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ORIGINAL PAPER

Spatial and temporal variability in the structure of the multiple-herbivore community of horsenettle, and evidence for evolutionary responses in host-plant resistance

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Abstract

The geographic mosaic model of plant–herbivore coevolution asserts that interactions between a plant species and an herbivore species vary in intensity among populations across the plant's geographic range. Despite this model's intuitive appeal, data to investigate its implications for the type of complex, multiple-herbivore communities that occur in nature are scant. This paper reports on the results of 2 years of field surveys of damage by five leaf herbivores and one stem herbivore in four *Solanum carolinense* (horsenettle) populations, combined with results of a common-garden study quantifying the mean resistance levels of the plants from each field against each of the six herbivores. The relative amounts of damage caused by each species (representing the "herbivore-community structure") differed significantly among the four fields. The plants were much more heavily damaged in the 2nd year than in the first, but the herbivore-community structure remained stable within each field between years. Overall, the amount of damage by species of herbivores in a field tended to be positively correlated with the plants' levels of resistance that were measured in the common garden ($r = 0.40$, $P = 0.05$). Specifically, for five of the six herbivores, greater damage in the field was associated with greater plant resistance. This result suggests that horsenettle's evolution of resistance against specific herbivores can occur rather quickly within fields, creating a local-scale mosaic of populations specifically adapted to the particular structure of the herbivore community that they are facing, but that herbivore-community structure is not strongly determined by plant resistance.

Keywords Community structure · Ecoevolutionary dynamics · Geographic mosaic · Plant–herbivore interactions · Spatial variation · Temporal variation

Introduction

A central goal of community ecology is to identify factors that contribute to the abundance of individuals of different species within groups of interacting organisms (i.e., a community's "structure") (Wisz et al. 2013; D'Amen et al. 2017). Traditional models of community assembly contend that community structure is controlled by historical contingency and stochastic processes based on the pool of species available in an area, plus perhaps abiotic or biotic "environmental-filtering" factors (Strong et al. 1984; Lawton et al. 1993; Lewinsohn et al. 2005; HilleRisLambers et al. 2012). In contrast, a growing body of theory suggests a more evolutionarily dynamic picture of community structure (Lankau 2011; Koch et al. 2014; Mittelbach and Schemske 2015; Andreazzi et al. 2018; terHorst et al. 2018). In particular, the discipline of ecoevolutionary dynamics is being built around the hypothesis that ecological interactions can lead to evolutionary changes that are rapid enough to affect the interactions among the species, which then feed back into more evolutionary responses, and so on (Schoener 2011; Vasseur et al. 2011; Barraclough 2015; Hendry 2017; Schreiber et al. 2018).

Communities of plants and their herbivores have been a popular focus for generating and testing ecoevolutionary

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hypotheses because these communities are ubiquitous, they are relatively easy to observe and manipulate, and they have played a central role throughout the history of coevolutionary studies (Ehrlich and Raven 1964; Rausher 2001; terHorst et al. 2018). In the context of plant–herbivore interactions, the ideas of ecoevolutionary dynamics mesh well with the ideas of the geographic mosaic theory of coevolution (Johnson and Stinchcombe 2007; Haloin and Strauss 2008; Muola et al. 2010). The geographic mosaic theory emphasizes spatial variation in herbivore-community structure, hypothesizing in part that there are hotspots and coldspots of plant–herbivore coevolution that can be caused by differences in herbivore-community structure throughout a host-plants' geographic range (Thompson 1994, 1999; Agrawal et al. 2006). Given enough time, signals of coevolution, such as increases in plant resistance to common herbivores, will be evident in the hotspots (Gómez and Zamora 2000; Haloin and Strauss 2008; Bischoff and Trémulot 2011; Garrido et al. 2012; Züst et al. 2012; De-la-Cruz et al. 2020a).

Indeed, a growing body of research is blurring the traditional distinction between ecological time and evolutionary time (Thompson 1998b; Hairston et al. 2005; Koch et al. 2014; Hendry 2017), and studies of plant–herbivore communities are helping to lead the way (Agrawal et al. 2012, 2013; Ramos and Schiestl 2019; Kalske and Kessler 2020). Several recent studies have found evidence of rapid evolutionary decreases in resistance in plant populations when herbivores are removed (Bode and Kessler 2012; Züst et al. 2012; Uesugi and Kessler 2016; Agrawal et al. 2018; Coverdale and Agrawal 2022), or rapid increases in resistance when plant populations are exposed to new herbivores (Castells et al. 2005). For example, in a 5-year field experiment, Agrawal et al. (2012) found that suppression of insect herbivores led to significant evolutionary decreases in resistance traits in evening primrose (*Oenthera biennis*). Such evidence suggests that spatial variation in herbivore levels could very well result in mosaics wherein plant populations vary in resistance levels.

Sizes of herbivore populations obviously vary among populations of their host plants over large geographic scales, such as across landscapes or among continents, due to such factors as barriers to dispersal and differences in abiotic conditions and biotic communities (Lawton et al. 1993; Baskett and Schemske 2018; Moreira et al. 2018a; Hahn et al. 2019; Núñez-Farfán and Valverde 2020). Surveys provide evidence for smaller, regional variation in herbivore densities and damage levels across populations of a variety of plant species (Gómez and Zamora 2000; Thompson and Cunningham 2002; Züst et al. 2012; Lynn and Fridley 2019; Verçosa et al. 2019; De-la-Cruz et al. 2020b). However, there has been less focus on documenting variation in herbivore community structure at even smaller scales (Karban and Nagasaka 2004; Bischoff and Trémulot 2011; Valdéz and Ehrlén 2017; Kalske and Kessler 2020; Sanczuk et al. 2021), such as among local plant populations that make up a metapopulation. Such populations are connected by at least some gene flow that can influence the rate of evolution of resistance. Data at this scale would shed insight into the question of whether interpopulation variation in herbivore-community structure tends to be caused by, to be a result of, or to be unrelated to resistance levels in the host-plant populations that have presumably evolved in response to damage by the herbivores (Loughnan and Williams 2019; Sanczuk et al. 2021).

The size of an herbivore population also can vary greatly from year to year in response to such factors as weather, intraspecific competition, disease, or predation. The resulting temporal variation in damage levels caused by the herbivore may slow evolutionary responses in the plant, as the selective benefit of resistance to that herbivore will vary from year to year, perhaps being outweighed by costs of resistance when herbivory is low (Løe et al. 2007; Agrawal 2011; Hare 2012; Rausher and Huang 2016). Temporal variation in the structure of a *multiple-herbivore* community could pose an even more complex set of constraints on the evolution of resistance (Lankau 2007; Lankau and Strauss 2008; Muola et al. 2010; Lay et al. 2011; Kalske and Kessler 2020). For instance, genetic correlations in resistances to different herbivores, ecological interactions among species of herbivores, or nonadditivity of combined impact of different herbivores on host-plant fitness can all act either to facilitate or to constrain the evolution of plant resistances against members of the herbivore community (Hougen-Eitzman and Rausher 1994; Rausher 1996; Stinchcombe and Rausher 2001; Wise 2009, 2023; terHorst et al. 2018). For a hotspot of coevolution to occur among plant populations, the rate of evolution must outpace temporal variation in selective forces across the lifetime of that plant population. Although there is no question that population sizes of herbivorous insects vary over time (Thompson 1998a; Karban and Nagasaka 2004), there is relatively little field data on year-to-year variation in the structure of multi-herbivore communities within host-plant populations on the metapopulation scale that may be most relevant to the geographic mosaic theory of plant–herbivore coevolution (Lawton and Gaston 1989; Lay et al. 2013).

Some insight into the dynamics of geographic mosaics of coevolution may be found by measuring, in a set of local host-plant populations within a metapopulation, both the herbivore-community structure and the genetically based resistance levels of the plants against those herbivores (Gómez and Zamora 2000; Karban and Nagasaka 2004; Woods et al. 2012; Verçosa et al. 2019; Kalske and Kessler 2020). A correlation between the abundance of an herbivore species and resistance of the plants to that species would be consistent with coevolution between the pair (Crémieux et al. 2008; Hahn et al. 2019; De-la-Cruz et al. 2020b). A negative correlation between an herbivore species' abundance and plant resistance to that herbivore would suggest that resistance limits the abundance of the herbivore. In contrast, a positive correlation would indicate that resistance does not play as large of a role in controlling an herbivore's abundance. However, a positive correlation still suggests that plant populations may be evolving higher levels of resistance in response to damage by that herbivore. Finally, a lack of correlation would suggest that the plant's evolution of resistance to an herbivore is not rapid enough to be detected at that spatial and temporal scale, and that the herbivore's abundance is controlled by factors other than plant resistance traits (Bischoff and Trémulot 2011).

To address these issues, I examined spatial and temporal variation in damage by leaf-feeding and stem-boring herbivores of the perennial herbaceous weed horsenettle (*Solanum carolinense*). Specifically, I measured herbivore damage in four horsenettle populations in northern Virginia in two consecutive years that exhibited extreme climatic variation (viz., El Niño and La Niña cycles). I compared these field data with damage levels in a common-garden experiment in which 24 clonal replicates of ten genets from each of the four fields were transplanted into an existing oldfield population of horsenettle. Here, I use these data sets to address the following questions: (1) How much does the community structure of herbivores (as characterized by relative levels of feeding damage) differ among horsenettle populations at a local scale? (2) How much variation is there in levels of herbivore damage from one year to the next? (3) How consistent is the herbivore-community structure between years with very different weather? 4) Does herbivore-community structure relate to genetic differences in resistance levels among horsenettle populations?

Methods

Study species

Solanum carolinense L. (Solanaceae), or horsenettle, is a perennial herb that thrives in disturbed sites, such as roadsides and old agricultural fields (Ilnicki et al. 1962; Bassett and Munro 1986). Horsenettle is native to the southeastern United States, but it is now considered to be a noxious weed throughout much of North America, and it is invasive in Europe and Asia (Gorrell et al. 1981; Nichols et al. 1991; NAPPO 2003; Follak and Strauss 2010). Horsenettle has been widely studied because of its economic relevance—both as a direct pest of crops and pastures (Albert 1960; Freeland 1982; Frank 1990; Whaley and Vangessel 2002) and as a reservoir of natural enemies of its taxonomic relatives, including potatoes, tomatoes, eggplants, peppers, and tobacco (Judd et al. 1991; Mena-Covarrubias et al. 1996; Aguilar and Servín 2000; Wise 2018). Thus, its community of herbivores has been rather well characterized (Somes 1916; Bailey and Kok 1978; Nichols et al. 1992; Imura 2003; Wise 2007b).

The current study focuses on the following five specialist leaf-feeding herbivores (folivores) and one stem borer:

1) *Tildenia inconspicuella* (Murtfeldt) (Lepidoptera: Gelechiidae). Larvae of the "eggplant leafminer" feed in mines on the edges of horsenettle leaves (Gross 1986). The browned leaf areas remain as evidence of their feeding long after the larvae pupate.
2) *Gratiana pallidula* (Boheman) (Coleoptera: Chrysomelidae). Larvae and adults of the "eggplant tortoise beetle" feed on areas of leaf tissue between veins, causing characteristic oval-shaped holes in the leaves' surface (Wise 2007b).
3) *Leptinotarsa juncta* (Germar) (Coleoptera: Chrysomelidae). Larvae (often in groups) and adults of the "false potato beetle" feed from the edges of horsenettle leaves, often consuming large sections of individual leaves, but only rarely consuming entire leaves (Wise 2007b).
4) *Epitrix fuscula* Crotch (Coleoptera: Chrysomelidae). Adults of the "eggplant flea beetle" chew small holes through horsenettle leaves, resulting in a "shotgun" appearance characteristic of flea-beetle damage (Wise and Sacchi 1996; Wise and Weinberg 2002). Larvae of this species feed underground on horsenettle roots.
5) *Gargaphia solani* Heidemann (Hemiptera: Tingidae). Both adults and nymphs of the "eggplant lace bug" suck fluids from leaf parenchyma cells, but most of the damage is done by nymphs as they feed in large groups that move from leaf to leaf, causing increasing amounts of damage as they grow (Wise and Mudrak 2021).
6) *Trichobaris trinotata* (Say) (Coleoptera: Curculionidae). Adult females of the "potato stalk borer" lay eggs singly in the apex of young horsenettle ramets, and larvae spend the spring and summer boring downward through the stem, pupating in the base of the stem near the soil surface (Wise 2018).

Field sites

In 1997, I chose four populations of horsenettle with different management histories to serve as sites for herbivore censuses. Two of these sites occurred on the University of Virginia's Blandy Experimental Farm in Clarke County, VA, USA: an old hayfield that was last disturbed in 1985 and a site managed as a wildflower and native grass meadow. These sites will be referred to respectively as the "Blandy Oldfield" and the "Blandy Meadow." The third site was located in an old horse pasture at Sky Meadows State Park in Fauquier County, Virginia (~ 13 km from Blandy Farm), and the fourth site was a ruderal field between a small woodlot and See Lane in an area in Frederick County that is quickly becoming engulfed by commercial development (~ 7 km from Blandy Farm). These two sites, which are ~ 22 km apart, will be referred to respectively as "Sky Meadows" and "See Lane." (These four sites also served as the source of horsenettle genets for the common-garden experiment described below.)

In the spring of 1998, soon after the emergence of horsenettle ramets (stems), I ran one or more linear transects through each of the four fields described above. To select 25 evenly spaced ramets, I placed a meter stick to the right of the transect tape at 2-m intervals and flagged the horsenettle ramet nearest to the end of the stick. Measurements of leaf herbivory were made on each of the flagged ramets 5 times throughout the growing season. (Only results from the census performed from 1 to 3 August are reported here, to correspond to the timing of the 1999 census. See below.)

On each plant, I counted the total number of leaves and the number of leaves demonstrating damage by the five most common folivores (described above). Because nearly every leaf experienced flea-beetle (*Epitrix*) feeding, damage by this insect was quantified more precisely. I placed a clear plastic grid consisting of a 92.7 mm^2 square divided into 25 squares to the right of the midvein of each of the three newest fully expanded main stem leaves and recorded the number of squares covering tissue that had been damaged by flea beetles. The percentage of the squares exhibiting flea-beetle damage for these three leaves combined served as an index for flea-beetle damage on that plant. Once the shoots had senesced at the end of the growing season, I harvested them and dissected their stems to search for evidence of feeding by the potato stalk-borer (*Trichobaris*). I also recorded the number of fruits that developed to maturity on each ramet.

In the spring of 1999, I again ran transects through the four fields and chose 30 ramets (32 at See Lane) in each horsenettle population in the same manner as the previous year. Observations of insects were conducted regularly in 1999, but detailed leaf counts and damage measurements were made only once (between 27 July and 2 August), after most feeding had occurred but before many leaves had senesced. The plants were harvested after shoot senescence and their stems were dissected to look for evidence of stalk-borer damage. The number of fruits matured was also recorded for each ramet. In both years, a small fraction of the plants were killed by herbivory, deer trampling, or vandalism before the final damage censuses. The number of plants with damage measures ranged from 23 to 25 per population in 1998 and from 27 to 30 in 1999.

Because damage levels of the six herbivores did not all use the same units, and because of the rather wide differences in damage levels among the species, it was difficult to visualize differences in herbivore-community structure using the raw damage data. To ameliorate these challenges, I relativized the damage levels for each herbivore by dividing the damage level measured on each ramet by the highest mean-damage level for that species in any site for either year. Thus, the field site and year with the maximum damage level for a species would have a mean relativized value of "one" for that species, and a site that suffered no damage by a particular herbivore in a year would have a mean relativized value of "zero."

Historical data on precipitation and temperatures at Blandy Farm were obtained from a database available online at: https://findtrees.blandy.virginia.edu/blandy/weather. The data used in the current study included daily precipitation values and high temperatures from January 1991 through December 2021.

Common-garden experiment

Because data from the common-garden experiment have been used in previous publications (Wise 2007b, a), the experiment is described only briefly here. In the spring of 1997, I excavated roots from 30 newly emerged horsenettle ramets from each of the four fields described above. The chosen ramets were growing at least 6-m apart to make it likely that the roots were from separate genetic individuals (genets). Because horsenettle is self-incompatible (in terms of sexual reproduction), I was able to confirm distinct identity of the genets eventually used in the experiment by a series of cross-pollinations performed in 1998 (Wise 2003).

The field-collected roots were transplanted into pots containing a peat-based commercial growing medium (Wesco Growing Media III, Wetsel Seed Company, Harrisonburg, VA), and the plants were placed in a semi-protected outdoor area where they were allowed to grow until shoot senescence. The perennial roots were removed from the pots and were kept in refrigeration over the winter, and new root growth from each genet was grown in pots in the same conditions as 1997. This process was repeated each year through 2001, which served to generate clonal replicates for a series of experiments as well as to purge the genets from potential non-genetic, carryover effects from environmental differences between and within the source fields.

In the spring of 2001, ten genets from each of the four source populations were selected for the common-garden experiment. Roots from each genet were cut into equal-volume segments (2 cm^3), which were then planted individually into 3.8 L (1-gallon) plastic pots in fresh growing medium. Between 28 June and 2 July, 24 healthy ramets from each of the 40 genets were transplanted into a grid amid a large horsenettle population in an oldfield at Blandy Farm that had been mowed (bush-hogged) each winter to stall secondary succession. The grid consisted of 960 planting positions allocated equally across three spatial blocks, with each block consisting of 10 rows (2 m apart), and with transplanting positions 1.5 m apart within the rows. Within each block, eight ramets of each of the 40 genets were transplanted into randomized planting positions. The ratio of naturally occurring horsenettle ramets to transplanted ramets was ~ 30:1, and there was a diverse community of horsenettle herbivores in this field (Wise 2007b).

Folivory measurements were taken in August and September—after most feeding had occurred but prior to leaf senescence—to obtain the most comprehensive and accurate damage estimates possible. Damage levels by *Tildenia* and *Gratiana* were quantified as the proportion of leaves displaying leaf mines or oval-shaped feeding holes, respectively. For *Leptinotarsa*, more precise measurements were made by a visual estimation of percentage categories for a sample of the ten youngest fully expanded leaves on each ramet (Wise 2007a). The same grid technique as described above was used to quantify damage by *Epitrix* flea beetles. For *Gargaphia*, a plant was considered damaged if lace bug eggs had been laid on it and there was evidence of feeding by a brood of nymphs. As in the field censuses, all stems in the garden experiment were dissected upon senescence to record evidence of damage by *Trichobaris*.

Statistical analyses

All statistical tests reported in this paper were performed using JMP-IN 4.0.4 (SAS Institute, Cary, NC, USA). To assess spatial and temporal patterns in plant growth and reproduction in the four field populations, I ran two ANOVAs with the following response variables: (1) the number of leaves present at beginning of August, and (2) the number of fruits matured. The number of leaves was natural-log transformed, and the number of fruits was square-root transformed to better meet the distributional assumptions of ANOVA. The explanatory variables for these ANOVAs were field site and year, both of which were treated as fixed-effects factors. ANOVAs with the same response variables were then run separately for each year (1998 and 1999), and Tukey HSD tests were performed to assess differences between all pairs of field sites in those 2 years. Similarly, ANOVAs with the same response variables were also run separately for each field site, and Tukey HSD tests were performed to assess differences between years within each field site.

To assess spatial and temporal patterns in damage levels by herbivores in the four field populations of horsenettle, a set of six ANOVAs similar to those described in the previous paragraph were run, with the response variables being the relativized-damage measurements for the six different herbivores included in the field censuses. (The inferences of the ANOVAs were the same when using the raw data instead of the relativized data because the response variates were divided by the same number within each ANOVA.) Tukey HSD tests were then performed within each year to assess the statistical significance of inter-field differences in damage levels for each herbivore. Likewise, Tukey HSD tests were performed within each field site to assess the statistical significance of between-year differences in damage levels for each herbivore.

To look for evidence of horsenettle's evolution of resistance to herbivory, I compared mean damage levels of herbivore species in each of the four field populations with horsenettle's mean-resistance levels against the respective herbivore species and source fields in the common-garden experiment. A few factors complicated these comparisons. For example, not only did the units and techniques of the damage measurements vary among the herbivore species, but for some species, they also differed in details between the field surveys and common-garden experiment. The range of variation in damage levels for the species also differed greatly among the field sites and between the common-garden experiment and the field sites. Finally, even with a small sample size of four means (one for each herbivore for each of the four field sites), it was apparent that the distributions of means were often quite skewed. To display and to analyze the field and garden comparisons in the most direct and assumption-free manner, I used rankings rather than raw damage levels.

In the field surveys, for each species of herbivore, I first ranked the fields from least-heavily damaged ("1") to most-heavily damaged ("4") by that herbivore in each year. That is, each of the six herbivores received its own set of four rankings for 1998 and for 1999. For the analysis presented in this paper, I used the mean value of the rankings for the 2 years for each species.

In the common-garden experiment, I also ranked the four source fields for mean-damage levels caused by each of the six herbivore species, with "1" assigned to the source population with the least damage, and "4" assigned to the source population with the most damage in the common garden. Each of these 24 mean-damage values included data from at least 231 (and at most 240) separate ramets in the common garden. Because a plant's "operational" resistance to an herbivore is defined as the inverse (or opposite or complement) of the amount of damage caused by that herbivore, a damage ranking of "1" in the garden would indicate that the source population had the highest (genetically controlled) resistance level of the four populations to that herbivore, while a damage ranking of "4" in the garden would indicate that a source population had the lowest level of resistance to that herbivore. If the population level of an herbivore species in a field was determined primarily by the level of genetically controlled resistance of its host-plant population, then rankings in the garden should be reflected in the rankings in the field (low with low, and high with high).

To quantify the overall relationship between herbivores' damage levels in the field and in the common-garden experiment, I calculated the Pearson product-moment correlation between the 24 pairs of damage rankings (four pairs for each of the six herbivores). A positive correlation would indicate that plant populations with higher levels of genetically controlled resistance tended to host lower densities of insect herbivores in the field. In contrast, a negative correlation would indicate that more-resistant plant populations actually hosted higher densities of herbivores in the field—a result that would suggest that plant resistance did evolve resistance levels in proportion to herbivore densities, but that herbivore densities in the field were not controlled by plant resistance.

Table 2 Summary of ANOVA results for the variation in leaf and fruit production across horsenettle populations (fields) and between years. The numbers of leaves were natural-log transformed and the numbers of fruits were square-root transformed prior to analyses

Source	df	MS	*F*-ratio	*P*-value
Leaves				
Field	3	7.52	30.30	< 0.0001
Year	1	23.60	95.12	< 0.0001
Field × year	3	0.42	1.69	0.17
Error	202	0.25		
Fruits				
Field	3	6.89	9.49	< 0.0001
Year	1	62.93	86.70	< 0.0001
Field × year	3	4.35	5.99	0.0006
Error	206	0.73		

Results

The overall weather conditions were substantially different in the 2 years of field-data collection (Table 1). In particular, the majority of the growing season of 1998 was much wetter than in 1999, with June of 1998 seeing 5 times more precipitation than June of 1999 at Blandy Farm. In addition, the amount of precipitation from January through April of 1998 was nearly twice the amount as during same span of 1999 (21.6 cm and 11.7 cm, respectively). Furthermore, the mean maximum-daily temperature for June was 7% higher in 1999 than in 1998, and it was 11% higher for July in 1999 than in 1998.

Horsenettle ramets in the field sites produced nearly twice as many leaves and 10 times as many fruits in 1998 as in 1999 (Table 2; Fig. 1). There were some significant differences in leaf and fruit production among the four populations, but each population showed the same pattern of much lower production in 1999 (Fig. 1).

Damage levels by five of the six species of horsenettle herbivores varied widely across the four field sites (Field main effect: $P < 0.0001$, Table 3; Fig. 2). Only for the tortoise beetles (*Gratiana*) were there no statistically significant differences between fields, even though the damage levels by this species differed fivefold among the fields in 1998 and 2.6-fold in 1999. The relative levels of damage caused by each species across the four fields were rather idiosyncratic, such that each field tended to be dominated by a different species of herbivore (Fig. 2). For instance, stalk borers (*Trichobaris*) were consistently high in the Blandy Oldfield; potato beetles (*Leptinotarsa*) had the highest relative damage in the Blandy Meadow; lace bugs (*Gargaphia*) were most damaging in Sky Meadows; and leaf miners (*Tildenia*) and tortoise beetles (*Gratiana*) tended to be at their most damaging in the See Lane population of horsenettle (Fig. 2).

Damage levels by all six herbivores in the field were also very different between years (Year main effect: $P < 0.0001$; Table 3). For all five folivores, damage tended to be greater in 1999 than 1998 (Fig. 3). However, the relative magnitudes of the differences between years tended to vary among fields, as evidenced by the significant Field-by Year interaction in the ANOVAs for three of the six species of herbivores (Table 3). Moreover, 19 of the 20 between-year comparisons of relative damage for the five folivores (across the four field sites) were in the direction of greater damage in 1999, and 11 of these differences were determined to be statistically significant by Tukey HSD tests (indicated by stars in Fig. 2). In contrast, damage by the potato stalk borer (*Trichobaris*) was greater in 1998 than in 1999 (Fig. 3), with the differences being statistically significant for two of the four field sites (Fig. 2).

Despite highly significant differences in damage levels between years, the relative importance of the six herbivore species within the four field populations of horsenettle remained rather consistent between years. That is to say, for none of the herbivores did the relative damage ranking across fields change drastically between 1998 and 1999

Table 1 Weather summary for Blandy Farm from Jan 1 through 31 July of 1998 and 1999. The 31-yr means cover 1991–2021

	Precipitation (cm)					Mean high temperature (°C)			
Year	Jan–Apr	May	June	July	Total	May	June	July	Mean
1998	21.6	10.2	16.2	1.4	27.8	25.8	27.9	31.3	28.3
1999	11.7	4.3	3.2	7.5	15.0	25.5	30.0	34.7	30.1
31-year mean	31.9	10.2	8.6	8.9	27.7	23.0	27.5	29.9	26.8

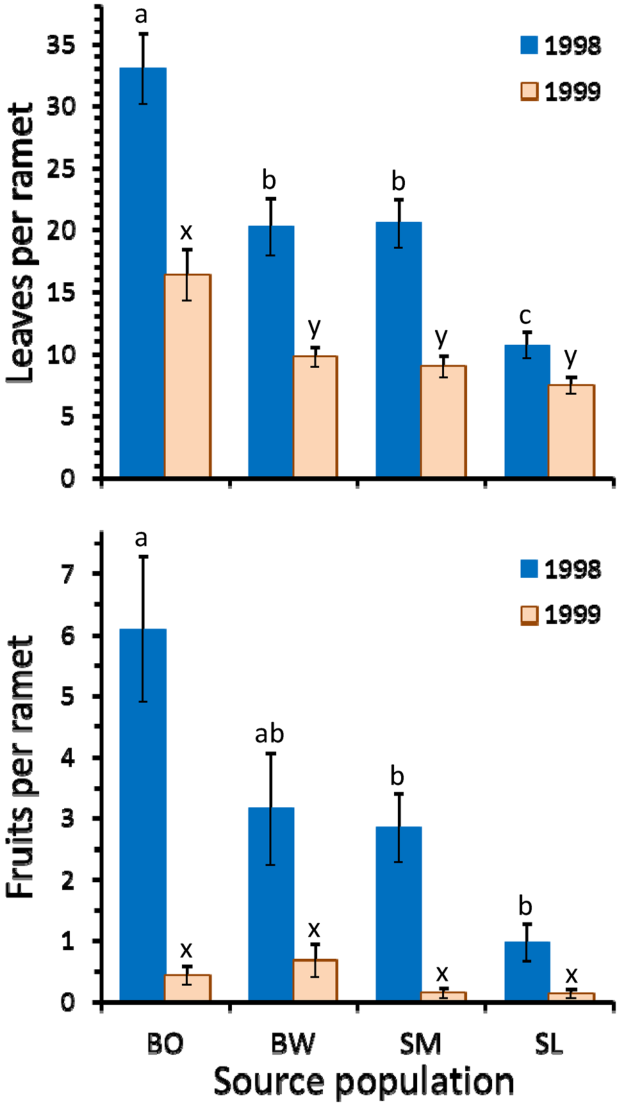

Fig. 1 Comparison of leaf and fruit production of horsenettle ramets among fields and between years. Columns and bars represent means ± one standard error. Within a year, bars that share a lowercase letter are not statistically significantly different at $P < 0.05$, as determined by Tukey HSD tests. *BO* Blandy Oldfield, *BM* Blandy Meadow, *SM* Sky Meadows, *SL* See Lane

Table 3 Summary of ANOVA results for the variation in damage levels across horsenettle populations (fields) and between years

Source	df	MS	*F*-ratio	*P*-value
Tildenia				
Field	3	1.30	47.93	< 0.0001
Year	1	0.82	30.15	< 0.0001
Field × year	3	0.31	11.35	< 0.0001
Error	205	0.027		
Gratiana				
Field	3	0.064	2.11	0.10
Year	1	0.83	27.19	< 0.0001
Field × year	3	0.050	1.64	0.18
Error	205			
Leptinotarsa				
Field	3	1.24	15.44	< 0.0001
Year	1	1.37	17.06	< 0.0001
Field × year	3	0.19	2.31	0.08
Error	205	0.080		
Epitrix				
Field	3	1.12	51.02	< 0.0001
Year	1	1.03	47.10	< 0.0001
Field × year	3	0.45	20.49	< 0.0001
Error	208	0.022		
Gargaphia				
Field	3	1.32	48.66	< 0.0001
Year	1	0.55	20.26	< 0.0001
Field × year	3	0.42	15.59	< 0.0001
Error	205			
Trichobaris				
Field	3	2.01	9.86	< 0.0001
Year	1	3.39	16.61	< 0.0001
Field × year	3	0.093	0.46	0.71
Error	205			

(Fig. 2). As one specific example, folivory by potato beetles was highest in the Blandy Meadow population and lowest at Sky Meadows in both 1998 and 1999 (Fig. 2).

The combined results suggest an overall negative relationship between an herbivore's damage levels in each field and that herbivore's damage levels on ramets from the corresponding source fields in the common-garden experiment. Specifically, for five of the six species of herbivores, the relationship was in the negative direction, with potato beetles (*Leptinotarsa*) being the lone exception (Fig. 4). Flea beetles (*Epitrix*) displayed a perfect inverse relationship, with the fourth, third, second, and first rankings among fields sites being the first, second, third, and fourth rankings, respectively, in the garden experiment. The correlation coefficient including all six species was on the cusp of traditional statistical significance ($r = -0.40$, $P = 0.053$; dotted line in Fig. 4).

Discussion

Spatial variation in herbivory

The four field populations of horsenettle in this study hosted a nearly identical suite of herbivore species, including five common folivores and a stem borer. Despite the fact that each field supported the same roster of these six focal herbivores, the relative amounts of damage inflicted on horsenettle by these species differed greatly among the four fields. Moreover, the fields showed great variation in the relative dominance of the different herbivore species feeding on horsenettle. To the extent that the relative amounts of damage are determined by the relative abundances of

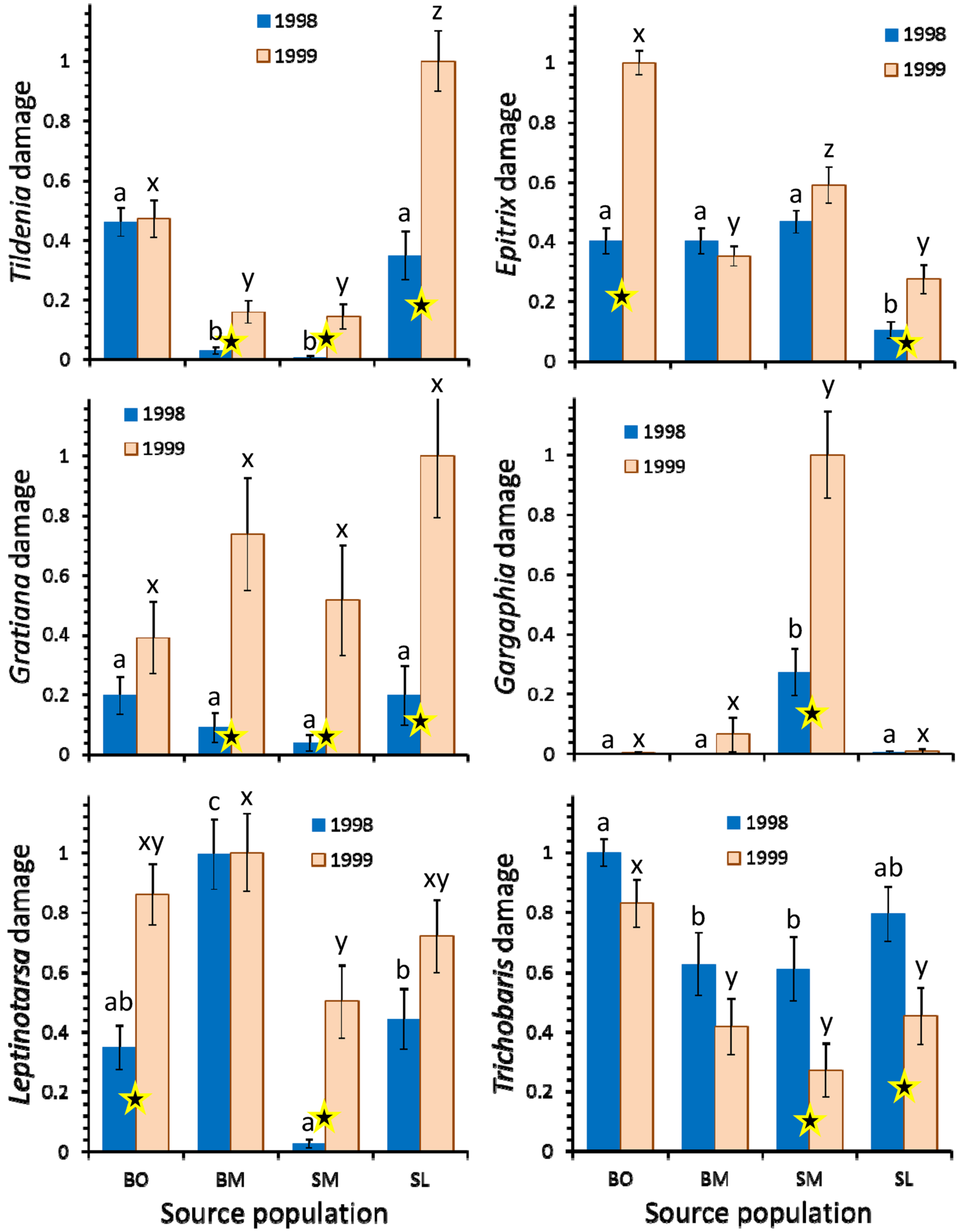

Fig. 2 Comparison of damage levels by the six species of horsenettle herbivores among field sites and between years. For each herbivore, the mean damage levels were relativized to a maximum value of one by dividing each mean by the largest mean-damage value across the four field sites and 2 years. Columns and bars represent relativized mean-damage levels ± one standard error. Within a year, bars that share a lower-case letter are not statistically significantly different at a pairwise $P < 0.05$, as determined by Tukey HSD tests. Stars between columns for the same field site indicate that the damage levels caused by the herbivore differed significantly ($P < 0.05$) between 1998 and 1999 at that site

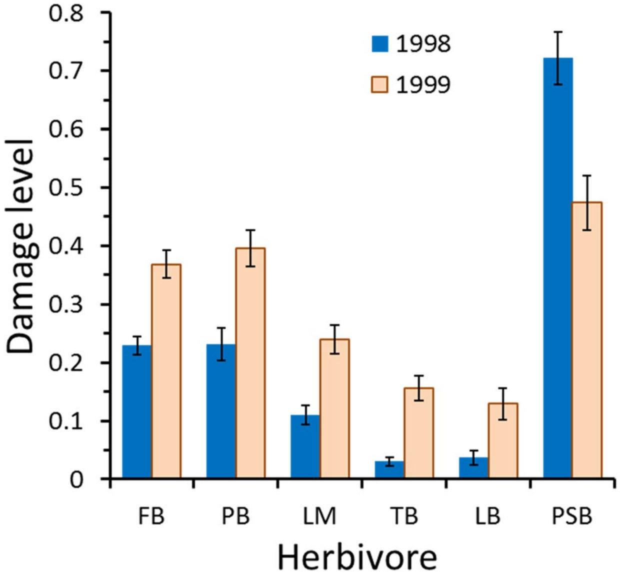

Fig. 3 Comparison of damage levels by the six species of horsenettle herbivores between years, averaged across the four field sites. Columns and bars represent mean-damage levels ± one standard error. Damage levels for each species were significantly different between 1998 and 1999 ($P < 0.0001$, Table 3). Herbivore-species are abbreviated as follows: *FB* eggplant flea beetle, *PB* false potato beetle, *LM* eggplant leafminer, *TB* eggplant tortoise beetle, *LB* eggplant lace bug, *PSB* potato stalk borer. As explained in the text, damage by FB was quantified by a unitless index proportional to the relative leaf area consumed; damage by PB, LM, TB, and LB was quantified as the proportion of leaves exhibiting feeding, and damage by PSB was indicated by the presence (1) or absence (0) of a PSB in the stem at the end of the growing season. $N = 100$ horsenettle ramets in 1998 and 124 horsenettle ramets in 1999

the herbivores, this study provided convincing evidence of spatial (among host-plant-population) variation in the community structure of the horsenettle herbivores at a metapopulation scale.

Differences in community structure among locations can be due to barriers to dispersal, including simply the locations being too far apart (Lawton et al. 1993; Verçosa et al. 2019; Núñez-Farfán and Valverde 2020). However, it seems highly unlikely that the differences in herbivore-community structure found in the current study could be due to dispersal barriers. First, all six species are flying insects—though not all are particularly strong or graceful fliers. The four fields were all within 22 km of each other, and the intervening landscape contained plenty of disturbed and field habitat ideal for horsenettle. Second, the similarities in community structures between fields were not related to the distance between the fields (MJ Wise, unpublished data). For instance, the herbivore-community structure of the Blandy Oldfield was less similar to that of the Blandy Meadow (only a few hundred meters) away than to that of See Lane (more than 7 km away).

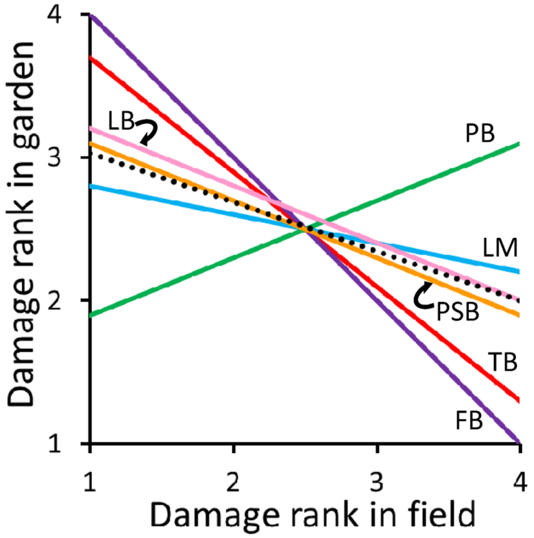

Fig. 4 Comparison of damage levels by six species of horsenettle herbivores in the four field sites with damage levels experienced by ramets from the same fields planted in the common garden. Ranks range from 1 to 4, with 1 representing the lowest damage level. Herbivore-species are as follows: *FB* eggplant flea beetle (purple line), *LB* eggplant lace bug (pink line), *LM* eggplant leafminer (blue line), *PB* false potato beetle (green line), *PSB* potato stalk borer (orange line), *TB* eggplant tortoise beetle (red line). The pink line (for lace bugs) was jittered upward for visibility, as its true location coincides with the orange line). The black, dotted line represents the correlation between damage ranks for all six species of herbivores combined ($r = -0.40$, $P = 0.053$)

Differences in the community structure of herbivores sharing a host plant could also be due to differences in abiotic conditions among the fields (Moreira et al. 2018b; Hahn et al. 2019; Lynn and Fridley 2019; Sanczuk et al. 2021). Although the field sites in the current study were close enough together that their macro-environments were similar, there were likely differences in micro-environmental conditions, such as soil type and moisture level, that could directly affect horsenettle and its herbivores.

The differences in species of plants sharing the different fields with horsenettle could have affected composition of horsenettle herbivores through associational (neighbor) effects (Barbosa et al. 2009; Underwood et al. 2014; Mutz et al. 2022). On one hand, neighboring plants that produce similar volatile chemicals to horsenettle's volatiles might attract horsenettle's herbivores to a field. On the other hand, neighboring plants might produce volatile chemicals that mask the presence of horsenettle in a field, thus reducing the attack rate on horsenettle. Importantly, the focal herbivores of this study are essentially monophagous on horsenettle in field sites (Wise 2007b). Therefore, the presence or absence of plant species that could serve as alternative hosts is not likely to have been a factor in the abundance of horsenettle's herbivores in this study.

Temporal variation in herbivory

The average proportion of the horsenettle ramets' leaves (or relative leaf area) that exhibited damage was greater for all five of the folivores in 1999 than in 1998. Such a result could be due to a greater density of all of the folivores in 1999, to the plants being smaller in 1999, or to a combination of both factors. Indeed, the horsenettle ramets were much smaller in 1999 across all four field sites—producing only half as many leaves as they did in 1998. If the density of a species of folivore was the same in 1999 as in 1998 in a field site, then one might expect the proportion of horsenettle's leaves damaged by that species to be twice as great in 1999 as it was in 1998.

For the eggplant leafminer (*Tildenia*), the overall relative damage level (all four sites combined) was indeed twice as high in 1999, suggesting that the density of this species was roughly the same in the 2 years. The relative damage levels by two other folivores (*Gratiana* and *Gargaphia*) were considerably greater than twice as high in 1999 than in 1998, a result that suggests that the densities of these two species were greater in 1999 than in 1998. For the two other folivores (*Epitrix* and *Leptinotarsa*), the relative damage levels were slightly less than twice as great in 1999, suggesting that the population densities of these species were lower in 1999 than in 1998. Finally, the proportion of stems infested by the potato stalk borer (*Trichobaris*) was considerably lower in 1999 than in 1998, which suggests that the stalk borer's population density was indeed lower in 1999.

Although changes in the abundances of the herbivores were only indirectly inferred using changes in relative damage levels, it is clear that the magnitude and direction of changes in abundance from 1998 to 1999 were not the same for all six species of the herbivores. Furthermore, the magnitudes of the temporal changes were not the same across the four field sites for most of the focal herbivore species. Importantly, however, the direction of the temporal changes in population density for each herbivore was quite consistent across the four fields. As a result, the spatial differences in the overall herbivore damage regimes (and by inference, the herbivore-community structures) among fields remained consistent across 2 years of vastly different growing conditions that were attributed to an intense El Niño in 1998 followed by a La Niña in 1999.

Implications for geographic mosaics of coevolution

Two major results from the field surveys are most relevant to the formation of a geographic mosaic of coevolution. First, the four horsenettle populations varied widely in the relative amounts of damage they experienced from each of the herbivores. Second, the differences in the patterns of relative amounts of damage caused by the different species of herbivores were largely maintained across years—even though these years represented opposite extremes of the spectrum of weather conditions. Previous studies have demonstrated that these particular horsenettle populations contain significant levels of genetic variation for resistance against herbivory, and that herbivores can have significant effects on horsenettle's fitness (Wise and Sacchi 1996; Wise 2007a; Wise et al. 2008; Wise and Rausher 2013). Altogether, these results suggest that horsenettle and its herbivores are prime candidates to demonstrate a geographic mosaic of coevolution between a plant and its multiple-herbivore community (Thompson 1994; Gómez and Zamora 2000; Thompson and Cunningham 2002; Züst et al. 2012; De-la-Cruz et al. 2020b).

Relationship between plant-resistance levels and herbivore-community structure

Consistent with the geographic mosaic model of coevolution, this study provided some intriguing evidence that the abundances of the insects that made up the herbivore community (inferred from levels of damage they caused) were related to genetically controlled differences in resistance levels among the plant populations. Specifically, for five of the six herbivores, the correlation between damage levels in the four field populations and damage levels in the common garden were in the negative direction. In other words, horsenettle populations with relatively higher levels of resistance to an herbivore tended to support relatively higher densities of that herbivore. From a purely ecological perspective, this result is rather counterintuitive. That is, one might expect that a high density of an herbivore in a host-plant population would suggest that the plant population was not very resistant. From an evolutionary perspective, it appears that higher herbivore pressures have tended to cause plants to evolve greater levels of resistance without a concomitant reduction in the herbivore population size. In other words, horsenettle's evolutionary response may be relatively rapid, while an ecological feedback in terms of herbivore abundance may lag behind.

This pattern of the level of damage caused by an herbivore being positively correlated with the plant populations' resistance was most striking for the eggplant flea beetles (*Epitrix*). Notably, flea beetles were not only the most abundant of the six herbivores in this study, they also exerted the strongest magnitude of natural selection for increased resistance in horsenettle in the common-garden experiment (Wise and Rausher 2013). Therefore, one might expect a more rapid evolution of resistance against flea beetles than against the other herbivores within horsenettle populations. As a result, one might expect densities (and thus damage levels) of flea beetles to be reduced to a greater degree in the fields with higher resistance. However, factors other than plant-resistance levels must have outweighed any effects that plant resistance had on the overall density of flea beetles in the field populations.

Although they were not a focus of this study, several other factors that may lead to differences in abundances of different species of herbivores among fields are worthy of mention. Most simply, differences in herbivore-community structure may be due to historical contingencies of how readily each species was able to colonize a field (Lawton et al. 1993; Stam et al. 2018). In addition, herbivore abundances could be controlled by tolerances of abiotic conditions that vary among fields (Lynn and Fridley 2019; Sanczuk et al. 2021). Finally, the abundances of an herbivore's predators or pathogens may vary among fields, which could lead to differences in population densities of herbivores among fields if these natural enemies exert top-down control on the herbivore populations (Gómez and Zamora 2000; Callejas-Chavero et al. 2020). These factors are not mutually exclusive with each other or with the effects of host-plant resistance on herbivore abundance. Although their relative roles in controlling herbivore abundance in horsenettle populations are not known, what is clear is that cumulative effect of the other factors outweighed the effects of plant resistance in limiting the abundance of at least five of the horsenettle herbivores in the current study.

The false potato beetle (*Leptinotarsa juncta*) was the only species for which horsenettle's resistance levels were negatively associated with levels of folivory in the field populations. That is, the horsenettle populations with higher levels of resistance to false potato beetles (determined operationally in the common garden) tended to suffer lower levels of leaf-feeding by this species in the source fields. Why false potato beetles would be the only herbivore showing this pattern is not clear. One reason why the patterns might differ among species of herbivores is that the more mobile species would be able to sample among populations and thus choose to feed and oviposit on plants in populations with relatively low resistance. Despite their bulky bodies and lumbering gait, adult potato beetles can fly long distances to locate host-plant populations (Boiteau 2001). Whether they are better at this than the other species of herbivores included in this study is not known.

It may also be important that false potato beetles do not restrict their feeding to leaves, but they also do considerable damage to flowers and fruits. Florivory and frugivory by potato beetles have been found to impose much stronger directional selection to increase resistance in horsenettle than does stem boring or leaf damage by any herbivore species (Wise and Rausher 2013). Resistance against potato beetles may thus be more important to horsenettle than to the other five herbivores in this study. As a result, resistance may be strong enough to affect potato beetle density more than it affects the density of the other herbivores included in this study. However, such rationale is not consistent with the observed pattern that flea beetle damage in the field was strongly positively correlated with resistance levels—even though selection for flea beetle resistance was stronger than selection for resistance to the stem borer or to any of the other folivores (Wise and Rausher 2013).

What is most clear from this study is that the community structure of herbivores that share a host plant does not necessarily reflect genetically controlled host-plant resistance levels against the array of herbivores it encounters. If the results for horsenettle are generalizable across systems, then it may be expected that higher densities of a species of herbivore in a host-plant population (relative to other populations of the host plant) are more likely to be associated with higher levels of plant resistance, rather than lower levels of plant resistance, against that herbivore.

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Data availability The data used in the analyses reported in this article are available upon reasonable request from the author.

Declarations

Competing interests The author has no competing interests to declare that are relevant to the content of this article.

References

Agrawal AA (2011) Current trends in the evolutionary ecology of plant defence. Funct Ecol 25:420–432. https://doi.org/10.1111/j.1365-2435.2010.01796.x

Agrawal AA, Hastings AP, Fines DM, Bogdanowicz S, Huber M (2018) Insect herbivory and plant adaptation in an early successional community. Evolution 72:1020–1033. https://doi.org/10.1111/evo.13451

Agrawal AA, Hastings AP, Johnson MTJ, Maron JL, Salminen J-P (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. Science 338:113–116. https://doi.org/10.1126/science.1225977

Agrawal AA, Johnson MTJ, Hastings AP, Maron JL (2013) A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedback to seed predator populations. Am Nat 181:S35–S45. https://doi.org/10.1086/666727

Agrawal AA, Lau JA, Hambäck PA (2006) Community heterogeneity and the evolution of interactions between plants and insect herbivores. Q R Biol 81:349–376. https://doi.org/10.1086/666727

Aguilar R, Servín R (2000) Alternate wild host of the pepper weevil, *Anthonomus eugenii*, Cano in Baja California Sur, Mexico. Southwest Entomol 25:153–154

Albert WB (1960) Control of horsenettle (*Solanum carolinense*) in pastures. Weeds 8:680–682. https://doi.org/10.2307/4040373

Andreazzi CS, Guimarães PR Jr, Melián CJ (2018) Eco-evolutionary feedbacks promote fluctuating selection and long-term stability of antagonistic networks. Proc R Soc London B 285:20172596. https://doi.org/10.1098/rspb.2017.2596

Bailey TE, Kok LT (1978) Insects associated with horsenettle (*Solanum carolinense* L.) in southwest Virginia. Va J Sci 29:37

Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szebdreu Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. Annu Rev Ecol Evol Syst 40:1–20. https://doi.org/10.1146/annurev.ecolsys.110308.120242

Barraclough TG (2015) How do species interactions affect evolutionary dynamics across whole communities? Annu Rev Ecol Evol Syst 46:25–48. https://doi.org/10.1146/annurev-ecolsys-112414-054030

Baskett CA, Schemske DW (2018) Latitudinal patterns of herbivore pressure in a temperate herb support the biotic interactions hypothesis. Ecol Lett 21:578–587. https://doi.org/10.1111/ele.12925

Bassett IJ, Munro DB (1986) The biology of Canadian weeds. 78. *Solanum carolinense* L. and *Solanum rostratum* Dunal. Can J Plant Sci 66:977–991. https://doi.org/10.4141/cjps86-120

Bischoff A, Trémulot S (2011) Differentiation and adaptation in *Brassica nigra* populations: interactions with related herbivores. Oecologia 165:971–981. https://doi.org/10.1007/s00442-010-1798-7

Bode RF, Kessler A (2012) Herbivore pressure on goldenrod (*Solidago altissima* L., Asteraceae): its effects on herbivore resistance and vegetative reproduction. J Ecol 100:795–801. https://doi.org/10.1111/j.1365-2745.2012.01958.x

Boiteau G (2001) Recruitment by flight and walking in a one-generation Colorado potato beetle (Coleoptera:Chrysomelidae) environment. Environ Entomol 30:306–317. https://doi.org/10.1603/0046-225X-30.2.306

Callejas-Chavero A, Martínez-Hernández D, Flores-Martínez A, Moncada-Orellana A, Diaz-Quiñones Y, Vargas-Mendoza CF (2020) Herbivory in cacti: fitness effects of two herbivores, one tending ant on *Myrtillocactus geometrizans* (Cactaceae). In: Núñez-Farfán J, Valverde PL (eds) Evolutionary ecology of plant-herbivore interaction. Springer, Cham, pp 109–134

Castells E, Berhow MA, Vaughn SF, Berenbaum MR (2005) Geographic variation in alkaloid production in *Conium maculatum* populations experiencing differential herbivory by *Agonopterix alstroemeriana*. J Chem Ecol 31:1693–1709. https://doi.org/10.1007/s10886-005-5921-x

Coverdale TC, Agrawal AA (2022) Experimental insect suppression causes loss of induced, but not constitutive, resistance in *Solanum carolinense*. Ecology. https://doi.org/10.1002/ecy.3786

Crémieux L et al (2008) Potential contribution of natural enemies to patterns of local adaptation in plants. New Phytol 180:524–533. https://doi.org/10.1111/j.1469-8137.2008.02545.x

D'Amen M, Rahbek C, Zimmermann N, Guisan A (2017) Spatial predictions at the community level: from current approaches to future frameworks. Biol Rev 92:169–187. https://doi.org/10.1111/brv.12222

De-la-Cruz IM et al (2020a) Evolutionary response to herbivory: population differentiation in microsatellite loci, tropane alkaloids and leaf trichome density in *Datura stramonium*. Arthropod-Plant Interact 14:21–30. https://doi.org/10.1007/s11829-019-09735-7

De-la-Cruz IM, Merilä J, Valverde PL, Flores-Ortiz CM, Núnez-Farfán J (2020b) Genomic and chemical evidence for local adaptation in resistance to different herbivores in *Datura stramonium*. Evolution 74:2629–2643. https://doi.org/10.1111/evo.14097

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18:586–608. https://doi.org/10.1111/j.1558-5646.1964.tb01674.x

Follak S, Strauss G (2010) Potential distribution and management of the invasive weed *Solanum carolinense* in central Europe. Weed Res 50:544–552. https://doi.org/10.1111/j.1365-3180.2010.00802.x

Frank JR (1990) Influence of horsenettle (*Solanum carolinense*) on snapbean (*Phaseolus vulgaris*). Weed Sci 38:220–223. https://doi.org/10.1017/S0043174500056435

Freeland TR (1982) The biology and control of horsenettle (*Solanum carolinense* L.). University of Arkansas, Fayetteville, p 37

Garrido E, Adraca-Gómez G, Fornoni J (2012) Local adaptation: simultaneously considering herbivores and their host plants. New Phytol 193:445–453. https://doi.org/10.1111/j.1469-8137.2011.03923.x

Gómez JM, Zamora R (2000) Spatial variation in the selective scenarios of *Hormathophylla spinosa* (Cruciferae). Am Nat 155:657–668. https://doi.org/10.1086/303353

Gorrell RM, Bingham SW, Foy CL (1981) Control of horsenettle (*Solanum carolinense*) fleshy roots in pastures. Weed Sci 29:586–589. https://doi.org/10.1017/s0043174500063773

Gross P (1986) Life histories and geographic distributions of two leafminers, *Tildenia georgei* and *Tildenia inconspicuella* (Lepidoptera: Gelechiidae), on solanaceous weeds. Ann Entomol Soc Am 79:48–55. https://doi.org/10.1093/aesa/79.1.48

Hahn PG, Agrawal AA, Sussman KI, Maron JL (2019) Population variation, environmental gradients, and the evolutionary ecology of plant defense against herbivory. Am Nat 193:20–34. https://doi.org/10.1086/700838

Hairston NG Jr, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. Ecol Lett 8:1114–1127. https://doi.org/10.1111/j.1461-0248.2005.00812.x

Haloin JR, Strauss SY (2008) Interplay between ecological communities and evolution: review of feedbacks from microevolutionary to macroevolutionary scales. Ann NY Acad Sci 1133:87–125. https://doi.org/10.1196/annals.1438.003

Hare JD (2012) How insect herbivores drive the evolution of plants. Science 338:50–51. https://doi.org/10.1126/science.1228893

Hendry AP (2017) Eco-evolutionary dynamics. Princeton University Press, Princeton

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. Annu Rev Ecol Evol Syst 43:227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411

Hougen-Eitzman D, Rausher MD (1994) Interactions between herbivorous insects and plant-insect coevolution. Am Nat 143:677–697. https://doi.org/10.1086/285626

Ilnicki RD, Tisdell TF, Fertig SN, Furrer AH Jr (1962) Life history studies as related to weed control in the Northeast—horse nettle.

Agricultural experimental station. University of Rhode Island, Kingston

Imura O (2003) Herbivorous arthropod community of an alien weed *Solanum carolinense* L. Appl Entomol Zool 38:293–300. https://doi.org/10.1303/aez.2003.293

Johnson MTJ, Stinchcombe JR (2007) An emerging synthesis between community ecology and evolutionary biology. Trends Ecol Evol 22:250–257. https://doi.org/10.1016/j.tree.2007.01.014

Judd GJR, Whitfield GH, Maw HEL (1991) Temperature-dependent development and phenology of pepper maggots (Diptera: Tephritidae) associated with pepper and horsenettle. Environ Entomol 20:22–29. https://doi.org/10.1093/ee/20.1.22

Kalske A, Kessler A (2020) Population-wide shifts in herbivore resistance strategies over succession. Ecology 101:e03157. https://doi.org/10.1002/ecy.3157

Karban R, Nagasaka K (2004) Are defenses of wild radish populations well matched with variability and predictability of herbivory? Evol Ecol 18:283–301. https://doi.org/10.1023/B:EVEC.0000035063.70344.03

Koch H, Frickel J, Valiadi M, Becks L (2014) Why rapid, adaptive evolution matters for community dynamics. Front Ecol Evol 2:1–10. https://doi.org/10.3389/fevo.2014.00017

Lankau RA (2007) Specialist and generalist herbivores exert opposing selection on a chemical defense. New Phytol 175:176–184. https://doi.org/10.1111/j.1469-8137.2007.02090.x

Lankau RA (2011) Rapid evolutionary change and the coexistence of species. Annu Rev Ecol Evol Syst 42:335–354. https://doi.org/10.1146/annurev-ecolsys-102710-145100

Lankau RA, Strauss SY (2008) Community complexity drives patterns of natural selection on a chemical defense of *Brassica nigra*. Am Nat 171:150–161. https://doi.org/10.1086/524959

Lawton JH, Gaston KJ (1989) Temporal patterns in the herbivorous insects of bracken: a test of community predictability. J Anim Ecol 58:1021–1034. https://doi.org/10.2307/5139

Lawton JH, Lewinsohn TM, Compton SG (1993) Patterns of diversity for the insect herbivores of bracken. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, pp 178–184

Lay CR, Linhart YB, Diggle PK (2011) The good, the bad and the flexible: plant interactions with pollinators and herbivores over space and time are moderated by plant compensatory responses. Ann Bot 108:749–763. https://doi.org/10.1093/aob/mcr152

Lay CR, Linhart YB, Diggle PK (2013) Variation among four populations of *Erysimum capitatum* in phenotype, pollination and herbivory over an elevational gradient. Am Midl Nat 169:259–273. https://doi.org/10.1674/0003-0031-169.2.259

Lewinsohn TM, Novotny V, Basset Y (2005) Insects on plants: diversity of herbivore assemblages revisited. Annu Rev Ecol Evol Syst 36:597–620. https://doi.org/10.1146/annurev.ecolsys.36.091704.175520

Løe G, Toräng P, Gaudeul M, Ågren J (2007) Trichome production and spatiotemporal variation in herbivory in the perennial herb *Arabidopsis lyrata*. Oikos 116:134–142. https://doi.org/10.1111/j.2006.0030-1299.15022.x

Loughnan D, Williams JL (2019) Climate and leaf traits, not latitude, explain variation in plant-herbivore interactions across a species' range. J Ecol 107:913–922. https://doi.org/10.1111/1365-2745.13065

Lynn JS, Fridley JD (2019) Geographic patterns of plant-herbivore interactions are driven by soil fertility. J Plant Ecol 12:653–661. https://doi.org/10.1093/jpe/tz002

Mena-Covarrubias J, Drummond FA, Haynes DL (1996) Population dynamics of the Colorado potato beetle (Coleoptera: Chrysomelidae) on horsenettle in Michigan. Environ Entomol 25:68–77. https://doi.org/10.1093/ee/25.1.68

Mittelbach GG, Schemske DW (2015) Ecological and evolutionary perspectives on community assembly. Trends Ecol Evol 30:241–247. https://doi.org/10.1016/j.tree.2015.02.008

Moreira X et al (2018a) Latitudinal variation in plant chemical defences drives latitudinal patterns of leaf herbivory. Ecography 41:1124–1134. https://doi.org/10.1111/ecog.03326

Moreira X, Petry WK, Mooney KA, Rasmann S, Abdala-Roberts L (2018b) Elevational gradients in plant defences and insect herbivory: recent advances in the field and prospects for future research. Ecography 41:1485–1496. https://doi.org/10.1111/ecog.03184

Muola A, Mutikainen P, Lilley M, Laukkanen L, Salminen J-P, Leimu R (2010) Associations of plant fitness, leaf chemistry, and damage suggest selection mosaic in plant-herbivore interactions. Ecology 91:2650–2659. https://doi.org/10.1890/09-0589.1

Mutz J, Heiling JM, Paniague-Montoya M, Halpern SL, Inouye BD, Underwood N (2022) Some neighbours are better than others: variation in associational effects among plants in an old field community. J Ecol 10:2118–2131. https://doi.org/10.1111/1365-2745.13935

NAPPO (2003) PRA/grains panel facts sheet-*Solanum carolinense* L. North American Plant Protection Organization, Ottawa, pp 1–7

Nichols RL, Cardina J, Gaines TP (1991) Growth, reproduction and chemical composition of horsenettle (*Solanum carolinense*). Weed Technol 5:513–520. https://doi.org/10.1017/s0890037x00027251

Nichols RL, Cardina J, Lynch RL, Minton NA, Wells HD (1992) Insects, nematodes, and pathogens associated with horsenettle (*Solanum carolinense*) in Bermudagrass (*Cynodon dactylon*) pastures. Weed Sci 40:320–325. https://doi.org/10.1017/S0043174500057416

Núñez-Farfán J, Valverde PL (2020) Natural selection of plant defense against herbivores in native and non-native ranges. In: Núñez-Farfán J, Valverde PL (eds) Evolutionary ecology of plant-herbivore interaction. Springer, Cham, pp 87–105

Ramos SE, Schiestl FP (2019) Rapid plant evolution driven by the interaction of pollination and herbivory. Science 364:193–196. https://doi.org/10.1126/science.aav6962

Rausher MD (1996) Genetic analysis of coevolution between plants and their natural enemies. Trends Genet 12:212–217. https://doi.org/10.1016/0168-9525(96)10020-2

Rausher MD (2001) Co-evolution and plant resistance to natural enemies. Nature 411:857–864. https://doi.org/10.1038/35081193

Rausher MD, Huang J (2016) Prolonged adaptive evolution of a defensive gene in the Solanaceae. Mol Biol Evol 33:43–51. https://doi.org/10.1093/molbev/msv205

Sanczuk P et al (2021) Small scale environmental variation modulates plant defence syndromes of understorey plants in deciduous forests of Europe. Glob Ecol Biogeogr 30:205–219. https://doi.org/10.1111/geb.13216

Schoener TW (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. Science 331:426–429. https://doi.org/10.1126/science.1193954

Schreiber SJ, Patel S, terHorst CP (2018) Evolution as a coexistence mechanism: does genetic architecture matter? Am Nat 191:407–420. https://doi.org/10.1086/695832

Somes MP (1916) Some insects of *Solanum carolinense* L., and their economic relations. J Econ Entomol 9:39–44. https://doi.org/10.1093/jee/9.1.39

Stam JM, Dicke M, Poelman EH (2018) Order of herbivore arrival on wild cabbage populations influences subsequent arthropod community development. Oikos 127:1482–1493. https://doi.org/10.1111/oik.05265

Stinchcombe JR, Rausher MD (2001) Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomoea hederacea*. Am Nat 158:376–388. https://doi.org/10.1086/321990

Strong DR Jr, Lawton JH, Southwood R (1984) Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge

terHorst CP et al (2018) Evolution in a community context: trait responses to multiple species interactions. Am Nat 191:368–380. https://doi.org/10.1086/695835

Thompson JN (1994) The coevolutionary process. The University of Chicago Press, Chicago

Thompson JN (1998a) Coping with multiple enemies: 10 years of attack on *Lomatium dissectum* plants. Ecology 79:2550–2554. https://doi.org/10.2307/176843

Thompson JN (1998b) Rapid evolution as an ecological process. Trends Ecol Evol 13:329–332. https://doi.org/10.1016/S0169-5347(98)01378-0

Thompson JN (1999) The evolution of species interactions. Science 284:2116–2118. https://doi.org/10.1126/science.284.5423.2116

Thompson JN, Cunningham BM (2002) Geographic structure and dynamics of coevolutionary selection. Nature 417:735–738. https://doi.org/10.1038/nature00810

Uesugi A, Kessler A (2016) Herbivore release drives parallel patterns of evolutionary divergence in invasive plant phenotypes. J Ecol 104:876–886. https://doi.org/10.1111/1365-2745.12542

Underwood N, Inouye BD, Hambäck PA (2014) A conceptual framework for associational effects: when do neighbors matter and how would we know? Q R Biol 89:1–19. https://doi.org/10.1086/674991

Valdéz A, Ehrlén J (2017) Caterpillar seed predators mediate shifts in selection on flowering phenology in their host plant. Ecology 98:228–238. https://doi.org/10.1002/ecy.1633

Vasseur DA, Amarasekare P, Rudolf VHW, Levine JM (2011) Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. Am Nat 178:E96–E109. https://doi.org/10.1086/662161

Verçosa D, Cogni R, Alves MN, Trigo JR (2019) The geographical and seasonal mosaic in a plant-herbivore interaction: patterns of defences and herbivory by a specialist and a non-specialist. Sci Rep 9:15206. https://doi.org/10.1038/s41598-019-51528-8

Whaley CM, Vangessel MJ (2002) Horsenettle (*Solanum carolinense*) control with a field corn (*Zea mays*) weed management program. Weed Technol 16:293–300

Wise MJ (2003) The ecological genetics of plant resistance to herbivory: evolutionary constraints imposed by a multiple-herbivore community. Department of biology. Duke University, Durham, p 169

Wise MJ (2007a) Evolutionary ecology of resistance to herbivory: an investigation of potential genetic constraints in the multiple-herbivore community of *Solanum carolinense*. New Phytol 175:773–784. https://doi.org/10.1111/j.1469-8137.2007.02143.x

Wise MJ (2007b) The herbivores of *Solanum carolinense* (horsenettle) in northern Virginia: natural history and damage assessment. Southeast Nat 6:505–522. https://doi.org/10.1656/1528-7092(2007)6[505:thosch]2.0.co;2

Wise MJ (2009) Competition among herbivores of *Solanum carolinense* as a constraint on the evolution of host-plant resistance. Evol Ecol 23:347–361. https://doi.org/10.1007/s10682-007-9230-4

Wise MJ (2018) The notoriously destructive potato stalk borer (*Trichobaris trinotata*) has negligible impact on its native host, *Solanum carolinense* (horsenettle). Arthropod-Plant Interact 12:385–394. https://doi.org/10.1007/s11829-017-9587-4

Wise MJ (2023) Why fitness impacts of different herbivores may combine nonadditively, and why it matters to the ecology and evolution of plant-herbivore communities. Plant Ecol Evol 156:13–28. https://doi.org/10.5091/plecevo.95982

Wise MJ, Cummins JJ, De Young C (2008) Compensation for floral herbivory in *Solanum carolinense*: identifying mechanisms of tolerance. Evol Ecol 22:19–37. https://doi.org/10.1007/s10682-007-9156-x

Wise MJ, Mudrak EL (2021) An experimental investigation of costs of tolerance against leaf and floral herbivory in the herbaceous weed horsenettle (*Solanum carolinense*, Solanaceae). Plant Ecol Evol 154:161–172. https://doi.org/10.5091/plecevo.2021.1805

Wise MJ, Rausher MD (2013) Evolution of resistance to a multiple-herbivore community: genetic correlations, diffuse coevolution, and constraints on the plant's response to selection. Evolution 67:1767–1779. https://doi.org/10.1111/evo.12061

Wise MJ, Sacchi CF (1996) Impact of two specialist insect herbivores on reproduction of horse nettle, *Solanum carolinense*. Oecologia 108:328–337. https://doi.org/10.1007/bf00334658

Wise MJ, Weinberg AM (2002) Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. Ecol Entomol 27:115–122. https://doi.org/10.1046/j.0307-6946.2001.00383.x

Wisz MS et al (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol Rev 88:15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

Woods EC, Hastings AP, Turley NE, Heard SB, Agrawal AA (2012) Adaptive geographical clines in the growth and defense of a native plant. Ecol Monogr 82:149–168. https://doi.org/10.1890/11-1446.1

Züst T, Heichinger C, Grossniklaus U, Harrington R, Kliebenstein DJ, Turnbull LA (2012) Natural enemies drive geographic variation in plant defenses. Science 338:116–119. https://doi.org/10.1126/science.1226397