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Historical land use and present-day canopy thinning differentially affect the distribution and abundance of invasive and native ant species

John D. Stuhler · John L. Orrock

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Abstract Disturbance may play a key role in affecting animal invasions; less appreciated is that past and present disturbances might interact to affect invasion. For example, although large portions of forest ecosystems worldwide are jointly affected by a history of past agricultural land use as well as contemporary timber harvest, it is unclear whether these disturbances facilitate biological invasions. We conducted a large-scale experiment that coupled adjacent non-agricultural and post-agricultural sites and a factorial canopy-thinning manipulation to understand how past agricultural land use might interact with contemporary canopy thinning to affect the distribution (i.e., presence/absence of mounds) and abundance of a highly invasive ant species, *Solenopsis invicta*, and common native ant species, *Dorymyrmex bureni*. Mounds of *S. invicta* were more likely to be present in unthinned post-agricultural habitats than unthinned non-agricultural habitats, but this legacy effect disappeared with canopy thinning. In unthinned habitats, the presence of *D. bureni* mounds did not differ based on past land use. However, presence of *D. bureni* mounds was greater in thinned non-agricultural habitats than thinned post-agricultural habitats. Once present in an area, mound abundance was largely related to temperature near the ground for both species, and negatively related to soil compaction for *D. bureni*. Our results provide large-scale evidence that an understanding of anthropogenic events that occur decades before present may be essential for interpreting contemporary invasion dynamics and the distribution of some species, and that local contemporary habitat characteristics play a key role in determining ant abundance once an area is colonized.

Keywords Agricultural legacy · *Dorymyrmex bureni* · Fire ant · *Solenopsis invicta* · Timber harvest

Introduction

Despite the potential for exotic species to generate profound changes in the communities they invade (Porter and Savignano 1990; Allan et al. 2010; Vilá et al. 2011), few generalities have emerged in terms of the factors that consistently promote invasion by exotic animals (Parker et al. 2013). One possibility is that our ability to understand invasion dynamics in the present is constrained by knowledge of activities in the distant past. For example, conversion of land for agriculture represents the largest use of land on the planet and is a major threat to biodiversity (Vitousek et al. 1997; Wilcove et al. 1998; Foley et al. 2011).

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J. D. Stuhler (✉) · J. L. Orrock
Department of Zoology, University of Wisconsin-Madison, 430 Lincoln Dr., Madison, WI 53706, USA
e-mail: john.stuhler@gmail.com

Following abandonment, post-agricultural lands can exhibit significant legacies that may persist for centuries after abandonment (Hermy and Verheyen 2007). Decades or centuries after abandonment, sites with a history of agricultural land use generally have altered over- and understory plant community composition (Flinn and Marks 2007; Baeten et al. 2010; Brudvig and Damschen 2011; Brudvig et al. 2013), overstory structure (Foster et al. 1998; Flinn and Marks 2007), and soil properties, including changes in soil nutrients (Davidson and Ackerman 1993; Fraterrigo et al. 2005), organic matter (Burke et al. 1995), and compaction (Bassett et al. 2005; Mattingly and Orrock 2013). However, although recent work suggests that historical land use can influence the contemporary establishment (Mattingly and Orrock 2013) and distribution (Kuhman et al. 2010, 2011) of invasive plants, the extent to which this is true for other exotic taxa remains unclear. Given the increasingly widespread abandonment of agricultural land worldwide (Flinn and Vellend 2005; Cramer et al. 2008), understanding the interplay between historical land use and contemporary invasion dynamics may be important for interpreting the present-day distribution and abundance of invasive species.

Understanding how land-use legacies affect biological invasions may require explicit consideration of both historical and contemporary disturbances because the two often coincide in space (Foster et al. 2003; Cramer et al. 2008) and may interact to affect invasion dynamics of exotic plants (Kuhman et al. 2010; Mattingly and Orrock 2013). Many areas that were previously used for agriculture have also experienced fire suppression, leading to increased tree abundance and canopy cover (Ramankutty and Foley 1999; Briggs et al. 2005; Nowacki and Abrams 2008). Consequently, canopy thinning is commonly used as a restoration technique (Gilliam and Platt 2006; Walker and Silletti 2006) or results from harvesting (Wear and Greis 2002). Fully understanding land-use legacy effects may therefore only be possible when considered in the context of contemporary land-use activities, and vice versa. Because both past and present-day disturbances have the potential to change the distribution and abundance of exotic and native species, studies capable of simultaneously evaluating historical land use and contemporary timber harvest may be useful for understanding patterns of invasion, predicting future invasion dynamics, and reversing invasions once underway.

In this paper, we use a replicated, landscape-scale experiment in the longleaf pine ecosystem to investigate the effects of land-use legacies and canopy thinning on the distribution and abundance of the invasive *Solenopsis invicta* and the native *Dorymyrmex bureni*, the two most abundant species in open canopy sites within our system (nearly 80 % of the individuals in pitfall traps; Resasco et al. 2014). *Solenopsis invicta* is one of the most noxious invasive species in the United States and is responsible for the displacement of native ants and a wide variety of other taxa (Holway et al. 2002; Tschinkel 2006). *Solenopsis invicta* tends to invade open and disturbed areas, and in particular soil disturbances created by human actions, such as roadsides, cultivated fields, and lawns (Buren 1972; Allen et al. 1974; Tschinkel 1986); recent work suggests that even subtle disturbances that open up canopy or ground cover can positively affect fire ant abundance (e.g., LeBrun et al. 2012; King and Tschinkel 2013; Tschinkel and King 2013). *Dorymyrmex* is a relatively aggressive ant genus found in warm, open habitats (Andersen 1995, 1997); changes in *Dorymyrmex* abundance may affect the evenness of the entire arthropod community (Orrock et al. 2011). The dynamics of *D. bureni* may be affected by the legacies of past land use because *D. bureni* occurs in disturbed habitats such as dunes, old fields, roadsides, lawns, pastures, and unpaved roads (Trager 1988). Although *S. invicta* and *D. bureni* are predominantly found in areas that have experienced contemporary disturbance, it is unclear whether the abundance of these two species is affected by past land use. One difficulty of understanding the effect of past land use on contemporary processes is that selection of areas is non-random: sites selected for agricultural use may be on different soils than sites not used for agriculture. As such, studies that seek to evaluate the effect of past land use must be carefully designed to ensure that sites differ only in their underlying land-use history, not in some other ecological characteristic.

We used a study design that minimizes the confounding effects of non-random land use by using paired plots (Brudvig et al. 2013). In these paired plots we experimentally imposed a canopy thinning treatment that makes it possible to explicitly study how past land use might interact with canopy thinning to determine the present-day distribution and abundance of invasive and native ant species. Our objectives were to (1) quantify the response of the focal species to present-day canopy thinning, (2) evaluate the degree to which past land use modifies the response of invasive and native species to contemporary disturbance, and (3) examine how specific ecological correlates of canopy cover (i.e., light availability or temperature near the ground) and land-use history (i.e., soil compaction) might drive ant mound distribution and abundance. In our approach, we explicitly evaluate distribution (measured as presence/absence) and abundance (measured as the number of mounds in an area where the species is present) as separate response variables. We take this approach because understanding the dynamics of invasions may benefit from focusing on the variables that affect the likelihood of successful colonization and persistence (i.e., whether a species is present in an area) as well as focusing on the factors that promote or deter increases in abundance of an invasive species in an area where it can occur (Mack et al. 2000).

Methods

Study area

Our study was conducted at the Savannah River Site (SRS) near Aiken, South Carolina, USA (Fig. 1), an 80,300 ha National Environmental Research Park containing large areas of forest dominated by longleaf pine, *Pinus palustris*, or loblolly pine, *P. taeda* (Kilgo and Blake 2005). Longleaf pine woodlands are traditionally characterized by sparse canopies and frequent understory fires (Frost 2006; Peet 2006). Longleaf pine savanna is a habitat of high conservation interest (Jose et al. 2006) and high ant diversity (Lubertazzi and Tschinkel 2003). Today, however, the longleaf pine ecosystem covers less than 3 % of its original area due to agricultural land use and fire suppression (Frost 2006; Noss 2012).

Experimental landscape manipulation

This study was conducted at 27 upland sites with 61 total paired plots (i.e., plots that pair post-agricultural and non-agricultural remnant woodlands). Cultivation for agriculture occurred in this area between 1865 and 1950, peaking in the 1920s; historical farms were small and dispersed across the landscape, leaving many pockets of untilled longleaf woodlands (Kilgo and Blake 2005). We determined historical land use across SRS by examining aerial photographs taken in 1951, just before acquisition of SRS by the government (Brudvig et al. 2013, 2014). Mature woodlands were classified as non-agricultural woodlands and cultivated fields were classified as post-agricultural woodlands, because they were subsequently replanted into pine plantations with *P. palustris* or *P. taeda* following abandonment (Kilgo and Blake 2005; see Supplementary Materials for more details). At the time of this study, unthinned post-agricultural woodlands were primarily dominated by *P. palustris* and *P. taeda* in the overstory (99 % of the total number of pine trees). Slash pine, *Pinus elliotti*, occurred at very low numbers. We selected 4- to 10-ha patches that border a non-agricultural/post-agricultural boundary. Earlier work at our sites indicated that there is no difference in the identity and area of soil series underlying non-agricultural and post-agricultural woodlands (Brudvig et al. 2013), which we confirmed for all of our paired plots (i.e., adjacent non-agricultural and post-agricultural plots). As such, any contemporary differences in soil characteristics between paired non-agricultural and post-agricultural plots are likely due to the act of agriculture itself and are unlikely to have arisen due to non-random past land-use decisions. Within this general design, we applied a factorial manipulation of canopy cover such that within each paired plot the canopy of the focal patch and the canopy of the adjacent patch were either thinned or unthinned (i.e., both patches within a pair were thinned, both patches remained unthinned, or one patch was thinned and the adjacent patch remained unthinned). This resulted in four unique patch types based on canopy cover and land-use history (Fig. 1). Canopy thinning took place in early 2012 and patches were thinned to 8–10 mature pine trees per hectare, a tree density within the range of natural variability in longleaf pine savannas (Platt et al. 1988; Kirkman et al. 2007). Ten of our sites were partially thinned in 2009; because this thinning was not to low densities, and because our results were not qualitatively different with or without these sites included, we report analyses that use all 27 sites.

Ant mound surveys

We established 10 × 10 m plots in each of the one-hectare patches (Fig. 1). Because edges are areas

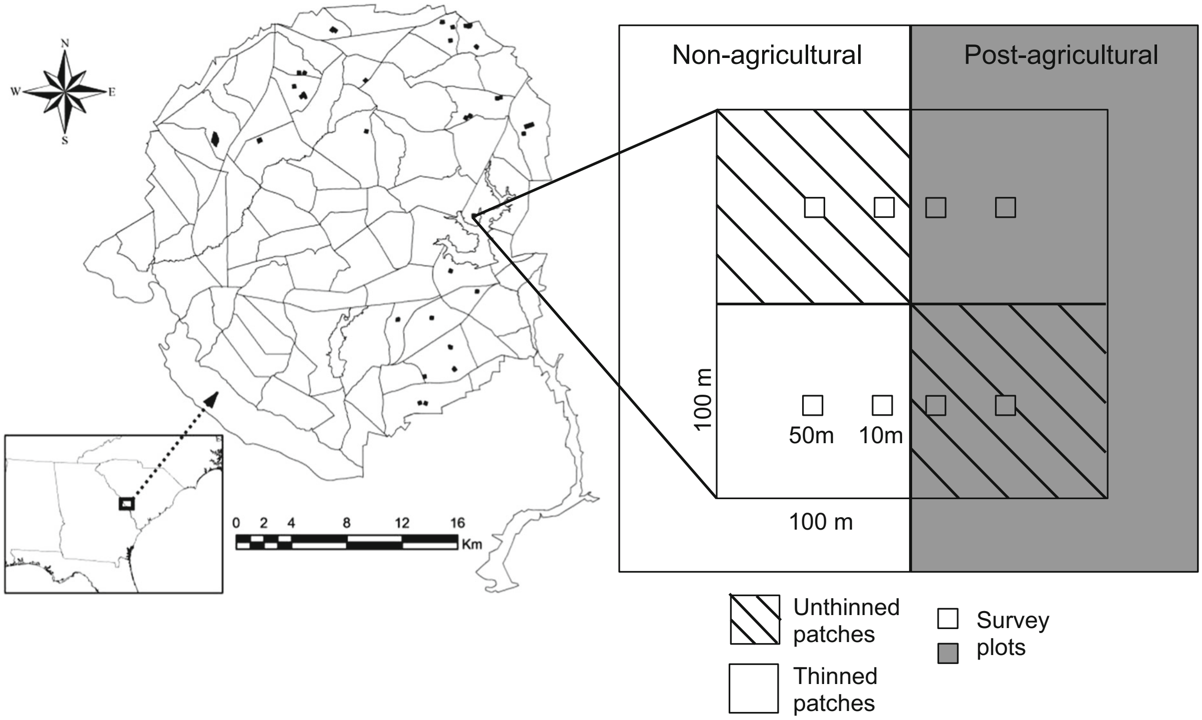

Fig. 1 Map of the 27 research sites and experimental design within the Savannah River Site, SC, USA. Overstory trees were thinned or left intact (unthinned). Survey plots (10 m^2; n = 244) were located 10 and 50 m from the boundary between non-agricultural and post-agricultural woodlands

where light levels and temperature can change abruptly (Yahner 1988; Matlack 1993), and may therefore affect ant colony dynamics, we surveyed at two distances (centered at 10 m and 50 m) from the edge of the non-agricultural/post-agricultural boundary within each patch (n = 244 plots) to determine whether distance from the land-use boundary affected species abundance (Ries et al. 2004; Ewers and Didham 2008; Ness and Morin 2008). Between 12 June and 5 August 2013 we surveyed plots for all active *S. invicta* and *D. bureni* mounds. We initially included another native species, *Pogonomyrmex badius*, in our survey, but omitted the species from analyses due to the low number of mounds in our plots (n = 8 total mounds). Due to the possibility of polydomy, particularly for *D. bureni*, the number of mounds may be greater than the number of colonies within each plot; as such, in this study we do not equate the number of mounds with the number of colonies of these two species. Nonetheless, because nests (e.g., ant mounds) are the reproductive units of social insects, nest counts provide a good measure of density (Gotelli et al. 2011). This relationship is indeed supported in our study system: Resasco et al. (2014) found qualitatively similar results from mound counts and bait surveys for *S. invicta*. Mound surveys have also been used in previous studies at Savannah River Site (Stiles and Jones 1998; Resasco et al. 2014) and elsewhere (e.g., Tschinkel 1988; Porter et al. 1992; Adams and Tschinkel 1995). Mound activity (i.e., active or abandoned) was determined by observing loose dirt on the mound and by gently disturbing mounds (Adams and Tschinkel 1995; Stiles and Jones 1998), which causes workers to rush out of the nest if the nest is inhabited. Following mound surveys, we revisited the mounds to collect individuals with an aspirator, and individuals were later identified to species. Voucher specimens were deposited in the Wisconsin Insect Research Collection at the University of Wisconsin-Madison.

Additional environmental data collection

We obtained data on several environmental variables that might contribute to differences in ant mound abundance between non-agricultural and post-agricultural patches. Light (lux) and temperature data were collected in a subset of sites (n = 32 plot pairs) as part of a related study in 2012 (Hahn and Orrock 2015c). Data were collected in 10-minute intervals by Hobo data loggers during daylight hours (0600–1900) for 9 days and all values for each location were averaged across days and time to produce one value per patch. We also quantified soil compaction in plots with a penetrometer by taking the mean of two measurements of the depth (in inches) at which 140 psi was obtained; smaller values indicate more compact soil.

Statistical analyses

We fit two models for each species to independently (a) model the presence and absence of ant mounds to understand factors influencing the distribution of ant mounds and (b) model positive counts to understand factors affecting the abundance of mounds where mounds were present. This approach allows separate interpretations of both components of count data, such that the presence-absence component (i.e., habitat suitability) and the abundance component (i.e., habitat quality) can be analyzed separately (Cunningham and Lindenmayer 2005; Martin et al. 2005). Our results were not qualitatively different when we fit a standard hurdle model to our data (i.e., a single model incorporating subcomponents to analyze both zeros and positive counts). Factors influencing the distribution of *S. invicta* and *D. bureni* mounds among habitats were determined with multiple logistic regression models, which assumed a binomial response to model the presence versus absence of ant mounds in our plots. Land-use history, canopy cover, adjacent canopy cover, and distance from the edge were included as fixed effects. Site, site × land-use history, and site × land-use history × canopy cover × adjacent canopy cover were included as random effects to account for the nestedness of distance. Factors influencing mound abundance (i.e., the number of mounds where mounds were present) were determined using similar generalized linear mixed-effects models, using a Poisson distribution (i.e., count data). We used the Kenward-Roger approximation for hypothesis tests (Littell et al. 2006). Because our hypotheses allow for multiple, interactive effects, we evaluated all possible interactions in our models.

We used generalized linear mixed models to assess the importance of specific ecological correlates of canopy cover (i.e., average daytime light levels and temperature near the ground) and land-use history (i.e., soil compaction) as determinants of habitat quality. The number of *S. invicta* or *D. bureni* mounds, where mounds were present, were treated as the response variable and abiotic variables were used separately as explanatory variables (i.e., six total models). Site, site × land-use history, and site × land-use history × canopy cover × adjacent canopy cover were included as random effects to account for the nestedness of distance. We used a similar model to compare differences in soil compaction (i.e., the depth at which 140 psi was obtained) across the four possible groupings of species occurrence within our plots (i.e., plots where both species were present, plots were neither species were present, plots where just *S. invicta* was present, and plots where just *D. bureni* was present). We tested for differences in soil compaction between non-agricultural and post-agricultural sites using a paired *t* test. All analyses were performed in R (R version 3.0.2, R Core Team, Vienna, Austria 2013) and SAS (SAS 9.3, Cary, NC, USA).

Results

Within our plots, we surveyed a total of 186 *Solenopsis* mounds and 166 *Dorymyrmex* mounds. All *Dorymyrmex* individuals were *D. bureni*. *Solenopsis invicta* made up 95 % of all *Solenopsis* specimens. However, 24 % of the mounds under canopy cover were identified as *S. geminata* based on collected specimens (n = 10 total mounds). All *Solenopsis* individuals collected in thinned plots were *S. invicta*. Given the limited number of sites where *S. geminata* was present in our surveys, we subsequently present the results for *S. invicta* mounds only. Soil compaction was greater in post-agricultural sites than in non-agricultural sites (depth at which 140 psi was obtained: 4.64 ± 0.40 SE in post-agricultural habitats, 16.32 ± 1.02 in non-agricultural habitats, $t = -11.91$, $P < 0.001$). Canopy thinning increased light levels (lux) near the ground in non-agricultural and post-agricultural habitats. Light levels near the ground were not different between thinned non-agricultural and post-agricultural habitats, but there were lower light levels near the ground in unthinned non-agricultural habitats than in unthinned post-agricultural habitats (Hahn and Orrock 2015c).

Solenopsis invicta presence and abundance

The presence of *S. invicta* mounds was strongly affected by canopy cover, with mounds more likely to be present in thinned patches than unthinned patches ($F_{1,\ 112.3} = 31.36$, $P < 0.001$; Fig. 2a). Similarly, mounds were more likely to be present in patches where the adjacent canopy was also thinned ($F_{1,\ 74.38} = 4.65$, $P = 0.034$). However, the main effects of land-use history ($F_{1,\ 86.99} = 0.51$, $P = 0.477$) and distance from the edge ($F_{1,\ 228} = 0.21$, $P = 0.646$) were not significant. There was an interaction between land-use history and canopy cover ($F_{1,\ 91.57} = 8.50$, $P = 0.005$; Fig. 2a): *S. invicta* mounds were more often present in unthinned post-agricultural patches than unthinned non-agricultural patches ($F_{1,\ 88.42} = 6.03$, $P = 0.016$), but there were no significant differences in mound presence between thinned non-agricultural and post-agricultural patches ($F_{1,\ 86.27} = 2.74$, $P = 0.102$). No other interactions were significant (all $P > 0.125$; Table 1). Canopy cover had a marginal effect on the abundance of *S. invicta* mounds at sites where *S. invicta* was present ($F_{1,\ 19} = 3.76$, $P = 0.067$; Fig. 3a): *S. invicta* mounds were more abundant in thinned patches than unthinned patches. However, no other main effects or interactions had a significant effect on *S. invicta* mound abundance (all $P > 0.357$; Table 1).

Dorymyrmex bureni presence and abundance

Canopy cover was a strong determinant of the presence of *D. bureni*, with mounds more often present in thinned plots than unthinned plots ($F_{1,109.4} = 34.62$, $P < 0.001$; Fig. 2b). The presence of *D. bureni* was also affected by a marginal interaction between land-use history and canopy cover ($F_{1,90.11} = 3.52$, $P = 0.064$): presence of *D. bureni* mounds was greater in thinned non-agricultural plots than thinned post-agricultural plots ($F_{1,\ 94.75} = 3.98$, $P = 0.049$), but there was no difference in the presence of *D. bureni* mounds between unthinned plots ($F_{1,\ 98.66} = 0.04$, $P = 0.842$). No other main effects (i.e., land-use history, opposite canopy cover, or distance) or interactions were significant for the presence or abundance of *D. bureni* mounds (all $P > 0.200$; Table 1).

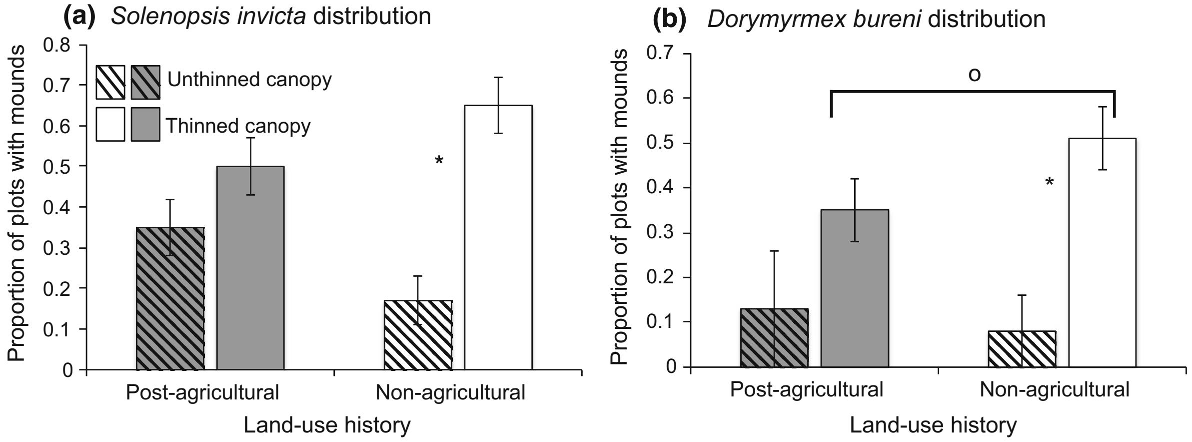

Fig. 2 The distribution (i.e., presence-absence) of **a** *S. invicta* and **b** *D. bureni* mounds across patches that differ by land-use history (non-agricultural or post-agricultural) and canopy cover (thinned or unthinned). *Values* represent an average of the number of mounds 10 and 50 m from the edge within each patch. *Bars* illustrate means ± one standard error. *Solenopsis invicta* mounds were more likely to be present in thinned patches than unthinned patches ($F_{1,\ 112.3} = 31.36$, $P < 0.001$), as well as in patches where the adjacent canopy was also thinned ($F_{1,\ 74.38} = 4.65$, $P = 0.034$). Moreover, *S. invicta* mounds were more often present in unthinned post-agricultural patches than unthinned non-agricultural patches ($F_{1,\ 88.42} = 6.03$, $P = 0.016$), but not between thinned non-agricultural and post-agricultural patches ($F_{1,\ 86.27} = 2.74$, $P = 0.102$). *Dorymyrmex bureni* mounds were more often present in thinned plots than unthinned plots ($F_{1,109.4} = 34.62$, $P < 0.001$). Similarly, *D. bureni* mounds were more often found in thinned non-agricultural habitats than thinned post-agricultural habitats ($F_{1,\ 94.75} = 3.98$, $P = 0.049$), but there was no difference in the presence of *D. bureni* mounds between unthinned habitats ($F_{1,\ 98.66} = 0.04$, $P = 0.842$)

Table 1 Results of the mixed-effects models evaluating *S. invicta* and *D. bureni* mound presence and abundance

Effect	S. invicta						D. bureni					
	Presence			Abundance			Presence			Abundance		
	df	F	*P*	df	F	*P*	df	F	*P*	df	F	*P*
Land-use history	86.99	0.51	0.477	19	0.20	0.663	88.3	0.25	0.618	3	1.63	0.292
Canopy cover	112.3	31.36	**<0.001**	19	3.76	**0.067**	109.4	34.62	**<0.001**	3	0.15	0.721
Landuse × canopy	91.57	8.50	**0.005**	19	0.05	0.821	90.11	3.52	**0.064**	3	0.34	0.602
Adjacent canopy cover	74.38	4.65	**0.034**	19	0.83	0.373	77.52	1.06	0.306	3	0.06	0.826
Landuse × adj	88.71	0.12	0.735	19	0.01	0.933	92.41	0.30	0.585	3	0.00	0.962
Canopy × adj	114.9	1.01	0.317	19	0.51	0.482	111.6	1.01	0.317	3	0.29	0.630
Landuse × canopy × adj	88.61	0.09	0.770	19	0.10	0.761	92.13	0.46	0.499	–	–	–
Distance from edge	228	0.21	0.646	32	0.13	0.722	228	1.05	0.307	15	0.33	0.575
Landuse × dist	228	0.48	0.491	32	0.05	0.832	228	0.04	0.842	15	0.04	0.838
Canopy × dist	228	0.51	0.477	32	0.87	0.357	228	1.65	0.200	15	0.01	0.924
Landuse × canopy × dist	228	0.19	0.663	32	0.01	0.916	228	0.05	0.823	–	–	–
Adj × dist	228	0.77	0.381	32	0.12	0.730	228	0.64	0.425	15	1.00	0.333
Landuse × adj × distance	228	0.07	0.785	32	0.02	0.887	228	0.09	0.765	15	0.29	0.600
Canopy × adj × dist	228	0.15	0.696	32	0.00	0.964	228	0.01	0.920	15	1.09	0.313
Landuse × canopy × adj × dist	228	2.37	0.125	32	0.28	0.602	228	0.10	0.752	–	–	–

Empty cells for *D. bureni* abundance represent levels that were not present when the data was subset to only plots where mounds were present

Significant ($P \leq 0.05$) and marginally significant ($P \leq 0.10$) *P* values are in bold

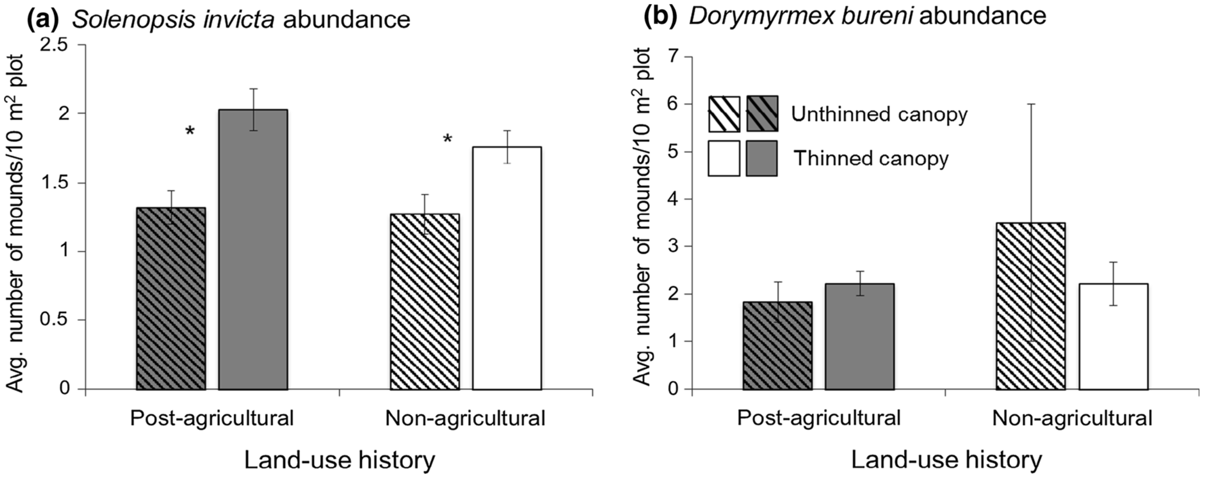

Fig. 3 The abundance (i.e., the *number* of mounds in patches where mounds were present) of **a** *S. invicta* and **b** *D. bureni* mounds in patches that differ by land-use history (non-agricultural or post-agricultural) and canopy cover (thinned or unthinned). *Values* represent an average of the *number* of mounds 10 and 50 m from the edge within each patch. *Bars* illustrate means ± one standard error. *Solenopsis invicta* mounds were more abundant in thinned patches than unthinned patches ($F_{1,\,19} = 3.76$, $P = 0.067$)

Ecological correlates of mound abundance

Temperature and light levels near the ground were strongly correlated ($r^2 = 0.93$; Fig. S1) and therefore had similar effects on both species: we found that the abundance of mounds where mounds were present increased with increasing average daytime light levels (*S. invicta*: $F_{1,43} = 28.28$, $P < 0.001$; *D. bureni*:

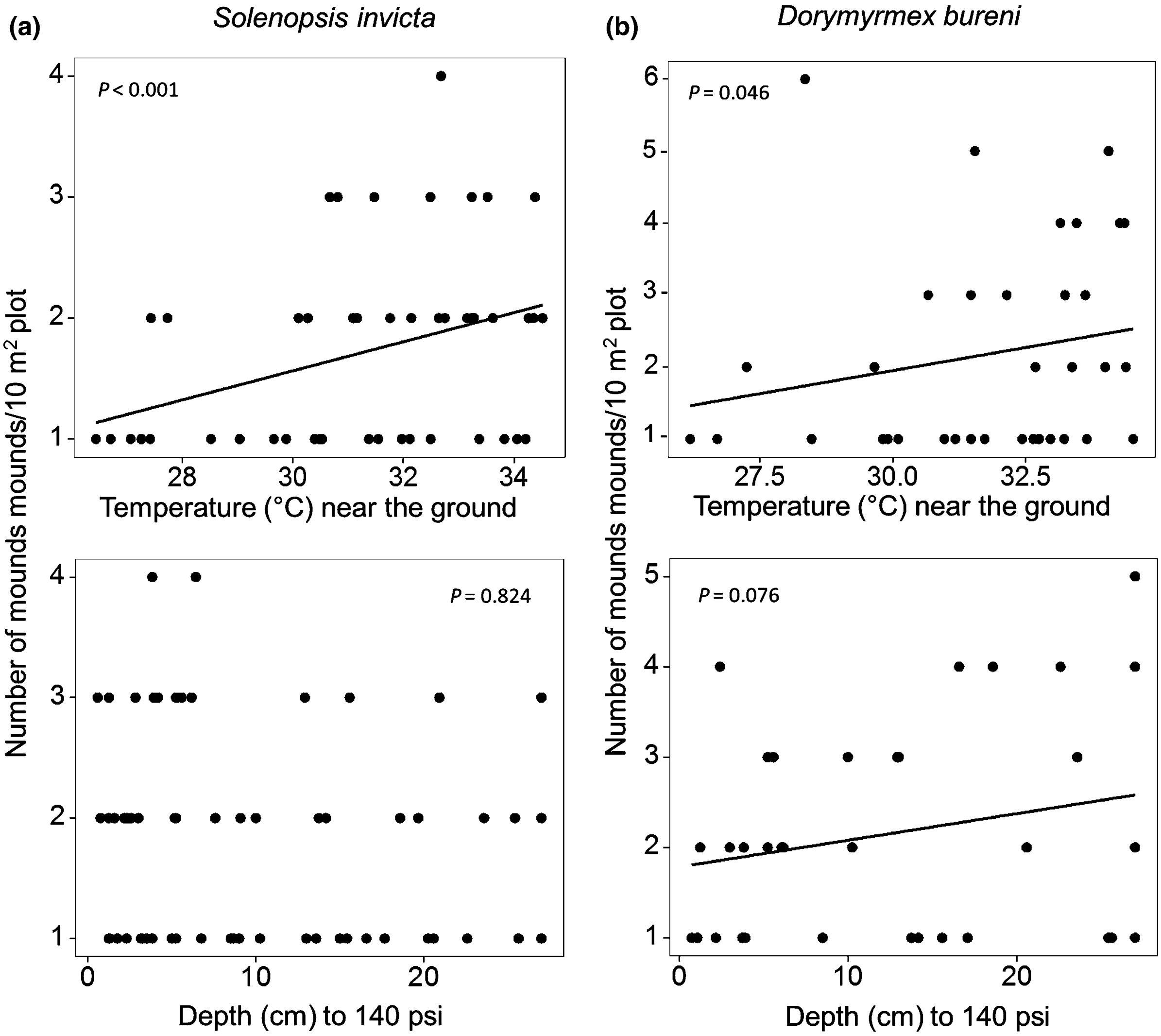

Fig. 4 Relationship between the number of **a** *S. invicta* and **b** *D. bureni* mounds and average daytime temperature (°C) near the ground and the depth (cm) to 140 psi (i.e., a measure of soil compaction; higher values indicate less compact soil). *Data* were collected from a subset of sites (n = 32 paired plots)

$F_{1,33} = 4.32$, $P = 0.046$) and average daytime temperature near the ground (*S. invicta*: $F_{1,43} = 28.63$, $P < 0.001$; *D. bureni*: $F_{1,33} = 4.74$, $P = 0.037$; Fig. 4). There was no relationship between the number of *S. invicta* mounds and soil compaction ($F_{1,47} = 0.05$, $P = 0.824$; Fig. 4a). However, there was a marginally significant negative effect of soil compaction on the number of *D. bureni* mounds ($F_{1,44} = 3.30$, $P = 0.076$; Fig. 4b), with fewer mounds in plots with more compact soil.

There was a marginally significant relationship between soil compaction and the four types of occurrence of the two species ($F_{1,3} = 7.40$, $P = 0.073$). Soil compaction was not significantly different between sites where just one of the two species occurred (*S. invicta* only: 9.00 ± 1.25; *D. bureni* only: 11.22 ± 3.33; $t = -0.63$, df = 10, $P = 0.543$). However, there was a significant difference in soil compaction between plots where both species were present versus plots where only *S. invicta* was found ($t = -2.37$, df = 49, $P = 0.022$), as well as a significant difference in soil compaction between plots where both species were present versus plots where neither species were present ($t = -2.22$, df = 43, $P = 0.032$).

Discussion

Using a large-scale manipulation of canopy cover in non-agricultural and post-agricultural longleaf pine woodlands, we show that historical and contemporary land-use activities may interact to differentially affect the present-day distribution (i.e., mound presence) of invasive and native ant species. Once present at a site, the abundance of invasive and native ant species was related to local variation in thermal characteristics associated with canopy cover, and was marginally related to soil compaction for the native species *D. bureni*. Together, these results indicate that historical land use may interact with contemporary management to provide an important lens through which to interpret the distribution of invasive ants, whereas contemporary management and local abiotic conditions may drive changes in local abundance of ants in habitats where they occur.

Historical and contemporary processes influence ant mound distribution whereas local processes most affect abundance

Our results demonstrate that both past land use and contemporary canopy thinning may affect the distribution of the invasive *S. invicta*, as well as the native *D. bureni* (albeit to a lesser degree than *S. invicta*). Specifically, presence of both species responded strongly and positively to canopy thinning, but past agricultural land use was important for affecting the presence of *S. invicta* mounds only in unthinned habitats, and past agricultural land use affected the presence of *D. bureni* mounds in thinned habitats (Figs. 2, 3). In demonstrating that past land use and present-day canopy thinning may interact to affect ant distribution, our study provides an important point of comparison with previous work. In a study conducted in unthinned forests, invasive plants were less likely to establish in post-agricultural forests (Mattingly and Orrock 2013); our work illustrates that the opposite is the case for *S. invicta*: unthinned post-agricultural habitats are more likely to contain *S. invicta* (Fig. 2a). Our study supports the findings of other studies that canopy thinning increases the prevalence of ants (Zettler et al. 2004; Cumberland and Kirkman 2012), but also illustrates that the effect of thinning may be modified by land-use history, as *D. bureni* mounds were found more often in thinned habitats with no history of agriculture (Figs. 2, 3). In light of our findings and recent work illustrating that land-use legacies may shape grasshopper communities (Hahn and Orrock 2015a), herbivory (Hahn and Orrock 2015b), and seed predation (Stuhler and Orrock 2016), large-scale historical agriculture may have important legacy effects extending to animal communities that warrant future work.

In addition to the effects of land-use history and canopy cover, we also found that the size of the disturbance may be important for invasion by *S. invicta*: mounds are more likely to be found when both patches are thinned, creating a larger disturbed area (Table 1). Dispersing alates (i.e., winged insects) respond to reflectance and vegetation cues from the ground (Maxwell 1982), so the creation of larger canopy gaps may facilitate the ability of alates to descend into thinned plots to begin colony establishment, which may promote greater establishment in plots with more open area (Vasconcelos and Cherrett 1995). The larger thinned area in adjacent cleared patches may also benefit *S. invicta* by reducing the amount of patch area that is shaded by the forest edge; the hypothesis that patch edge is important for affecting ants is further supported by community-level data indicating that patches with less area near a forest edge had higher levels of ant species turnover (Orrock et al. 2011).

Our study highlights potential mechanisms contributing to the effects of past land use and canopy thinning by demonstrating the importance of local conditions on ant mound abundance once mounds are present in an area. Increased soil compaction is a persistent legacy of historical agriculture (Compton et al. 1998; Parker et al. 2010), and previous work has implicated soil compaction as a mechanism capable of creating persistent land-use effects on plant establishment (Kyle et al. 2007; Mattingly and Orrock 2013). Within our research sites soil compaction was 3.5 times greater in post-agricultural patches than in non-agricultural patches (see Results), and our data suggest a negative relationship between the number of *D. bureni* mounds and increasing soil compaction. The relationship between *D. bureni* mound abundance and soil compaction, despite no overall effect of land-use history on mound abundance, may reflect variation in compaction among our sites and contribute to the observed differences in *D. bureni* mound distribution in thinned non-agricultural patches versus thinned post-agricultural patches. Because soil compaction levels that exceed 2 MPa are generally considered to limit plant performance (Bassett et al. 2005), soil compaction could indirectly affect *D. bureni* mound abundance by changing either plant resource availability or the invertebrate community since liquid carbohydrates and arthropods make up a large component of the diet of *D. bureni* (Smith 1965; Hung 1974). Importantly, soil compaction did not have the same effect on *S. invicta* mound abundance in areas where the species was present. The additional energy investment that is likely required for colonization of more compact soils may be balanced by the increased thermal conductivity that occurs in more compact soils (Willis and Raney 1971). The ability to colonize areas with greater soil compaction could increase the spread, population densities, and ecological impacts of the species, and might explain why *S. invicta* frequently colonizes habitats that are likely highly compacted (e.g., roadsides and cultivated fields; Buren 1972; Allen et al. 1974; Tschinkel 1986).

In our study, canopy thinning increased light levels and temperature near the ground in thinned plots relative to unthinned plots (Hahn and Orrock 2015c), and our results indicate a positive relationship between mound abundance and these abiotic variables. The general importance of soil temperature and lack of effect of soil compaction on *S. invicta* mound abundance may help explain the difference in *S. invicta* mound distribution between unthinned post-agricultural and non-agricultural habitats that disappears when the canopy is thinned. In unthinned plots, light levels are greater in post-agricultural woodlands than non-agricultural woodlands, likely because of a sparser canopy in the former, whereas there is no such difference in thinned plots (Brudvig et al. 2013; Hahn and Orrock 2015c). Indeed, results from Stiles and Jones (1998) suggest that direct sunlight is a requirement for *S. invicta* colonization. Porter (1988) showed that the growth of established *S. invicta* colonies only occurs between 24 and 36 °C, although we detected no significant differences between habitats in the amount of time the temperature at ground level was within this range during daylight (100 % of the time) or non-daylight hours (approximately 28–33 % of the time; PG Hahn *unpublished data*). Nevertheless, this pattern of *S. invicta* mound distribution and abundance may also explain our observation of *S. geminata* exclusively in unthinned habitats: *S. invicta* has been known to restrict native fire ants to less desirable wooded locations (Wilson and Brown 1958; Tschinkel 1988).

Our focus on recently disturbed systems (i.e., areas recently thinned) is important because these disturbed habitats are places where *S. invicta* invasions often begin (Tschinkel 1986; King and Tschinkel 2008). However, it is important to note that mound abundance may still be increasing in these habitats, as the density of *S. invicta* mounds may be much higher in habitats in areas where *S. invicta* has been established for a considerable time (Tschinkel 2006). Temporal dynamics of increasing mound abundance may also help explain why our experiment detected stronger patterns of mound distribution relative to mound abundance. Viewed in light of recent work suggesting that soil conditions and habitat disturbance can be important drivers of *S. invicta* prevalence (LeBrun et al. 2012; King and Tschinkel 2013; Tschinkel and King 2013), the potential clearly exists for past land use and canopy thinning to lead to eventual shifts in the abundance of *S. invicta* mounds, although future studies will be needed to evaluate this possibility.

Implications for invasion, conservation, and restoration

Thinning of overstory trees is a common conservation and restoration practice for understory plant communities in longleaf forests (Gilliam and Platt 2006; Walker and Silletti 2006), and thinning is often a consequence of active forest management (e.g., the southern United States' status as the largest timber producer worldwide; Wear and Greis 2002). Our findings suggest that all of these activities will affect the distribution of invasive and native ants. In having a positive effect on the distribution and, to a lesser extent, abundance of *S. invicta*, thinning for restoration or management may have deleterious effects on the taxa and processes affected by *S. invicta*, such as the diversity of native invertebrates (Porter and Savignano 1990; Holway et al. 2002; Resasco et al. 2014), foraging of native rodents (Orrock and Danielson 2004), abundance of native vertebrates (Allen et al. 1994; Holway et al. 2002), and the removal and dispersal of seeds of native plant species (Ness 2004; Ness et al. 2004; Zettler et al. 2004).

The effect of land-use history and canopy thinning on *D. bureni* may further exacerbate the effect of *S. invicta*. Recent work has illustrated that the effects of *S. invicta* on native ant communities may depend on habitat conditions, such as soil moisture, with native species being affected more strongly by the presence of *S. invicta* in wet environments (LeBrun et al. 2012). Our results suggest that the same may be true in the context of soil compaction. For example, *D. bureni* can be significant seed dispersers, even in sites invaded by *S. invicta* (Stuble et al. 2010). However, if *D. bureni* were to occur less frequently in thinned post-agricultural habitats due to land-use legacy effects on soil compaction, then the effects of *S. invicta* invasion could be exacerbated by the lower occurrence of a species that can typically coexist with *S. invicta* and fulfill important ecological roles. Our results also suggest that effective management to mitigate invasion into thinned habitats may require special attention to the amount of area thinned, particularly in the context of canopy thinning for restoration (Table 1; Fig. 2, 3). Future work that examines the degree to which other ant functional groups, and arthropods in general, are affected by land-use history will also provide important information for fully characterizing the effects of *S. invicta* on conservation and restoration efforts in post-agricultural habitats.

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