



Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity

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Nomenclature

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Introduction

Altered fire regimes and agricultural conversion are two pervasive forms of human-induced environmental change (Foster et al. 2003). Agriculture can impose dramatic and persistent changes to ecosystems, including losses of

Abstract

Question: Human-altered disturbance regimes and agricultural land uses are broadly associated with reduced plant species diversity in terrestrial ecosystems. In this study, we seek to understand how fire frequency and agricultural land-use history influence savanna understorey plant diversity through complex relationships (i.e. indirect effects) among multiple biophysical variables.

Location: Fort Bragg, NC, US, Savannah River Site, SC, US and Fort Stewart, GA, US.

Methods: We use structural equation modelling (SEM) to evaluate the relationships among six groups of predictor variables and their influence on local-scale species richness in pine savannas at 256 sites from three locations in the southeastern USA. In the model, fire frequency and agricultural history are hypothesized to control richness through a combination of direct effects, and indirect effects mediated by resource availability, tree abundance, understorey plant abundance and the O horizon (litter and duff depth).

Results: Frequent fires promote richness by limiting tree abundance, which increases understorey abundance and reduces the O horizon. Frequent fires also limit the O horizon independent of tree abundance. Of the total positive effect of fire on richness, 70% is attributable to reductions in the O horizon and 30% to reduced tree abundance. Agricultural history has a negative effect on richness through a positive correlation with tree abundance, which decreases understorey abundance and increases the O horizon. Agricultural history has a modest negative effect on richness by reducing resource availability as well as a strong direct negative effect (38% of the total effect) that is unrelated to other modelled variables.

Conclusions: Through a multivariate framework and large-scale data set, this study unites and tests our understanding of the factors that control plant species diversity in a fire-dependent ecosystem. We show that the effects of fire frequency and agricultural history on richness are largely mediated through other ecosystem attributes, including vegetation structure (i.e. tree and understorey abundance), resource availability and the O horizon. Persistent, negative effects of agricultural history demonstrate the slow rates of savanna plant community recovery on post-agricultural land and highlight the conservation value of frequently burned savanna remnants.

biodiversity (Flinn & Vellend 2005). When plant communities are eliminated by intensive agriculture, it can take centuries or longer for locally extinct species to re-colonize (Turner et al. 1997; Verheyen et al. 2003). The mechanisms by which past agricultural land use continues to influence contemporary species diversity are not fully

understood, but are likely to involve multiple biophysical factors (e.g. altered soils and vegetation structure, or dispersal limitation) that determine plant community diversity and composition (Flinn & Vellend 2005; Verheyen et al. 2006; Cramer et al. 2008). The lasting effects of agriculture are particularly pronounced in understorey plant communities of woodlands, savannas and grasslands (e.g. Ostertag & Robertson 2007) where plant species have evolved life-history strategies to survive frequent fires, often at the expense of colonization potential (Kirkman et al. 2004; Zaloumis & Bond 2011).

Altered fire regimes (i.e. changes in frequency, intensity or seasonality of fires) pose a global threat to biodiversity, and are often associated with agricultural land uses. Human colonization and land clearing along agricultural frontiers are initially associated with increased fire frequencies that are catastrophic for forest ecosystems composed of fire-intolerant species (e.g. Nepstad et al. 2001). In contrast, agricultural expansion in fire-dependent ecosystems can incentivize fire exclusion (e.g. Frost 1993). Biodiversity losses from fire exclusion are particularly severe in ecosystems where frequent fires are required to limit tree abundance, prevent forest succession and promote understorey plant diversity (Rogers et al. 2008; Noss 2013). Recognition of the complex relationships between understorey plants, trees, fire and resource gradients that are characteristic of savannas (e.g. Hoffmann et al. 2012a) calls for a multivariate approach to studying plant diversity in these systems (Weiher 2003; Gilliam et al. 2006; Veldman et al. 2013).

Distinct from treeless grasslands and closed-canopy forests, a defining characteristic of savanna ecosystems is the co-existence of scattered trees and understorey plants. Fire and the availability of limiting resources (e.g. precipitation, soil nutrients) are key determinants of vegetation structure (i.e. tree and understorey abundance) and savanna distributions from local to continental scales (Staver et al. 2011; Murphy & Bowman 2012). In 'mesic savannas' where resources are sufficient to support forest development, frequent fires are required to limit tree abundances that can otherwise constrain fine fuel production by the understorey and reduce ecosystem flammability (Lehmann et al. 2011; Hoffmann et al. 2012b). In addition to fueling fires, savanna understorey plant communities often support species-rich assemblages of graminoids, forbs and shrubs of high conservation value (Ratter et al. 1997; Kirkman & Mitchell 2006; Sankaran 2009; Bond & Parr 2010). As such, we should expect the determinants of savanna vegetation structure to be integral to understanding relationships between fire, land use and understorey plant diversity (Fig. 1).

In many ecological systems, including savannas, it can be challenging to understand the controls over species

diversity because of complex relationships that exist among organisms and their environments. Contributing to this complexity is the potential for indirect effects (i.e. relationships that are influenced by one or more intermediaries; Grace 2006). Indirect effects are widespread in natural systems, and studies of the roles of indirect effects have informed our thinking about food webs (e.g. Estes et al. 2011), species diversity (e.g. Harrison et al. 2006) and vegetation structure (e.g. van Langevelde et al. 2003). Because of the prevalence of indirect effects, analyses of simple bivariate relationships are often insufficient for understanding ecological systems and their biological diversity (Grace 2006). Indeed, analytical frameworks such as structural equation modelling (SEM) that incorporate direct and indirect relationships among multiple biotic and abiotic factors are proving useful for understanding species diversity in a variety of systems (e.g. Weiher 2003; Grace et al. 2011; Stomp et al. 2011).

In this study, we use SEM to determine how fire frequency and agricultural land-use history influence local-scale understorey plant species richness in pine savannas of the southeastern USA. Specifically, we investigate how six factors (fire frequency, agricultural history, resource availability, tree abundance, understorey plant abundance and the O horizon) directly and indirectly influence species richness. We begin by developing a multivariate conceptual model, based on previous work in pine savannas and current theory regarding savanna vegetation globally, of how these factors affect each other and influence understorey species richness (Fig. 1). We then assess these hypothesized relationships using a large-scale vegetation data set from 256 sites at three locations that span broad environmental gradients (Table 1), including gradients in prescribed fire frequency (from frequently burned to fire-excluded from 1991 to 2009). We include sites on former agricultural land (fields abandoned for 60–90 yr) as well as remnant savannas with no evidence of past cultivation. This is the first broad-scale investigation of how fire and agricultural legacies directly and indirectly (through influences on additional factors) control savanna plant diversity in a model study system. Our results provide a conceptual framework that may be tested in other mesic savannas around the world, and provide insight into the future of other fire-dependent ecosystems that are currently experiencing widespread agricultural conversion and fire exclusion.

Methods

Study system

We carried out this study in savannas and woodlands (hereafter 'savannas'; Glitzenstein et al. 1995; Ratnam et al. 2011) within the longleaf pine (*Pinus palustris*)

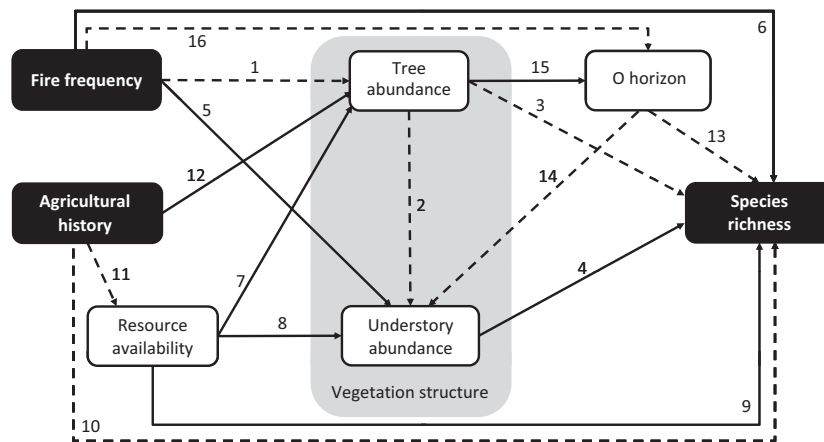


Fig. 1. The meta-model that guided the structural equation modelling. Rounded boxes represent system components (i.e. measurable variables, conceptual factors and theoretical constructs). Arrows indicate the hypothesized direction of influence, with positive and negative relationships represented by solid and dashed lines, respectively. Black shading denotes the components of primary interest whose relationships are thought to be mediated by other system components (in white). Path numbers correspond to the hypotheses in Appendix S1. In this framework, fire frequency and agricultural history are hypothesized to effect species richness by influencing vegetation structure (i.e. the balance between tree and understorey plant abundance; grey shading) and through alternative pathways that involve resource availability, the O horizon and direct (unmediated) effects.

Table 1. Summary of observed variables included in the structural equation model.

Variables (units)	Mean	Median	Range
Understorey plant species richness (species·m ⁻²)	5.6	4.9	0.1–17.9
Fire frequency (number of fires 1991–2009)	4.7	5	0–17
Litter depth (cm)	2.2	1.5	0.1–7.7
Duff depth (cm)	0.9	0.3	0–5.2
Total understorey cover (total %)	64	54	1–225
Tree basal area (m ² ·ha ⁻¹)	18	17	2.7–49
Tree canopy cover (%)	56	56	30–78
Soil moisture holding capacity (% by mass)	40	39	28–57
Soil organic matter (% by mass)	1.9	1.6	0.7–5.6
Cation exchange capacity (mEq·100·g ⁻¹)	2.2	2	0.4–6.9
Agricultural history	97 post-agricultural, 159 remnant sites		

ecosystem of the southeastern USA. This ecosystem is characterized by scattered pine trees and species-diverse understorey plant communities (Peet 2006). Frequently burned pine savannas with high moisture availability are among the most species-rich ecosystems in North America, supporting up to 35 species·m⁻² (Walker & Peet 1984). Like many of the world's savannas (Bond & Parr 2010), this high understorey plant diversity includes not just grasses (i.e. Poaceae) but a mixture of graminoid, forb and shrub species. Savannas have probably existed in parts of the southeastern USA throughout the past 2.6 Ma, resulting in many endemic fire-adapted species (see discussion by Noss 2013 and references therein).

Pine savannas are a model ecosystem for studying mesic savannas in fragmented agricultural landscapes. We specify 'mesic' because the subtropical climate, mild seasonality and ample precipitation of the region can support either savannas of C₄ graminoids or forests of fire-intolerant tree species, depending on the fire regime (Heyward 1939; Beckage & Stout 2000; Gilliam et al. 2006). Pine savannas once covered much of the southeastern USA but have been reduced to ~3% of their original area due to the combined effects of fire suppression, logging, resin extraction, agricultural and silvicultural conversion, and urbanization (Frost 1993; Gilliam & Platt 2006). Given this regional land-use history, studies of the ecology, conservation and restoration of pine savannas may offer insight into the future of other mesic savannas that are currently undergoing rapid agricultural conversion (e.g. Ratter et al. 1997; Klink & Machado 2005).

Meta-model development

An important part of SEM is meta-model development, the *a priori* conceptual framework that provides the basis for the statistical model (Grace et al. 2010). We based our SEM on a meta-model that depicts hypothesized relationships among factors that are thought to influence species richness in savannas (Table S1), with a specific emphasis on fire frequency and agricultural land-use history (Fig. 1). We began with a simple framework derived from current ecological theory of savanna vegetation structure, in which tree abundance and understorey abundance are a function of fire frequency and resource availability. Similar frameworks have proven to be relevant at both global

(Staver et al. 2011) and local scales (Hoffmann et al. 2012a), and thus provide a starting point to link fire frequency and agricultural land-use history to patterns of species richness via effects on vegetation structure. We incorporated agricultural history into the model based largely on mechanisms documented in forest ecosystems, because agricultural history has rarely been considered in studies of savanna plant diversity (Table S1). We also included the O horizon (litter and duff depth), a factor that is often neglected in plant community studies (Fridley et al. 2012), but that can be important in fire-dependent ecosystems, particularly in the context of fire exclusion (Varner et al. 2005; Hiers et al. 2007). In Appendix S1 we describe the theoretical basis for each of the hypothesized paths in the meta-model and provide additional literature references.

Field sampling

We selected 256 sites at three study locations that include a wide range of conditions typical of savannas in the eastern range of the longleaf pine ecosystem (Frost 1993; Peet 2006). The locations were: Fort Bragg, NC (73 000 ha; elevation, 43–176 m; mean annual precipitation [MAP], 1270 mm; mean annual temperature [MAT], 16 °C; $n = 85$ sites); Savannah River site (a National Environmental Research Park), SC (SRS, 80 000 ha; elevation, 20–130 m; MAP, 1225 mm; MAT, 18 °C; $n = 89$ sites) and Fort Stewart, GA (114, 000 ha; elevation, 2–56 m; MAP, 1220 mm; MAT, 19 °C; $n = 82$ sites). We used historical maps and aerial photographs from the time of public acquisition (1919 for Ft. Bragg, 1951 for SRS, 1947 for Ft. Stewart) to identify areas with agricultural land-use histories (i.e. former cultivated fields and improved pastures), as well as areas with no known history of cultivation (as in Brudvig & Damschen 2011). Although we distinguished between post-agricultural sites and savanna remnants, it is important to note that, like much of southeastern USA, all of our study sites (including the savanna remnants) have been influenced to varying degrees by a history of human land uses, including livestock grazing, resin extraction and logging by European settlers (Frost 1993) as well as fire management, megafaunal hunting and cultivation by Native Americans (Fowler & Konopik 2007). All potential sites supported mature overstorey trees, were at least 250 m apart, and covered ≥ 1 ha of relatively uniform habitat that did not cross topographical, hydrological or land-use boundaries. After identifying potential sites, we used annual prescribed fire records (available from 1991) to select sites that represented the range of fire frequencies at each location (Table 1); fire frequency is the number of fires that occurred at a site between 1991 and 2009.

Using a modified version of the sampling protocol developed by Peet et al. (1998), we conducted vegetation surveys from August–November 2009 within a 20×50 -m sampling plot that was randomly positioned within each site. We identified all plant species present within each of eight 1-m^2 subplots nested within the 20×50 -m plot and calculated the mean number of species per 1-m^2 subplot, including graminoids, forbs, shrubs and small trees (< 2.5 cm diameter at 1.37 m) rooted in or overhanging each subplot. We estimated the percentage cover of each species in the subplots and used the sum of all species cover values to determine total percentage cover per 1 m^2 . As indicators of O horizon development, we measured the depth of litter and duff in the centre of each of the eight subplots. To determine tree basal area, we measured the diameter of all trees ≥ 2.5 cm diameter at 1.37 m within the 20×50 -m plot. We used a spherical densiometer to estimate tree canopy cover at six points, spaced 10 m apart, along the centre line of the plot (Lemmon 1956). To assess water availability, a correlate of understorey diversity and site productivity (Kirkman et al. 2001) and tree growth rates (Grady & Hoffmann 2012), we extracted six 20-cm soil cores from each site and processed them following Brudvig & Damschen (2011) to obtain an estimate of moisture content at field capacity by mass. We also sent soil samples to Brookside Laboratories, Inc. (New Knoxville, OH, US) to determine soil organic matter (SOM, an indicator of post-agricultural soil conditions; Flinn & Marks 2007) and cation exchange capacity (CEC, an indicator of cation availability related to tree distributions and abundances in savannas; Hoffmann et al. 2009).

Statistical analyses

Using the meta-model as a guide (Fig. 1), we developed a structural equation model comprised of 11 observed variables (Table 1) and four latent variables (resource availability, tree abundance, understorey abundance and O horizon). Latent variables represent theoretical constructs that are not directly measured, but are inferred from measured (observed) variables. In our model, we specified the latent variables as combinations of one, two or three indicator variables. We inferred: (1) resource availability from soil moisture-holding capacity, SOM and CEC (interrelated variables that are indicators of water, nitrogen and cation availability, respectively); (2) tree abundance from basal area and canopy cover; (3) understorey abundance from total percentage plant cover; and (4) the O horizon from litter and duff depth. Before fitting the model, we inspected univariate distributions and bivariate relationships in the data (Grace 2006). It is common in SEM to explore relationships between key model variables (e.g. Harrison et al. 2006); we performed select regressions

using the `lm` function in R 2.15.1 (R Foundation for Statistical Computing, Vienna, AT). To meet assumptions of linearity and to correct skew, we applied a \log_{10} transformation to species richness and SOM. We fit the model in IBM SPSS Amos 20.0 (Amos Development Corp., Meadville, PA, US). To improve overall fit, we modelled several correlations that are due to unknown causes (Grace 2006; Table S2). To achieve an analysis that encompassed a wide range of conditions and that spanned regional gradients in edaphic factors that influence plant species richness, we combined data from all three study locations (Veldman et al. 2013).

Results

In bivariate analyses, fire frequency is positively correlated with species richness (Fig. 2a), and agricultural land-use history is associated with decreased richness (Fig. 2b). In a multiple regression, the main effects of these two factors combine to explain 31% of variance in species richness ($R^2 = 0.31$, $F = 56.0$, $df = 2$ and 253 , $P < 0.001$); additional factors are likely to be involved. Indeed, species richness is correlated with multiple variables related to resource availability (Fig. 3a), tree abundance (Fig. 3b), understorey abundance (Fig. 3c) and the O horizon (Fig. 3d). We use SEM to disentangle these interrelated variables (Fig. 4, Fig. S1).

The SEM provides a good fit to the data ($\chi^2 = 18.7$, $df = 23$, $P = 0.72$; saturated model $\Delta AIC = 17.3$), and explains 65% of the variance in understorey species richness ($R^2 = 0.65$; Fig. 4). The model is a good predictor of the O horizon ($R^2 = 0.55$), and explains a significant fraction of the variance in tree abundance ($R^2 = 0.20$) and understorey abundance ($R^2 = 0.21$). The model explains relatively little variation in resource availability ($R^2 = 0.07$). All modelled factors (i.e. fire frequency,

agricultural history, resource availability, tree abundance, understorey abundance and O horizon) contribute directly or indirectly to understorey plant species richness (Tables S3, S4 and Fig. 4). Thirteen of 16 hypothesized paths are statistically significant ($P < 0.05$; Table S3), although the strength of these relationships range widely (Fig. 4, Table S4).

The SEM shows that bivariate patterns of species richness in relation to fire frequency and agricultural history can be largely explained through indirect effects. For fire frequency, 70% of the total positive effect on species richness is through reductions in the O horizon, and 30% through reductions in tree abundance (Table S4). There is no significant direct effect of fire frequency on species richness or understorey abundance. Instead, fire frequency limits trees, which increases understorey cover and species richness (Fig. 4). Fire influences richness independent of vegetation structure (i.e. tree and understorey abundance) by limiting the development of the O horizon, a factor with strong negative effects on richness (Table S4, Fig. 4). For agricultural history, 51% of the total negative effect on species richness is explained through increased tree abundance, 10% through decreased resource availability and 38% through direct negative effects (Table S4, Fig. 4).

In addition to fire frequency and agricultural history, the model reveals the influences of other biophysical factors on species richness. The relationship between resource availability and species richness is complex, with both strongly positive effects and indirect negative effects due to increases in tree abundance (Table S4, Fig. 4); when these contrasting effects are combined, the total effect of resource availability on richness is weakly positive (Table S4). Understorey abundance, which is completely controlled by resource availability and tree abundance, is a strong predictor of species richness (Table S4, Fig. 4). The O horizon, which was controlled by fire frequency and tree

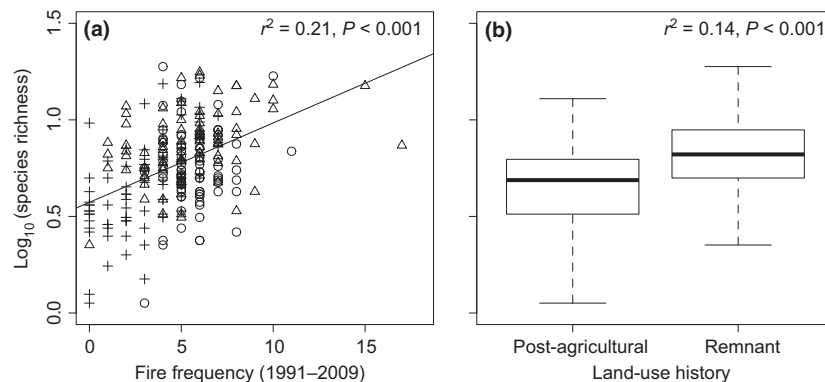


Fig. 2. Species richness in relation to (a) fire frequency and (b) agricultural land-use history. Symbols correspond to study locations: Fort Bragg, \circ ; Fort Stewart, Δ ; and Savannah River Site, $+$. The boxplots display quartiles.

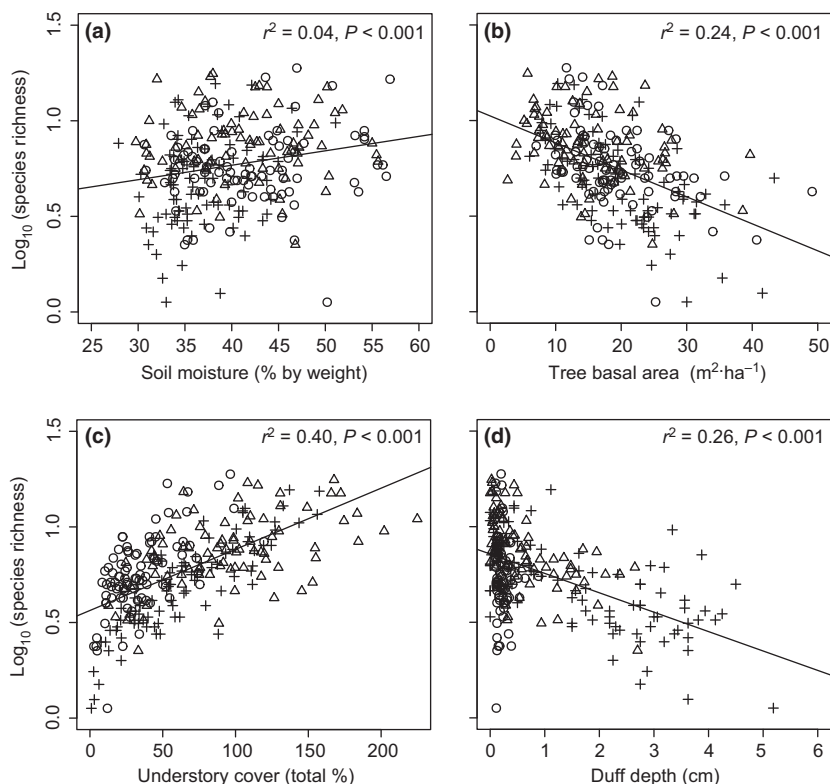


Fig. 3. Bivariate scatter plots of species richness and select measured variables. In the SEM, (a) soil moisture holding capacity, (b) tree basal area, (c) understory plant cover and (d) duff depth contribute to the latent variables: resource availability, tree abundance, understory abundance and O horizon, respectively. Symbols correspond to study locations: Fort Bragg, ○; Fort Stewart, △; and Savannah River Site, +.

abundance, has a strong direct negative effect on richness (Table S4, Fig. 4). Contrary to our hypotheses, there are no direct effects of fire frequency on understory abundance or richness, and no direct effect of the O horizon on understory abundance (Table S3, Fig. 4).

Discussion

In pine savannas of the southeastern United States, fire exclusion and agricultural land-use history are associated with decreased understory plant species richness (Fig. 2; Walker & Silletti 2006). Our results provide mechanistic insight into these relationships by modelling direct and indirect effects among multiple factors that are thought to broadly influence plant diversity in savanna ecosystems, including: resource availability, tree abundance, understory abundance and the O horizon. Our study presents the first model of its kind for savannas anywhere in the world. The SEM analytical framework enables us to explore the controls over savanna understory plant diversity in a way that would be difficult or impossible with other statistical approaches or manipulative experiments (Grace 2006). Our model incorporates indirect effects, includes many

interrelated variables, uses data that cover wide biophysical gradients and a large geographic region, and includes information on site history that is not available for most study systems. The similarities between the fitted model and the *a priori* meta-model suggest that in combination, decades of fire research in pine savannas, ecological theory on grass–tree co-existence, and previous studies of agricultural legacies in a variety of systems have given us a good understanding of the factors that control understory plant species richness. Nonetheless, some unexpected results did emerge. We find no direct effect of fire frequency on either species richness or understory abundance; all positive effects of fire on the understory are mediated by tree abundance and the O horizon.

A history of agriculture is an important determinant of plant community composition and diversity in many ecosystems (e.g. Flinn & Vellend 2005), including pine savannas (Hedman et al. 2000; Kirkman et al. 2004). Our results suggest that post-agricultural sites have reduced species richness compared to savanna remnants for three reasons. First, intensive agriculture appears to constrain richness by depleting soil resource availability (Fig. 4; Flinn & Marks 2007). But because a reduction in resources

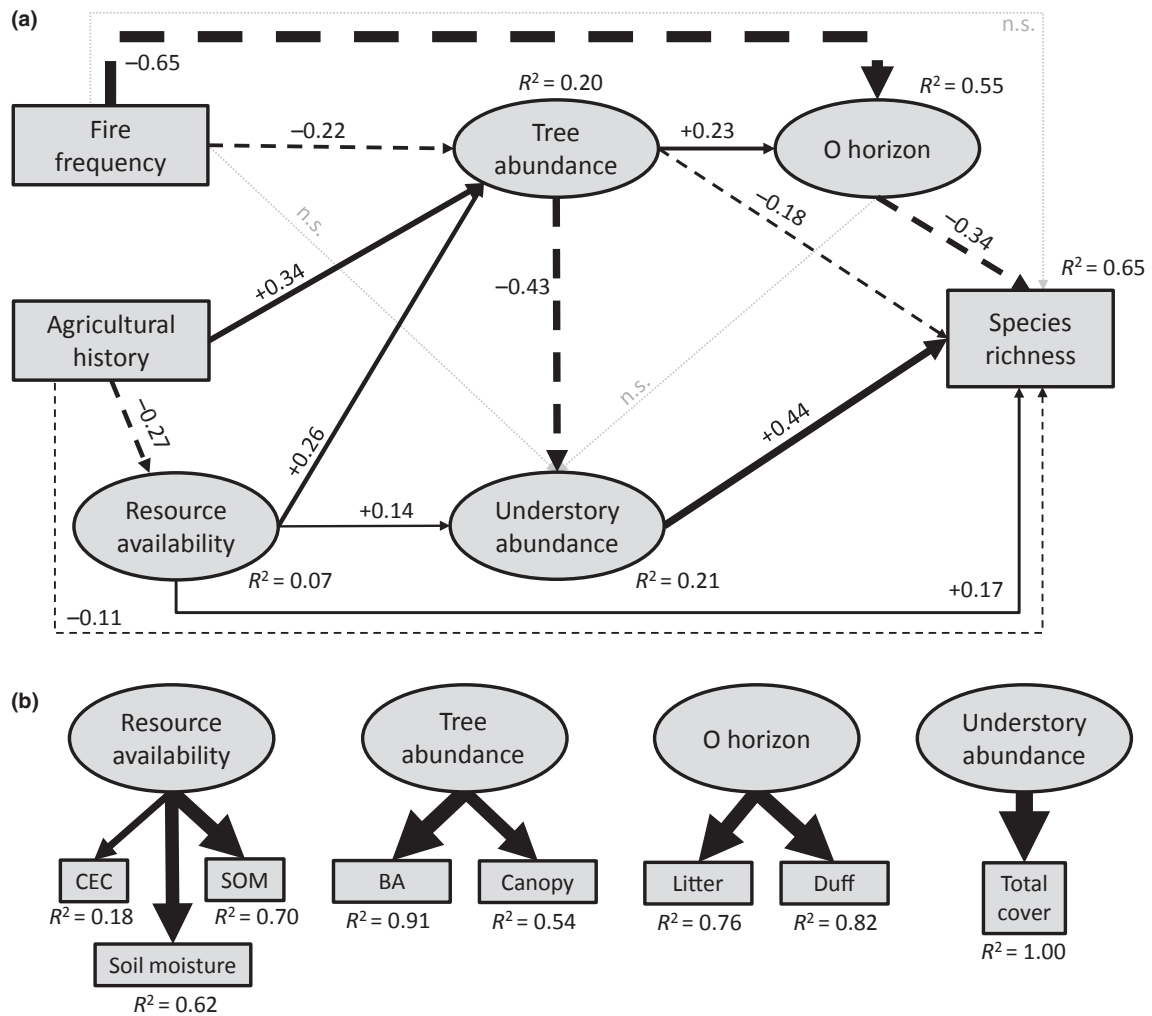


Fig. 4. Results of the structural equation modelling: **(a)** path diagram of relationships among the main variables of interest, and **(b)** the structure of the latent variables. Rectangles represent observed (measured) variables; ovals represent latent (unmeasured) variables that are inferred from observed variables. Arrows indicate the hypothesized direction of influence, with positive and negative relationships indicated by solid and dashed lines, respectively. The thickness of each significant ($P < 0.05$) path is scaled to the strength of the correlation (i.e. the standardized effect); thin grey arrows indicate modelled (hypothesized) paths that were not significant. CEC, cation exchange capacity; SOM, soil organic matter; BA, tree basal area; Canopy, tree canopy cover; n.s., not significant.

can also constrain tree abundance, the overall effect of agricultural history on richness mediated by resource availability is modest (10% of the total effect, Table S4; see discussion on resource availability below). The consequences of altered biophysical conditions (e.g. reduced soil organic matter) on post-agricultural land can be quite different in savannas, where diversity is heavily influenced by tree–understorey interactions, compared to grasslands and forests (e.g. Baer et al. 2003; Plue et al. 2008). Second, agricultural history reduces richness by increasing tree abundance. We suspect that this effect represents the legacy of post-agricultural tree community succession and historic fire exclusion (before 1991) not captured in our fire data. In the initial years following abandonment, old

fields may have been less likely to burn compared to savanna remnants and thus developed dense stands including fire-intolerant tree species (Heyward 1939; Frost 1993) that inhibit the spread of fire (Kane et al. 2008; Kreye et al. 2013). Additionally, if old fields were preferentially managed for timber, fire suppression would have been incentivized (Frost 1993), resulting in high tree abundances and low species richness on post-agricultural sites. Such a relationship between past land use and fire frequency may still be evident in contemporary prescribed fire management; we model a weak, marginally significant correlation between contemporary fire frequency and agricultural history (Table S2). The SEM accounts for this correlation, but the relationship needs further investigation.

Finally, there is a direct negative effect of agricultural history on richness. Statistically, this direct effect represents covariance not explained through other model variables and, as such, does not reveal a specific mechanism. Nonetheless, we suspect that this direct negative effect represents a combination of dispersal limitation and successional time, influenced by the degree of spatial isolation of post-agricultural sites from savanna remnants (Kirkman et al. 2004; Brudvig & Damschen 2011). This hypothesis would be consistent with Verheyen et al. (2003) and Vellend (2003) who conclude that forest colonization by understorey herbs is strongly influenced by distance from seed sources and forest age, with effects on plant communities persisting for at least 195–350 yr after agricultural abandonment. For long-lived fire-adapted savanna grasses, forbs and shrubs that are poor colonizers (Kirkman et al. 2004) and do not form persistent seed banks (Cohen et al. 2004), savanna plant community recovery following agricultural abandonment is slow in the absence of intensive restoration efforts (e.g. seeding or seedling transplants).

Fire frequency is correlated with species richness in many fire-dependent plant communities, including our study system (Fig. 2a). Our results suggest that frequent fires promote plant diversity by preventing trees from reaching sufficient abundance to limit understorey plant cover and species richness (Fig. 4; Peterson & Reich 2008). As such, fire may be viewed as a factor that limits the growth of dominant competitors (e.g. forest trees; Hoffmann et al. 2009) and indirectly favours fire-adapted understorey plants (Cavender-Bares & Reich 2012). There are a number of mechanisms by which fire might directly promote richness (e.g. through reduced competition among understorey plants; Myers & Harms 2009), but such effects were not detected in our model. If a direct effect of fire on the understorey exists, it may be more important to community composition than to richness, or may be more related to other aspects of fire regimes such as season of burn or variation in fire-return interval (e.g. Brewer et al. 2009).

In addition to limiting tree abundance, fire also promotes richness by reducing the O horizon. O horizon development, caused by fire exclusion and high tree abundance, is thought to be a primary factor limiting understorey plant communities in our study system (Hiers et al. 2007), but the effects of the O horizon have not previously been examined at a regional scale or in concert with other factors in our model. For example, our model, which separates understorey cover and species richness, suggests that the O horizon is a strong filter on communities, directly limiting the number of species without influencing understorey abundance; previous studies had not made this distinction (e.g. Hiers et al. 2007). The linkages between fire

exclusion, increased abundance of fire-intolerant trees, and decreased plant diversity are well documented for many open-canopied ecosystems (Ratajczak et al. 2012), but the potential role of the O horizon is often neglected (Fridley et al. 2012). Fire-intolerant, mesophyllitic, forest trees appear to be particularly important contributors to the O horizon because they produce low-flammability leaf litter that can impede the spread of fire (Kane et al. 2008). To keep our model tractable, we do not distinguish between tree functional groups that are thought to differ in the strength of their negative relationships with understorey plants (Veldman et al. 2013). More work is needed to fully understand the relationships between tree community composition, litter characteristics, ecosystem flammability and understorey plant diversity (Trauernicht et al. 2012; Kreye et al. 2013; Veldman et al. 2013).

Vegetation structure figures prominently in ecological theory of grass–tree co-existence, vegetation–fire feedbacks and savanna–forest distributions (Hoffmann et al. 2012a; Murphy & Bowman 2012). In our model, we depict vegetation structure as two separate factors: tree abundance and understorey abundance. Numerous studies have concluded that tree abundance controls savanna understorey species richness (e.g. Beckage & Stout 2000; Platt et al. 2006), but typically without considering the role of understorey abundance. Our results suggest that both tree abundance and understorey abundance are important determinants of understorey species richness (Weiher 2003; Grace et al. 2011) that mediate the effects of fire frequency, agricultural history and resource availability. We expected to see direct positive effects of fire frequency on understorey abundance (Fig. 1); instead, all effects of fire on understorey abundance are mediated by tree abundance (Fig. 4). In our model, which is static and hierarchical (i.e. lacking looping paths and feedbacks), trees exert a negative effect on understorey abundance. We should expect that in a model that incorporates vegetation–fire feedbacks, understorey plant abundance would have a negative influence on tree abundance by increasing fuel loads and fire intensity (Gilliam et al. 2006; Beckage et al. 2009). Although such feedbacks are potentially important, our model confirms that a focus on tree abundance, a dominant paradigm in savanna ecology (e.g. Sankaran et al. 2005), can be both predictive and ecologically meaningful for understanding other important parameters of savanna ecosystems (e.g. understorey abundance, species richness, O horizon development). Given the dynamic nature of savanna ecosystems, our approach is just one of many ways to look at causal relationships among multiple variables that influence plant diversity.

As hypothesized, understorey abundance is a strong predictor of species richness (Table S4, Fig. 4) and a critical factor that links fire frequency, agricultural history, soil

resources and tree abundance with species richness. The concept of a causal relationship between plant diversity and measures of abundance, biomass or productivity has existed for several decades (Grime 1973). Although once assumed to be unimodal, bivariate productivity–diversity relationships in grasslands without trees may assume many different forms, including positive linear (Adler et al. 2011). When considering productivity–diversity relationships in savannas, it is important to note that biomass is not limited to understorey plants, but is partitioned between overstorey trees and understorey plants (House et al. 2003); where tree biomass is high (as in fire-excluded savannas), understorey cover and diversity decline (Veldman et al. 2013). Biomass also accumulates in the O horizon and is thus another carbon pool that should be factored into studies of these relationships (Fridley et al. 2012).

Resource availability plays a complex role in the regulation of understorey species richness, involving relationships that are obscured in bivariate analyses. In the sandy soils of the southeastern USA, small differences in organic content and moisture-holding capacity (which is related to SOM, silt and clay content; Salter & Williams 1967) are thought to influence understorey productivity and diversity (Kirkman et al. 2001) as well as tree distributions (Goebel et al. 2001). In our model, the total effect of resource availability on species richness is weakly positive, but the role of resource availability is complicated because it includes both positive and negative effects (Table S4). Favourable resource conditions promote species richness directly and indirectly through understorey abundance, but these positive effects are offset by the contribution of soil resources to trees, which compete with understorey plants and contribute to O horizon development. These results are consistent with a wider body of literature on the interactions of resource availability, tree growth, grass abundance and fire in savannas: on high resource sites, frequent fires are required to limit trees, prevent closed-canopy forest development and maintain a grassy understorey (Lehmann et al. 2011; Hoffmann et al. 2012a; Murphy & Bowman 2012). Our study shows how these same factors are causally linked to understorey plant diversity and are influenced by agricultural land-use history.

Conclusion

This study demonstrates how multiple factors influence local-scale plant species richness in pine savannas and details specific indirect effects of fire frequency and agricultural land-use history on plant diversity. By bringing together biophysical variables that had not previously been incorporated in a single model, this study improves our understanding of how multiple factors (which are often examined independently) may limit the recovery of

species-diverse savanna plant communities in post-agricultural landscapes. Given the many obstacles to recovery, conservation efforts should prioritize the protection of savannas that have never been cultivated and maintain historic fire regimes through prescribed fire and wildfire. Where restoration efforts are undertaken, manipulation of several ecosystem attributes (i.e. fire regimes, soils, tree abundances, O horizon depth and propagule dispersal) may be necessary to facilitate understorey plant diversity.

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Supporting Information

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

Appendix S1. Theoretical basis for the hypothesized relationships in the meta-model.

Table S1. Examples of studies on savanna understorey plant species diversity.

Table S2. Summary of modeled correlations.

Table S3. Unstandardized path coefficients for hypothesized causal relationships.

Table S4. Direct, indirect, and total standardized effects on species richness.

Fig. S1. Bivariate relationships between variables that mediate the influence of fire frequency and agricultural history on species richness.