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ORIGINAL PAPER

Use of invasive Amur honeysuckle (*Lonicera maackii*) by native caterpillars

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Abstract Nonnative plant invasion is among the most severe environmental threats facing terrestrial ecosystems. When introduced into new regions, nonnative plants are thought to shed adapted herbivores. This enemy release may contribute to plant invasiveness, but it also implies that by hosting fewer herbivores, nonnative plants contribute little to supporting diverse food webs and ecosystem services. However, for many widespread invasive plants, arthropod communities have not been extensively surveyed, limiting our ability to assess their contribution to ecosystems. Here, we report on the caterpillar fauna of an important invasive shrub in the Midwest U.S, Amur Honeysuckle (*Lonicera maackii*). We find that, despite its nonnative status, *L. maackii* hosts a surprising diversity of caterpillar and sawfly species. We recorded 91 caterpillar species from *L. maackii*, and though some were likely vagrants, we were able to rear 61 species to pupation on this host. This diversity is similar to that found on common native woody plant genera in the region. The caterpillar community on *L. maackii* is dominated by generalist Noctuidae, Geometridae, and Erebidae, but also includes species specialized on native relatives. Overall survival was relatively low on *L. maackii,* suggesting that despite the diverse community we documented, physiological barriers may hamper its colonization by native herbivores. Size at collection, date and caterpillar family all significantly affected the likelihood of caterpillar survival on *L. maackii*. Our results provide a foundation for understanding the ecological impacts of *L. maackii* on insect herbivore communities and the processes by which invasive plants are integrated into local food webs.

Keywords Lepidoptera · Enemy release · Host use · Ecological assimilation · Invasive plant · Ecological impacts

Introduction

Among the greatest concerns about the spread of invasive plants is their negative impacts on the biodiversity and ecosystem services of higher trophic levels. As they proliferate in their introduced range and usurp resources, invasive plants are unlikely to contribute to local food webs and ecosystem processes to the same degree as the native species they are replacing (Vilá et al. 2011; Schirmel et al. 2016), leading to disrupted ecosystems that are both less diverse and less productive. These detrimental effects of invasive plants on consumer abundance, diversity, and ecosystem services are particularly severe for herbivores,

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especially phytophagous insects (Schirmel et al. 2016). Indeed, release from such herbivores appears to be a significant factor contributing to plant invasiveness in the first place (Keane and Crawley 2002; Liu and Stiling 2006; Meijer et al. 2012; though see, e.g., Parker et al. 2006, Chun et al. 2010). The "enemy-release hypothesis" posits that introduced plants lack coevolved enemies from their native range, providing them a competitive advantage over native taxa in their introduced range and allowing them to allocate less energy to enemy defenses and more energy to growth and reproduction (Blossey and Nötzold 1995; Keane and Crawley 2002).

Due to a deficit of adapted herbivores in their introduced ranges, nonnative plants have been considered ecological wastelands, motivating efforts to limit their spread and eradicate them from invaded habitats. Even alien plants with phylogenetically close (e.g., congeneric) relatives in their introduced range have been shown to support depauperate herbivore communities, lower in abundance, species richness, specialization, and interaction diversity than their native counterparts (Richard et al. 2019; Burghardt et al. 2010). Furthermore, "generalist" herbivores, which might be expected to rapidly expand on to novel host plants, have been observed to perform poorly on nonnative plants (Tallamy et al. 2010). Indeed, the spread of invasive plants has even been suggested as a contributor to global declines in insects (Tallamy et al. 2021).

Interactions between invasive plants and insect herbivores are not static, however, and herbivore communities may accumulate over time as more potential herbivores encounter spreading invasives and natural selection favors traits that facilitate their use (Hawkes 2007). Such colonization of introduced plants by native herbivores may largely be due to the process of ecological fitting (Janzen 1985), whereby herbivores expand on to novel host plants as a result of host finding and performance traits they already possess. This is expected to occur with polyphagous taxa employing broad host-recognition cues and the ability to tolerate a wide range of plant defenses. However, more specialized herbivores may also colonize invasive plants if the plant is phylogenetically and/or biochemically similar to native plant species in the invaded range (Agarwal and Kotanen 2003). Over time, such colonization may result in a form of ecological assimilation, whereby invasive plants accumulate herbivores over time, gradually becoming integrated into ecological networks with faunas increasingly resembling those of native members of the local plant community (Sheppard and Shurr 2019).

A number of studies have documented such patterns of increasing herbivore diversity on introduced plants over time (Strong et al. 1984; Hawkes 2007; Brändle et al. 2008). For example, Schilthuizen et al. (2016) found that herbivore communities on invasive black cherry (*Prunus serotina*) in the Netherlands were more diverse than those on native bird cherry (*Prunus padus*). In addition, *P. serotina* and *P. padus* exhibited similar proportions of specialist and generalist herbivores (Schilthuzien et al. 2016). This study and others have revealed evidence of adaptation by herbivores to the novel invasive host plants and even genetic differentiation of herbivore populations on introduced plants (e.g., Bush 1969; Filchak et al. 2000; Carroll and Boyd 1992; Carroll 2007).

Surprisingly, many invasive plants, particularly in North America, have not been extensively surveyed for arthropod herbivores, and their contributions to native food webs have not been evaluated. Here, we assess the diversity and pattern of colonization of native herbivores on a key invasive shrub in the Midwestern U.S., Amur Honeysuckle (*Lonicera maackii*). The primary questions we sought to address include: (1) Do native caterpillar species use *L. maackii* and, if so, which taxa and functional groups? (2) How do caterpillar assemblages on *L. maackii* compare to those on common native trees and shrubs in the same community? And (3) What factors explain variation in the ability of native caterpillars to develop on *L. maackii*?

Study system

Lonicera maackii, or Amur Honeysuckle, is among the most widespread and pernicious invasive plants in the Midwestern and Eastern United States. This large shrub was originally introduced to the U.S. in the 1890's and was widely planted as an ornamental (Luken and Thieret 1996). High phenotypic plasticity allows *L. maackii* to thrive in a variety of environments (Luken et al. 1997; Lieurance and Lansbergen 2016) and it is a strong disperser, producing abundant fruits that are fed on and dispersed by native birds and mammals (Castellano and Gorchov 2013; McNeish and McEwan 2016). These factors, along with its strong competitive ability, have allowed *L. maackii* to colonize forest edges and interiors, hedgerows, roadsides, and disturbed habitats throughout much of the Eastern United States, where it can dominate the shrub layer (Hutchinson and Vankat 1997). Its detrimental effects on native plant communities are well-documented (e.g., Gorchov and Trisel 2003; Dorning and Cipollini 2006).

Previous research has found that *L. maackii* experiences relatively low herbivory (Lieurance and Cipollini 2012, 2013; Lieurance et al. 2015; though see Bodawatta et al. 2019), suggesting that release from enemies may be contributing to its successful invasion of Eastern North America. Furthermore, feeding assays of generalist caterpillars on *L. maackii* have revealed evidence of both feeding deterrence (Cipollini et al. 2008) and reduced fitness (McEwan et al. 2009). However, no published studies have surveyed *L. maackii* to characterize the community of insect herbivores found on this invasive shrub in its introduced range or assessed which species may be able to successfully develop on it.

Methods

Caterpillar surveys

We explored these questions by surveying caterpillars, and ecologically similar sawflies (Symphyta), on *L. maackii* and other woody shrubs and trees as they were encountered in forested woodlands in Southwest Ohio (for simplicity, we refer to both groups as caterpillars, except where distinctions are made). These surveys were conducted as part of broader studies of U.S. Eastern Forest caterpillar communities (e.g., Stireman et al. 2014) and were conducted during the years 2006–2009 (old) and 2017–2020 (recent). Surveys were opportunistic and effort was not quantified, limiting our ability to compare caterpillar densities among native and non-native hosts. They were conducted at a variety of local woodland sites in the Dayton Metropolitan Area ("Miami Valley") including state and local parks, nature preserves, and private woods. Major sampling sites included the Wright State University Woods (39.781, −84.057), Huffman Metropark (39.811, −84.092), and Glen Helen Preserve/John Bryan State Park (39.795, −83.880). Caterpillars were located either by visual searching of foliage (all years) or beating foliage with a stick onto a hand-held beat-sheet (primarily recent surveys). Once caterpillars were located, they were placed in a marked plastic bag or tub with foliage of the plant they were found on and transported to our laboratory rearing facility at Wright State University for processing.

In the laboratory, caterpillars were given a unique identification code and the following data was recorded: date collected, initial identification (often simply a morphospecies designation), family, host plant, size (length), and defensive traits (e.g., gregariousness, shelter building, etc.). A subset of caterpillars was photographed for later reference. Caterpillars were placed individually (or in groups, if gregarious) in labeled clear plastic rearing tubs (450 ml) with foliage from the plant on which they were found and a piece of damp paper towel. These were reared under fluorescent light banks at ambient temperature (ca. 21–25 ºC) under a 16L:8D light cycle. Caterpillars were checked and plant material and paper towels were replaced at least every other day until death, pupation, or evidence of parasitism. Rearing outcomes and their dates were recorded for each caterpillar including attainment of obvious prepupal stage (e.g., cocoon spinning), pupation, death, and/or parasitism.

Identification

Trees and shrubs were identified using field guides to woody plants of the region (e.g., Braun 1969). Caterpillars were initially identified to families, genera and species where possible using Wagner (2005). Once adults emerged, they were mounted and spread and identified using Covell (2005), Microleps.org, The North American Moth Photographer's Group (http://mothphotographersgroup.msstate.edu), and other traditional and digital resources. Some specimens were identified by comparison with specimens in the C.A. Triplehorn Insect Collection (Ohio State University) with the help of USDA/APHIS National Lepidoptera Specialist S. Passoa. Some could not be identified to species because they died before an identification could be made or because we were unable to definitively identify the species using external traits (we did not dissect genitalia). In these cases, we took a conservative approach. If the caterpillar appeared to be distinct it was assigned a morphospecies based on its appearance. If it could possibly correspond to a species known from the host plant it was found on based on morphological resemblance, we lumped it with that species. If images or descriptions were insufficient to assign it to a unique morphospecies or known species, it was considered unknown. Thus, the unknown category contains species that may or may not correspond to recognized taxa, and these (N = 13) were excluded from most analyses. Vouchers of adult taxa were deposited in the J.O. Stireman Collection at Wright State University.

We broadly characterized caterpillar species found on *L. maackii* and a set of common native forest trees (see below) as either host plant specialists or generalists based on whether they are restricted to one host-plant family or a closely related taxonomic clade (rare records on other hosts were ignored) or if they regularly use hosts belonging to more than one family, respectively (Bernays and Chapman 1994). Information on host plant use was based on our rearing database as well as Wagner (2005) and the Natural History Museum's HOSTS database of lepidopteran host-plants (https://www.nhm.ac.uk/our-science/data/hostplants/search/index.dsml). Some caterpillars had unknown host-plant ranges and were not scored. In a few cases we made conservative inferences based on diet breadths of related taxa (e.g. our *Autographa* sp. is probably polyphagous).

Analysis

We compared the diversity of the caterpillar fauna of *L. maackii* to that of five dominant taxa of native woody plants: *Acer* (mostly sugar maple, *A. saccharum*), *Lindera benzoin* (Spicebush), *Prunus* (Mostly black cherry, *Prunus serotina*), *Quercus* (Oaks), and *Viburnum*. We lumped plant species within genera in order to achieve greater sample sizes. Although native species of *Lonicera* occur in Ohio, they are extremely rare in the region we surveyed. However, *Viburnum* is a closely related genus, belonging to the family Adoxaceae that was formerly subsumed within the honeysuckle family, Caprifoliaceae (Angiosperm Phylogeny Group 2009). In analyzing the caterpillar fauna of *L. maackii* (and other taxa), we excluded likely vagrants, i.e., infrequently collected caterpillars known to be specialists on other taxa (e.g., *Euphydryas phaeton*, *Pieris rapae*, *Atteva aurea*) that showed no evidence of feeding or growth on *L. maackii*. These records likely involved prepupae seeking pupation sites, caterpillars that dropped from other host plants, inadvertent beating of non-target plant foliage mixed with the focal plant, or similar "accidents." Furthermore, we excluded unknown specimens that we could not assume were distinct taxa (see above). Although our characterization of the "caterpillar" community includes sawflies, we omit them in several analyses and tables to facilitate comparison with other studies that exclude them.

Rearing of caterpillars in the laboratory allowed us to compare survival rates on *L. maackii* relative to native plant taxa. For these comparisons, caterpillars with unknown fates (or that escaped or were lost for other reasons) were excluded. Mortality of reared caterpillars across all plant hosts was high, with only about one third of collected caterpillars reaching adulthood. Adults often failed to eclose from pupae, especially those requiring an overwintering period. For this reason, we considered pupation as indicative of successful development on a host plant. It is unclear whether to consider caterpillars killed by parasitoids as successful or not in terms of their ability to grow and develop on a plant. In many cases, caterpillars grew and developed on a plant and even pupated before they were parasitized, but in other cases parasitoid emergence occurred soon after collection, and thus suitability of the host plant was uncertain. Therefore, we examined patterns of successful development among plant taxa both considering parasitism as a success and by excluding parasitized caterpillars. We also compared parasitism frequencies of caterpillars from *L. maackii* with those from other host plant taxa. These estimates excluded caterpillar that died from other causes, i.e., $P = N_p/N_s + N_p$, where P is parasitism frequency, Np is the number of caterpillars (and pupae) that produced parasitoids, and Ns is the number of unparasitized caterpillars reaching pupation or adulthood (as in Stireman and Singer 2002 and Stireman et al. 2017).

To compare communities of caterpillars on invasive *L. maackii* to those on native woody plant taxa in a standardized manner we used the R package *iNext* (Hsieh et al. 2020) to conduct individual-based rarefaction for each plant taxon and calculate Shannon (e^H, effective number of species) and (inverse) Simpson diversity indices. Furthermore, to allow direct comparisons among plant taxa, we extrapolated caterpillar richness on each taxon to a sample 693 individual caterpillars, the highest sample size of any one plant taxon (*Acer* sp.). We estimated the total species richness expected on each plant taxon using the Chao estimator (Chao 1984; Chao et al. 2014). These analyses excluded likely vagrants, unknown caterpillars, and sawflies. We also used rarefaction to compare caterpillar faunas associated with *L. maackii* between our old samples (2006–2009) and more recent surveys (2017–2020) interpolated/extrapolated to 459 individuals (the total number from the later sampling period).

We constructed a generalized linear model (GLM) in R 4.1.1 (R Core Team 2021) to examine what biological and environmental factors may explain variation in the ability of caterpillars to successfully develop on *L. maackii*. This binomial model (with log–log link function) assessed the likelihood of successful development (0 or 1) as a function of caterpillar family (ten most well-represented families), date of collection, host breadth category (see previous), and size (length in mm) at collection. Caterpillar size is an important covariate in this model as caterpillars collected at earlier stages are less likely to successfully complete development. Significance of factors was assessed by comparing models with and without each factor using Analyses of Deviance. This model considered individual caterpillar as the sampling unit; however, we also analyzed a parallel model examining effects of family and host breadth with species as the sampling unit, including only non-vagrant species represented by at least four individuals (N = 33 spp.).

Results

Caterpillar diversity

In all, we collected and attempted to rear 590 individual caterpillars (and sawflies) belonging to an estimated 93 species from *L. maackii* over eight years (Fig. 1; Table S1). Seven of these species (16 individuals) were considered to be vagrants due to specialized associations with unrelated hosts (with *Malacosoma americanum* considered another likely vagrant), and another seven species were not identified sufficiently to categorize as vagrants or otherwise (although individuals of several of these were able to develop on *L. maackii*). Approximately 40% of collected caterpillars either died as a larva or prepupa or were unaccounted for, about one half reached pupation or adulthood, and about 9% were parasitized (Table 1). Excluding vagrants and taxa that could not be assigned to a species/morphospecies, we recorded at least 61 species of caterpillars that were able to successfully develop to pupation on *L. maackii*. Most individuals and species found on *L. maackii* were collected in the recent, more focused surveys (474 individuals of 81 species, excluding unknowns), as opposed to the older 2006–2009 surveys (102 individuals of 29 species), with 20 species being recovered from both periods.

Caterpillars were found on *L. maackii* from late March through October. An apparent peak in caterpillar abundance was observed in May, with another, smaller peak in August (Fig. S1). This pattern is consistent with previous surveys of caterpillar abundance showing a late spring peak and smaller peak in late summer (Stireman et al. 2014).

The species of caterpillars and sawflies recovered from *L. maackii* were distributed among 19 families, including 4–5 vagrant families (Figs. 1, 2). The vast majority of individuals (> 90%) and species (> 80%, excluding vagrants) belong to four families, in decreasing order of abundance: Geometridae, Noctuidae, Erebidae, and Tortricidae (Fig. 2). As is typical of surveys of diverse insect communities, most species encountered on *L. maackii* were represented by relatively few (< 5) individuals (Fig. S2), suggesting that the true number of species using this host is much higher. This conclusion is supported by the rarefaction analysis, which predicts (based on the Chao estimator) that the community of caterpillars and sawflies using *L. maackii* may exceed 120 species.

Rarefaction analysis of caterpillar communities on *L. maackii* and five common native woody plant taxa (*Prunus* sp., *Acer* spp., *Quercus* spp., *Viburnum* spp. and *Lindera benzoin*) suggests that this invasive honeysuckle hosts a caterpillar community comparable to that of native plants in the region (Table 2; Fig. 3b). This is particularly evident when rarefaction curves are extrapolated to the same total abundance, in which case *L. maackii* is only exceeded by *Prunus* spp. in our surveys (Fig. 3b). Similarly, only *Prunus* spp. exceeds *L. maackii* in the total (Chao) estimated number of caterpillar species it is predicted to host in this region. Even more striking is the finding that estimates of

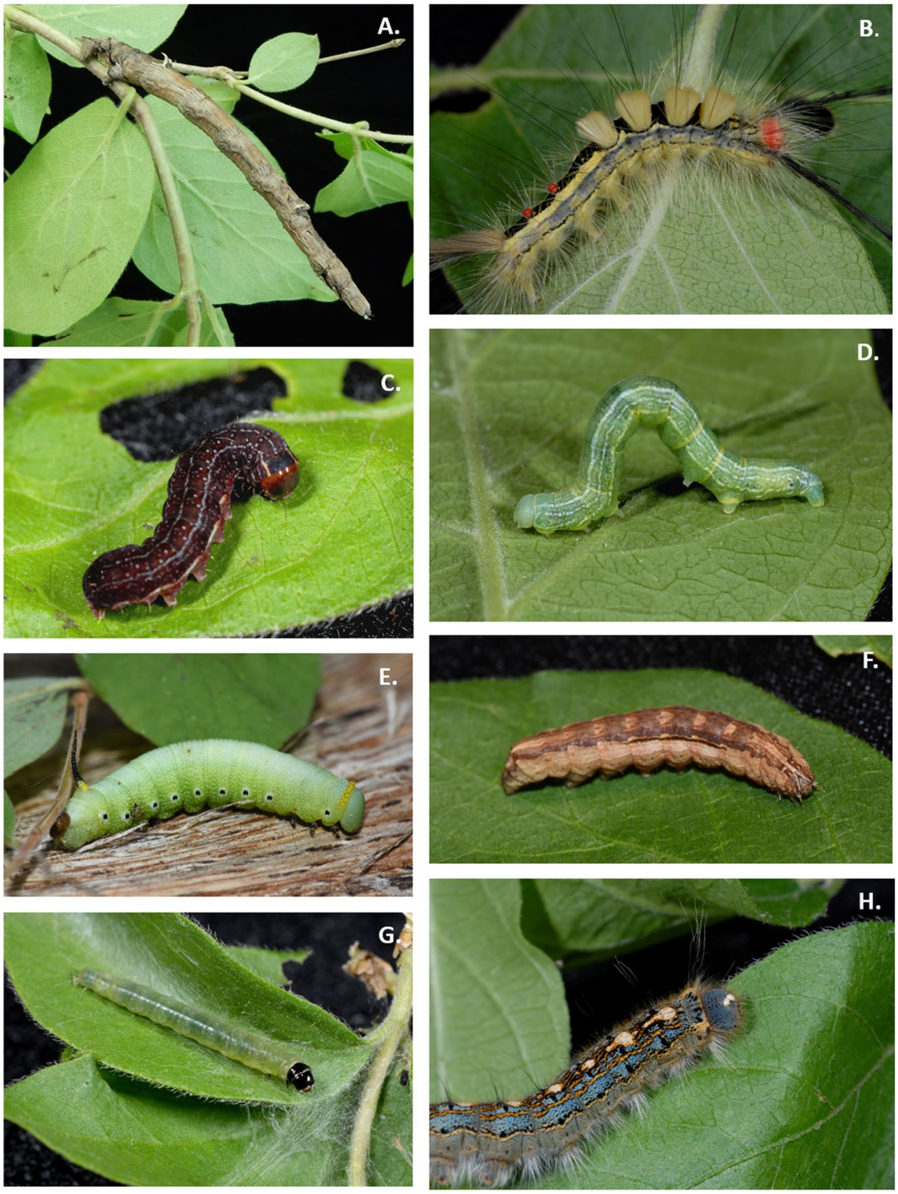


Fig. 1 Representative caterpillars found on *L. maackii*. **A** *Lytrosis unitaria* (Geometridae), **B** *Orgyia leucostigma* (Erebidae), **C** *Eupsilia* sp. (Noctuidae), **D** *Alsophila pometeria* (Geometridae), **E** *Hemaris diffinis* (Sphingidae), **F** *Sympistis badistriga* (Noctuidae), **G** *Choristoneura rosaceana* (Tortricidae), **H** *Malacosoma disstria* (Lasiocampidae, with tachinid fly eggs on head capsule)

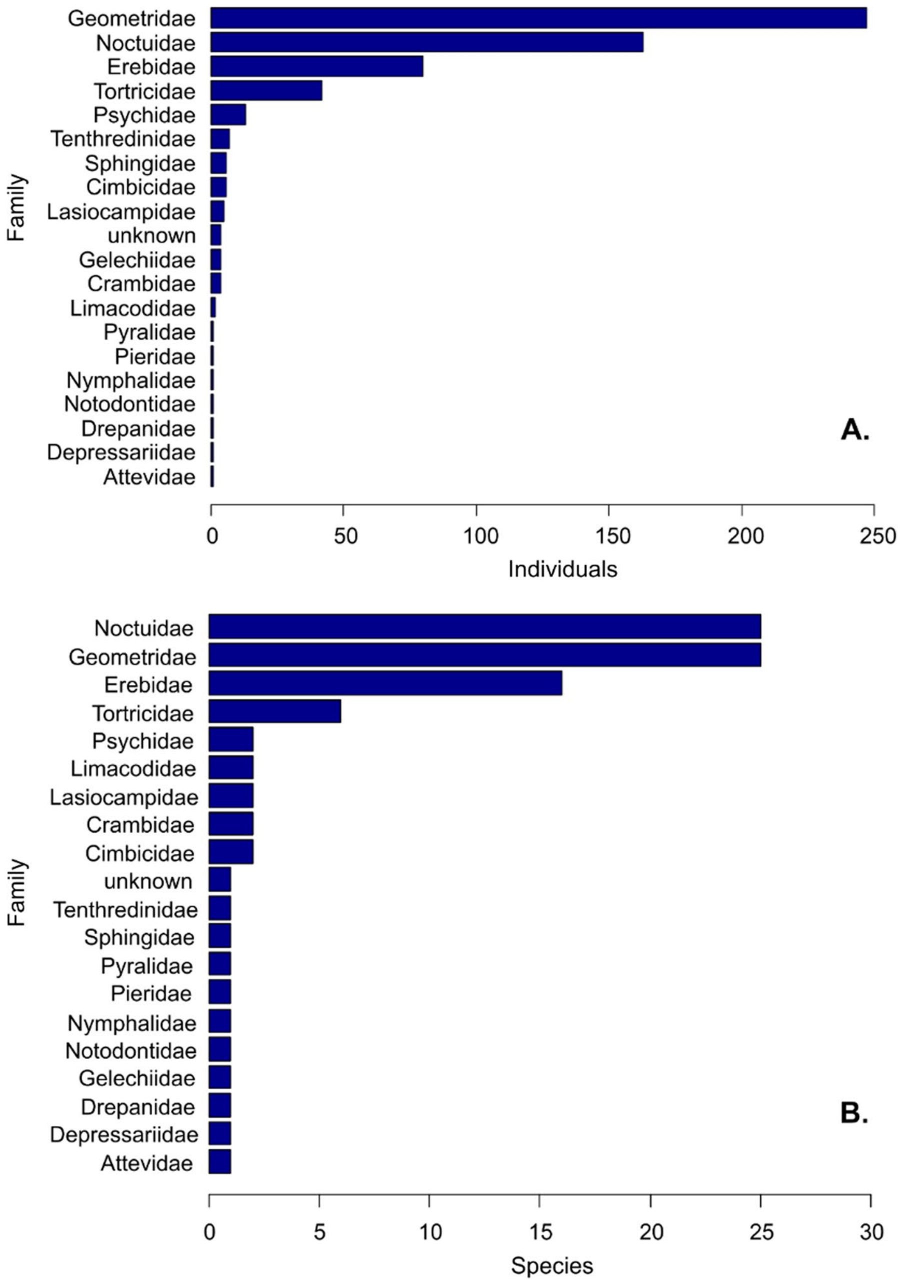
diversity, which account for relative abundance, are greater for *L. maackii* than any of the native taxa examined (Table 2). These high estimates of species richness and diversity of caterpillars on *L. maackii* are driven by the more recent, 2017–2020 surveys. If only the more limited older (2006–2009) surveys are considered, *L. maackii* ranks lower than all of the native woody plant taxa in estimated caterpillar richness (Table 2; Fig. 3a).

Table 1 Fates of caterpillars collected from *Lonicera maackii* in Southwest Ohio

Caterpillar fate	N	%
Adult	189	32.0
Pupation but no adult	98	16.6
Parasitism	52	8.8
Dead (as larva/prepupa)	175	29.7
Unknown	76	12.9
Total	590	100

N = number of individuals

Fig. 2 The family distribution of caterpillar individuals (**A**) and species (**B**) collected from *L. maackii*



Diet breadth

Of the 80 caterpillar species for which we classified host range, six species (7.5%) were specialists or likely specialists on *Lonicera* or related taxa (Caprifoliaceae and Adoxaceae; e.g., *Abia inflata, Hemaris diffinis*). The remaining 74 species were either generalists feeding on plants from several families (85%) or specialists on other plant taxa (7.5%; mostly vagrants). When sawflies are included, the proportion of specialists increases across taxa, as Symphyta as a group tend to be highly specialized (e.g. Nyman et al. 2006). As expected for a non-native plant, the proportion of generalists found on *L. maackii* was relatively high and the proportion of specialists low (Table 3).

Table 2 Observed caterpillar species richness (S), Shannon Diversity (e^H), Simpson diversity (inverse Simpson Index), and Chao estimator with standard errors on invasive honeysuckle (*L. maackii*; overall and divided into older or more recent sampling periods) and five native plant genera

Plant taxon	N	S	e^H	D	Chao ± se
Lonicera maackii	560	84	36.1	17.5	123.3 ± 18.7
2017–2020	459	75	36.4	21.0	119.9 ± 22.7
2006–2009	98	26	11.2	5.6	39.9 ± 10.3
Acer spp.	693	86	33.7	16.5	107.1 ± 10.8
Lindera benzoin	205	35	12.9	7.3	57.4 ± 16.0
Prunus spp.	134	39	20.4	12.5	126.5 ± 63.0
Quercus spp.	122	33	17.3	10.5	80.8 ± 36.7
Viburnum spp.	107	25	10.9	6.4	45.9 ± 16.3

Survey effort varied widely among plant taxa

N = total caterpillar individuals collected on each species (vagrants, sawflies, and unknowns are omitted)

Caterpillar performance on *L. maackii*

As indicated previously, approximately 30% of caterpillars collected from *L. maackii* died as larvae and another 17% pupated but failed to eclose as adults (excluding parasitism; Table 1). This failure to develop, particularly during the larval stage, may reflect physiological barriers to using this novel host. Indeed, caterpillars on *L. maackii* had slightly lower overall survivorship to pupation (62%) than those on common native woody plants (68% overall). This variation in survivorship among plants was significant, both when including parasitism as successful development ($X^2 = 20.8$, d.f. = 5, $P < 0.0008$) or excluding parasitized caterpillars ($X^2 = 18.6$, d.f. = 5, $P = 0.0023$; Fig. 4A). Caterpillars on *L. maackii* experienced relatively low risk of parasitism among the plant taxa examined (13.3% versus 15.6% across other taxa); however, variation in parasitism among host-plant taxa was not significantly greater than expected by chance ($X^2 = 4.1$, d.f. = 5, $P = 0.540$; Fig. 4B).

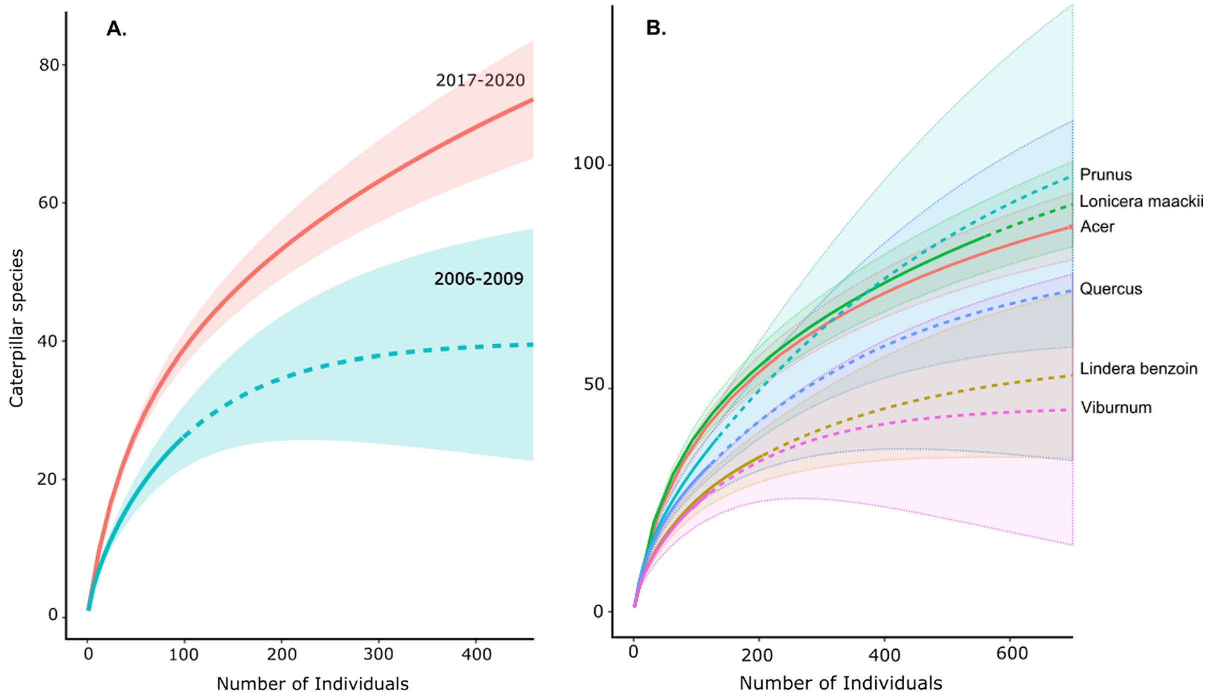


Fig. 3 Individual based rarefaction curves of caterpillars on invasive honeysuckle (*L. maackii*) for **A** from early (2006–2009) and later (2017–2020) survey periods extrapolated to 459 individuals (the number from later surveys) and **B** overall relative to five co-occurring woody plant taxa extrapolated to 693 individuals (the number found on *Acer* spp.). Dashed lines indicate extrapolated values. Background colors indicate 95% confidence intervals. Note: survey effort varied widely among plant taxa

Table 3 Estimated percentage of generalist and specialist caterpillar species (including sawflies in parentheses) on *L. maackii* and five native plant taxa surveyed in Southwest Ohio

Plant taxon	N	% spec	%gen	% other
Lonicera maackii	80 (83)	7.5 (9.6)	85 (81.9)	7.5 (8.4)
Acer spp.	86 (87)	23.3 (24.1)	74.4 (73.6)	2.3 (2.3)
Lindera benzoin	35 (36)	14.3 (13.9)	83.7 (83.3)	0.0 (2.8)
Prunus spp.	39 (41)	25.6 (29.3)	71.8 (68.3)	2.6 (2.4)
Quercus spp.	33 (35)	24.2 (28.6)	75.8 (74.3)	0.0 (0.0)
Viburnum spp.	25 (26)	40.0 (42.3)	52.0 (50.0)	8.0 (7.7)

Species for which host ranges could not be inferred are omitted. Note: survey effort varied widely among plant taxa (see Table 1)

N = number of caterpillar species recovered

spec. = specialists

gen. = generalists

other = specialists on other taxa (including vagrants)

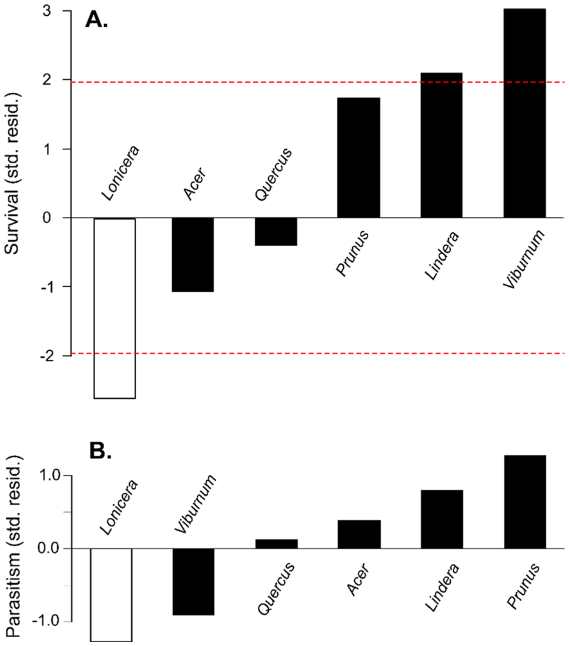


Fig. 4 Deviation from expected values of **A** caterpillar survival and **B** parasitism of caterpillars reared from *L. maackii* (left, white bars) and five genera of native woody plants (Pearson standardized residuals). The zero line represents expected frequencies, with positive bars indicating relatively high survival or parasitism rates and negative bars indicating relatively low rates. Dashed red lines indicate approximate significance thresholds

Comparison of generalized linear models revealed that caterpillar size (length) at collection, date of collection, and family significantly influenced the likelihood of successful development to pupation on *L. maackii* (Table 4). As expected, caterpillars that were collected at a larger size were more likely to survive to pupation, and this was the strongest predictor of caterpillar success ($z = 4.94$). Caterpillars collected earlier in the year were more likely to survive than those collected later, although this effect was relatively weak ($z = -2.10$). Caterpillars belonging to families including Erebidae, Lasiocampidae, and Gelechiidae were more likely to complete development on *L. maackii* than Noctuidae and Geometridae (Fig. 5). We found similar, but stronger, effects of caterpillar family on developmental success when analyzed at the species level (i.e. proportion of caterpillars of a given species developing to pupation), with species of Erebidae experiencing significantly elevated survival rates on *L. maackii* ($z = 2.115$, $P = 0.034$) and those belonging to Geometridae ($z = -2.00$, $P = 0.034$) and Noctuidae ($z = -2.78$, $P = 0.005$) experiencing relatively lower survival rates on this novel invasive host plant. Diet breadth did not significantly influence likelihood of caterpillar survival.

Discussion

Caterpillar richness and diversity

Contrary to expectation, we found that the invasive shrub *L. maackii* hosts a surprisingly diverse caterpillar community, comparable in richness to communities found on common native woody plant species.

Table 4 Analysis of Deviance table showing effects of single factor deletions of binomial GLM models assessing the likelihood of successful (individual) caterpillar development on *L. maackii*

Factor	d.f	Dev	AIC	LR	P
model		471	497.1		
Caterpillar size	1	496	519.9	24.8	**< 0.0001**
Caterpillar family	9	12.9	497.3	18.3	**0.032**
Date collected	1	20.4	499.5	4.4	**0.036**
Diet Breadth	1	17.3	496.6	1.5	0.214

Estimates are given for model deviance (Dev), AIC, likelihood ratio (LR), and significance (P)

Statistically significant effects are highlighted with bold P-values

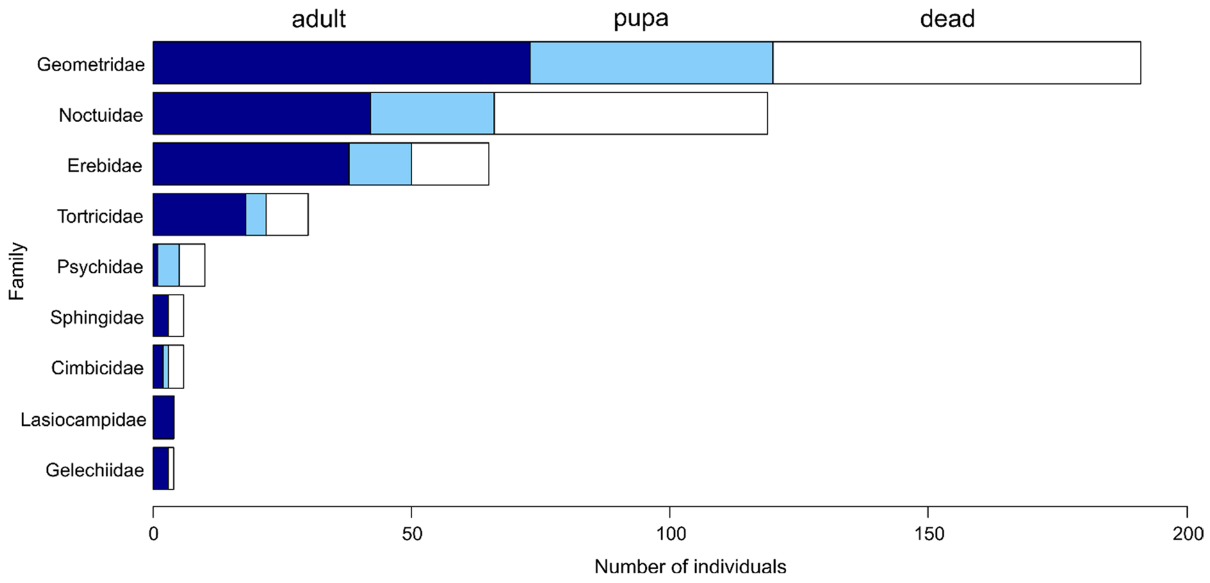


Fig. 5 Fates of reared caterpillars from major families found on *L. maackii* (likely vagrants are excluded)

Even so, our estimates of caterpillar richness on *L. maackii* are likely low due to our conservatism in excluding presumed vagrants and in recognizing distinct species (i.e., potentially lumping morphologically similar species of caterpillars). Furthermore, rarefaction analysis suggests that the species accumulation curve on *L. maackii* is only beginning to saturate and well over 100 caterpillar species are likely to be found on this host in the region surveyed.

Approximately one third of the species we collected from *L. maackii* failed to develop to pupation, suggesting that not all of the species found on this host can actually develop on it. Caterpillars are frequently found on plants on which they do not normally feed due to dropping from overlying foliage (e.g., to escape predators) and prepupal wandering. Despite this, we were able to collect and rear to pupation 61 caterpillar and sawfly species on *L. maackii*, demonstrating that this novel, invasive plant hosts a rich and varied caterpillar assemblage.

Rarefaction analysis revealed both expected and unexpected patterns of caterpillar diversity. Cherry (*Prunus* spp.) exhibited the highest expected richness among the taxa examined, consistent with its high ranking as a host for Lepidoptera found in other studies (Tallamy and Shropshire 2009; Narango et al. 2020). However, oaks (*Quercus* spp.), which rank highest in caterpillar richness based on literature records (Tallamy and Shropshire 2009; Narango et al. 2020), were intermediate in diversity in our surveys, possibly reflecting limited sampling. This may also be the case for *Viburnum*, the closest relative of *Lonicera* among the taxa examined, which exhibited the lowest caterpillar richness despite the presence of several, relatively abundant species in this genus. Narango et al. (2020) also found that *Viburnum* ranked relatively low in caterpillar diversity compared to other common woody plant genera in Eastern North America. Spicebush (*Lindera benzoin*) hosts a relatively low richness of caterpillars, however we recovered approximately three times the number of caterpillar species from this host than is reported from the literature (Narango et al. 2020). These comparisons reflect individual-based species rarefaction and are not standardized with respect to survey effort. Quantitative surveys (in progress) will provide additional insight into the relative value of these plants as hosts for caterpillars.

The difference in rarefaction curves for caterpillar richness between our older and more recent sampling periods is striking (Fig. 3a). It is tempting to attribute the greater diversity in recent surveys to an accumulation of native herbivores that are expanding over time to utilize the plentiful resource that *L. maackii* presents. This process is expected and may have contributed to the increased richness we observed over sampling periods, but it is unlikely to account for the magnitude of the observed increase over a relatively short time period (~ 10 years) on an invasive plant that has been well-established in the region for more than 30 years (DeMars and Runkle 1992). Much of the observed increase is likely attributable to our more focused sampling of *L. maackii* in recent surveys and our more consistent use of foliage beating, which more efficiently surveys cryptic caterpillars.

Even more unexpected than the relatively high richness of caterpillars on *L. maackii*, are the high indices of diversity, indicating elevated species evenness as well as high richness. The effective number of species (Chao et al. 2014) on *L. maackii* is greater than any of the native plant genera examined. There are several possible explanations for this. First, it could reflect our more complete sampling of *L. maackii* versus other plant taxa. Second, there may be fewer rare (perhaps more specialized) species on this nonnative plant given its lack of coevolutionary history with native herbivores. Third, the sheer abundance of *L. maackii* in the region could make it a major host for generalist caterpillars that are broadly permissive in host selection (e.g., ballooning caterpillars). Finally, low predation rates on *L. maackii*-feeding caterpillars (Piel et al. 2021) could result in elevated richness and diversity.

Community composition

The representation of lepidopteran families recovered from *L. maackii* reflects the relative abundance and richness of those families on woody plants generally. The four dominant families found on this host are also the four most diverse families of Lepidoptera (van Nieukerken et al. 2011), which also contain the vast majority of generalist caterpillar species. More specialized lineages may be underrepresented. For example, Notodontidae are underrepresented and although this family contains broad generalists, most species feed on a relatively limited range of hosts (e.g., *Quercus*). Papilionoidea are also poorly represented and tend to be relatively specialized.

One taxonomic and ecological void in the caterpillar fauna we recovered on *L. maackii* are concealed-feeding microlepidoptera such as Pyraloidea, Gelechioidea, and Gracillarioidea. Although we reared a number of Tortricidae, leaf rolls and shelters were relatively uncommon on *L. maackii* (see also Lieurance and Cipollini 2012) and we never noted leaf-mining caterpillars (but we did observe mines of the agromyzid fly, *Aulagromyza cornigera*, pers. obs.). This may be due to high specificity of internal and concealed feeders, with some tortricines such as *Choristoneura roscaceana* and *Pandemis limitata* being the exception (Brown et al. 2008). Still, our reliance on foliage beating in later surveys may have missed some endophytic and shelter building taxa. High densities of the leafminer *Phyllonorycter emberizaepenella* (Gracillariidae) have been reported on *L. maackii* in Michigan (Craves 2017), less than 300 km to the north of our study area, but we have not observed this species.

The overwhelming majority of herbivorous larvae found on *L. maackii* were generalists, and while this is also true for the native plant genera examined, only *Li. benzoin* had a similarly high proportion of generalists. This finding is surprising as *Li. benzoin* (family Lauraceae) is relatively taxonomically isolated in Ohio forests and is known to host a number of relatively specialized species (e.g., spicebush swallowtail, *Papilio troilus*).

Lonicera maackii hosts the smallest proportion of specialists of the plant taxa examined. Eight species are specialists or likely specialists on *Lonicera* or related taxa (i.e., Caprifoliaceae and Adoxaceae). This includes the sawflies *Abia inflata* and the introduced *A. lonicerae*, the noctuids *Metaxaglaea inulta* and *Sympistis badistriga*, the sphingid *Hemaris diffinis*, and three shelter builders (2 Crambidae and 1 Gelechiidae [*Anacampsis* sp.]). These last three taxa are not fully identified and may turn out to have broader host ranges. Laboratory studies have confirmed that the native specialist sawflies *Abia inflata* and *A. americana* perform relatively well on *L. maackii*, although females prefer to oviposit on native hosts (Lieurance and Cipollini 2013; Shewart 2016). Seven of the 83 herbivore species we found on *L. maackii* with diet breadth estimates were likely vagrants, all specialists on other host plants. This proportion of vagrants was relatively high, supporting the suggestion that many species may inadvertently occur on this host simply due to its abundance in the subcanopy.

Predictors of successful development

The high mortality (almost 40%) of the caterpillars collected from *L. maackii* suggests that it may be a relatively poor host for many native caterpillars. This conclusion is supported by our finding of significant variation in overall caterpillar survival across host plant taxa, with those on *L. maackii* experiencing the lowest of the six plant taxa we examined. However, caterpillar rearing studies on native plants often report high levels of mortality (>40%) due to disease, improper rearing conditions and other causes (Stireman et al. 2017). In addition, survival rates of many particular caterpillar species on *L. maackii* were relatively high. For caterpillar species with five or more collections on *L. maackii* (N = 31), in only one (*Autographa* sp.) did no caterpillars survive to pupation (and 2 of 6 were parasitized). Even rarely collected species often developed to pupation: of 49 species only collected once or twice, more than 60% (30) developed to pupation. These results indicate that *L. maackii* is not merely a sink for populations of caterpillars feeding on other plant taxa, but can also be a source. It is possible that the pupal stage could be a sensitive period to accumulated plant secondary metabolites, but we see no clear pattern in percent of adults eclosing from pupa relative to host plant (e.g., *L. maackii*: 65.8%, overall across plant taxa, 68.7%).

Although we did not find significant variation in parasitism among host plants, caterpillars on *L. maackii* exhibited relatively low parasitism risk. Further sampling might reveal evidence of "enemy free space" for herbivores on *L. maackii* (Jeffries and Lawton 1984) that may facilitate its colonization by native herbivores and perhaps accelerate its ecological assimilation into the community. However, we find little support for *L. maackii* acting as a refuge for the caterpillars that feed on it. The lack of convincing enemy free space on this novel host may be due to the preponderance of generalist caterpillars found on it, whose parasitoids are likely adapted to using broad-spectrum cues in host location (Vet and Dicke 1992).

The strong effect of caterpillar size on survival is expected simply due to statistical probability given a constant daily death rate and is found across our rearing data; however, lack of adaptation to *L. maackii* could also contribute to higher mortality of younger caterpillars, as early instars may be more sensitive to plant nutritional deficiencies and defenses (e.g., Zalucki et al. 2002). The underlying cause of the effect of season on developmental success is unclear, but it may be related to plant quality. Younger, softer leaves produced in spring may be more nutritious than the tougher, mature leaves available later in the summer (Coley et al. 2006). Disease prevalence may also increase throughout the season, potentially contributing to higher mortality in the late summer and fall.

Variation in developmental success among caterpillar families appears to be driven by high tolerance of generalist arctiine (Erebidae) species (e.g., *Haploa* spp., *Hyphantria cunea*) as well as relatively low success in common generalist Geometridae (e.g. *Melanolophia canadaria*, *Ectropis crepuscularia*) and Noctuidae (*Eupsilia cirripalea*, *Crocigrapha normani*). Many arctiines are extremely polyphagous (Wagner 2009; Singer and Bernays 2009) and adapted to tolerate wide variation in plant quality and defenses. Still, at least one extreme generalist, the spongy moth (*Lymantria dispar*), has been shown to perform relatively poorly on *L. maackii* (McEwan et al. 2009). Generalist geometrids and noctuids feed on a wide range of forest trees, but they tend to be more host-restricted than Erebidae. To some degree, patterns of success may be driven by individual species rather than being phylogenetic properties of families, yet we found similar patterns when analyzing our data at the level of species versus individuals within families.

Why does nonnative honeysuckle host such a rich caterpillar community?

The results of our surveys and analyses lead to the question: Why does *L. maackii* host such a diverse caterpillar community given its lack of eco-evolutionary history with native herbivores? One possibility is that *L. maackii* is special relative to other nonnative plants and is particularly well-suited for colonization by native herbivores. This could be due to the existence of native congeners in the region (as well as ecologically and phylogenetically related *Viburnum* spp.) which may serve as a source for colonizing herbivores. Yet most caterpillars we recorded from *L. maackii* were generalists and native *Lonicera* are generally rare in the region, with several species being of conservation concern (e.g., *L. dioica*; Hill 2003).

L. maackii's abundance may be another reason for the high caterpillar diversity we observed. Amur honeysuckle often dominates the subcanopy and understory of Eastern U.S. forests, facilitating interactions with adult and larval Lepidoptera. As suggested previously, both caterpillars dropping from above and those wandering up from the forest floor are likely to encounter *L. maackii*, creating opportunities for interaction. Furthermore, several other species of invasive *Lonicera* are abundant in the region (e.g., *L. japonica*, *L. tatarica*, *L. morrowi*), potentially favoring adaptations for more efficient recognition and feeding on the genus as a whole.

In addition to being an abundant resource, *L. maackii* may be relatively nutritious for herbivores. It lacks obvious physical defenses (e.g. sharp trichomes) and its leaves are relatively soft and thin. Decomposition studies indicate that the leaves are low in indigestible lignin and high in Nitrogen content (Arthur et al. 2012). Also, laboratory studies suggest that both specialist and generalist insect herbivores can perform well on *L. maackii* (Lieurance and Cipollini 2013; Shewart 2016). However, *L. maackii* is known to possess defensive secondary compounds (Cipollini et al. 2008; Watling et al. 2011; Lieurance and Cipollini 2013) and has been previously recorded to experience low (1–3%) herbivory in our study area (Lieurance and Cipollini 2012, 2013). Interestingly, our preliminary surveys in Southwest Ohio have found somewhat higher herbivory levels of approximately 4–5% on *L. maackii*, although this is lower than that experienced by the co-occurring dominant natives, *Li. benzoin* and *A. saccharum* (both ca. 7%) and in some environmental contexts (forest interior) we have also found low herbivory on *L. maackii* (1%). Bodawatta et al. (2019) also report appreciable (6.2%) but variable herbivory (0.5–8.0% among years) on *L. maackii* at a site in neighboring Indiana. We are gathering additional data to better estimate herbivory on *L. maackii* in its introduced range and how it varies over space and time.

Another possibility is that *L. maackii* is not particularly special, and the paradigm that nonnative invasive plants as a group host reduced herbivore diversity is faulty. Although reviews and metanalyses have found evidence of lower richness of herbivores on nonnative plants, the effect is often weak (Keane and Crawley 2002; Meijer et al. 2012; Spafford et al. 2013) and some studies have found no pattern or even the opposite pattern, with nonnative plants hosting more diverse communities of herbivores (see Maron and Vilà 2001; Grandez-Rios et al. 2015; Allen et al. 2021). Although they did not assess herbivore diversity, Chun et al. (2010) failed to detect a difference in herbivory level between 35 co-occurring pairs of native and nonnative species. Furthermore, field studies in aquatic and terrestrial systems have shown that native generalist herbivores often prefer to feed on nonnative plants and may provide "biotic resistance" to plant invasions (Parker and Hay 2005, 2006). We note however, that one field study found that herbivory on *L. maackii* was far lower than on sympatric native *Lonicera* species (Lieurance and Cipollini 2013).

Certain nonnative plants accumulate herbivores rapidly in their introduced range (e.g., Auerbach & Simberloff 1988; Eckberg et al 2012, Schilthuizen et al. 2016), such that their herbivore communities are not obviously depauperate relative to native relatives. The rate of herbivore accumulation may be function of the degree of phylogenetic novelty of the invader (Grandez-Rios et al. 2015), although some phylogenetically isolated nonnatives experience high herbivory (see Parker et al. 2012). Much of the herbivore diversity on nonnative plants in their introduced ranges is likely due to rapid colonization by generalists, which are more catholic in host selection and are broadly tolerant of plant defenses, with slower accumulation of more specialized taxa (e.g., leaf miners). This appears to be the case with *L. maackii*. However, a recent metanalysis of 30 local plant communities found no differences in mean herbivore specialization among native and nonnative plants (Grandez-Rios et al. 2015).

Our results demonstrate a rich and diverse set of caterpillars (and sawflies) using *L. maackii* in its introduced range, suggesting that this invader is being assimilated into local ecological communities in the Midwest U.S. Whether these herbivores are present in sufficient quantity to restore ecological balance and dampen the spread of *L. maackii* is unclear, but at least this invasive appears to be contributing to local food webs. Our caterpillar surveys were not standardized, and further research is needed to determine if the density of herbivores differs between *L. maackii* and native plants, if herbivory is increasing over time, and how herbivore communities and herbivory levels vary over space and across habitat types. Additional herbivore rearing studies that include monitoring of performance will aid in assessing the physiological costs and possible ecological benefits of using *L. maackii*. Such studies will not only aid in our understanding of how *L. maackii* is impacting the ecosystems it is invading, but may also provide insights into evolutionary processes of host expansions and shifts, and the assembly of ecological communities in general.

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Data availability The datasets generated during and/or analysed during the current study are not publicly available because we are using these data in additional analyses for be published in future manuscripts. However, the data are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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