

# Can alien plants support generalist insect herbivores?

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**Abstract** Simple rearing experiments were conducted to address two questions relevant to understanding how generalist lepidopteran herbivores interact with alien plants. Yellow-striped armyworm (*Spodoptera ornithogalli*), luna moth (*Actias luna*), bagworm (*Thyridopteryx ephemeraeformis*) and white-marked tussock moth (*Orgyia leucostigma*) were reared from egg to 5th instar on excised foliage in the laboratory to determine the degree to which highly polyphagous lepidopteran herbivores are physiologically capable of surviving and developing on the suite of alien plants naturalized in the mid-Atlantic. *Actias luna* larvae from a single population were similarly reared on a representative of each of the 25 native plant genera recorded as hosts for this species to compare the diet breadth of a local population with that listed over the entire geographic range of the species. With few exceptions, all four generalists either quickly starved or grew at an unsustainably low rate on alien foliage. *Actias luna* larvae survived for 18 days on only 44% of the native

plants recorded as hosts over the entire range of this insect and thrived on only 7%. The data suggest that (1) alien plants are unlikely to produce as much generalist insect biomass as the native plants they replace and (2) Lepidoptera that qualify as generalists when host breadth is considered over their entire geographic range may express a far more specialized diet within local populations. Both of these conclusions support the hypothesis that alien plant invasions may seriously disrupt terrestrial food webs by reducing the insect biomass required by insectivores in higher trophic levels.

**Keywords** Alien plants · Invasive species · Biotic resistance · Enemy release · Generalist · Specialist · Insect herbivores

## Introduction

The rapid replacement of native vegetation by plant species that evolved elsewhere (both noxious invasive species and ornamentals widely used in lieu of native species in suburban landscaping) has renewed interest in the evolutionary and ecological interactions between insect herbivores and their host plants (Keane and Crawley 2002; Tallamy 2004; Agrawal et al. 2005). Despite this we still have a poor understanding about how well alien vegetation supports insect-based food webs, and we know little

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about the extent to which generalist insect herbivores interact with alien plants. If replacing native vegetation with plants that do not share an evolutionary history with other organisms in a community reduces the insect biomass available to insectivores, alien plant invasions may trigger a “bottom-up” cascade that reduces biomass and diversity in higher trophic levels (Wilson 1987; Martin 1992; Tallamy 2004). However, the degree to which the biomass of insect herbivores is affected by increasing the percentage of alien plants in an ecosystem has not yet been quantified.

Theory backed by decades of empirical support predicts that most alien plants, particularly those without native relatives, should be unable to support the growth and reproduction of insects that have specialized on native plants in a particular lineage or on plants that share particular chemical traits (Ehrlich and Raven 1965; Rosenthal and Janzen 1979; Kennedy and Southwood 1984; Strong et al. 1984; Bell 1987; Bernays and Graham 1988; Berenbaum 1990; Scriber et al. 2008). Although the response of specialist herbivores to alien plants has not yet been tested explicitly (but see Tallamy and Shropshire 2009), the logic behind the prediction that specialists should do poorly on alien vegetation has not been challenged. How generalist insect herbivores respond to alien plants is not as easily predicted. Although they are less diverse (Bernays and Graham 1988), generalists may be far more abundant than specialists (Futuyma and Gould 1979; Crawley 1989) and therefore fulfill the bulk of the dietary needs of insectivores such as birds, amphibians, and small mammals. If common generalists can use alien plants for growth and reproduction as well as they use the native plants that they replace, insect biomass production in ecosystems with a high percentage of alien plants may support communities of insectivores as large and diverse as those found in ecosystems dominated by native vegetation. Moreover, recent meta-analyses support the biotic resistance hypothesis that states that at least some generalists actually prefer alien plant hosts over native plants because aliens have not yet evolved effective defenses against evolutionarily novel generalists (Hokkanen and Pimentel 1989; Parker and Hay 2005; Parker et al. 2006).

As a first step toward understanding how generalist insect herbivores respond to alien plants, we used simple rearing assays to determine the degree to

which alien plant species that now dominate the understory in the mid-Atlantic can potentially support four highly polyphagous species of Lepidoptera. We also used these assays to determine whether or not the local host range of a generalist lepidopteran is actually a subset of all its recorded host plants.

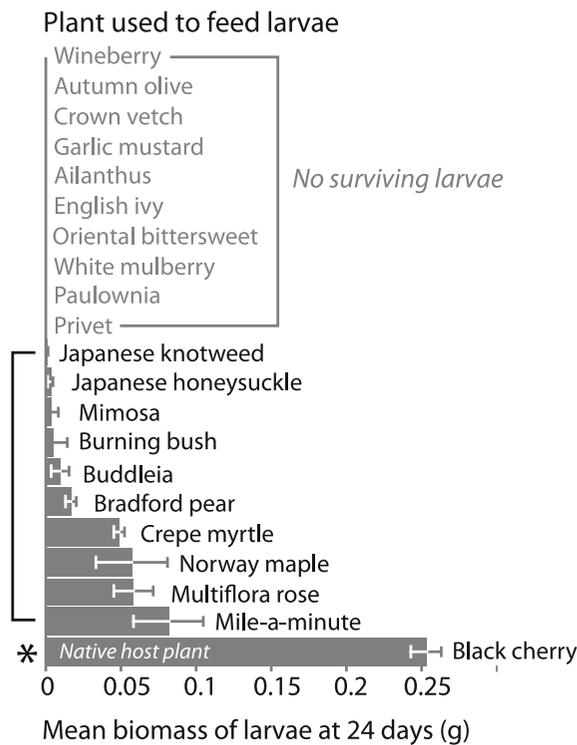
## Methods

To measure the ability of alien plants to support the growth of local native lepidopteran generalists, we reared larvae of luna moth (*Actias luna*; Saturniidae), yellow-striped armyworm (*Spodoptera ornithogalli*, Noctuidae), bagworm (*Thyridopteryx ephemeraeformis*; Psychidae), and white-marked tussock moth (*Orgyia leucostigma*; Lymantriidae) from egg hatch until the first larvae reached 5th instar. These species were chosen because gravid females were easily collected, they represent four unrelated families, and they are among the most generalized lepidopteran species in the area (that is, they have exceptionally long host lists recorded in the literature). Combined, these four species have been recorded from 165 plant genera representing 71 families (Tallamy and Shropshire 2009) and are extraordinary examples of insect polyphagy.

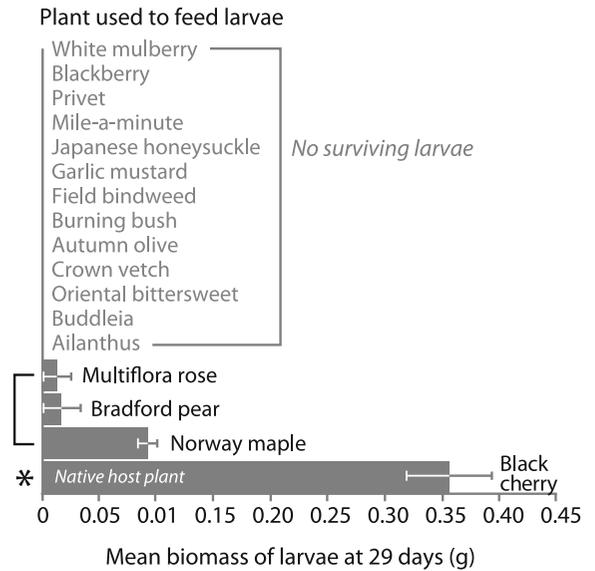
We reared ten larvae of each species on each plant species examined. Because initial ingestion of one plant can have a powerful influence on subsequent growth and survival on other plants (Renwick and Huang 1995, 1996), we placed all larvae on fresh, excised foliage in glass screw-top jars 4 cm in diameter without prior exposure to any other plant species. Foliage was changed and the jars were cleared of frass, debris, and excess moisture every other day. Because the adults that produced the eggs used in this experiment were collected in the field, the larvae were reared on foliage at the same phenological stage that would have been encountered under field conditions. For yellow-striped armyworm and bagworm, all larvae used in this experiment were siblings derived from a single mother. Two females collected at the same light supplied all of the larvae for the luna moth. Two females collected within 2 weeks of each other were the source of all white-marked tussock moths. Temperature was not controlled across species, but all larvae within species were reared simultaneously in the same place. The

rearing was terminated when the first larva reached fifth instar and all surviving larvae in all treatments were weighed at this time.

The plant species examined for each generalist (Figs. 1, 2, 3, 4, and 5) were selected from the type of plant most commonly represented on published host lists. For example, Wagner (2005) lists herbaceous perennials and low-growing shrubs as common hosts of the yellow-striped armyworm. Therefore, we chose herbaceous alien species for this generalist. By the same reasoning, luna moth and bagworm were largely restricted to woody plants. For comparison, at least one native host was included in the test plants of each generalist. We used available literature to determine the native plants that are common hosts of the insect species in question. All species commonly occur in the mid-Atlantic region of the USA list of latin names, authors and geographical areas of origin is available from <http://copland.udel.edu/~dtallamy/pubs.html>.



**Fig. 1** Mean biomass (and SE) of all white-marked tussock moth larvae at day 24. Means are significantly different from one another (Kruskal-Wallis;  $P < 0.05$ ). The asterisk denotes the control against which all the other plant species were tested using a non-parametric version of Dunnett’s test that was significantly different ( $P < 0.05$ ) for all comparisons enclosed within the bracket to the left of the y-axis

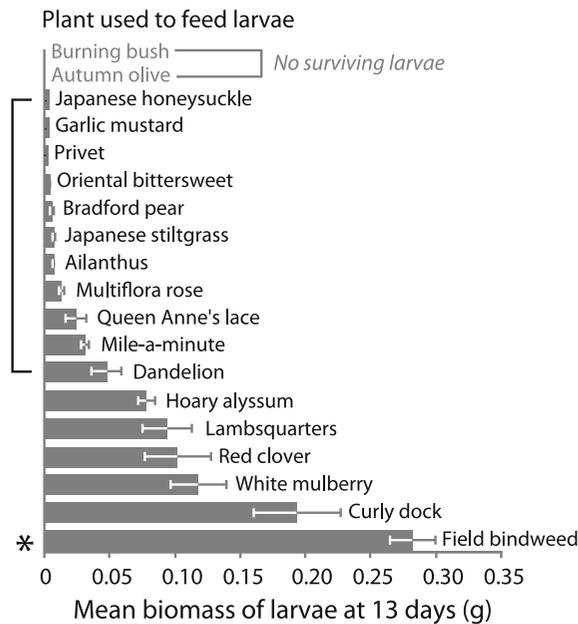


**Fig. 2** Mean biomass (and SE) of all bagworm larvae day 29. Means are significantly different from one another (Kruskal-Wallis;  $P < 0.05$ ). The asterisk denotes the control against which all the other plant species were tested using a non-parametric version of Dunnett’s test that was significantly different ( $P < 0.05$ ) for all comparisons enclosed within the bracket to the left of the y-axis

A second experiment was conducted using luna moth larvae to determine whether published host lists for a species over its entire geographic range accurately reflect the host range of local populations. We reared luna moth larvae on all of the recorded host plants for this species (Fig. 5) as described above. An intensive search of the literature revealed recorded hosts in 25 genera of native woody plants spanning 17 plant families. Larval performance was measured as biomass achieved by the time the first larvae attained 5th instar.

Statistical methods

We analyzed the mean biomass of larvae at the termination of the experiment using the Kruskal-Wallis test performed via Proc NPAR1WAY in SAS (SAS 2000). Many of the treatments resulted in no surviving larvae at the end of the experiment and these treatments were left out of analyses. If necessary, post-hoc testing was performed when the Kruskal-Wallis test showed significant differences in the ranked means. We used a non-parametric version of Dunnett’s test to compare each treatment

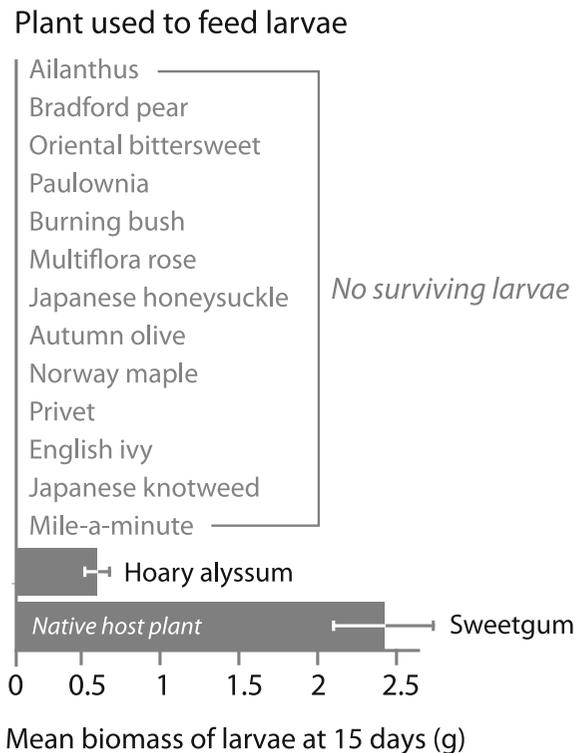


**Fig. 3** Mean biomass of all *yellow-striped* armyworm larvae at 13 days. Means are significantly different from one another (Kruskall-Wallis;  $P < 0.05$ ). The *asterisk* denotes the control against which all the other plant species were tested using a non-parametric version of Dunnett's test that was significantly different ( $P < 0.05$ ) for all comparisons enclosed within the bracket to the left of the y-axis

to the treatment which produced the largest larvae (Zar 1999). This was appropriate with bagworm, white-marked tussock moth, armyworm and luna moth on all its recorded native hosts. The Dunnett-type test was calculated by hand.

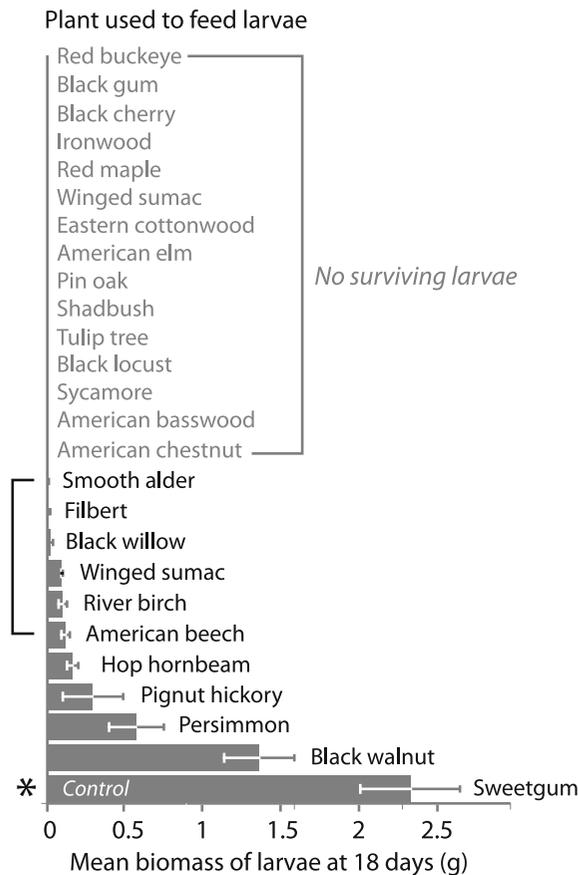
## Results

Figures 1, 2, 3, 4, and 5 show the mean biomass of all larvae on the final day of each rearing experiment. For many of the plant species in each feeding trial there were no larvae surviving. By the end of the experiment, all ten white-marked tussock moths died on 10 of the 20 alien plants tested, all bagworms died on 13 of the 16 alien plants tested and all luna moths died on 13 of the 15 alien plants tested. Yellow-striped armyworm performed slightly better, with only 2 of the 20 plants causing death of all the larvae. On 18 of the 20 plants tested, however, mean biomass production was less than half of the mean biomass obtained by larvae reared on field bindweed, the plant on which armyworm grew best.



**Fig. 4** Mean biomass (and SE) of all luna moth larvae reared on alien plants at 15 days. Means are significantly different from one another (Kruskall-Wallis;  $P < 0.05$ ). No post-hoc testing was necessary

Of the alien plants offered to white-marked tussock moth, crepe myrtle provided the greatest rate of survival (100%); however, larvae fed crepe myrtle reached a mean biomass less than 20% of that achieved by those fed native black cherry (Fig. 1). The alien plant species that produced the largest tussock moth larvae on average was mile-a-minute weed. Yet these larvae obtained only one-third the size of larvae fed black cherry. The largest single larva reared on any alien plant species (Norway maple) was 83% of the mass of the smallest larva reared on the native black cherry (0.1855 vs. 0.2211 g). Differences between the ranked mean biomass were significant (Kruskall-Wallis;  $\chi^2 = 62.23$ ,  $P < 0.0001$ ) and the non-parametric Dunnett-type test showed that larvae that ate black cherry, a recorded native host, were significantly larger than larvae reared on all other plant species with respect to ranked mean biomass ( $q_{0.05, \infty, 11}$ ) (Dunnett's test tables are available online at <http://copland.udel.edu/~dtallamy/pubs.html>).



**Fig. 5** Mean biomass (and SE) of all luna moth larvae reared on native hosts at 18 days. Means are significantly different from one another (Kruskall-Wallis;  $P < 0.05$ ). The asterisk denotes the control against which all the other plant species were tested using a non-parametric version of Dunnett’s test that was significantly different ( $P < 0.05$ ) for all comparisons enclosed within bracket to the left of the y-axis

While survivorship of bagworm on Norway maple was high (90%), these larvae were less than one-quarter the size of those reared on black cherry, a recorded native host (Fig. 2). The largest bagworm larva reared on any alien plant (Norway maple) was 64% of the size of the smallest larva reared on black cherry (0.1230 vs. 0.1937 g). Only a single bagworm larva survived 28 days on Bradford pear and multiflora rose. Differences among the mean ranked biomass of larvae were significant (Kruskall-Wallis;  $\chi^2 = 34.32$ ,  $P < 0.0001$ ). The Dunnett-type test showed that larvae reared on black cherry were significantly larger than larvae reared on all other treatments (q 0.05,  $\infty$ , 4) (Fig. 2).

The results for the feeding trials on yellow-striped armyworm are more complicated because we failed to identify a native host species of this moth at the onset of the experiment. Consequently, we offered no acceptable native plant as a control for our experiments. We did, however, test yellow-striped armyworm on field bindweed (*Convolvulus arvensis*), an invasive plant not native to North America, and found that armyworm performance on this plant was superior to that on any other plant tested. Yellow-striped armyworm is a migratory species that occurs in Central and South America, and moves eruptively into North America when conditions are right. Its natural range overlaps with many species of neotropical *Convolvulus*, a plant genus to which it is clearly adapted. Thus, we compared growth and survivorship of yellow-stripe armyworm on all other plant species to that achieved on field bindweed.

Survivorship of armyworm larvae was 100% on five of the 19 species (field bindweed, hoary alyssum, mile-a-minute weed, ailanthus, and oriental bitter-sweet). Thus, the survivorship of yellow-striped armyworm on non-native plants was much better than any other lepidopteran we tested. However, while survivorship was good on comparatively more plant species, the larvae in most cases were very small at the end of the experiments. Only the larvae reared on curly dock had a mean biomass of more than 50% of the mean biomass of the larvae on field bindweed (the largest larvae) at the termination of the experiment (Fig. 3). Ranked means were significantly different (Kruskall-Wallis;  $\chi^2 = 124.2$ ,  $P < 0.0001$ ), and a Dunnett’s test (q 0.05,  $\infty$ , 17) found that the ranked biomass of larvae reared on field bindweed was significantly different than the ranked biomass of larvae reared on all treatments except red clover, lambsquarters, hoary alyssum, white mulberry, and curly dock ( $P < 0.05$ ; Fig. 3).

Luna moth was tested on both aliens (Fig. 4) and all of its recorded native host plants (Fig. 5). Among the alien plants tested, only larvae reared on hoary alyssum survived to the last day of the experiment. While survivorship on hoary alyssum was equal to that on the native host sweetgum (90%), the mean biomass of larvae reared on sweetgum was more than 4.5 times that of larvae reared on hoary alyssum (2.353 vs. 0.5169 g). Ranked means were significantly different (Kruskall-Wallis;  $\chi^2 = 9.38$ ,  $P = 0.0022$ ).

The trial of luna moth reared on all of its recorded native host plants (Fig. 5) reflected the trend seen throughout our experiments. Survivorship of luna moth larvae was 70% or better on persimmon, hop hornbeam, river birch, American beech, black walnut, and sweetgum. On all other treatments, three or fewer of the 10 initial larvae survived. The treatments with the largest mean biomass were black walnut and sweetgum, with sweetgum producing larvae about 1.7 times larger than those on black walnut (2.353 vs. 1.374 g). The differences between ranked means were significant (Kruskal-Wallis;  $\chi^2 = 54.78$ ,  $P < 0.0001$ ) a Dunnett's test ( $q_{0.05, \infty, 11}$ ) found that the ranked biomass of larvae reared on sweetgum was significantly different than the ranked biomass of larvae reared on all treatments except hop hornbeam, persimmon and black walnut.

## Discussion

This study addresses the potential role of lepidopteran generalists, those species recorded from numerous plant lineages, in slowing the growth and reproduction of alien plants and in compensating by biomass production for the predicted loss of specialist herbivores from areas in which native plants have been replaced by alien species. The results of our simple rearing experiments are clear; with one exception, lepidopteran generalists that were offered plant species with which they have had no evolutionary history either died or developed at extremely slow rates. Such slow growth would undoubtedly affect their ability to pupate as well as their future fecundity (Barbosa et al. 1986).

We found no evidence that the alien plants pervasive in the mid-Atlantic region of North America can support a productive fauna of insect generalist herbivores. Although we only examined the response of four generalists to alien plants, they represented four different lepidopteran families, include the most generalized herbivores in the region, and should serve as conservative surrogates for other lepidopteran generalists. If alien plants in the mid-Atlantic region (and, by inference, alien plants in other regions of North America) cannot support generalist herbivores to the extent that native plants do, it is doubtful that generalists will compensate for the predicted loss of specialists on alien plants in terms of supplying the

insect biomass required by insectivores in higher trophic levels.

The loss of insect biomass from areas heavily invaded by alien plant species may have serious consequences for the sustainability of insectivores, particularly terrestrial birds, in wide areas of North America that have been invaded by alien plants. Although birds use fruits and seeds for food during much of the year, 96% rely on arthropod protein, primarily insects and the spiders that eat insects, for feeding young (Dickinson 1999). Because reproductive success in birds is typically limited by food availability (Martin 1987; Rodenhouse and Holmes 1992; Burke and Nol 1998; Marra et al. 1998; Duguay et al. 2000; Zanette et al. 2000), a loss in available insect resources during the breeding season should reduce reproductive success in nearly all birds. A recent meta-analysis of bird fitness in urban ecosystems supports this contention (Chamberlin et al. 2009).

Our results also do not support the hypothesis that native generalists will be able to slow or limit the establishment or spread of alien plants (the biotic resistance hypothesis; Hokkanen and Pimentel 1989; Maron and Vilà 2001; Colautti et al. 2004). One would expect rapid growth and the ability to achieve large size from herbivores with the potential to eat enough foliage to slow plant growth and reproduction. With a few exceptions (yellow-striped armyworm on dock and field bindweed), the generalists in this study either died in an early instar or were significantly smaller on alien plants compared to a native control.

Recent meta-analyses and re-analysis of data from past studies suggest that some vertebrate and invertebrate herbivores may prefer alien foliage over native foliage (Parker and Hay 2005; Parker et al. 2006). The biotic resistance hypothesis predicts such a preference if alien plants lack the physical or chemical properties required to deter native generalists. In contrast, the enemy release hypothesis predicts that alien plant species are unacceptable hosts for native herbivores that lack the evolutionary exposure required to adapt to the invaders' defenses (Elton 1958; Keane and Crawley 2002). Our study was not designed to test the biotic resistance hypothesis or the enemy release hypothesis and should not be used as evidence for or against either one. We purposefully studied invasive plant species

common in the mid-Atlantic area to examine how such invasions might impact the production of Lepidoptera biomass. Introduced plants negatively impacted by native insect herbivores, as predicted by the biotic resistance hypothesis, would consequently have been uncommon or absent in the study area and therefore overlooked in our study. Similarly, our study is not a good test of the enemy release hypothesis because only invasives not suffering in obvious ways from herbivore pressure were examined. Nevertheless, these plants are precisely the species that are increasingly dominating native plant communities in the study area. If successful invasives do not produce as much insect biomass as the native plants they replace, their invasions will block energy flow from plants to insect herbivores and from there to higher trophic levels.

The results of rearing luna moth larvae on all of their recorded host genera remind us that the concept of “generalist” is often inflated beyond the physiological capabilities of individual caterpillars or even local populations. Larvae derived from adults captured in Milford, Delaware, survived on only 44% of their recorded host genera and reached the 5th instar within 28 days on only 7% of their “host” plants. Actual host use in the field may be even more specialized than these results indicate for luna moth because they do not account for any host discrimination by ovipositing females (Singer 1983). To our knowledge, this is the first time larval performance has been measured across the full breadth of recorded host genera for any lepidopteran species, but the notion that diet breadth is a property of a species over its entire geographic range has been challenged for decades (Fox and Morrow 1981; Scriber 1983; Futuyuma and Peterson 1985). Ecological, chemical, morphological, and/or genetic factors typically constrain local populations of “generalists” to a small fraction of the host plants recorded for that species over its entire geographic range. The consequences of such local specialization from the perspective of alien plant invasions is that, like true host specialists, even species purported to be generalists may be too specialized in local diet preference and physiological tolerance to develop on plants with which they have no evolutionary experience.

One could argue that local host specialization by generalist species might explain the results of all of our rearing experiments. By this reasoning, the

generalists examined in our study did poorly on the 28 species of non-native plants we fed them but may have done well on other introduced species that we did not test. This is certainly a possibility but does not dilute our central interpretation of our data. The non-native plants that we examined are the most common invasives in the Delaware Valley and already comprise much of the first trophic level in thousands of hectares. If generalist insect herbivores cannot develop or reproduce on these plants as well as they do on native hosts, they will not compensate for the loss of specialist insect herbivores in terms of supporting insectivores in higher trophic levels and invaded food webs will be compromised.

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