Drivers of plant functional group richness and beta diversity in fire-dependent pine savannas

Johanna E. Freeman1,2 | Leda N. Kobziar3 | Erin H. Leone1 | Kent Williges1

1Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida
2School of Forest Resources and Conservation, University of Florida, Gainesville, Florida
3Department of Natural Resources and Society, University of Idaho, Moscow, Idaho

Correspondence
Johanna E. Freeman, Lovett E. Williams Jr. Wildlife Research Laboratory, 1105 SW Williston Road, Gainesville, FL 32601. Email: Johanna.Freeman@MyFWC.com

Funding information
U.S. Joint Fire Science Program, Grant/Award Number: 14-3-01-43

Abstract
Aim: To assess the drivers of plant functional group richness and beta diversity in fire-maintained North American Coastal Plain (NACP) savannas.

Location: The southern portion of the NACP, a global biodiversity hotspot. This region is characterized by fire-dependent pine savanna fragments that are isolated within a matrix of agriculture, urban development, non-pyrogenic plant communities and plantation forestry.

Methods: We used nested quadrats to sample plant species on 30 fire-maintained savanna preserves in Florida and Georgia, USA. We analysed between-site Sørenson dissimilarity, a measure of beta diversity, using NMDS and PerMANOVA. We measured nestedness using NODF, and we used Betapart to partition Sørenson dissimilarity into nestedness and turnover components. We used linear and generalized linear mixed models to explore drivers of functional group richness and composition, including fire regime (return interval, number of fires, time since fire and seasonality), vegetation structure (herbaceous cover, woody cover and tree density) and spatial factors (surrounding landscape and geographic distance).

Results: We found turnover-dominated beta-diversity patterns in all functional groups. Turnover was explained partly by spatial and environmental gradients, but roughly half of the turnover between sites was unexplained. Species richness was higher on sites where fire and fire surrogates had been used longer and more consistently, and these effects were partly independent of current vegetation structure. Fire regimes containing more growing season fire and more diversity of burn seasons promoted higher species richness. Relationships between small-scale and large-scale species richness varied by soil type and functional group.

Main conclusions: Fire-maintained savannas in the southeastern NACP vary greatly in their plant functional group richness, but high beta diversity resulting primarily from species turnover suggests that even species-poor sites can harbour less-common members of the regional plant metacommunity. Prescribed fire regimes that include growing season fire as well as a diversity of burn seasons may best promote species and functional group richness.
INTRODUCTION

The North American Coastal Plain (NACP), a global biodiversity hotspot due to its high vascular plant diversity and endemism, is a fire-prone region in which conservation depends upon the widespread application of prescribed fire to maintain native savanna and grassland biodiversity (Noss et al., 2015). At last count, over three million hectares of NACP savanna were in active prescribed fire rotation (Mitchell & Duncan, 2009), representing a massive ecosystem management achievement following decades of anthropogenic fire suppression (Van Lear, Carroll, Kapeluck, & Johnson, 2005). The reintroduction of fire has yielded a regional landscape dotted with fire-maintained savanna fragments. Many studies have provided valuable information about the factors affecting within-preserve plant species diversity and composition (i.e., fire frequency, land use history, hydrologic and soil gradients, and overstory-understory relationships) (Glitzenstein, Streng, Masters, Robertson, & Hermann, 2012; Kirkman, Mitchell, Helton, & Drew, 2001; Platt, Carr, Reilly, & Fahr, 2006; Veldman et al., 2014), but data on plant diversity patterns at the regional metacommunity level are lacking. With so many savanna preserves in the NACP now returned to a fire-maintained grass-tree structure, expanding to metacommunity-level biodiversity questions is timely.

Regional approaches to biodiversity conservation are increasingly recommended for stemming global biodiversity loss in the face of accelerating anthropogenic change (Socolar et al., 2016). Fire-dependent NACP savanna plant communities exist within a largely inhospitable matrix of agriculture, plantation forestry, fire-impeding hardwood forest, wetlands, water bodies and urban development, wherein only a small proportion of native savanna species are found (Brudvig & Damschen, 2011; Freeman, Williges, Gardner, & Leone, 2017; Volk et al., 2017). As such, island biogeography concepts are a useful framework for understanding large-scale biodiversity patterns in this region. One such concept is beta diversity, the component of species diversity that accumulates due to site-to-site differences in local species assemblages (Socolar et al., 2016).

Two patterns of beta diversity with profound implications for conservation are turnover (species present at one site are absent at another, but are replaced by other species absent from the first) and nestedness (species present at one site are absent at another, but are not replaced by other species, resulting in smaller assemblages that are nested subsets of larger assemblages) (Baselga, 2010). In landscapes with high species turnover, biodiversity is best conserved by protected area networks that capture the full range of variation within a metacommunity, a conservation strategy that may necessitate protecting smaller and/or more species-poor sites alongside larger and/or richer ones (Socolar et al., 2016). In contrast, networks with high nestedness may benefit from conservation strategies that focus resources on fewer, higher-diversity sites (Socolar et al., 2016).

A related aspect of plant community composition with regional biodiversity implications is the relationship between species richness at small and large scales. Small-scale (<1 m$^2$ quadrat) species richness has been a topic of interest among those researching NACP savannas as the first modern plant surveys documented very high plant species richness at these scales (Walker & Peet, 1984). Small-scale richness has been posited as an important conservation target in NACP savannas due to the possibility that species loss at small scales could be a leading indicator of population declines at the whole-preserve level, raising the risk of local extirpation (Glitzenstein et al., 2012; Palmquist, Peet, & Weakley, 2014).

In addition to scaling up to broader spatial perspectives, longer temporal perspectives may also help reveal previously unrecognized patterns and help inform conservation priorities. This is particularly true with respect to the study of fire regime-biota interactions, which are scale- and context-dependent, with outcomes that may only become apparent after many repeated fire cycles (Driscoll et al., 2010; Westgate, MacGregor, Scheele, Driscoll, & Lindenmayer, 2018). Due to the fire-dependent and relatively productive nature of NACP savannas, woody encroachment during the period of intense anthropogenic fire suppression (from the 1930s to the 1990s) was nearly ubiquitous within relic savanna fragments (Heyward, 1939; Van Lear et al., 2005). Managing agencies have since had widespread success in re-establishing the grass-tree vegetation structures thought to be representative of the historical reference condition, through frequent fire and accompanying mechanical and chemical woody reduction treatments. Many savanna preserves throughout the region now experience frequent (<5-year return interval) prescribed fire regimes (Kobziar, Godwin, Taylor, & Watts, 2015), but little is known about the lasting effects of past fire suppression and landscape fragment isolation on the plant species composition of savanna preserves, or how these individual species assemblages fit into the larger regional plant metacommunity.

Like all aspects of fire regime research, understanding the effects of seasonality requires study over long timescales and a variety of contexts. Fire seasonality may have important effects on plant species composition in NACP savannas, as repeated early- and mid-growing season fires result in greater woody mortality and growth reduction (Hmilewski, Robertson, & Platt, 2014), much less vigorous woody resprouting (Drewa, Platt, & Moser, 2002) and higher flowering and seed germination rates among native herbaceous species (Shepherd, Miller, & Thetford, 2011; Streng, Glitzenstein, & Platt, 1993). It has been hypothesized that there may be widespread, undocumented plant adaptations to fires conducted during the months of greatest lightning and wildfire activity (May and June), which is thought by some to constitute the “natural” or pre-anthropogenic...
fire season to which native species would have adapted (Frost, 2006). Fire season variation has also been identified as a potentially important component of conservation strategies, due to phenological differences between species (Hiers, Wyatt, & Mitchell, 2000; Knapp, Estes, & Skinner, 2009), but no studies have examined the plant community effects of NACP savanna fire regimes that are seasonally variable within the same spatial extent.

In this study, we explored fire regime, spatial and vegetation structural drivers of beta diversity and species richness in NACP savannas, focusing on functional groups known to be important for grassland and savanna productivity and biodiversity. NACP savannas are low-N systems, in which some of the most important plant traits with regard to ecosystem functioning are related to N-cycling and availability (Kirkman et al., 2001; Reich et al., 2012). Studies in North American tallgrass prairie communities, which are phylogenetically and functionally similar to NACP savannas, have shown that C_3 graminoids, C_4 graminoids, legumes and non-leguminous forbs exhibit complementarity in root depth distribution and N-acquisition traits, and productivity is maximized when all four of these functional groups are present and species richness within groups is highest (Fargione, Brown, & Tilman, 2003; Fornara & Tilman, 2009; Reich et al., 2012). Woody species are also prominent members of NACP savanna assemblages, which likely add more complexity to the root depth and N-acquisition spectrum, and which have unique direct and indirect relationships with fire regime and understory plant diversity (Veldman, Mattingly, & Brudvig, 2013). We examined functional group richness and beta-diversity patterns within C_3 graminoid, C_4 graminoid, legume, non-leguminous forb (hereafter “forb”), shrub and tree assemblages across a regional sample of 30 different fire-managed savanna preserves in Florida and Georgia, USA. We hypothesized that functional group richness and composition would vary between sites and that some of this variation would be explained by fire regime (return interval, number of fires, time since fire and seasonality), vegetation structure (herbaceous cover, woody cover and tree density) and spatial factors (composition of the surrounding landscape and distance between sites). The scope

**FIGURE 1** Locations of the study sites in Florida and Georgia. The subregions (GA south, FL north, FL panhandle and FL central) correspond with differences in mean annual temperature and precipitation due to peninsular climate patterns (PRISM, 2018), which are described further in Appendix 2. The inset map shows the location of the study area within the North American Coastal Plain floristic province.
of the study also allowed us to test the hypothesis that small-scale richness and whole-site species richness are correlated, both overall and within functional groups.

2 | METHODS

2.1 | Study sites

We sampled the understories of 30 fire-maintained savannas in north Florida and south Georgia, all of which are managed with biological conservation as either a primary or secondary goal (Figure 1: Appendix 1). Though the longer-term natural and fire history details of any given preserve vary widely, most agencies in the region have been working to implement 2- to 4-year fire return intervals for the past 10–25 years (Kobziar et al., 2015). We sought study sites with little to no history of agriculture other than native range grazing, or forestry practices other than tree removal, as the legacies of more intensive agricultural and forestry activities are known to be associated with novel communities in this region (Brudvig, Grman, Habeck, Orrock, & Ledvina, 2013; Freeman, Kobziar, Rose, & Cropper, 2017).

We evaluated these criteria through communication with managing agencies, historical aerial photographs and the presence of indicator species associated with old-growth sites that have not experienced soil disturbance (primarily wiregrass, Aristida stricta Michx., as well as various Asteraceae, Fabaceae and Ericaceae species) (Kirkman, Coffey, Mitchell, & Moser, 2004). We also sought sites that had undergone at least three documented fire and/or fire surrogate (mechanical or chemical) treatments, and all but one of the sites met this criterion (the only exception was Osceola National Forest, which was later determined to have had only two recorded treatments). Exotic and weedy species were all but absent from the study sites, which generally typify old-growth savanna communities (sensu Veldman et al., 2015) subjected only to fire suppression.

2.2 | Field sampling methods

The study sites were sampled using a nested quadrat sampling design, a modified version of the methods of Peet, Wentworth, and White (1998). At each study site, five randomly placed 10 m × 10 m (100 m²) species–area sampling modules were established. Sampling modules were placed at least 50 m from one another and 20 m from roads or other boundaries. Nested in one corner of each 100 m² module were 10, 1 and 0.1 m² quadrats. Understory species presence/absence was recorded in all quadrats, and percentage cover to the nearest 5% was recorded in the two smallest quadrats. We classified all understory species by functional group (C₃ graminoid, C₄ graminoid, forb, legume, shrub, tree). C₃ and C₄ graminoid classifications followed Waller and Lewis (1979) and Bruhl & Wilson (2007). Overstory tree data were collected in the north-west corner of each 100 m² module using the point-centred quarter method, from which tree density was then calculated. Field data collection occurred during fall 2014 and fall 2015.

To the greatest extent possible, we located each five-module sampling array within a single burn unit at each preserve, so that all five of the sampling modules shared the same fire and management history. Sampling sites were approximately 9 ha on average, though they varied in shape and size somewhat depending on the shape and size of the surrounding burn unit. At three preserves (Pt. Washington, Bell Ridge and Half Moon), it was necessary to locate sampling modules across more than one burn unit because of size constraints, but in these cases, the units shared the same recorded treatment history.

2.3 | Site histories

Fifty-year fire and management histories for the sampling sites (including dates and descriptions of all known fires and fire surrogate treatments) were collected via detailed questionnaires distributed to the managing agencies. In six cases, personnel reported that burning had occurred prior to their agency’s acquisition of the land and/or prior to the advent of consistent recordkeeping, but they did not have specific dates or details about the fires. When constructing the 50-year fire histories for the sites in question, we added a single
placebo fire to the record in the appropriate decade. The quality of record was much better for the 25-year histories (only one agency noted unrecorded fires during that period), and the 10-year histories contained no omissions.

2.4 Spatial and landscape factors

We stratified the study sites into three soil types, all of which are common NACP savanna substrates, and which are characterized by markedly different plant community compositions (Peet, 2006): Spodosols (mesic/wet sands, known regionally as flatwoods)—12 sites; Entisols (xeric/extremely xeric sands, known regionally as sandhills)—12 sites; and Ultisols (mesic sandy loams, known regionally as clayhills)—six sites. The study area can be roughly divided into subregions (GA south, FL north, FL panhandle and FL central) corresponding with differences in mean annual temperature and total precipitation (PRISM, 2018) (Figure 1; Appendix 2). The somewhat disjunct distribution of study sites reflects the topography, geologic history and agricultural development patterns of the region, as well as the availability of sites meeting our study criteria.

We collected data on the geographic distances between sites and the landscape composition surrounding sites using the open-access Florida Geographic Data Library and the Georgia GIS Clearinghouse (FGDL, 2016; GGISC, 2016) and derived the relevant parameters in ArcMap 10.3 (ESRI, 2014). For each study site, we created 500- and 1,000-m-radius landscape buffers and calculated the area within each buffer belonging to vegetation types the same as, or very similar to, those of the sample site. For the Florida sites, we used the most recent Florida Land Use and Cover vector shapefiles (FGDL, 2016). These shapefiles classify plant communities and land uses according to the Florida Land Use Cover Class System (FLUCCS), which is a three-tiered classification system that includes specific habitat types (i.e., hydric pine savanna and xeric pine-oak woodland). For the Georgia sites, we used the Georgia Land Use Trends (GLUT) 2008 Land Use Cover raster dataset (GGISC, 2016). The GLUT land cover categories are much broader than the FLUCCS categories (i.e., evergreen forest and woody wetlands), but were descriptive enough to allow us to roughly calculate the area of each buffer in similar natural vegetation types.

2.5 Analysis of functional group richness

We developed generalized linear mixed models using PROC GLIMMIX in SAS v9.4 (SAS Institute, Inc. 2013) to explore the influence of fire regime, spatial and vegetation structure variables on functional group richness. From the fire history questionnaires, we developed a variety of quantitative fuel treatment history parameters, based on histories dating back to 1965 (approximately 50 years from the time of data collection). We began with eleven fire regime variables as potential predictors of functional group richness: total number of fires over 50 years, total number of fire surrogate treatments over 50 years, total number of fire + fire surrogate treatments (weighted equally) over 50 years, mean fire-only intervals over the past 10, 25 and 50 years, mean fire + fire surrogate intervals over the past 10, 25 and 50 years, number of years in active fire rotation and time since fire on the date the data were collected. We began with five landscape/vegetation variables: number of hectares in same/similar community within 500- and 1,000-m-radius landscape buffers, overstory tree density (trees/ha), percentage shrub cover and percentage herb cover. We included "site" as a random factor in all models and dropped non-significant variables from the models sequentially, in order of least significance, until the lowest AIC was achieved. We calculated the amount of variance explained by each model ($R^2$) using the method of Nakagawa & Schielzeth (2013).

In a separate set of generalized linear mixed models, we analysed the effects of fire seasonality since 1990 (the 25-year period of record), dividing the year into five fire seasons that reflect the climate and plant phenology in the south-eastern portion of the NACP: dormant season (months 11–2, November–February), very early-growing season (months 3–4, March–April), lightning season (months 5–6, May–June), middle-growing season (months 7–8, July–August) and late-growing season (months 9–10, September–October). This analysis was conducted only for Entisol and Spodosol sites because of missing seasonality data for a number of the Ultisol sites and only for the 25-year period of record because of too much missing seasonality information in the 50-year records. We calculated the number of fires that had occurred in each of the five fire seasons on each site (Appendix 3) and compiled the following variables: diversity of seasons (calculated using the Shannon–Weiner diversity index), number of growing season fires (months 3–10) and number of lightning season fires (months 5–6). We also included three of the non-seasonal fire variables in order to disentangle the influences of frequency and seasonality: total number of fire and fire surrogate treatments over the past 25 years, mean fire interval over the past 25 years and time since fire. We began each model with all of the variables, their soil interactions and “site” as a random factor. We dropped variables from the models in order of least significance until the lowest AIC was achieved for each functional group and then calculated the total amount of variance explained by each model (Nakagawa & Schielzeth, 2013).

2.6 Analysis of beta diversity

We analysed site-to-site dissimilarity, a measure of beta diversity, between functional group and overall species assemblages in PC-ORD version 7 (McCune & Mefford, 2016). We used non-metric multidimensional scaling (NMS) to ordinate the 100 m$^2$ module data using a Sørensen distance measure (Sørenson, 1948). For the NMS ordination and PerMANOVA, species within each 100 m$^2$ module were given weighted presence/absence values based on the number of nested quadrat scales at which they occurred (1, 2, 3 or 4). We used PerMANOVA and multivariate pairwise comparisons in PC-ORD, also with a Sørensen distance measure, to test for significant differences in community composition between sites (both overall and within functional groups). We used a Benjamini–Hochberg
correction at a false discovery rate of 0.05 to adjust for multiple site-to-site pairwise comparisons.

We performed nestedness analysis using vegan (Oksanen et al., 2013) in R (R Core Team, 2017), with the NODF metric (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). We tested the NODF results for significance using the Tuning Peg null model R program (Strona, Ulrich, & Gotelli, 2018), which generates results from 100 null models offering all possible types of row and column constraint, from fully constrained (FF), to partially constrained (PP), to fully unconstrained. FF is the most conservative null model with respect to type I error (falsely detecting nestedness), but has a somewhat higher likelihood of type II error (failing to detect nestedness in a truly nested matrix), while the converse is true for the PP null model (Ulrich & Gotelli, 2012). We report p-values from the fully constrained FF model alongside four incrementally less-constrained null models that lie in the most accurate region of null model space between FF and PP.

We used Betapart (Baselga & Orme, 2012) in R to disentangle the influences of nestedness and turnover on beta diversity, since most real-world metacommunities are characterized by a mix of both patterns (Baselga, 2010). Betapart partitions the Sørenson distance ($\beta_{S\text{OR}}$, which ranges from 0 to 1) into two additive components, $\beta_{S\text{IM}}$ (Simpson dissimilarity, i.e., turnover) and $\beta_{S\text{NE}}$ (nestedness). These two additive metrics are not direct measures of turnover or nestedness, but rather account for the relative contributions of each phenomenon to the observed overall beta diversity (Baselga, 2010). It is therefore possible for $\beta_{S\text{NE}}$ to be low even when NODF detects significant nestedness, due to a larger turnover component ($\beta_{S\text{IM}}$) in the matrix (Baselga, 2010).

$\beta_{S\text{NE}}$ (also denoted $\beta_{S\text{ES}}$ in some publications) has an inconsistent and somewhat non-intuitive relationship with absolute nestedness, which is measured most reliably by NODF, and as a result the metric has generated criticism (Almeida-Neto, Frensel, & Ulrich, 2012). The biggest weaknesses of the $\beta_{S\text{NE}}$ metric arise when comparing matrices of unequal sizes and in certain limited cases where $\beta_{S\text{NE}}$ can yield false positives (Almeida-Neto et al., 2012; Baselga, 2012). As we were not comparing $\beta_{S\text{NE}}$ between matrices (rather we assessed nestedness and turnover within each functional group × soil matrix separately), and could use NODF results as a benchmark to protect against $\beta_{S\text{NE}}$ false positives, we found the $\beta_{S\text{OR}} = \beta_{S\text{IM}} + \beta_{S\text{NE}}$ calculation provided by Betapart, as well as site-to-site pairwise comparisons (\$\beta_{S\text{OR}} = \beta_{S\text{IM}} + \beta_{S\text{NE}}\$), to be a useful complementary technique. We focused the pairwise analysis primarily on the forb functional group, which is of particular interest because much of the plant diversity of NACP savannas lies in this group and it is among the most vulnerable to species loss via fire suppression (Peet, 2006).

In order to identify drivers of beta diversity, we analysed unfolded Sørenson distance matrices using linear mixed models in the R package lme4 (Bates, Maechler, Bolker, & Walker, 2015). We calculated the Euclidean distance (in km) between sites, as well as the difference between pairs in the following environmental variables determined to be important in the functional group richness models: 25-year fire/fire surrogate total, diversity of seasons, time since fire and 500-m-radius landscape buffer composition. We built linear mixed models to estimate the proportion of variability explained in the Sørenson distances according to the different sources. We included each site in the pair (i.e., site 1 and site 2) as random effects in the models. To estimate the proportion of variation explained we built a null, or intercept-only model (including the random variables), for each soil type. We then built a space, environment and global (i.e., space + environment) model. We calculated pseudo-$R^2$ based on the proportion of total variance the null model explained compared to the space, environment and global model (Feng, Diehr, Peterson, & McLerran, 2001).

We used Mantel correlograms to quantify the spatial structure in the Sørenson distance matrices, following the geographic lag class method described in Lichstein (2007). We tested for autocorrelation between 100 m² modules within different distance classes, the first of which (class 1, 1 km) represents within-site comparisons. The remaining distance lag classes increased by roughly 100-km increments, with some variation in increment size among the different soil types due to the irregular spatial distribution of study sites. Mantel tests were calculated in PC-ORD between each functional group/soil type Sørenson distance matrix and each binary geographic lag class matrix, yielding a standardized Mantel statistic (r) that was then tested for significance using a permutation test with 2,000 iterations and a Bonferroni correction.

2.7 Analysis of small-scale versus large-scale richness

We conducted linear regressions between whole-site species richness and richness at the 0.1, 1, 10 and 100 m² levels, in order to determine the degree of correlation between small-scale and whole-site richness.

3 RESULTS

3.1 Patterns and drivers of functional group richness

We found pronounced differences in functional group richness between sites. Whole-site species richness (the cumulative number of species found across all five sampling modules at each site) varied widely, and the richest sites with respect to any given functional group typically contained anywhere from two to five times more species per functional group than the poorest sites (Table 1).

The final generalized linear mixed model parameters for functional group richness varied by functional group, and there were many significant soil interactions (Table 2). Appendix 4 contains the means and 95% confidence intervals for all species richness parameters used in the GLMMs. For all functional group models, the lowest AICs were achieved with the parameters that gave fire and fire surrogates equal weight in the record. In the final models, the 25-year fire/fire surrogate interval (hereafter “25-year interval”)
had the most consistent negative influence on species richness both overall and within functional groups, a result that may be partially attributable to the greater accuracy of that parameter relative to the 50-year interval. Years in rotation × soil had a significant positive influence on forb, legume and overall species richness. For forbs and legumes, the number of years a site was in consistent fire rotation was more significant than the 25-year interval. Time since fire (which ranged from 0.5 to 4 years) had a significant influence on forb, shrub and overall species richness, with a negative effect on Spodosols and Ultisols and a positive effect on Entisols.

Trees/ha × soil influenced forb, legume and overall species richness (negatively for Spodosols and Entisols and positively for Ultisols), and shrub cover had an influence on legume richness in the final model—this was a small but significant positive relationship that was evident across all soil types. The other final model that included shrub cover was the C₄ graminoid model, in which case there was a negative relationship. Herb cover influenced both forb and shrub richness (positively in the latter and negatively in the former). The legume, shrub and total richness models contained a significant interaction between 500-m landscape buffer composition and soil type, whereas none of the models contained the 1,000-m buffer. For total richness and legume richness, the effect of vegetation extent in the 500-m buffer was positive for Spodosols, negative for Entisols and neutral for Ultisols. These results suggest some degree of correlation between vegetation extent and fire regime, but the reason for the different relationships could not be determined from our data. R² values were highest for the forb, legume and total models (ranging from 0.66 to 0.75), and lowest in the C₃ graminoid, C₄ graminoid and shrub models (ranging from 0.14 to 0.47).

All three of the seasonality variables (diversity of seasons, growing season fire and lightning season fire) had significant effects, either alone or with soil interactions, in the total richness model (Table 3). Both diversity of seasons and growing season fire had significant positive influences on forb richness, while the effects of growing season and lightning season fire varied with soil type in the C₃ graminoid and

---

**Table 2** Final generalized linear mixed models for understory functional group richness at the 100 m² level, including fire regime, vegetation and landscape predictor variables

| Variables                | Total F p | Forb F p | Legume F p | C4 gram. F p | C3 gram. F p | Shrub F p |
|--------------------------|-----------|----------|------------|--------------|--------------|-----------|
| Soil                     | 4.2 0.02  | 3.7 0.03 | 13.5 0.00  | 2.3 0.10     | 4.2 0.02     | 4.9 0.01  |
| Trees/ha                 | 0.3 0.34  | 2.8 0.10 | 0.0 0.88   |              |              |           |
| Trees/ha × soil          | 5.7 0.00± | 3.6 0.00±| 6.2 0.00±  |              |              |           |
| Shrub cover              | 10.8 0.00+| 2.9 0.09 |           |              |              |           |
| Shrub cover × soil       | 1.26 0.29 |          |            |              |              |           |
| Herb cover               | 4.1 0.05+ |          |            |              |              |           |
| Herb cover × soil        |           |          |            |              |              | 6.2 0.01- |
| Landscape 500 m          | 2.5 0.12  |          | 0.0 0.88   |              | 9.9 0.00-   |           |
| Landscape × soil         | 3.5 0.04± | 4.9 0.01±|            |              | 5.7 0.01-   |           |
| 50-year fire Int         |           |          |            |              | 2.7 0.10    | 4.0 0.05+ |
| 50-year Int × soil       |           |          |            |              | 3.2 0.05±   |           |
| 25-year fire Int         | 0.5 0.50  | 0.9 0.35 | 5.7 0.02-  | 4.0 0.05    | 2.5 0.12    |           |
| 25-year Int × soil       | 4.0 0.02- | 3.6 0.03-| 2.6 0.08   | 4.8 0.01±   |           |           |
| 10-year fire Int         | 6.7 0.01- |          |            |              |             |           |
| 10-year Int × soil       |           |          |            |              | 2.9 0.09    |           |
| Time since fire          | 5.1 0.03- | 6.0 0.02-|            |              | 5.9 0.00±   |           |
| TSF × soil               | 4.8 0.01± | 8.1 0.00±|            |              | 9.9 0.00-   |           |
| Years in rotation        | 3.9 0.09  | 4.8 0.03+| 0.0 0.89   |              |             |           |
| Years in rot. × soil     | 4.7 0.01+ | 4.6 0.01+| 5.4 0.01+  |              |             |           |
| Site covariance χ²       | 6.2 0.01  | 56.4 0.00| 0.65 0.21  | 0.7 0.20     | 0.2 0.32    | 2.7 0.05  |
| AIC                      | 1,080.08  | 870.36   | 519.42     | 673.58       | 481.67      | 728.67    |
| R²                       | 0.66 0.75 | 0.72 0.72| 0.24 0.24  | 0.14 0.47    |             |           |

Note. The model for each functional group was selected based on the combination of variables that achieved the lowest AIC. The table shows F statistics and p-values for each included parameter, with significance denoted in bold. The direction of each significant relationship is indicated with a +, − or ± in the case of soil interactions in which the direction differed by soil type. Specifics regarding divergent soil interactions are discussed in the text. The R² value is a measure of the percentage of variance explained by each model, derived using the method of Nakagawa and Schielzeth (2013), and the site covariance chi-square is based on a Wald test.
shrub models: positive for Spodosols, negative for Entisols and neutral for Ultisols (Table 3). $R^2$ values indicate that the fire seasonality models explained roughly half the variation in forb, shrub and overall richness, and very little of the variation in $C_4$ graminoid richness. None of the seasonality variables had significant effects on $C_4$ graminoid richness. Legumes did not have any relationships with seasonal variables, though others have documented sensitivity to fire season in this group (Hiers et al., 2000); this may have been partly due to the fact that our seasonality model contained only Spodosols and Entisols, and the former are relatively inhospitable to legumes.

### 3.2 Patterns and drivers of beta diversity

Three-dimensional NMS solutions were chosen for all three soil types, with a final stress of 14.0 for the Entisol plot, 13.5 for the Spodosol plot and 12.3 for the Ultisol plot. NMS ordination of the Sørensen distances between overall communities at the 100-m² sampling scale revealed that Entisol and Ultisol communities showed distinct separation between sites, even within subregions, while Spodosol sites varied less distinctly (Figures 2–4). Within functional groups, PerMANOVA showed that site was a significant effect for all functional group assemblages on all soil types, and multivariate pairwise $t$ tests showed significant differences between the great majority of site pairs following a Benjamini–Hochberg correction (including within-region pairs), particularly among forb, $C_4$ grass and legume assemblages (Table 4).

Nestedness analysis using the NODF metric and the Tuning Peg null model algorithm showed that no assemblages were nested at the 0,0 or 1,1 null model positions (the most conservative in identifying nestedness) (Table 5). However, some assemblages tested positive for nestedness from the still-conservative 2,2 position onward (Entisol forbs, Entisol trees and Spodosol $C_3$ graminoids), and many tested positive at the less-constrained 3,3 and 4,4 positions (shrubs and $C_4$ graminoids on all soil types), suggesting that some degree of nestedness may be present in those assemblages. There was no evidence of legume nestedness on any soil type.

---

**Table 3** Final generalized linear mixed models for understory functional group richness at the 100 m² level, based on 25-year fire regime seasonality data for Entisol and Spodosol communities

| Variables                      | Total | Forb | Legume | $C_4$ gram. | $C_3$ gram. | Shrub |
|-------------------------------|-------|------|--------|-------------|-------------|-------|
|                               | $F$   | $p$  | $F$    | $p$         | $F$         | $p$   |
| Soil                          | 8.3   | 0.01 | 14.0   | 0.00        | 1.3         | 0.26  |
| 25-year Int                   | 1.2   | 0.27 | 1.9    | 0.18        | 8.0         | 0.01- |
| 25-year Int × soil            | 8.0   | 0.01-| 1.7    | 0.19        |             |       |
| Total fire/Trt 1990+          | 8.6   | 0.00+| 3.0    | 0.09        | 6.9         | 0.01+ |
| Total fire/Trt × Soil         | 4.5   | 0.04 | 4.2    | 0.04+       |             | 24.4  |
| Burn Season diversity         | 6.5   | 0.01+| 9.6    | 0.00+       |             |       |
| Growing season fire           | 0.1   | 0.76 | 5.1    | 0.03+       | 0.1         | 0.75  |
| Lightning season fire         | 8.8   | 0.00+|       |             | 10.3        | 0.00± |
| Time since fire               | 1.6   | 0.20 | 0.0    |             | 0.0         | 0.86  |
| Lightning season × soil       | 5.9   | 0.02+|       |             | 14.5        | 0.00± |
| TSF × soil                    | 7.6   | 0.01±|       |             | 6.8         | 0.01- |
| Site covariance $\chi^2$      | <0.0001| <0.0001| <0.0001| 0.0296      | 1.0000      | 1.0000|
| AIC                           | 829.39| 663.43| 393.90 | 544.80      | 363.32      | 556.69|
| $R^2$                         | 0.55  | 0.48 | 0.67   | 0.20        | 0.08        | 0.53  |

Note. The final model for each functional group was selected based on the combination of variables that achieved the lowest AIC. The table shows $F$ statistics and $p$-values for each included parameter, with significance denoted in bold*. The direction of each significant relationship is indicated with a +, − or ± in the case of soil interactions in which the direction differed by soil type. Specifics regarding divergent soil interactions are discussed in the text. The $R^2$ value is a measure of the percentage of variance explained by each model, derived using the method of Nakagawa and Schielzeth (2013), and the site covariance chi-square is based on a Wald test.
Betapart confirmed the Sørensen dissimilarity results derived using PC-ORD, with all functional group × soil type assemblages showing high dissimilarity (i.e., beta diversity) between sites (Table 6). Partitioning the turnover and nestedness components of Sørensen dissimilarity, we found that beta diversity was explained largely by turnover ($\beta_{\text{SIM}}$) rather than nestedness ($\beta_{\text{SNE}}$) in all functional group × soil combinations, even those identified by NODF as having some degree of nestedness (Tables 5 and 6). Betapart pairwise comparisons for Spodosol forbs showed that while overall $\beta_{\text{SNE}}$ was very low, five of 66 site pairs showed roughly equivalent contributions of nestedness and turnover to site-to-site forb assemblage dissimilarity. Three of these pairings occurred between the species-rich Caravelle Ranch and other, more depauperate sites in the FL-north subregion (Appendix 5). Both Entisol and Ultisol forbs showed minimal nestedness-resultant dissimilarity, the only source in both cases being a single very species-poor site that was nested within all others (General Coffee and Manatee Springs, respectively) (Appendices 6 and 7).

The Mantel correlograms showed positive autocorrelation between 100 m$^2$ module species assemblages at Lag 1 (within-site, <1 km) across all soil types and functional groups (Table 7). Positive autocorrelation was also present, though to a lesser degree, at Lag 2 (1–99 km) within Entisol forb, shrub and overall assemblages, and in Spodosol shrub and overall assemblages. Significant negative
autocorrelation was present in most Entisol functional group assemblages from 300 km onward and many Spodosol assemblages from 200 km onward. Ultisol assemblages only showed positive autocorrelation at Lag 1 (within-site) level, but negative autocorrelation was present in most Ultisol functional groups beginning at Lag 3 (100–230 km).

Our comparison of null, spatial, environmental and shared space–environment linear mixed models showed that the proportion of site-to-site Sørenson dissimilarity explained by geographic distance ranged from 17.5% among Ultisol sites to 26.7% among Spodosol sites, and the proportion of dissimilarity explained by environment ranged from 6.2% among Spodosol sites to 42% among Ultisol sites (Figure 5). The shared space–environment model explained 0.8% of the variation among Ultisol sites, 7.1% of the variation among Entisol sites and 14% of the variation among Spodosol sites. For both Entisols and Spodosols, a little more than half of the between-site dissimilarity remained unexplained (58.1% and 53%, respectively), while 39.7% of Ultisol site dissimilarity was unexplained by spatial or environmental factors.

3.3 | Species richness at different scales

The strongest correlations between quadrat-level and whole-site richness were found among Spodosol sites, particularly in the forb functional group, which had $r^2$ values of 0.36, 0.48, 0.69 and 0.75 at the 0.1, 1, 10 and 100 m$^2$ levels, respectively (Table 8). No other soil × functional group combination showed a correlation between whole-site and quadrat richness at the very smallest scale (0.1 m$^2$), and Ultisols also had no correlations between whole-site richness and the next larger scale (1 m$^2$). Entisol forb, legume and total richness at the 1 m$^2$ level were weakly correlated with whole-site richness. Correlations between whole-site richness and quadrat richness at the two larger scales (10 and 100 m$^2$) were stronger across the board, particularly at the 100 m$^2$ level (Table 8). Figure 6 shows a boxplot of 100 m$^2$ quadrant forb richness superimposed on whole-site forb richness, with sites sorted from highest to lowest mean forb richness at the 100 m$^2$ level.

4 | DISCUSSION

We found pronounced variation in functional group richness among NACP savanna sites, with the richest sites typically containing two to five times more species per functional group than the poorest. Beta-diversity patterns were turnover-dominated for all plant functional groups, a finding that largely held true among sites in the same climatic subregions of the study area. Though we did find some evidence of nestedness (particularly among Entisol forbs,
Entisol trees and Spodosol C₃ graminoids), in all cases it was balanced by equivalent or higher turnover, and ultimately, nestedness had only a limited effect on beta diversity for any functional group. The prevalence of turnover rather than nestedness suggests that even species-poor sites in this portion of the NACP can harbour less-common members of the regional plant metacommunity and may be important targets for conservation despite having smaller assemblages. Our findings indicate that protecting and investing in many sites, regardless of their current species richness, may be the most beneficial conservation strategy for NACP savannas.

The species turnover we observed was due in part to spatial gradients, with many functional group assemblages showing positive autocorrelation in the 1- to 99-km distance band, and most transitioning to negative autocorrelation at 200 km + distances. Fire regime and landscape composition also explained a portion of between-site variation, though more than half of the observed beta diversity remained unexplained for Entisol and Spodosol assemblages. Some of the unexplained variation likely stems from gradients that were not captured by our set of variables, such as edaphic factors beyond our categorical soil distinctions, or

### TABLE 5

Nestedness analysis using the NODF metric, tested against five progressively less-constrained null models generated by the Tuning Peg algorithm

| Functional group | Soil   | NODF | 0.0 (FF) | 1.1 | 2.2 | 3.3 | 4.4 |
|------------------|--------|------|----------|-----|-----|-----|-----|
| Forbs            | Spodosol | 27.28| 0.999    | 0.998| 0.976| 0.758| 0.216|
|                  | Ultisol | 33.47| 1.000    | 1.000| 1.000| 1.000| 0.994|
|                  | Entisol | 31.26| 0.936    | 0.457| 0.005*| <0.001*| <0.001*|
| C₃               | Spodosol | 38.14| 0.274    | 0.103| 0.020*| 0.005*| 0.001*|
|                  | Ultisol | 23.13| 0.849    | 0.816| 0.755| 0.722| 0.656|
|                  | Entisol | 33.77| 0.418    | 0.158| 0.113| 0.087| 0.029*|
| C₄               | Spodosol | 35.83| 0.963    | 0.860| 0.578| 0.243| 0.024*|
|                  | Ultisol | 39.55| 0.815    | 0.715| 0.495| 0.225| 0.030*|
|                  | Entisol | 41.85| 0.970    | 0.740| 0.187| 0.009*| <0.001*|
| Legumes          | Spodosol | 23.38| 0.371    | 0.683| 0.657| 0.325| 0.353|
|                  | Ultisol | 27.99| 0.904    | 0.915| 0.839| 0.744| 0.642|
|                  | Entisol | 30.23| 0.985    | 0.951| 0.855| 0.502| 0.142|
| Shrubs           | Spodosol | 48.15| 1.000    | 0.948| 0.592| 0.154| 0.003*|
|                  | Ultisol | 41.23| 0.675    | 0.420| 0.099| 0.005*| <0.001*|
|                  | Entisol | 34.50| 0.617    | 0.410| 0.190| 0.045*| 0.003*|
| Trees            | Spodosol | 18.85| 0.966    | 0.958| 0.923| 0.872| 0.837|
|                  | Ultisol | 41.88| 0.938    | 0.965| 0.960| 0.911| 0.786|
|                  | Entisol | 71.66| 0.772    | 0.062| <0.001*| <0.001*| <0.001*|

Notes. The 0,0 (fixed row totals, fixed column totals) model fully constrains row and column totals, while null models 1,1 through 4,4 allow increasingly more variation in row and column totals, increasing sensitivity to a variety of real-world nestedness patterns but also increasing the risk of type I error. Significant *p*-values are denoted in bold.

### TABLE 6

Betapart partitioning of beta diversity (βSOR) into nestedness (βSNE) and turnover (βSIM) components, broken down by soil type and functional group

| Entisols | Spodosols | Ultisols |
|----------|-----------|----------|
| βSIM     | βSNE      | βSOR     | βSIM | βSNE | βSOR | βSIM | βSNE | βSOR |
| Forbs    | 0.82      | 0.06     | 0.88  | 0.71  | 0.08  | 0.79  | 0.80  | 0.03  | 0.84  |
| C₃ gram  | 0.75      | 0.09     | 0.85  | 0.80  | 0.03  | 0.83  | 0.79  | 0.06  | 0.85  |
| C₄ gram  | 0.77      | 0.07     | 0.83  | 0.65  | 0.09  | 0.74  | 0.74  | 0.06  | 0.80  |
| Legumes  | 0.81      | 0.10     | 0.91  | 0.77  | 0.05  | 0.82  | 0.80  | 0.06  | 0.86  |
| Shrubs   | 0.70      | 0.06     | 0.76  | 0.66  | 0.08  | 0.74  | 0.78  | 0.06  | 0.84  |
| Trees    | 0.85      | 0.04     | 0.89  | 0.64  | 0.11  | 0.75  | 0.45  | 0.24  | 0.69  |
differences in longer-term fire history beyond the period of record. Still more of the unexplained variation is probably due to long histories of stochastic environmental filtering events not addressed by our study, since droughts, rainfall events and the severity/heterogeneity of individual fires are known to interact with seed arrival to influence NACP savanna community assembly (Myers & Harms, 2011). Finally, a documented lack of dispersal and colonization by native herbaceous species in NACP savannas (Brudvig et al., 2013; Kirkman et al., 2004; Ostertag & Robertson, 2007) indicates that these communities are effectively islanded, and the persistence of less-common assemblage members on species-poor fragments suggests a role for neutral immigration and extinction processes in the beta-diversity patterns we observed (Socolar et al., 2016). Our finding that the 500-m-radius landscape buffer composition had a more significant influence on species richness than the 1,000-m-radius buffer composition supports the conclusion that NACP savanna fragments have a limited range of interaction with the surrounding landscape.

As interaction between NACP savanna fragments appears to be relatively limited, the species richness of individual sites may be of critical importance for regional biodiversity. Among Spodosol forb assemblages, we found support for the hypothesis that species richness at small scales is correlated with richness at larger scales, with moderate correlations between whole-site and small-scale (0.1 and 1 m²) richness. On Entisols and Ultisols, however, relationships between whole-site richness and richness at the two smallest scales were weak or absent across all functional groups, a result that we suspect may be due to lower shrub encroachment.

### Table 7

| Lag class distance (km) | Entisols | Spodosols | Ultisols |
|-------------------------|----------|-----------|----------|
|                         | All species | Forbs | Legumes | C4 gram. | C3 gram. | Shrubs | All species | Forbs | Legumes | C4 gram. | C3 gram. | Shrubs |
| <1                      | 0.450*    | 0.548*    | 0.599*    | 0.345*    | 0.325*    | 0.449*    | 0.776*    | 0.585*    | 0.707*    | 0.230*    | 0.569*    | 0.565*    |
| 1–99                    | 0.099*    | 0.101*    | -         | 0.058     | 0.069     | 0.115*    | 0.195*    | -         | 0.058     | 0.069     | 0.011     | 0.334*    |
| 100–199                 | 0.006     | 0.007     | 0.032     | 0.013     | 0.020     | -0.005    | -0.086    | -0.046    | 0.018     | 0.206*    | -0.028    | -0.210*   |
| 200–299                 | -0.086    | -0.046    | 0.018     | 0.206*    | -0.028    | -0.210*   | -0.186*   | -0.214*   | -0.219*   | -0.169*   | -0.046    | -0.064    |
| 300–399                 | -0.146*   | -0.118    | -0.128*   | -0.194*   | -0.033    | -0.103*   | -0.468*   | -0.139*   | -         | -         | -         | -         |
| 400–550                 | -         | -         | -         | -         | -         | -         | -         | -         | -         | -         | -         | -         |

Note. The <1 km distance class is within-site, and all others are between-site. n = the number of module-to-module comparisons. The standardized Mantel statistic (r) is shown in bold* where values were significant, based on a 2,000-iteration permutation test and a progressive Bonferroni adjustment (αi = 0.05/2i for the ith lag) (Legendre & Legendre, 1998).

### Figure 5

Percentage of beta diversity (as measured by between-site Sørenson distance) explained by null, spatial, environmental and shared spatial–environmental factors, based on linear mixed models. The percentage of variation explained is a pseudo-\( R^2 \) based on the proportion of total variance the null model explained compared to the space, environment and global models (Feng et al., 2001).
pressure on those soil types. Nonetheless, differences in small-scale richness on these soils could still have implications for trophic interactions, plant population dynamics and fuel structures (Glitzenstein et al., 2012). It is important to note that the Ultisol sites in this study were all well drained, whereas other studies in the region have examined plant community change on wetter Ultisol sites, which may be more vulnerable to shrub encroachment (Palmquist et al., 2014). Within-site edaphic heterogeneity is another known correlate of whole-site plant species richness in NACP savannas (Costanza, Moody, & Peet, 2011; Palmquist, Peet, & Mitchell, 2015; Provencher, Litt, & Gordon, 2003) and was likely important on our study sites.

The most consistent fire regime predictors of species richness across functional groups and soil types were the average fire/fire surrogate interval over the past 25 years, and the total number of years a site was in fire rotation. For many variables, only the soil interaction was significant, or the soil interaction was more significant than the main effect. In many cases, the direction of these relationships was the same across soil types, but the slope differed, whereas in several other cases, the relationships varied from positive to

| Quadrat richness | Entisols (m²) | Spodosols (m²) | Ultisols (m²) |
|------------------|--------------|--------------|--------------|
|                  | Correlation with whole-site richness (r²) | All species | Forbs | Legumes | C4 gram. | C3 gram. | Shrubs |
|                  | Entisols (m²) | 0.1 | 0.24 | 0.28 | 0.31 | – | – | – | 0.14 |
|                  | 0.55 | 0.65 | 0.44 | 0.28 | 0.31 | 0.57 |
|                  | Spodosols (m²) | 0.1 | 0.11 | 0.36 | – | – | – | – | – |
|                  | 0.36 | 0.48 | – | 0.31 | – | – |
|                  | 0.56 | 0.69 | 0.24 | 0.20 | 0.11 | – |
|                  | 0.61 | 0.75 | 0.29 | 0.40 | 0.37 | 0.21 |
|                  | Ultisols (m²) | 0.1 | – | – | – | – | – | – | – |
|                  | 0.24 | 0.28 | – | – | – | – | 0.14 |
|                  | 0.32 | 0.50 | 0.21 | 0.36 | 0.18 | 0.36 |

TABLE 8 Correlations ($r^2$) between quadrat-level species richness and whole-site species richness based on simple linear regression, broken down by soil types and functional groups

FIGURE 6 Boxplots of the 100 m² level forb richness for the five sampling modules at each site, superimposed on whole-site forb richness. Sites are sorted from highest to lowest mean forb richness at the 100 m² level.
negative depending on the soil type. This result was not surprising, as the three soil types differ in many ways that influence vegetation structure, fire regime and the abundance of species within functional groups (i.e., hydrology, edaphic properties, elevations and fuel structures) (Peet, 2006). Of particular note was the positive association between time since fire (up to 4 years) and total Entisol species richness, versus a negative association between time since fire and total species richness on Spodosols and Ultisols, an effect that may point to different woody-herbaceous dynamics on the different soil types. Most of the final models contained current vegetation/landscape parameters as well as fire history parameters, which suggests that the fire regime in previous decades has had effects on species richness that are independent of current vegetation structure, possibly due to within-fragment species extirpation or other compositional changes that occur during periods of fire suppression.

We found empirical support for the theory that fire regimes containing an abundance of growing season fire (March–October) in general, and lightning season fire (May–June) in particular, promote plant species richness in NACP savannas. Diversity of seasons also had a significant positive influence on overall and forb species richness, and these relationships were consistent across soil types. Though our study did not examine the mechanistic causes of the relationships between burn season diversity and species richness, one logical hypothesis is that burn season variation may better promote coexistence among functional groups and among spring-, summer- and fall-flowering forb species. It may be that prescribed fire regimes with an emphasis on lightning season fire, but also containing variation among the fire seasons we identified (March–April, May–June, July–August, September–October and November–February), would best capture the positive effects of both seasonal diversity and growing season fire. Experimental research would be necessary in order to develop definitive management recommendations regarding fire season variability.

The continued application of fire in the coming decades will likely foster conditions hospitable to higher species richness, but evidence from this study and others suggests limited dispersal of native species between fire-maintained fragments (Brudvig et al., 2013; Kirkman et al., 2004; Ostertag & Robertson, 2007). More research is needed into the details of species and functional group-specific relationships with fire regimes of varying seasonality and frequency, within the larger 1- to 5-year fire return interval that is widely recognized as being biologically and logistically appropriate for NACP savannas. The mechanistic relationships between fire and plant population dynamics are poorly documented for most NACP savanna plant species. More information of this type would greatly improve the ability of managing agencies to fine-tune fire prescriptions, in order to address the unique conservation needs of each NACP savanna fragment.

ACKNOWLEDGEMENTS

This work was made possible by a Graduate Research Innovation grant from the U.S. Joint Fire Science Program, a Graduate School Fellowship from the University of Florida, and institutional support from the Fish and Wildlife Research Institute. Debbie Miller, Hollie Ober, Jack Putz, David Kaplan, Matthew Stoddard, Bobby Hattaway, Kyle Paris and Samantha Baraoidan provided helpful input and contributions to this project. We thank all of the government agencies who participated in this project.

DATA AVAILABILITY

The data supporting this study are being archived with the United States Department of Agriculture: Forest Service Research Data Archive: https://www.fs.usda.gov/rds/archive/.

BIOSKETCHES

Johanna E. Freeman is a plant ecologist at the Fish and Wildlife Research Institute (FWRI), with research interests in fire ecology and conservation biology. She completed this work in fulfillment of a PhD from the University of Florida’s School of Forest Resources and Conservation.

Kent Williges is a plant ecologist at FWRI with expertise in pyro-genic plant communities of Florida.

Erin H. Leone is the programme leader for the Center for Biostatistics and Modeling at FWRI.

Leda N. Kobziar is a fire scientist at the University of Idaho whose work focuses on the ecological repercussions of managed fire regimes in pine-dominated forests.

ORCID

Johanna E. Freeman https://orcid.org/0000-0002-9201-6581

REFERENCES

Almeida-Neto, M., Frenzel, D., & Ulrich, W. (2012). Rethinking the relationship between nestedness and beta diversity: A comment on Baselga (2010). Global Ecology and Biogeography, 21(7), 772-777. https://doi.org/10.1111/j.1466-8238.2011.00709.x

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. Oikos, 117(8), 1227-1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19(1), 134-143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography, 21(12), 1223-1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. Methods in Ecology and Evolution, 3(5), 808–812.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), 1–48.

Brudvig, L. A., & Damschen, E. I. (2011). Land-use history, historical connectivity, and land management interact to determine longleaf pine
woodland understory richness and composition. *Ecography*, 34(2), 257–266. https://doi.org/10.1111/j.1600-0587.2010.06381.x

Bruel, J. J., & Wilson, K. L. (2007). Towards a comprehensive survey of *C3* and *C4* photosynthetic pathways in Cyperaceae. *Aliso: A Journal of Systematic and Evolutionary Botany*, 23, 99–148. https://doi.org/10.5049/aliso.20072301.11

Costanza, J. K., Moody, A., & Peet, R. K. (2011). Multi-scale environmental heterogeneity as a predictor of plant species richness. *Landscape Ecology*, 26(6), 851–864. https://doi.org/10.1007/s10980-011-9613-3

Drewa, P. B., Platt, W. J., & Moser, E. B. (2002). Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. *Ecology*, 83(3), 755–767. https://doi.org/10.1890/0012-9658(2002)083[0755:FEORSF]2.0.CO;2

Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J., ... York, A. (2010). Fire management for biodiversity conservation: Key research questions and our capacity to answer them. *Biological Conservation*, 143(9), 1928–1939. https://doi.org/10.1016/j.biocon.2010.05.026

Environmental Systems Research Institute (ESRI). (2014). *ArcGIS Release 10.3. Redlands, CA: ESRI.*

Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral vs. niche processes. *Proceedings of the National Academy of Sciences*, 100(15), 8916–8920.

Feng, Z., Diehr, P., Peterson, A., & McLerran, D. (2001). Selected statistical issues in group randomized trials. *Annual Review of Public Health*, 22, 167–187.

Florida Geographic Data Library. (2016). http://www.fgdl.org/metadata/metadata_archive fgdl html sfu95.htm.

Fornara, D. A., & Tilman, D. (2009). Ecological mechanisms associated with the positive diversity–productivity relationship in an N-limited grassland. *Ecology*, 90(2), 408–418. https://doi.org/10.1890/08-0325.1

Freeman, J., Kobziar, L., Rose, E. W., & Cropper, W. (2017). A critique of the historical-fire-regime concept in conservation. *Conservation Biology*, 31(5), 976–985. https://doi.org/10.1111/cobi.12942

Freeman, J. E., Williges, K., Gardner, A. G., & Leone, E. H. (2017). Plant functional group composition on restored longleaf pine—wiregrass (*Pinus palustris—Aristida stricta*) savannas with a history of intensive agriculture. *Natural Areas Journal*, 37(4), 434–456.

Frost, C. C. (2006). History and future of the longleaf pine ecosystem. In S. Jose, E. Jokela, & D. L. Miller (Eds.), *The longleaf pine ecosystem: ecology, silviculture, and restoration* (pp. 9–47). New York, NY: Springer Science + Business Media, LLC.

Georgia GIS Clearinghouse. (2016). https://data.georgiaspatial.org.

Glitsenstein, J. S., Streng, D. R., Masters, R. E., Robertson, K. M., & Hermann, S. M. (2012). Fire-frequency effects on vegetation in north Florida pinelands: Another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. *Forest Ecology and Management*, 264, 197–209. https://doi.org/10.1016/j.foreco.2011.10.014

Heyward, F. (1939). The relation of fire to stand composition of longleaf pine forests. *Ecology*, 20(2), 287–304. https://doi.org/10.2307/1930747

Hier, J. K., Wyatt, R., & Mitchell, R. J. (2000). The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? *Oecologia*, 125(4), 521–530.

Hmielewski, T. L., Robertson, K. M., & Platt, W. J. (2014). Influence of season and method of topkill on resprouting characteristics and biomass of Quercus nigra saplings from a southeastern US pine-grassland ecosystem. *Plant Ecology*, 215(10), 1221–1231. https://doi.org/10.1007/s11258-014-0380-5

Kirkman, L. K., Coffey, K. L., Mitchell, R. J., & Moser, E. B. (2004). Ground cover recovery patterns and life-history traits: Implications for restoration obstacles and opportunities in a species-rich savanna. *Journal of Ecology*, 92, 409–421.

Kirkman, L. K., Mitchell, R. J., Helton, R. C., & Drew, M. B. (2001). Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany*, 88(11), 2119–2128. https://doi.org/10.2307/3558437

Knapp, E. A., Estes, B. L., & Skinner, C. N. (2009). Ecological effects of prescribed fire season: a literature review and synthesis for managers. United States Department of Agriculture Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-224.

Kobziar, L. N., Godwin, D., Taylor, L., & Watts, A. C. (2015). Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern US. *Forests*, 6(3), 561–580.

Legendre, P., & Legendre, L. (1998). *Numerical ecology*, volume 24, developments in environmental modelling.

Lichstein, J. W. (2007). Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecology*, 188(2), 117–131. https://doi.org/10.1007/s11258-006-9126-3

McCune, B., & Mefford, M. J. (2016). *PC-ORD*. Multivariate Analysis of Ecological Data. Version 7.03. MJM Software, Glenden Beach, Oregon, USA.

Mitchell, R. J., & Duncan, S. L. (2009). Range of variability in southern coastal plain forests: Its historical, contemporary, and future role in sustaining biodiversity. *Ecology and Society*, 14(1), 17. https://doi.org/10.5751/ES-02562-140117

Myers, J. A., & Harms, K. E. (2011). Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology*, 92(3), 676–686. https://doi.org/10.1890/10-1001.1

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142.

Noss, R. F., Platt, W. J., Sorrie, B. A., Weakley, A. S., Means, D. B., Costanza, J., & Peet, R. K. (2015). How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Diversity and Distributions*, 21(2), 236–244. https://doi.org/10.1111/dad.12278

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’Hara, B., ... Oksanen, M. J. (2013). The Vegan Package. *Community Ecology Package*, 29, 631–637.

Ostertag, T. E., & Robertson, K. M. (2007). A comparison of native versus old-field vegetation in upland pinelands managed with frequent fire. South Georgia, USA. In *Tall Timbers Fire Ecology Conference Proceedings*, vol. 23, pp. 109–120.

Palmquist, K. A., Peet, R. K., & Mitchell, S. R. (2015). Scale-dependent responses of longleaf pine vegetation to fire frequency and environmental context across two decades. *Journal of Ecology*, 103(4), 998–1008. https://doi.org/10.1111/1365-2745.12412

Palmquist, K. A., Peet, R. K., & Weakley, A. S. (2014). Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North America. *Journal of Vegetation Science*, 25(6), 1426–1437. https://doi.org/10.1111/jvs.12186

Peet, R. K. (2006). Ecological classification of longleaf pine woodlands. In S. Jose, E. Jokela, & D. L. Miller (Eds.), *The longleaf pine ecosystem: ecology, silviculture, and restoration* (pp. 95–133). New York, NY: Springer Science + Business Media LLC.

Peet, R. K., Wentworth, T. R., & White, P. S. (1998). A flexible multipurpose method for recording vegetation composition and structure. *Castanea*, 63, 262–274.
Platt, W. J., Carr, S. M., Reilly, M., & Fahr, J. (2006). Pine savanna overstorey influences on ground-cover biodiversity. *Applied Vegetation Science, 9*(1), 37–50. https://doi.org/10.1111/j.1654-109X.2006.tb00654.x

PRISM Climate Group, Oregon State University. (2018). http://prism.oregonstate.edu/normals/

Provencher, L., Litt, A. R., & Gordon, D. R. (2003). Predictors of species richness in northwest Florida longleaf pine sandhills. *Conservation Biology, 17*(6), 1660–1671. https://doi.org/10.1111/j.1523-1739.2003.00416.x

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F., & Eisenhauer, N. (2012). Impacts of biodiversity loss escalate through time as redundancy fades. *Science, 336*(6081), 589–592.

SAS Institute Inc. (2013). SAS 9.4. Cary, NC: SAS.

Shepherd, B. J., Miller, D. L., & Thetford, M. (2011). Fire season effects on flowering characteristics and germination of longleaf pine (Pinus palustris) savanna grasses. *Restoration Ecology, 20*(2), 268–276. https://doi.org/10.1111/j.1526-100X.2010.00759.x

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution, 31*(1), 67–80.

Sørensen, T. A. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter Kongelige Danske Videnskabernes Selskab, 5, 1–34.*

Streng, D. R., Glitzenstein, J. S., & Platt, W. J. (1993). Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. In *Proceedings of the tall timbers fire ecology conference* (vol. 18, pp. 227–263). Tallahassee, FL: Tall Timbers Research Station.

Strona, G., Ulrich, W., & Gotelli, N. J. (2018). Bi-dimensional null model analysis of presence-absence binary matrices. *Ecology, 99*(1), 103–115. https://doi.org/10.1002/ecy.2043

Ulrich, W., & Gotelli, N. J. (2012). A null model algorithm for presence–absence matrices based on proportional resampling. *Ecological Modelling, 244*, 20–27. https://doi.org/10.1016/j.ecolmodel.2012.06.030

Van Lear, D. H., Carroll, W. D., Kapeluck, P. R., & Johnson, R. (2005). History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. *Forest Ecology and Management, 211*(1–2), 150–165. https://doi.org/10.1016/j.foreco.2005.02.014

Veldman, J. W., Brudvig, L. A., Damschen, E. I., Orrock, J. L., Mattingly, W. B., & Walker, J. L. (2014). Fire frequency, agricultural history, and the multivariate control of pine savanna understory plant diversity. *Journal of Vegetation Science, 25*, 1438–1449. https://doi.org/10.1111/jvs.12195

Veldman, J. W., Buisson, E., Durigan, G., Fernandes, G. W., Le Stradic, S., Mahy, G., ... Bond, W. J. (2015). Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment, 13*(3), 154–162. https://doi.org/10.1890/140270

Veldman, J. W., Mattingly, W. B., & Brudvig, L. A. (2013). Understory plant communities and the functional distinction between savanna trees, forest trees, and pines. *Ecology, 94*(2), 424–434. https://doi.org/10.1890/12-1019.1

Volk, M. I., Hoctor, T. S., Nettles, B. B., Hilsenbeck, R., Putz, F. E., & Oetting, J. (2017). Florida land use and land cover change in the past 100 years. In *Florida’s Climate: Changes, Variations, & Impacts* (Edition 1).

Walker, J., & Peet, R. K. (1984). Composition and species diversity of pine-wiregrass savannas of the Green Swamp. *North Carolina Vegetatio, 55*(3), 163–179. https://doi.org/10.1007/BF00045019

Wallr, S. S., & Lewis, J. K. (1979). Occurrence of C4 and C3 photosynthetic pathways in North American Grasses. *Journal of Range Management, 32*, 12–28. https://doi.org/10.2307/3897378

Westgate, M. J., MacGregor, C., Scheele, B. C., Driscoll, D. A., & Lindenmayer, D. B. (2018). Effects of time since fire on frog occurrence are altered by isolation, vegetation and fire frequency gradients. *Diversity and Distributions, 24*(1), 82–91. https://doi.org/10.1111/ddi.12659

How to cite this article: Freeman JE, Kobziar LN, Leone EH, Willigles K. Drivers of plant functional group richness and beta diversity in fire-dependent pine savannas. *Divers Distrib.* 2019;25:1024–1044. https://doi.org/10.1111/ddi.12926
**APPENDIX 1**

List of study preserves with the soil type of the sampling site, basic fuel treatment history over 50 years, number of years in active prescribed fire rotation (defined as the most recent continuous period of fire with no gaps >10 years) and total species richness found on the sampling site (all five modules combined). FL-P = Florida panhandle, FL-N = Florida north, FL-C = Florida central and GA-S = Georgia south.

| Site                                | Site code | Subregion | Soil type | Total # fires | Total # non-fire treatments | Years in active rotation | Total spp richness |
|-------------------------------------|-----------|-----------|-----------|---------------|-----------------------------|--------------------------|-------------------|
| Apalachicola National Forest        | ANF       | FL-P      | Ultisol   | 6             | 0                           | 16                       | 112               |
| River Rise State Park               | RR        | FL-N      | Ultisol   | 7             | 1                           | 27                       | 110               |
| Moody Forest Preserve               | MOO       | GA-S      | Ultisol   | 6             | 1                           | 11                       | 101               |
| Joe Budd Wildlife Mgmt Area         | JB        | FL-P      | Ultisol   | 14            | 0                           | 28                       | 94                |
| Apalachicola Wildlife Env. Area     | ARWEA     | FL-P      | Spodosol  | 6             | 2                           | 14                       | 93                |
| Reed Bingham State Park             | RB        | GA-S      | Entisol   | 6             | 0                           | 19                       | 88                |
| Brixton Rocks Preserve               | BR        | GA-S      | Ultisol   | 9             | 0                           | 20                       | 82                |
| Julington Durbin Preserve           | JD        | FL-N      | Entisol   | 3             | 4                           | 10                       | 82                |
| St. Marks Nat’l Wildlife Refuge     | SM        | FL-P      | Entisol   | 17            | 0                           | 49                       | 81                |
| Black Creek Ravines Preserve        | BC        | FL-N      | Entisol   | 7             | 0                           | 16                       | 76                |
| Caravelle Wildlife Mgmt Area        | CV        | FL-N      | Spodosol  | 4             | 1                           | 16                       | 74                |
| Aucilla Wildlife Mgmt Area          | AUC       | FL-P      | Spodosol  | 5             | 3                           | 14                       | 72                |
| Withlacoochee State Forest          | WITH      | FL-C      | Entisol   | 11            | 0                           | 19                       | 69                |
| Pt Washington State Forest          | PTW       | FL-P      | Entisol   | 5             | 1                           | 18                       | 66                |
| Bell Ridge Wildlife Env. Area       | BR        | FL-N      | Entisol   | 35            | 1                           | 49                       | 65                |
| Longleaf Flatwoods Preserve         | LF        | FL-N      | Entisol   | 2             | 1                           | 7                        | 65                |
| Jennings State Forest               | JEN       | FL-N      | Spodosol  | 8             | 0                           | 22                       | 62                |
| Manatee Springs State Park          | MAN       | FL-N      | Ultisol   | 10            | 0                           | 22                       | 62                |
| Eglin Air Force Base                | EG        | FL-P      | Entisol   | 4             | 3                           | 17                       | 60                |
| Seminole State Forest               | SEM       | FL-C      | Entisol   | 3             | 1                           | 11                       | 60                |
| Gold Head Branch State Park         | GH        | FL-N      | Entisol   | 10            | 1                           | 28                       | 56                |
| Ochlockonee River State Park        | OCH       | FL-P      | Spodosol  | 17            | 0                           | 39                       | 56                |
| Half Moon Wildlife Mgmt Area        | HM        | FL-C      | Spodosol  | 4             | 1                           | 14                       | 55                |
| Osceola National Forest             | OSC       | FL-N      | Spodosol  | 1             | 1                           | 6                        | 53                |
| Guana River Wildlife Mgmt Area      | GR        | FL-N      | Spodosol  | 7             | 4                           | 12                       | 52                |
| Austin Cary Memorial Forest         | AC        | FL-N      | Spodosol  | 5             | 0                           | 16                       | 50                |
| Newnans Lake Preserve               | NEW       | FL-N      | Spodosol  | 4             | 1                           | 11                       | 50                |
| General Coffee State Park           | GC        | GA-S      | Entisol   | 3             | 1                           | 9                        | 45                |
| Crooked River State Park            | CR        | GA-S      | Spodosol  | 3             | 2                           | 17                       | 42                |
| Goethe State Forest                 | GOE       | FL-C      | Spodosol  | 6             | 0                           | 21                       | 36                |
### APPENDIX 2
Mean annual precipitation and temperature in the four subregions of the study area, based on 1981–2010 normals (PRISM, 2018)

| Study area subregion | Total annual precipitation (cm) | Mean annual temperature (°C) |
|----------------------|---------------------------------|-----------------------------|
| GA South             | 102–127                         | 18°–20°                     |
| FL Panhandle         | 152–178                         | 18°–20°                     |
| FL North             | 127–152                         | 20°–22°                     |
| FL Central           | 102–127                         | 22°–24°                     |

### APPENDIX 3
Burn season summary by site, 1990–2015

| Site                  | Agency     | Months in which prescribed burns occurred | Very early-growing (3–4) | Lightning (5–6) | Mid-growing (7–8) | Late-growing (9–10) | Dormant (11–2) | Unknown |
|-----------------------|------------|-------------------------------------------|--------------------------|-----------------|-------------------|--------------------|-----------------|---------|
| Broxton               | TNC-GA     |                                           | -                        | 1               | 1                 | -                  | -               | 2       |
| Caravelle             | FWC-FL     |                                           | 1                        | -               | -                 | -                  | -               | 1       |
| Crooked River         | DNR-GA     |                                           | -                        | -               | -                 | -                  | -               | 1       |
| Eglin                 | USDOD      |                                           | -                        | -               | -                 | -                  | -               | 1       |
| Gen. Coffee           | DNR-GA     |                                           | 1                        | 1               | -                 | -                  | -               | 1       |
| Goethe                | FFS-FL     |                                           | -                        | -               | -                 | -                  | -               | 5       |
| Gold Head             | DEP-FL     |                                           | 2                        | 2               | -                 | -                  | -               | 1       |
| Guana River           | FWC-FL     |                                           | 2                        | 2               | -                 | -                  | -               | 3       |
| Half Moon             | FWC-FL     |                                           | -                        | 2               | 1                 | 1                  | -               | -       |
| Jennings              | FFS-FL     |                                           | 3                        | 1               | -                 | 1                  | 2               | -       |
| Joe Budd              | FWC-FL     |                                           | 4                        | -               | 2                 | 1                  | 4               | -       |
| Julington             | SJRWMD-FL  |                                           | -                        | 2               | -                 | -                  | -               | 1       |
| Longleaf              | SJRWMD-FL  |                                           | 1                        | 1               | -                 | -                  | -               | -       |
| Manatee               | DEP-FL     |                                           | 5                        | -               | -                 | -                  | -               | 3       |
| Moody                 | TNC-GA     |                                           | 1                        | -               | -                 | -                  | -               | 3       |
| Newmans               | SJRWMD-FL  |                                           | 2                        | 1               | -                 | -                  | -               | -       |
| Ochlockonee           | DEP-FL     |                                           | -                        | 6               | 2                 | -                  | 1               | -       |
| Osceola               | USFS       |                                           | -                        | -               | -                 | -                  | -               | 1       |
| Pt. Wash              | FFS-FL     |                                           | -                        | -               | -                 | -                  | -               | 4       |
| Reed Bingham          | DNR-GA     |                                           | 2                        | 1               | -                 | -                  | 2               | 1       |
| River Rise            | DEP-FL     |                                           | -                        | -               | -                 | -                  | -               | 6       |
| Seminole              | FFS-FL     |                                           | -                        | 1               | 2                 | -                  | -               | -       |
| St. Marks             | USFWS      |                                           | 1                        | 6               | 1                 | 1                  | 1               | -       |
| Withlacoochee         | FFS-FL     |                                           | 3                        | 2               | 4                 | 1                  | -               | -       |
| **Totals**            |            |                                           | **38**                   | **38**          | **20**            | **10**            | **50**          | **20**  |
### APPENDIX 4

Means and 95% confidence intervals for 100 m² species richness parameters used in generalized linear mixed models

| 100m² species richness          | Mean, [95% CL]               |
|---------------------------------|------------------------------|
| **Entisols (n = 60)**           |                              |
| C3 graminoids                   | 1.7, [1.47, 1.93]            |
| C4 graminoids                   | 6.7, [6.1, 7.3]              |
| Forbs                           | 12.5, [11.2, 13.8]           |
| Legumes                         | 5.0, [4.3, 5.7]              |
| Shrubs                          | 5.9, [5.2, 6.6]              |
| Trees                           | 4.0, [3.5, 4.5]              |
| All species                     | 35.6, [33.2, 38.0]           |
| **Spodosols (n = 60)**          |                              |
| C3 graminoids                   | 2.4, [2.1, 2.7]              |
| C4 graminoids                   | 5.1, [4.5, 5.7]              |
| Forbs                           | 8.4, [6.8, 10.0]             |
| Legumes                         | 0.6, [0.4, 0.8]              |
| Shrubs                          | 9.9, [9.1, 10.6]             |
| Trees                           | 1.5, [1.2, 1.8]              |
| All species                     | 27.9, [25.3, 30.5]           |
| **Ultisols (n = 30)**           |                              |
| C3 graminoids                   | 2.4, [1.9, 2.9]              |
| C4 graminoids                   | 6.0, [5.2, 6.8]              |
| Forbs                           | 15.3, [12.6, 18.0]           |
| Legumes                         | 3.6, [2.7, 4.5]              |
| Shrubs                          | 10.0, [8.6, 11.4]            |
| Trees                           | 4.1, [3.4, 4.8]              |
| All species                     | 41.4, [36.8, 46.0]           |

### APPENDIX 5

Betapart pairwise comparisons for Spodosol Forbs

| ACMF | ARWEA | AUC | CV | CR | GOE | GR | HM | JEN | NEW | OCH |
|------|-------|-----|----|----|-----|----|----|-----|-----|-----|
| **B_{sim}—Spodosol forbs (turnover-resultant dissimilarity)** |                      |
| ARWEA | 0.91  |     |    |    |     |    |    |     |     |     |
| AUC   | 0.91  | 0.46|    |    |     |    |    |     |     |     |
| CV    | 0.27  | 0.66| 0.50|    |     |    |    |     |     |     |
| CR    | 0.80  | 0.70| 0.70| 0.60|    |    |    |     |     |     |
| GOE   | 0.36  | 0.91| 0.82| 0.36| 0.80|    |    |     |     |     |
| GR    | 0.73  | 0.63| 0.56| 0.50| 0.80| 0.73|    |     |     |     |
| HM    | 0.82  | 0.77| 0.64| 0.55| 0.70| 0.73| 0.81|     |     |     |
| JEN   | 0.82  | 0.58| 0.42| 0.53| 0.70| 0.73| 0.63| 0.63|     |     |
| NEW   | 0.70  | 0.70| 0.70| 0.30| 0.60| 0.70| 0.70| 0.40| 0.50|     |
| OCH   | 0.73  | 0.64| 0.59| 0.73| 0.30| 0.64| 0.75| 0.77| 0.68| 0.70|
| OSC   | 0.91  | 0.42| 0.50| 0.58| 0.80| 0.91| 0.67| 0.67| 0.58| 0.60|
| **B_{sne}—Spodosol forbs (nestedness-resultant dissimilarity)** |                      |
| ARWEA | 0.06  |     |    |    |     |    |    |     |     |     |
| AUC   | 0.04  | 0.16|    |    |     |    |    |     |     |     |

(Continues)
### APPENDIX 5 (Continued)

|        | ACMF   | ARWEA | AUC   | CV    | CR    | GOE   | GR    | HM    | JEN   | NEW   | OCH   |
|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| CV     | 0.33   | 0.09  | 0.03  |       |       |       |       |       |       |       |       |
| CR     | 0.01   | 0.20  | 0.13  | 0.19  |       |       |       |       |       |       |       |
| GOE    | 0.00   | 0.06  | 0.07  | 0.29  | 0.01  |       |       |       |       |       |       |
| GR     | 0.05   | 0.19  | 0.10  | 0.14  | 0.05  | 0.05  |       |       |       |       |       |
| HM     | 0.06   | 0.08  | 0.03  | 0.06  | 0.11  | 0.09  | 0.03  |       |       |       |       |
| JEN    | 0.05   | 0.18  | 0.09  | 0.10  | 0.09  | 0.07  | 0.03  | 0.03  |       |       |       |
| NEW    | 0.01   | 0.20  | 0.13  | 0.34  | 0.00  | 0.01  | 0.07  | 0.23  | 0.16  |       |       |
| OCH    | 0.09   | 0.14  | 0.03  | 0.04  | 0.26  | 0.12  | 0.04  | 0.00  | 0.02  | 0.11  |       |
| OSC    | 0.00   | 0.35  | 0.18  | 0.17  | 0.02  | 0.00  | 0.05  | 0.10  | 0.09  | 0.04  | 0.07  |

\( B_{\text{soc}} \) — Spodosol forbs (Sorenson dissimilarity)

|        |        |       |       |       |       |       |       |       |       |       |       |
|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| ARWEA  | 0.97   |       |       |       |       |       |       |       |       |       |       |
| AUC    | 0.95   | 0.62  |       |       |       |       |       |       |       |       |       |
| CV     | 0.60   | 0.74  | 0.53  |       |       |       |       |       |       |       |       |
| CR     | 0.81   | 0.90  | 0.83  | 0.79  |       |       |       |       |       |       |       |
| GOE    | 0.36   | 0.97  | 0.89  | 0.65  | 0.81  |       |       |       |       |       |       |
| GR     | 0.78   | 0.81  | 0.67  | 0.64  | 0.85  | 0.78  |       |       |       |       |       |
| HM     | 0.88   | 0.86  | 0.67  | 0.61  | 0.81  | 0.82  | 0.84  |       |       |       |       |
| JEN    | 0.87   | 0.76  | 0.51  | 0.63  | 0.79  | 0.80  | 0.66  | 0.66  |       |       |       |
| NEW    | 0.71   | 0.90  | 0.83  | 0.64  | 0.60  | 0.71  | 0.77  | 0.63  | 0.66  |       |       |
| OCH    | 0.82   | 0.77  | 0.63  | 0.76  | 0.56  | 0.76  | 0.79  | 0.77  | 0.71  | 0.81  |       |
| OSC    | 0.91   | 0.77  | 0.68  | 0.76  | 0.82  | 0.91  | 0.71  | 0.76  | 0.68  | 0.64  | 0.82  |

### APPENDIX 6

Betapart pairwise comparisons for Ultisol Forbs

|        | ANF    | BX     | JB     | MAN    | MOO    |
|--------|--------|--------|--------|--------|--------|
| \( B_{\text{gin}} \) — Ultisol forbs (turnover-resultant dissimilarity) |
| BX     | 0.76   |        |        |        |        |
| JB     | 0.61   | 0.45   |        |        |        |
| MAN    | 0.56   | 0.22   | 0.22   |        |        |
| MOO    | 0.75   | 0.45   | 0.61   | 0.56   |        |
| RR     | 0.79   | 0.48   | 0.47   | 0.33   | 0.50   |
| \( B_{\text{gin}} \) — Ultisol forbs (nestedness-resultant dissimilarity) |
| BX     | 0.04   |        |        |        |        |
| JB     | 0.05   | 0.04   |        |        |        |
| MAN    | 0.30   | 0.44   | 0.48   |        |        |
| MOO    | 0.02   | 0.05   | 0.01   | 0.28   |        |
| RR     | 0.00   | 0.09   | 0.06   | 0.45   | 0.04   |
| \( B_{\text{soc}} \) — Ultisol forbs (Sorenson dissimilarity) |
| BX     | 0.80   |        |        |        |        |
| JB     | 0.65   | 0.49   |        |        |        |
| MAN    | 0.86   | 0.67   | 0.70   |        |        |
| MOO    | 0.77   | 0.51   | 0.62   | 0.84   |        |
| RR     | 0.79   | 0.58   | 0.53   | 0.79   | 0.54   |
## APPENDIX 7

### Betapart pairwise comparisons for Entisol Forbs

|       | BR | BC | EG  | GCOF | GHB  | JD   | LF  | PTW | RB   | SEM  | SM   | WITH |
|-------|----|----|-----|------|------|------|-----|-----|------|------|------|------|
| **B_{sim}** — Entisol forbs (turnover-resultant dissimilarity) |    |    |     |      |      |      |     |     |      |      |      |      |
| BC    | 0.57 |    |     |      |      |      |     |     |      |      |      |      |
| EG    | 0.79 | 0.58 |     |      |      |      |     |     |      |      |      |      |
| GCOF  | 0.71 | 0.43 | 0.71 |     |      |      |     |     |      |      |      |      |
| GHB   | 0.65 | 0.35 | 0.79 | 0.64 |      |      |     |     |      |      |      |      |
| JD    | 0.57 | 0.33 | 0.58 | 0.43 | 0.45 |      |     |     |      |      |      |      |
| LF    | 0.64 | 0.36 | 0.63 | 0.57 | 0.40 | 0.50 |     |     |      |      |      |      |
| PTW   | 0.52 | 0.50 | 0.58 | 0.64 | 0.60 | 0.56 | 0.55 |     |      |      |      |      |
| RB    | 0.61 | 0.42 | 0.68 | 0.43 | 0.50 | 0.56 | 0.41 | 0.56 |      |      |      |      |
| SEM   | 0.64 | 0.50 | 0.74 | 0.64 | 0.45 | 0.50 | 0.55 | 0.59 | 0.35 |      |      |
| SM    | 0.61 | 0.38 | 0.68 | 0.50 | 0.55 | 0.48 | 0.50 | 0.48 | 0.48 | 0.50 |      |
| WITH  | 0.52 | 0.54 | 0.68 | 0.50 | 0.55 | 0.46 | 0.59 | 0.58 | 0.62 | 0.50 | 0.65 |

|       |    |    |     |      |      |      |     |     |      |      |      |      |
| **B_{one}** — Entisol forbs (nestedness-resultant dissimilarity) |    |    |     |      |      |      |     |     |      |      |      |      |
| BC    | 0.01 |    |     |      |      |      |     |     |      |      |      |      |
| EG    | 0.02 | 0.05 |     |      |      |      |     |     |      |      |      |      |
| GCOF  | 0.07 | 0.15 | 0.04 |     |      |      |     |     |      |      |      |      |
| GHB   | 0.02 | 0.06 | 0.01 | 0.06 |      |      |     |     |      |      |      |      |
| JD    | 0.03 | 0.04 | 0.07 | 0.18 | 0.08 |      |     |     |      |      |      |      |
| LF    | 0.01 | 0.03 | 0.03 | 0.10 | 0.03 | 0.05 |     |     |      |      |      |      |
| PTW   | 0.04 | 0.03 | 0.07 | 0.11 | 0.06 | 0.00 | 0.05 |     |      |      |      |      |
| RB    | 0.06 | 0.08 | 0.08 | 0.22 | 0.12 | 0.04 | 0.11 | 0.04 |      |      |      |      |
| SEM   | 0.01 | 0.02 | 0.02 | 0.08 | 0.03 | 0.05 | 0.00 | 0.04 | 0.08 |      |      |      |
| SM    | 0.06 | 0.08 | 0.08 | 0.19 | 0.10 | 0.04 | 0.08 | 0.04 | 0.01 | 0.08 |      |      |
| WITH  | 0.03 | 0.02 | 0.05 | 0.15 | 0.06 | 0.01 | 0.03 | 0.01 | 0.04 | 0.04 | 0.03 |      |

|       |    |    |     |      |      |      |     |     |      |      |      |      |
| **B_{sor}** — Entisol forbs (Sorensen dissimilarity) |    |    |     |      |      |      |     |     |      |      |      |      |
| BC    | 0.57 |    |     |      |      |      |     |     |      |      |      |      |
| EG    | 0.81 | 0.63 |     |      |      |      |     |     |      |      |      |      |
| GCOF  | 0.78 | 0.58 | 0.76 |     |      |      |     |     |      |      |      |      |
| GHB   | 0.67 | 0.41 | 0.79 | 0.71 |      |      |     |     |      |      |      |      |
| JD    | 0.60 | 0.37 | 0.65 | 0.61 | 0.53 |      |     |     |      |      |      |      |
| LF    | 0.64 | 0.39 | 0.66 | 0.67 | 0.43 | 0.55 |     |     |      |      |      |      |
| PTW   | 0.56 | 0.53 | 0.65 | 0.76 | 0.66 | 0.56 | 0.59 |     |      |      |      |      |
| RB    | 0.67 | 0.50 | 0.76 | 0.65 | 0.62 | 0.59 | 0.52 | 0.59 |      |      |      |      |
| SEM   | 0.64 | 0.52 | 0.76 | 0.72 | 0.48 | 0.55 | 0.55 | 0.52 | 0.63 | 0.63 |      |      |
| SM    | 0.67 | 0.45 | 0.76 | 0.69 | 0.65 | 0.52 | 0.58 | 0.52 | 0.49 | 0.58 |      |      |
| WITH  | 0.55 | 0.56 | 0.73 | 0.65 | 0.61 | 0.47 | 0.63 | 0.58 | 0.66 | 0.54 | 0.68 |      |