COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Historical agriculture alters the effects of fire on understory plant beta diversity

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Abstract Land-use legacies are known to shape the diversity and distribution of plant communities, but we lack an understanding of whether historical land use influences community responses to contemporary disturbances. Because human-modified landscapes often bear a history of multiple land-use activities, this contingency can challenge our understanding of land-use impacts on plant diversity. We address this contingency by evaluating how beta diversity (the spatial variability of species composition), an important component of regional biodiversity, is shaped by interactions between historical agriculture and prescribed fire, two prominent disturbances that are often coincident in terrestrial ecosystems. At three study locations spanning 450 km in the southeastern United States, we surveyed longleaf pine woodland understory plant communities across 232 remnant and post-agricultural sites with differing prescribed fire regimes. Our results demonstrate that agricultural legacies are a strong predictor of beta diversity, but the direction of this land-use effect differed among the three study locations. Further, although beta diversity increased with prescribed fire frequency at each study location, this effect was influenced by agricultural land-use history, such that positive fire effects were only documented among sites that lacked a history of agriculture at two of our three study locations. Our study not only highlights the role of historical agriculture in shaping beta diversity in a fire-maintained ecosystem but also illustrates how this effect can be contingent upon fire regime and geographic location. We suggest that interactions among historical and contemporary land-use activities may help to explain dissimilarities in plant communities among sites in human-dominated landscapes.

Keywords Agriculture · Beta diversity · Fire · Land-use legacies · Longleaf pine

Communicated by Scott Collins.

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Introduction

Human land use is a major force shaping the diversity and distribution of plant communities (Vitousek et al. 1997; Sala et al. 2000; Foster et al. 2003). Although a great deal of attention has been paid to land-use impacts on local-scale (alpha) diversity (e.g., Hermy and Verheyen 2007; Brudvig and Damschen 2011; Vellend et al. 2013), a growing body of literature illustrates how beta diversity, or variation in species composition among sites (Anderson et al.

2011), may be altered by human activities (e.g., via land-use changes and habitat fragmentation; Olden and Rooney 2006; Vellend et al. 2007; La Sorte et al. 2008; McKinney 2008; Britton et al. 2009; Jamoneau et al. 2012). Beta diversity is a fundamental diversity parameter, linking local (alpha) and regional (gamma) scales of diversity, and one that may be particularly sensitive to land-use impacts, as suggested by the mounting evidence of biotic homogenization (e.g., Qian and Ricklefs 2006; Baiser et al. 2012; Ross et al. 2012). However, very little is known about how multiple forms of land use together structure beta diversity, despite the fact that most ecosystems are simultaneously impacted by many types of land-use activities (Foster et al. 2003; Cramer et al. 2008). As such, the potential for legacies of historical land use to interact with contemporary disturbances can make it difficult to discern how human activities influence beta diversity. In this study, we assess the interaction between historical agriculture and prescribed fire, two prominent disturbances that shape plant communities and often coincide in space across large portions of the terrestrial biosphere.

Agricultural land use and prescribed fire are two fundamentally different types of disturbances: agriculture completely displaces native plant communities, repeatedly disturbs soils, depletes soil resources, and introduces non-native species, whereas fire consumes aboveground biomass with no subsoil disturbance, increases plant available nutrients, and promotes native plant species in fire-maintained ecosystems. Nonetheless, studies that have investigated either historical agriculture or prescribed fire management illustrate that each of these disturbances (separately) can have strong effects on beta diversity. For example, beta diversity among post-agricultural sites is often lower than that of sites lacking a history of cultivation (Vellend et al. 2007; Rogers et al. 2009; Baeten et al. 2010), a legacy effect that may result from both plant dispersal- and recruitment-limitation and may persist for decades following agricultural abandonment (Flinn 2014). On the other hand, in fire-maintained communities (e.g., grasslands, savannas, and woodlands), frequent fires can facilitate plant recruitment in ways that increase beta diversity (Dodson and Peterson 2010). Fire can increase plant recruitment opportunities by reducing standing biomass and litter, which in turn may yield unique combinations of species among frequently burned sites. Further, spatially discontinuous fires create heterogeneous environments that can provide variation in recruitment opportunities following propagule dispersal (Myers and Harms 2011), also leading to increased beta diversity. On the other hand, frequent fires may decrease beta diversity by promoting species dominance (Uys et al. 2004; Kirkman et al. 2014). Clearly, agricultural land use and prescribed fires can both influence patterns of beta diversity, manifested in part by

their sometimes opposing effects on plant recruitment, yet the extent to which historical agriculture alters the effects of contemporary fire regimes on plant diversity is poorly understood.

Although agricultural land-use and human-altered fire regimes are often studied separately, these disturbances may interact to shape patterns of beta diversity. For example, agricultural legacies have been attributed to reduced habitat quality (e.g., degraded soil environments; McLauchlan 2006; Flinn and Marks 2007) and reduced connectivity (Brudvig and Damschen 2011) that may limit plant establishment (Baeten et al. 2010). As a result, increased recruitment opportunities provided by frequent fires may be inconsequential in post-agricultural sites where reduced colonization and strong environmental filters constrain community membership (e.g., via reduced soil moisture holding capacity, Foster et al. 2003; increased soil compaction, Mattingly and Orrock 2013; or altered soil microbial communities and nutrient availability, Fraterrigo et al. 2005, 2006), whereas the positive effects of fire on beta diversity may be more pronounced in areas that lack a history of agriculture. Presently, however, we lack understanding of whether historical disturbances influence the manner in which plant communities respond to contemporary disturbances due to a lack of studies designed to investigate such an interaction.

In this study, we evaluated the effects of historical agriculture and human-altered fire regimes on beta diversity by surveying longleaf pine (*Pinus palustris*) woodland understory plant communities at 232 sites spanning 450 km across three study locations in the southeastern United States. For several reasons, longleaf pine woodlands provide an ideal system in which to evaluate land-use impacts on beta diversity. First, agricultural practices were widespread in this system, and, currently, both historically cultivated and uncultivated lands vary considerably in fire management practices (Frost 2006). Second, agricultural and fire disturbances are known to affect local-scale (alpha) diversity (Veldman et al. 2014), and because dispersal- and recruitment-limitation are known to constrain plant community membership in this system (Myers and Harms 2011), these disturbances are likely to shape patterns of beta diversity. Further, longleaf pine woodlands contain many rare and endemic plant species, yet this system is highly threatened by human land-use activities, including agriculture and fire-suppression (e.g., Frost 2006; Noss 2013). As such, understanding the factors that drive multiple components of biodiversity, including beta diversity, is of interest to land management and conservation. At each of our three study locations, we tested the following predictions: (1) post-agricultural woodlands have lower beta diversity among sites compared to woodlands lacking a history of agricultural land use; (2) frequently burned

Table 1 Comparison of measured environmental variables for remnant and post-agricultural sites at three study locations

Location	Remnant		Post-agricultural		t	P
	Mean ± SE (n)	Range	Mean ± SE (n)	Range		
Fort Bragg, NC						
Fire frequency (# of fires)	6.0 ± 0.2 (51)	3–11	5.5 ± 0.2 (34)	3–8	1.76	0.08
Soil moisture holding capacity (% by weight)	43.6 ± 0.9 (51)	34.2–56.5	37.8 ± 0.9 (34)	30.7–54.2	4.57	<0.001
Savannah River Site, SC						
Fire frequency (# of fires)	3.0 ± 0.3 (39)	0–7	3.1 ± 0.3 (41)	0–7	0.31	0.76
Soil moisture holding capacity (% by weight)	35.8 ± 0.6 (39)	27.9–47.0	37.7 ± 0.7 (41)	30.3–51.1	1.97	0.052
Fort Stewart, GA						
Fire frequency (# of fires)	4.8 ± 0.5 (40)	0–17	5.2 ± 0.4 (27)	1–8	0.67	0.51
Soil moisture holding capacity (% by weight)	41.9 ± 1.0 (40)	30.2–55.7	39.0 ± 1.2 (27)	29.8–51.0	1.90	0.062

woodlands have greater beta diversity among sites than infrequently burned woodlands; and (3) the positive effect of fire on beta diversity is more pronounced among sites that lack a history of agricultural land use. To show how patterns of beta diversity differ from the well-established patterns of alpha diversity in this system (e.g., Veldman et al. 2014), we also assessed the separate and combined effects of agriculture and fire on species richness, thereby providing a broader view of how human land uses shape local and landscape patterns of plant diversity.

Materials and methods

Study system

The longleaf pine ecosystem historically covered much of the southeastern U.S. (Frost 2006). Today, this fire-dependent open tree canopy ecosystem, which is variably referred to as savanna, woodland, and forest (hereafter "woodlands"; Peet 2006), covers <3 % of its original area due to conversion to agriculture, intensive timber production, and fire suppression (Frost 2006; Noss 2013). Remnant longleaf pine woodlands that have no recent history of agriculture are characterized by a sparse overstory and a highly diverse understory that may contain up to 30 or more plant species per m² (e.g., Walker 1995; Peet 2006). In this ecosystem, understory plant communities are shaped and maintained by frequent, low-intensity surface fires that consume leaf litter and top-kill fire-intolerant trees (Thaxton and Platt 2006; Walker and Silletti 2006; Hiers et al. 2007). Historically, fire return intervals were as frequent as 1–3 years (Frost 2006; Peet 2006).

We conducted this study at three locations within the historical range of longleaf pine woodlands: Ft. Bragg (North Carolina), the Savannah River Site (SRS, South Carolina; a National Environmental Research Park), and Ft. Stewart (Georgia). A map of our study locations is provided

in Brudvig et al. (2014). These locations span 450 km, 3° of latitude, and a broad gradient in soil moisture (Table 1), a factor known to influence patterns of understory plant species richness in this study system (Kirkman et al. 2001; Peet et al. 2014). Within each location, sites themselves encompassed a large area, spanning the extent of Ft. Bragg (730 km²), SRS (770 km²), and Ft. Stewart (1,140 km²). Because species richness tends to increase with soil moisture, this environmental factor will likely influence the effects of agriculture and fire on beta diversity (e.g., the recruitment opportunities provided by frequent fires are more likely to yield unique combinations of species among sites exhibiting high soil moisture). As such, we accounted for underlying gradients in soil moisture in our models to better evaluate the effects of these land-use activities on beta diversity. At each study location, habitat encompasses a mosaic of formerly cultivated woodlands ("post-agricultural" sites) intermixed with areas with no known history of agriculture ("remnant" sites). In this sense, our use of the phrase "remnant woodland" is synonymous with that of "ancient forest", another common descriptor of sites lacking a history of agricultural land use (e.g., Dupouey et al. 2002; Hermy and Verheyen 2007). Over the past several decades, managers at each location have used prescribed fires to restore and maintain longleaf pine woodlands. Because fire management is not uniform across the landscape, each study location contains fire-suppressed sites interspersed among more frequently burned areas. More detailed description of each study location is provided as supplementary material.

Site selection

At each location, we stratified our site selection to include both remnant and post-agricultural woodlands. We selected sites by using a Geographic Information System that contained location boundaries, a digitized historical map and aerial photographs from the year of agricultural

abandonment (Ft. Bragg: 1919; SRS: 1951; and Ft. Stewart: 1947), and annual prescribed fire records from 1991 to 2009. We classified sites as either remnant or post-agricultural based on their land-use status in these historical documents, using methods similar to Brudvig and Damschen (2011) and Mattingly and Orrock (2013). Although locations of agricultural sites may be chosen on the basis of certain soil characteristics (Kirch et al. 2004), soil texture, an important determinant of plant diversity in this system (Peet 2006; Peet et al. 2014), was similar between remnant and post-agricultural sites at each study location (supplementary material: Table A1). Across both land-use categories, sand was the dominant soil component at each location: Ft. Bragg (85.1 ± 1.3 % sand), SRS (90.6 ± 0.6 % sand), and Ft. Stewart (87.7 ± 1.0 % sand). All sites occurred in habitat with *Pinus palustris* present in the current overstory, were separated from one another by at least 250 m, and contained at least 1 ha of relatively uniform habitat (i.e. lacked apparent age or compositional discontinuities, drainages, and roads). Although the extent of uniform habitat (patch size) varied among replicate sites, previous work in this system shows that patch size has no effect on plant species richness or composition (Brudvig and Damschen 2011). We used annual fire records to select a final set of sites to encompass a range of fire return intervals, from 0 to 17 fires between 1991 and 2009. For each study location, mean values of fire frequency were similar between the two land-use categories (Table 1). A total of 232 sites were selected across three study locations (Ft. Bragg: $n = 85$ sites; SRS: $n = 80$ sites; and Ft. Stewart: $n = 67$ sites). Importantly, for each study location, this high level of replication allowed for a multitude of pairwise site comparisons, thereby providing a robust analysis of beta diversity.

Understory vegetation survey

We surveyed understory vegetation at the 232 sites between 20 August and 13 November 2009. To determine plant species richness and community composition, we used a modified version of the protocol developed by the Carolina Vegetation Survey (Peet et al. 1998; http://cvs.bio.unc.edu/), recording all understory plant species present within a 20 × 50 m area at each site, as in Brudvig and Damschen (2011) and Brudvig et al. (2014). This sampling area was randomly oriented and positioned within the interior of the site. Soil moisture holding capacity was determined for each site, wherein six soil cores (each 2.5 cm in diameter and 15 cm in depth) were collected at 10-m intervals along the center line of the 20 × 50 m area. For each site, soil cores were homogenized and processed by determining the proportional difference between saturated wet and oven-dry weights of the soil samples, as in Brudvig and Damschen

(2011) and Brudvig et al. (2014). For a subset of sites at each study location, homogenized soil cores were processed for texture analysis (Brookside Laboratories, New Knoxville, OH, USA).

Data analysis

Various metrics of beta diversity have been used to evaluate spatial variation in community composition, ranging from classical measures that incorporate species richness at local (alpha) and regional (gamma) scales (Whittaker 1960; Tuomisto 2010a, b) to multivariate approaches that calculate the average dissimilarity of sampled communities to group centroids (e.g., Anderson 2006). Indeed, suitable methods for quantifying beta diversity have been at the forefront of recent discussions (reviewed in Jurasinski et al. 2009; Anderson et al. 2011; see also Ellison 2010 and references therein). In this study, we used the Raup-Crick metric (Beta$_{RC}$) to quantify community dissimilarity (Raup and Crick 1979), which employs a null model approach to evaluate compositional dissimilarity between two communities relative to a null expectation derived from the numbers of observed and expected shared species between the two communities. This approach was recently advocated by Chase et al. (2011) and subsequently employed in several analyses of beta diversity (e.g., Azeria et al. 2011; Barlow et al. 2012; Jamoneau et al. 2012; Grman and Brudvig 2014). Unlike other common dissimilarity metrics (e.g., Jaccard or Sørenson), this metric is not biased by differences in alpha diversity among compared communities. Because human land-use activities can have profound effects on plant species richness (Hedman et al. 2000; Vellend 2004; Hermy and Verheyen 2007; Vellend et al. 2007; Brudvig and Damschen 2011), controlling for potential differences in alpha diversity while evaluating beta diversity is particularly important (Chase et al. 2011). Indeed, for each of our three study locations, replicate sites encompassed a broad range of alpha diversity values (Ft. Bragg: 20–98 species per 1,000 m^2; SRS: 16–99 species per 1,000 m^2; Ft. Stewart: 25–92 species per 1,000 m^2). As such, some pairwise site comparisons involve sites that differ considerably in alpha diversity, thus warranting the use of this null model approach.

For this null model approach, the species pool from which species are drawn to determine Beta$_{RC}$ must be defined (Chase et al. 2011). Here, we defined the species pool as all species occurring within the sampled plots across all sites per study location: Ft. Bragg (142 species), SRS (168 species), and Ft. Stewart (260 species). We constructed null models by sampling from the respective species pool, wherein species were weighted by their frequency of occurrence across all sites per study location. We used the R code presented in Kraft et al. (2011) to generate
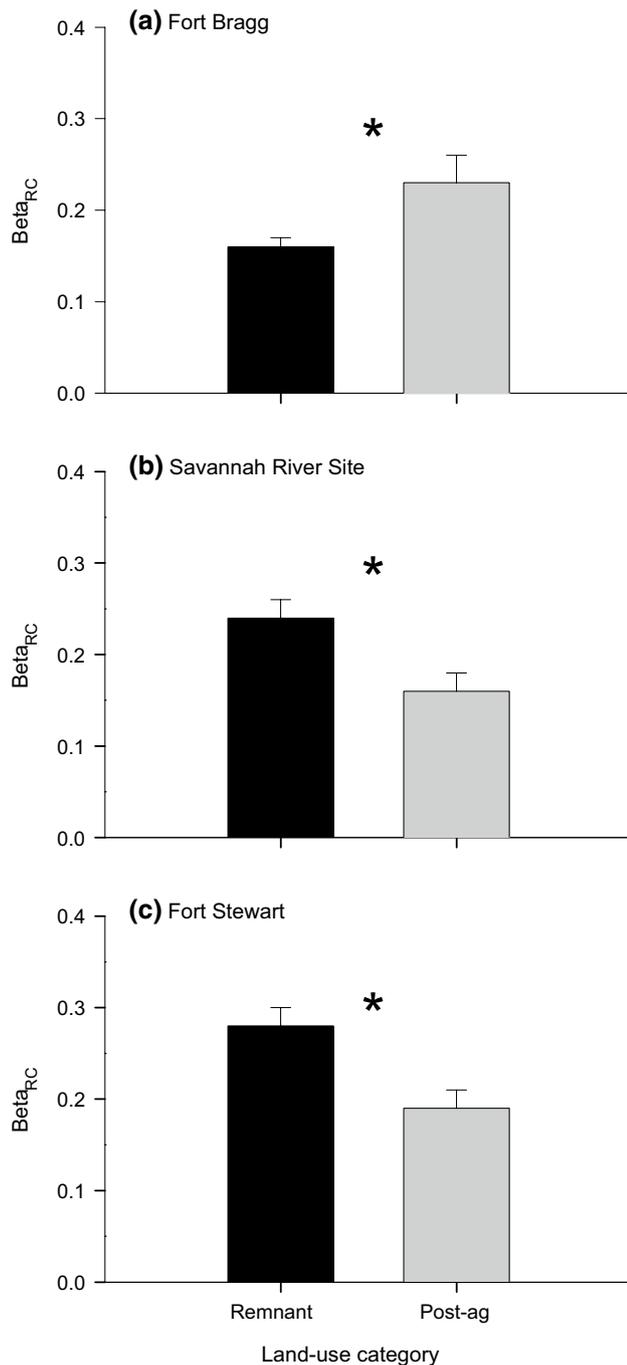
Fig. 1 Values of $Beta_{RC}$ (mean ± SE) among remnant and post-agricultural sites at the three study locations. For each location, an *asterisk* denotes a significant difference ($P < 0.05$) in mean $Beta_{RC}$ values between the two land-use categories

a $Beta_{RC}$ value for all possible pairwise site comparisons per study location, based on 9,999 simulations per comparison. From the resulting site × site dissimilarity matrix, we calculated a $Beta_{RC}$ value for each site using the approach of Vellend et al. (2007), where $Beta_{RC}$ is calculated as the mean of two separate means: (1) the mean of all pairwise

site comparisons for a given site against remnant sites, and (2) the mean of all pairwise site comparisons for a given site against post-agricultural sites. This approach controls for a source of bias that may arise when sample sizes are unequal between the two land-use categories (Vellend et al. 2007), as is the case with our study (Table 1).

We used general linear models to test the effects of fire frequency (number of fires between 1991 and 2009) and soil moisture holding capacity (% by weight) on $Beta_{RC}$ across remnant and post-agricultural sites at each study location (SAS v.9.1; SAS Institute, Cary, NC, USA). Similar models were used to evaluate patterns of alpha diversity (i.e. species richness per 1,000 m^2). We used a separate analysis for each land use × study location combination, evaluating the role of fire frequency, soil moisture holding capacity, and their interaction in affecting diversity. We analyzed remnant and post-agricultural sites separately because soil moisture holding capacity differed significantly between these land-use categories for several sites (Table 1). We adopted this approach because a model using the soil moisture × land use interaction term would be extrapolating over different domains of the soil moisture data for each level of the land-use factor (i.e. an implicit assumption of GLMs that evaluate interactions between factors and covariates is that the values of the covariate are similar among factor groups; Quinn and Keough 2002). By analyzing data separately for each land-use category, inference from the model is appropriately constrained to the range of data for soil moisture in that model. We determined confidence intervals for fire and soil moisture effects on $Beta_{RC}$ to facilitate comparisons between the remnant and post-agricultural sites at each study location. Following analysis, variances of the residuals appeared homoscedastic and normally distributed for each model. To assess the extent to which our results were contingent on the use of the Raup-Crick metric ($Beta_{RC}$), we performed similar analyses based on the Sørensen similarity coefficient. We used Indicator Species Analysis (ISA) to identify the understory plant species that distinguished groups based on land-use history (remnant vs. post-agricultural) and fire frequency (≤4 burns since 1991 vs. >4 burns since 1991, based on the model results of Brudvig et al. 2014) (R v.3.0; R Foundation for Statistical Computing, Vienna). We used *t*-tests to evaluate site-level environmental differences between land-use categories.

Results

Agricultural land use was consistently an important determinant of beta diversity, but the direction of this effect differed among the three study locations (Fig. 1). At Ft. Bragg, beta diversity was greater among post-agricultural

Table 2 Results of general linear models testing the effects of fire and soil moisture on beta diversity (Beta$_{RC}$) across remnant and post-agricultural sites at each study location. Where significant, a positive relationship was detected between fire frequency and beta diversity

Location	Remnant			Post-agricultural		
	df	F	P	df	F	P
Fort Bragg, NC						
Fire frequency (number of fires)	1,50	5.79	0.020	1,33	0.38	0.54
Soil moisture holding capacity (% by weight)	1,50	0.43	0.52	1,33	0.77	0.39
Fire frequency × Soil moisture holding capacity	1,50	3.58	0.06	1,33	0.88	0.36
Savannah River Site, SC						
Fire frequency (number of fires)	1,38	2.35	0.13	1,40	9.91	0.003
Soil moisture holding capacity (% by weight)	1,38	0.49	0.49	1,40	<0.01	0.96
Fire frequency × Soil moisture holding capacity	1,38	6.84	0.013	1,40	0.38	0.54
Fort Stewart, GA						
Fire frequency (number of fires)	1,40	10.25	0.003	1,26	0.09	0.77
Soil moisture holding capacity (% by weight)	1,40	0.01	0.93	1,26	0.08	0.78
Fire frequency × Soil moisture holding capacity	1,40	0.07	0.79	1,26	0.39	0.54

sites (mean Beta$_{RC}$ ± 1SE: 0.23 ± 0.03) than among remnant sites (0.16 ± 0.01; $F_{1,84} = 6.4$, $P = 0.014$; Fig. 1a). In contrast, remnant sites exhibited greater beta diversity than post-agricultural sites at both SRS (remnant: 0.24 ± 0.02; post-agricultural: 0.16 ± 0.02; $F_{1,79} = 9.5$; $P = 0.003$; Fig. 1b) and Ft. Stewart (remnant: 0.28 ± 0.02; post-agricultural: 0.19 ± 0.02; $F_{1,67} = 9.3$; $P = 0.003$; Fig. 1c). Analysis of community dissimilarity (100 − Sørensen similarity coefficient) provided qualitatively similar results (supplementary material: Fig. A1).

Frequent fires increased beta diversity at each study location, but this positive effect of fire was contingent on agricultural land-use history (Table 2; Fig. 2). Frequent fires increased beta diversity among remnant sites at Ft. Bragg (main effect of fire frequency: remnant: $F_{1,50} = 5.8$, $P = 0.020$; post-agricultural: $F_{1,33} = 0.4$, $P = 0.54$; Fig. 2a) and Ft. Stewart (main effect of fire frequency: remnant: $F_{1,40} = 10.3$, $P = 0.003$; post-agricultural: $F_{1,26} = 0.1$, $P = 0.77$; Fig. 2c). However, these findings were inconsistent with results from SRS where frequent fires also increased beta diversity among post-agricultural sites (main effect of fire frequency: remnant: $F_{1,38} = 2.4$, $P = 0.13$; post-agricultural: $F_{1,40} = 9.9$, $P = 0.003$; Fig. 2b).

Soil moisture holding capacity was greater among remnant sites than among post-agricultural sites at Ft. Bragg. At SRS and Ft. Stewart, however, differences in soil moisture holding capacity between the two land-use categories were marginal (Table 1). The positive effects of fire frequency on beta diversity were contingent on soil moisture holding capacity at SRS ($F_{1,38} = 6.84$, $P = 0.013$) and marginally so at Ft. Bragg ($F_{1,50} = 3.58$, $P = 0.06$; Table 2), such that the effects of frequent fires were more pronounced among remnant sites under conditions of high soil moisture holding capacity (Fig. 2). This contingency was not apparent at Ft. Stewart ($F_{1,40} = 0.1$, $P = 0.79$; Table 2; Fig. 2).

Analysis of community dissimilarity provided qualitatively similar results (supplementary material: Table A2).

ISA revealed differing suites of species among the four site classes defined by land-use history and fire frequency (supplementary material: Tables A3–A5). In general, plant species characteristic of fire-maintained understory communities (e.g., *Aristida stricta*, *Gaylussacia dumosa*, and *Tephrosia virginiana*) were indicative of frequently burned remnant sites, whereas post-agricultural sites were more often defined by the presence of ruderal species typical of disturbed habitats (e.g., *Vitis rotundifolia*, *Gelsemium sempervirens*, and *Rhus toxicodendron*). Woody species (e.g., *Vaccinium stamineum*, *Carya pallida*, and *Lyonia mariana*) were often indicative of infrequently burned sites at each of the three study locations (supplementary material: Tables A3–A5).

Alpha diversity (understory plant species richness per 1,000 m²) was similar between remnant and post-agricultural sites at Ft. Bragg (remnant: 49.2 ± 2.7 species; post-agricultural: 47.5 ± 2.4 species; $F_{1,84} = 0.2$, $P = 0.66$; Fig. 3a) and Ft. Stewart (remnant: 53.2 ± 3.1 species; post-agricultural: 47.0 ± 2.4 species; $F_{1,67} = 2.1$, $P = 0.16$; Fig. 3c). At SRS, however, more understory plant species occurred in remnant than in post-agricultural plots (remnant: 56.5 ± 2.4 species; post-agricultural: 47.1 ± 2.2 species; $F_{1,79} = 8.4$, $P = 0.005$; Fig. 3b). At Ft. Bragg, species richness increased with fire frequency only in remnant sites, whereas at SRS this positive effect of fire was detected at both remnant and post-agricultural sites. In contrast, fire had a negligible effect on species richness for both land-use categories at Ft. Stewart (supplementary material: Table A6). Unlike the effects of fire, soil moisture holding capacity did not affect species richness in either remnant or post-agricultural sites at each study location (supplementary material: Table A6). In general,
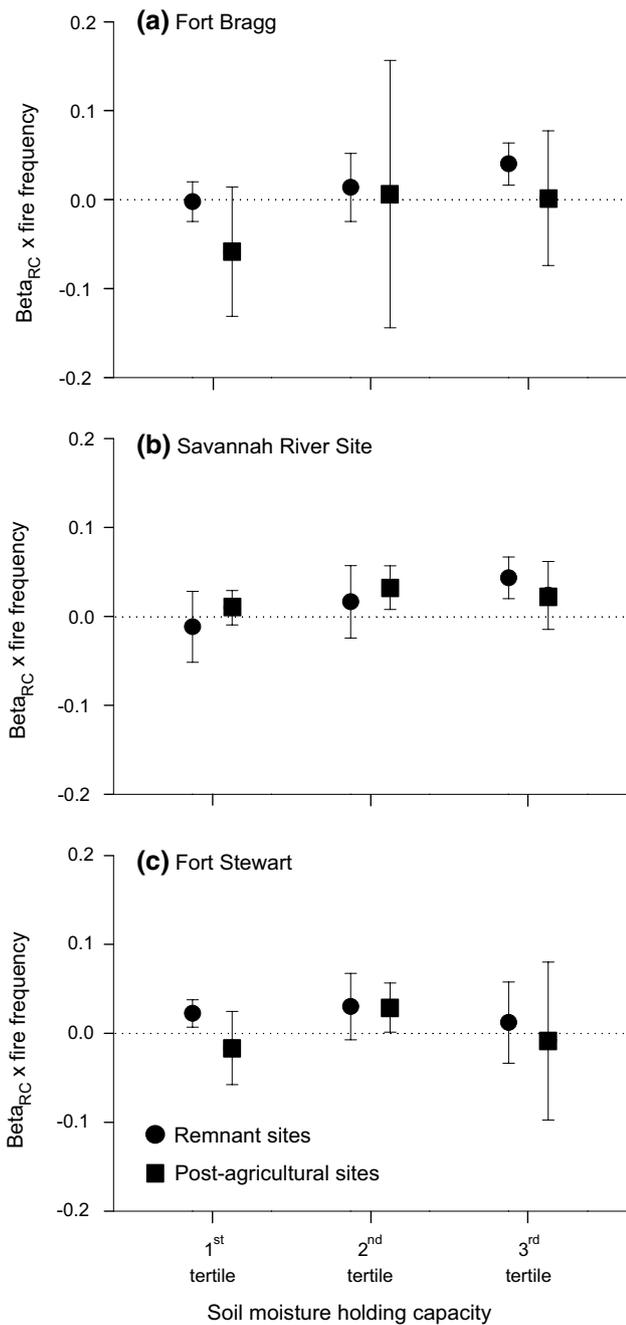
Fig. 2 Slope and 95 % confidence intervals for the effect of fire frequency on $Beta_{RC}$ among remnant and post-agricultural sites at the three study locations. To illustrate interactions between fire frequency and soil moisture holding capacity (SMHC), paired plots in each panel are based on the 1st, 2nd, and 3rd tertiles for SMHC values, respectively

Fig. 3 Species richness (mean ± SE) at remnant and post-agricultural sites at the three study locations. For each location, an *asterisk* denotes a significant difference ($P < 0.05$) in mean richness values between the two land-use categories

correlation analyses revealed non-significant relationships between species richness and soil texture. At SRS, however, we detected a negative relationship between sand content and species richness (supplementary material: Table A7).
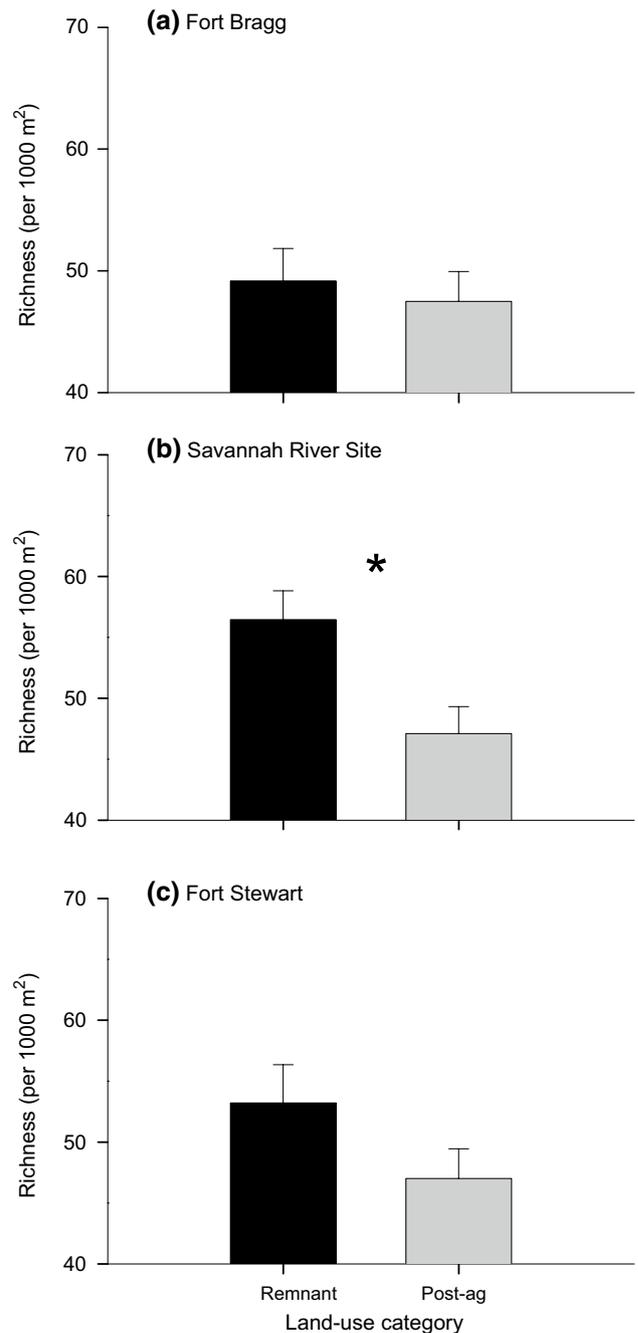
Discussion

Agricultural legacy and beta diversity

We predicted that beta diversity would be lower among sites that have a history of agriculture, since agricultural

legacies are known to limit recruitment and constrain the identity of plant species occurring at local scales (Foster et al. 2003; Cramer et al. 2008). Using 232 sites at three locations spanning 450 km in the longleaf pine ecosystem, our results clearly demonstrate that historical agriculture is a key determinant of beta diversity. Yet, the nature of this relationship differed among locations, with remnant sites illustrating greater beta diversity at two locations and post-agricultural sites supporting greater beta diversity at one location. Importantly, by coupling multiple geographic locations with high levels of large-scale replication within each location, our study provides strong evidence that the nature of this land use effect on beta diversity is itself contingent.

At SRS and Ft. Stewart, beta diversity was lower among post-agricultural sites, a result consistent with our predictions and with studies conducted in temperate forests (e.g., Vellend et al. 2007; Rogers et al. 2009). In post-agricultural landscapes, low beta diversity among plant communities can arise from reduced levels of environmental heterogeneity (e.g., via the homogenization of soils from tilling) that are often a consequence of historical disturbances (Christensen and Peet 1984; Foster et al. 2003; but see Vellend et al. 2007; Grman et al. 2014). Further, such disturbances can decouple associations between plant communities and environmental gradients. For example, Vellend et al. (2007) attributed the homogenization of plant communities on post-agricultural land to the combined effects of dispersal limitation and reduced habitat quality (e.g., degraded soil environments that limits plant recruitment upon dispersal). Together, these factors can determine—and limit—the number and identity of species that arrive and establish in historically disturbed sites (Flinn et al. 2010; De Frenne et al. 2011; Brudvig et al. 2013), leading to low levels of beta diversity among plant communities.

Contrary to our predictions, beta diversity was higher among post-agricultural sites at Ft. Bragg. We suspect that the spatial isolation of post-agricultural patches played a role in generating relatively high beta diversity at this study location, a pattern that has also been documented within the context of forest fragmentation (Jamoneau et al. 2012). Unlike land-use patterns at SRS and Ft. Stewart, agriculture at Ft. Bragg was confined to small, spatially-isolated patches within a matrix of non-agricultural remnant pine woodlands (Aragon 2004); such isolation can increase the relative importance of stochastic processes (e.g., ecological drift) in community assembly, leading to divergent communities and higher beta diversity (Vellend 2010). Historical and contemporary disturbances, such as those in our study, may further reduce the number of interacting individuals in a community (i.e. community size; Orrock and Fletcher 2005), enhancing ecological drift (e.g., Vellend and Orrock 2009; Orrock and Watling 2010) and, ultimately, beta

diversity. Although we do not have data to directly address the role of drift in our system, we show that, in contrast to previous work (e.g., Vellend et al. 2007), agricultural legacies can in some cases be associated with increased beta diversity. Importantly, beta diversity in these post-agricultural landscapes reflects turnover among communities that have vastly different species compositions compared to plant communities typically found in habitats not used for agriculture (Kirkman et al. 2004; Brudvig et al. 2014). Thus, like other summary measures of diversity that are based on dissimilarity metrics, high levels of beta diversity per se may not reflect the quality of habitat because species identities are obscured. However, additional analysis (e.g., ISA; supplementary material: Tables A3–A5) may provide some insight into how community composition differs in response to human land use.

Prescribed fire frequency and beta diversity

We predicted that beta diversity would increase with prescribed fire frequency because in this system frequent fires have been shown to increase recruitment opportunities that in turn promote plant community heterogeneity (Walker and Silletti 2006; Mitchell et al. 2009; Myers and Harms 2011). Our results demonstrate that prescribed fire frequency, like historical agriculture, is not only an important determinant of beta diversity but that historical land use can interact with contemporary disturbances (e.g., fire) to shape plant community heterogeneity among sites. For example, although beta diversity increased with prescribed fire frequency at each study location, this positive effect of fire was contingent on historical land-use patterns. Further, the nature of this contingency was not consistent among the three locations: at two of our study locations (Ft. Bragg and Ft. Stewart), frequent fires increased beta diversity only among sites lacking a history of agricultural land use, whereas at SRS this effect of fire was also detected among post-agricultural sites. Clearly, agricultural legacies can influence how plant communities respond to subsequent disturbance regimes (Cramer et al. 2008), but, as seen with our results, the nature of this response is variable, suggesting that the timing and intensity of previous disturbance or other environmental factors (e.g., soil moisture) may be important in shaping patterns of beta diversity. For example, Dodson and Peterson (2010) demonstrate that prescribed fire increased the beta diversity of understory plant communities only when combined with overstory tree thinning.

We predicted that the positive effects of fire on beta diversity would be more pronounced among sites lacking a history of agriculture. We expected this interaction because, although fire can increase recruitment opportunities (Myers and Harms 2011), this effect may be inconsequential

among post-agricultural sites where strong environmental filters are likely to limit plant establishment (e.g., via reduced soil moisture holding capacity, Foster et al. 2003; increased soil compaction, Mattingly and Orrock 2013; or altered soil microbial communities and nutrient availability, Fraterrigo et al. 2005, 2006). Our data at Ft. Bragg and Ft. Stewart were consistent with this reasoning. However, at SRS, fire frequency affected beta diversity among remnant sites as well as among post-agricultural sites. SRS has a longer history of fire suppression compared with the other two study locations, and 11 post-agricultural sites (27 %) at SRS experienced one or fewer fires since 1991. Consequently, these sites were characterized by a deep litter layer that likely limits plant species recruitment. Indeed, for this study location, Veldman et al. (2014) demonstrated that fire frequency is strongly (and negatively) correlated with litter depth, which in turn is negatively correlated with local-scale plant species richness. Further, in this study system, Brudvig et al. (2014) showed that understory plant species indicative of frequently-burned post-agricultural sites (e.g., *Chamaecrista nictitans*, *Desmodium marilandicum*, and *Prunus serotina*) differ from those of fire-suppressed sites (e.g., *Vitis rotundifolia*, *Gelsemium sempervirens*, and *Quercus incana*). Thus, variation in burn frequency in these extremely fire-suppressed landscapes may generate compositional differences among sites when the baseline condition (i.e. zero fires) is ecologically extreme. In this case, even a small increase in fire frequency—relative to zero—may generate vastly different plant communities. Further, the dense canopy cover characteristic of pine plantations in post-agricultural sites, like at SRS (Brudvig et al. 2014), further contributes to litter accumulation (Veldman et al. 2014), which, when combined with chronic fire suppression, may explain the observed positive effects of fire on beta diversity among post-agricultural sites at SRS. Under these conditions, the benefits of frequent prescribed fires may overcome agricultural legacy effects on beta diversity, but more work would be necessary to directly address this hypothesis. Additionally, it is worth noting that beta diversity among post-agricultural sites was high and unaffected by prescribed fire frequency at one of our study locations (Ft. Bragg), suggesting that, in some cases, other factors (e.g., species pools, dispersal limitation, species interactions, or plant community age) likely determine local species composition and may thus exert a greater influence than fire in shaping patterns of beta diversity. Nonetheless, our results do suggest that fire can be an important determinant of beta diversity, depending on land-use history.

The positive effect of frequent fires on beta diversity was additionally contingent on soil moisture availability at two of our study locations (Ft. Bragg and SRS); further, this contingency was observed only among sites lacking a history of agriculture. In longleaf pine woodlands, soil

moisture is one of the most important environmental determinants of plant alpha diversity (Kirkman et al. 2001; Peet et al. 2014). As such, because soil moisture and local diversity are often positively correlated, the recruitment opportunities provided by frequent fires are more likely to yield unique combinations of species among sites exhibiting high soil moisture holding capacity. Further, soil moisture is strongly positively correlated with productivity in this system (Mitchell et al. 1999), including the dominance of understory species, and thus the removal of standing vegetation and accumulated litter by frequent fires will likely have a more pronounced effect on plant species recruitment in productive habitats. Together, the relationships between soil moisture and the local diversity and productivity of understory plant communities may contribute to the interaction between soil moisture and fire frequency in shaping beta diversity, an interaction that was not detected among post-agricultural sites perhaps because such sites in this system typically exhibit low levels of local diversity and productivity (Mattingly and Orrock 2013).

Alpha and beta diversity

Our integration of information on alpha and beta diversity highlights scale-dependent effects of fire and agricultural land use on understory plant diversity in this system. Interestingly, at two of our study locations (Ft. Bragg and Ft. Stewart), historical land use was a significant determinant of beta diversity but alpha diversity did not differ between remnant and post-agricultural sites, suggesting that agricultural legacy effects may be more readily detected by evaluating changes in the identities rather than the numbers of plant species in human-modified landscapes. Further, the importance of fire as a determinant of diversity (and its interaction with historical land use) varied with respect to the diversity component under consideration. For instance, fire did not influence alpha diversity in remnant or post-agricultural sites at Ft. Stewart, but frequent fires did increase compositional differences among remnant sites at this study location. Consequently, the interaction between historical land use and contemporary fire management on diversity was only evident by examining diversity at a landscape-scale, taking into account compositional differences among sites. At SRS and Ft. Bragg, fire increased both alpha and beta diversity in remnant sites, illustrating the importance of fire management for maintaining diversity of remnant forests. Only at SRS did fire increase alpha and beta diversity among post-agricultural sites, likely reflecting the history of burn suppression across this study location. Although we quantified alpha diversity across a relatively large spatial scale per site (1,000 m^2), it is possible that the effects of historical agriculture and fire are more apparent when alpha diversity is assessed across smaller

spatial scales (e.g., 1 m^2), where local environmental factors are likely to constrain community membership. Additional work is needed to address this hypothesis.

Conclusions

Our results show that historical agriculture can have strong effects on the beta diversity of understory plants in one of the most diverse terrestrial systems in North America. Importantly, this study demonstrates that agricultural legacies can shape plant diversity in fire-maintained ecosystems that function quite differently compared to temperate deciduous forests where land-use impacts on beta diversity are most often assessed. These agricultural legacies can result in both positive and negative effects on beta diversity. Our study also demonstrates that the effects of prescribed fire frequency on beta diversity can be contingent on historical land-use activities as well as environmental characteristics (e.g., soil moisture). As such, our results suggest that although fire plays a crucial role in maintaining understory structure in longleaf pine woodlands, efforts to promote and maintain beta-diverse understory plant communities through prescribed fire management alone may in some cases be ineffective in human-modified landscapes. Because human-modified landscapes are often subjected to multiple forms of anthropogenic disturbances (e.g., prescribed fire, timber harvesting, changing land-use patterns), additional beta diversity studies designed to evaluate potential interactions between historical agriculture and other contemporary disturbance regimes are needed.

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