

Land-use history alters contemporary insect herbivore community composition and decouples plant–herbivore relationships

Philip G. Hahn* and John L. Orrock

Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706, USA

Summary

1. Past land use can create altered soil conditions and plant communities that persist for decades, although the effects of these altered conditions on consumers are rarely investigated.
2. Using a large-scale field study at 36 sites in longleaf pine (*Pinus palustris*) woodlands, we examined whether historic agricultural land use leads to differences in the abundance and community composition of insect herbivores (grasshoppers, families Acrididae and Tettigoniidae).
3. We measured the cover of six plant functional groups and several environmental variables to determine whether historic agricultural land use affects the relationships between plant cover or environmental conditions and grasshopper assemblages.
4. Land-use history had taxa-specific effects and interacted with herbaceous plant cover to alter grasshopper abundances, leading to significant changes in community composition. Abundance of most grasshopper taxa increased with herbaceous cover in woodlands with no history of agriculture, but there was no relationship in post-agricultural woodlands. We also found that grasshopper abundance was negatively correlated with leaf litter cover. Soil hardness was greater in post-agricultural sites (i.e. more compacted) and was associated with grasshopper community composition. Both herbaceous cover and leaf litter cover are influenced by fire frequency, suggesting a potential indirect role of fire on grasshopper assemblages.
5. Our results demonstrate that historic land use may create persistent differences in the composition of grasshopper assemblages, while contemporary disturbances (e.g. prescribed fire) may be important for determining the abundance of grasshoppers, largely through the effect of fire on plants and leaf litter. Therefore, our results suggest that changes in the contemporary management regimes (e.g. increasing prescribed fire) may not be sufficient to shift the structure of grasshopper communities in post-agricultural sites towards communities in non-agricultural habitats. Rather, repairing degraded soil conditions and restoring plant communities are likely necessary for restoring grasshopper assemblages in post-agricultural woodlands.

Key-words: abandoned agriculture, community composition, grasshoppers, insect diversity, longleaf pine, old field, plant–insect interactions

Introduction

The single greatest threat to biodiversity is habitat destruction, with a major source of destruction being land transformation for agriculture (Wilcove *et al.* 1998; Foley *et al.* 2011). Since the 1950s, more than 200 million hect-

ares of croplands in North America have been abandoned and are regenerating into semi-natural areas, creating potential habitat for diverse taxa (Ramankutty & Foley 1999; Foley *et al.* 2011). However, the legacies of agricultural practices can alter plant community composition for decades to centuries after abandonment (Foster *et al.* 2003; Flinn & Vellend 2005). Many native herbaceous plant species typical of habitats with no history of agriculture fail to reestablish in post-agricultural sites partially

*Correspondence author. E-mail: pghahn@wisc.edu

because of dispersal limitation (Kirkman *et al.* 2004; Flinn & Vellend 2005; Vellend *et al.* 2007). Tilling also has major effects on soil characteristics (Foster *et al.* 2003), including increasing soil nutrients, particularly phosphorous (Davidson & Ackerman 1993), decreasing soil organic matter (Burke, Lauenroth & Coffin 1995) and compacting soil (Bassett, Simcock & Mitchell 2005; Hamza & Anderson 2005). Altered soil conditions can further affect plant communities by reducing establishment of native plants or promoting establishment of ruderal plants species (Dambrine *et al.* 2007; Baeten *et al.* 2009). Because of the strong legacy effects of historic agriculture on both abiotic and biotic components of ecosystems, recovery trajectories of post-agricultural ecosystems often differ from ecosystems recovering from natural disturbances and can result in alternative stable states (Egler 1954; Cramer, Hobbs & Standish 2008; Kepfer-Rojas *et al.* 2014). Despite these well-documented effects of agricultural land-use history on soil conditions and plant communities, less work has examined the effects of land-use legacies on other organisms, such as consumers.

Understanding how anthropogenic drivers alter consumer communities is important, because consumers contribute significantly to ecosystem productivity, biodiversity and ecosystem functioning (Duffy 2002; Schmitz 2008; Metcalfe *et al.* 2014). Recent evidence suggests that the responses of consumer communities to land-use legacies are highly variable, likely because land-use legacies affect a suite of environmental characteristics (Foster *et al.* 2003). A recent meta-analysis showed that land use affects multiple taxa in tropical systems, but that different land uses had differing effects on biodiversity and that the effects were taxa specific, with agricultural activities (either current or historic) causing the largest declines in species richness for most taxa (Gibson *et al.* 2011). Debiniski *et al.* (2011) found taxa-specific responses of arthropod communities to land-use legacies (historic agriculture, grazing or fire regimes) in Midwestern grasslands, with herbivorous taxa responding most strongly to characteristics of the plant community. Furthermore, the effects of land-use legacies were stronger than contemporary management regimes (i.e. burning and grazing). A study in the Argentine pampas found higher densities of pest grasshoppers in disturbed sites dominated by introduced forbs and pasture grasses compared to adjacent natural areas dominated by native vegetation (Torrusio, Cigliano & De Wysiecki 2002). Although these recent studies demonstrate clear contingencies in how land-use legacies affect consumer communities, whether historic agriculture alters relationships between environmental (plant or soil) characteristics and consumer communities remains unresolved.

Grasshoppers are common generalist herbivores in grassland systems world-wide (Otte 1981) and may be particularly sensitive to the effects of historic agriculture through changes to plant community composition, because grasshopper assemblages respond to changes in plant communities from disturbances such as fire and

grazing (Joern 2005; Knight & Holt 2005; Branson & Sword 2010). Longleaf pine (*Pinus palustris*) woodlands occur in upland areas of the south-eastern United States and are characterized by a patchy overstorey of open-grown pines, with a high diversity of herbaceous plants (Walker & Peet 1984) and grasshoppers (Hill & Dakin 2011) in the understorey. Historically, longleaf pine woodlands were maintained by low-intensity understorey fires ignited by lightning or Native Americans as frequently as every 2–3 years (Frost 1998). Prior to European settlement in the 1700s, longleaf pine woodlands were used for grazing cattle and hogs by early European colonists (White 2004). Throughout the 1700–1800s, longleaf pine woodlands were extensively logged, tapped for turpentine and tilled for agriculture (Frost 1998; White 2004). Fire suppression was also actively practised after around 1920, resulting in the conversion of open pine woodlands to closed canopy secondary forests (Frost 1998; White 2004). Over the last several decades, large tracts of agricultural land have been abandoned, allowing longleaf pine woodlands to regenerate and prescribed fire has been reintroduced to many managed areas (Jose, Jokela & Miller 2005). However, the legacies of historic agriculture persist throughout the historic range of the longleaf pine ecosystem through altered soil conditions and altered plant community composition, which generally results in reduced plant diversity and the loss of plant species with a strong affinity for undisturbed longleaf woodlands (Kirkman *et al.* 2004; Brudvig & Damschen 2011; Brudvig *et al.* 2014). Since characteristics of the plant community, such as productivity or composition, are strong regulators of consumer community structure, changes to the plant and soil conditions likely propagate up to consumer communities, although this has not been investigated.

In this study, we conduct comprehensive sampling of the plant community, environmental variables and grasshopper communities across 36 separate sites to provide the first large-scale evaluation of how past land use affects the abundance and composition of grasshopper communities. Specifically, we ask: (i) does land-use history affect grasshopper abundance or community composition? and (ii) does past land use alter the relationship between plant cover or environmental variables and grasshopper abundance or community composition?

Materials and methods

SITE SELECTION

This study was conducted at 36 upland longleaf pine (*P. palustris*) woodlands at the Savannah River Site (SRS), an c. 80 000-ha National Environmental Research Park in South Carolina, USA (Fig. 1). The area around the SRS was heavily affected by open grazing, logging, turpentine and agriculture throughout much of the 1700–1800s. However, the most intensive human activities, such as logging and agriculture, were restricted to lowland areas near major rivers and tributaries, leaving pine uplands

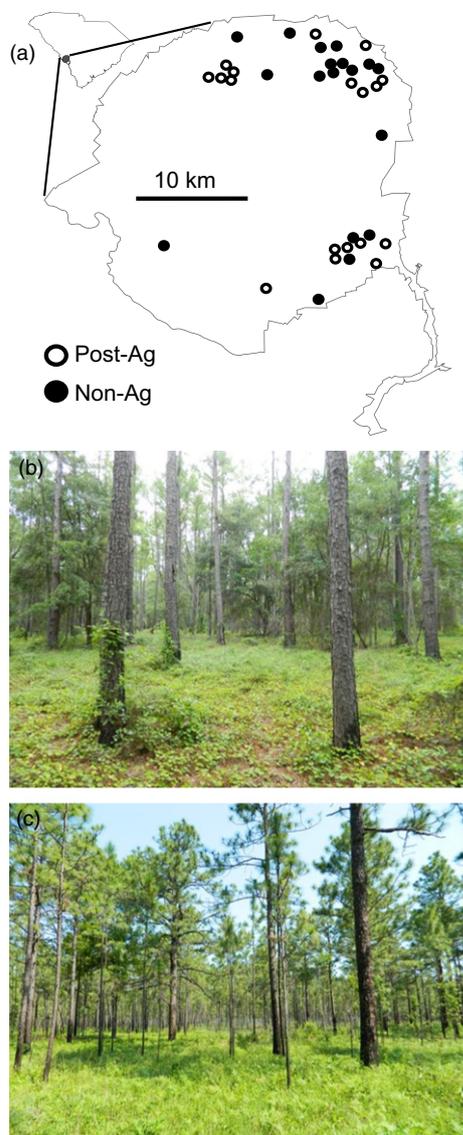


Fig. 1. (a) Map of the study sites within upland longleaf pine woodlands at the Savannah River Site, South Carolina, USA. ‘Post-Ag’ sites have a history of agriculture (>50 years since abandonment); ‘Non-Ag’ sites have no known history of agriculture. Longleaf pine woodland sites with (b) a history of agriculture and (c) no history of agriculture. Photo credit: P. G. Hahn.

relatively undisturbed by human activities (White 2004). Fertilizers became more common in the southern USA after 1865, allowing for more intensive tilling of upland pine forests, which peaked in the 1920s (White 2004). Tilling for agriculture peaked at SRS around this time, but occurred between about 1865 and 1950 (White & Gaines 2000). Farms were small and dispersed across the landscape, and approximately half of the land remained as untilled woodlands through 1950 (White 2004). Woodlands were used by farmers as timber lots and for grazing, and were fire-suppressed starting around 1920 (White 2004), but they have no history of tilling, which is a major destructive force that eliminates all existing vegetation (Foster *et al.* 2003; Cramer, Hobbs & Standish 2008). Historic agriculture has dramatic effects on contemporary plant community composition, more so than grazing or fire suppression (Brudvig & Damschen 2011; Brudvig

et al. 2014), and therefore is the focus of our study. We selected sites that varied in land-use history: non-agricultural or post-agricultural woodlands. Land-use histories were determined from aerial photographs taken in 1951, just prior to governmental acquisition of SRS. All agricultural fields were abandoned after governmental acquisition and subsequently planted with pine trees (White & Gaines 2000). Tilled fields in the 1951 aerial photographs were classified as post-agricultural woodlands; non-agricultural sites were mature open woodlands in the 1951 aerial photographs. We examined aerial photographs taken in 1938 to verify that land-use histories were consistent for at least 13 years (Appendix S1, Supporting information). All of our non-agricultural sites were located on mature woodlands in the aerial photographs taken in both 1938 and 1951. One of our 18 post-agricultural sites was mature woodland in 1938 and tilled by 1951, but the rest were located on tilled fields at both time periods. The land-use history types were interspersed across the landscape. All sites were separated by >250 m, covered >1 ha of relatively uniform habitat and were buffered by >50 m of the same land-use history. We also stratified our site selection along a fire frequency gradient. Fire history (number of fires since 1991) was obtained for each site from the USDA Forest Service.

GRASSHOPPER SAMPLING

We used sweep nets to sample grasshopper assemblages (Acrididae and Tettigoniidae), which is the most common method used to sample grasshopper assemblages (Evans, Rogers & Opfermann 1983; Belovsky & Slade 1995; Joern 2005). At each site, we established three 5 m × 5 m plots, separated by >5 m. Plots were vigorously swept for three 3-min periods, with *c.* 15-min rest periods between sweeps so that any grasshoppers dislodged from the vegetation could crawl back up onto the vegetation. The three sweep samples per plot and the three plots (nine total subsamples) were pooled for each site. Preliminary analyses indicate that, on average, the sample from each plot contained more than half the grasshoppers species captured at a site (Appendix S2, Supporting information), suggesting this sampling method captured a representative sample of the grasshoppers present at each site. Sampling was conducted between 23 July and 6 August 2011. Sweeps were restricted to 09.00–15.00 on sunny days, when grasshoppers are most active at our site (Evans *et al.* 2012; P. G. Hahn, pers. obs.). Sites were visited in a random order, and sampling of the different land-use histories was equally spread across different times of day. Immediately after collection, grasshoppers were frozen and later identified to genus or species using taxonomic guides (Capinera, Scott & Walker 2004; Eades *et al.* 2013). Identifications of a subset of the collection were verified by a regional expert (J. Hill, Mississippi Entomology Museum), and these voucher specimens have been deposited in the Insect Research Collection of the Department of Entomology, University of Wisconsin-Madison. Adults and nymphs were included in the analysis.

VEGETATION AND GROUND COVER

At each 5 m × 5 m plot, vegetation was sampled in four 1-m² quadrats (*n* = 12 quadrats per site) between 19 and 21 July 2011. We recorded per cent cover of plant functional groups (grasses, forbs, legumes, ferns, woody vegetation, vines) and leaf litter. These functional groups are common at our field site (Parresol,

Blake & Thompson 2012), and broad functional groups (grasses and forbs) are commonly used in grasshopper studies because they comprise the dominant food source for grasshoppers (e.g. Behmer & Joern 1993; Belovsky & Slade 1995; Specht *et al.* 2008; Joern, Provin & Behmer 2012). The per cent cover of the six plant functional groups and leaf litter was averaged by site for analysis. We also summed grasses, forbs and legumes into one variable (herbaceous cover) because they were highly correlated.

ENVIRONMENTAL DATA

At each site, we collected environmental data (e.g. canopy cover, substrate temperature) potentially related to grasshopper activity. We calculated the mean proportion of visible sky in photos taken with a hemispherical lens 1 m above the ground in three plots per site following standard protocol (HEMIVIEW version 2.1; Dynamax Inc., Houston, TX, USA). Temperature of the substrate (bare ground, leaf litter, or vegetation) was recorded in the corner of each 5 m × 5 m plot using an infrared temperature gun (Fluke Corp., Everett, WA, USA) immediately after the sweep netting. We measured soil hardness as the depth at which 2 MPa was attained (max of 72 cm), which is a level of soil compaction that affects plant performance (Bassett, Simcock & Mitchell 2005). Soil hardness measurements were taken at six locations adjacent to the 5 m × 5 m plots and averaged to produce one value per site. Plant and environmental variables are summarized in Table 1 and Appendix S3 (Supporting information). Data are available in the Dryad Digital Repository (Hahn & Orrock 2014).

DATA ANALYSIS

To describe the differences in the cover of plant functional groups and environmental variables between post-agricultural and non-agricultural longleaf pine woodlands, we conducted univariate *t*-tests for each variable.

Prior to analysis, we removed grasshopper taxa that occurred in fewer than three sites of each land-use history. Removing rare taxa was important for our analysis because we are interested in the response of individual taxa to environmental gradients and

Table 1. Mean values of environmental variables and plant functional groups in post-agricultural and non-agricultural longleaf pine woodlands

Description	Mean (SE)	
	Post-Ag	Non-Ag
Prop visible sky	0.45 (0.02)	0.43 (0.02)
Soil Hardness [depth (cm) to 2 Ma] [†]	11.2 (0.73)	22.2 (2.41)**
Number of burns since 1991	4.28 (0.46)	4.11 (0.50)
Substrate temperature (°C)	40.2 (1.09)	36.7 (1.08)*
% leaf litter cover	63.5 (3.46)	63.73 (3.11)
% herbaceous cover	5.44 (1.32)	3.43 (0.98)
% woody cover	14.3 (2.04)	18.56 (2.51)
% vine cover	7.64 (0.51)	3.79 (0.39)*
% fern cover [†]	0.00 (0.0)	2.13 (0.85)*

* $P < 0.05$; ** $P < 0.005$ (Bonferroni correction, $\alpha = 0.05$, 8 corrections, P -value = 0.0055). [†]Variables that were analysed separately to avoid multicollinearity with land-use history.

the resulting consequences for community composition. Therefore, inclusion of rare taxa would mask the response of the community composition to environmental variation (see also the description of the MLM below). We used criterion for rare taxa from McCune and Grace (2002). The resulting data set contained counts of the six most common grasshopper taxa at 36 sites (Appendix S4, Supporting information). All predictor variables were centred ($\mu = 0$, $\sigma = 1$) before analysis, which allows regression coefficients to be compared among all variables.

We used multilevel models (MLMs) described by Jackson *et al.* (2012) for analysis of community data to evaluate our questions. Multilevel models are desirable for our data set and question for several reasons. First, MLM is similar to other common multivariate techniques (e.g. redundancy analysis or canonical correspondence analysis) but allows for generalized error distributions (e.g. Poisson distribution for counts). Secondly, we are interested in changes to both grasshopper abundance and community composition. MLM analyse the responses of individual grasshopper species to predictor variables as random-effect slopes using a series of Poisson regressions. The standard deviations of these slopes can be interpreted as changes in community composition assuming that two communities with the same relative abundances of species have the same composition, regardless of the total abundances (Jackson *et al.* 2012). Finally, the results can be plotted in an ordination to aid in visual interpretation, if appropriate (Jackson *et al.* 2012). Although MLM is our primary analytical approach, we conducted ancillary univariate Poisson regressions for comparison.

We addressed our two questions (i.e. does land-use history affect grasshopper abundance and community composition? and does past land use alter the relationship between plant cover or environmental variables and grasshopper abundance or community composition?) using MLM. We followed the general recommendations of Bolker *et al.* (2009) and Grueber *et al.* (2011) for fitting MLMs that include random intercepts and slopes. We first constructed a global model that included our seven environmental and plant functional predictor variables as continuous fixed effects (Table 1), land-use history as a binary (0 = post-agricultural or 1 = non-agricultural) fixed effect, and an interaction term for land-use history and each of the seven continuous variables. These interaction terms allowed us to formally examine our second question (does past land use alter the relationship between plant cover or soil characteristics and grasshopper abundance or community composition?) because a significant interaction would indicate different relationships (slopes) between land-use histories. We did not include interaction terms among any continuous variables or any three-way interactions to avoid over-fitting our model and to ensure that our global model converged (Bolker *et al.* 2009). We did not include fern cover or soil hardness in these models to avoid multicollinearity with land-use history (see Table 1). Instead, we analyse these two variables separately. The global model included random intercepts for site, species, and a unique number for each observation to account for overdispersion. The observation-level random-effect models variation beyond the Poisson distribution (i.e. overdispersion) using a Poisson log-normal distribution (Elston *et al.* 2001). We used a two-step AIC selection approach, a model-reduction step and then a model-selection step. First, we reduced the global model using the dredge function in the MuMIn package in R, which runs all possible models based on the global model and selects the top model(s) based on AIC (Barton 2013). Then we added random slope terms to the top models within 2 AIC units of the best

model and selected the best model that included fixed and random effects. The random slope terms (i.e. each fixed effect \times taxa) in these models tested for taxon-specific responses to each predictor variable (i.e. changes to community composition). In other words, these random effects test the standard deviation of parameter estimates (slopes) for each taxon in response to an effect, such that a significant random effect can be interpreted as altering community composition because the responses of the different taxa differ in response to the effect (Jackson *et al.* 2012). Furthermore, as in Jackson *et al.* (2012), we consider changes in relative abundances, not absolute abundances, as a change in community composition. Mean relative abundances for two variables following a Poisson distribution is $\lambda_1/\lambda_2 = \exp(a_1 - a_2)$, where a_i are intercepts, such that proportional changes (i.e. both species double in abundance) would not change the relative abundance of the two species (Jackson *et al.* 2012). We avoided model averaging because our top models contained different random effects, which are not able to be incorporated into model averaging procedures (Grueber *et al.* 2011). P -values for the random slopes were tested using the `rand` function in the `LMERTEST` package (Kuznetsova, Brockhoff & Christensen 2012).

We interpret three products of the final MLMs: (i) the fixed-effect parameter estimates, which report the mean response of all grasshopper taxa to a predictor variable (i.e. changes in abundance), (ii) the random effects, calculated as the standard deviations of coefficients, which report the variability in responses of all grasshopper taxa in response to a predictor variable (i.e. changes in community composition), and (iii) the random slope parameters, which report the response of individual grasshopper species to a predictor variable. We used the `glmer` function in the `LME4` package version 1.1-6 for the MLM analysis (Bates, Maechler & Bolker 2013).

Results

Two plant cover variables differed between land-use histories, with greater vine cover in post-agricultural sites and greater fern cover in sites not used for agriculture. Substrate temperature was also lower in woodlands with no history of agricultural use, and the depth at which 2 MPa was reached was greater in non-agricultural sites, indicating less soil compaction (Table 1).

We collected 459 individuals representing 18 taxa (species or genera), six of which were abundant enough to include in further analysis (Appendix S4, Supporting information). In the best-supported MLM (Appendix S5, Supporting information), land-use history alone did not affect grasshopper abundance, but there was a significant interaction between land-use history and herbaceous cover (Table 2). Herbaceous cover was not related to grasshopper abundance in post-agricultural woodlands ($z = 1.39$, $P = 0.16$), but the relationship between grasshopper abundance and herbaceous cover was significantly more positive in non-agricultural woodlands ($z = 1.96$, $P = 0.05$). Leaf litter cover was negatively related to grasshopper abundance ($z = -2.34$, $P = 0.019$). The land-use history \times grasshopper taxa random term, which allowed each grasshopper taxa to vary with land-use history, was also significant ($\chi^2 = 7.16$, $P = 0.007$, Table 2), suggesting that

Table 2. Analysis of deviance table for the fixed effects, including analysis of random effects, from the best MLM on grasshopper assemblages at the Savannah River Site, South Carolina, USA

Fixed effects	χ^2	P
Land-use history	0.32	0.572
Herbaceous cover	8.78	0.003
Leaf litter	5.48	0.019
History \times HerbCov	3.84	0.050
Random effects		
Species	40.48	0.000
History \times Spp	7.16	0.007
Site	18.60	0.000

land-use history altered grasshopper community composition (Fig. 2). Fixed- and random-effect coefficients for the best model are presented in Appendix S5 (Supporting information). The two variables that were analysed separately to avoid multicollinearity with land-use history generally support the results of the best model, with fern cover positively affecting grasshopper abundance and soil hardness associated with altered grasshopper community composition (Appendix S6, Supporting information). Moreover, the grasshopper taxa responses to land-use history and soil hardness were highly correlated between these two models (Fig. S6, Supporting information).

To aid in interpretation of the MLM, we plotted the raw abundance values for each grasshopper taxa to highlight difference in abundances between land-use histories, including best-fit Poisson regression lines (Fig. 3, Appendix S7, Supporting information). Three of the six taxa match the results of the MLM in that their abundance was positively related to herbaceous cover in non-agricultural sites, but not in post-agricultural sites. Of the mixed

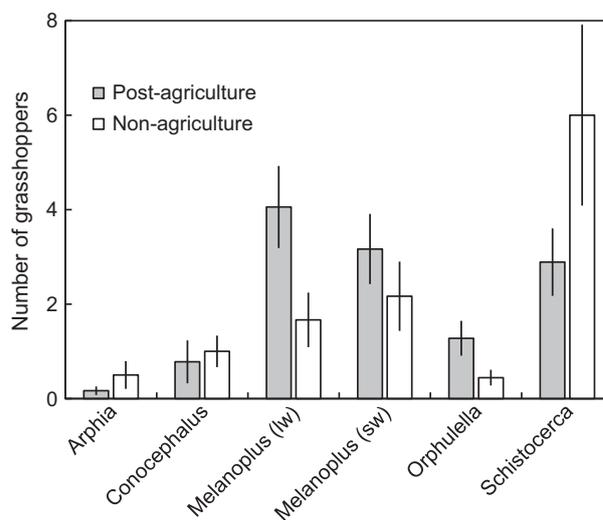


Fig. 2. Mean abundance (± 1 standard error in three 5 m \times 5 m plots per site) of the six most common grasshopper taxa (Acrididae and Tettigoniidae) collected at the Savannah River Site, South Carolina, USA, as a function of land-use history.

feeders (i.e. grasshoppers that consume grasses, forbs and some woody foliage; Ueckert & Hansen 1971; Joern 1985), the two most common *Melanoplus* taxa (subfamily Melanoplinae) both had higher abundances in post-agricultural woodlands (Fig. 2), although only slightly for short-wing species, and only long-winged *Melanoplus* were significantly related to herbaceous cover (Fig. 3c,d). *Schistocerca* (subfamily Cyrtacanthacridinae) had lower abundance in post-agricultural woodlands (Fig. 2) and responded positively to herbaceous cover only in non-agricultural woodlands (Fig. 3f). *Arphia xanthoptera* (subfamily Oedipodinae), a banded-winged grasshopper that likely specializes on grasses but may also consume forbs (Ueckert & Hansen 1971; Joern 1985), had similar abundance in both land-use histories (Fig. 2), but increased positively with herbaceous cover only in woodlands without a history of agricultural use (Fig. 3a). *Orphulella pelidna* (subfamily Gomphocerinae), a grass specialist, had higher abundance in post-agricultural woodlands (Fig. 2) and similar (positive) responses to herbaceous cover in both land-use histories (Fig. 3e). *Conocephalus* (family Tettigoniidae) had similar mean abundances in both land-use histories (Fig. 2) but increased positively with herba-

ceous cover only in non-agricultural woodlands (Fig. 3b). The second best MLM model captured this taxon-specific variation to herbaceous cover via a land-use history \times herbaceous cover \times grasshopper taxa random effect, although the increase in model parameters did not justify it over the more simple MLM with only the land-use history \times grasshopper taxa random effect, based on AIC (Appendix S5, Supporting information).

Discussion

Past agricultural land use generates persistent changes in plant communities and soil conditions in many ecosystems (Flinn & Vellend 2005; Cramer, Hobbs & Standish 2008). We found a positive relationship between herbaceous plant cover and grasshopper abundance, but only in habitats without a history of agriculture. We also found taxon-specific effects of historic agriculture on grasshopper abundance, which resulted in shifting dominance from *Schistocerca* in sites with no history of agriculture to dominance of *Melanoplus* in sites with a history of agriculture (Fig. 2). Collectively, these results suggest that the effect of historic agricultural land use extends beyond

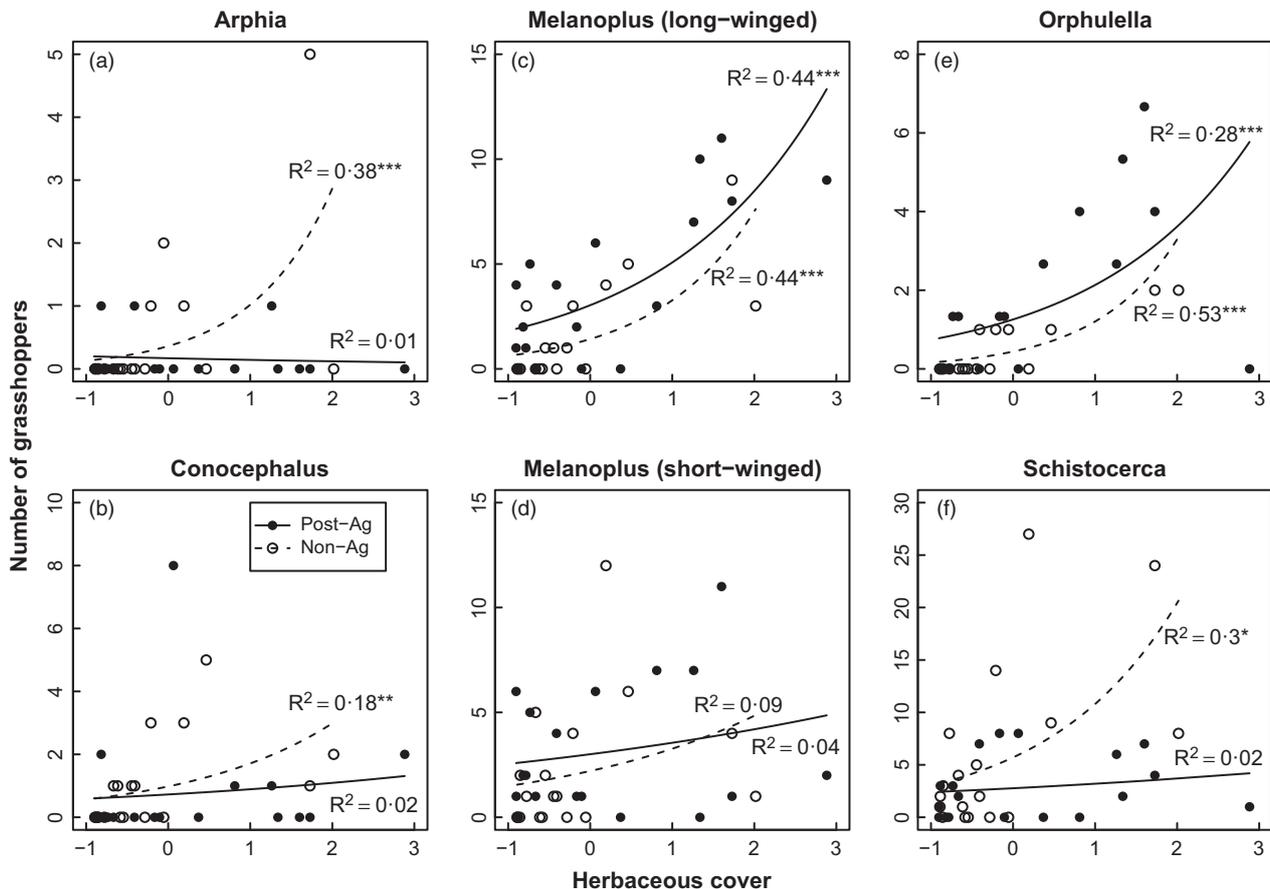


Fig. 3. Total number of grasshoppers collected at the Savannah River Site, South Carolina, USA in three 5 m \times 5 m plots per site regressed against herbaceous cover (averaged across the three plots and centred). Fit lines are from Poisson regressions conducted for each land-use history type: post-agricultural or non-agricultural land-use history. R^2 is the proportion of deviance explained by the model (i.e. pseudo- R^2). * $P \leq 0.05$; ** $P \leq 0.01$; *** $P < 0.001$.

plants and soils to decouple plant–herbivore relationships, leading to a strong legacy of past agriculture on present-day insect herbivore assemblages. Below we discuss the changes in grasshopper assemblages in response to land-use history and environmental drivers, including the potential indirect role of fire, as well as how altered plant community composition and soil conditions resulting from historical agricultural land use may have contributed to the differences in grasshopper assemblages we found. Our results shed light on how human activities can decouple otherwise well-established plant–herbivore relationships and suggest that management efforts should consider the role of historic land use on herbivore assemblages, as well as plant communities.

Plant productivity is often a good predictor of insect abundance and diversity in grasslands around the world (Joern & Laws 2013), but our results suggest that agricultural land-use legacies may decouple this relationship. For instance, we found a strong relationship between herbaceous cover and grasshopper abundance, but only in non-agricultural woodlands for most grasshopper taxa (Fig. 3; Appendix S7, Supporting information). Furthermore, our data suggest that the abundance of certain grasshopper taxa is sensitive to historic agriculture (e.g. *Schistocerca*), whereas other taxa responded positively to historic agriculture (e.g. *Melanoplus*) (Fig. 2). Two other studies conducted within the longleaf pine ecosystem found that grasshopper species that were common in anthropogenic habitats (e.g. old fields, roadsides, power-line right of ways), including *Melanoplus* and some potential pest species, were not common in natural habitats (Squitier & Capinera 2002; Hill 2009). Because of widespread anthropogenic land use, including abandonment of agricultural fields in North America (Ramankutty & Foley 1999), land-use legacies may have underappreciated effects on grasshopper assemblages, and potentially other insects, in grasslands or savannas regenerating from anthropogenic land use.

Agricultural land-use legacies have well-documented effects on plant community composition (Flinn & Vellend 2005; Cramer, Hobbs & Standish 2008), as well as nutrients in the soil and plant tissues (Baeten *et al.* 2011), both of which may provide a potential mechanism altering grasshopper community composition. In the longleaf pine ecosystem, agricultural land-use history is known to reduce plant diversity, to alter community composition and also tends to eliminate long-lived perennial plant species (Kirkman *et al.* 2004; Brudvig & Damschen 2011; Brudvig *et al.* 2014). Although we did not measure plant community composition at the species level, altered plant community composition between post-agricultural and non-agricultural woodlands likely contributed to the different relationships we found between herbaceous cover and grasshopper abundance. For instance, altered or reduced host plant availability in post-agricultural sites could affect grasshopper abundance. Plant diversity can increase grasshopper fitness by providing more diverse

nutritional options (Specht *et al.* 2008; Unsicker *et al.* 2010), and differences in plant species richness or community composition among land-use histories may have contributed to altering grasshopper assemblages in our study. Agricultural land-use history also affects soil nutrients, generally resulting in an increase in soil phosphorous and other nutrients (Verheyen *et al.* 1999; Fraterrigo, Turner & Pearson 2006; Brudvig *et al.* 2014) and this can increase nutrients in plant tissues (Baeten *et al.* 2011). Grasshopper assemblages respond to plant phosphorus (Bishop *et al.* 2010) and other nutrients (Joern, Provin & Behmer 2012) measured at the plant community level. Thus, it seems likely that land-use-mediated changes in plant nutrients may contribute to the changes to grasshopper community composition that we observed. Furthermore, other changes to soil conditions related to agriculture land use, such as compaction or soil organic matter (Burke, Lauenroth & Coffin 1995; Hamza & Anderson 2005), could potentially affect grasshopper oviposition preference or egg development in the soil and alter composition (Appendix S6, Supporting information). Studies that incorporate detailed measures of plant community composition, functional traits (e.g. van der Plas, Anderson & Olf 2012) and plant nutrients (Joern, Provin & Behmer 2012) may provide further mechanistic insight into how land-use history alters plant–herbivore relationships.

Fire can affect grasshopper abundance and community composition in grasslands around the world (Joern 2005; Knight & Holt 2005; Branson & Sword 2010; van der Plas, Anderson & Olf 2012) by killing either grasshoppers or eggs directly or by eliminating vegetation, which is their main food source (Evans 1984; Swengel 2001; Branson & Vermeire 2013). Although we found no evidence for direct effects of fire, fire effects on grasshopper assemblages can be subtle and are usually indirectly driven by concurrent changes to the plant community (Evans 1984). Several studies of grasshopper assemblages in tallgrass prairies in Kansas found that the effects of weather or grazing are stronger than the direct effects of fire on regulating grasshopper abundance and community composition (Joern 2004, 2005; Jonas & Joern 2007). van der Plas, Anderson & Olf (2012) found that the effects of fire and environmental variables on grasshopper assemblages in a South African savanna were indirect, driven through changes to vegetation structure and plant traits. Although we found no effect of the total number of burns since 1991 on grasshopper abundance or community composition, we did find a negative relationship between leaf litter cover, which decreases with frequent fires in our system (Hiers *et al.* 2007), as well as a positive relationship between herbaceous plant cover (although only significantly in remnant woodlands), which generally increases with frequent fires (Glitzenstein *et al.* 2012), and grasshopper abundance (Table 2, Appendix S5, Supporting information). At our sites, the number of burns was negatively related to leaf litter cover and was positively, although not significantly, related to herbaceous plant

cover (Appendix S3, Supporting information). This suggests that, through its influence on leaf litter, fire may negatively affect grasshopper abundances by reducing microsites suitable for oviposition. The indirect effects of fire on grasshoppers driven through the plant community appear to be weaker in our system compared to herbaceous-dominated tallgrass ecosystems (e.g. Joern 2005; van der Plas, Anderson & Olff 2012), possibly because the understorey of our sites was composed of woody plants and vines, in addition to herbaceous plants (Table 1). Finally, we reiterate that we only found significant relationships between plant cover and grasshopper abundance in non-agricultural habitat, which might suggest that potential indirect effects of fire on grasshopper assemblages are also decoupled by agricultural land-use history, although this requires future experimental examination.

Grasshoppers contribute significantly to biodiversity (Steck *et al.* 2006; Hill & Dakin 2011; Orrock *et al.* 2011), secondary productivity (Joern & Rudd 1982; Belovsky, Slade & Stockhoff 1990; Champlin, Kilgo & Moorman 2009) and ecosystem processes such as nutrient cycling (Belovsky & Slade 2000; Joern & Laws 2013). Our findings show that land-use history decoupled the relationship between herbaceous plant cover and abundance for most grasshopper species, even over 50 years after agricultural abandonment, which could have implications for conservation and management of insect communities. Prescribed fires are common management techniques used in grasslands and savannas to promote plant diversity, insect diversity and endangered species such as the red cockaded woodpecker in the longleaf pine ecosystem (Panzer 2002; Jose, Jokela & Miller 2005; Pyke, Brooks & D'Antonio 2010). Consistent with conclusions from a recent study examining insect diversity in Midwestern grasslands (Debinski *et al.* 2011), our data suggest that current management strategies alone (e.g. prescribed fire) may not shift grasshopper abundance or community composition in post-agricultural woodlands to more resemble assemblages in woodlands without a history of agricultural use and highlight the need to consider the effect of land-use legacies on contemporary biodiversity of primary consumers. Although our study is not able to disentangle agricultural legacies from natural succession processes, the trajectories of plant communities recovering from intensive cultivation have been shown to be drastically altered compared to recovery from less intensive, natural disturbances (Dupouey *et al.* 2002; Kepfer-Rojas *et al.* 2014). Therefore, our results suggest that a comprehensive approach including restoration of the plant community and soil conditions may be required to promote grasshopper assemblages typical of habitats with no agricultural history over disturbance-adapted pest species that are often considered undesirable (Branson, Joern & Sword 2006). Alternatively, focusing conservation and management efforts on less degraded habitat may have a more desirable effect on conserving both plants and arthropods than trying to reintroduce management practices to highly degraded

sites. Because grasshoppers are important herbivores, potential feedbacks between plants and herbivores, and how they are altered by historic agriculture (Hahn & Orrock *in press*), should receive more attention by both land managers and research ecologists.

Acknowledgements

We thank N. Boyea, D. Fegan and S. Gorsline for assistance with grasshopper collection and sorting; J.G. Hill and S.J. Krauth for assistance with grasshopper identification; M. Jackson and A. Ives for invaluable statistical advice; J. Blake, E. Olson and K. Wright for logistical support at SRS. K. Bartowitz, L. Brudvig, T. Kim, J. Stuhler, M. Turner and two anonymous reviewers provided valuable comments on the manuscript. L. Brudvig, E. Damschen, R. Jackson, W.B. Mattingly, A. Ives, M. Turner and J. Veldman provided helpful suggestions on the design and analysis. This work was funded by the Strategic Environmental Research and Development Program (Project RC-1695), the USDA Forest Service, Savannah River, under Interagency Agreement DE-AI09-00SR22188, and the Noland Fund from the UW-Madison Department of Zoology.

Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.465t5> (Hahn & Orrock 2014).

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Received 24 February 2014; accepted 3 October 2014

Handling Editor: Spencer Behmer

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Aerial photographs of select sites at the Savannah River Site, SC, USA in 1938, 1951 and 2010.

Appendix S2. Accumulation of grasshopper species in plots within sites.

Appendix S3. Correlation matrix of predictor variables used in the analysis.

Appendix S4. Information about the grasshopper taxa collected at the Savannah River Site, SC, USA.

Appendix S5. Multilevel model reductions and section results, coefficients and R code.

Appendix S6. Results of the analysis of fern cover and soil compaction.

Appendix S7. Results of the supplemental Poisson regression analyses.