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Specialist Herbivore Performance on Introduced Plants During Native Host Decline

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1                   **Specialist herbivore performance on introduced plants**  
2                                   **during native host decline**

3  
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15  
16   **Abstract**

17           Ash (*Fraxinus* spp.) is in rapid decline across the northeastern USA due to the invasive  
18   emerald ash borer (*Agrilus planipennis* Fairmaire). Three recently co-occurring confamilial  
19   species may serve as alternative larval host plants for ash-reliant Lepidoptera. These prospective  
20   hosts are non-native shrubs often planted in managed suburban landscapes and are sometimes  
21   invasive or naturalized in North America. Given the imminent decline of ash trees, we  
22   considered potential downstream effects on insect herbivores historically specialized on ash  
23   foliage. We measured the performance of three ash-specialist hawkmoths (Lepidoptera:

24 Sphingidae) on native white ash (*Fraxinus americana* L.) and alternative host plants: common  
25 lilac (*Syringa vulgaris* L.), weeping forsythia (*Forsythia suspensa* (Thunb.) Vahl), and European  
26 privet (*Ligustrum vulgare* L.). We found the non-native host plants provided varied support for  
27 larval survival to pupation, with biomass and growth rate affected differently by both plant and  
28 insect identity. Nearly all caterpillars reared on one alternative host, European privet, exhibited  
29 distinct malformations of the wing buds at pupation. Given caterpillar presence on privet in the  
30 field, privet may constitute an ecological trap (i.e., when female moths select a sub-optimal host,  
31 offspring survival and fitness are reduced). This work demonstrates how performance testing can  
32 reveal species-specific effects of host plant loss on mono- or oligophagous insects. For some ash  
33 specialists, alternative non-native host plants may be suboptimal, but some cultivated host plants  
34 may be able to support certain specialist insects during native host decline. We suggest that  
35 landscaping decisions can be tailored to support threatened insect species.

36 **Keywords:** Lepidoptera, invasive species, insect decline, global change, community science

37

## 38 **Introduction**

39 Coevolution of many plants and herbivorous insects has resulted in specialized or  
40 oligophagous relationships, such that most insect herbivores only feed on a small number of  
41 plant species, genera, or families (Berenbaum 1990, Futuyma and Agrawal 2009, Forister et al.  
42 2015). Compared to many regionally native plants capable of hosting large communities of  
43 locally-adapted insect herbivores, introduced and invasive plants generally support less  
44 biodiverse food webs, and host fewer insect populations, fewer species, and less insect biomass  
45 than native congeners (Zuefle et al. 2007, Burghardt et al. 2010, Fickenscher et al. 2014, Richard  
46 et al. 2019). Mechanistically, invasive plants can present a threat to native insect communities by

47 extirpating less-competitive native plants (Heleno et al. 2009) or by replacement as inferior-  
48 quality host plants for native herbivores (Evans 2013, Tallamy et al. 2020). Examining the ability  
49 of insects to switch onto novel hosts is an active area of research in entomology and ecology  
50 (Yoon and Read 2016) and is particularly timely as insect population declines become prominent  
51 (van Klink et al. 2020, Outhwaite et al. 2022). However, few studies have quantified the extent  
52 to which non-native plants can support native insects when their host plants have been extirpated  
53 or driven to extinction. Further, there is a paucity of diet breadth data for many insect herbivores,  
54 resulting in a lack of understanding of many organisms' basic biologies and ecologies (Hardy et  
55 al. 2020). Recognizing that diet breadth is unique for each population adds complexity and  
56 unpredictability to assessing the potential for persistence of specialist insect fauna.

57         The degree to which moth and butterfly communities will suffer from the loss of their  
58 native host plants is of concern for multiple trophic levels. Lepidoptera are among the preferred  
59 prey for insectivorous birds (Razeng and Watson 2015, Piel et al. 2021), a group experiencing  
60 well-documented population losses (Smith et al. 2015, Bowler et al. 2019, Rosenberg et al.  
61 2019). Moths and butterflies represent the most diverse order of insects associated with  
62 angiosperm plants (New 2004). With the introduction of exotic plants to novel ecosystems, some  
63 native lepidopteran species have adopted, and in some cases prefer, exotic plants as larval hosts  
64 (Shapiro 2002). Occasionally, new associations support larger insect populations and promote  
65 range expansions. For instance, adopting the invasive tree-of-heaven (*Ailanthus altissima* (Mill.)  
66 Swingle) as a host allowed the Ailanthus webworm (*Atteva aurea* Fitch) to expand its range  
67 north, following the tree's introduced range (Becker 2009). The larvae of Blackburn's sphinx  
68 moth (*Manduca blackburni* Butler), an endangered species in Hawai'i, are able to survive on  
69 both native and invasive nightshade (Solanaceae) family plants, including tobacco weed

70 (*Nicotiana glauca*). Crucially, tobacco weed may constitute the moth's most abundant and  
71 reliable host plant in some regions of Maui (Rubinoff and Jose 2010). Novel associations can be  
72 deleterious, such as the adoption of invasive garlic mustard (*Alliaria petiolata* (M.Bieb.) Cavara  
73 & Grande) by the native mustard white butterfly (*Pieris oleracea* Harris). Female mustard whites  
74 are attracted to the plant for oviposition, but the larvae perform poorly when feeding on its  
75 foliage (Keeler and Chew 2008). Like many graminoid-feeding Lepidoptera in grassland  
76 habitats, females of the imperiled Dakota skipper (*Hesperia dacotae* Skinner), a specialist of  
77 northern tallgrass and dry upland prairies, will oviposit nearly randomly among habitat substrate,  
78 including on native and non-native grasses. Larvae accept common non-native grasses such as  
79 Kentucky bluestem (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss) but feeding on  
80 these species negatively impacts Dakota skipper larval mass, time to pupation, and survivorship  
81 (Nordmeyer et al. 2021). Overall, a minority of novel associations have been documented as  
82 beneficial or neutral for lepidopteran populations (Yoon and Read 2016). Associations that  
83 produce negative effects on the attracted herbivores are considered to be "ecological traps." The  
84 extent to which such interaction occurs is understudied due to the wide diversity of possible  
85 interactions and the challenges associated with assessing both oviposition preference and larval  
86 performance (Tallamy et al. 2020). Increasingly widespread community science observations  
87 represent a potential complementary source of species-interaction and host plant use data  
88 (Gazdic and Groom 2019, Gardiner and Roy 2021).

89         In the eastern forests of North America, tree communities are undergoing major shifts  
90 following the introduction of novel pests over the last century (Tobin 2015, Wagner and Turo  
91 2015, Liebhold et al. 2017). Ash trees (*Fraxinus* spp.) represent the dominant indigenous  
92 members of the olive family (Oleaceae) in North America and have known associations with

93 nearly 300 species of arthropods on the continent (Gandhi and Herms 2010), including at least  
94 110 native Lepidoptera in the eastern United States according to the HOSTS database for  
95 Lepidopteran host plants (Robinson et al. 2022). An invasive forest pest, the emerald ash borer  
96 (*Agrilus planipennis* Fairmaire), threatens mature ash across the trees' North American range.  
97 Since its introduction to the Great Lakes region in 2002, this phloem-feeding beetle has killed  
98 millions of ash trees in the United States and Canada, radically altering the trajectory of forest  
99 ecosystems where ash is dominant or subdominant (Poland and McCullough 2006, Klooster et  
100 al. 2014). Emerald ash borers are moving eastward into New England states (Herms and  
101 McCullough 2014). Given that most species within *Fraxinus* are at risk (Anulewicz et al. 2008)  
102 and that regeneration appears unlikely (Klooster et al. 2014), the survival of the 26 known at-risk  
103 ash-specialist Lepidoptera remains uncertain (Gandhi and Herms 2010, Wagner and Turo 2015,  
104 2016). Hope for associated herbivore persistence exists in the presence of 'lingering ash' in  
105 emerald ash borer invaded forests where lone ash trees remain amongst stands of greater than  
106 95% mortality (Knight et al. 2014) and in white ash stands capable of regeneration (Robinett and  
107 McCullough 2019). However, the presence of ash in forests may become marginalized to the  
108 point that tree populations are no longer capable of sustaining specialist insects. A loss of such  
109 ecosystem functionality was observed in the last century with the decline of the American  
110 chestnut and subsequent extinction of five associated Lepidoptera (Wagner and van Driesche  
111 2010).

112         Should ash become functionally extinct due to EAB, no native members of Oleaceae will  
113 remain in the northeastern United States. A small suite of non-native, confamilial relatives of ash  
114 exist in managed properties and as escaped shrubs across the USA. In New England, privet  
115 (*Ligustrum* spp.), forsythia (*Forsythia* spp.), and lilac (*Syringa* spp.) are historically popular

116 landscaping plants in Oleaceae, all originating from Eurasia (Haines 2010). Privets are  
117 widespread invasive shrubs, which form dense thickets propagated by berry-eating birds and are  
118 capable of displacing native vegetation (Maddox et al. 2010). Privet species are particularly  
119 noxious in the southeastern states, where European privet (*L. vulgare* L.), Chinese privet (*L.*  
120 *sinense* Lour.), and border privet (*L. obtusifolium* Siebold & Zucc.) have invaded approximately  
121 ten percent of southern forest land (Maddox et al. 2010, Wang and Grant 2012). Privet species  
122 are less aggressive in regions with colder winters where they rarely thrive beyond forest edges  
123 and roadsides (Wang and Grant 2012, Zhao et al. 2013). Lilacs are popular flowering shrubs that  
124 spread slowly through seed dispersal and, in the case of common lilac (*S. vulgaris* L.), rhizomes  
125 (Springer and Parfitt 2007). Many populations have been established outside of cultivation, and  
126 while it is not widely considered invasive, common lilac can become locally common away from  
127 cultivation (Falck and Olson 2008). Forsythia species have also naturalized but do not appear to  
128 spread easily, with patchy colonies cropping up around homesteads and reproducing  
129 predominantly asexually by rooted pendulous branches (Ebinger and McClain 1997, Serviss et  
130 al. 2015). Outside of urban and suburban plantings, these three shrubs are found mostly in  
131 artificial or disturbed habitat in New England, and co-occur with ash mostly at forest edges  
132 (Haines 2010). If ash specialists exhibit host-switching capability, these genera are the only  
133 related host-plant genera that could “rescue” at-risk specialist ash phytophages.

134         The main objective of this study was to quantify larval growth and survival of North  
135 American ash-specialist Lepidoptera feeding on non-native oleaceous plants and, further, to  
136 identify how these plants may influence lepidopteran communities experiencing ash decline. We  
137 examined three species in the family Sphingidae: *Ceratomia undulosa*, *Sphinx kalmiae*, and  
138 *Sphinx chersis*. Wagner and Turo (2016) project that each species will face marked population

139 declines due to native host-plant loss and other drivers of global change. Given both anecdotal,  
140 published (i.e., Wagner 2005), and community-scientist-reported records of each species of  
141 caterpillar on various alternative host plants, we predicted that exotic confamilial plant species  
142 can support caterpillar growth to adulthood. However, we also expected that all three species  
143 would experience reduced performance on non-native plants. To address these hypotheses, we  
144 examined the growth rate and biomass attained at developmental benchmarks to quantify  
145 changes in fitness on alternate host plants. We also carried out a survey of focal plant-insect  
146 interactions captured in photographic observations posted to the community science platform,  
147 iNaturalist.

148

## 149 **Materials and Methods**

150 *Study system.* We conducted our study in the summer of 2020 in southern New  
151 Hampshire, USA. We reared three ash-specialist Lepidoptera species (*Ceratomia undulosa*  
152 Walker, *Sphinx kalmiae* J. E. Smith, and *Sphinx chersis* Hübner) from hatch to pupation on four  
153 confamilial plants in Oleaceae: white ash (*Fraxinus americana* L.), European privet (*Ligustrum*  
154 *vulgare* L.), weeping forsythia (*Forsythia suspensa* (Thunb.) Vahl), and common lilac (*Syringa*  
155 *vulgaris* L.). We chose our focal moth species for the ease of collecting a gravid female and for  
156 their high-moderate endangerment risk from the loss of ash (Wagner and Turo 2016). We  
157 collected eggs from wild females lured to a sheet illuminated by mercury vapor light. Plant  
158 species were selected based on their phylogenetic relatedness to *Fraxinus*, a documented  
159 predictor of host usage (Pearse and Altermatt 2013), and their prominence in New England  
160 suburban landscapes.



161           *Larval performance.* From mid-June to August, we reared caterpillars (*Ceratonia*  
162 *undulosa*, n = 154; *Sphinx kalmiae*, n = 120; *Sphinx chersis*, n = 166) individually on one of the  
163 four host plants in food-grade containers under identical light and temperature conditions (13-15  
164 hours of daylight (ambient conditions) at ~21°C). We maintained subequal larval sample sizes  
165 for each host-plant treatment (*C. undulosa*, n = 34 to 41; *S. kalmiae*, n = 30; *S. chersis*, n = 41 to  
166 42), with small deviations in sample size mostly due to accidental early mortality during  
167 container maintenance. We also conducted a pilot study with a geometrid species, *Plagodis*  
168 *kuetzingi* Grote, a species with high endangerment risk in the event of the ecological loss of ash  
169 (Wagner and Turo 2016). For this pilot, we placed 30 neonates in a single container with the  
170 treatments in our main study. *Plagodis kuetzingi* tends to prefer new leaves, so we also included  
171 a treatment with new ash leaves only (S.P.J. pers. obs.). To assess survival, we marked the  
172 number of dead caterpillars at 48 hours, 96 hours, 4 days, 8 days, 10 days, 15 days, and 20 days.

173           Caterpillars were fed with harvested foliage in the same phenological stage as plants  
174 found in the field, with no prior introduction to other host plants. Each day, we cleared away  
175 frass and replaced foliage to avoid differences in quality and moisture content. On days 15 and  
176 25 after hatch and continuous feeding, we counted each surviving caterpillar and measured  
177 individual biomass. For the remaining time, we continued our feeding protocol and checked  
178 daily for prepupal caterpillars (no longer feeding and expelling characteristic watery frass). We  
179 noted the ‘wandering’ date (i.e., when a caterpillar leaves its host plant in search of a suitable  
180 environment for pupation), and the caterpillars were allowed to pupate in individual rearing  
181 containers under identical conditions. We measured the weight of each pupa and noted any  
182 abnormalities. To confirm the results of our laboratory study with non-excised foliage, we  
183 sleeved six individuals of *C. undulosa* per treatment on trees in the field. Caterpillars were 10

184 days old at the time of placement in the field. After two weeks, we counted survivors and  
185 caterpillars remained in sleeves for another week. At the conclusion of the third week, we  
186 counted survivors and allowed the caterpillars to pupate in conditions identical to those reared in  
187 the laboratory experiment.

188 *iNaturalist survey.* We surveyed host-plant associations with our focal lepidopteran  
189 species by identifying plants in the documented photographs of three sphingid larvae on  
190 iNaturalist. While community science platforms such as iNaturalist historically garner single-  
191 taxon observations, incidental species interaction data are often captured in images associated  
192 with the sighting (Gazdic and Groom 2019). Such data are already being used to document  
193 pollinator-floral resource interactions (Roy et al. 2016). Other researchers have used museum  
194 specimen label metadata similarly to complement field-based data (González-Vaquero et al.  
195 2014). In the present study, we screened images uploaded to iNaturalist by a broad population of  
196 observers to visually identify the associated host plants being used by the caterpillars of our three  
197 study species. All images of caterpillars were analyzed and scored using a standardized protocol  
198 to ensure accuracy and reduce possible confusion or misidentifications. Our search parameters  
199 were constrained by region (eastern United States) and life stage (larval records only) in order to  
200 maintain relevance to the current work. Eastern United States was defined by a 1250 km by 1100  
201 km box encompassing Washington, DC, USA, north to Quebec City, Canada, and Toronto,  
202 Canada, east to the Atlantic Ocean. We ignored iNaturalist determined identification and instead  
203 confirmed the identity of the caterpillar and associated host plant directly. Further, we removed  
204 observations fitting one or more of the following criteria: (a) larval misidentifications, (b)  
205 duplicate observations, (c) caterpillars showing evidence of being from captive origin, (d)  
206 prepupal or wandering caterpillars with no host association, and (e) feeding stage caterpillars

207 with no identifiable host association. From our subsetted data, we manually scored each record  
208 based on plant identification: 1 = host unidentified, 2 = host unidentified but is not *Fraxinus*, 3 =  
209 caterpillar associating with ash (*Fraxinus*) species, 4 = caterpillar associating with privet  
210 (*Ligustrum*) species, 5 = caterpillar associating with lilac (*Syringa*) species, 6 = caterpillar  
211 associating with forsythia (*Forsythia*) species, and 7 = caterpillar associated with non-focal host  
212 species.

213 To further confirm the use of the alternative, non-native plants by sphinx caterpillars in  
214 the field, we conducted evening field surveys along two adjacent suburban roadsides (Depot and  
215 Joslin Roads, Keene, NH 03455) and one managed landscape (Aldworth Manor, 184 Aldworth  
216 Manor Rd, Harrisville, NH 03450) that featured the target alternative host plants (n > 5 plants per  
217 species). For each survey, we used an ultraviolet black light to illuminate caterpillars after  
218 sunset. This survey method is well-described in other caterpillar species (Moskowitz 2017) and  
219 has been previously observed in *C. undulosa*, *S. kalmiae*, and *S. chersis* larvae (S.P.J, pers. obs.).  
220 We conducted our in-situ surveys on 15-VII-2020 and 19-VIII-2020.

221 *Statistical analysis.* We conducted data analysis using R (R Core Team 2022) and data  
222 visualization using the package *ggplot2* (Wickham et al. 2021). All caterpillars not surviving to  
223 pupation were omitted from growth rate, biomass, and growth period analysis to eliminate  
224 outliers from caterpillars “failing to thrive” (i.e., caterpillars dying shortly after the first  
225 weighing) and those dying from pathogen infection in later instars. We analyzed absolute growth  
226 rates and median biomass at 15 and 25 days after hatch for caterpillars reared on native (white  
227 ash) and non-native (all other) host plants using the Wilcoxon rank sum test with a Bonferroni  
228 correction. Growth rate is defined as biomass gained over time. Starting weight was considered  
229 negligible as egg weight was below the threshold of precision of the scale. Caterpillars were at

230 middle (15 days) and late (25 days) instars when we took the weighing measurements (*sensu*  
231 Tallamy et al. 2010). We used Fisher's exact test to analyze survivorship for the native control  
232 group and the non-native treatments. Additionally, we calculated the growth period defined as  
233 the time from hatch to pupation for each caterpillar. To compare insect growth periods by the  
234 host plant, we used the Wilcoxon rank sum test with a Bonferroni correction between the native  
235 and non-native plants.

236

## 237 **Results**

238 *Larval performance.* Larval growth periods for all three species varied significantly by  
239 native and non-native host plant (*C. undulosa*,  $W = 240.5$ ; *S. kalmiae*,  $W = 1590.5$ ; *S. chersis*,  $W$   
240  $= 260.5$ ; for all,  $p < 0.001$ ); *S. chersis* and *C. undulosa* caterpillars reared on ash exhibited  
241 shorter times from hatch to pupation than the non-native plants taken together. The median  
242 growth period for *S. chersis* on ash was 35 (interquartile range, IQR 34 to 36) days versus 37  
243 (IQR 30.75 to 43.25) days on the non-native plants. Similarly, the median growth period for *C.*  
244 *undulosa* was 33 (IQR 29 to 37) days for ash-reared caterpillars and 40 (IQR 34 to 46) days for  
245 all others together. This pattern was reversed for *S. kalmiae*, with caterpillars exhibiting a median  
246 growth period of 32 (IQR 29 to 35) days on non-native plants compared to 35 (IQR 32.5 to 37.5)  
247 days on the native plant. Of the 440 sphingid caterpillars across the three species, 269 survived to  
248 pupation (61.1%). Survival varied by species, with *C. undulosa* and *S. chersis* caterpillars  
249 surviving to pupation in greater numbers on the native host than the non-native host plants (for  
250 both,  $p < 0.001$ ) and *S. kalmiae* caterpillars exhibiting no significant survival differences across  
251 plant species ( $p = 0.492$ ) (Table 1). Despite showing normal caterpillar growth, most moth pupae  
252 of all three species reared on privet exhibited a malformation of the wing buds and were likely

253 unviable (Fig. 1). We subsequently adjusted the ultimate survival of caterpillars reared on privet  
254 to reflect this unviability. After this adjustment, the survival trends remained similar, but the  
255 negative survival impacts of the non-native plants on *S. kalmiae* caterpillars neared significance  
256 ( $p = 0.061$ ) (Table 1). For sleeved caterpillars, several individuals perished before being placed  
257 outdoors (ash,  $n = 1$ ; privet,  $n = 2$ ; forsythia,  $n = 3$ , lilac,  $n = 3$ ). Of those placed outdoors, four  
258 survived on ash to pupation, two on privet, none on forsythia, and three on lilac. Both pupae of  
259 caterpillars raised on privet outdoors exhibited the same deformities of those reared in laboratory  
260 conditions. For our pilot, of 30 *Plagodis kuetzingi* caterpillars in each experimental group, 21  
261 survived to 20 days on ash, 22 on young ash leaves, two on lilac, one on forsythia, and zero on  
262 privet.

263 *Ceratonia undulosa* growth rates (Fig. 2) varied significantly by host plant origin, with  
264 larvae reared on the native host outperforming those reared on the non-native plants at both time  
265 periods (days 0 - 15,  $W = 2092.5$ ; days 15 - 25,  $W = 1985$ ; for both,  $p < 0.001$ ). Conversely, for  
266 *S. kalmiae*, larval growth rates were higher on the non-native hosts than on the native host (days  
267 0 - 15,  $W = 648.5$ ,  $p = 0.003$ ; days 15 - 25,  $W = 257$ ,  $p < 0.001$ ). (Fig. 2). The growth rates for *S.*  
268 *chersis* caterpillars did not significantly differ across host plants at either time period (days 0 -  
269 15,  $W = 493$ ,  $p = 0.23$ ; days 15 - 25,  $W = 454$ ,  $p = 0.56$ ) (Fig. 2). Similarly, caterpillar biomass  
270 attained at 15 and 25 days from hatch (Fig. 3) varied by the host plant. At both time points, the  
271 biomass of *S. kalmiae* caterpillars reared on non-native plants was higher than on the native host  
272 plant (day 15,  $W = 648.5$ ,  $p = 0.003$ ; day 25,  $W = 326$ ,  $p < 0.001$ ), while biomass for *C. undulosa*  
273 was significantly lower (day 15,  $W = 2092.5$ ; day 25,  $W = 2026$ ; for both,  $p < 0.001$ ). Biomass  
274 did not vary significantly across native or non-native plants for *S. chersis* at both 15 and 25 days  
275 (day 15,  $W = 493$ ,  $p = 0.23$ ; day 25,  $W = 457$ ,  $p = 0.53$ ). Median pupal biomass was significantly

276 higher for caterpillars of all three species reared on the non-native plants (*C. undulosa*, W = 302;  
277 *S. kalmiae*, W = 88; *S. chersis*, W = 176; for all,  $p < 0.001$ ).

278 *iNaturalist* survey. We analyzed 5659 records of larval *S. kalmiae*, *S. chersis*, and *C.*  
279 *undulosa* recorded in the northeastern United States. Of 1274 total records on iNaturalist of *S.*  
280 *kalmiae*, 517 were of the larval stage, and of those, 161 had visual host plant information.  
281 Twelve observations were of caterpillars on unknown plants, including six on unknown,  
282 distinctly non-ash plants. Of the positively identified specimens, 119 were on ash species, seven  
283 on privet, 19 on lilac, zero on forsythia, and four on a non-focal plant, common winterberry (*Ilex*  
284 *verticillata* (L.) A. Gray). For *S. chersis*, we processed 614 images. Of those records, 358 were  
285 of caterpillars and 12 retained visual host plant information. Six caterpillars were on ash, one  
286 caterpillar was on privet, five caterpillars were on lilac, and zero caterpillars were on forsythia.  
287 There were 3771 New England records of *C. undulosa* on iNaturalist, 346 of these observations  
288 were of caterpillars. Of the 74 images with visual host plant information, 69 caterpillars were on  
289 ash, three were on privet, two were on lilac, and zero were on forsythia.

290 Walking nighttime surveys revealed the use of privet by late instar *C. undulosa*  
291 caterpillars (n = 2) in the field in mid-July (15-VII-2020) on the suburban roadside and a final  
292 instar *S. kalmiae* caterpillar (n = 1) at Aldworth Manor in August (19-VIII-2020). We collected  
293 and reared wild caterpillars found on privet to pupation. Pupae from caterpillars obtained from  
294 the field as late instars exhibited the same wing malformation as lab-reared pupae. We also  
295 collected a *C. undulosa* (n = 1) and a *S. chersis* caterpillar (n = 1) from ash trees at Aldworth  
296 Manor (19-VIII-2020). No Sphingidae larvae were found on lilac or forsythia.

297 **Discussion**

298           As plant communities undergo rapid changes from the displacement of native species and  
299 the introduction of non-natives, the fate of specialist insects is uncertain. Our study represents an  
300 important assessment of the impacts of non-native plants on specialist herbivores during the  
301 decline of a confamilial native host plant. We found differential effects on each of our focal ash-  
302 feeding species, with *C. undulosa* and *S. chersis* caterpillars experiencing higher mortality rates  
303 on non-native plant foliage than on native ash foliage. In contrast, *S. kalmiae* caterpillar mortality  
304 rates did not differ significantly across treatments. However, despite the differences in  
305 performance metrics across sphingids, all three species experienced pupal malformations when  
306 reared on privet. Individuals of *C. undulosa* collected from outdoor sleeve cages on privet  
307 likewise showed the same pupal deformities as those raised in the lab as did pupae from  
308 caterpillars collected from the field.

309           Anecdotal associations garnered from images posted to the community science platform,  
310 iNaturalist, support the wide-ranging host use of privet in eastern North America by *C. undulosa*  
311 and *S. kalmiae* (iNaturalist, 2022). We were able to circumvent a common pitfall of non-expert  
312 collected data, misidentification (Roy et al. 2016), by expert validation of observation images,  
313 including the identity of caterpillars and their associated plants. Using images from iNaturalist,  
314 we confirmed associations between each of our focal species and ash, as expected. In addition, a  
315 few individuals of each species were associated with each of the alternative host plants, with the  
316 notable exception of forsythia, on which zero caterpillars were found. Further, we found middle-  
317 instar caterpillars of two of our focal sphingid species (*C. undulosa* and *S. kalmiae*) on privet in  
318 our field surveys, and utilization of the plant by both species has been previously observed  
319 (S.P.J., pers. obs.) and documented (Wagner 2005, Robinson et al. 2022). Given that community  
320 science data suffers from spatial bias (Di Cecco et al. 2021), we make no claims about caterpillar

321 abundance on alternative host plants; rather, we show that caterpillar presence on our focal plants  
322 is observable in the field.

323 We found that privet feeding stunted the biomass accumulation rate for *C. undulosa* and  
324 *S. kalmiae*. Given the detrimental effect of privet consumption on pupal development, this  
325 species may constitute an ecological trap for some ash-feeding insects in North America.

326 However, this assertion requires further verification to ensure moths preferentially lay on privet  
327 leaves (Yoon and Read 2016). The developmental deficiencies observed in privet-reared pupae  
328 may be due to several possible interactions with the novel host plant, including differences in  
329 foliar structural compounds, specific leaf area, nutrient levels, and water content (Montti et al.  
330 2016). Privet foliage contains an iridoid glycoside, oleuropein, which has been found to cause  
331 lysine deficiencies and adverse growth impacts in non-privet specialists (Konno et al. 2009).  
332 Moreover, others have shown lysine to be an essential amino acid in lepidopteran growth  
333 (Kasting and McGinnis 1962). A previous study of the corn earworm (*Heliothis zea* Boddie,  
334 1850) found that caterpillars reared on lysine-deficient diets required twice as long as control  
335 caterpillars to reach the pupal stage and that nutrient-deficient diets produced adults with wing  
336 deformities (Rock and Hodgson 1971). Longer growth periods allow more time to accumulate  
337 biomass, lending credence to our finding that pupal weight for all three focal species was higher  
338 on the non-native plants. We offer lysine deficiency as one possible, untested mechanism for the  
339 observed malformations in the current study.

340 Feeding on lilac, forsythia, and privet also negatively affected the growth period, growth  
341 rate, and biomass accumulation of *C. undulosa* compared to feeding on ash, with these metrics  
342 varying by the host plant and severity for *S. chersis*. *Sphinx kalmiae*, in contrast, exhibited  
343 shorter growth periods, and higher growth rates and biomass when feeding on the non-native



344 Oleaceae compared to the native ash. In addition to existing documentation (Wagner 2005), our  
345 results, including a multitude of community scientist reports, suggest *S. kalmiae* has successfully  
346 expanded its host range to include lilac. The variable outcomes observed in our three focal  
347 species reflect the complexity in determining the impacts of non-native plants on native insect  
348 communities, demonstrating that one species of focal host or herbivore is unlikely to adequately  
349 represent the range of interactions. While lilac is potentially a suitable host for *S. kalmiae*, it  
350 proved to be detrimental for *S. chersis* in our study. The differences exhibited by the two *Sphinx*  
351 species further exemplify how sampled focal taxa may not accurately capture the effects of  
352 ecosystem changes for all species even within a single genus.

353         First instar tests are important for determining local population host plant use, which may  
354 differ regionally and from later instars (Tallamy et al. 2020). Two of the three sphingids we  
355 tested may take longer to complete development and accumulate less biomass on select non-  
356 native Oleaceae, but may be able to adopt non-ash hosts. Other ash-specialists may fail entirely if  
357 their early instars cannot accept alternate hosts. For example, our pilot survival assessment of the  
358 ash-specialist geometrid *Plagodis kuetzingi* revealed that hatchling larvae exhibited near-total  
359 failure on any non-native Oleaceae foliage. Given that degree of specialization for many  
360 herbivores is unclear or unknown, first instar tests may aid in our understanding of how host  
361 plant choice and quality impacts population dynamics (Despland 2018).

362         Our results add to the growing record of non-native plants contributing sub-optimally as  
363 host plants for specialist species (Zuefle et al. 2007, Burghardt et al. 2010, Tallamy et al. 2010,  
364 Fickenscher et al. 2014, Sunny et al. 2015, Richard et al. 2019). Burghardt (2010) observed that  
365 93% of native caterpillars in their study were found only on native plant species, with non-native  
366 species contributing to reductions in abundance and richness of lepidopteran species. Other

367 analyses also note the differential performance of lepidopterans on non-native plants, with  
368 specialist species bearing the brunt of the impacts if the non-native plants are not congeneric  
369 with the insects' native hosts (Burghardt et al. 2010). Poor performance on non-native hosts may  
370 partially explain accumulating evidence that dietary and ecological specialist taxa are declining  
371 at faster rates than generalists (Wagner, Fox, et al. 2021, Wagner, Grames, et al. 2021). Of  
372 similar concern is the impact on food webs reliant on foundational species which, if lost without  
373 replacement, will result in the extirpation of native insects and associated macrofauna (Adkins  
374 and Rieske 2013, Youngquist et al. 2017), though more studies examining the impacts of non-  
375 native plants on multiple and higher trophic levels are still needed (Harvey et al. 2010). Reduced  
376 larval biomass impacts adult fecundity and dispersal capability, particularly for Lepidoptera  
377 species that do not feed as adults, which may negatively affect the regional population (Tanmaru  
378 and Haukioja 1996, Jahant-Miller et al. 2021) and could ultimately affect the foraging and  
379 nutritional efficiency of insectivores (Zanette et al. 2000, Threlfall et al. 2012, Razeng and  
380 Watson 2015).

381         The reduced performance of *C. undulosa* and *S. chersis* on non-native plants suggests  
382 that preserving ash and removing privet should be priorities for supporting ash-associated  
383 Lepidoptera. The persistence of specialist caterpillars during the decline of their ash host will  
384 depend on the species composition of habitat experienced by the species (Tallamy et al. 2020).  
385 Landscape homogenization pushes biotic communities into isolated habitat fragments,  
386 emphasizing the need for habitat connectivity between patches (Habel et al. 2020). Such  
387 corridors may take the form of cultivated plants in urban and suburban backyards, which may act  
388 as reservoirs for biodiversity (MacGregor-Fors et al. 2016). Thus, the choices made by zoning  
389 commissions, city planners, landscape architects, and homeowners determine integral

390 components of food webs, and the size of the native insect community that can be supported is  
391 becoming increasingly relevant when making landscaping decisions (Burghardt et al. 2009).  
392 Targeted conservation efforts focused on host-plant-specific plant-insect interactions can have  
393 wide-ranging impacts on arthropod taxa at large but are especially important for communities of  
394 dietary specialists reliant on scarce host plant resources (Khelifa and Mellal 2017) which are less  
395 likely to be supported in novel urban environments (Bergerot et al. 2011, Lee et al. 2015).

396         Given the three non-native Oleaceae we assessed are common shrubs in managed urban  
397 and suburban landscapes, we demonstrate how landscape management decisions can have  
398 supportive or detrimental impacts on insect communities, especially if new horticulturally-  
399 introduced species become invasive (Reichard and White 2001, Niemiera and Holle 2008).  
400 However, *Fraxinus* spp. and these cultivated relatives largely occupy different habitats in New  
401 England. White ash is a forest tree and a once-popular street tree, while lilac, forsythia, and  
402 privet are typically found in disturbed habitats or as ornamental plantings. As such, uncertainty  
403 remains about whether adult moths will exhibit behavioral changes allowing populations to  
404 disperse to appropriate alternate host plants. To mitigate these challenges, connectivity and  
405 quality of matrix habitat are important in uniting populations. Regionally, these interactions may  
406 differ as host plant communities shift. In the Southeastern United States, non-native privet  
407 (*Ligustrum* spp.) is an invading genus of concern (Maddox et al. 2010), but other native  
408 confamilials such as swamp privet (*Forestiera* spp.), white fringetree (*Chionanthus virginicus*),  
409 and American olive (*Cartrema americana*) overlap with *Fraxinus* spp. and may prove supportive  
410 for populations of ash-specialists. Assessing the ash-associated lepidopteran community in the  
411 southeastern region of the United States is necessary to determine potential population declines  
412 and the potential role of privet as a catalyst or antagonist of the process.

413 Our study is limited by the small number of species we considered and the presence of  
414 disease in later stadia caterpillars. The relevance of the pupal weights we recorded is attenuated  
415 by the existence of a pathogen affecting later instar caterpillars. Caterpillar mortality from the  
416 disease was not unique to a single treatment but occurred for a few caterpillars reared on all  
417 hosts. Disease in large-scale caterpillar rearing has been previously documented (Taschenberg  
418 and Roelofs 1970, Kasting et al. 1971) and observed (S.P.J, R.M., G.M.H., pers. obs.).  
419 Fortunately, early instar caterpillars showed no incidence of disease. We suggest that early instar  
420 assessments are of particular relevance to testing the suitability of prospective host plant species  
421 for insect herbivores given that plant physical and chemical defenses are often most effective on  
422 early instar caterpillars, especially neonates (Despland 2018).

423 Our results demonstrate that specialist insect herbivore communities exhibit variation in  
424 their capacity to shift to non-native host plants during the extirpation of their native host. One of  
425 our examined moth species performed better on the three non-native hosts and two of our focal  
426 species performed equivocally or worse on non-native hosts. However, all three species  
427 experienced detrimental pupal deformities after feeding on non-native European privet  
428 (*Ligustrum vulgare*), and larval presence on this plant in the wild suggests this plant is likely an  
429 ecological trap in its invaded range. Our study organisms represent only three of approximately  
430 100 threatened insect taxa specializing on North American ash trees (Wagner and Turo 2015,  
431 2016). Future studies investigating the performance of other ash-specialist arthropod taxa on  
432 alternate hosts, including the rich diversity of other at-risk specialist phloem-, gall-, and root-  
433 feeders, would be beneficial to understand the full impact of ash loss on biodiversity and food  
434 web stability. As eastern and northern forests continue to experience the loss of mature ash trees  
435 to the emerald ash borer, it is becoming evident that ash-reliant herbivores may need to associate

436 with alternate hosts in order to persist. Given the lack of native confamilial Oleaceae in New  
437 England, dietary specialists are imperiled by ash's impending functional or complete extinction.  
438 In the face of unprecedented change, conservation efforts may be necessary to ensure the future  
439 of ash specialists and their connected communities.

440

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447

#### 448 **Contributions of the authors**

449 Grace Horne and Sam Jaffe designed the project and collected data. Grace Horne conducted data  
450 analysis and wrote the first draft of the manuscript. Grace Horne and Rea Manderino contributed  
451 to revisions. All authors approved of the submission.

452

#### 453 **Conflict of interest**

454 The authors have no competing interests to declare.

455

456

#### 457 **Data availability statement**

458 Data will be made available through Dryad at the time the manuscript is accepted for publication.

459

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671 **Figures and Tables**

672 *Figure 1.* Exemplar pupae for (a) malformed, privet-reared *C. undulosa* and (b) healthy *C.*  
673 *undulosa*. Malformations of the wing buds were observed in *C. undulosa*, *S. kalmiae*, and *S.*  
674 *chersis* caterpillars reared on privet.

675

676 *Figure 2.* Kernel densities and interquartile ranges of caterpillar growth rates for caterpillars  
677 surviving to pupation from (a) 0 - 15 days and (b) 15 - 25 days. The median growth rate was  
678 significantly different for caterpillars reared on the native host plant compared to the non-native  
679 plants (for both time periods,  $p < 0.001$ ) except for *S. chersis* ( $p = 0.23$  and  $p = 0.56$ ,  
680 respectively). Growth rates for *S. kalmiae* were significantly higher on the non-native plants,  
681 while growth rates for *C. undulosa* were significantly lower.

682

683 *Figure 3.* Kernel densities and interquartile ranges of caterpillar biomass for caterpillars  
684 surviving to pupation at (a) 15 days and (b) 25 days. The median biomass was significantly  
685 different for caterpillars reared on the native host plant compared to the non-native plants (for  
686 both time periods,  $p < 0.001$ ) except for *S. chersis* ( $p = 0.23$  and  $p = 0.53$ , respectively). Biomass  
687 for *S. kalmiae* was significantly higher on the non-native plants, while biomass for *C. undulosa*  
688 was significantly lower.

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692 Table 1. Survival rates for all caterpillars (*C. undulosa*, n = 154; *S. kalmiae*, n = 120; *S. chersis*,  
693 n = 166) during the first 15 days (early instars), 25 days (middle instars), at pupation, and overall  
694 (pupal viability as a proxy). Survival for *C. undulosa* and *S. chersis* was significantly higher on  
695 the native host than on the non-native plants, whereas survival for *S. kalmiae* was not  
696 significantly different across host plants.

	<b>Species</b>	<b>Native (%)</b>	<b>Non-native (%)</b>	<b>p-value</b>
Early instars				
	<i>C. undulosa</i>	94.87	67.83	< 0.05
	<i>S. kalmiae</i>	90.00	92.22	0.709
	<i>S. chersis</i>	83.33	43.55	< 0.05
Middle instars				
	<i>C. undulosa</i>	94.87	63.48	< 0.05
	<i>S. kalmiae</i>	90.00	92.22	0.709
	<i>S. chersis</i>	73.81	41.13	< 0.05
At pupation				
	<i>C. undulosa</i>	94.87	57.39	< 0.05
	<i>S. kalmiae</i>	86.67	91.11	0.492
	<i>S. chersis</i>	61.90	25.81	< 0.05
Lifetime				
	<i>C. undulosa</i>	94.87	36.52	< 0.05
	<i>S. kalmiae</i>	92.86	76.40	0.061
	<i>S. chersis</i>	54.76	16.13	< 0.05

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