

Research



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Community ecology

An invasive herbivore structures plant competitive dynamics

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Species interactions are central to our understanding of ecological communities, but may change rapidly with the introduction of invasive species. Invasive species can alter species interactions and community dynamics directly by having larger detrimental effects on some species than others, or indirectly by changing the ways in which native species compete among themselves. We tested the direct and indirect effects of an invasive aphid herbivore on a native aphid species and two host milkweed species. The invasive aphid caused a 10-fold decrease in native aphid populations, and a 30% increase in plant mortality (direct effects). The invasive aphid also increased the strength of interspecific competition between the two native plant hosts (indirect effects). By investigating the role that indirect effects play in shaping species interactions in native communities, our study highlights an understudied component of species invasions.

1. Introduction

The destructive impacts of invasive species on native communities and ecosystems are widely recognized [1,2]. Several traits commonly associated with invasive species including strong competitive ability, rapid reproduction and generalist diets can allow them to outcompete native competitors and exert strong top-down pressure on their food sources [2–4]. For example, invasive insect herbivores have been responsible for the displacement of native competitors and the restructuring of native flora worldwide [3,4]. More generally, invasive species impact communities by negatively affecting some species more than others (direct effects), or by altering the strength or direction of interactions among native species (indirect effects). For example, invasive herbivores can alter competitive dynamics between native plant hosts by precipitating the competitive release of less-preferred hosts [3,5], or altering how host relative density structures herbivore impacts [6]. However, experimental tests of these indirect effects of invasive herbivores which manifest as changes in competitive interactions between native plant hosts are lacking [4,5].

The stability of competitive interactions, and ultimately, the coexistence of plant species, arise from the response of a focal plant to its neighbouring competitors [6,7]. Stable coexistence is promoted when individuals of each species limit their population growth by responding more negatively to conspecific than heterospecific individuals (negative frequency dependence), whereas species that respond more positively to conspecifics (positive frequency dependence) generate unstable dynamics that can lower diversity [6]. If competing plant species share herbivores which move between them and differentially impact their performance, the presence of herbivores could alter the relative strength of interspecific and intraspecific competition [8]. Furthermore, invasive herbivores are likely to alter the competitive dynamics of host plants whenever invasive herbivores generate different impacts on host plant species from native herbivores, or when they respond to the relative densities of host plant species

in different ways. Investigating the role that invasive herbivores play in structuring plant competition would broaden our understanding of the complex and pervasive impacts of invasive species on native communities.

We tested the effects of an invasive aphid herbivore, *Aphis nerii*, on its native congener, *Aphis asclepiadis*, and two closely related, co-occurring native milkweed hosts, common milkweed and butterfly milkweed. We tested the impact of the invasive herbivore on three aspects of the native community: (i) direct impacts on the native herbivore, (ii) direct impact on the performance of each native plant host, and (iii) indirect impacts on the competitive dynamics of the native plant hosts. We show that in addition to its strong direct effects, the invasive herbivore also exerts subtle, indirect impacts on plant competitive dynamics that could have long-term consequences for native community structure.

2. Material and methods

Asclepias syriaca (common milkweed) and *Asclepias tuberosa* (butterfly milkweed) are native perennials that co-occur in old field and prairie habitats throughout eastern North America and have a suite of chemical and physical defences. Several insects specialize on *Asclepias* species, including two phloem-sucking aphids, *A. asclepiadis* and *A. nerii*. *Aphis asclepiadis* is a native specialist, while *A. nerii* is an invasive from the Mediterranean region that feeds on a wider diversity of plants [9].

We grew each milkweed species from seed (electronic supplementary material), and planted seedlings in pairs in 2 litre pots in the treatments described below. We used colonies of each aphid species that were started from individuals collected at or near our field site (Koffler Scientific Reserve (KSR; 44°03' N, 79°53' W)).

We ran a fully factorial experiment that crossed three levels of plant composition (two common milkweed plants, two butterfly milkweed plants or one plant of each species) with four levels of aphid composition (*A. asclepiadis* only, *A. nerii* only, both aphid species, or no aphids). This resulted in 12 treatments, each replicated eight times, for a total of 96 experimental communities arranged in a randomized design. The experiment was conducted in a cleared area paved with clay, with each experimental community consisting of a pot with two plants (plus added aphids) contained within a mesh cage (Skeeta, Bradenton, FL, USA) to prevent aphid dispersal and colonization by other insects. In treatments with a single aphid species, we placed six individuals on each plant at the beginning of the experiment, while in treatments with both aphid species, we added three individuals of each species on each plant.

Over six weeks, we counted the number of aphids of each species on each plant once a week. At the end of the experiment, we recorded how many plants had died (greater than 50% of leaves senesced), and harvested and dried dead and live biomass separately at 60°C for 48 h.

To test for differences in performance and determine the impacts of the *A. nerii* on *A. asclepiadis* and vice versa, we used a linear mixed effects model (LMM) with aphid treatment, plant treatment and time as fixed effects, and 'cage' as a random factor. Models were run with log abundance or log finite rate of increase in each aphid species as the response variable. The finite rate of increase was calculated as N_{t+1}/N_t , where N_{t+1} and N_t are the population sizes at time $t + 1$ and time t , respectively. To determine the impacts of the aphids on plant performance and plant competitive dynamics, we ran LMMs with aphid treatment, focal plant identity and neighbour plant identity as predictor variables, log live biomass or survival as the response variable, and 'cage' as a random factor (electronic

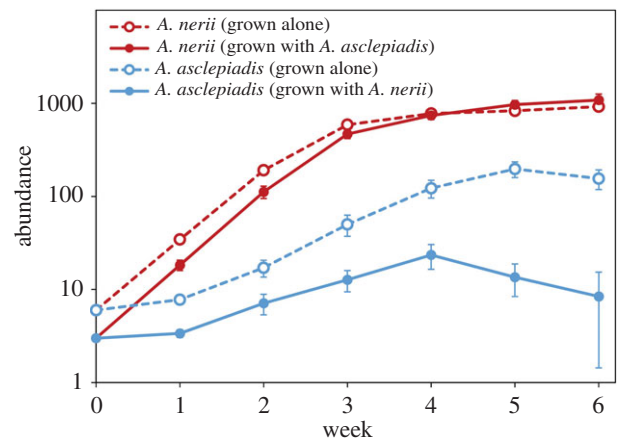


Figure 1. Effect of invasive *A. nerii* on native *A. asclepiadis*. Mean aphid abundances (total number of aphids of that species per plant) over the six-week experiment when species are grown with or without interspecific competition (averaged across all three plant treatments). Data points are mean values \pm one standard error. (Online version in colour.)

supplementary material). All analyses were performed in R (v. 3.2.3). All data used in our analyses are deposited in the Dryad Digital Repository at <http://dx.doi.org/10.5061/dryad.7r826> [10].

3. Results and discussion

Overall, we found that the invasive herbivore had faster population growth and a broader diet breadth than its native competitor, and impacted the dynamics of the invaded community in three distinct ways: *A. nerii* (i) suppressed populations of its native competitor *A. asclepiadis*, (ii) reduced plant performance of both milkweed species more than its native competitor, and (iii) altered competitive dynamics between common milkweed and butterfly milkweed by amplifying the negative impacts of competing with heterospecific neighbours. We outline these results below and highlight how these direct and indirect effects shape community responses to this widespread invasive species.

We found that *A. nerii* was a stronger competitor with a broader host range than *A. asclepiadis* [9,11]. *Aphis nerii* had higher abundances than *A. asclepiadis* in all treatments (figure 1; $F_{1,158} = 104.1$, $p < 0.001$), and was unaffected by plant species identity ($F_{1,162} = 3.04$, $p = 0.083$), while *A. asclepiadis* population sizes were reduced on butterfly milkweed as the experiment progressed ($F_{1,294} = 58.4$, $p < 0.001$; electronic supplementary material, figure S1). This result is somewhat consistent with Smith *et al.* [12], who showed that host genotype can alter aphid competitive dynamics, but generally not enough to promote the coexistence of these unequal competitors. As is commonly observed with invasive species [4], the higher growth rates of *A. nerii* translated into a reduction of *A. asclepiadis* growth rates when the two species were grown together (figure 1; $F_{1,161} = 18.95$, $p < 0.001$). Previous researchers that have likewise demonstrated the strong competitive dominance of *A. nerii* over *A. asclepiadis* have hypothesized that the long-term coexistence of these two competitors may be aided by the earlier arrival of *A. asclepiadis* each season or the mutualistic relationship that *A. asclepiadis* has with ants [11–13].

The invasive *A. nerii* had stronger negative impacts on plant performance than its native counterpart for both

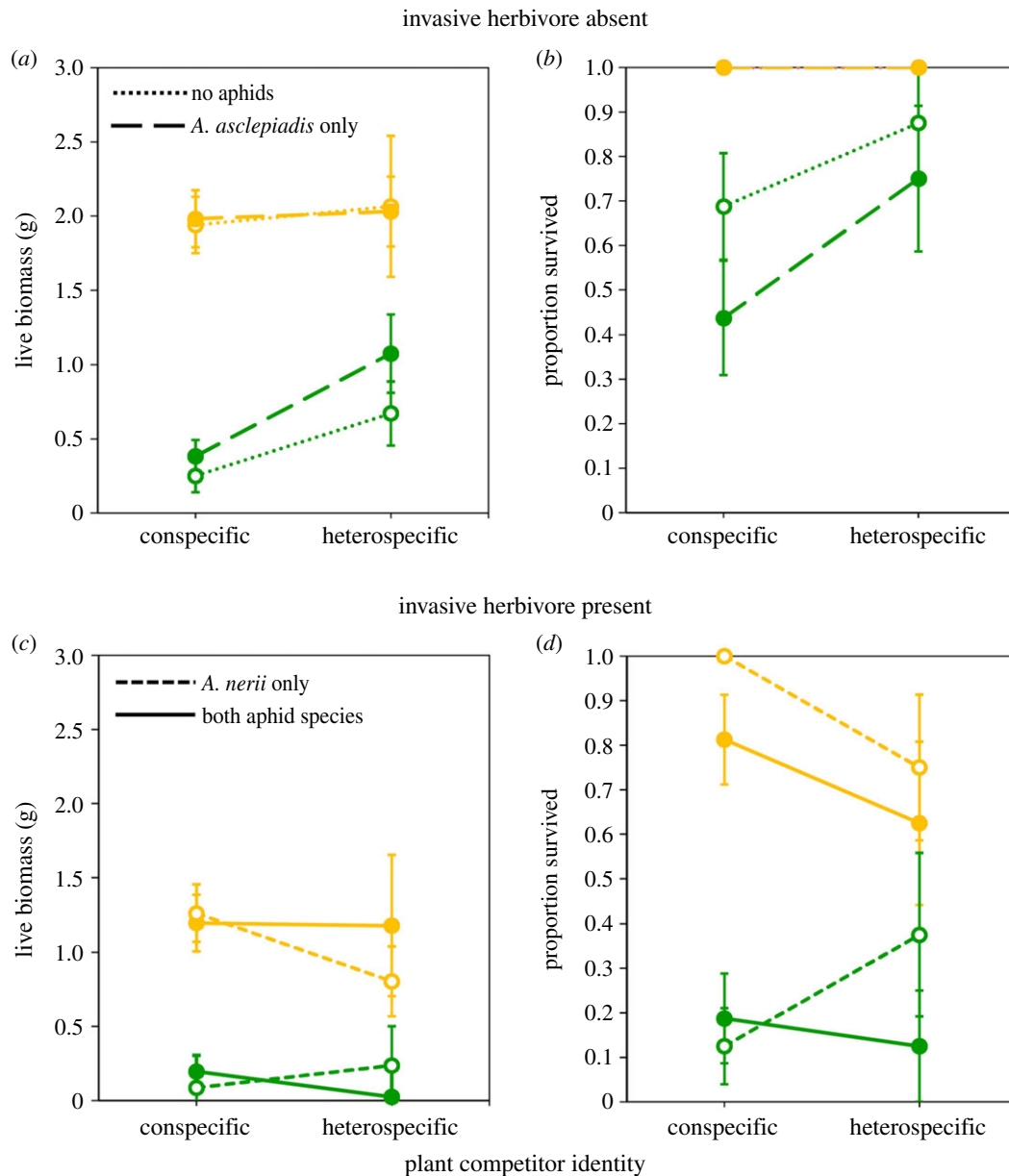


Figure 2. Performance of plants in the absence (*a,b*) and presence (*c,d*) of the invasive aphid *A. nerii* for common milkweed (dark, green) and butterfly milkweed (light, yellow). Upper panels show live biomass (*a*) and plant survival until the end of the experiment (*b*) in treatments where *A. nerii* was absent: control plants grown with no aphids (dotted lines) and treatments with only *A. asclepiadis* (dashed lines). Lower panels show (*c*) live biomass and (*d*) plant survival in treatments with *A. nerii* present: *A. nerii* only (dashed lines) and mixed aphid treatments (solid lines). Data points are mean values \pm 1 s.e. (Online version in colour.)

milkweed species. *Aphis nerii* reduced live biomass and survival (dotted green and yellow lines in figure 2*a,b* (control plants) versus lines of the same colour in figure 2*c,d* (plants with *A. nerii*); $F_{1,86} = 38.1$ for biomass, $\chi^2_1 = 14.7$ for survival, both $p < 0.001$). In contrast, *A. asclepiadis* did not significantly impact the performance of either milkweed species (dotted lines (control plants) versus dashed lines (plants with *A. asclepiadis*) in figure 2*a,b*; $F_{1,86} = 1.29$, $p = 0.26$ for biomass and $\chi^2_1 = 2.0$, $p = 0.15$ for survival). This larger impact of *A. nerii* on plant performance may have arisen not only from its larger population sizes, but also as a result of high *per capita* feeding rates [11].

We also found that the invasive herbivore changed inter- and intraspecific competitive dynamics that mediate plant coexistence (figure 2). Only the invasive *A. nerii* affected competitive interactions between our two milkweed species, and, for both milkweed species, it caused the presence of a heterospecific plant neighbour to more negatively impact plant

performance of the focal plant (figure 2; significant focal plant \times neighbour plant \times aphid interaction for live biomass $F_{3,174} = 4.95$, $p = 0.003$ and survival $t_{66.7} = 2.47$, $p = 0.004$). These results suggest that invasive herbivores may be more likely to induce indirect competitive effects among plants owing to the intense top-down pressure they exert [3].

Common milkweed performed better in the presence of a heterospecific neighbour than a conspecific neighbour when grown with no aphids or only the native aphid (green lines in figure 2*a,b*). Therefore, in the absence of the invasive herbivore, there was a beneficial effect of competing with a heterospecific neighbour, which is often associated with the maintenance of stable local coexistence [6]. However, when the invasive aphid was present (*A. nerii* only and mixed aphid treatments), this benefit of competing with a heterospecific neighbour was reduced for common milkweed (flat or negative slopes of green lines in figure 2*c,d*). Similarly, butterfly milkweed was only negatively impacted by a

heterospecific neighbour in the presence of *A. nerii* (slopes of yellow lines shift from flat in figure 2*a,b*, to negative in figure 2*c,d*). These results indicate that the presence of this invasive herbivore altered the competitive dynamics between native plant species by increasing the negative impact of heterospecific neighbours [14]. This type of dynamic, in which a species competes more strongly with heterospecific neighbours than conspecific neighbours, can lead to positive frequency dependence and unstable community dynamics [6,14].

Plant neighbours can mediate herbivory through associational effects, such as associational susceptibility which increases herbivory on a focal species [15]. However, it is not immediately clear how herbivory might cause plants of both species to be at a disadvantage in the presence of one another. One intriguing hypothesis is that these effects may arise from shifts in root foraging strategies, which vary among plant species and depend on neighbour identity [16]. Previous research has suggested that aboveground herbivory alters root mycorrhizae [17], and that herbivores and neighbours can interactively influence performance through changes in root foraging [16]. Although we can only speculate on this and other mechanisms through which herbivory alters plant competitive dynamics, the importance of frequency dependence for coexistence suggests that future research should investigate these mechanisms [6].

The shifts in community dynamics that arose from the direct and indirect effects of an invasive herbivore demonstrate the severity and complexity of community responses to species invasions [3,4]. In contrast with the weak effects of herbivory by the native aphid, the invasive aphid reduced the performance of its competitor and plant hosts, as has been widely observed in invaded ecosystems [4,5], and also generated top-down effects that restructured plant competitive dynamics. While the implications of these changes for the long-term coexistence of these species remain to be tested, this study provides a first indication of a distinct and potentially destabilizing change to plant communities that can manifest in systems invaded by non-native herbivores.

Data accessibility. Datasets supporting this article are included as the electronic supplementary material, and uploaded to the Dryad Digital Repository at <http://dx.doi.org/10.5061/dryad.7r826> [10].

Authors' contributions. All authors contributed to the conception and study design, L.W. collected the data, L.W. and B.G. analysed the data, and all authors contributed to the interpretation and writing. All authors agree to be held accountable for the manuscript content and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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