insure fitness (e.g. aphid-ant mutualisms), and many of these mutualisms readily establish between species that lack evolutionary history of interaction [29]. A possible exception regards internal symbionts of insect herbivores. When vertically transmitted, these mutualistic microorganisms may travel with the invader in its new range, relieving the insect from the need to form associations with the native microfauna. However, recent studies revealed that, first, herbivores are capable of adopting novel symbionts [30*], with major consequences on their invasiveness [31], and second, host-symbiont associations may not have the same pathogenicity in the native and introduced range of the invading herbivore [32].

What is the overall impact of herbivore versus plant invasions for the invaded community? The ecological and evolutionary impacts of exotic plants and herbivores on native communities are broad and have been the subject of detailed reviews [28*–33–35]. Plants can directly affect their environment in ways that herbivores cannot (Table 1). For instance, the physical presence of invasive plants can directly alter the landscape (via changes in soil structure, ground cover, light regimes for neighboring plants, and so on), with far-reaching consequences on nutrient cycles [36] and multitrophic interactions [37]. Furthermore, plants release a variety of chemical compounds in the atmosphere and the rhizosphere, principally under the form of: first, root exudates, second, herbivore-induced volatile compounds, and third, floral scents. While some of these compounds directly exert a detrimental effect on receivers (e.g. allelochemicals), most of them will blend in the ‘smellscape’ of the new habitat, with the potential of disruptingInfochemical networks existing between plants, herbivores, natural enemies, and pollinators [38]. By spreading in the new environment, plant products have the potential to reach and affect numerous native organisms not necessarily directly associated with the invader [39]. In contrast, the direct structural and chemical impact of exotic insects on native environments is probably limited to very specific interactions, for example [40]. Most of the ecological consequences of invasions by exotic herbivores occur indirectly, via effects on their host plant(s) that cascade through the food chain. Such indirect effects are comparable to the direct effects of exotic plants in terms of diversity, strength, and scale [24,34].

Non-native plants and herbivores are new resources to be exploited by native organisms. Rates of colonization and consumption of non-native plants by native herbivores, as well as visitation rates from pollinators on non-native flowers, have been thoroughly investigated and reviewed [28*], while studies on the general use of non-native herbivores by natural enemies are scarce [41,42]. Interestingly, there seem to be fundamental similarities in the rates and patterns of colonization of novel plants and herbivores by consumers in their introduced range: both non-native plants and insects are rapidly consumed by native herbivores and natural enemies, respectively, but these assemblages of new consumers typically show reduced diversity and a higher proportion of generalists compared to assemblages of consumers of native plants and herbivores [41].

The presence of a new plant resource in a native environment can have long-term evolutionary consequences at the community level, for example by affecting feeding and oviposition preferences of certain native herbivores and by changing plant-herbivore-natural enemy dynamics in native plants [37]. These effects can escalate up the food chain and affect higher trophic levels [14]. Similarly, exotic herbivores are a new resource for native natural enemies such as predators and parasitic wasps. However, most studies related to use of exotic hosts by parasitoids focus on the consequences of shared natural enemies for native herbivores, neglecting some concepts that have been explored in the context of plant invasions. For example, the notion of ‘ecological trap’, which designates a non-native plant that is favored for oviposition by native herbivores but is not suitable for the development of their offspring, has a possible parallel in the context of insect invasions: non-native herbivores readily attacked by native parasitoids, but unable to support the development of their offspring. Such ecological traps at the third trophic level remain to be explored. Another notion developed in the context of plant invasions is that non-native plants can act as enemy-free space for native herbivores, for example if natural enemies are unable to detect them on the non-native plant. A possible parallel exists with invasions by insect herbivores: a native parasitoid may escape its own competitors (other parasitoids) and enemies (hyperparasitoids) by exploiting a novel non-native host [43]. Such enemy-release at the third trophic level has only been examined for non-native natural enemies used as biological control agents thus far [44].

The interplay between non-native plants and non-native herbivores and its effects on invasion processes Most of the world’s ecosystems face invasions by numerous plants and herbivorous insects. There is increasing evidence, for example [45], that past invasions can affect future invasions (Table 1). In many cases, such as biological control, we attempt to use the invasion of a novel herbivore to limit the success of a previous plant invasion [46]. However, successful invaders can also facilitate the establishment and spread of other exotic species [47]. One example of facilitative interactions between exotic herbivores and plants is invasive forest pests in eastern North America such as the hemlock woolly adelgid and emerald ash borer. These invasive insects create canopy gaps that increase light availability and facilitate the establishment of alien plant species in the forest interior [48]. Similarly, exotic plants can facilitate the establishment of alien insects, first, simply as ‘hitchhikers’ associated with the
alien plant and its native range and following it in its introduced range [49], and second, by benefiting from the lack of natural enemies associated with habitats with poor plant diversity, as commonly observed in agroecosystems (e.g. monocultures) [50].

Conclusions

Do novel antagonistic plant–insect interactions differ whether the non-native species is the plant or the insect? We suggest that, in many cases the answer will be ‘yes’ for several reasons. From the outset, different invasion pathways for plants and herbivorous insects will skew which organisms come in contact. Once in contact, aspects of the biotic and abiotic environment can shape the outcome of novel herbivore plant interactions and likely differ between the native ranges of plant and herbivore. Furthermore, the main ecosystem-level effects of novel herbivore–plant interactions seem to be mediated by the plant, so those effects will be direct when the plant is introduced and indirect (i.e. mediated through its host) when the herbivore is introduced. Finally, invasion ecology would strongly benefit from applying some notions developed in the context of plant invasions to exotic herbivores. For examples, the concepts of ‘ecological trap’ and ‘enemy-free space’ are typically addressed with the exotic plant (or the herbivore consuming the plant) being the focal organism. The examination of such notions higher in the food chain would be fascinating to investigate.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

• of special interest
•• of outstanding interest

A study that offers a sobering view on the ability to predict invasiveness and invasibility. It advocates for large scale comparisons of invasions, but caution in the predictions made from them.
By extrapolating from native food webs, most novel interactions between European Lepidoptera and plants were predicted based on shared ancestry of those plants with native hosts.
A demonstration of an herbivore ‘offensive’ behavior that overcomes the defenses of the invasive herbivore’s novel host.
A careful set of experiments that manipulate the thermal environment of a novel herbivore-plant interaction and show that success on the novel host depends on temperature.
An insightful review that highlights the numerous ways in which invasive plants affect native insect communities.
A genotyping study that demonstrates that fungal symbionts can be exchanged between native and introduced wood-boring herbivores.


