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Neighbor palatability generates associational effects by altering herbivore foraging behavior

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Abstract. Despite increasing evidence that herbivory on a focal plant may hinge upon the identity of its neighbors, it is not clear whether predictable mechanisms govern the nature and magnitude of such associational effects. Using a factorial field experiment replicated at 14 sites across 80,000 hectares, we evaluated the mechanisms driving associational effects between two plant species mediated by grasshopper herbivores. Our experiment manipulated local neighborhood plant density (two levels) and frequency (three levels), nested within two larger-scale habitat contexts (habitats that did or did not have past agricultural land use). We found that the more palatable plant species, *Solidago nemoralis,* experienced reduced herbivory (associational resistance) when rare due mainly to reduced grasshopper foraging activity. Damage to the less palatable plant species, *S. odora*, was affected by the interaction between plant frequency and the land-use history of the site: it experienced increased damage (associational susceptibility) in even-frequency neighborhoods, but only in sites with a history of agricultural use. Behavioral assays generally corroborated the results from the field, further supporting the importance of foraging behavior in generating associational effects. In finding that associational effects are contingent upon relative palatability among plants and events in the distant past that modify contemporary habitat structure (i.e., past agricultural land use), our work suggests that foraging decisions made at the neighborhood level are important for generating associational effects and that in some cases these neighborhood interactions also depend on the larger-scale environmental context resulting from legacies of past land-use events.

Key words: associational effects; context-dependent interactions; grasshoppers; herbivory; land-use history; plant–insect interactions.

INTRODUCTION

Herbivory is an important ecological process that can affect plant performance and regulate the abundance and distribution of plants (Maron and Crone 2006, Allan and Crawley 2011). However, the degree to which plants are damaged by herbivores often depends on characteristics of the large-scale habitat (i.e., scale of hectares or more; Bakker et al. 2006, Hillebrand et al. 2007), the local neighborhood (i.e., scale of meters; Orrock and Witter 2010, Orrock et al. 2010*a*, Stastny and Agrawal 2014, Kim and Underwood 2015), or selection between neighboring plants (Baraza et al. 2006, Miller et al. 2009). Importantly, different mechanisms typically govern herbivore damage at larger (i.e., habitat or site) and smaller (i.e., neighborhood) spatial scales. For instance, habitat context can affect how herbivores select among patches (i.e., "extent" sensu Kotliar and Wiens 1990) and neighborhood context can affect foraging decisions at smaller scales (i.e., "grain" sensu Kotliar and Wiens 1990) (Baraza et al. 2006, Miller et al. 2009, Castagneyrol et al. 2013). However, understanding the mechanisms whereby larger-scale habitat-context can interact with neighborhood-scale associational effects remains limited by a lack of studies that have explicitly evaluated the mechanisms driving herbivory rates at multiple spatial scales. Experiments conducted in different habitat types that also manipulate neighborhood plant communities are necessary for disentangling herbivore effects at multiple spatial scales.

Associational effects (AE) are indirect interactions among neighbors, mediated by a consumer, that arise when the effect of an herbivore on a focal plant depends upon the presence or identity of a neighboring plants (Root 1973, Barbosa et al. 2009, Underwood et al. 2014). Neighboring plants can generate AE through processes at two spatial scales. First, neighbors can affect the number of herbivores arriving to or leaving a patch (i.e., a change in herbivore abundance within a patch; Hambäck et al. 2014). Second, within a patch, neighbors can affect food selection among plants (i.e., a change in behavior within a patch; Hambäck et al. 2014). The outcome of these neighborhood interactions can take two forms: associational resistance (AR) occurs when a neighboring plant reduces damage to a focal plant and associational susceptibility (AS) occurs when neighbors

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increase damage to a focal plant. Several unique mechanisms can generate AR or AS that hinge upon herbivore behavior within a patch. The outcome (AS or AR) of each mechanism can depend on the relative palatability between the focal plant and its neighbors or the degree of detectability of the plant to the herbivore (Table 1). Here we focus on potential mechanisms generated by generalist herbivores, which most likely depend on the relative palatability between the focal plant and its neighbors. We outline these potential mechanisms, how they depend on the relative palatability between neighbors, and the outcome in Table 1.

The strength of associational effects is likely to vary as a consequence of anthropogenic activities that alter both plant abundance and community composition (i.e., density or frequency) (Loranger et al. 2013, Salazar et al. 2013, Kim and Underwood 2015). For instance, agricultural land-use legacies have substantial effects on plant communities by altering plant community composition and reducing the richness of species typical of intact habitats (Flinn and Vellend 2005, Cramer et al. 2008). Abandoned agricultural fields occupy more than 200 million hectares of North American natural areas (Flinn and Vellend 2005, Cramer et al. 2008), and thus could have widespread consequences on the strength of associational effects. We have previously documented altered herbivory rates on some plant species (Hahn and Orrock 2015*a*, *b*) in post-agricultural longleaf pine woodlands compared to woodlands without a history of agriculture. Land-use history affected herbivory through reductions in plant cover, as we found the highest levels of herbivore damage in sites with intermediate levels of herbaceous cover (Hahn and Orrock 2015*a*). Non-agricultural sites that were maintained by frequent fires had the highest levels of plant cover, but despite higher grasshopper abundance, focal palatable plants experienced low levels of herbivore damage, consistent with the dilution hypothesis (Table 1). In contrast, sites that were fire suppressed or historically used for agriculture had reduced plant cover and herbivory rates on the focal palatable plants were elevated (Hahn and Orrock 2015*a*). However, the mechanisms that generate these neighborhood-level associational effects, and whether they depend upon the larger-scale habitat context, remain incompletely resolved.

In this paper, we evaluated how several habitat characteristics may generate associational effects at the neighborhood scales by altering insect herbivore behavior. To test the potential mechanisms that may generate associational effects (Table 1), we created experimental plant neighborhoods (10 m^2) within two habitat types: post-agricultural and non-agricultural (remnant) longleaf pine habitats (n = 14 study sites). At the neighborhood scale, we manipulated plant density (two levels) and frequency (three levels) of two plant species that differ in palatability. The abundance of grasshoppers, the dominant insect herbivore in this system (Hahn and Orrock 2015*a*), varies widely among study sites, and plant community composition varies with land-use history, allowing us to examine the role of grasshopper abundance and environmental context on herbivore damage to focal plants. If differences we documented in herbivory rates between post-agricultural and non-agricultural habitats (Hahn and Orrock 2015*a*) are driven largely by characteristics of the plant neighborhood (i.e., plant density and frequency), we expected to find the same results in our experimental plant neighborhoods in both habitat types. However, if herbivory is habitat-dependent, then we expected to find an interaction between land-use history and neighborhood plant composition. Because behavioral foraging decisions can be an important determinant of associational effects (Holt and Kotler 1987, Hambäck et al. 2003, Hambäck et al. 2014, Orrock et al. 2010*a, b*), we also used foraging

TABLE 1. Potential mechanisms of how generalist herbivores can generate different types of associational effects.

Hypothesis		Relative palatability†	Mechanism	Predicted associational effect outcome‡
1	Dilution hypothesis	Lower or higher	Neighbors dilute per-capita herbivory	AR occurs in high plant density
2	Selective grazing hypothesis	Higher	Herbivores selectively graze on focal plant	AS occurs in all treatments
3	Decoy hypothesis	Lower	Herbivores preferentially graze on neighbors	AR occurs in treatments with high frequency of palatable neighbors
4	Repellent hypothesis	Higher	Neighbors repel herbivores from neighborhood or reduce residence time	AR occurs in treatments with high frequency or density of unpalatable neighbors
5	Attractant hypothesis	Lower	Neighbors attracts herbivores	AS occurs in treatments with high density or high frequency of palatable neighbors

†Relative palatability is of the focal plant to neighbor.

‡Outcome is the type of associational effect: AR, associational resistance; AS, associational susceptibility. If the outcome of associational effects are habitat-dependent, we would expect different outcomes in habitat types. References to hypotheses are as follows: H1 (Hambäck et al. 2014, Otway et al. 2005); H2-3: (Atsatt and O'dowd 1976); H4: (Atsatt and O'dowd 1976, Baraza et al. 2006); H5: (Palmer et al. 2003, Rand 2003).

experiments to assess neighborhood-level behavioral foraging decisions made by the dominant consumer in our system: the grasshopper *Melanoplus angustipennis*.

METHODS

Study system

This experiment was conducted in the longleaf pine (*Pinus palustris*) ecosystem at the Savannah River Site (SRS), South Carolina, USA, an approximately 80,000-ha National Environmental Research Park (Fig. 1). The longleaf pine ecosystem contains one of the most diverse plant communities in North America, but large tracts of land have been converted to agriculture or urbanized (Frost 1998). Over the past century, agricultural plots that replaced historic longleaf woodlands have been abandoned, allowing woodlands to regenerate (Frost 1998). However, these post-agricultural woodlands lack or have reduced cover of many herbaceous plant species typical of longleaf pine woodlands (Kirkman et al. 2004, Brudvig et al. 2014). Although many studies have examined the role of abiotic factors and competition on the responses of the plant communities to management activities in longleaf ecosystems, there remains a lack of information regarding the effects of important biotic factors, such as herbivory.

Grasshoppers are a dominant invertebrate herbivore in the longleaf pine ecosystem and the most common herbivores on small, first year juvenile plants (Evans et al. 2012, Hahn and Orrock 2015*b*, PG Hahn, *unpublished data*). Grasshoppers are mobile enough to move several meters within a site over the course of our experiment. However, they typically forage at scales of a few meters (e.g., 3–17 m over a 5-week period; Haynes et al. 2007), likely making foraging decisions between neighboring plants. The size of our neighborhood plots (10 m^2; see below) was selected to be large enough for grasshoppers to move or select among the plots but small enough that most foraging decisions were most likely made among plants contained within a plot.

Experimental design

We conducted a split-plot 2 × 3 × 2 factorial experiment (Fig. 1) manipulating plant density (two levels; split-plot) and plant frequency (three levels; split-plot), within two habitat types (post-agricultural or non-agricultural land-use

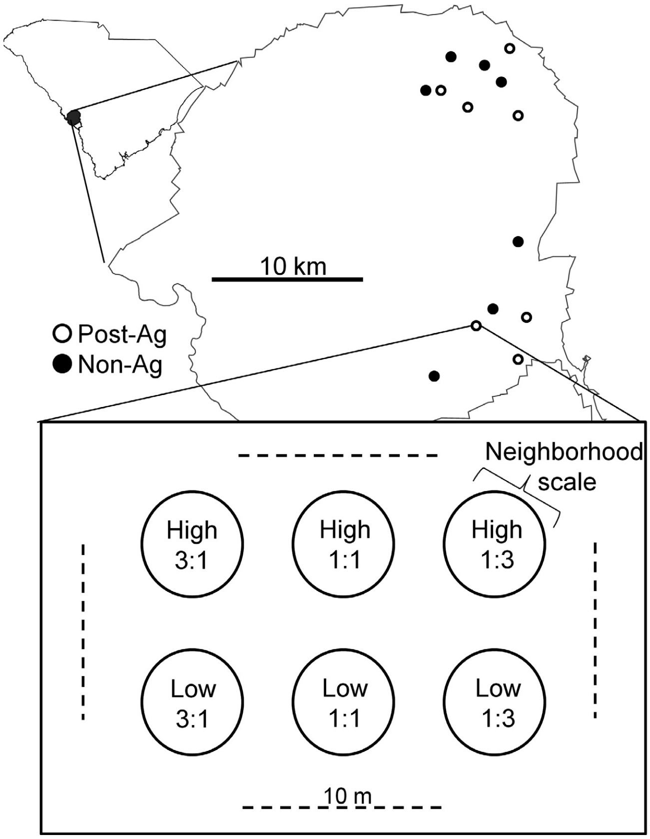

FIG. 1. Study sites within the Savannah River Site, South Carolina, USA. We manipulated plant density (low = 8 and high = 16 plants) and the frequency of *S. nemoralis* to *S. odora* (3:1, 1:1, or 1:3) in 10 m^2 plots within two habitat types: post-agricultural and non-agricultural (remnant) longleaf pine woodlands. We also measured grasshopper abundance at four 10 m transects at each site (dashed lines).

histories; whole-plot). We selected 14 sites, seven of each habitat type (post-agricultural and non-agricultural), interspersed across the SRS, resulting in an incomplete block design (Fig. 1). Sites encompassed at least 1,000 m^2 area of relatively homogenous vegetation. Sites received between three and eight prescribed fires in the previous 23 yr and were not burned the year of the study. We propagated plants in a greenhouse at the Savannah River Ecology Laboratory beginning in late May 2014. Plants were either a more palatable species (*Solidago nemoralis*) or a less palatable species (*Solidago odora*). Palatability was determined via feeding trials conducted in September 2013 using the grasshopper *Melanoplus angustipennis*. In these trials more than twice as much leaf tissue of *S. nemoralis* was consumed compared to *S. odora* (Hahn and Orrock 2015b). In June 2014, we prepared six 10 m^2 plots at each field site by removing existing vegetation using a brush saw followed by an herbicide application (glyphosate, Rodeo, Dow AgroSciences LLC, Indianapolis, Indiana, USA). Between 07 and 25 July 2014, we created our experimental neighborhoods by transplanting the greenhouse-propagated plants into the prepared field sites at two densities: eight or 16 plants per 10 m^2 plot. We also manipulated the relative frequency of *S. nemoralis* to *S. odora* at three levels: 3:1 (high *S. nemoralis*), 1:1 (even), and 1:3 (high *S. odora*). All plants were transplanted in biodegradable 10 cm diameter peat pots (Jiffy International AS, Kristiansand, Norway) containing a 1:1 mixture of potting soil and sand to minimize potentially confounding effects of varying soil conditions among land-use histories. The plants were spaced apart to reduce competition for sunlight and transplanting the plants in individual peat pots reduced competition for soil resources.

Quantifying herbivores and herbivory

At 2–3 week intervals, we measured grasshopper abundance at four 10 m × 1 m transects surrounding each block of plots. We disturbed the vegetation with a long stick and counted the grasshoppers as they flushed. Each site was surveyed 3–4 times during July and August. We averaged the counts along the four transects to get the average number of grasshoppers per 10 m^2 at the site (habitat) level. Grasshopper abundance did differ with sampling period ($F_{1,32} = 10.1$, $P = 0.003$) but did not differ between land-use histories ($F_{1,12} = 1.7$, $P = 0.22$) or with the land-use history × sampling period interaction ($F_{1,32} = 1.7$, $P = 0.21$). Since our study was focused on cumulative damage accrued over the course of the season rather than temporal fluctuations in damage related to temporal fluctuations in grasshopper abundance, we also averaged across survey periods to get one estimate of grasshopper abundance per site. At the end of the experiment in late August 2014, we recorded the total number of plants with herbivore damage.

We also recorded herbivore damage on three plants of each species within each plot. On each plant, we visually examined five haphazardly selected leaves and estimated the proportion of leaf tissue removed by chewing insects. If five or fewer leaves were present on a plant, we estimated the proportion of leaf tissue removed on all leaves. In cases where an original focal plant died, we haphazardly selected a neighbor to measure. We also counted the total number of leaves and the number of leaves with greater than 5% tissue removed by chewing invertebrates. All measurements were averaged by plant species at the plot level to avoid pseudo-replication.

Grasshopper foraging experiment

During August 2014 we conducted a grasshopper foraging experiment in a greenhouse at the Savannah River Ecology Laboratory. Within 30.5 cm^3 rearing cages, we created experimental plant arrays by manipulating the frequency of *S. nemoralis* to *S. odora* at three levels to match the field experiment (3:1, 1:1, and 1:3). Each array contained eight plants planted in one tray. *Melanoplus angustipennis* nymphs (3rd–4th instars) were collected and kept individually in small cages, where they were fed leaf lettuce ad libitum. Grasshoppers were starved for a 24-h period prior to use in the experiments. One *Melanoplus* was added to each array at approximately 09:00 h on the start of the experiment. At 10 min intervals, we recorded the position of each grasshopper within the array and if feeding, the identity of the plant species it was feeding upon. Trials were conducted during daylight hours (09:00–19:30) for two consecutive days ($n = 113$ observations per array). We conducted the feeding experiments over three periods between 04 August and 12 August 2014, with eight, four, and five trials per day, respectively. Replicates per treatment are as follows: 3:1 ($n = 7$), 1:1 ($n = 4$), 1:3 ($n = 6$). The trials were conducted on mostly sunny days and the temperature within the greenhouse ranged from 23°C to 32°C.

Statistical analysis

We used the number of plants attacked in each plot as a proxy of foraging activity in the field experiment to evaluate how habitat-scale and neighborhood-scale factors affect the total number of attacks on all plants, as well as on each species. We constructed a generalized linear mixed model using the number of plants damaged (a proxy of foraging activity) as the response variable with a Poisson error structure. Fixed-effect predictor variables measured at the habitat scale included land-use history (post-agricultural or non-agricultural), mean abundance of grasshoppers (continuous variable), and the number of prescribed burns in the past 23 yrs. Neighborhood plant frequency (three levels) and density treatments (high or low) were treated as fixed effects at the neighborhood scale. We included all possible interactions among land-use history, neighborhood frequency, and density. Grasshopper abundance and the number of prescribed fires in the past 23 yrs were treated as covariates and we did not include these in interactions. To account for the incomplete split-plot experimental design, we included site × land-use history as a random effect, which served as the error term for the land-use history, grasshopper abundance, and the number of prescribed fires. The residual error was the error term for all other effects. We conducted additional analyses on each of the two plant species using the same model structure.

To examine the effects of the habitat-scale and neighborhood-scale factors on the amount of herbivore damage to the experimental plant species, we constructed linear mixed-models with an index of plant damage as the response variable. The index of plant damage represented the estimated proportion of leaf tissue removed on the entire plant and was calculated as the proportion of leaf tissue removed by chewing insects averaged across five leaves on each plant multiplied by the proportion of the total leaves with chewing damage. This value was logit transformed to improve normality (Warton and Hui 2011). Fixed and random effects were the same as for the number of plants damaged described previously. We conducted separate analyses for each of the two focal species. To verify that the results were driven by the presence of neighboring plants instead of density of the focal plant, we conducted an additional analysis using the density of the focal plant in each plot (i.e., 2, 4, 8, or 12) as a predictor variable instead of the frequency and density treatments.

To evaluate foraging activity in the greenhouse feeding experiment, we used a generalized linear mixed model with the total number of attacks on all plants analyzed as a Poisson distributed response variable. We conducted additional analyses of the number of attacks on each species using the same model structure. To evaluate how plant frequency affects associational effects on each plant species, we used the per capita number of attacks on *S. nemoralis* and *S. odora* using linear mixed models. Per-capita attacks were calculated as the mean number of attacks on each individual plant within an array (i.e., total number of attacks on a given species divided by the number of individuals of that species within an array). The frequency of *S. nemoralis* to *S. odora* (three levels) was the predictor variable for all models. We included a period term as a random effect to account for the three experimental periods.

For all models, we considered $\alpha = 0.05$ significant and $\alpha = 0.1$ marginally significant. For generalized linear mixed models, we included an observation-level random effect to account for overdispersion and denominator degree of freedom were estimated using the Kenward–Roger method (Littell et al. 2006). All post-hoc linear contrasts were made using Tukey-adjusted *P*-values. Analyses were conducted using SAS version 9.4 (SAS Institute Inc., Cary, North Carolina, USA).

Results

The total number of plants attacked was affected by the neighborhood plant frequency treatment ($F_{1,61.1} = 6.0$, $P = 0.004$), with the highest number of plants attacked in the high *S. nemoralis* treatment and the lowest number of plants attacked in the high *S. odora* treatment (Fig. 2A). The density treatment had a marginally significant effect on the total number of plants attacked ($F_{1,61.7} = 3.2$, $P = 0.080$), with more plants tending to be attacked in the high-density (mean = 4.0 ± 0.38 SE) compared to the low-density treatment (mean = 3.1 ± 0.35 SE). Land-use history also had a marginal effect on the total number of plants attacked ($F_{1,14.6} = 3.9$, $P = 0.068$), with more plants tending to be attacked in post-agricultural sites (mean = 4.2, SE = 0.43) compared to non-agricultural sites (mean = 3.0, SE = 0.36). No other factors or interactions affected the total number of plants damaged (Appendix S1: Table S1). Attacks on *S. nemoralis* followed the same patterns as the total number of attacks (Fig. 2A; Appendix S1: Table S1). Attacks on *S. odora* were only affected by the frequency treatment ($F_{1,61.5} = 8.2$, $P = 0.001$), with fewer attacks when it was rare (i.e., in the high-palatability neighborhoods; Fig. 2A).

The proportion of leaf tissue removed on *S. nemoralis* plants at the end of the field experiment was affected by the neighborhood frequency treatment (Table 2), where *S. nemoralis* plants received less damage when they were rare relative to *S. odora* (Fig. 2B). *Solidago nemoralis* plants in the high *S. odora* treatment (1:3, *S. nemoralis* : *S. odora*) received significantly less damage compared to the even (1:1) treatment (linear contrast: $t = 3.0$, $P = 0.011$) and marginally less damage compared to the high *S. nemoralis* (3:1) treatment ($t = 2.3$, $P = 0.065$). Plants in the even frequency (1:1) and high *S. nemoralis* (3:1) treatments did not differ in damage ($t = 0.7$, $P = 0.77$). The number of burns had a marginally significant positive effect on damage to *S. nemoralis* ($\beta = 0.37$, SE = 0.18, $t = 2.1$, $P = 0.065$).

The proportion of leaf tissue removed on *S. odora* at the end of the field experiment was affected by the neighborhood frequency treatment, the interaction between land-use history and the frequency treatment, and marginally by the three-way interaction between neighborhood frequency, plant density, and land-use history (Table 2). However, the simple effect of plant density, given all combinations of land-use history and frequency treatments, were never significant (all *P*'s > 0.1), so we only interpret the land-use history-by-frequency interactions. In post-agricultural sites, plants in the even frequency (1:1) treatment received significantly more damage compared to when it was more frequent (1:3) ($t = 3.0$, $P = 0.044$) and marginally more damage compared to when *S. odora* was rare (3:1) (linear contrast: $t = 2.8$, $P = 0.068$; Fig. 2C). There was no effect of the frequency treatment in the non-agricultural sites (simple effect: $F = 0.4$, $P = 0.65$). The proportion of leaf tissue removed on *S. odora* was also marginally and positively related to grasshopper abundance ($\beta = 0.54$, SE = 0.31, $t = 1.8$, $P = 0.100$). The proportion of leaf tissue removed on either *S. nemoralis* or *S. odora* was not affected by

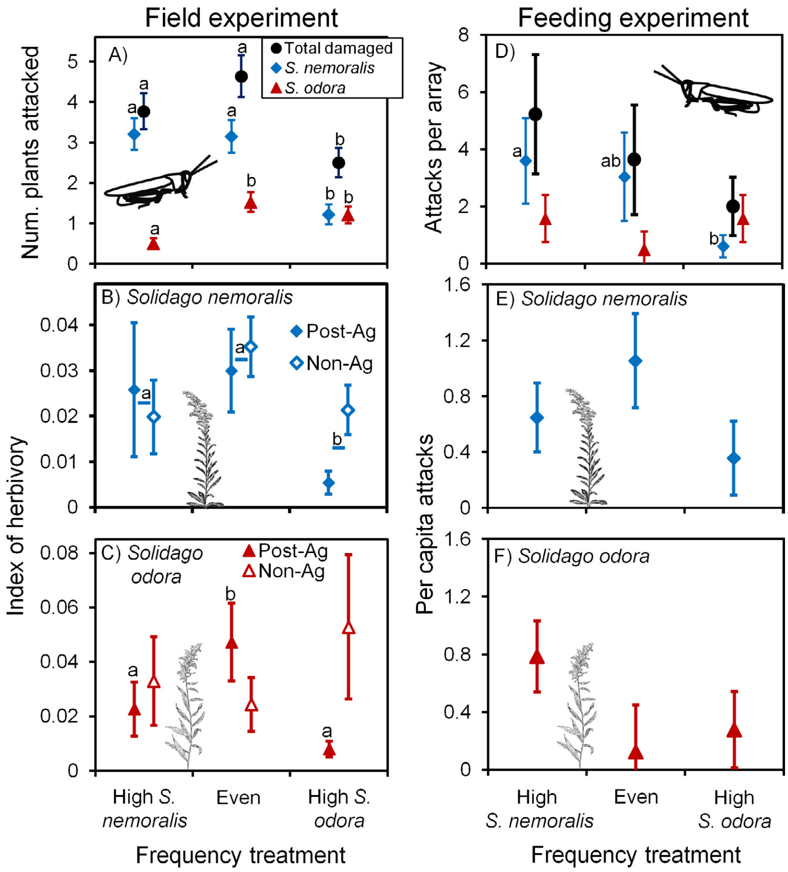

FIG. 2. (A–C) Results from the field experiment. (A) Mean number of plants with herbivore damage, a proxy for foraging activity, by frequency treatment. (B–C) Index of herbivory is the proportion of leaf tissue removed, estimated for the whole plant, on (B) *Solidago nemoralis* and (C) *Solidago odora* in the three frequency treatments and two land-use history habitats. Note that analyses were conducted on logit-transformed data, although we present back-transformed means for clarity. (D–F) Results from the grasshopper feeding experiment. (D) mean number of total attacks by herbivores in the three frequency treatments, a proxy for foraging activity. Per-capita number of attacks on (E) *So. nemoralis* and (F) *So. odora*, which are plant-centric metrics of damage. All bars are ±1 SE. Letters above data points indicate significant (or marginal) differences based on Tukey-adjusted *P*-values. Letters in (B) compare means pooled across land-use histories (bars) to aid in comparing among frequency treatments. Letters in (C) compare frequency treatments only within post-agricultural habitats (frequency treatments in non-agricultural sites do not differ). Letters in (A and D) are comparisons made within species, when there are significant differences.

intraspecific density (Appendix S1: Table S2), further supporting that changes in herbivore damage were driven by neighbors of the other species.

In the feeding experiment, the frequency of *S. nemoralis* to *S. odora* did not affect the total number of attacks on all plants ($F_{2,12.9}$ = 1.7, *P* = 0.23, Fig. 2D). Total attacks on *S. nemoralis* was affected by the frequency treatment ($F_{2,12.8}$ = 4.1, *P* = 0.043). *Solidago nemoralis* received fewer total attacks when it was rare (i.e., 1:3 treatment; Fig. 2D) and attacks in this treatment were marginally less than the 1:1 treatment (linear contrast: *t* = 2.5, *P* = 0.07) and significantly less than the 3:1 treatment (*t* = 2.8, *P* = 0.037). Total attacks between the 3:1 and 1:1 treatments did not differ (*t* = 0.4, *P* = 0.92). Total attacks on *S. odora* were not affected by the frequency treatment ($F_{2,14}$ = 0.40, *P* = 0.68; Fig. 2D). Per-capita attacks on *S. nemoralis* ($F_{2,13.1}$ = 1.9, *P* = 0.19; Fig. 2E) or *S. odora* ($F_{2,12}$ = 1.64, *P* = 0.23, Fig. 2F) were not significantly affected by the frequency treatment. However, because of the small sample size and that the patterns of total attacks and per-capita attacks on *S. nemoralis* were approaching significance and the patterns matched the results of the field experiment (Fig. 2), we conducted a retrospective power analysis (Thomas 1997). The retrospective power analysis revealed that our feeding experiment had fairly low power to detect significant effects across a range of ecologically relevant effect sizes that are similar to those we observed in the field (i.e., a 2.5–7.5 × change in per-capita consumption among the frequency treatments (Appendix S1: Table S3).

DISCUSSION

Understanding the mechanisms governing the direction and magnitude of plant-herbivore interactions that are mediated by neighbors (i.e., associational effects) is a

Table 2. ANOVA table of the reduced models for the results of the proportion of leaf tissue removed on the two focal plant species in the field experiment. A model-reduction procedure was used to remove non-significant higher-order interactions.

	Solidago nemoralis			*Solidago odora*		
Effect	*ddf*	*F*	*P*	*ddf*	*F*	*P*
Land-use history	9.6	0.0	0.982	8.6	1.2	0.301
Plant frequency	57.3	4.9	0.011*	50.2	3.0	0.061**
Plant density	57.5	0.2	0.700	50.9	0.3	0.566
Land-use × frequency	57.3	0.2	0.804	50.3	3.2	0.050*
Land-use × density	57.5	0.0	0.993	51.5	0.1	0.772
Frequency × density	57.3	0.9	0.412	51.0	0.3	0.720
Land-use × freq × density	57.3	0.0	0.989	51.3	2.7	0.079**
Burns since 1991	9.8	4.3	0.065**	8.7	3.2	0.108
Grasshopper abundance	9.7	2.7	0.134	14.3	3.1	0.100**

$^*P \leq 0.05$; $^{**}P \leq 0.1$.

primary challenge in the study of indirect species interactions (Agrawal et al. 2006, Barbosa et al. 2009, Underwood et al. 2014). Our experimental results demonstrate that foraging behavior is a key driver of the direction of associational effects (i.e., associational resistance or susceptibility) and depends on both neighborhood plant frequency and the relative palatability between plant species. For the more palatable species in our study (*Solidago nemoralis*), herbivore foraging activity was reduced in the less-palatable neighborhoods in the field experiment (Fig. 2A), resulting in reduced damage (i.e., associational resistance) when the more palatable plant was rare (Fig. 2B). The results for foraging activity and the pattern for per-capita attack rates from our feeding experiment, although not significant, matched the patterns from the field experiment (Fig. 2). In contrast, damage to the less-palatable species (*Solidago odora*) was driven by a combination of habitat context (both herbivore abundance and land-use history) and neighborhood plant frequency. We found increased damage (i.e., associational susceptibility) in the even frequency treatment neighborhoods only in post-agricultural habitats (Fig. 2C). Our study suggests that associational effects are one likely explanation for the common finding that herbivory is often context-dependent and varies widely among different plant species and habitats (Maron et al. 2014).

Foraging behavior at the level of the plant neighborhood appears to be important for determining the amount of damage received by palatable plants based on results of both our field and greenhouse-feeding experiments. Grasshoppers consume a variety of food sources to meet their nutritional requirements (Behmer and Joern 1993, Unsicker et al. 2008), but will preferentially consume the optimal food source even when it is rare relative to a sub-optimal food source (Behmer et al. 2001). This was not the case in our study, as we found that the more palatable species, *S. nemoralis,* received less damage in the field when it was rare relative to the less-palatable *S. odora* (Fig. 2B). Reduced herbivory on *S. nemoralis* seemed to be driven by reduced foraging activity in the neighborhoods with high frequency of the less palatable *S. odora* (Fig. 2A). Furthermore, the behavioral observations from our greenhouse feeding experiment generally support the finding of lower feeding activity in the high *S. odora* treatments. Our results also suggest that grasshopper foraging on the more palatable *S. nemoralis* is in part frequency-dependent, because total attacks on *S. nemoralis* were higher when *S. nemoralis* was more common or in even frequency compared to when it was rare (Fig. 2D). Collectively, the results for the more palatable species are most consistent with the herbivore repellent hypothesis (Table 1), where the presence of the less palatable species acts to reduce foraging activity in the less-palatable neighborhoods or reduce residence time within the neighborhood. When *S. nemoralis* was not rare, herbivores preferentially foraged on this more palatable species (Fig. 2), consistent with the selective grazing hypothesis (Table 1). Thus, associational effects on *S. nemoralis* appear to be driven by overall foraging activity as well as partially frequency-dependent foraging.

Herbivore abundance is sometimes, but not always (Cronin et al. 2010, Hakes and Cronin 2012), a good predictor of herbivore damage. Our findings provide insight into when a relationship between herbivore abundance and herbivore damage might be expected (and when it might not). We previously found that herbivory exhibited a hump-shaped response to plant cover and that grasshopper abundance was a poor predictor of herbivory in the same system as the present study, although this previous study did not manipulate local plant neighborhoods (Hahn and Orrock 2015*a*). In the present study we found only a weak relationship between herbivore abundance and herbivore damage and only for the less palatable species, *S. odora*. These findings and the results of our feeding experiment suggest that herbivores preferentially feed on the more-palatable species and thus foraging behavior is more important than herbivore abundance for predicting damage on these plant species.

We expected a dilution effect (Table 1) to occur in the high-density plots, especially the plots with high density and high frequency of the more palatable plant. However, the density of plants used in our experiment may not have been high enough to create a dilution effect. We also found that neighboring plant frequency affected damage to *S. odora*, but only in post-agricultural habitats, suggesting an interplay between neighborhood-scale and larger-scale, habitat-level factors in dictating herbivore damage. Although it is unclear why only the less palatable plant species was affected by land-use history, recent studies have found relationships between land-use history, neighboring plant cover, and herbivory (Hahn and Orrock 2015*a*, Kim et al. 2015). Our finding of higher herbivory in post-agricultural sites is consistent with previous results, where we found higher herbivory rates in some post-agricultural sites due to differences in vegetation composition (Hahn and Orrock 2015*a*). Collectively, the results for the less-palatable *S. odora* are consistent with the attractant hypothesis (Table 1) if herbivores are preferentially moving from the surrounding post-agricultural habitat, which support lower quality food resources (Hahn and Orrock 2015*a*), into the experimental neighborhoods. This appears to be the case because we also found that more total plants tended to be attacked in post-agricultural sites compared to non-agricultural sites (Appendix S1: Table S1). More broadly, our study highlights that any factor that alters plant community composition, such as land-use legacies in our case, could potentially alter levels of herbivory via associational effects. Associational effects are likely a valuable tool for understanding the outcome of plant-herbivore interactions and how herbivory might affect community structure in natural or anthropogenically altered systems.

Our study provides some of the first experimental evidence from complementary field and greenhouse studies that plant frequency affects the foraging behavior of generalist insects and that this can generate associational effects. Understanding associational effects that are driven by foraging behavior rather than abundance may be particularly important, because behaviorally mediated consumer effects can be disproportionate to consumer abundance and occur more rapidly than abundance-mediated consumer effects (Holt and Kotler 1987, Orrock et al. 2008, 2010*b*, Silliman et al. 2013). Our results suggest that associational effects can benefit individual plants, although how this might scale up to affect population dynamics remains unclear. Future research that seeks to further understand the mechanisms that generate associational effects and how these interactions scale-up to alter population dynamics will be essential for understanding the large-scale implications of associational effects. Foraging behavior may provide a useful framework for generating predictions and hypotheses for such future work.

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