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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

Table 1

Potential differences between plant and herbivorous insect invasions.

	Invasive plant	Invasive herbivorous insect
Primary mode of introduction	Intentional; escape from cultivation, forage, plantings [3,7]	Accidental; hitchhikers on plant material, soil, wood products [3,7]
Likelihood to find resources	High (but non-directed dispersal may limit ability to find adequate habitats)	Variable (depends on host range: generalist–specialist)
Antagonistic interactions with consumers/enemies	Herbivores (fitness consequences variable based on herbivore pressure and tolerance of herbivory)	Predators, parasitoids (fitness consequences variable based on toxicity, concealment, and presence of related species)
Mutualist interactions	Resource acquisition: mycorrhizae, rhizobia; reproduction: pollinators; protection from herbivores: predators and parasitoids [27]	Protection for resource mutualisms with ants [29]; digestive mutualisms with gut microbes [30•]
Long term consequences of novel interaction at the community level	Direct consequences (new resource — potentially inducing host shifts at second and third trophic level) [28•,39]	Primarily indirect consequences via host plants [24,34]
Interplay with the 'other' exotic type	Facilitation by exotic herbivores [47]; Antagonism with specialist exotic herbivores such as biological control agents	Facilitation due to lack of natural enemies in degraded environments [50]; facilitation when exotic plant is host [49]

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.

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 adelgid) 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