

Geographic variation in performance of a widespread generalist insect herbivore

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Abstract. 1. Generalist herbivores are often widespread and occur in a variety of environments. Due to their broad distribution, it is likely that some populations of generalists will encounter host plants with geographic variation in traits that could affect the herbivore's growth and survival (i.e. performance). However, the geographic pattern of performance has rarely been studied for generalists, especially across large geographic ranges.

2. This study used one of the most generalist herbivore species known, the fall webworm (*Hyphantria cunea* Drury 1773, Erebidae, Lepidoptera), to experimentally test how the performance of a local population of fall webworms varies with increasing geographic distance of the host plant population from the local herbivore population. Specifically, a transplant experiment was used to compare the performance of one fall webworm population feeding on its local host plants with its performance on host populations from two other locations, 1300 and 2600 km away.

3. It was found that fall webworms performed better on their local host plant populations than on populations from other regions, with performance at its lowest when reared on hosts of the same species from the farthest region. It was also found that local fall webworms do not perform well on hosts commonly used by fall webworms at the other two, more distant sites.

4. This study helps to elucidate how the performance of generalist herbivores varies along their geographic range and suggests possible local adaptation to different sets of hosts across sites.

Key words. Bottom-up effects, diet breadth, fall webworm, fitness, insect herbivore, performance.

Introduction

The fitness of generalist herbivores (here defined as a species feeding on hosts from more than two plant families; see also Forister *et al.*, 2015) is relatively unaffected by variation in the quality of host plants as compared with specialist herbivores (Vidal & Murphy, 2018a). The ability to feed on a large array of host plant species that vary geographically in quality could facilitate the expansion in geographic range of generalist herbivores (Janz & Nylin, 2008). Indeed, generalist herbivores

are typically widespread (Hardy *et al.*, 2016) and there is a positive correlation between diet breadth and geographic range (Slatyer *et al.*, 2013). One consequence of this broad range is that widespread generalist herbivores are likely to encounter variable plant traits and variable plant community composition across their range, which could alter performance (i.e. growth and survival) with increasing distance. Furthermore, when the geographic range is broad, some populations of generalists may become geographically isolated. Variable performance together with geographic isolation could influence the genetic divergence of generalist herbivores (e.g. Vidal *et al.*, 2019). Knowing how much the performance of a generalist herbivore varies across its geographic range will aid in understanding their diet breadth evolution and ecology. For instance, significant geographic

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variation in performance together with limited gene flow across sites might facilitate local adaptation. Similarly, evidence of survival on hosts used by allopatric populations but not local populations could indicate their potential to establish in novel environments.

Many factors could influence the pattern of performance of generalist herbivores across their geographic range. For instance, geographic variation in the relative abundance of realised and potential host plant species can lead to variable selection on generalist herbivores across environments (Thompson, 2005). Similarly, although generalist herbivores typically have a wider array of host species to feed on than specialist herbivores, the quality of these hosts is likely to vary depending on the species identity and plant population. Furthermore, generalist herbivores can be locally adapted to their resident plant populations (Traxler & Joern, 1999; Calcagno *et al.*, 2007; Soudi *et al.*, 2015). All these factors, acting in combination or singly, could lead to variation in performance across sites, potentially resulting in local specialisation. In fact, some generalist herbivore species are composed of locally specialised populations (Fox & Morrow, 1981). However, there are still species of generalist herbivores that remain generalised at the population level (e.g. Normark & Johnson, 2011; Clarke, 2017). For these generalist species, it remains unclear how much their performance may vary on the array of host plant they encounter and utilise across their range.

Geographic variation in diet-related aspects of herbivore performance has been mostly shown for specialist herbivores (e.g. Blau & Feeny, 1983; Nitao *et al.*, 1991). These studies found that specialist herbivores are adapted to feed on their local host plant species, enjoying better performance on their local hosts compared with hosts used by other populations (but see Leimu *et al.*, 2005). Of the few cases testing the geographic pattern of performance of generalist herbivores, results suggest that performance can vary even at relatively small geographic scales. For example, Bowers (1986) showed that at least one population of the variable checkerspot (*Euphydryas chalcedona*) had better performance on its local host than on a host used by another population; however, the other variable checkerspot population tested did not vary in performance across hosts (c. 250 km). Hanks and Denno (1994) showed that an armoured scale insect (*Pseudaulacaspis pentagona*) had better performance on nearby hosts (<5 m) than on hosts of the same species farther away (≥ 300 m). On a relatively larger scale, a recent study showed that an extreme generalist (*sensu* Normark & Johnson, 2011), fall webworm (*Hyphantria cunea*), varied in performance on the same plant species across a 700-km range (within the state of Colorado; Vidal & Murphy, 2018b). This last study indicates that the performance of generalist herbivores can vary even when there is considerable gene flow among populations (Vidal *et al.*, 2019). Experiments on an even larger spatial scale (e.g. continent-wide) are needed to elucidate how both geographic distance and turnover in plant community composition together influence generalists' performance in allopatry.

To describe the geographic patterns of generalists' performance on their host plants, we used an extreme case of generalist herbivore: the fall webworm (hereafter FW, *Hyphantria cunea*,

Lepidoptera: Erebidae). Fall webworms feed on hundreds of plant species over their cosmopolitan range. At the population level the FW diet includes dozens of host species from a variety of plant families (Warren & Tadic, 1970; Vidal & Murphy, 2018b). Although most populations are still considered generalists, the number of species of host plants that they use locally and the identity of those species vary considerably across their wide native geographic range (e.g. Vidal & Murphy, 2018b).

Using the FW system, we tested how the geographic distance of hosts influences the performance of an extreme dietary generalist across a 2600-km geographic range. We compared performance of larvae from Colorado feeding on their native hosts with performance on those same host species but from localities 1300 and 2600 km away. We would expect the performance of FW on their host plants to decrease with increasing distance of the local host population. This could be because the plant community composition and traits are more distinct and/or because gene flow among FW populations decreases with geographic distance (Wright, 1943; e.g. Vidal *et al.*, 2019). Besides testing for the possible effects of geographic distance of plant population, we also tested for evidence of local adaptation of FW to the array of host plants used in each location. To do that, we compared the performance of Colorado FW on their commonly used host species in Colorado with performance on hosts used by FW in the other two rearing locations. If Colorado FWs in general have better performance on their native host species across the three sites than on non-native hosts and they perform better on their local populations than on foreign populations, this would indicate possible local adaptation to these host species.

Materials and methods

Study system

Fall webworm is a generalist insect herbivore native to North America that feeds on more than 600 host plant species over its geographic range (Warren & Tadic, 1970). At the species and population levels, FW is a dietary generalist; individual FW larvae, however, typically feed only on the plant species on which the eggs were oviposited. Fall webworm larvae pupate in mid- to late summer and overwinter as pupae. The adults emerge from early May to late July, females lay eggs in a single large clutch on a host plant leaf and sibling larvae feed gregariously, forming a web that encompasses the host plant branches, usually including hundreds of sibling larvae. There are two types of FW that are morphologically, genetically and behaviourally distinct and probably comprise different species (Oliver, 1964; Vidal *et al.*, 2019), the black- and the red-headed larvae; here, we focus on the red-headed type.

Although FW is widespread throughout North America, at least three clear geographic barriers potentially isolate FW populations: the Appalachian Mountains, the Great Plains, and the Rocky Mountains (Fig. 1; Vidal *et al.*, 2019). These three barriers likely restrict gene flow among regions, thus increasing the likelihood that populations are adapted to their set of regional host plants. Vidal *et al.* (2019) showed that the Colorado FW is genetically divergent from eastern red-headed FW (from Connecticut, Illinois, Kansas, Missouri, Maryland, Ohio, and

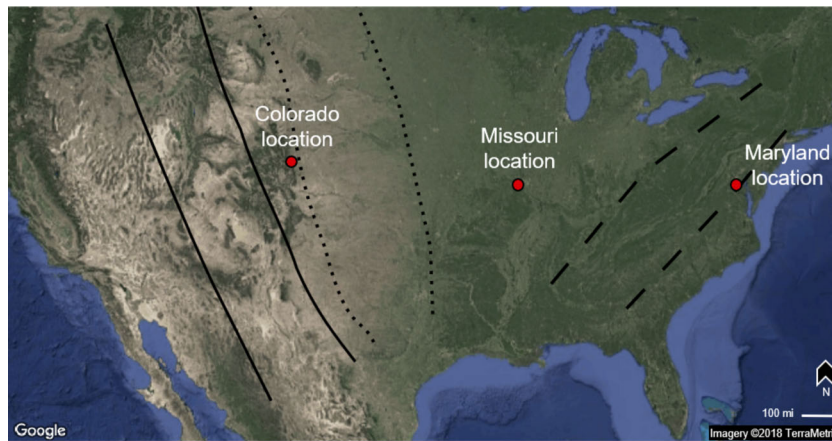


Fig. 1. Map showing the geographic barriers among populations of fall webworms; solid line, Rocky Mountains; dotted line, Great Plains; dashed line, Appalachian Mountains. Red circles represent the locations of the host plants used by red-headed fall webworms in our experiment. Map from Google Earth®. Although the Rocky Mountains represent one important geographic barrier, we did not include populations separated by this barrier in our experiment. [Colour figure can be viewed at wileyonlinelibrary.com].

Pennsylvania), and the Great Plains probably contribute to this divergence. Furthermore, these authors found that geographic distance explained a greater proportion of genetic divergence than did the use of different host plant species (Vidal *et al.*, 2019). Here, we define FW populations as a group of individuals that most likely breed with each other and that have low gene flow with individuals from other locations (as in Vidal & Murphy, 2018b; Vidal *et al.*, 2019).

We examined the performance of FW on host plants used by three populations that are separated by the Great Plains and the Appalachian Mountains: Colorado, Missouri, and Maryland. Using Vidal *et al.* (2019) genetic data, Weir and Cockerham's F_{ST} pairwise comparison between red-headed FW from Colorado and Missouri is 0.158, that between Colorado and Maryland is 0.132, and that between Missouri and Maryland is 0.059. These F_{ST} values indicate low gene flow between Colorado FWs and those from the other two locations, whereas there is a slightly higher gene flow between Missouri and Maryland FWs that are separated by the Appalachian Mountains. In the Colorado Front Range, the most common hosts used by FW are as follows: *Alnus tenuifolia*, *Malus* sp., *Populus angustifolia*, *Populus deltoides*, *Prunus virginiana*, *Salix* sp., and *Ulmus* sp. (Murphy & Loewy, 2015). There is not a current published description of host use by red-headed FW in Missouri or Maryland. However, based on our previous observations, in Missouri the hosts that are usually used are *Betula nigra*, *Carya* sp., *Cercis canadensis*, *Diospyros virginiana*, *Fraxinus* sp., *Liquidambar styraciflua*, *Morus alba*, *Po. deltoides*, and *Prunus serotina*. In Maryland, the most common hosts for red-headed FWs are *Betula* sp., *D. virginiana*, *Juglans nigra*, *Platanus occidentalis*, and *Pr. serotina*.

Experimental design

We reared 10 maternal lines of red-headed FW, in which the egg clutch from each maternal line was divided into three

parts (Fig. 2), with one part reared in Denver, Colorado (all 10 maternal lines), a second part reared in Missouri (University of Missouri-St Louis; nine out of the 10 maternal lines were shipped) and a third part reared in Washington, D.C. (George Washington University – although the larvae were reared in D.C., the host plants were collected from nearby sites in suburban Maryland; all 10 maternal lines were used). We reared all larvae in the same conditions and with similar temperature and day length in laboratories across sites (LD 12:12 h, 25 °C), thus controlling for environmental differences. The Maryland site is *c.* 2600 km from Denver, while the Missouri site is approximately half that distance (1300 km). Of the 10 maternal lines of FW, four were obtained from the laboratory colony at the University of Denver, which was started the previous generation from field-collected third-instar larvae that were feeding on *Alnus* sp., *Po. angustifolia*, *Pr. virginiana*, or *Salix* sp. (captive larvae were fed foliage from the same host individuals as originally collected in the field until pupation). The other six maternal lines were obtained in the field as neonate larvae; all maternal lines originated from Colorado [nine from Boulder (40.090013°N, 105.359962°W) or Jefferson County (39.746944°N, 105.210833°W), and one from Garfield County (39.7273511°N, 108.6020411°W)]. Of the six maternal lines collected in the field, four were collected from choke cherry (*Pr. virginiana*) and two were collected from narrow leaf cottonwood (*Po. angustifolia*). Subdivisions of each maternal line were shipped as eggs or neonate larvae to Missouri or Maryland using overnight shipping. The transfer of neonates from their original host plant in the field to the treatment plants and the origin of maternal lines (laboratory or field) did not affect their survival (transfer: $\chi^2 = 0.88$, d.f. = 4, $P = 0.93$; origin: $z = -0.42$, $P = 0.67$). Each subdivision of each maternal line was then subdivided again at each site (Colorado, Missouri, and Maryland) onto the three host plant treatments used in each specific location (Fig. 2). We chose to use three host species per location because we were limited by how many larvae we would be able to use per maternal line. Although egg clutches can sometimes

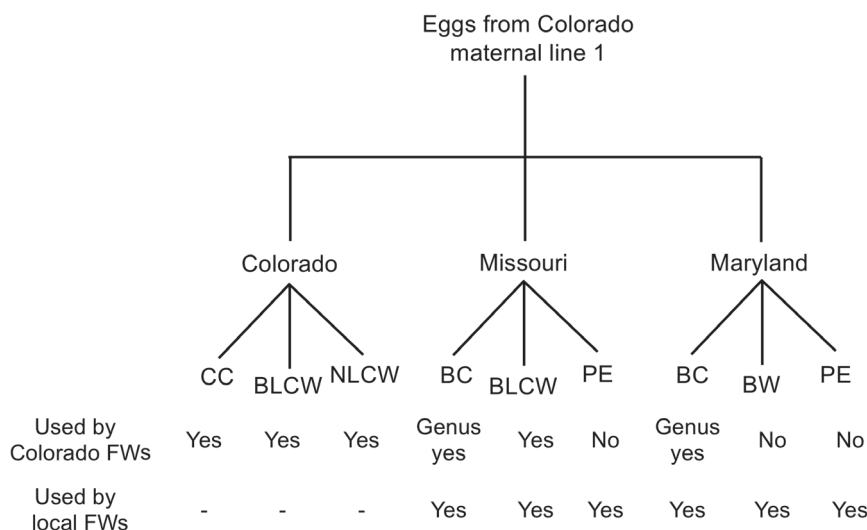


Fig. 2. Experimental design. The diagram shows how eggs were split for maternal line 1 (repeated similarly for all 10 maternal lines). The state names (Colorado, Missouri and Maryland) are where the larvae were reared and the host plant abbreviations below each state indicate on which plants the larvae were reared in each location, as follows: CC, choke cherry; BLCW, broad leaf cottonwood; NLCW, narrow leaf cottonwood; BC, black cherry; PE, persimmon; BW, black walnut. The information immediately below the plant abbreviations shows the use in nature of these different host plants by red-headed fall webworms from Colorado and the use by the local fall webworm population outside Colorado (Missouri or Maryland).

include > 150 eggs, not all are viable, and neonate larvae can also experience high mortality. Thus, we designed the experiment to include three hosts per location so that we would be able to obtain reasonable subdivisions of larvae per host at each locality (each locality would have around 40 eggs/neonates to set up the experiment, which, combined, would require 120 eggs per clutch).

In each location, we fed Colorado larvae a mix of host species that are frequently used by the local populations of red-headed FW (at the rearing site) based on previous observations, and hosts that are shared among locations (Fig. 2). The hosts that are shared among locations were used to test the hypothesis that performance would vary with distance. The hosts that are unique in each location were used to consider the possibility that FW larvae use locally the best quality host available, or the alternative hypothesis that local larvae are locally adapted to different sets of hosts in different locations. We chose the hosts from Colorado based on plant species frequently used by Colorado FWs and, when possible, that are present in Missouri and Maryland (Murphy & Loewy, 2015; Vidal & Murphy, 2018b). Hosts uniquely used in Missouri and Maryland were chosen based on previous observations of local red-headed larvae feeding frequently on these hosts for many consecutive years (R.J. Marquis and J.T. Lill, pers. obs.). In Colorado, the host plants were choke cherry, broad leaf cottonwood (*Po. deltoides*, Salicaceae), and narrow leaf cottonwood. In Missouri, the host plants were broad leaf cottonwood, black cherry (*Pr. serotina*, Rosaceae), and persimmon (*Diospyros virginiana*, Ebenaceae). In Maryland, the host plants were persimmon, black cherry, and black walnut (*Juglans nigra*, Juglandaceae) (Fig. 2). Therefore, Colorado and Missouri shared broad leaf cottonwood as a host plant, Missouri and Maryland shared persimmon, and the genus *Prunus* (either *P. serotina* or *P. virginiana*) was

common to all locations. While black cherry and choke cherry are different species, our results from previous rearing efforts of FW from Colorado suggested that FW exhibits similar performance on the two congeners.

All rearing methods followed Loewy *et al.* (2013), where more detailed information is provided. Briefly, we reared the larvae in containers providing foliage *ad libitum*. Early-instar larvae do not survive well by themselves, and therefore we started the experiment with multiple larvae in the same container and split them into individual containers as the larvae grew. We checked larvae every other day and changed or included new leaves when necessary, and we removed frass weekly. We recorded the development time, pupal mass, and survival to pupation of 10–15 larvae from each maternal line reared on each host plant, totalling *c.* 90 larvae per maternal line (854 larvae total). We classified the sexes following Loewy *et al.* (2013) and measured pupal mass to the nearest 0.01 mg, at 10 (± 1) days after pupation. Development time may be an important feature impacting larval survival under natural conditions due to its predicted positive relationship with frequency of predation and parasitism (Price *et al.*, 1980). Pupal mass and survival are fitness measures related to plant quality; larvae reared on plants of high quality have greater survival and greater pupal mass than larvae reared on poor-quality hosts, and as pupal mass is directly related to female fecundity, it is often used as a reliable fitness proxy (Gripenberg *et al.*, 2010; Loewy *et al.*, 2013). To facilitate comparisons, we used a composite measure of fitness, which we called ‘fitness score’ (e.g. Murphy & Loewy, 2015), by multiplying the mean pupal mass per maternal line on each host by the proportion of surviving individuals for that same maternal line. We did not include development time in the measure of fitness score because we did not know the exact hatching date of individuals collected as neonates.

Statistical analyses

To quantify how performance varies across host plant populations, we first tested if geographic distance influenced performance by comparing the fitness score of Colorado FWs on the different populations of the same host plant species. We used the three hosts that were found on at least two locations: broad leaf cottonwood, persimmon, and black cherry. We compared the performance of Colorado FWs within each of these shared host plants using ANOVA. For each of these three host plants, fitness score was the response variable, and the location reared (i.e. the source location of host plant) was the fixed term.

To test if there is possible local adaptation of Colorado FWs to the host plants they normally use, we then determined if FWs had higher performance on frequently versus infrequently used plants, in which cherries (*Prunus* sp.) and cottonwoods (*Populus* sp.) were considered to be frequently used by Colorado FWs, whereas persimmon and black walnut were classified as infrequently used (following Murphy & Loewy, 2015). We used generalised linear mixed models (GLMMs) using the package AFEX (Singmann *et al.*, 2017) and function 'mixed' to test the prediction that larvae would have better performance on frequently used host plants (with 1 = frequent host and 0 = infrequent host); maternal line was considered as a random effect. We included sex of pupa as a fixed effect in the models testing pupal mass, as usually females have higher values of pupal mass than do males (Loewy *et al.*, 2013). For pupal mass and development time, we conducted a linear mixed model with a normal distribution. For survival we used a generalised linear mixed model with 'likelihood-ratio test' method. We further compared the performance of FW on each host plant using GLMM. The fixed effects were rearing host and location, as well as rearing host \times location interaction, with maternal line as a random effect. We again included sex of pupa as a fixed effect in the model with pupal mass. For the fitness score measurement, we performed an ANOVA with the interaction between rearing location and host treatment as the fixed effect. We performed Tukey's honestly significant difference pairwise comparisons with all our models to determine on which hosts larvae had higher performance using the package MULTCOMP with function 'ghlt' to test linear hypotheses for the mixed models, and we used Bonferroni corrections for more than six comparisons (Hothorn *et al.*, 2008). All analyses were performed in R environment 3.4.1 (R Development Core Team, 2011).

Results

Red-headed FW larvae from Colorado had a greater fitness score on near than on farther away populations of the same host plant species (considering all three species of shared hosts together: $F_{1,47} = 16.37$, $P = 0.0002$). When considering each host species individually, Colorado FW larvae had similar fitness on broad leaf cottonwood from Colorado and Missouri (Fig. 3a, top; $F_{1,14} = 2.4$, $P = 0.14$); however, when we excluded maternal lines that failed to develop entirely (two maternal lines in Colorado and two in Missouri; Table S1), Colorado FW larvae had greater fitness on Colorado broad leaf cottonwood than

Table 1. Statistical tests summary from (generalized) linear mixed models. Models testing pupal mass also included sex of pupa as a fixed effect with $P < 0.0001$.

Fixed effects	d.f.	<i>F</i>	<i>P</i> -value
Pupal mass			
Host plant	4, 212.92	4.67	0.001
Rearing site	2, 213.92	0.73	0.49
Frequent versus infrequent	1, 474.31	32.34	< 0.0001
Host plant \times rearing site	2, 212.81	20.78	< 0.0001
Development time			
Host plant	4, 214.7	4.66	0.001
Rearing site	2, 215.3	0.50	0.61
Frequent versus infrequent	1, 14.9	4.04	0.06
Host plant \times rearing site	2, 215.6	22.42	< 0.0001
Fitness score			
Host plant	4, 77	8.56	< 0.0001
Rearing site	2, 77	8.16	0.0006
Frequent versus infrequent	1, 84	23.94	< 0.0001
Host plant \times rearing site	2, 77	7.33	0.001
Fixed effect	d.f.	χ^2	<i>P</i> -value
Survival			
Host plant	4	36.56	< 0.0001
Rearing site	2	55.96	< 0.0001
Frequent versus infrequent	1	11.54	0.0007
Host plant \times rearing site	2	15.23	0.0005

on Missouri broad leaf cottonwood ($F_{1,10} = 10.42$, $P = 0.009$). Even on the hosts not used by Colorado FWs, the distance from the source population also predicted performance. Specifically, Colorado FWs had greater fitness on persimmon and black cherry from the closer region of Missouri than on these same host species from the more distant region of Maryland (Fig. 3a, bottom; persimmon, $F_{1,14} = 10.64$, $P = 0.006$; black cherry, $F_{1,15} = 9.59$, $P = 0.007$). There was no effect of maternal line on fitness score ($F_{1,8} = 1.01$, $P = 0.5$).

Colorado FW larvae had better performance when reared on their frequently used Colorado hosts than on plants that are not used in Colorado (Table 1). The local source of host plants was an important factor as we found a significant interaction between rearing host plant species and rearing location for pupal mass, development time, and survival (Table 1). When considering pupal mass and survival together (fitness score), there was no difference in fitness on the hosts used in Colorado, whereas in Missouri, Colorado FW larvae performed better on black cherry than on broad leaf cottonwood, and in Maryland, black cherry was a better host than persimmon (Fig. 3b; see Fig. S1 for pupal mass, development time, and survival rate across host plants).

Discussion

Generalist herbivores are geographically widespread in their distribution, occurring in a variety of environments (e.g. Hardy *et al.*, 2016). As such, it is likely that some populations will experience reduced gene flow, which can lead to local adaptation to their host plant populations (Kawecki & Ebert, 2004). Here,

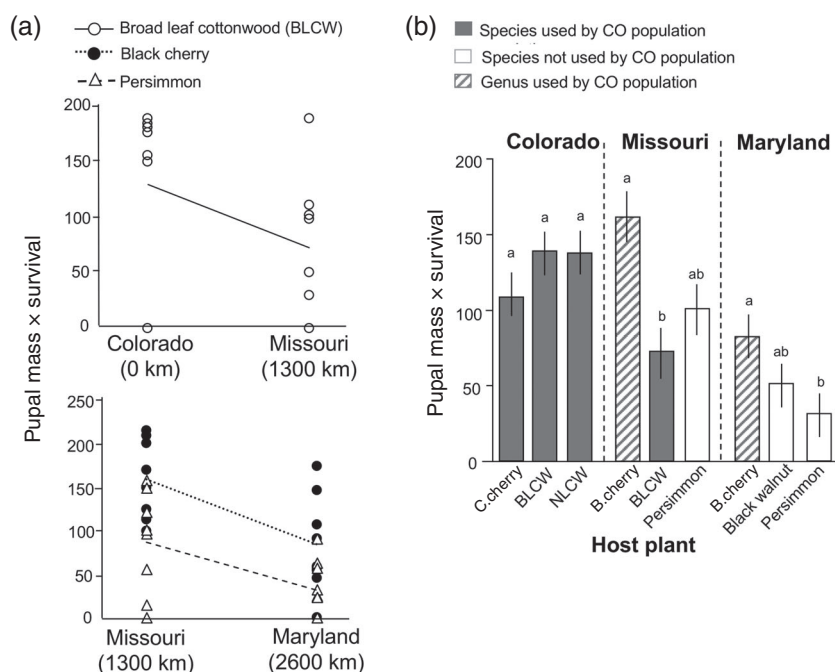


Fig. 3. Fitness score of Colorado fall webworms measured as survival \times pupal mass. (a) Comparison between near and far away populations of each host plant species. The x -axis represents the location of the host plant used and the distance from Colorado (the source population of fall webworms). (b) Comparison among the three host plant species used in each location (mean \pm SE). Dark grey bars represent hosts used by red-headed fall webworms in Colorado. White bars are hosts that are used by red-headed fall webworm in Missouri or Maryland, but not by fall webworm in Colorado. Striped bars represent a shared genus across location, but we used different species in Colorado compared with the eastern locations. Letters represent pairwise comparisons within each rearing location. All Tukey's pairwise comparisons were Bonferroni-corrected. Number of larvae per host plant are as follows: Colorado – choke cherry (C. cherry, $n = 96$), broad leaf cottonwood (BLCW, $n = 101$), narrow leaf cottonwood (NLCW, $n = 100$); Missouri – black cherry (B. cherry, $n = 79$), broad leaf cottonwood (BLCW, $n = 74$), persimmon ($n = 72$); Maryland – B. cherry ($n = 118$), black walnut ($n = 107$), persimmon ($n = 107$).

we found evidence of possible local adaptation of FW to the set of host plants they use locally (Table 1). Furthermore, we found that FW performance decreased with increasing geographic distance of host plant populations (Fig. 3a). These results suggest that generalist herbivores, even an extreme generalist such as the FW, are sensitive to variation in host plant quality across locations. However, the ability of generalist herbivores to survive in spite of lower performance on unfamiliar host plants could enable their range expansion.

We showed that FWs had higher performance on foliage from their local host plant population of broad leaf cottonwood compared with that of a distant population of the same host plant species. The performance of Colorado FWs was also higher on persimmon and black cherry from the near plant population of Missouri compared with Maryland. Our finding supports the conclusion that plants from the same species might vary geographically in traits that can influence insect herbivore performance (see also Moles *et al.*, 2011). For instance, broad leaf cottonwood quality as a host for FW can vary even at relatively small geographic scales of < 30 km (S.M. Murphy, unpublished). Cottonwoods have phenolic glycosides as chemical compounds that can negatively affect insect herbivores, especially generalists (Boeckler *et al.*, 2011). The concentration of phenolic glycosides seems to be genetically determined and can also vary with environmental factors, which can result

in high variation between genotypes (Boeckler *et al.*, 2011). Thus, variation in phenolic glycosides in cottonwoods could have accounted for the decreased FW performance on Missouri plants compared with Colorado plants.

Variation in environmental factors across sites could also have influenced the quality of persimmon and cherry as hosts for FW. For instance, both persimmons and cherries have tannins, and the amount of tannin in plant material can vary with nutrient availability in soil and can correlate with nutritional quality of the plant itself for the herbivore (Bernays *et al.*, 1989). Furthermore, it is known that other herbivores feeding on the same host can decrease its quality for other competing herbivores (Kaplan & Denno, 2007). For example, early-season herbivory by western tent caterpillars (*Malacosoma californicum*, Lasiocampidae) on choke cherry in Colorado makes the remaining and sprouting leaves tougher (Barnes & Murphy, 2018), which may negatively affect FWs later in the season. Thus, the factors leading to geographic variation in performance on different populations of the same plant species could be a combination of genetic and environmental (abiotic and biotic) differences across sites.

Regardless of the trait influencing the variation in performance across sites, the overall pattern of better performance when reared on hosts from nearby populations suggests that the quality of hosts for the source population of FW decreases with increasing distance from the source population. Spatial

scale has been argued to be an important aspect of the mosaic of local adaptation in host–parasite systems at large (Gandon & Van Zandt, 1998). Cogni and Futuyama (2009) found evidence of local adaptation by *Utetheisa ornatrix* (Erebidae) to the sympatric host only at the continental scale (> 6000 km), yet there was no evidence of local adaptation when testing nearer populations (160–200 km apart). Kalske *et al.* (2016) found that the strength of local adaptation increases with increasing distance for populations of the herbivore *Abrostola asclepiadis* (Noctuidae) and their host plants. Similarly, our results also show that a generalist herbivore may be adapted to its local host populations. The communities of plants occurring in the geographic range we studied are drastically different, especially when comparing host plant communities in Colorado with those in Missouri and Maryland. Thus, the pattern of performance might depend on there being turnover in either plant quality or plant species community composition across locations, which can be more pronounced with increased distances.

Our results demonstrate that the Colorado FW does not perform well on hosts that are used by FWs in the east (i.e. infrequently used or unavailable hosts in Colorado), which is consistent with local adaptation of Colorado FWs to local host species. Gene flow, or lack thereof, between FW populations could account for the variation in performance we encountered within and across locations. The low level of gene flow of Colorado FWs with FWs from Missouri and Maryland ($F_{ST} = 0.158$ and 0.132, respectively; Vidal *et al.*, 2019) could facilitate local adaptation of Colorado FWs to host species that are used locally. However, although our results indicate possible local adaptation, we lack data to definitely support this proposition. According to Kawecki and Ebert (2004), local adaptation can be tested using the home versus away (i.e. comparing fitness of an organism locally with its fitness in a different location) and the local versus foreign (i.e. comparing fitness of the local population with fitness of a foreign population in the same local condition) criteria, the latter constituting stronger evidence of local adaptation than the former. Here, we employed the home versus away criterion; however, we do not currently have data to test the local versus foreign criterion. Thus, to have reliable evidence of local adaptation, future research should compare performance of Colorado FWs with that of eastern FWs on their local hosts.

The ability to feed on many host plant species is thought to facilitate geographic range expansion of generalist herbivores (e.g. Janz & Nylin, 2008; Slatyer *et al.*, 2013). Furthermore, generalism has been linked with invasion success (Ehrllich, 1986). The FW is an invasive species outside its native range of Central and North America and is now considered a pest in its non-native ranges of Asia and Europe (Kiritani & Morimoto, 2004). Although Colorado FWs had lower performance on most non-local host plant populations, including lower survival rate, a considerable portion of individuals survived on every treatment host, even hosts that are not commonly used in Colorado (e.g. persimmon and black walnut). Fall webworms that survived on infrequently encountered hosts could eventually become locally adapted to the new host plant species or population. The history of FW range expansion in North America is unknown, and thus

hosts used by eastern FWs could represent ancestral hosts and hosts used in Colorado could be novel hosts, or vice versa. Regardless, although we found that Colorado FWs experienced low fitness on the hosts that are never used because they do not occur in Colorado, the ability to feed and survive on these disparate hosts indicate the possibility of establishing in novel environments.

Geographic variation in performance does not mean that generalist herbivores will ultimately become locally specialised. It has been argued that generalist herbivores are composed of locally specialised populations or of a complex of cryptic specialist species (Fox & Morrow, 1981; Loxdale & Harvey, 2016). However, the FW constitutes a clear example of a generalist that is neither of these things. Vidal *et al.* (2019) showed that FWs in Colorado, with populations that are up to c. 700 km apart, are composed of somewhat panmictic subpopulations, thus rejecting the possibility of being cryptic species. We have now shown that even though FWs can vary in performance across locations, possibly leading to local adaptation, they are still local generalists. Furthermore, Loxdale *et al.* (2011) argue that generalism is a transitory phase and that specialisation is required for genetic divergence and speciation. However, there is strong genetic divergence between Colorado FWs and eastern FWs (Vidal *et al.*, 2019), providing evidence that genetic divergence can occur without diet specialisation. More studies focusing on generalists are needed to advance our knowledge of the generalist/specialist debate (e.g. Clarke, 2017), especially with generalists at population and even individual scales.

Our study is an important step forwards in understanding the interactions between generalist herbivores and their host plants. The variation in performance at the continental scale that we found suggests that the differences in plant traits can potentially deter a generalist herbivore from expanding its range, but the few individuals that survive may become locally adapted to their novel host population. Ultimately, geographic isolation and local adaptation could facilitate genetic divergence among populations of widespread insect herbivores, an important step for their diversification, without necessarily requiring local specialisation. The FW provides an excellent system to test diversification without specialisation in insect herbivores, especially considering that there are currently two types of FW that are probably different species.

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Author contributions

SMM and JTL conceived the experiment. MCV, SMM, JTL and RJM designed and performed the experiments. MCV analysed the data and wrote the first draft. MCV, SMM, JTL and RJM contributed equally to revisions.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Fitness score (survival \times pupal mass) of all maternal lines used for the geographic distance comparison on shared host plants. Fitness scores from hosts that were not used in this comparison are not included. A fitness score of 0 represents maternal lines for which none of the larvae survived, and asterisks represent data excluded from the analysis with broad leaf cottonwood.

Fig. S1. Performance measures (\pm SE) of fall webworms on the different host plant treatments, pupal mass, development time, and proportion of survival, respectively, of Colorado red-headed fall webworms on choke cherry, broad leaf cottonwood (BLCW) and NLCW from Colorado, black cherry, BLCW and persimmon from Missouri, black cherry, black walnut, persimmon and Maryland. Letters above bars represent Tukey's pairwise comparisons; a–c, comparisons within locations, x–z, comparisons of the same plant genus/species across sites.

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