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Maximizing the monitoring of diversity for management activities: Additive partitioning of plant species diversity across a frequently burned ecosystem

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ABSTRACT

Monitoring understory plant diversity is important, allowing managers to track current diversity status and trends both spatially and temporally at a landscape-scale. Improving precision in quantifying patterns in understory plant diversity improves efficiency in monitoring design and more accurate measures of success of management intervention over time. Patterns of species diversity are dependent upon the scale in which they are examined – an increase in small-scale diversity across a gradient can convert to a decrease in large-scale diversity across that same gradient. Using two extensive datasets including both mined historical data and supplemental experimental data, we performed an additive partitioning of plant diversity to elucidate the hierarchical spatial patterns of understory plant species richness, and independent measures of alpha and beta diversity in the species-rich longleaf pine ecosystem at Eglin Air Force Base in northwestern FL, USA. This analysis allowed us to identify the spatial scale that most effectively captures plant diversity to inform monitoring efforts by using measures of species turnover, specifically beta diversity. We found that while species richness and alpha diversity increased with spatial scale, beta diversity began to reach an asymptote at smaller ($1\ \text{m}^2$) scales. Furthermore, we found the sampling effort at this $1\ \text{m}^2$ scale required as few as 60 plots to effectively estimate plant diversity within management blocks. While our results are attributable to Eglin AFB specifically, these scaling analyses can help to streamline monitoring efforts in other ecosystems that seek to elucidate the individual contributions of diversity components.

1. Introduction

Enumerating and monitoring biodiversity is a critical activity for land managers, allowing for the assessment of management activities and evaluating effects of disturbance on biotic communities (Lindenmayer and Likens, 2010, Legg and Nagy, 2006). Effective monitoring helps to elucidate spatio temporal variation in plant diversity patterns and informs strategies to maintain diversity. Successful monitoring programs are targeted, objective driven, and test *a priori* hypotheses which allow for adaptive management strategies (Nichols and Williams, 2006; Yoccoz et al., 2001). Furthermore, an effective monitoring program measures success with quantifiable objectives (Lindenmayer and Likens, 2010).

Long-term biodiversity sampling schemes often represent a legacy, having been established in the past for many reasons that may no longer be currently relevant, but still represent a valuable resource for interpreting trends in species abundance, impacts of management interventions, and impacts of invasive species colonization (Enquist and Enquist, 2011). Monitoring efforts require costly data collection (Caughlan and Oakley, 2001). Recent literature suggests that despite considerable investment of resources and effort to optimize sampling, the wide range of sampling techniques employed in studies of diversity can negatively effect the accuracy of landscape or regional scale inferences (Eigenbrod et al., 2010). As a result, generalization from targeted monitoring efforts are limited to the local scale at which data are collected (i.e. management unit, Lindenmayer and Likens, 2010). However, efficiency can be gained through the identification of the appropriate spatial scale to monitor biodiversity (Yoccoz et al., 2001).

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One of the most general patterns in nature is the species-area relationship (Lomolino, 2000, MacArthur and Wilson, 1967). As greater spatial areas are sampled, species richness accumulates as a wider range of environmental conditions and associated species are encountered (Sandel, 2015). While this pattern may be repeatable across systems it does not always provide an accurate measure for those interested in managing biodiversity. For instance, richness alone does not provide information regarding community composition at varying spatial scales nor allow for monitoring how community dynamics change in response to management activities. More nuanced studies on the scale-dependence and distribution of species diversity (richness, evenness, and abundance) have contributed significantly to understanding patterns of biodiversity and community structure (Condit et al., 2002; Crawley and Harral, 2001). If patterns detected at larger scales are the result of complex processes occurring at smaller scales, then it is necessary to examine how patterns at variable scales relate to one another (Tello et al., 2015; Levin, 1992).

Whittaker (1972, 1960) partitioned diversity, defining alpha (α) diversity as the local diversity within a single sampling unit, beta (β) diversity as the variation in species composition and abundance (turnover) between sampling units in a geographic area, and gamma (γ) diversity as a measure of regional diversity. Building upon these definitions, Lande (1996) demonstrated analytically that γ-diversity could be partitioned into additive components with total diversity as the sum of average α-diversity and β-diversity ($\gamma = \alpha + \beta$). Therefore, the relative contributions of α-diversity and β-diversity to γ-diversity can be calculated and used to describe changes in diversity across spatial scales (Tello et al., 2015; Tuomisto, 2010; Gering et al., 2003).

Under this framework, an informative metric of diversity for managers interested in the effect of management intervention on plant communities is species turnover or beta diversity. β-diversity reflects the variation of species assemblages in response to management actions, thereby providing greater insight into drivers of community composition across spatial, temporal, or environmental gradients. β-diversity is a key concept for understanding the functioning of ecosystems, patterns in community assembly, and informing ecosystem management (Barwell et al., 2015; Chao et al., 2012; Jost, 2007; Legendre et al., 2005). For example, reduction in β-diversity represents a homogenization in community composition which may reduce ecosystem function by affecting productivity, resilience to disturbance, and vulnerability to biological invasion (Balata et al., 2007). The utility of β-diversity as a measure that can be compared between sites with differing levels of α-diversity requires that the two components be independent (Jost, 2007). In doing so, partitioning diversity into spatially explicit components identifies the most important scale for targeting management efforts. For instance, identifying the spatial scale at which β-diversity is maximized provides a more accurate estimate of biodiversity, allowing monitoring programs to implement a standardized plot size for sampling biodiversity.

Our goal was to examine the impact of sampling area on plant diversity estimates and investigate the influence of sampling intensity to help guide efforts to effectively capture and monitor biodiversity in longleaf pine (*Pinus palustris* Mill.) stands. Longleaf pine ecosystems are ideal for management related studies of plant species diversity as they are characterized by high levels of floristic diversity at fine scales, including numerous rare and endemic species that are maintained in managed landscapes through the use of prescribed fire (Palmquist et al., 2015; Walker, 1993; Hardin and White, 1989; Walker and Peet, 1984). We estimated diversity components in plot areas sampled hierarchically in space (i.e., area), which act as a surrogate for inventorying larger and larger plots, to test hypotheses about optimal scales and metrics for measuring biodiversity in longleaf pine systems. We proposed that spatial scale would have differential impact on alpha and beta diversity components due to spatial aggregation of understory plant species. Specifically, we were interested in finding the spatial scale where β-diversity was maximized over the fixed extent of Eglin Air Force Base (AFB; Sandel, 2015); i.e., – what is the best sampling scale to assess management effects on biodiversity?

2. Methods

2.1. Study site

All data were collected at Eglin AFB located in the Gulf Coastal Plain of the Florida panhandle, USA. Eglin AFB is over 180,000 ha in size, includes over 3500 ha of the estimated 5100 ha of old-growth longleaf pine remaining in the region, and is actively managed by frequent prescribed fire (Mitchell et al., 2009, Hiers et al., 2007; Varner et al., 2005; Varner and Kush, 2004). The climate is typified by hot, humid summers with frequent thunderstorms and lightning strikes, mild winters (Provencher et al., 2001), mean annual temperature of 18.6 °C, and 169.2 cm of annual precipitation during the period of data collection (Vose et al., 2014). The area has relatively little topography (0–100 m ASL) and is dominated by well-drained Lakeland series soils (Overing and Watts, 1989). Past land uses at Eglin included timber extraction and naval stor however the deep, coarse-textured entisols precluded extensive tilling or agricultural land use (B. Williams, personal communication).

Xeric sandhills and mesic flatwoods are the dominant vegetative communities found at Eglin AFB. Longleaf pine is a foundation species and is typically monodominant in the overstory with a relatively open canopy throughout the site. Sandhill ground cover vegetation contains many plant species and is dominated by several grasses, such as wiregrass (*Aristida stricta* Michx.), little bluestem (*Schizachyrium scoparium* Michx.), broomsedge (*Andropogon virginicus* L.), as well as dwarf huckleberry (*Gaylussacia dumosa* (J. Kenn) Torr. and A. Gray), evergreen blueberry (*Vaccinium darrowii* Camp), and saw palmetto (*Serenoa repens*). Ground cover vegetation in flatwood communities are dominated grasses such as wiregrass, toothache grass (*Ctenium aromaticum* Walter) and shrubs such as dwarf live oak (*Quercus minima* (Sarg.) Small), saw palmetto, and gallberry (*Ilex glabra* (L.) A. Gray).

2.2. Data collection

To quantify the patterns of diversity found in understory plant communities of longleaf pine ecosystems, we collected species area data and supplemented it with Eglin AFB vegetation monitoring data. Datasets included species richness and abundance measures from hierarchically nested plots (> 1–78 m^2), and 201 monitoring plots representing over a decade of sampling at hierarchical scales (1–100 m^2; Hiers et al., 2007). Data were collected by Eglin AFB natural resource technicians, and professional botanists. Due to differences in data collection and study design as described below, datasets were analyzed separately. Additionally, fire history records were available for the majority of plots extending over the entire sampling time period.

2.3. Datasets

2.3.1. Eglin AFB vegetation monitoring dataset

The Eglin AFB Natural Resources Branch monitoring program began collecting fuel and vegetation data for 201, one-hectare plots randomly located across the base in 2001. Plots were stratified within sandhill, flatwood, and plantation plant communities managed as reference stands or for restoration, or as plantations. All plots in the program were sampled one year following management activities (fire, herbicide treatments, and timber harvest) to determine the effects on plant communities. With the regular application of fire occurring every 15–24 months, plots were revisited and resampled on 2–5 occasions between the years 2001–2012. Each plot visit included the measurement of understory species richness in four, 10-m x10-m subplots nested within each monitoring plot based on the North Carolina Vegetation Survey dimensions (Peet et al., 1998). Within each subplot species richness and abundance were recorded in 8, 1 m^2 nested quadrats. Groundcover richness and abundance data were collected in all plots through 2005. From 2005 through 2012 richness and abundance data were only collected in 35 reference sandhill and flatwood plots. A total of 376 plant species were recorded in this dataset (Table S1). Additional details on the monitoring program can be found in Hiers et al. (2007).

2.3.2. Inventory dataset

Nine circular plots with a 5-m radius were sampled in the summers of 2014 and 2015 for species richness and abundance from sandhill sites located across Eglin AFB with various time since fire and 20-year burn histories. A total of 121 plant species were recorded in this dataset (Table S1). A rod at the center of the circle was attached to a cable that could be adjusted from 0 to 0.4 m to a 1-m aluminum bar. Individual plants were counted as the bar swept by. Plots were sampled in quarter arcs starting in the outer northwest arc moving clockwise and inwards. This method was manageable for multi-day sampling and prevented trampling of areas to be sampled later. Each arc could be analyzed individually or in combination with others for multiple scale analyses (arcs, circles, nested circles, pie sections) ranging in size from 1 m^2 (a single arc at interior radius) to 78 m^2 (the entire plot).

2.4. Statistical analyses

2.4.1. Diversity partitioning

We defined and calculated diversity components in an additive manner (Tuomisto, 2010; Jost, 2007; Chandy et al., 2006; Veech et al., 2002; Lande, 1996). Regional diversity represented the sum of alpha and beta diversity, such that $\gamma = \alpha + \beta 1 + \beta 2 + \beta i$. Where γ = regional diversity, α = mean diversity within plots, β1 = mean diversity between plots, β2 = mean diversity between plots of increasing scale (see Table 1 for β values associated with each spatial grain (*i*)). At each spatial scale within each dataset, α-diversity was calculated as the mean diversity within the sampling unit and β-diversity was calculated between sampling units of the same size. This allowed us to additively partition the total diversity across Eglin AFB into scale-specific diversity components, thereby calculating the relative contribution of each component to overall diversity. Diversity is reported using Hill numbers or species equivalents of Shannon's entropy, to allow for independence in measures of α and β-diversity (Jost, 2007).

In order to visualize how the distribution of species abundances impacted diversity, we plotted alpha and beta components as a continuous function of diversity order (q), where increasing values of q correspond to greater contributions from more abundant species (Chao et al., 2014). q = 0 corresponds to species richness, q = 1 reflects the exponentiated form of Shannon's entropy, and q = 2 equals the inverse of Simpson's concentration. As an alternative measure of species turnover or dissimilarity between samples, we also calculated the mean pairwise Chao-distance between samples within each spatial scale (Chao et al., 2005). Finally, for comparative purposes, we also partitioned diversity multiplicatively (Supplemental).

To assess temporal changes in community composition within the monitoring dataset, we quantified β-diversity over time in plots that had been sampled on more than one occasion. Plots were located within reference stands (n = 25), undergoing restoration (n = 52), or located within plantations (n = 19). The amount of turnover within each individual plot was calculated and aggregated by management status to visualize the distribution of diversity values within each category. In this case, lower values of β-diversity indicated conservation of species composition while larger values represent a greater response to management in terms of community composition.

Table 1

Empirical additive partitioning of plant diversity in the inventory (N = 9) and monitoring (N = 201) datasets collected at Eglin AFB. Observed values were significantly higher (+) or lower (−) than expected from null model comparisons ($P < 0.0001$). α and β-diversity are reported in species equivalents of Shannon's index (H'). As an alternative measure of turnover, mean pairwise distance between plots using Chao's dissimilarity is also reported at each spatial scale.

Partition	Scale (m^2)	Richness	α-Diversity (H')	β-Diversity (H')	Distance
Inventory dataset					
α	1	9.25 (−)	4.94 (−)	–	–
β1	btwn 1	9.25 (−)	–	3.93 (+)	0.7474
β2	3	22.75 (−)	10.76 (−)	2.65 (−)	0.5629
β3	13	35.08 (−)	12.94 (−)	2.41 (−)	0.5408
β4	28	44.41 (−)	14.15 (−)	2.26 (−)	0.4582
β5	50	51.19 (−)	14.71 (−)	2.21 (−)	0.4277
β6	78	58.00 (−)	15.23 (−)	2.17 (−)	0.3904
Monitoring dataset					
α	1	8.99 (−)	4.47 (−)	–	–
β1	btwn 1	8.99 (−)	–	13.60 (+)	0.9235
β2	2	14.10 (−)	6.12 (−)	9.77 (+)	0.8964
β3	8	27.35 (−)	8.88 (−)	6.81 (+)	0.8624
β4	100	33.68 (−)	16.17 (−)	5.24 (+)	0.8023

2.4.2. Comparison to null model

We created a null model for each dataset that produced local assemblages constructed from randomly assigned individuals from the species pool (Tello et al., 2015). Within the null model, all individuals had the same chance of becoming part of any local assemblage. Furthermore, the total number of individuals at each local assemblage and the regional abundances of species were constrained to be the same as the empirical data. The null model was run 1000 times with replacement to create a distribution of additively partitioned diversity values at each spatial scale which were then compared against empirical distributions for statistical significance. Positive deviations from the null indicate deterministic processes favorable to diversity, whereas negative differences indicate processes that diminish diversity.

2.4.3. Rarefaction

Sample-based rarefaction analyses were performed to estimate the number of samples needed to adequately capture diversity following Chao et al. (2014). Using 2698 quadrats of 1 m^2 from the monitoring dataset and 36 samples at 1 m^2 from the inventory dataset, we calculated the slope at each level of sampling intensity (i.e., sample number). The point where mean slope began to asymptote indicates effective sample number. We also calculated the non-parametric Chao$_1$ asymptotic estimate at the identified sampling level to determine sample coverage level. A sample coverage of 50% indicates the point where half of the total species richness has been observed and represents the minimum sample coverage required to estimate diversity (Chao and Jost, 2012). All statistical analyses were performed in R (v.3.2.3, R Core and Team, 2013).

3. Results

Within both datasets, richness and α-diversity increased with area sampled (Table 1, Fig. 1). β-diversity and pairwise distance between plots in both datasets were highest between 1 m^2 plots with increases in spatial grain adding little to compositional difference in the understory community. This pattern was consistent in both additive and multiplicative partitioning (Tables 1 and S2). Nearly 50% of total or γ-diversity was found within the smallest spatial scales, with larger areas contributing relatively less towards overall diversity (Fig. 2). In comparison to the null models, all levels of observed species richness and α-diversity were lower than expected in both datasets. However, observed β-diversity was higher than expected at the smallest scale in the inventory dataset and at all spatial scales in the monitoring dataset (Table 1).

Looking at individual components of diversity with increasing

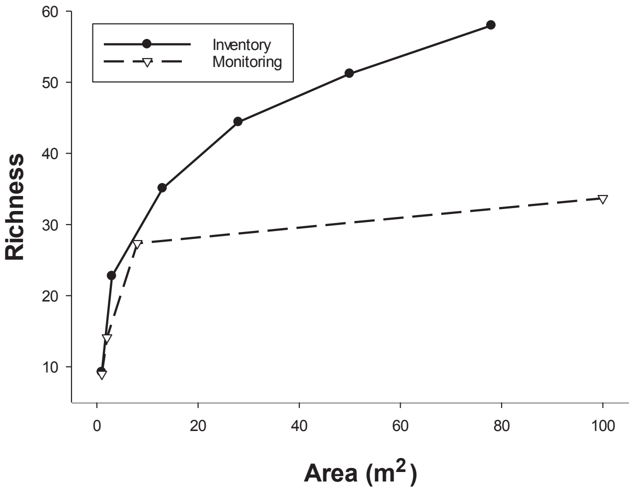

Fig. 1. Species area relationship between richness and sampling grain for the inventory and monitoring datasets.

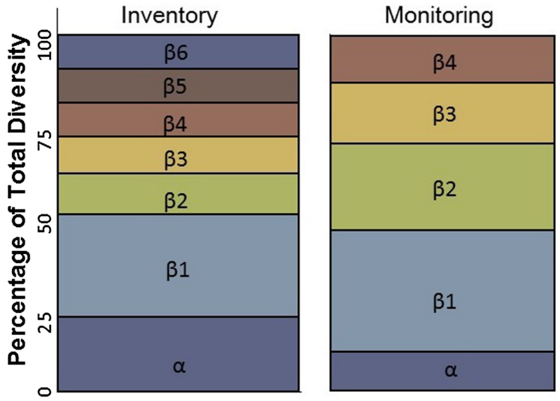

Fig. 2. Relative contributions of individual diversity components from additive partitioning of inventory (left panel) and monitoring (right panel) datasets. α-diversity refers to mean within-plot diversity at the smallest spatial scale sampled while β-diversity is the between-plot diversity at each scale. β1 refers to the smallest spatial scale sampled and consecutive β-diversities represent increasing hierarchical areas sampled up to the largest spatial area.

diversity order (q) showed opposing relationships between spatial scale and influence of relatively abundant taxa. Less abundant taxa contributed considerably to α-diversity with increasing spatial scale (Fig. 3). As more abundant taxa were considered, α-diversity variation between scales was reduced. When looking exclusively at β-diversity the opposite pattern was found, where less abundant taxa contributed more with decreasing spatial scales. Once again, as more abundant taxa were considered, species turnover between plots within each spatial scale decreased (Fig. 3).

Further analysis by rarefaction based on 1 m^2 plots indicated that mean slope began to asymptote around 60 samples (Fig. 4). At this sampling intensity, Chao$_1$ estimates yielded an inference of 89% sample coverage. This indicates an effective level of sampling intensity to achieve an accurate measure of plant species richness. A sample coverage of 50% was reached within 6 samples – meaning half of the species richness had been observed and representing the minimum sample coverage required to estimate diversity (Chao and Jost, 2012).

Temporal analysis of β-diversity within monitoring plots showed that reference stands had the lowest amount of species turnover with increasing amounts in restoration plots and plantation plots, respectively. Furthermore, reference plots had the smallest amount of

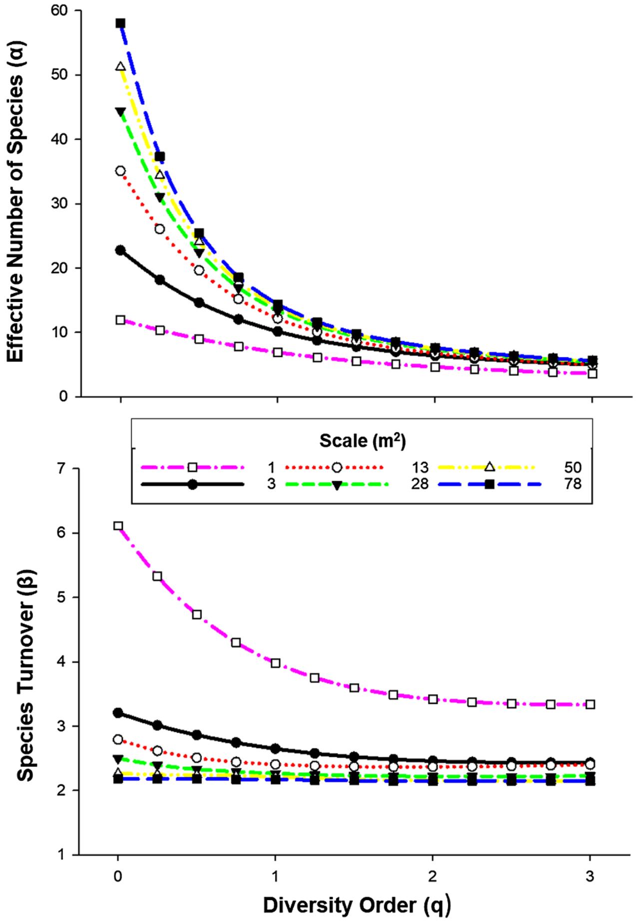

Fig. 3. Diversity profile illustrating the relationship between individual diversity components at various spatial scales and diversity order (q) using the inventory dataset. Top Panel: The mean effective number of species (α-diversity) within samples at each spatial scale. Bottom Panel: turnover between samples (β-diversity) at each scale. Diversity order refers to the weight given to abundant taxa during the calculation of diversity equivalents. q = 0 corresponds to species richness and as q increases, the relative influence of more abundant species increases.

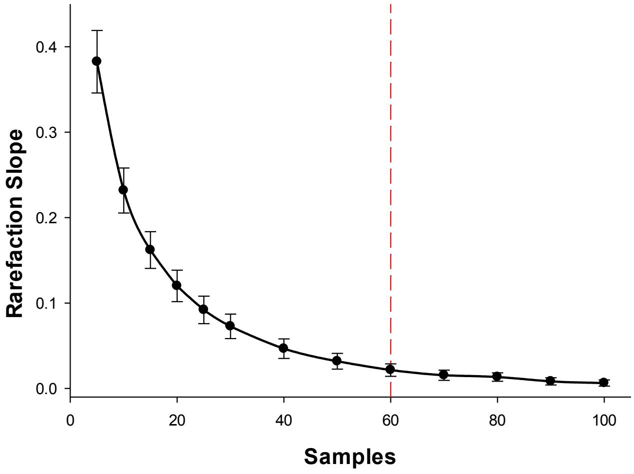

Fig. 4. Mean slope of 2734 rarefaction curves based on 1 m^2 samples from the monitoring and inventory datasets calculated at various sampling intensities. Error bars represent ± SE. Where the mean slope begins to asymptote at 60 samples indicates an effective level of sampling intensity to achieve an accurate measure of plant species diversity.

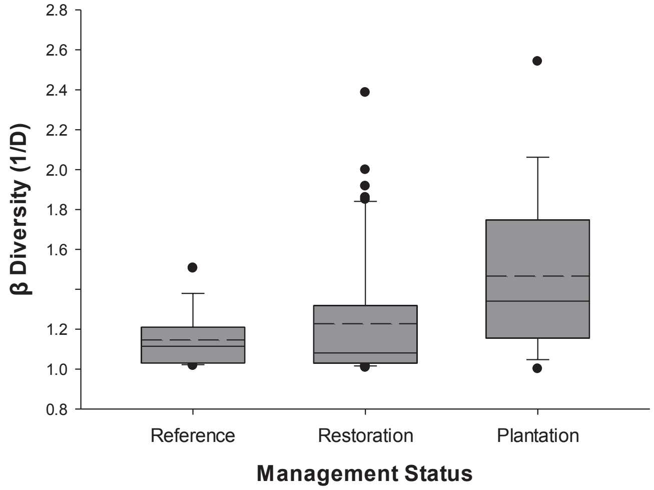

Fig. 5. Box plots showing the distribution of beta diversity values or amount of species turnover over time within each monitoring plot management category. Inside each box, median values are indicated by solid lines and mean values by dashed lines. Diversity is reported in species equivalents using inverse Simpson's (1/D).

variation, indicating plots are conserved in composition over time while restoration and plantation plots have more variation in turnover (Fig. 5).

4. Discussion

The positive relationship between spatial scale and within plot diversity in terms of richness and α-diversity (Figs. 1 and 3) indicated that rare and relatively less abundant species contribute considerably to understory plant diversity. More abundant species were also more common and homogenized variance in α-diversity at all spatial scales. As larger areas were sampled, a greater amount of less abundant species were encountered and added to differentiation in values of α-diversity. Furthermore, the negative relationship between area sampled and between-plot β-diversity (Figs. 2 and 3) indicated that these less common species have an unaggregated distribution across the extent of Eglin AFB, providing a high-level of species turnover between areas sampled. The greater species turnover at smaller scales was uninfluenced by the relative abundance of individual species, given that common species have a broad distribution across Eglin AFB (Fig. 3).

The fact that β-diversity was maximized at the smallest scale supports a focus on 1 m^2 plots as an appropriate size for monitoring changes in understory plant diversity in this particular ecosystem. Utilizing this framework, rarefaction results based on 1 m^2 samples indicate that sampling efficiency can be greatly improved with diversity being accurately estimated in as few as 60 samples. Over the course of the 12 years represented in the Eglin monitoring database, 201 individual plots were being sampled and understory vegetation quantified in areas of up to 8 m^2 (Hiers et al., 2007). The identification of suitable sampling size and intensity represents an increase in sampling efficiency for continued monitoring efforts (Yoccoz et al., 2001). However, management occurs at the stand level. At Eglin AFB, stands comprise 425 individual management units (Hudak et al., 2016), each with unique management regimes including burning, herbicide, mechanical, and overstory thinning treatments; therefore, samples should be stratified across different management units to fully understand the impacts of management activities on understory community responses.

Monitoring β-diversity over time is useful for assessing the efficacy of management interventions. β-diversity is a quantitative measure of spatial background variation that informs temporal assessments; it provides insight into basic system level noise, referred to as a dynamic reference (Hiers et al., 2012). The conservation of β-diversity values within reference plots over the entire monitoring period indicates that management by fire is maintaining the stability of understory plant communities. The higher variation within restoration sites illustrated that species composition is changing in response to management intervention. Plantations within Eglin AFB were harvested prior to the monitoring period, therefore the large amount of variation in β-diversity is attributable to successional processes. Quantification of compositional change in understory communities is an example of a measurable objective, a key component to a successful monitoring program (Lindenmayer and Likens, 2010). While Eglin AFB has been relatively undisturbed by agricultural activities, future studies conducted in post-agricultural areas should consider land use history and associated legacy effects on plant communities (Brudvig et al., 2014).

Frequently burned, low-latitude coniferous forest understories often have high diversity; longleaf pine forests and woodlands are classic examples of highly diverse plant communities at fine scales and very frequent fire return intervals (1–3 years). The frequent fires within these stands are the major force driving the high levels of ground cover plant diversity, with up to 50 species m^{-2} (Palmquist et al., 2015; Walker and Peet, 1984). Although our inferences are limited to Eglin AFB (Lindenmayer and Likens, 2010), our findings that fine-scale beta components of diversity were greater than expected supports previous studies that patterns in plant species richness and composition are structured by small-scale processes in frequently burned longleaf pine forests (Hiers et al., 2009; Thaxton and Platt, 2006).

Specifically, understory community structure is influenced by fine-scale processes such as dispersal limitation and random mortality and recruitment (O'Brien et al., 2016; Wiggers et al., 2013). Furthermore, using a spatially explicit fuel cell concept, Loudermilk et al. (2012) empirically linked fine-scale variation in fuel as the driver of heterogeneity in fire behavior and fine-scale fire intensity. Gagnon et al. (2012) found fine-scale processes governed bunchgrass dynamics in this ecosystem. Dell et al. (2017) then showed mechanistically that this fine-scale variation in fuels contributes significantly to species richness in longleaf pine ecosystems by creating a mosaic of bare patches for seedling establishment.

These varied responses in understory plants may contribute to fine-scale species turnover in heterogeneous light and nutrient environments found in mixed-age longleaf pine stands (Battaglia et al., 2003). Pecot et al. (2007) found differential response of understory vegetation to manipulations of overstory density and light limitation. While shade-intolerant herbaceous plants thrived in open areas created within small gaps, shade-tolerant grasses increased in productivity underneath overstory trees. Nutrient-limited woody plants experienced increased growth in large gaps free from belowground competition with overstory trees.

To fully understand the community-level effects of management actions, such as prescribed fire and overstory thinning, appropriate measurements of diversity via monitoring need to be made in conjunction with management actions and quantifiable objectives (Nichols and Williams, 2006). Furthermore, in light of changing climate and future uncertainty, long term monitoring data are essential for understanding how ecosystems change in response to management (Hiers et al., 2016); these monitoring programs often require substantive labor and financial inputs (Caughlan and Oakley, 2001). Improving precision in quantifying patterns of understory plant diversity will allow for more efficient monitoring design and more accurate measures of success over time (Yoccoz et al., 2001). While our results are relevant to Eglin AFB specifically, the overall methodology of partitioning diversity to identify spatial scale and utilizing rarefaction to identify sampling intensity, could be applied to other ecosystems where investigations into the individual contributions of diversity components are warranted.

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Appendix A. Supplementary material

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