University of Nevada, Reno

Untangling patterns of plant and arthropod diversity in a fire-adapted ecosystem: Dynamic relationships between fire, scale, and trophic interactions in longleaf pine forests.

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ABSTRACT

Fire has been a part of terrestrial ecosystems since the Silurian Period and is an essential process for maintaining both ecosystem function and biological diversity in fire dependent ecosystems, such as longleaf pine (*Pinus palustris* Mill.). In these frequently burned fire-dependent ecosystems, fire frequency is positively correlated with high species diversity. The removal of fire from the landscape initiates a shifting ecosystem trajectory where fire-adapted species are replaced by other species assemblages, yielding an alternative stable state.

Patterns of biodiversity and the mechanisms driving them must be thoroughly understood to guide an effective monitoring and resource management programs. I describe cross-scale spatial and temporal patterns of plant and arthropod diversity, identification of the grain size and sampling effort to maximize efficiency in monitoring diversity, fine-scale examination of the role of fire in driving patterns of diversity, and mechanisms linking fire, biological diversity, and forest structure. Understanding these links mechanistically is critical for both guiding management now and in the future under the novel conditions expected with global change.

By sampling arthropod diversity and creating linkages to plant diversity at multiple spatial and temporal scales, I could better understand how both plant and animal communities, as well as their interactions, are organized with respect to presence or absence of fire. My quantification of multiple dimensions of diversity, including taxonomic and functional metrics, reflect the current focus of biodiversity researchers in both basic and applied realms and further provides novel insight into debates about neutrality and

correlations between diversity, stability, resiliency, and ecosystem services The interaction diversity measure is particularly important for linking biodiversity to the trillions of dollars of ecosystem services that are provided by natural ecosystems, since those services are all due to a diverse mix of ecological interactions. Taken together, these metrics of diversity can act as more sensitive indicators of how ecological communities respond to management activities, disturbances, or global change parameters.

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"If I have seen further, it is by standing upon the shoulders of giants."
Sir Isaac Newton

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INTRODUCTION

Fire has been a part of ecosystems since at least the Silurian and is an influential disturbance that should be included in development of basic ecological theory (Pausas and Keeley 2009). Longleaf pine (*Pinus palustris*) forests are dependent on fire to maintain ecosystem function and stability (Mitchell et al. 2009, O'Brien et al. 2008, Kirkman et al. 2004). Similar to other disturbances, the key mechanisms by which fire affects communities and ecosystems are attenuation of competition between understory species; reduction of surface fuels, allowing for seedling establishment; and addition of nutrients to the soil (Glitzenstein et al. 2003, Mitchell et al. 2006). Fires burning in longleaf pine forests are typically high-frequency, low-intensity and predominately run through surface fuels. These fires are a major driver of the high levels of small-scale alpha diversity found in longleaf pine stands, with up to fifty understory plant species possible in a single square meter (Palmquist et al. 2015, Kirkman et al. 2001, Walker and Peet 1984).

Fire also shapes patterns of fine-scale community assembly. Neutral processes as outlined in Hubbell's (2001) Unified Neutral Theory of Biodiversity (UNTB), seem to be a likely determinant of plant community assembly in frequently burned longleaf forests because the high-levels of richness occur at scales too small for niche differentiation in the relatively uniform sandy soils. While there has been much debate about whether or not neutral processes and niche differentiation can together affect community structure (Adler et al. 2007, Gavel et al. 2006) or whether UNTB is best treated as a null model (Alonso et al. 2006), the frequently burned longleaf pine community might be the closest example of a truly neutral community.

Using an autonomous agent model with UNTB-based assumptions, Loudermilk et al. (in review) successfully simulated plant community richness and revealed that community dynamics were not predicted by species traits and UNTB parameters alone could explain fine-scale groundcover assemblages, supporting the notion that understory plants are neutral communities at high fire frequencies. Since local patches of high severity fire can act as a random agent of mortality at fine scales (O'Brien et al. 2016), understory plant community structure could indeed be driven by demographic stochasticity rather than competitive processes in these longleaf stands. Frequent fire provides an element of randomness and keeps competition in check. As sites burn less frequently, neutral processes break down and competition-based dynamics are more likely to contribute to community assembly and fire sensitive species can flourish.

Today's longleaf pine forests are a fraction of their historic range. Deforestation, logging, and development have reduced forested areas and decades of fire exclusion policies and practices have given competitive advantage to faster growing tree species that thrive in the absence of fire, resulting in extensive habitat degradation and reductions in biodiversity (Mitchell et al. 2006, Frost 2006, Noss et al. 1995). Conservation of longleaf ecosystems has even greater significance as they are also characterized by high levels of endemism and are located within a global hotspot of biodiversity (Noss et al. 2014). Prescribed burning or allowing wildfires is critical for continued function of longleaf ecosystems. A focus of longleaf ecological research and management is to uncover mechanisms linking fire to diversity and detail how that diversity is distributed across the landscape. More generally, ecological theory would benefit from a better understanding of relationships between fires and diversity, while for conservation biology the focus is on making links to management objectives focused on the remaining stands of longleaf.

While we know fire contributes to the maintenance of plant biodiversity, little is known about the impacts of fire on arthropods in longleaf pine. Arthropods are the most abundant and species-rich group of animals in terrestrial systems and have tremendous impacts on ecological processes such as nutrient cycling, net primary production, and food web structure (Weisser and Siemann 2004). Clearly arthropods should be included in studies of fire-diversity-ecosystem function relationships, and since arthropod diversity is tightly linked to changes in diversity of plants, mammals, and birds (Tallamy 2004), arthropod-fire relationships should be relevant to entire communities. Results from studies on how fire affects insects vary due to differences in weather, burn intensity, focal taxa studied, and season of burn. In any investigation it is necessary to consider not only that burning has differential ecological effects based on ecosystem sensitivity and/or dependency on fire, but also the variant spatial distribution of fire across these different landscapes in terms of extent (i.e. 10 ha^2 vs. 10,000 ha^2), fuel heterogeneity within fire perimeters which affects burn patchiness and localized energy release (i.e. direct mortality), and distance to refugia. As a result, potential insect adaptations towards fire will also be taxa specific and highly variable. Therefore, it has been suggested that inclusion of multiple taxa is necessary for more accurate assessments of fire effects on arthropod diversity (Pryke and Samways 2012).

Numerous ecological studies have focused on how disturbance affects taxonomic diversity, especially for plants. However, an additionally informative response variable could be diversity of interactions between plants and animals. Interaction diversity is the number of interactions linking species together into dynamic biotic communities (Thompson 1996, Janzen 1974). For this metric of diversity, the calculation of richness and diversity indices are based on links between interacting species in the network rather than species alone. Interaction diversity is affected by taxonomic, genetic, and functional diversity and the quantitative measure of interaction diversity provides significant insight into correlations between diversity, stability, productivity, and ecosystem services (Dyer et al. 2010).

Analyzing how trophic interaction network topology responds to disturbance, or in the case of longleaf pine communities, how interaction diversity responds to variation in fire frequency, is an effective approach for generating informative patterns about the relationship between disturbance and biodiversity. For example, interaction networks with greater connectivity are indicative of higher levels of functional stability within an ecosystem (Thyliankis et al. 2010). From the perspective of the insurance hypothesis (Yachi and Loreau 1999), in a high interaction diversity community, if a disturbance removes one of several predator species controlling a dominant herbivore species, then other predators are still able to control that herbivore population, and ecosystem function is maintained by this redundancy.

Understanding the relationship between diversity and ecosystem stability has been topic of debate for decades (Hooper et al.2005). While the most commonly used metric of diversity is typically measures of species richness, the definition of stability is more broad and complex. Ecosystem stability can refer to response and resilience of various abiotic and biotic parameters to perturbations (Hooper et al. 2005), which is relevant to frequently-disturbed ecosystems, such as the longleaf pine. The diversity-stability relationship posits that increased levels of diversity will result in greater community stability due to the asynchronous responses to disturbance by individual species in a community, providing functional redundancy and a greater response diversity (Elmqvist et al. 2003). Resilient stability has been documented in diverse communities that have experienced repeated disturbances (van Ruijven and Berendse 2010), but this has not been examined carefully using any measure of interaction diversity (Dyer et al. 2010). Therefore, investigations of both taxonomic and interaction diversity as well as community responses along a gradient of fire return intervals in the frequently burned longleaf pine ecosystem may provide additional insight and support for diversity-stability theory.

The overall theme of my dissertation research is to investigate patterns and processes of plant-arthropod diversity changes in a fire-adapted landscape.
My research focuses on three specific objectives:

1. Quantify patterns of diversity in understory vegetation and arthropod communities across a continuum of spatiotemporal scales in relation to disturbances by prescribed fire.
2. Investigate specific, small-scale mechanisms that contribute to changes in diversity patterns.
3. Examine patterns of trophic interaction diversity and test hypotheses about how fire and spatial scale affect trophic networks.

The above objectives are addressed within the following six data chapters. Chapter one involves an investigation into the spatial distribution of plant diversity culminating in the identification of the scale and intensity at which sampling efficiency is maximized. Chapter two details a mechanism by which remotely sensed forest fuels individually contribute to understory plant diversity. Chapter three is an amalgamation of two studies that looked at arthropod community responses over time to a singular fire, as well as arthropod diversity patterns within defined fire frequency regimes. Chapter four highlights observations made during prescribed fires and focuses on what happens to less-mobile arthropods during burns**.** Chapter five describes a new taxonomic species record for North America discovered in longleaf pine while documenting arthropod diversity post-burn. Finally, chapter six represents a wholistic view of the ecosystem through quantification of interaction diversity between plants, insect herbivores, and their natural enemies along a fire return interval gradient.

CHAPTER 1

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

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ABSTRACT

Improving precision in quantifying patterns in understory plant diversity improves efficiency in monitoring design and more accurate measures of success 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 northwest 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 m^2) scales. Furthermore, we found the sampling effort at this 1 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 to any ecosystem where investigations into the individual contributions of diversity components are warranted.

INTRODUCTION

Enumerating and monitoring biodiversity is a critical activity for land managers, allowing for the assessment of management activities and evaluating the effects of disturbance on biotic communities (Lindenmayer and Likens 2010, Legg and Nagy 2006). Effective monitoring helps to elucidate patterns in temporal and spatial variation in plant diversity which informs strategies to maintain diversity. Successful monitoring programs are targeted, meaning they are objective driven by testing *a priori* hypotheses which allow for adaptive management strategies (Nichols and Williams 2006, Yoccoz et al. 2001). Furthermore, a monitoring program's efficacy is enhanced by measures of success in terms of 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 of species abundance, impact of management interventions, and the impact of invasive species colonization (Enquist and Enquist 2012). Monitoring efforts are costly, with data collection being the main expense (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 have a large negative effect on the accuracy of landscape or regional scale inferences (Eigenbrod et al. 2011). As a result, generalization from targeted monitoring efforts are limited to the local scale at which data is 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).

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 (Crawley and Harral 2001, Condit et al. 2002). 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 (1960, 1972) 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, the more informative metric of diversity for managers is species turnover or beta diversity because it 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 beta 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 for the creation of a standardized plot size to in which to sample for biodiversity monitoring programs.

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. 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 with the goal of testing 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. In other words, we sought to increase plant sampling efficiency by identifying the spatial grain (i.e. plot size) that maximizes the capture of diversity for monitoring activities over the fixed extent of Eglin Air Force Base (AFB; Sandel 2015) - what is the best sampling scale to assess management effects on biodiversity?

METHODS

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, is home to over half of the remaining stands of old-growth longleaf pine and is actively managed by frequent prescribed fire (Varner et al. 2005, Holliday 2001, Hiers et al. 2007). 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).

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).

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 over 200 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.

Datasets

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 in reference, restoration, and plantation management status. All plots in the program were sampled one year following management activities including 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, 1m^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).

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 - 0.4 meters 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 can be analyzed individually or in combination with others to examine 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).

Statistical Analyses

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 within plot diversity, β1 = mean diversity between plots, β2 = mean diversity between plots of increased 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 the Hill numbers or species equivalents, 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 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.

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 indicated there are deterministic processes favorable to diversity, whereas negative differences indicate processes that diminish diversity.

Rarefaction

Sample-based rarefaction analyses were performed to estimate the number of samples needed to adequately capture diversity following Chao et al. (2014). Using 2,698 1m^2 quadrats from the monitoring dataset and 36 samples from the inventory dataset at 1 m^2, 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 (Chao and Jost 2012). All statistical analyses were performed in R (v.3.2.3, R Development Core Team 2013).

RESULTS

Within both datasets, richness and α-diversity increased with area sampled (Table 1, Figure 1). β-diversity and pairwise distance between plots in both datasets was highest between 1m^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 (Figure 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 in the inventory dataset at the smallest scale and at all spatial scales in the monitoring dataset (Table 1).

Looking at individual components of diversity with increasing 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 (Figure 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 (Figure 3).

Further analysis by rarefaction based on $1m^2$ plots, indicated mean slope began to asymptote around 60 samples (Figure 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 value 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 variation, indicating plots are conserved in composition over time while restoration and plantation plots have more variation in turnover (Figure 5).

DISCUSSION

The positive relationship between spatial scale and within plot diversity in terms of richness and α-diversity (Figures 1 and 3) indicated that rare and relatively less abundant species provide a considerable contribution 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 (Figures 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, providing evidence that common species have a broad distribution across Eglin AFB (Figure 3).

The fact that β-diversity was maximized at the smallest scale supports a focus on $1m^2$ plots as an appropriate size for monitoring changes in understory plant diversity in this particular ecosystem. Utilizing this framework, rarefaction results based on $1\text{-}m^2$ 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, over 200 individual plots were being sampled and understory vegetation quantified in areas up to $8m^2$ (Hiers et al. 2007). The identification of suitable sampling size and intensity represent an increase in sampling efficiency for continued monitoring efforts (Yoccoz et al. 2001). However, management occurs at the stand level which can encompass hundreds of individual management units, 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 in assessments of the efficacy of management intervention. β-diversity is a quantitative measure of spatial background variation that informs temporal assessments; this measure 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).

Frequently burned low-latitude coniferous forests often have a high diversity understory. Longleaf pine forests and woodlands are classic examples with exceptionally high diversity 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 2015, Kirkman et.al 2004, 2001, Walker and Peet 1984). Although our inferences are limited to Eglin AFB (Lindenmayer and Likens 2010), results 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, Loudermilk et al. 2018, in review, 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 could be applied to any ecosystem where investigations into the individual contributions of diversity components are warranted.

ACKNOWLEDGEMENTS

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TABLES

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 reported in species equivalents of the 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.

Inventory Dataset

Partition	Scale (m^2)	Richness	**α-Diversity (H')**	**β-Diversity (H')**	**Distance**
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

Partition	Scale (m^2)	Richness	**α-Diversity (H')**	**β-Diversity (H')**	**Distance**
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

FIGURE LEGENDS

Figure 1: Species area relationship between richness and sampling grain for the monitoring and inventory datasets. Richness and area are represented using the log scale.

Figure 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.

Figure 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.

Figure 4: Mean slope of 2,698 rarefaction curves based on 1 m^2 samples from the monitoring dataset calculated at various sampling intensities. 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.

Figure 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 indicated by dashed lines. Diversity reported in species equivalents using inverse Simpson’s (1/D).

FIGURES

Figure 1

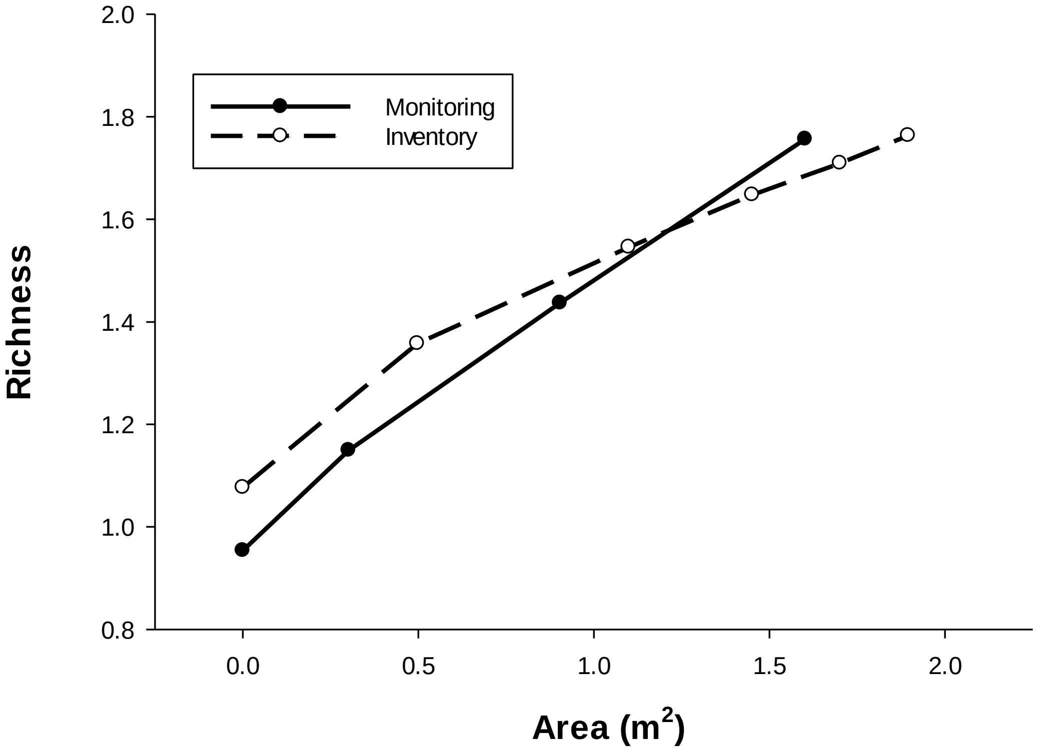


Figure 2

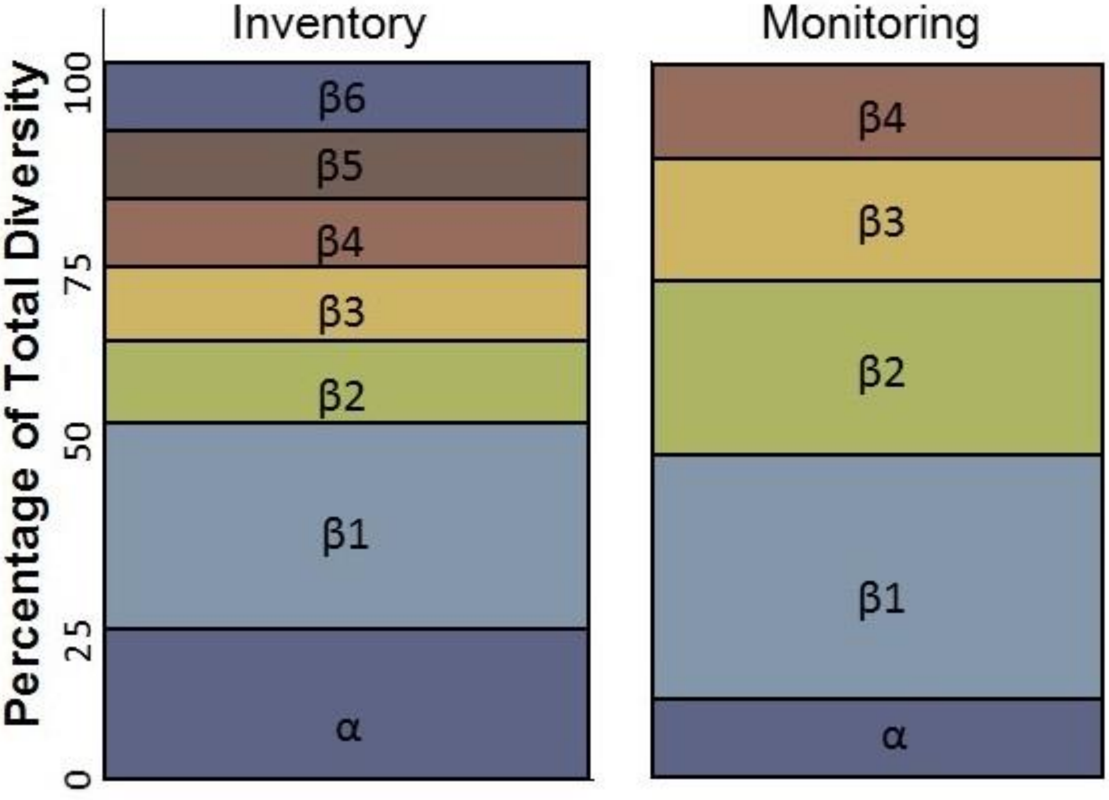

Inventory
Monitoring
Percentage of Total Diversity
100
75
50
25
0
β6
β5
β4
β3
β2
β1
α
β4
β3
β2
β1
α

Figure 3

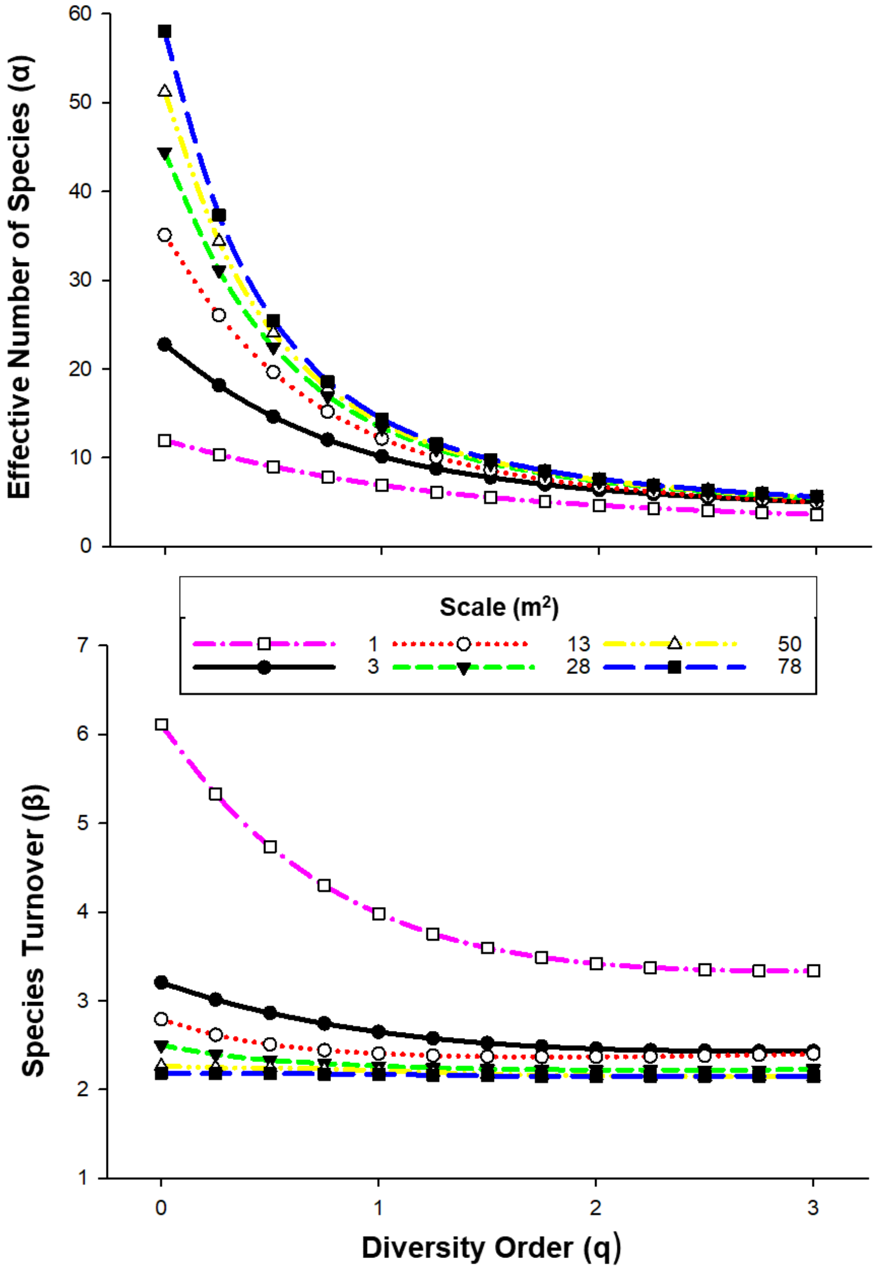

Effective Number of Species (α)
60
50
40
30
20
10
0
Scale (m²)
1
3
13
28
50
78
Species Turnover (β)
7
6
5
4
3
2
1
0
1
2
3
Diversity Order (q)

Figure 4

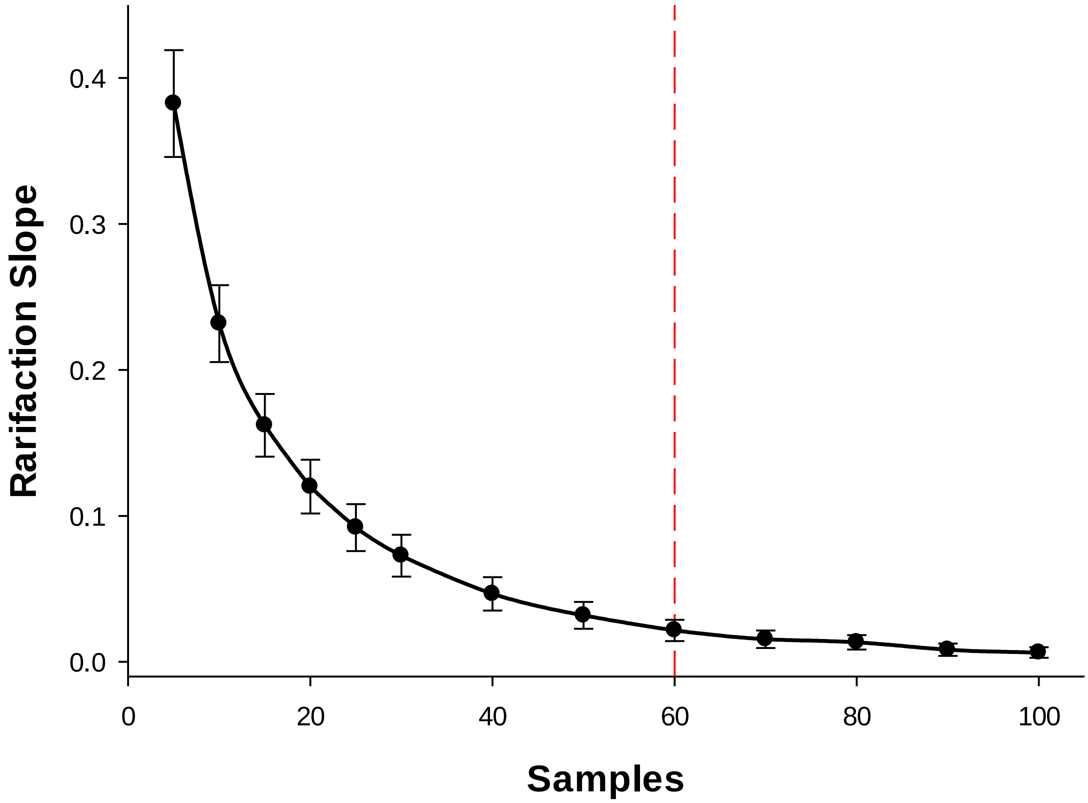
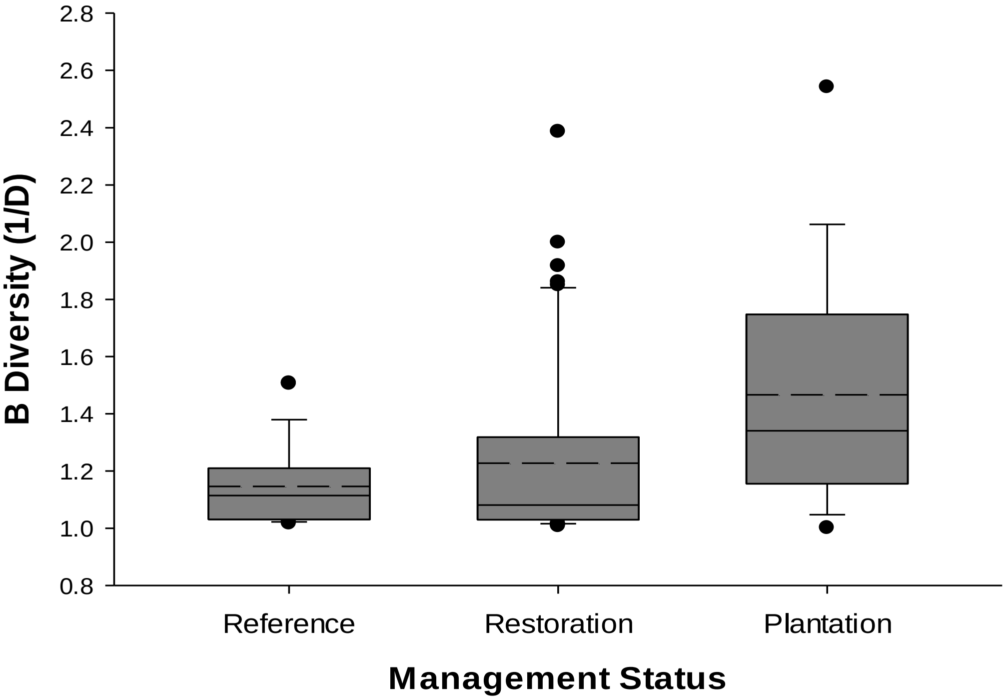


Figure 5


2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
B Diversity (1/D)
Reference
Restoration
Plantation
Management Status

SUPPLEMENTAL INFORMATION

Table S1: List of most commonly occurring plant species from the monitoring and inventory datasets (121 inventory, 376 monitoring)

Acalypha gracilens
Acer rubrum
Agalinis divaricata
Agalinis fasciculata
Agalinis setacea
Ageratina aromatica
Albizia julibrissin
Aletris lutea
Allium canadense
Andropogon glomeratus
Andropogon gyrans
Andropogon spp.
Andropogon ternarius
Andropogon virginicus
Anthaenantia rufa
Anthaenantia villosa
Aristida condensata
Aristida lanosa
Aristida longespica
Aristida mohrii
Aristida palustris
Aristida purpurascens
Aristida stricta
Aristolochia serpentaria
Arundinaria gigantea
Asclepias cinerea
Asclepias connivens
Asclepias humistrata
Asclepias tuberosa
Asclepias verticillata
Axonopus fissifolius
Baccharis halimifolia
Balduina angustifolia
Balduina uniflora
Baptisia calycosa
Baptisia lanceolata
Digitaria ciliaris
Digitaria cognata
Digitaria filiformis
Diodia teres
Diospyros virginiana
Drosera capillaris
Drosera tracyi
Elephantopus elatus
Eragrostis spectabilis
Eragrostis spp.
Eragrostis virginica
Erechtites hieraciifolius
Erigeron strigosus
Eriogonum tomentosum
Eryngium yuccifolium
Eupatorium compositifolium
Euphorbia discoidalis
Euphorbia floridana
Euthamia caroliniana
Froelichia floridana
Galactia erecta
Galactia regularis
Galactia volubilis
Galium hispidulum
Galium pilosum
Gaura filipes
Gaylussacia dumosa
Gaylussacia frondosa
Gaylussacia mosieri
Gelsemium sempervirens
Gratiola hispida
Gymnopogon ambiguus
Gymnopogon brevifolius
Hamamelis virginiana
Helianthemum carolinianum
Helianthus radula
Pinus clausa
Pinus palustris
Pityopsis aspera
Pityopsis graminifolia
Pityopsis oligantha
Polygala lutea
Polygala nana
Polygala polygama
Polygonella gracilis
Polypremum procumbens
Prunus angustifolia
Prunus caroliniana
Prunus serotina
Pseudognaphalium obtusifolium
Pteridium aquilinum
Pterocaulon pycnostachyum
Pycnanthemum pycnanthemum
Quercus chapmanii
Quercus geminata
Quercus incana
Quercus laevis
Quercus laurifolia
Quercus margaretta
Quercus minima
Quercus myrtifolia
Quercus spp.
Rhexia alifanus
Rhexia lutea
Rhexia mariana
Rhexia petiolata
Rhus copallinum
Rhynchosia cytisoides
Rhynchosia reniformis
Rhynchospora baldwinii
Rhynchospora grayi
Rhynchospora plumosa

Berlandiera pumila
Bigelowia nudata
Bigelowia nuttallii
Bulbostylis ciliatifolia
Bulbostylis warei
Calamintha coccinea
Calamintha dentata
Callicarpa americana
Carex tenax
Carphephorus odoratissimus
Castanea pumila
Ceanothus microphyllus
Centrosema virginianum
Chamaecrista fasciculata
Chamaecrista nictitans
Chaptalia tomentosa
Chrysoma pauciflosculosa
Chrysopsis gossypina
Clematis reticulata
Clethra alnifolia
Cliftonia monophylla
Clitoria mariana
Cnidoscolus stimulosus
Commelina erecta
Conyza canadensis
Crataegus michauxii
Croptilon divaricatum
Crotalaria purshii
Crotalaria rotundifolia
Croton argyranthemus
Ctenium aromaticum
Cyperus croceus
Cyperus filiculmis
Cyperus retrofractus
Cyperus retrorsus
Cyrilla racemiflora
Dalea pinnata
Danthonia sericea
Desmodium ciliare
Desmodium floridanum
Desmodium laevigatum
Desmodium lineatum
Hieracium gronovii
Houstonia procumbens
Hypericum crux-andreae
Hypericum gentianoides
Hypericum hypericoides
Hypericum tetrapetalum
Hypoxis juncea
Ilex ambigua
Ilex cassine
Ilex coriacea
Ilex decidua
Ilex glabra
Ilex opaca
Ilex vomitoria
Ionactis linariifolius
Iris verna
Juncus dichotomus
Juncus marginatus
Kalmia hirsuta
Krameria lanceolata
Lachnocaulon beyrichianum
Lechea sessiliflora
Lespedeza capitata
Lespedeza hirta
Lespedeza repens
Liatris elegans
Liatris graminifolia
Liatris secunda
Liatris tenuifolia
Licania michauxii
Linum floridanum
Lobelia brevifolia
Ludwigia virgata
Lupinus diffusus
Lyonia lucida
Magnolia grandiflora
Magnolia virginiana
Mimosa quadrivalvis
Minuartia caroliniana
Mitchella repens
Muhlenbergia capillaris
Myrica cerifera
Rubus cuneifolius
Ruellia caroliniensis
Salvia azurea
Sassafras albidum
Schizachyrium sanguineum
Schizachyrium scoparium
Schizachyrium tenerum
Scleria ciliata
Scleria triglomerata
Scutellaria incana
Serenoa repens
Sericocarpus tortifolius
Seymeria cassioides
Sideroxylon lanuginosum
Silphium compositum
Sisyrinchium nashii
Smilax auriculata
Smilax bona-nox
Smilax glauca
Smilax laurifolia
Smilax pumila
Smilax smallii
Solidago odora
Sorghastrum nutans
Sorghastrum secundum
Sporobolus compositus
Sporobolus junceus
Stillingia sylvatica
Stipulicida setacea
Stylisma patens
Stylosanthes biflora
Symphyotrichum adnatum
Symphyotrichum concolor
Symphyotrichum dumosum
Tephrosia chrysophylla
Tephrosia florida
Tephrosia hispidula
Tephrosia spicata
Tephrosia virginiana
Tradescantia hirsutiflora
Tragia smallii
Tragia urens

Desmodium strictum
Dichanthelium aciculare
Dichanthelium acuminatum
Dichanthelium chamaelonche
Dichanthelium commutatum
Dichanthelium ensifolium
Dichanthelium oligosanthes
Dichanthelium ovale
Dichanthelium portoricense
Dichanthelium ravenelii
Dichanthelium sphaerocarpon
Dichanthelium spp.
Dichanthelium strigosum
Opuntia humifusa
Opuntia pusilla
Panicum verrucosum
Panicum virgatum
Paronychia patula
Paspalum praecox
Paspalum setaceum
Pediomelum canescens
Penstemon australis
Persea borbonia
Persea palustris
Physalis angustifolia
Physalis arenicola
Trichostema setaceum
Triplasis americana
Vaccinium arboreum
Vaccinium corymbosum
Vaccinium darrowii
Vaccinium spp.
Vernonia angustifolia
Viola palmata
Vitis rotundifolia
Xyris brevifolia
Xyris caroliniana
Xyris elliottii
Yucca filamentosa

Multiplicative Partitioning of Diversity

Partitioning of diversity into independent alpha and beta components can be done in more than one manner. In additive partitioning (β = γ - α), beta represents the magnitude of difference between samples at each spatial scale. An alternative method is multiplicative partitioning (β = γ/α), where beta represents the distinct amount of species within each spatial scale (Marion et al. 2015). While the definition of the beta diversity component differs with method, quantitatively the values remain unchanged with the exception of a reduction in beta at the smallest scale (Table S2).

Table S2: Empirical multiplicative partitioning of plant diversity in the inventory (N=9) and monitoring (N= 201) datasets collected at Eglin AFB.). α and β-diversity reported in species equivalents of the Shannon’s index (H’).

Inventory Dataset		
Scale (m^2)	**α-Diversity (H’)**	**β-Diversity (H’)**
1	4.94	-
btwn 1	-	3.98
3	10.76	2.65
13	12.94	2.41
28	14.15	2.26
50	14.71	2.21
78	15.23	2.17
Monitoring Dataset		
Scale (m^2)	**α-Diversity (H’)**	**β-Diversity (H’)**
1	4.47	-
btwn 1	-	13.60
2	6.12	9.77
8	8.88	6.81
100	16.17	5.24

CHAPTER 2

Overstory-Derived Surface Fuels Mediate Plant Species Diversity in Frequently Burned Longleaf Pine Forests*

*Citation: Dell, J.E., Richards, L.A., O'Brien, J.J., Loudermilk, E.L., Hudak, A.T., Pokswinski, S.M., Bright, B.B., and Dyer, L.A. (2017) Overstory derived surface fuels mediate plant species diversity in frequently burned longleaf pine forests. Ecosphere 8(10), e01964.

Keywords: *Pinus palustris*, species richness, prescribed fire, overstory derived fuels, structural equation model, LiDAR

ABSTRACT

Frequently burned low-latitude coniferous forests maintain a high diversity understory. Longleaf pine (*Pinus palustris* Mill.) forests and woodlands have exceptionally high diversity at fine scales and very frequent fire return intervals (1-3 years). Furthermore, the positive association between high-frequency, low-intensity surface fires and high species richness in longleaf pine ecosystems is well documented but poorly understood. Recent studies have demonstrated additional linkages between specific fuel assemblages and fire intensity at small spatial scales. In this study, we build upon both patterns by using long term data sets to examine the relationship between fire and specific fuel types, and how the combination of these two elements contributes to ground cover species diversity. We used 11 years of monitoring data from longleaf pine forests at Eglin Air Force Base, Florida (USA) to parameterize a structural equation model (SEM) that examines causal relationships between fuels and fire history on ground cover plant diversity. Overstory derived fuels, including pine needle litter, pine cones and other 10-hour and 100-hour woody fuels, had the greatest positive impact on diversity in relatively open-canopied, frequently-burned reference stands. A second model examined surface fuel components originating from the forest overstory as characterized by airborne LiDAR and found that pine needle litter was positively associated with canopy density. Our parameter estimates for causal relationships between easily measured variables and plant diversity will allow for development of management models at the stand scale while being informed by fuels measured at the plot scale.

INTRODUCTION

Frequently burned coniferous forests often share a similar forest structure globally, with a monospecific overstory of pine, a sparse midstory, and a high diversity understory. These forests are widely distributed around the lower latitudes of the Northern Hemisphere and constitute a global conservation concern (Veldman et al. 2015). Longleaf pine (*Pinus palustris* Mill.) forests represent an archetype of these systems and are dependent on very frequent fires for maintenance of biodiversity and ecosystem function (O'Brien et al. 2008, Kirkman et al. 2004, Mitchell et al. 2009, Glitzenstein et al. 2003). For any terrestrial ecosystem, fire can be a catalyst of community interactions via attenuating competition between plant species, allowing for seedling establishment by reducing surface fuels, and adding nutrients to the soil (Mitchell et al. 2006, 2009, Kirkman et al. 2004, 2001). Fires burning in longleaf pine forests are typically high-frequency, low-intensity disturbances that predominately run through surface fuels and understory shrubs with little effect on the canopy. These frequent fires are the major force driving the high levels of ground cover plant diversity found in longleaf pine stands, with up to 50 species m^{-2} (Palmquist et al. 2015, Kirkman et al. 2004, 2001, Walker and Peet 1984).

Today longleaf pine forests occupy a fraction of their historic range. Deforestation, logging, and development have reduced forested areas, and decades of fire exclusion policy and practice have given a competitive advantage to faster growing tree species that thrive in the absence of fire. Combined, these events have resulted in extensive habitat degradation and reductions in biodiversity (Mitchell et al. 2006, Frost

2006, Noss et al. 1995). Conservation of longleaf pine ecosystems is also warranted because these forests possess high levels of endemism and are located within a proposed “global hotspot” of biodiversity (Noss et al. 2015). While effective management via prescribed burning or low-intensity wildfire is critical for continued health of the longleaf pine ecosystem, mechanistic models of the role of fire in maintaining diversity need considerable development. Variation in fire intensity within burned areas has been found to be a driver of plant community function and structure, including high ground cover diversity and horizontal or vertical distribution of plant and debris layers within a forest, or “forest structure” (Hiers et al. 2009, Wiggers et al. 2013, O’Brien et al. 2016a, Loudermilk et al. 2016). One possible source leading to variation in local-scale fire intensities is the variation in distributions of surface fuels, or fuels found near the forest floor (O’Brien et al. 2016a). These fuels are derived from the overstory, midstory, and understory. This variation in fuel sources and effects on fire intensities is a critical part of the “ecology of fuels” concept (Mitchell et al. 2009), which focuses on cycles of impacts of forest structure and vegetative composition on fuel heterogeneity, which in turn affects fire behavior and community responses to fire, including changes in plant diversity and long-term forest structure.

Heterogeneity in fuels across the landscape directly affect fire intensities in these surface fire regimes. Woody fuels, such as pine cones and branches, are spatially associated with pine tree distribution and temporally associated with changing canopy cover (tree mortality, growth), and episodic cone production cycles (Boyer 1998). These dense fuels burn for extended periods with up to 12 times more energy release than finer fuels (grasses, forbs, shrubs) and vary at scales less than $0.25m^2$ (O’Brien et al. 2016a, Mitchell et al. 2009, Fonda and Varner 2004). Understory derived fuels such as shrubs and deciduous oaks comprise a significant portion of the litter on the forest floor, and volatile shrubs and other fine fuels, such as pine needle litter, grasses, forbs, and legumes are important for carrying fire across the landscape. Using the spatially explicit wildland 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. We know that fire is the critical element in maintaining biodiversity in longleaf pine forests (Kirkman et al. 2004), thus understanding the causal mechanisms linking plant community composition to fuel type and understanding the contribution of various fuel types to fire effects are major goals for ecology (Thaxton and Platt 2006, Gagnon et al. 2010, Mitchell et al. 2009).

The issue is that different fuels burn simultaneously, making it difficult through retrospective assessments alone to disentangle each fuel type’s contribution to the ecological consequences of fire. New empirical methods utilizing infrared thermography can capture in-fire, spatially resolved, radiative heat flux and relate these patterns to fire effects (O’Brien et al. 2016a, 2016b). While these data are informative at fine scales, they need to be linked to coarser scale patterns in forest structure in order to investigate the impacts of forest management on different scales of diversity (Hiers et al. 2003). Structural Equation Modeling (SEM) is a statistical approach that allows the testing of hypothesized causal relationships among complex associations of variables (Shipley 2016, Grace et al. 2015). It is especially useful for testing proposed causal linkages between fine scale fuel measurements and landscape scale patterns of forest structure. For example, the use of active remote sensing, specifically airborne light detection and ranging (LiDAR), can provide detailed information on forest structure at the landscape scale and can be used to test hypotheses about how such forest structure affects diversity at smaller scales.

In this study, we created SEMs to examine associations between fire, fuels, and plant species richness at fine scales (<1 m^2) in frequently burned longleaf pine forests of northwest Florida and then assessed whether LiDAR maps of forest structure over a landscape (100’s of km^2) could predict relevant patterns of fuel types driving patterns of diversity. We initially tested for associations among the number of fires and the distribution of six common litter fuel types. We hypothesized that spatiotemporally variable distribution of these common fuel types drives heterogeneous fire behavior. We also examined associations between each fuel type and associated ground cover diversity. From this, we modeled the indirect effects of fire on ground cover diversity mediated by fuel type. Finally, at a coarser scale we investigated and modeled how forest structure predicts each fuel type (Hudak et al. 2016a, 2016b). Combined, we were able to test causal relationships responsible for maintaining high levels of plant diversity in longleaf pine ecosystems based on fuel types and forest structures that are common in other forests with similar structure and burn frequency.

The statistical modeling was guided by two primary objectives; first to model the effects of burning different fuel types on variation in ground cover plant diversity in reference stands, and second to evaluate the ability to up-scale patterns of fuel, fire, and diversity to a management context through linkages to overstory forest structure as characterized by airborne LiDAR data and the field measurements of the fuel bed. While many fire modeling applications consider litter as a uniform component of surface fuels for increased ease of simulation (Keane 2015), separating out the specific types of litter can be highly informative when assessing fuel type contributions to fire effects. We used 11 years of vegetative monitoring data (collected by the Natural Resources Branch, Eglin Air Force Base, Hiers et al. 2007) from forested longleaf pine stands to parameterize a SEM comprised of hypothesized relationships between fire history, plant diversity, and ground measured surface fuel variables, represented by commonly occurring types of litter: woody fuels, oaks and shrubs, forbs, grasses, saw palmettos, and longleaf pine needles (Table 1). In an effort to better create a foundation upon which to understand the ecology of fuels, we focused our efforts on regularly-burned reference stands. A second SEM was then created to assess LiDAR as an effective indicator of the origin of these fuel components within these reference plots (Table 1).

As a secondary objective relevant to both the generality and context dependency of our findings, we tested for differences in modeled effect size between vegetative community types and stand quality. To examine litter effects in the two predominant community types, we extended our main model by running the SEM separately through plots located in sandhills and flatwoods. In a second comparison, we examined how effect sizes vary along a gradient of stand quality represented by increased fire return intervals found in sandhill plots located within reference, restoration, and plantation stands.

METHODS

Study area

All data were collected at Eglin Air Force Base (EAFB) located in the Gulf Coastal Plain of the Florida panhandle, USA. Eglin AFB is over 180,000 ha in size, is home to over half of the remaining stands of old-growth longleaf pine, and is actively managed by frequent prescribed fire (Varner et al. 2005, Holliday 2001, Hiers et al. 2007). The climate is typified by hot, humid summers with frequent thunderstorms and lightning strikes, mild winters, mean annual temperature of 18.3°C, and 1580 mm of annual precipitation (Provencher et al. 2001). The area has relatively little topography (0-100 m ASL) and is dominated by well-drained Lakeland series soils.

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. The sandhills are also comprised of shrubby hardwoods species such as turkey oak (*Quercus laevis*), blackjack oak *(Q. incana*), and persimmon (*Diospyros virginiana*), however these species are generally absent from the flatwoods. Most of the hardwoods are in a shrub state, as they are continuously top-killed by fire. The ground cover vegetation contains most plant species and is dominated by several grasses, such as wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium*), broomsedge (*Andropogon virginicus*), as well as dwarf huckleberry (*Gaylussacia dumosa*), evergreen blueberry (*Vaccinium darrowii*), runner oak (*Quercus minima*), saw palmetto (*Serenoa repens*), and gallberry (*Ilex glabra*).

Eglin AFB contains a diverse array of longleaf pine forests including reference stands representing high-quality habitat with relatively open understories, stands undergoing the process of ecological restoration via chemical and mechanical treatments towards reference conditions, and plantations of longleaf pine. Current EAFB natural resource policies of increasing fire frequency for Red-Cockaded Woodpecker (*Picoides borealis*) management began in 1995. Reference plots in the dataset experienced fire nearly every other year, from at least the mid 1990’s through the time of data collection with variation in fire return intervals of 1.6 – 6 years, while restoration and plantation plots had a broader range of fire return intervals of 2.1 – 18 years.

Monitoring data

The Eglin AFB Natural Resources Branch monitoring program began collecting fuel and vegetation data in 201, one-hectare plots randomly located across the base in 2001. All plots in the program were sampled one year following management activities including 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, as well as collection of fuels data. During each sampling event, fuels were measured every 10m along two, 50-m point-intercept transects and averaged for each plot. Woody fuels were counted when they intercepted transects by time lag classes (Brown 1974), with intact pine cones and 2.54 – 7.62 cm diameter branches recorded as 100-hour fuels, and broken cones and branches 0.635 –

2.54 cm in diameter designated as 10-hour fuels. Total litter depth was measured at each intercept, litter type determined from original form, and then tallied by individual litter class including: longleaf pine needles, grasses, saw palmetto, oaks, shrubs, and forbs. The depth of the combined fermentation (Oe) and humus (Oa) layers, also known as duff, was recorded along transects. Live fuels for these same vegetation classes were also recorded with shrubs and oaks being classified into volatile and non-volatile categories. At the time of fuel measurement, grass litter was closely associated with live fuels as bunch grass represents a combination of some percentage of live fuels and litter. Additionally, a tally was taken along transects of intercept with bare ground. Historical records were used to determine fire frequency over the last 40 years. Additional details about the EAFB monitoring protocol can be found in Hiers et al. (2007).

In this study, we analyzed a subset of plots that were sampled between 2001 and 2012 in the EAFB monitoring dataset including those located within reference stands (35 plots: 26 sandhill and 9 flatwoods), monitoring plots within sandhill restoration stands (67 plots), and plots located within sandhill plantation stands (30 plots). Because individual plots were sampled numerous times over the 11 years, measured fuel variables and species richness were averaged across time for each plot prior to analyses. While live fuels are an important consideration in terms of fuel continuity and fire intensity, they are consumed quickly when burned, resulting in brief residence times and little effect on plant mortality (Wenk et al. 2011, Gagnon et al. 2015, Fill et al. 2016). Therefore, we focused our analyses exclusively on dead and downed surface fuels. Furthermore, oak litter, which included both deciduous and evergreen species, was combined with shrub litter prior to analyses. For ease of interpretation (Table 1), fuels were converted into mass per area (kg m^{-2}) measurements with woody fuels following conversions outlined in Brown (1974) and litter loadings as described in Pritchard et al. (2013).

LiDAR data

Airborne LiDAR uses high-frequency laser pulses to measure distances between the LiDAR sensor and underlying vegetation and terrain. When flown over a forest, LiDAR characterizes the forest structure as a 3-dimensional cloud of points. These points resemble the spatial configuration of forest vegetation within the canopy, understory, and near the ground surface (Hudak et al. 2009). LiDAR processing for forest management often entails reducing the 3-dimensional data of canopy elements to metrics of canopy height and density that can serve as informative inputs into predictive models (Hudak et al. 2016a). By calculating these metrics within defined monitoring plot areas, the LiDAR metrics can serve as predictor variables to the observational data collected at finer spatial scales.

LiDAR data covering Eglin AFB were downloaded from a public repository (http://www.nwfwmdLiDAR.com/); data were collected in 2006-2008 at mean return densities ranging from 0.5-2.9 points m^{-2}. Returns were classified as ground or nonground and normalized to height above ground using the ‘lasground’ tool of the LAStools software program (Isenburg 2015). The ‘lascanopy’ tool was then used to generate canopy density metrics within four vertical strata (Table 2) calculated at two levels: 1) within the discrete plot footprints where monitoring data were collected in the field (i.e., model level) and 2) within contiguous 30-m x 30-m grid cells across the entirety of Eglin AFB (i.e., map level). The calculated density metrics for the overstory, midstory, understory, and surface strata were then used as predictor variables in a SEM investigating the vertical canopy strata of origin for the plot measured litter categories described above. In addition, Eglin AFB managers maintain a geodatabase of fire history that includes the fire boundary, date of burn, and fuel type for each fire that has occurred at Eglin AFB since 1972. We summarized this geodatabase to produce a GIS layer that consisted of a 30-m x 30-m raster of the number of fire occurrences between 1995 and 2012 (Figure 1). Additional details regarding LiDAR processing and analysis are available in Hudak et al. (2016a).

Structural equation model formulation

The first structural equation models were formulated to test hypothesized causal relationships between fire, fuels, and ground cover plant species diversity (Table 1A). Ubiquitous fuel types found in longleaf pine forests may contribute to ground cover diversity when consumed by fire; these fuel types include woody fuels (10-hour and 100-hour time lag fuels, which includes both weathered and recently fallen pine cones), and litter (longleaf pine needles, shrub and oak, grass, forb, and saw palmetto). A second approach focused on the hypothesis that remotely sensed LiDAR metrics predict how forest layers (overstory, midstory, understory, and surface vegetation) contribute to the different fuel types examined in the first path analysis (Table 1B).

For all path models, all variables were standardized, transformed to meet assumptions of normality, and models were run using the lavaan package in R (Rossell 2012, R Core Team 2015). All models were specified based on our predictions (Table 1), estimated by maximum likelihood (ML), and tests of model fit followed guidelines outlined in Shipley (2016). Model fit indices including chi-square and Akaike Information Criterion (AIC) were used to determine the specific model that best fit the data after removal of non-significant associations, with P-values of greater than 0.05 considered to indicate a good model fit. Direct effects were estimated directly using standardized path coefficients, while indirect effects of fire through each fuel type were simply the products of direct effects for each pathway from fire to diversity.

The SEM was run separately for flatwoods and sandhills reference plots to test differences in fuel contributions based on the two main vegetative community types found at EAFB. Additionally, the same SEM approach was utilized for different sandhill forest stand types: reference sites, restoration sites, and longleaf pine plantations to represent a gradient in forest quality. Because vegetation structure and composition are tightly linked with frequency of fire in longleaf systems, the gradient was based on lower number of fires and longer fire return intervals (FRI). Over the 18-year period of fires at Eglin AFB used in the models, the mean FRI was 3.19, 5.89, and 7.87 years in the reference stands, restoration sites, and plantations, respectively.

RESULTS

Fuel-diversity model

Fuel type had varied effects on species richness following fire in reference plots. Insignificant pathways with negligible effect on diversity included both shrub and oak litter, and forb litter, which were removed from the final model to improve model fit (Full model: AIC = 649; Reduced model: AIC = 407), yielding a parsimonious model that was a good fit to the data (Figure 2; $\chi 2$ = 5.5; df = 7; P = 0.60). As hypothesized (Table 1), regular burning had negative effects on all litter types; longleaf pine litter (standardized path coefficient (spc) = -0.23; slope (β = -1.8), grass litter (spc = -0.01; β = -0.03), saw palmetto litter (spc = -0.11; β = -0.13) and woody fuels (spc = -0.12; β = -0.96). Additionally, all fuel types were significantly and negatively (i.e. in their consumption) associated with ground cover plant species diversity (Table 3, Figure 2). Specifically, saw palmetto litter had a significant negative effect on diversity (spc = -0.15, β = -0.68) followed by woody fuels (spc = -0.44, β = -0.31), grass litter (spc = -0.37, β = -0.31), and longleaf pine litter (spc = -0.39, β = -0.25).

Overall, the indirect effects of fire on species richness, based on the products of measured direct effects from fire, through fuel type, to diversity, were positive for all fuel types (Table 3). The burning of overstory derived fuels had the greatest positive effects on ground cover diversity with longleaf pine needle litter producing the largest indirect effect (spc = 0.09; β = 1.2) as well as pine cones and other woody fuels (spc = 0.05; β = 0.74). Saw palmetto litter also exerted a positive effect on species richness (spc = 0.02; β = 0.22; Table 3). The burning of grass litter provided little contribution to ground cover diversity (spc = 0.004; β = 0.03). Summing these individual contributions together results in a clear mechanism for the well documented positive association between fires and ground cover diversity in longleaf pine systems and is indicated by the significant indirect effect (spc = 0.16, β = 2.2) as shown in the black dashed line in Figure 2.

LiDAR model

In longleaf pine ecosystems, fuels are contributed from different forest layers, including the overstory (trees above 5 m), understory (plants 0.5 - 1.37 m height), and surface vegetation (0-0.5 m). Since reference stands do not typically have a well-developed midstory, this component of the forest canopy was excluded from the model. In reference stands, LiDAR density measurements were effective in representing most fuel types based on correlations with forest structure (χ^2 = 3.98; df = 12; P = 0.98, Figure 3). Overstory density was a strong predictor of pine needle litter (spc = 0.36; β = 0.77) and understory density predicted shrub and oak litter (spc = 0.20; β = 0.74). Overstory LiDAR was not an effective indicator of woody fuels (spc = -0.18; β = -0.36). The double headed arrows indicate unestimated relationships, including a positive correlation between near surface LiDAR (0-0.5 m) and forb litter (spc = 0.25; β = 0.36), a weaker association with saw palmetto litter (spc = 0.28; β = 0.07), and even less with grass litter (spc = 0.02; β = 0.03).

Forest community type

In a separate SEM, we compared fuel contributions in flatwood and sandhill reference plots (Figure 4). Pine needles provided the greatest positive contribution to diversity in sandhills with 0.34 kg m^{-2} fuel loads resulting in a larger increase in diversity (spc = 0.09; β = 1.3) compared to flatwoods (spc = 0.03; β = 0.50). However, in flatwoods the burning of 0.16 kg m^{-2} of woody fuels resulted in a larger increase to diversity (spc = 0.16; β = 1.94) with a smaller increase in sandhills (spc = 0.04; β = 0.59). There was little difference in direction of the contribution of saw palmetto and grass litter between the sandhills and flatwoods; however, the magnitude of indirect effect on ground cover diversity increases for each fuel type in the flatwoods (Figure 4). Fuel loading of 0.02 kg m^{-2} of saw palmetto litter had little effect in sandhills (spc = 0.002; β = .03) but a slight diversity increase in flatwoods (spc = 0.12; β = 0.18). Finally, grass exerted negative influences in sandhills (spc = -0.06; β = -0.925) and flatwoods (spc = -0.06; β = -0.69).

Stand quality

Finally, we ran the SEM for differing longleaf forest types located exclusively within intact sandhill communities. The model included reference sites, plots in the midst of restoration, and plots located within plantation stands to represent a gradient of stand quality based on fewer total burns and increased fire return intervals. Approximately 0.30 kg m^{-2} loading of pine needles had a positive effect on diversity in reference (spc = 0.09; β = 1.3) and restoration plots (spc = 0.05; β = 0.73), and negligible negative effect in plantations (spc = -0.001; β = -0.007). Similarly, woody fuels had a positive effect in reference stands (spc = 0.04; β = 0.59) and negative effect in restoration plots (spc = -0.007; β = -0.11).

However, woody fuels were the only fuel type to have a positive effect on diversity in plantations (spc = 0.09; β = 2.0). Additionally, there was a positive correlation between woody fuel loading and fire return interval with 0.08 kg m^{-2} in reference sites increasing to 0.22 kg m^{-2} in plantations. With a small contribution in terms of fuel loading (0.02 kg m^{-2}), saw palmetto had a positive influence on diversity in sandhill reference plots (spc = 0.002; β = 0.03), a negligible effect in restoration plots (spc = -0.05; β = -0.003), and was associated with declines in diversity in plantations (spc = -0.04; β = - 0.82). Finally, a 0.08 kg m^{-2} loading of grass litter had little effect in restoration plots (spc = 0.001; β = 0.007), and negative effects in reference plots (spc = -0.06; β = -0.93), and plantations (spc = -0.03; β = -0.62; Figure 5).

DISCUSSION

Our results that overstory derived fuels help maintain plant diversity in longleaf pine forests are not surprising, but it is important to recognize that these effects are dependent on fuel types, which in turn are affected by the forest structure. These results should be generalizable to other coniferous forests based on the variety of systems we examined, including flatwood and sandhill communities and a reasonable gradient of stand quality experiencing variable total burns and fire return intervals. Similarly, the predictive power of LiDAR data for detecting these positive effects of fuels on diversity is likely to be similar in other forested systems and clearly demonstrates the indirect effects of basic forest structure characteristics on overall plant diversity.

Overstory-derived fuels

This study documented a positive influence of overstory on diversity in EAFB’s characteristically open stands with canopy openness remaining similar across reference (51.5%), restoration (42.4%), and plantation stands (50.9%) (Figure 5, Hiers et al. 2007, Battaglia et al. 2003). In stands with few historical fires and which were undergoing restoration by tree removal, Platt et al. (2006) suggested that a dense overstory of longleaf pine hindered ground cover plant species diversity due to light limitation. In the stands we studied, light limitation was unlikely a factor. This was demonstrated by Hiers et al. (2007), where forest floor development, not canopy light interception, was the main driver of the loss in plant biodiversity. This occurs when forests remain unburned. We found that the overstory-derived fuels in stands maintained by frequent fire, provided a significant contribution to species richness, particularly in flatwoods. We also found that longleaf pine litter exerted the greatest positive influence on ground cover richness in reference plots, where a mean fuel loading of 0.34 kg m^{-2} added a mean of 1.2 plant species with each additional fire (Table 3, Figure 2).

Overstory-derived fuels, mainly longleaf pine needles and cones on the forest floor, are a critical component of longleaf pine fire ecology (Mitchell et al. 2009, Loudermilk et al. 2012, Hiers et al. 2009, O'Brien et al. 2016a). Pine needles facilitate fire by supplying a continuous and highly combustible fuel bed (Rebertus et al. 1989, Loudermilk et al. 2012, Hiers et al 2009). Ellair and Platt (2013) found that pine litter acted synergistically with other fuels to increase fire intensity, resulting in longer heating duration of understory vegetation, and increased consumption of hardwood litter. Additionally, variation in the amount of pine litter had significant impact on fire behavior and fire effects, which in turn alters forest structure by determining the prevalence of midstory hardwood species, like the turkey oak (*Quercus laevis*) (Hiers et al. 2009, Ellair and Platt 2013).

We found that woody fuels, which include small branches and pine cones derived from the longleaf canopy, significantly promoted ground cover diversity when burned, adding a mean 0.74 species in reference stands at loadings of 0.1 kg m^{-2} (Table 3, Figure

2). Woody debris burns at high intensity, releasing 12 times the radiative energy as fine fuels (O’Brien et al. 2016a) and has significantly longer residence times (Loudermilk et al. 2012, 2014, Fonda and Varner 2004). These ‘hot spots’ of fire intensity can influence understory mortality as plants near woody debris have been found to be 3 times as likely to die from increased energy release from burning woody fuels (O’Brien et al. 2016a). These patches of increased mortality likely result in open areas of bare mineral soil for seedling establishment of both herbaceous species and longleaf pine resulting in increased variation in recruitment patterns post fire (Wiggers et al. 2013, O’Brien et al. 2008).

When fire is removed from the landscape, litter and woody fuels accumulate on the forest floor contributing to an O horizon, decomposing to fermentation (Oe) and humus (Oa) layers, which is also described as duff or forest floor (Kreye et al. 2017, Varner et al. 2005). Hiers et al. (2007) showed that understory health is inversely linked with the amount of duff that has accumulated in the absence of fire in longleaf pine. Consistent with that study, we found that species richness was indirectly reduced with elevated litter in plantations, resulting from longer fire return intervals (Figure 5). This was not the case, however, with the consumption of woody fuels. Pine cones and woody fuels, especially during dry conditions, increase the probability of duff ignition and consumption (Kreye et al. 2017). When fire is reintroduced, the increased fire intensity and radiative energy released by woody fuels (O’Brien et al. 2016a, Kreye et al. 2013), coupled with longer residence times (Loudermilk et al. 2012, Fonda and Varner 2004), will result in the consumption of duff and exposure of bare mineral soil for seedling establishment (Wiggers et al. 2013, Hiers et al. 2009, O’Brien et al. 2008). Therefore, woody fuels consumption may be a key process maintaining diversity in forested stands characterized by more extended fire return intervals (Figure 5). Additionally, the positive effects on vegetative diversity resulting from burning woody debris such as pine cones, may be significantly greater following longleaf pine masting events when individual trees may produce > 100 cones (Brockway 2015, Mitchell et al. 2009). This potentially high contribution to diversity by woody debris consumption in flatwoods (Figure 4) and pine plantations (Figure 5) warrants further investigations into issues such as the fire radiative heat flux necessary to create open space in shrubby flatwoods or the consumption of duff in pine plantations (Varner et al. 2005).

Detrital fuels

Although oak litter often has been assumed to be associated with decreased plant diversity (Thaxton and Platt 2006, Provencher et al. 2001), oak litter did not appear to be associated with lower levels of diversity in this study. This may be due to the inclusive nature of this litter category which incorporated oaks with variable flammability. Pyrophytic oaks such as turkey oak (*Quercus laevis),* are characterized by production of flammable leaf litter which burns with similar characteristics to longleaf pine needles (Varner et al. 2015, Kane et al. 2008). In contrast, fire-avoiding oak species such as live oak (*Quercus virginiana)* produce non-flammable litter which prevents fire from reaching the plant (Varner et al. 2016). Removal of deciduous oaks in xeric sandhill habitat have often been the inappropriate target of intense management, but recent evidence suggests that they are benign at worst and can actually add to conservation value of stands (Hiers et al. 2014). Our study confirms that xeric oaks native to sandhill habitat at Eglin have little influence on patterns of understory diversity. Moreover, data now suggest deciduous oaks facilitate longleaf pine regeneration on xeric sites (Loudermilk et al. 2016). Additional insights may be gained if these flammable guilds were separated in future analyses.

Graminoids are a common feature of longleaf pine plant communities (Holliday 2001, Kirkman et al. 2001), yet we found that variation in grass litter had negligible influence on ground cover diversity in reference and restoration stands (Figure 5). Furthermore, grass litter had an intermediate negative effect in pine plantations (Figure 5). In the absence of fire, grass litter can accumulate, limiting light resources and competitively excluding lower stature plants (Walker and Peet 1984). Grasses do play a role in fire ecology by contributing an abundant fine fuel source that dries out quickly, is highly ignitable and combusts rapidly, thus promoting fire spread (Simpson et al. 2016, Fill et al. 2016). Grasses have also been shown to have similar peak heat flux to pine litter when burned, although residence times are shorter (Fill et al. 2016, Loudermilk et al. 2014). Therefore, grasses represent a self-perpetuating fuel load that also limits hardwood growth and reduce post-fire competition (Ripley et al. 2015, Simpson et al. 2016). The small effect size in our models suggests that the positive association that exists between grass and ground cover plant species diversity may be more likely due to subtle factors, such as pine needles that are caught and suspended on bunch grasses, contributing to aeration and continuity of the fuel bed (Loudermilk et al. 2014).

Saw palmetto litter had a small, positive effect on diversity in reference stands and flatwoods, and a negligible effect in restoration stands and sandhills (Figures 4, 5).

Although the effect was minimal, this litter may be an important source of depleted soil nutrients such as nitrogen (N) and phosphorus (P) to plants. While unmeasured and outside the scope of this study, nutrient input post-fire is highly variable (Lavoie et al. 2014) and has been shown to stimulate the growth of understory species (Certini 2009).

Relevance to management

Understanding how forest structure interacts with fire management to conserve biodiversity is critical for conservation in pine-grassland ecosystems (Mitchell et al. 2006, O'Brien et al. 2008). This study shows plant diversity is linked to variation in fire intensity from canopy derived overstory fuels. While it is documented that fire intensity is linked to heterogeneous fuels at fine spatial scales (Mitchell et al. 2009), it is important to also understand the role of forest structure – which is the most common attribute targeted by conservation managers. The focus of management for specific forest structure alone without understanding mechanisms has led to negative conservation outcomes (Hiers et al. 2014). This study provides a mechanistic link and documents specific patterns between the burning of canopy-derived fuels and high levels of ground cover diversity commonly found in high-quality, frequently burned longleaf pine forests. Such patterns allow managers to discern the critical elements of forest structure, fuels, and subsequent fire behavior that drive biodiversity conservation in managed forests.

In light of changing climate and future uncertainty, long-term monitoring data are critical for understanding how ecosystems change in response to management (Jackson and Hobbs 2009, Hiers et al. 2016). As demonstrated here, long-term monitoring programs are critical in identifying and quantifying these changes, however, high-quality monitoring often require substantive labor and financial inputs that cannot be sustained. Therefore, using remote sensing metrics to link to observed fuels data can contribute to more cost-effective management models conducted at broader scales or fill breaks in monitoring data acquisition. Our results from the LiDAR SEM demonstrate specific linkages and contributions of fuels from various vertical canopy strata within the forest structure using landscape scale LiDAR data and plot scale ground observations (Figure 3).

While our fuel-diversity model (Figure 2) explained over half of the variance in plant species richness, there are other factors that contribute to the fire-fuels-diversity relationship. Incorporating empirical fire intensity data could give increased insight to these models, by adding causal linkages between fuel types and heat flux. Improvements in the capture of empirical fire intensity data (O'Brien et al. 2016a, 2016b) are providing insights into explicit contributions of fuels to fire behavior and can help understand dose dependent mortality (Sparks et al. 2017). Our analysis was also limited to common litter types and down woody debris. Other fuel variables, such as the structure and composition of live fuels and respective moisture content or fuel complexes (i.e. fuel cells) could also contribute to ground cover diversity through modification of the combustion environment, especially if measured immediately pre-ignition.

Conclusion

Feedbacks from fuels differentially affecting fire behavior and intensity leading to post-fire community dynamics and forest structure at multiple scales are a critical principle of fire ecology (Mitchell et al. 2009). The path models in this study illustrated distinct forest structure and fuel attributes that drive biodiversity patterns at both plot and landscape scales. This study represents a new way of exploiting long-term monitoring datasets collected at the stand level by linking fuel characteristics and plant diversity. Our results reinforce the concept of the “ecology of fuels” where studies initially focused on the fine-scale linkages (Mitchell et al. 2009, O’Brien et al. 2016a, 2016b, Wiggers et al. 2013), where this study expands this work to incorporate landscape structure and processes. This relationship is part of a more general property of disturbance in natural systems; as disturbances impact ecosystems at regular intervals, there should be predictable associations between vegetation in disturbed patches, fire (or other disturbance) intensity, and fuel composition. While neutral theory and empirical results still provide challenges to the utility of the “intermediate disturbance hypothesis” (Hubbell et al. 1999), it is clear that moderate disturbances, such as surface fires, contribute to biodiversity via complex pathways. Further investigations examining hypotheses focused on post-fire establishment and community composition will continue to be relevant to major biodiversity theories, such as the neutral theory of biodiversity (Hubbell 2001) or the continuum hypothesis (Gravel et al. 2006).

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TABLES

Table 1: A) Names and descriptions of variables in the SEMs with associated hypotheses. Model variables represent monitoring data collected over the years 2001 – 2102 by Jackson Guard, Eglin AFB, FL. B) LiDAR metrics collected during 2006 and 2008. Data ranges are for plots located within longleaf pine reference stands.

(A)Variable	**Descriptor**	**Range**	**Associated Assumptions/Hypotheses**
Longleaf Pine Litter	Detection of long-needle conifer litter found along fuel transect	0.22 – 0.58 kg m^{-2}	The burning of pine needles will be positively associated with diversity by acting as continuous, highly flammable fuel source conducive for fire spread.[1]
Woody Fuels	Detection of 10-hour and 100-hour fuels (including pine cones) found along fuel transect	0.04 – 0.29 kg m^{-2}	Pine cones will have longer residence burn times creating open spaces on forest floor for seedling establishment which will increase diversity.[1,2]
Shrub and Oak Leaf Litter	Detection of litter from shrub and oak species: *Ilex spp., Quercus laevis, Q. minima, Smilax spp., Gaylussacia spp., Vaccinium spp.*	0.06 – 0.45 kg m^{-2}	Volatile shrubs will increase diversity by providing increased fuel flammability for more complete burns. Oak leaves will increase diversity by acting as a continuous, highly-flammable surface fuel.[3,4]
Forb Litter	Detection of forb contributed litter found along fuel transect	0.01 – 0.13 kg m^{-2}	Forbs will contribute to fuel bed depth providing surface level fuels which will moderately increase diversity.[5]
Grass Litter	Detection of litter from all graminoid species	0 – 0.27 kg m^{-2}	Grass litter will increase diversity by providing another source of continuous fine fuels.[1]
Saw palmetto Litter	Detection of litter from *Serenoa repens*	0 – 0.09 kg m^{-2}	Saw palmetto is highly flammable and will provide to added fire intensities and increase diversity with post-fire soil nutrient input.[6]
Number of Fires	Number of prescribed fires conducted from 1995 - 2012	3 – 11 fires (FRI: 1.2 -4.3 Yrs.)	Frequent fire will have negative associations with fuels as they are consumed by burning.[2]
Ground cover Diversity	Mean species richness of ground cover vegetation (<1.37 m in height)	49 – 84 species in 400m^2 subplots	Response variable in all SEMs[5,7-9]

(B)Variable	**Descriptor**	**Range**	**Associated Assumptions/Hypotheses**
Overstory Density	LiDAR: % vegetation located above heights of 5m.	11.1 – 36.5%	Overstory LiDAR will indicate canopy derived fuels.[10,11]
Understory Density	LiDAR: % vegetation located between heights of 0.5 - 1.37m.	0.3 – 17.4%	Understory LiDAR will indicate the amount of shrub and oak litter fuels.[10,11]
Surface Density	LiDAR: % vegetation located between heights of 0 – 0.5m	52.1 – 81.3%	Surface level LiDAR will indicate fuels on or near the forest floor.[10,11]

Supporting Citations: [1]Loudermilk et al 2012 [2]Mitchell et al 2009 [3]Hiers et al 2014 [4]Ellair and Platt 2013 [5]Kirkman et al 2001 [6]Shaffer and Mack 2010 [7]Palmquist et al.2015 [8]Kirkman et.al 2001 [9]Walker and Peet 1984 [10]Hudak et al. 2016a [11]Hudak et al. 2016b

Table 2: LiDAR canopy density metrics.

Metric Name	Height of LiDAR Returns (m)	Measurement
d1	≥ 0 and < 0.5 meters	Surface vegetation
d2	≥ 0.5 and < 1.37 meters	Understory
d3	≥ 1.37 and < 5 meters	Midstory
d4	≥ 5 and < 30 meters	Overstory

Table 3: Indirect effects of fire on diversity for each fuel type. Total effects are calculated as the sum of the product of individual standardized path coefficients (spc). Significant pathways denoted with asterisk. Effect size in terms of species richness (S) also shown as indicated by calculated slope (β) from fuel-diversity SEM.

Fuel	**Fire Effect on Fuel**	**Fuel Effect on Diversity**	**Indirect Effect (spc)**	**Indirect Effect (S)**
Longleaf Pine Litter	-0.23*	-0.39*	**0.09**	**1.17**
Woody Fuels	-0.12	-0.44*	**0.05**	**0.74**
Grass Litter	-0.01	-0.37*	**0.004**	**0.03**
Saw palmetto Litter	-0.11	-0.15	**0.02**	**0.22**
Total Effects of Fire on Diversity			**0.16***	**2.16**

FIGURE LEGENDS

Figure 1: Map of research locations at Eglin Air Force Base (EAFB) in northwestern Florida, USA. Shaded areas correspond to the number of fires occurring at EAFB during the 1995-2012 period and red dots indicate location of reference monitoring plots within EAFB.

Figure 2: Structural equation model including hypothesized causal relationships between the burning of individual fuel categories and plant diversity in longleaf pine reference stands. In fire dependent ecosystems such as the longleaf pine forest, greater numbers of fires have positive effects on ground cover species richness. This relationship is mediated by the composition and consumption of different surface fuel types, including longleaf pine litter, pine cones and other 10-hour and 100-hour woody fuels, grass litter, and saw palmetto litter. Numbers next to lines are the standardized path coefficients (spc). Line thickness corresponds to strength of path coefficient and asterisks denote statistical significance ($P < 0.05$). Black dashed line represents total indirect effects of fire on diversity as indicated in Table 3. The model is a good fit to the data ($\chi2 = 5.2$; df = 7; $P = 0.64$) as indicated by P-values larger than 0.05. Insets within fuel types are partial correlation plots of the paths between individual fuel types and species richness while accounting for the effects of all other fuel types.

Figure 3: SEM illustrating LiDAR detection of forest layers as predictors of each individual fuel category in longleaf pine reference stands. LiDAR data measured at various canopy heights (m) in the forest overstory, understory, and surface returns are hypothesized to predict various surface fuels that commonly occur within longleaf pine

forests. Positive correlations are shown in black and negative correlations in red. Numbers next to lines are the standardized path coefficients (spc). Line thickness corresponds to strength of path coefficient and asterisks denote statistical significance ($P < 0.05$). Surface fuels originating from surface returns are modeled as covariates; indicated by double-headed arrows. The hypothesized model provides a good fit to the data ($\chi^2 = 3.98$; df = 12; $P = 0.98$).

Figure 4: Effect of different fuel types on diversity in each plant community. Indirect effect or combined effect of burning each fuel type on ground cover diversity, measured here as species richness (S) for reference sandhill and flatwood plant communities.

Figure 5: Effect of the burning of each fuel type along a gradient of ecosystem quality. Indirect effects are calculated as the combined effect of burning each fuel type as it relates to ground cover diversity, measured here as species richness (S). Gradient of ecosystem quality in reference, restoration, and plantation sandhill stands are based on longer periods between burning. Numbers in parentheses next to each stand type refer to mean fire return interval.

FIGURES

Figure 1

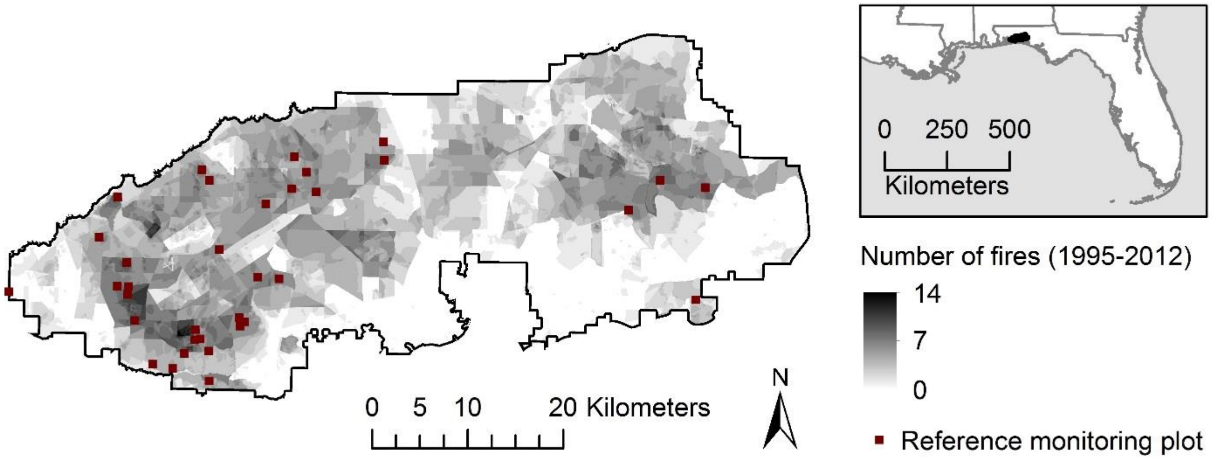


Figure 2

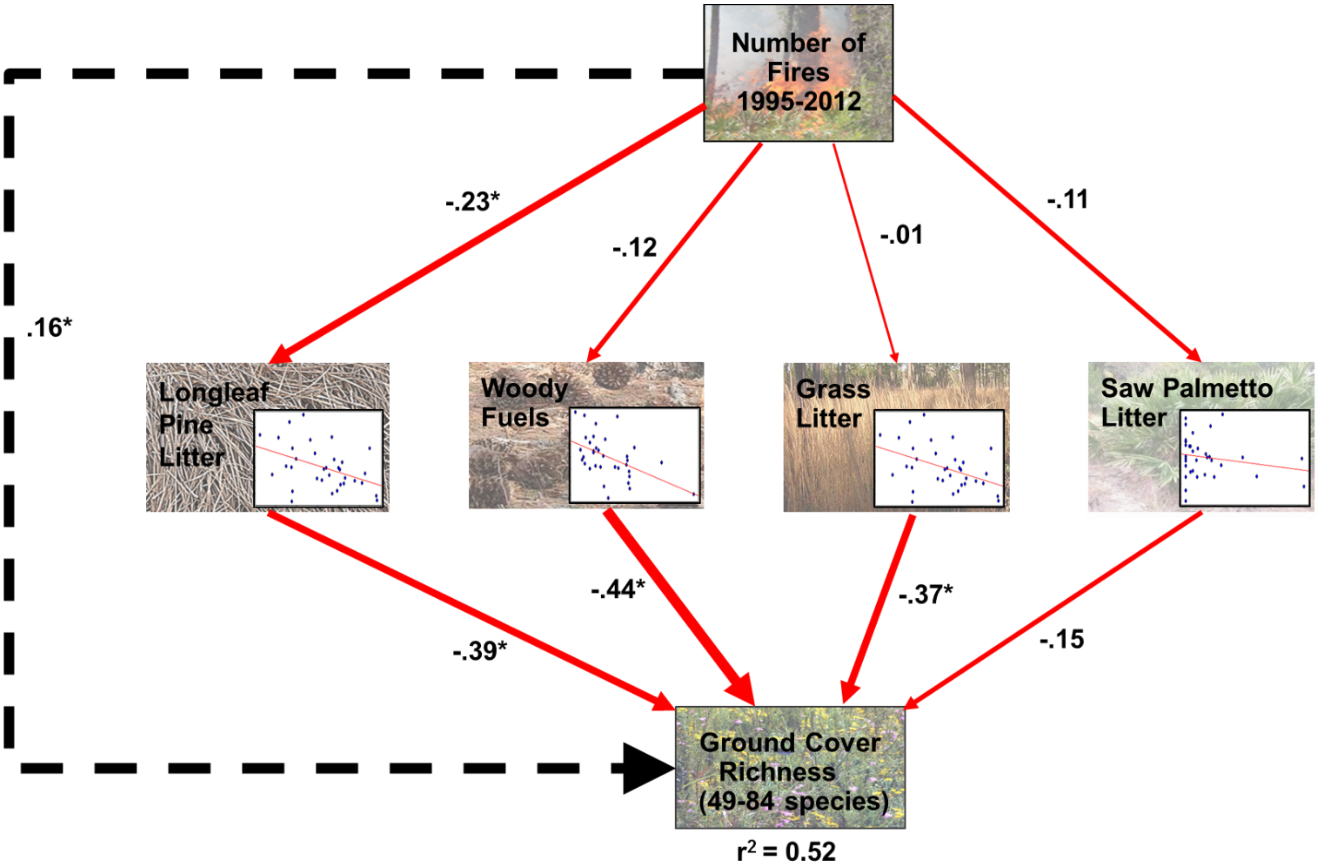

Number of Fires 1995-2012
-.23*
-.12
-.01
-.11
.16*
Longleaf Pine Litter
Woody Fuels
Grass Litter
Saw Palmetto Litter
-.44*
-.37*
-.39*
-.15
Ground Cover Richness (49-84 species)
r2 = 0.52

Figure 3

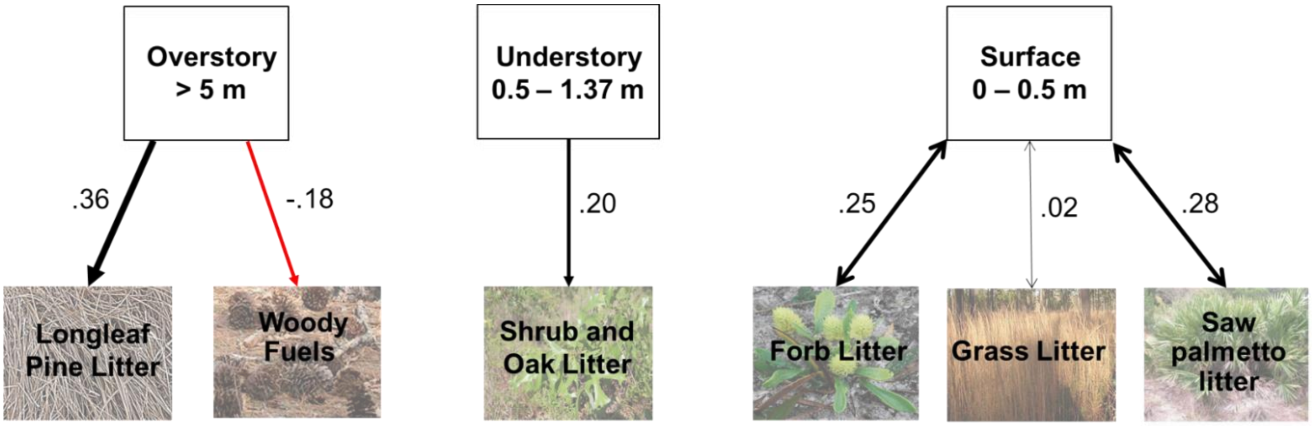

Overstory
> 5 m
Understory
0.5 – 1.37 m
Surface
0 – 0.5 m
.36
-.18
.20
.25
.02
.28
Longleaf Pine Litter
Woody Fuels
Shrub and Oak Litter
Forb Litter
Grass Litter
Saw palmetto litter

Figure 4

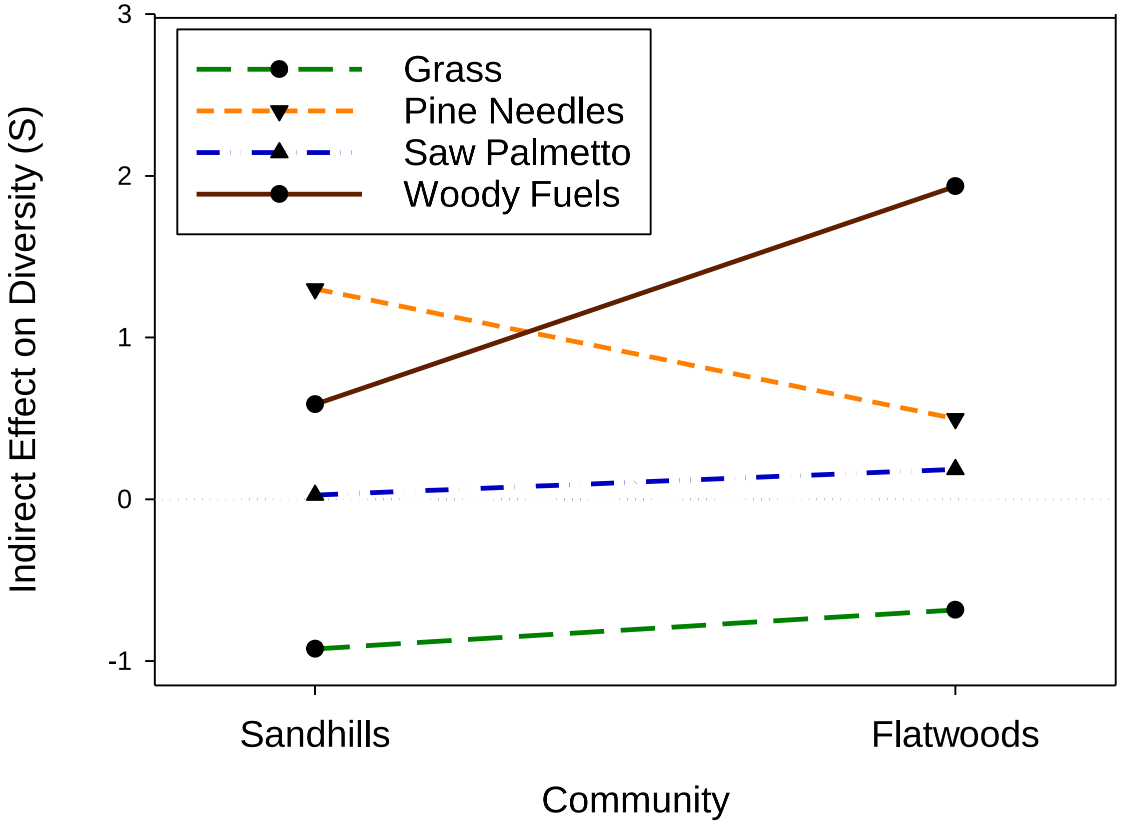
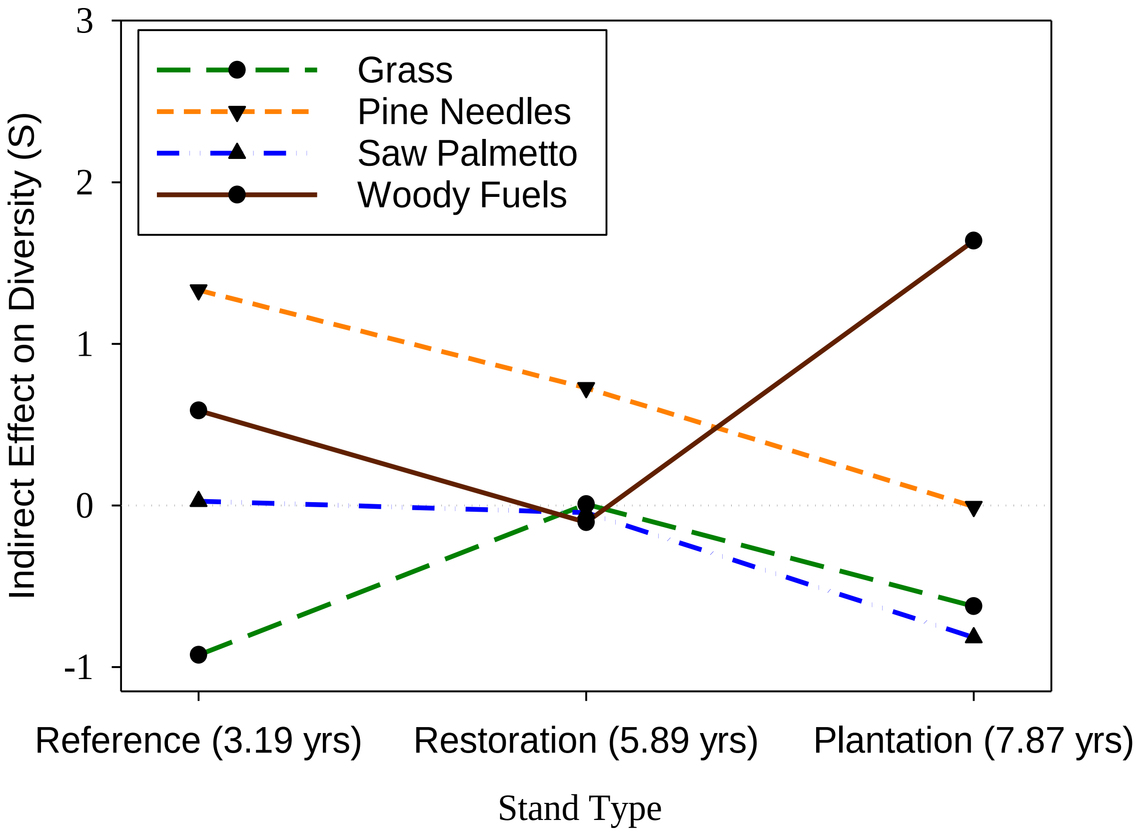

Grass
Pine Needles
Saw Palmetto
Woody Fuels
Indirect Effect on Diversity (S)
3
2
1
0
-1
Sandhills
Flatwoods
Community

Figure 5


Grass
Pine Needles
Saw Palmetto
Woody Fuels
Indirect Effect on Diversity (S)
3
2
1
0
-1
Reference (3.19 yrs)
Restoration (5.89 yrs)
Plantation (7.87 yrs)
Stand Type

CHAPTER 3

Quantifying the effects of burning on the diversity of arthropods in a fire-adapted longleaf pine (*Pinus palustris*) forest.

INTRODUCTION

Fire is a natural and key disturbance mechanism in terrestrial ecosystems, especially those that are adapted to regular burning. Ecological benefits include nutrient cycling, serotinous seed dispersal, reduction of competitive species, and creation of habitat heterogeneity (Pausas and Keely 2009). However, fire may also result in negative ecological consequences such as habitat alteration and destruction, increased predation, and release of competitive species (DeBano et al. 1998). There has been a wealth of research performed on the effects of fire on a multitude of biological communities such as all vegetative guilds, birds, mammals, and aquatic taxa, yet general consensus regarding fire's effect on arthropod communities remains lacking (New 2014).

In the numerous studies investigating the effects of fire on arthropod communities in fire adapted systems there are no clear patterns in the response of arthropods to fire (Pryke and Samways 2012, Swengel 2001, Whelen 1995). Positive effects have included removal of ground vegetation which facilitates movement in ground-dwelling arthropods (Brown et al. 2013, Pryke and Samways 2012), increases in taxonomic and functional diversity in Mediterranean Hymenoptera (Mateos et al. 2011), and increases in herbaceous understory linked to arthropod abundance (Campbell et al. 2006). However, patterns are often difficult to attribute to fire alone as results vary due to differences in weather, burn intensity, focal taxa studied, and season of burn. In any investigation it is necessary to consider not only that burning has differential ecological effects based on ecosystem sensitivity and/or dependency on fire, but also the variant spatial distribution of fire across these different landscapes in terms of extent (i.e. 10 ha^2 vs. 10,000 ha^2), fuel heterogeneity within fire perimeters which affects burn patchiness and localized energy release (i.e. direct mortality), and distance to refugia (Pryke and Samways 2012). Furthermore, arthropods possess complex life histories, and responses are typically species and system specific (Joern and Laws 2012).

Despite this fact, most studies focus on a single taxon or functional group to gauge specific fire effects and usually involve post-fire assessment of a singular burn. While this adds much to the current state of knowledge, numerous taxa and multiple fires should be studied in order to get a more robust picture of arthropod assemblages and the range of effects on numerous orders and functional groups (Pryke and Samways 2012). Arthropods are the most abundant and species-rich group of animals in terrestrial systems and have tremendous impacts on ecological processes such as nutrient cycling, net primary production, and food web structure (Weisser and Siemann, 2004). Thus, arthropods should be included in assessments of the role of fire on biodiversity and other ecosystem parameters. Additionally, identifying arthropod traits which confer greater fitness to taxa living within fire-prone ecosystems remains an essential undertaking in efforts to understand maintenance of ecology function (New 2014).

Longleaf pine (*Pinus palustris* Mill.) forests are dependent on frequent fire to maintain ecosystem function and stability (O’Brien et al. 2008, Kirkman et al. 2004, Mitchell et al. 2009, Glitzenstein et al. 2003). The fire regime in longleaf pine forests is characterized by high-frequency, low-intensity surface fires with return intervals of 1-5 years (Mitchell et al. 2009, Provencher et al. 2001). In the absence of fire competitive advantage is given to faster growing, non-fire dependent broadleaved vegetation, resulting in a closed canopy, extensive habitat degradation, and reductions in biodiversity (Mitchell et al. 2006, Frost 2006, Noss et al. 1995). Arthropod diversity is tightly linked to changes in diversity of plants, mammals, and birds (Tallamy 2004); therefore, we expect there to be concurrent alterations to arthropod community composition as successional processes unfold post-fire and as the fire return intervals increase within longleaf pine stands.

To test this hypothesis, we conducted two separate studies that examined specific questions concerning arthropod community response to prescribed fires in longleaf pine forests. Q1: How does the arthropod composition and diversity change over time post-fire? The study was based on changes in arthropod assemblages over time in relation to single fires in frequently burned stands and utilized sampling techniques geared towards more mobile taxa. To examine the role of fire in maintenance of arthropod assemblages, the second study assessed patterns in community composition along a fire return interval gradient. Here we investigated the effect of altered fire regimes in terms of reduced fire frequency ranging from frequently to infrequently burned, specifically asking Q2: How does arthropod diversity differ in longleaf pine forest stands with different fire return intervals? We predict that when fire is removed from the landscape in infrequently burned areas, the forest transitions to closed canopy system and results in a reduced diversity in understory vegetation. Because arthropod community metrics are tightly linked to plant biomass and diversity, we expect to find reductions in arthropod diversity when sampled along a gradient from frequently (1-5years) burned, to infrequently (20+ years) burned longleaf pine stands. In both studies we utilized numerous taxa and functional guilds in an effort to more accurately describe how fire shapes patterns in arthropod diversity.

METHODS

Study system

The studies were conducted at Eglin Air Force Base (EAFB) located in the Gulf Coastal Plain of the Florida panhandle, USA during 2014 to 2015. Eglin AFB is over 180,000 ha in size, is home to over half of the remaining stands of old-growth longleaf pine and is actively managed by frequent prescribed fire (Varner et al. 2005, Holliday 2001, Hiers et al. 2007). The climate is typified by hot, humid summers with frequent thunderstorms and lightning strikes, mild winters, mean annual temperature of 18.3°C, and 1580 mm of annual precipitation (Provencher et al. 2001). The area has relatively little topography (0-100 m ASL) and is dominated by well-drained Lakeland series soils. The fire regime in longleaf pine forests are characterized by high-frequency, low-intensity surface fires with a return interval of 1-5 years.

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. The sandhills are also comprised of shrubby hardwoods species such as turkey oak (*Quercus laevis*), blackjack oak *(Q. incana*), and persimmon (*Diospyros virginiana*); however, these species are generally absent from the flatwoods. Most of the hardwoods are in a shrub state, as they are continuously top-killed by fire. The ground cover vegetation contains most plant species and is dominated by several grasses, such as wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium*), broomsedge (*Andropogon virginicus*), as well as dwarf huckleberry (*Gaylussacia dumosa*), evergreen blueberry (*Vaccinium darrowii*), runner oak (*Quercus minima*), saw palmetto (*Serenoa repens*), and gallberry (*Ilex glabra*).

Community changes over time since fire

To address the question of how the arthropod composition and diversity change over time post-fire, we erected a series of six malaise traps (BioQuip Products Inc., model #2875AG, Rancho Cordova, CA, USA or Townes Style) to sample before, during, and five periods post-fire. Sampling was done in conjunction with three separate prescription fires conducted as part of regular management burning in late May 2014. Burn blocks were located within sandhill vegetation communities, ranged in size from (10-200ha), and were surrounded by contiguous blocks of frequently burned longleaf stands segmented by fire breaks in the form of sand roads. Two locations at least 50m from a fire break were randomly selected within each burn block and GPS coordinates recorded. At each location, a malaise trap was erected for 72h immediately before ignition and removed while burn operations were conducted. During the execution of each burn prescription, two traps were set downwind and outside of each burn block on the edge of the fire break to capture fire-related dispersal. In order to assess arthropod community assemblage over time since fire, at each of the six geo-referenced locations malaise traps were deployed for 24-92h at five post-fire sampling events over the course of a year. Sampling was conducted immediately after each burn and at 2, 5, 10, and 12 months post-fire during the months of May 2014, July, October, March, and May 2015 respectively.

Community changes with reduced fire frequency

To address the question how arthropod diversity differs with increasing fire return intervals, we established eighty-six, 30m diameter plots (Figure S1) in forested stands represented by variable time since last disturbance by fire. Based on available fire history records and vegetative indicator species associated with known fire return intervals, plots were placed into a burn category; frequently burned (fire return interval (FRI): 1-5 years, n=69), intermediately burned (FRI: 5-25 years, n=8), and infrequently burned (FRI: >25 years, n=9). Plots were visited on a single occasion between the years 2013-2016. Arthropod specimens were collected with sweepnets in a standardized format with sweeping starting at the edge of each plot and moving towards the plot center in concentric circles. Sampling was constrained to the understory vegetation. Plots were stratified by vegetation community type (sandhills, n=46; flatwoods, n=40), and season of collection (Spring, n=15; Summer, n=44; Fall, n=27).

Quantifying Diversity and Statistical Analyses

Specimens were pooled by sampling event, identified at minimum to taxonomic family, and assigned a morphospecies based on coarse morphological features, which for most taxa, correspond to taxonomic identification (Longino and Colwell 1997). Based on taxonomic family identification and trophic associations within published literature, specimens were assigned to one of four trophic guilds: herbivore, detritivore, predator, or parasitoid. A reference collection of morphospecies was created, curated, and housed within the research collection at the University of Nevada, Reno's Museum of Natural History.

To control for the differing number of hours each trap was erected, trap abundances were standardized by numbers of hours of collection. Abundance and richness of morphospecies were used to calculate alpha and beta diversity components with the inverse Simpson concentration (1/D) used as the response variable for multivariate statistical analyses. As described by Jost (2007), the inverse Simpson gives the effective species numbers instead of a measure of entropy given by the untransformed index. Therefore, this makes for allowable and informative comparisons across studies.

To address unequal sampling efforts in terms of number of plots within each fire return interval category, we performed sample-based rarefaction for species and richness. We also calculated nonparametric asymptotic estimators at equal sample coverage levels following Chao et al. (2014) to allow for community comparison across the fire return interval gradient.

To visualize a reduced complexity in the data, ordination techniques were employed including non-metric multidimensional scaling (NMDS) and correspondence analysis constrained (CCA) by fire return interval. To identify variables contributing to arthropod community diversity we utilized generalized linear models fit with the appropriate distributions to deal with violations of non-linearity in the data with diversity components predicted by date of collection, taxonomic order, and trophic guild for both studies, as well as by fire return interval, season, and vegetation community for the reduced fire frequency study.

In an attempt to uncover how the environment filters certain life history traits, we also performed an RLQ analysis, also known as the fourth corner method. Here we analyzed the relationships between fire return interval and arthropod life history traits including developmental strategy, annual reproductive output, body size and feeding habit. Arthropod traits were based on data were taken from numerous published sources or from direct observation and assigned to 128 taxonomic families. Statistical significance was evaluated through 1000 permutations where rows and columns were randomized.

RESULTS

Community changes over time since fire

Malaise sampling efforts resulted in a collection of 9,896 individuals comprised of 11 arthropod orders represented by 454 morphospecies and four trophic guilds (Table 1). Overall arthropod diversity had a variable pattern in relation to time since fire. Diversity increased both during and immediately after fire and continued to increase 2 months post burn in the month of July (Figure 1). Diversity then decreased 5 and 10 months post burn corresponding to October and March collections, respectively. Overall diversity increased again in the May sample collected 1 year after the fires and had higher diversity than the pre-burn collection. Ordination with non-metric multidimensional scaling (NMDS) indicates that the arthropod communities were easily distinguishable based on collection period, with most distinct community being the insects that were collected during the fire (Figure 1). Model results indicated diversity was significant effected by date of collection ($F_{6,445}$ = 13.848, P = 0.001) and taxonomic order ($F_{10,435}$ = 34.885, P = 0.001), with trophic guild not a significant predictor ($F_{3,451}$ = 2.487, P = 0.060).

Focusing in on arthropod taxonomic order, there was significant interactions between date and order ($F_{44,367}$ = 4.220, P = 0.001). Diptera, Lepidoptera, Orthoptera, and Hemiptera showed an overall increase in diversity 1-year post fire (Figure 2). Hymenopteran diversity decreased during and immediately post burn, increased in July after 2 months after the fires, and then decreased in diversity to lower than pre-burn levels. Orthoptera were the only order to increase in diversity during the fires.

There were also significant interactions between collection date and trophic guild ($F_{18, 417}$ = 4.351, P = 0.01) as well as between guild and taxonomic order ($F_{6,411}$ = 28.409, P = 0.001). Trophic guild analyses indicated increased diversity for herbivores and predators at all collections during and post burn compared to pre-burn levels (Figure 3). Detritivores and parasitoids had more variable patterns in diversity over time in post burn collections with 1-year after the fire matching pre-burn levels. There was not a significant effect of date, order, and trophic guild ($F_{20, 347}$ = 0.939, P = 0.537). The greatest changes in diversity within post-burn collections were seen in Dipteran detritivores and herbivores, Hymenopteran predators and parasitoids, and herbivorous Coleopterans, Hemipterans, Lepidopterans, and Orthopterans.

Community changes with reduced fire frequency

The overall sweepnet sampling effort resulted in 7,686 individual arthropods, with 658 morphospecies from 16 different taxonomic orders and 124 families (Table 2). Species richness was significantly higher in frequently burned plots than infrequently burned plots ($F_{2, 84} = 4.689$, $P = 0.01$). Rarefaction analyses also illustrated that species richness was highest within frequently burned plots as compared to intermediately and frequently burned plots. Comparing Chao's asymptotic estimates of species richness at an equal level of coverage of 20 samples, the most species were found within frequently burned plots ($\text{Chao1}_{\text{frequent}} = 322$) followed by intermediate ($\text{Chao1}_{\text{intermediate}} = 253$) and infrequently burned plots ($\text{Chao1}_{\text{infrequent}} = 213$).

Conversely, alpha diversity did not differ across the fire return interval gradient ($F_{2, 703} = 1.179$, $P = 0.308$; Table 3, Figure 4). Beta diversity was highest in frequently burned plots and saw the greatest proportion of species turnover between plots, followed by infrequently then by intermediately burned plots (Table 3, Figure 4). While arthropod diversity did not differ between sandhill and flatwood vegetative communities ($F_{1, 702} = 0.161$, $P = 0.690$), it was significantly affected by arthropod order ($F_{15, 687} = 23.927$, $P = 0.001$), trophic guild ($F_{3, 684} = 20.606$, $P = 0.001$) and season of collection ($F_{2, 682} = 5.961$, $P = 0.003$).

Araneae as well as herbivorous Hemiptera and Orthoptera taxonomic orders had the highest diversity in frequently burned plots and declined with increasing time since fire (Figure 5). Lepidopteran diversity values were the relative lowest among taxonomic orders and also had a negative relationship with longer periods between fires. Coleopteran, Dipteran, and Hymenopteran diversity was variable along the gradient and did not have a linear relationship with fire return interval. Throughout all three fire types, herbivores had the highest alpha diversity while parasitoids had the lowest and all trophic guild diversity was inversely related to fire return interval (Figure 6). Diversity was highest in arthropods collected during the fall season (Figure 7). There was also significant interaction between fire return interval and trophic guild ($F_{6, 643} = 2.199$, $P = 0.042$), taxonomic order and guild ($F_{8, 640} = 11.413$, $P = 0.001$), and order and season of collection ($F_{22, 606} = 1.922$, $P = 0.007$).

Ordination by constrained correspondence analysis (CCA) showed community compositional overlap between the three fire return intervals (Figure 8). The greatest spread of plots within ordination space was among frequently burned stands. The orientation of ellipses in frequently burned plots and plots with longer fire return intervals were in opposite directions along the first axis indicating further distinction between arthropod community composition along the gradient.

The fourth corner analysis resulted in 8 correlations with an overall model inertia of 1.57 at $P = 0.07$. Positive correlations included between frequently burned plots and multivoltine reproduction, intermediately burned plots and ametametabolous development and univoltine reproduction, and between infrequently burned plots and parasitoids as well as univoltine reproduction. Negative correlations were found between frequently burned plots and ametametabolous development and univoltine reproduction as well as between infrequently burned plots and multivoltine reproduction (Figure 9).

DISCUSSION

Frequent fires not only maintain plant diversity but also higher levels of arthropod species richness and beta diversity which both erode as fire is removed from the system

(Table 3, Figure 4). Reduction in beta 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). Our results from singular fires within these frequently burned stands indicate that arthropod communities are re-assembling in patterns that suggest bottom-up regulation. As longleaf pine ecosystems are fire-adapted, plants readily resprout quickly after fire, often times in a matter of days (O’Brien et al. 2008, Kirkman et al. 2004, Dell, personal observation). As the vegetation returns post-burn the arthropod community also reestablishes as habitat is restored and diversity increases as the vegetative community becomes more complex. For instance, herbivore abundances commonly increase post-fire, especially for Orthopterans as they take advantage of re-sprouting vegetation (Knight and Holt 2005) and fire-induced changes in habitat structure benefit herbivore community diversity (Kim and Holt 2012).

Arthropod diversity also mirrors plant diversity in terms of collection season as both understory plants and arthropods experience highest levels in the early fall (S. Pokswinski, unpublished data). Subsequent decreases in overall arthropod diversity in late fall collections follow as plants enter senescence. Alternatively, when looking over the course of one year after an individual burn, this late in the year drop in overall diversity could also indicate delayed recolonization or population seasonality. However, ecosystem recovery can be seen as communities became compositionally similar to pre-burn assemblages after one year. Expanding out beyond a single fire, bottom up regulation is also evident with longer fire return intervals as illustrated by the negative correlation between herbivores and fire. Plant diversity decreases, so as a result we see concomitant reductions in diversity of upper trophic levels.

For both predators and parasitoids, responses to fire are likely to be deeply tied to those of their prey. Predator diversity increased immediately post-burn, agreeing with studies suggesting spiders and predaceous recover rapidly from fire disturbances (Polchaninova 2016, Jansen et al. 2013). Other studies have found that predators can be either positively or negatively affected by fire and that, as in other trophic levels, habitat type, taxonomic group, dispersal ability, and time-since-fire are important components of recovery (Kwok and Eldridge 2015, Samu et al. 2010, Valko et al. 2016). In general, parasitoids showed latent recovery post-fire and reduced diversity as fire is removed from the ecosystem, further indicating bottom-up regulation. Parasitoids tend to be more specialized on specific hosts and therefore to be more sensitive to fire effects and post-fire community structure. Parasitoid responses to fire may also be taxon-specific, as has been shown with other types of disturbances (Stireman et al. 2005). Decreased diversity in parasitoids along the fire return interval gradient could have significant impact on population regulation of the arthropod communities in long unburnt stands.

Diversity patterns among detritivores were variable both for single fires and across the fire return interval gradient. While soil arthropod abundance is not commonly affected, diversity tends to decrease after fire and can remain altered for decades (Malmstrom 2012). Responses to fire by soil-dwelling arthropods are therefore likely to reflect not only post-fire shifts in plant composition and litter availability, similar to surface-dwelling arthropods (Samu et al. 2010, Venier et al. 2017), but also the pre-fire plant composition and soil quality (Bokhorst et al. 2017). Thus, understanding detritivore responses to shifting fire regimes will require considering the short- and long-term effects of fire on plant communities and soil quality.

One clear generalization is that direct effects such as exposure to high temperatures may be ameliorated via seeking refuge (Engstrom 2010). Refugia are areas adjacent to or within a burn area that enhance arthropod survival during a fire that facilitate persistence of individuals, or that allow for post-fire recovery (Robinson et al. 2013, Brennen et al. 2011, Sandoval 2000, Williams 1995). As the greatest increased taxonomic diversity was seen in three highly vagile orders, dispersal ability may give greater resilience to mobile taxa and provide increased recolonization potential as the vegetative habitat returns post fire. Furthermore, the increase in Orthopteran diversity during fires indicates a dispersal response to burning. Specific triggers remain unknown but the highly sensitive sensory systems in arthropods suggest dispersal cues could include olfactory receptors and smoke, sensation of temperature and thermal energy release, and even auditory receptors and response to sound waves (Dell et al. 2017).

Life history traits that can improve survival to fire include living some or all life stages belowground (Kral et al. 2017, Love and Cane 2016), high-dispersal capability (New 2014), and being a trophic generalist (Rojas et al. 2018, Garcia et al. 2016, Dell et al. 2018, in review). Some of the interesting results of the RQL analysis included the correlation between multivoltine reproductive strategies and frequent fire as relatively short generation times and large population sizes, may facilitate rapid evolution and adaption to disturbance. Our ability to link environmental filtering to community composition would be greatly enhanced by the inclusion of additional arthropod traits.

Furthermore, refining the resolution of taxonomic identification down to species level would increase correlational strengths.

Our results are biased towards the methods of collection used in the study. While malaise traps are designed for the collection of flying or highly-vagile orders of arthropods, sweepnets are biased towards herbivores and plant-dwelling orders. However, when used in combination, we were able to describe informative community diversity patterns. Further understanding could be gained by replicating methods over additional burn seasons and fire intensities as additional fire regime attributes beyond frequency may have significant impacts on particular orders and guilds (New 2014). Regardless, quantifying the diversity of the overall arthropod community allows for multiple comparisons in the responses of numerous taxa enhancing the understanding of ecosystem response to disturbance.

How fire affects insects can vary depending on differences in weather, fire severity, focal taxa, and season of burn. Similarly, the ecological effects of burning depend not only on ecosystem sensitivity to and dependency on fire, but also on the spatial distribution and extent of the fire, fuel heterogeneity, burn patchiness, and distance to refugia. As a result, when considering the potential effects of changes in fire regimes, it will be worthwhile to consider that the actual traits that enable insects to survive fire may vary widely across sites. Furthermore, as fire regimes continue to shift as a result of climate change (IPCC 2014), insects and the ecological communities they inhabit are likely to change as well. While our understanding of ecological feedbacks in insect responses to fire and other types of disturbance remains limited, this is a promising area of research that deserves more attention.

ACKNOWLEDGEMENTS

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TABLES

Table 1: Summary of malaise trap contents from 39 samples collected in relation to events before three separate prescribed burns, during the fires, and over the course of 1-year post fire. The number of morphospecies and taxonomic families are detailed for each arthropod order represented in the samples. Trophic guilds: Herbivore(H), detritivore (D), predator (Pr), and parasitoid (Pa).

Order	Morphospecies	Families	Guild
Araneae	2	1	Pr
Coleoptera	41	12	H, D, Pr
Diptera	139	41	H, D, Pr, Pa
Hemiptera	80	16	H, Pr
Hymenoptera	116	18	H, Pr, Pa
Isoptera	1	1	D
Lepidoptera	41	4	H
Neuroptera	4	2	Pr
Opiliones	1	1	Pr
Orthoptera	25	3	H
Psocodea	4	1	Pa

Table 2: Summary of sweepnet contents from 86 samples collected along a time since fire gradient. Order refers to taxonomic classification and guild represents trophic functional assignment. Guilds: Herbivore(H), detritivore (D), predator (Pr), and parasitoid (Pa).

Order	Individuals	Morphospecies	Families	Guild
Araneae	898	89	10	Pr
Coleoptera	475	77	19	H, D, Pr
Collembola	693	3	1	H
Diptera	1,077	103	21	H, D, Pr, Pa
Hemiptera	1,978	197	25	H, Pr
Hymenoptera	672	108	23	H, Pr, Pa
Lepidoptera	41	15	6	H
Mantodea	6	2	1	Pr
Neuroptera	19	7	4	Pr
Odonata	21	4	2	Pr
Opiliones	72	2	2	Pr
Orthoptera	1,092	25	4	H
Parasitiformes	2	2	2	Pa
Phasmatodea	14	1	1	H
Thysanoptera	317	2	2	H, Pr
Trombidiformes	309	1	1	H

Table 3: Diversity measures for arthropod communities in each fire return interval category. Alpha and beta diversity components were estimated using inverse Simpson's index (1/D). Plot level means are reported (+/- SE). Letters denote significant differences between fire return interval (FRI) categories based on Tukey's test at $P < 0.05$. Turnover measures dissimilarity between plots within each FRI category and is defined as 1 – plot richness/FRI richness.

Fire Return Interval	**Richness**	**α**	**β**	**Turnover**
Frequent	24.60^{a} (1.63)	10.18^{a} (0.62)	10.49	0.960
Intermediate	19.25^{ab} (3.87)	7.41^{a} (1.31)	7.40	0.849
Infrequent	13.44^{b} (1.98)	8.27^{a} (1.36)	8.53	0.878

FIGURE LEGENDS

Figure 1: Right Panel: Box plots showing the distribution of arthropod diversity values based on aggregated collection time. The first three collections occurred in May with subsequent sampling months indicated below individual boxes. Diversity reported in species equivalents using inverse Simpson's (1/D). Left Panel: Non-metric multidimensional scaling (NMDS) plot showing aggregation of samples by collection time denoted by different colored circles. Arthropod communities were easily distinguishable based on collection period, with most the distinct community being the insects that were collected during the fire, suggesting fire affects insect behavior and dispersal.

Figure 2: Taxonomic diversity sampled during collection periods before, during, and five times post burn. Mean diversity of the seven most abundant arthropod orders are denoted with unique colored symbols and aggregated based on time of collection. Diversity reported in species equivalents using inverse Simpson's (1/D). Error bars represent +/- SE.

Figure 3: Functional group diversity sampled during collection periods before, during, and five times post burn. Mean diversity of the four trophic guilds are denoted with unique colored symbols and aggregated based on time of collection. Diversity reported in species equivalents using inverse Simpson's (1/D). Error bars represent +/- SE.

Figure 4: Box plots showing the distribution of arthropod community diversity components calculated from frequently, intermediately, and infrequently burned plots. Right panel: Species richness values within each burn category. Left panel: Alpha diversity values calculated within individual plots are shown in boxes and beta diversity values between plots within each fire return interval category are indicated by black diamonds. Diversity values are reported in (1/D).

Figure 5: Taxonomic diversity of samples collected along a fire return interval gradient. Mean diversity of the seven most abundant arthropod orders are denoted with unique colored symbols and aggregated based on time of collection. Diversity reported in species equivalents using inverse Simpson's (1/D). Error bars represent +/- SE.

Figure 6: Functional group diversity sampled along a fire return interval gradient. Mean diversity of the four trophic guilds are denoted with unique colored symbols and aggregated based on time of collection. Diversity reported in species equivalents using inverse Simpson's (1/D). Error bars represent +/- SE.

Figure 7: Arthropod community diversity in spring, summer, and fall seasons along a fire return interval gradient. Intermediately burned plots were not sampled in the fall nor infrequently burned plots in the spring. Diversity reported in species equivalents using inverse Simpson's (1/D). Error bars represent +/- SE.

Figure 8. Correspondence analysis of arthropod communities constrained by fire return interval. Plots within each fire category are denoted with colored ellipses with crosses

representing +/- SE around each ellipse centroid. Plotted circles represent site scores and triangle linear constraint scores from the correspondence analysis.

Figure 9: Plot of significant correlations between fire return intervals and arthropod life history traits determined through RQL or fourth corner analysis. Light grey indicates non-significant correlations, blue indicates significant negative correlation, and red indicates significant positive correlation. Significance determined at P = 0.10.

FIGURES

Figure 1

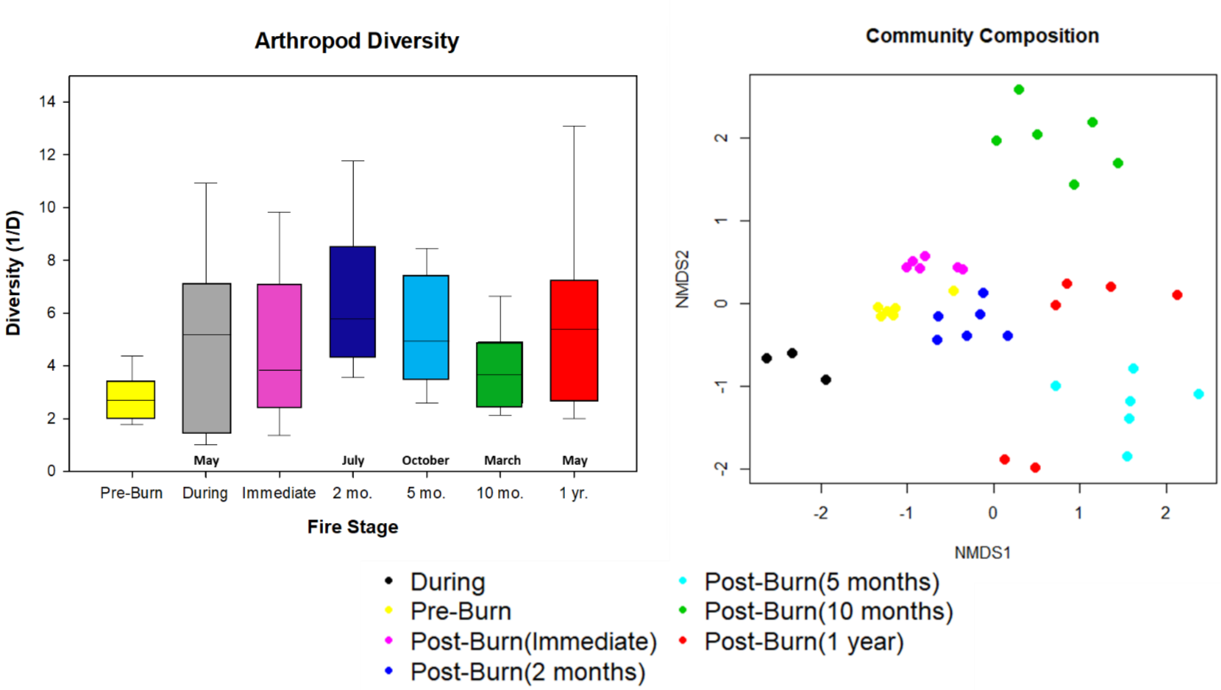


Figure 2

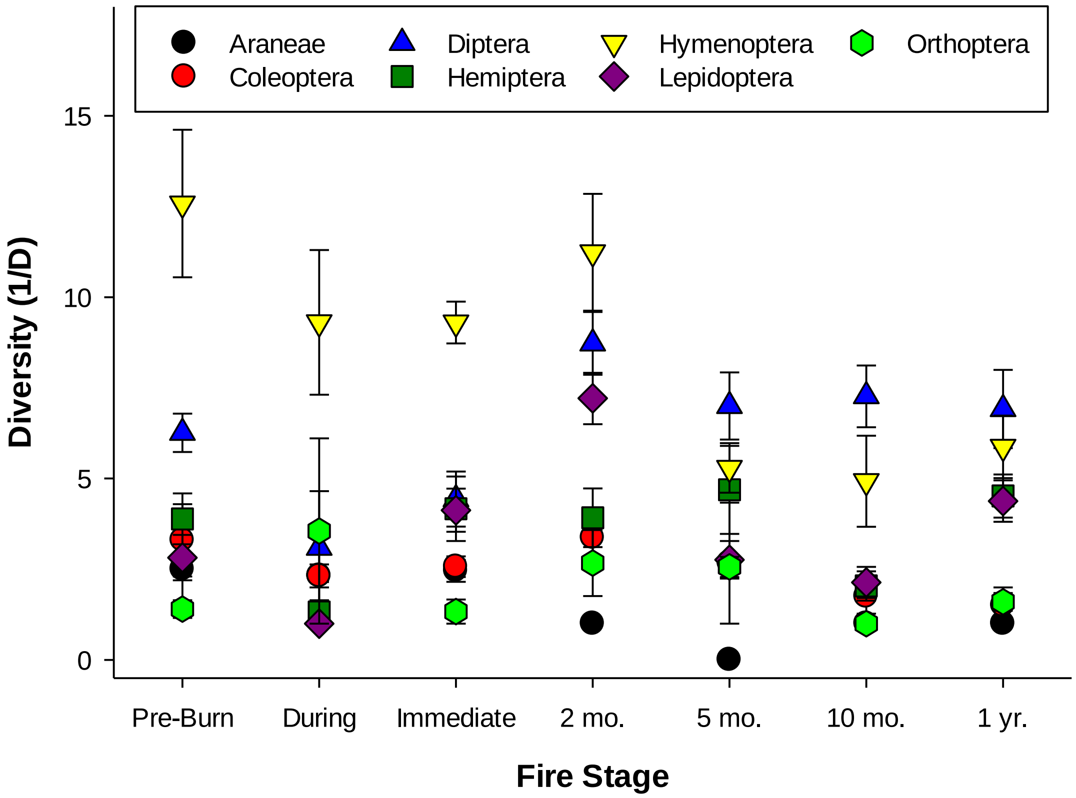

Araneae
Coleoptera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Orthoptera
Diversity (1/D)
0
5
10
15
Pre-Burn
During
Immediate
2 mo.
5 mo.
10 mo.
1 yr.
Fire Stage

Figure 3

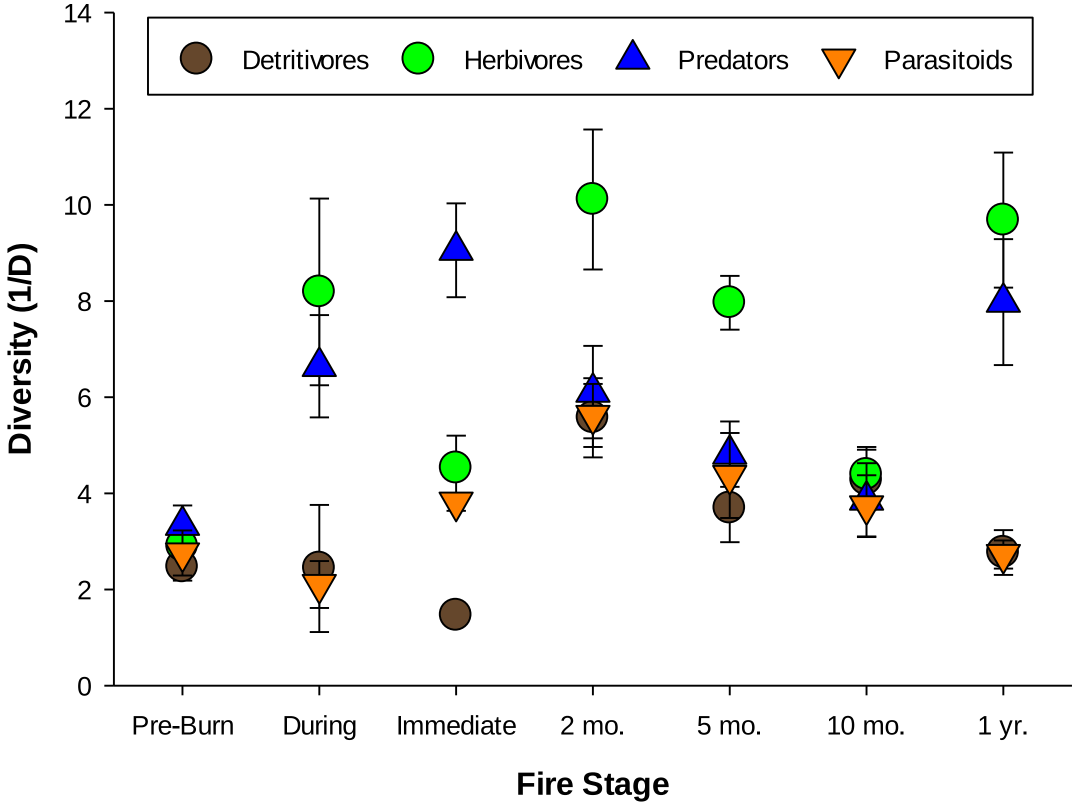

14
12
10
8
6
4
2
0
Diversity (1/D)
Detritivores
Herbivores
Predators
Parasitoids
Pre-Burn
During
Immediate
2 mo.
5 mo.
10 mo.
1 yr.
Fire Stage

Figure 4

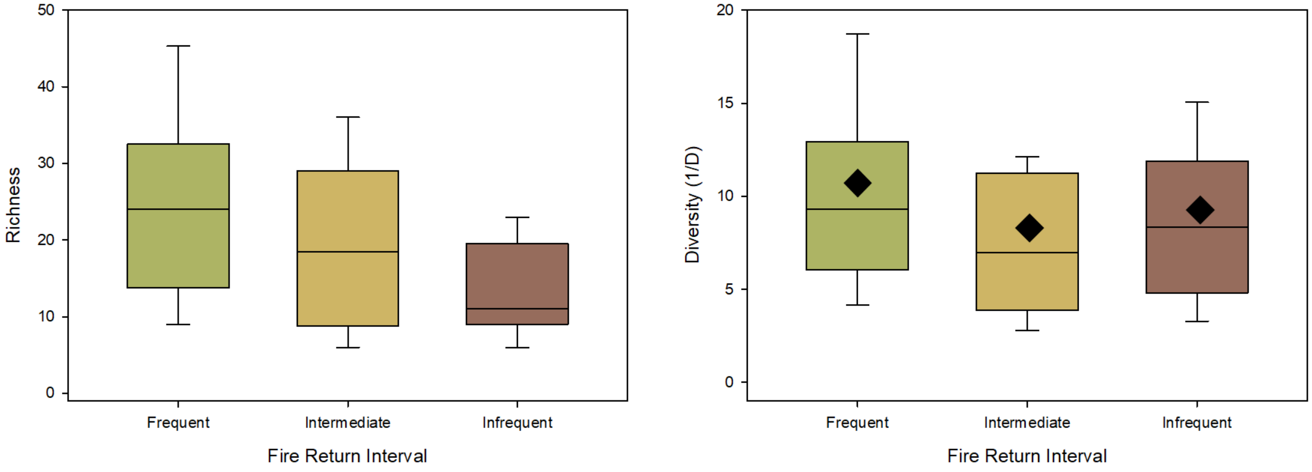

50
40
30
20
10
0
Richness
Frequent
Intermediate
Infrequent
Fire Return Interval
20
15
10
5
0
Diversity (1/D)
Frequent
Intermediate
Infrequent
Fire Return Interval

Figure 5

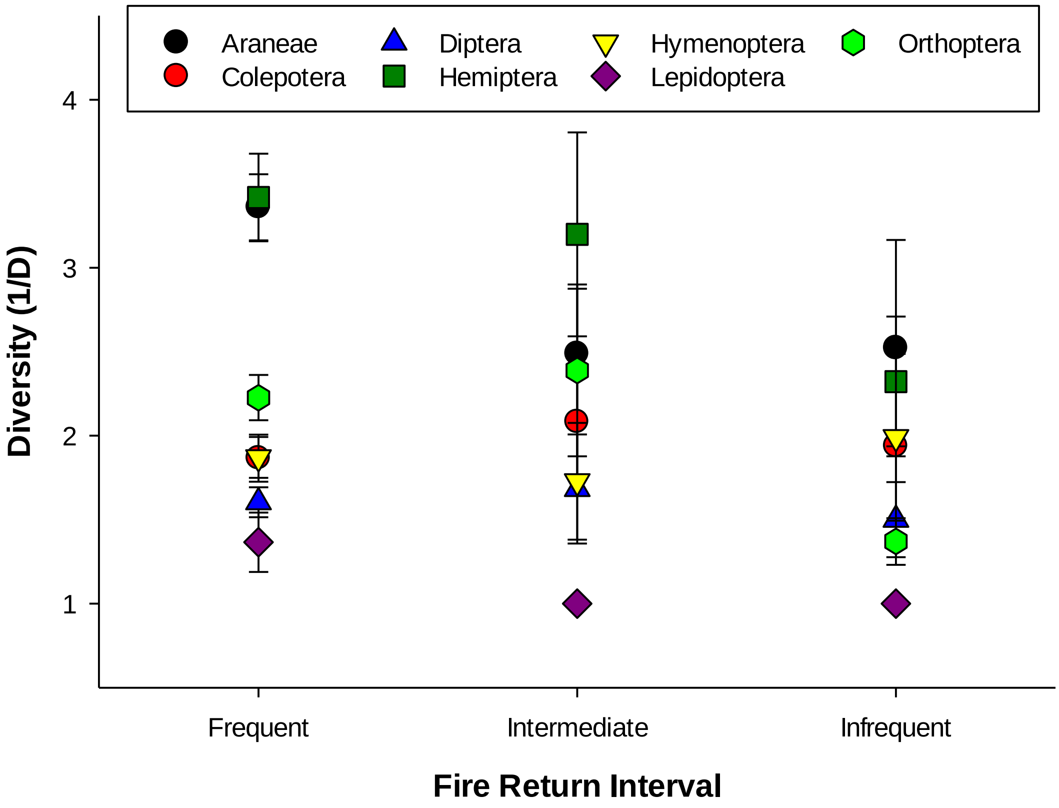

Araneae
Colepotera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Orthoptera
Diversity (1/D)
4
3
2
1
Frequent
Intermediate
Infrequent
Fire Return Interval

Figure 6

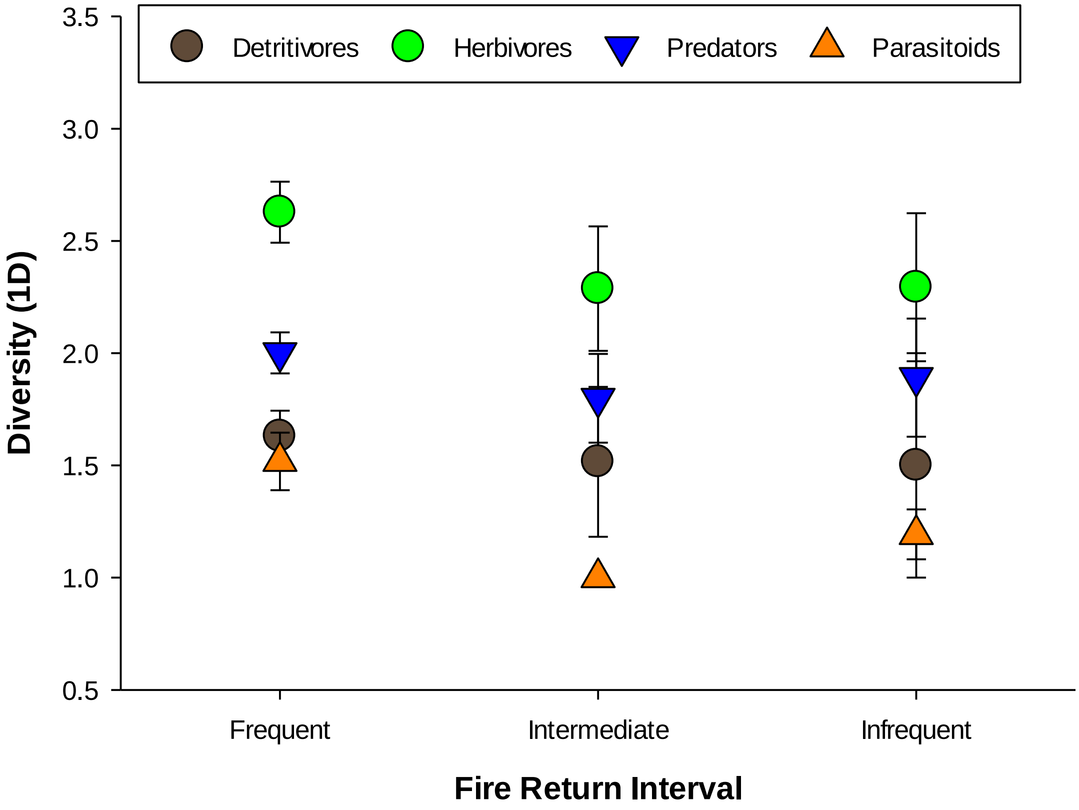

Detritivores
Herbivores
Predators
Parasitoids
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Diversity (1D)
Frequent
Intermediate
Infrequent
Fire Return Interval

Figure 7

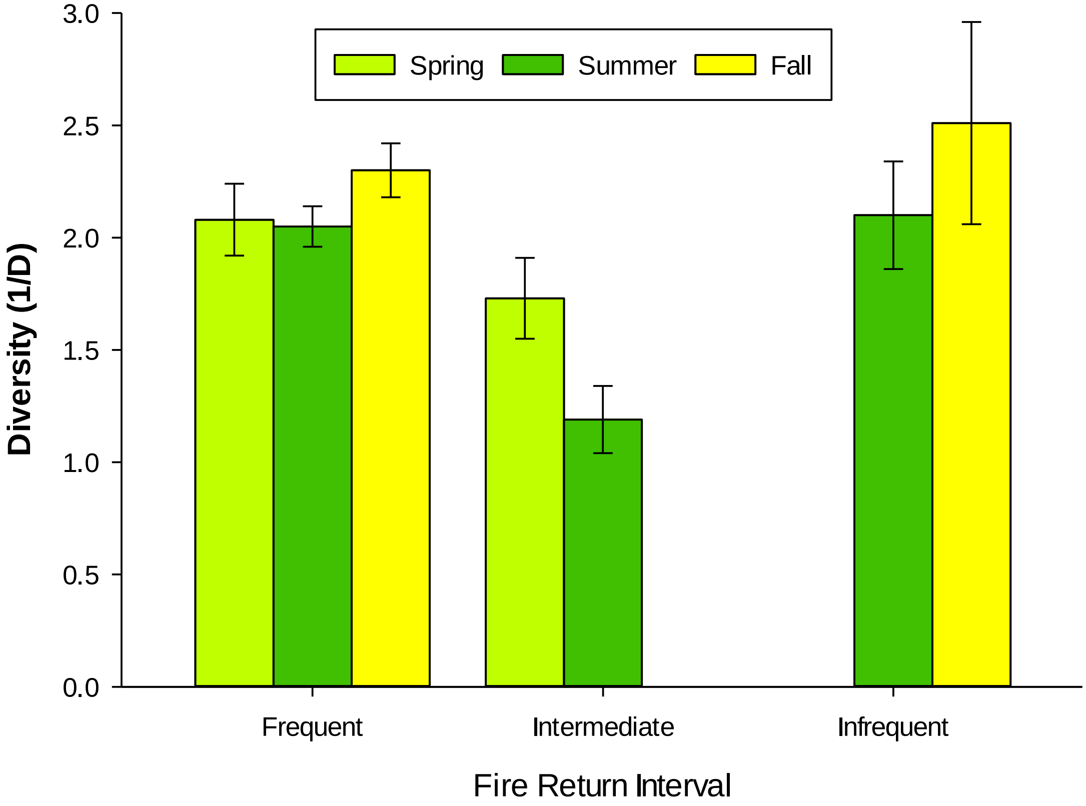

3.0
2.5
2.0
1.5
1.0
0.5
0.0
Diversity (1/D)
Spring
Summer
Fall
Frequent
Intermediate
Infrequent
Fire Return Interval

Figure 8

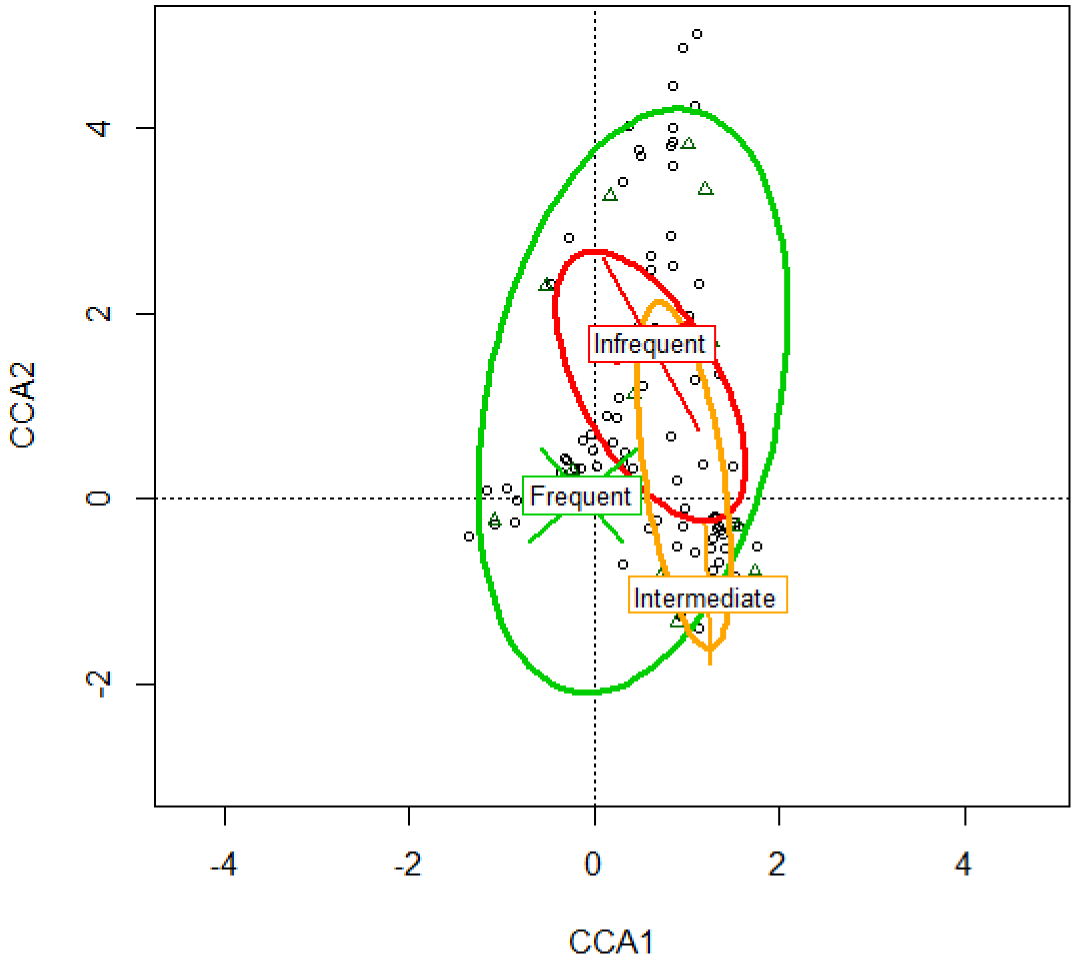
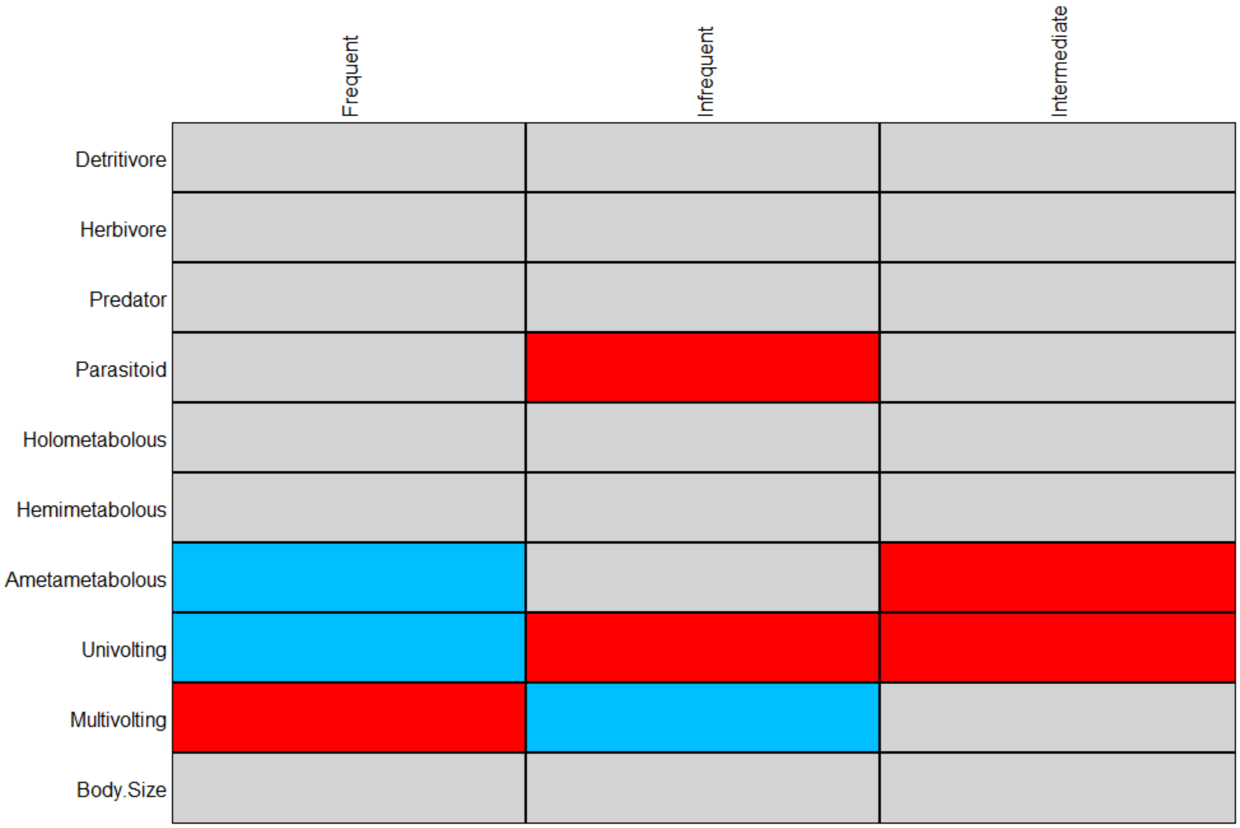


Figure 9



	Frequent	Infrequent	Intermediate
Detritivore	⬜	⬜	⬜
Herbivore	⬜	⬜	⬜
Predator	⬜	⬜	⬜
Parasitoid	⬜	🟥	⬜
Holometabolous	⬜	⬜	⬜
Hemimetabolous	⬜	⬜	⬜
Ametametabolous	🟦	⬜	🟥
Univolting	🟦	🟥	🟥
Multivolting	🟥	🟦	⬜
Body.Size	⬜	⬜	⬜

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CHAPTER 4

An arthropod survival strategy in a frequently burned forest*

*Citation: Dell, J.E., O’Brien, J.J., Doan, L., Richards, L.A., and Dyer, L.A. (2017) An arthropod survival strategy in a frequently burned forest. Ecology 98, 2972-2974.

The sound of burning stems and leaves filled our ears and smoke swirled as we marched into the longleaf pine forest to assess the experimental burn. As we walked over the ash of burnt vegetation, seedbanks and plant parts lay beneath our feet waiting to grow. But what we couldn’t see were the arthropods fleeing the fire. How are these invertebrates adapted to fire? They probably smell it coming, but do they feel the heat or see the smoke? Do they hear the noise that we hear as we near the flames?

Fire has been structuring terrestrial ecosystems since the Silurian Period (Glasspool et al. 2004, Pausas and Keeley 2009) and remains a key process in these systems. Prairies, savannas, and coniferous forests, like longleaf pine (*Pinus palustris* Mill.), cannot persist without periodic burning (Bradstock et al. 2005). Fire-adapted plant species have physiological adaptations such as thick, insulating bark and the ability to rapidly resprout post-burn. These adaptations confer greater resiliency to frequent disturbance. While we know fire maintains plant diversity in these ecosystems, less is known about the impacts of fire on other taxa in fire-adapted systems. Recently, we discovered a potential mechanism by which arthropods, the smallest animals in the longleaf pine ecosystem, survive frequent disturbance by fire. We suggest that tiny, yet highly-sensitive sensory adaptations may aid in an interesting arthropod behavior that takes place before the fire arrives: *insect ears.*

Arthropods found in fire-adapted habitats have specific traits and dispersal strategies to deal with frequent fires (New 2014). For example, they seek refugia during fires where temperatures may be lower (Robinson et al. 2013). Refugia are areas adjacent to or within a burn area that enhance arthropod survival during a fire, facilitate persistence of individuals, or allow for post-fire recovery. These may include insulated underground burrows, fire-resistant termite mounds, or patches of unburned vegetation (Robinson et al. 2013). Dispersal is another obvious response to fire for arthropods, and as a result, winged orders have higher survivorship than less-mobile taxa (New 2014).

When we arrived in the middle of our prescribed fire at Eglin Air Force base in Florida in May 2014, we noticed the maneuvering of a group of Mississippi kites as they gorged themselves on arthropods fleeing in front of the oncoming flames. We also spotted a group of several wingless juvenile grasshoppers walking up the side of a tree towards the canopy. Longleaf pine forests are characteristically open, with a monospecific overstory of pine, a sparse midstory, and a high-diversity understory. Fires burning in longleaf pine forests are typically high-frequency, low-intensity and predominately run through surface fuels with little effect on the canopy. Later that afternoon, we started wondering out loud if these marching arthropods were also escaping the flames and what warning signals they used to make a timely getaway. If refugia and dispersal are the most crucial factors in predicting success of arthropod fire avoidance, how were these less-mobile, and immature arthropods avoiding the dangers of natural fires?

To address this question, we formulated methods for an experiment using sticky traps to capture insects moving up tree boles during the fire. We chose such traps as they can be engineered from any sticky substance, including duct tape purchased that night from the local hardware store. For each of the subsequent burns, sticky traps were set approximately 2m high, putting them out of reach of the surface flames. Ten traps were set on the boles of longleaf pine trees pre-ignition and also in paired unburned sites, with contents collected after fires had moved through. Sticky traps are ideal as they effectively capture small arthropods and preserve orientation upon contact with the sticky surface allowing for documentation of upward movement (Figure 1).

After a subsequent fire, we saw that our sticky traps were covered with mostly juvenile, wingless, and non-flying arthropods. Traps within the fires caught 615% more arthropods compared to traps outside the fire perimeter (n=1666 inside, n=271 outside). Most specimens collected were grasshoppers and crickets (n=1361), including a few winged adults (n=56), but primarily wingless nymphs (n=1305; Orthoptera: Acrididae, Gryllidae, Tettigoniidae). Traps also yielded several other non-flying arthropods such as spiders (n=67; Araneae: Buthidae, Salticidae) and arachnids (n=134; Opiliones), walking sticks (n=17; Phasmatodea), cockroaches (n=3; Blattodea), praying mantids (n=57; Mantodea), ants (n=89; Hymenoptera: Formicidae), and immature stages of antlions (n=24; Neuroptera: Myrmeleontidae) and true bugs (n=128; Hemiptera: Cercopidae, Cicadellidae, Pentatomidae). Although there was not much difference between burned and unburned areas in flying arthropods, there were proportionately more non-flying arthropods collected from the burn treatment.

Unique arthropod survival strategies exist in other fire-adapted systems. In Australia, during experimental burning of the flammable grass tree (*Xanthorrhoea spp.*), a diverse assemblage of arthropods sought refuge and survived between the tightly packed tree leaves (Brennen et al. 2011). In longleaf pine forests, arthropods fly towards adjacent unburned areas, or as we documented in Florida, walk, crawl, or jump up tree boles towards the canopy. What cues are used for dispersal towards refugia during fires? Shortly after cutting down our first set of arthropod-laden sticky traps, we came up with additional hypotheses related to arthropod sensilla that respond to touch, smell, light, and sound. We all agreed there must be some sensory cue responsible for the initiation of the dispersal response.

The highly-developed sensory systems in arthropods suggest several hypotheses, such as specialized chemoreceptors that sense compounds unique to smoke associated with longleaf fires, or perhaps sensilla that respond to radiant heat. Pyrophilous insects possess both adaptations (New 2014). Yet from our vantage point, we were well-upwind of the advancing flames and smoke, and distant enough to not feel any of the heat from combustion. Thus, we present a third hypothesis: the auditory sensilla in arthropods, such as tympana in Orthopterans and Lepidopterans, respond to acoustic signals from the burning fuels and may trigger dispersal behavior. Therefore, the arthropods may be responding to the sounds of the fire. This hypothesis has been tested by Grafe et al. (2002), who showed that estivating frogs flee from the sounds of fire.

Both vertebrates (Beane 2006) and arthropods use specialized hearing organs for intraspecific communication and detection of predators. The hearing range of arthropods with tympanal structures are commonly within the 100 Hz to 3 kHz range, with some Lepidopterans able to detect frequencies up to 240 kHz (Hedwig 2014). Characterizations of fire acoustics indicate that clearest signals of burning are found in the frequency range of 200-500 Hz (Viegas et al 2008). Because the frequency ranges associated with fire lie well within the arthropod hearing range (Figure 2), it is feasible that fire acoustics serve as a dispersal cue for arthropods in this system.

Although many studies have investigated arthropod recolonization before and after fires, determining whether the populations sampled post-burn have survived the fire or are new colonizers has proven difficult (Robinson et al 2013, New 2014). The survival of arthropods that have dispersed into the canopy during fires and their potential as a source of recolonization remains unknown. Fires are characteristically heterogeneous in terms of severity and impact (Bradstock et al 2005). In forests with low-intensity surface fires and short residence times, such as those found in the longleaf pine ecosystem, the canopy has cooler temperatures and reduced combustion compared with the understory. Thus, it is likely that arthropods may move upwards into the cooler canopy. This may allow them to survive the burn, and subsequently recolonize the burned area below. Future studies linked with prescribed burns could focus on these dispersal patterns to provide insight to the mechanisms of post-burn colonization. Additionally, documenting dispersal, survival, and colonization events could be an important consideration for arthropod conservation strategies in longleaf pine and other fire-adapted ecosystems.

ACKNOWLEDGEMENTS

We’d like to thank B Williams and the Jackson Guard personnel at Eglin Air Force Base for assistance with and access to prescribed fires; also S Pokswinski, B Hornsby and Earthwatch volunteers for assistance in the field. This work was made possible through funding by SERDP (RC-2243).

FIGURE LEGENDS

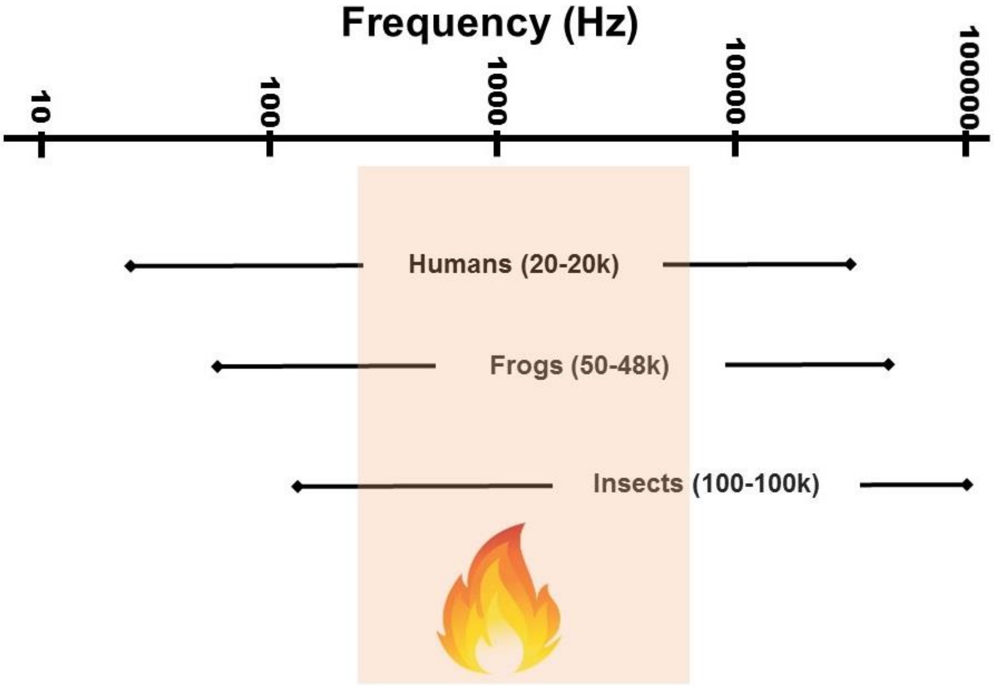
Figure 1: Sticky trap contents collected during a fire from within a burn unit. Arthropods were engaged in vertical dispersal as indicated by their orientation which is preserved upon contact with the trap.

Figure 2: The overlapping acoustic frequency ranges of fire and arthropod sound detection support the hypothesis that the sounds of fire may serve as an audible cue for dispersal.

FIGURES

Figure 1

Figure 2


Frequency (Hz)
10
100
1000
10000
100000
Humans (20-20k)
Frogs (50-48k)
Insects (100-100k)

Chapter 5

A New tachinid genus and species record for North America: *Iceliopsis borgmeieri* Guimarães*

*Citation: Stireman, J.O. and Dell, J.E. (2017) A New tachinid genus and species record for North America: *Iceliopsis borgmeieri Guimarães*. *The Tachinid Times*, 30: 9-13.

INTRODUCTION

The Iceliini are a small, enigmatic New World tribe of Tachininae consisting of three genera, *Icelia, Iceliopsis,* and *Erviopsis*, and five recognized species (Guimarães 1976). All known species are Neotropical in distribution with the exception of *Icelia triquetra* (Olivier), which ranges from Brazil, through Central America, and as far North as New York state (O'Hara and Wood 2004). Members of the tribe are generally medium sized (ca. 7-12 mm), elongate, yellowish or grayish in color, and resemble Dexiini or Leskiini in general appearance. Members of the tribe are relatively rarely collected and there is but a single host record (Lepidoptera; see below). Here, we report on the discovery of a specimen of *Iceliopsis borgmeieri* Guimarães from the U.S. state of Florida, a species never before recorded outside of Brazil.

Collection and identification

The specimen reported here was collected during the course of a large scale ecological study examining the effects of fire on insect communities in the fire-dependent longleaf pine (*Pinus palustris*) forests at Eglin Air Force Base (EAFB) in northwest

Florida (Fig. 1). EAFB is over 180,000 ha in size, is home to over half of the remaining stands of old-growth longleaf pine and is actively managed by prescribed fire on a 2-5 year return interval (Varner et al. 2005, Holliday 2001, Hiers et al. 2007). The climate is typified by hot, humid summers with frequent thunderstorms and lightning strikes, mild winters, mean annual temperature of 18.3°C, and 1580 mm of annual precipitation (Provencher et al. 2001). The area has little topography (0-100 m ASL) and is dominated by well-drained Lakeland series soils. Xeric sandhills and mesic flatwoods are the dominant vegetative communities found at EAFB. Longleaf pine is a foundation species and is typically monodominant in the overstory with a relatively open canopy throughout the site and high levels of understory plant diversity. The xeric sandhills habitat is comprised of shrubby hardwood species such as turkey oak (*Quercus laevis*), blackjack oak (*Q. incana*), and persimmon (*Diospyros virginiana*). The understory vegetation is dominated by several grasses, such as wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium*), broomsedge (*Andropogon virginicus*), as well as dwarf huckleberry (*Gaylussacia dumosa*), evergreen blueberry (*Vaccinium darrowii*), runner oak (*Q. minima*), saw palmetto (*Serenoa repens*), and gallberry (*Ilex glabra*).

To address the question of fire’s impact on insect communities, a series of six, georeferenced malaise traps (BioQuip Products Inc., model #2875AG) were erected to sample before, during, and five periods post-fire (immediately after, then at 2, 5, 10, and 12 months) (Fig. 2). Sampling was done in conjunction with three separate fires conducted as part of regular management burning in late May 2014.

One Malaise trap sampled two months post-burn in a xeric sandhills stand, captured a male of *Iceliopsis borgmeieri*. The information from the three labels is as follows (a diagonal line [/] indicates a new line on the label:

(1) FL: Okaloosa Co./Eglin Air Force Base/30.60997, -86.70266/Malaise 8-July 2014/J. E Dell/Earthwatch

(2) FL: Okaloosa Co./Burn Block 3, Trap #6/Earthwatch/8 July 2014 [original locality label]

(3) FL-S-M2708 [QR (quick response) code label with reference number for database]

Unfortunately, the specimen is in poor condition, lacking postpedicels, many legs, and most of the dorsal bristles and with one wing broken (Figs. 3, 4). In an attempt to remove the dusting of moth scales that covered the body, further damage was done to an already broken right wing (shown in its original condition in Fig. 3) and the distal portion was lost. Despite its poor condition, the specimen clearly matches *Iceliopsis*. Most crucially, the hind tibia is "…swollen on middle, with a longitudinal hairy groove on inner side" (Guimarães 1976) (Fig. 5), an unusual trait in Tachinidae. In addition, the specimen possesses setal sockets for three strong genal bristles (Icelia has one or two) and tergite 1+2 bears sockets indicating the presence of a pair of strong marginal setae (lacking in *Icelia*). In addition to these characters, the cerci and to a lesser extent the surstyli are somewhat exposed and bear a strong resemblance to those of *I. borgmeieri* (Fig. 6). In particular, in lateral view the fused (suture-less) cerci terminate in a knob-like process, and the surstyli are slender, elongate, and slightly spatulate, contrasting strongly with the broad, lobate surtstyli of *Icelia triquetra* (Olivier) (the only known N. American iceliine). These unique genitalic structures, along with features of the external morphology indicate that the specimen is very likely *Iceliopsis borgmeieri*, or a similar species. It does deviate slightly from the original description of *I. borgmeieri* in having the surstyli slightly spatulate rather than parallel-sided subapically, the dorsum of the thorax yellowish, and the abdomen less black on syntergite 1+2 and tergite 3, but *I. borgmeieri* was described from nine specimens and this difference could be intraspecific variation. We have not yet had the opportunity to compare the specimen directly with the holotype or with paratypes (housed in the Museu de Zoologia, Universidad de São Paulo; MZSP). The specimen currently resides in Stireman's personal collection at Wright State University (JOSC).

DISCUSSION

This record of *I. borgmeieri* represents a dramatic expansion of the known range of this genus and species. Previously, the species was only known from a restricted region of the Atlantic coast of Southeastern Brazil in the states of São Paulo and Rio de Janeiro (Guimarães 1976). This suggests one of two possibilities, either *I. borgmeieri* is a widespread but rarely collected species (or species complex) across the Neotropical region and into subtropical North America, or it has recently been introduced to Florida. The first hypothesis is possible, as some other tachinid species are known to exhibit similar broad ranges spanning the Neotropical and Nearctic regions (e.g. *Cholomyia inaequipes* Bigot; de Santis and Nihei 2016). But, it seems unlikely that this species of *Iceliopsis*, with its distinctive characteristics, would have so broad a range and yet not be collected or reported anywhere outside of Southeastern Brazil. The second possibility seems much more likely.

Both São Paulo and Rio de Janeiro are densely populated states with large ports and extensive shipping trade with North America and elsewhere. Furthermore, Florida (and to a lesser extent the gulf coast of the U.S.) is well known for the hundreds if not thousands of alien tropical species that have colonized and established populations there. It is a likely site for inadvertent tachinid introductions from tropical regions, especially via parasitized hosts that may be associated with agricultural or forest products.

Only a single host record has been reported for any member of the tribe Iceliini. The species *Icelia guagliumi* Guimarães was reared from *Diatraea impersonates* (Walker) (recorded as *D. flavipennella* Box), a crambid stem borer of sugar cane (Guimarães 1975). This is among the most important pests of sugar cane in Brazil, having garnered the common name *broca pequena da cana-de açúcar* or "small sugar-cane drill" (Do Rosário et al. 2007). Their planidia-form larvae are likely deposited in the vicinity of entrance holes and crawl through the tunnels in search of host larvae, similar to the strategy of the stem-borer parasitoid *Lixophaga diataeae* (Roth et al. 1982). We infer that *Iceliopsis* probably also attacks some sort of stem boring lepidopteran larvae that might be easily overlooked if transported within host plant tissue from Brazil to the U.S. It may take some time before we understand if *Iceliopsis borgmeieri* is truly established in the United States, what hosts it is using there, and how it may have been introduced (or if it has been here all along).

Notes on Iceliini Systematics

Although the Iceliini was originally placed within the Dexiinae by Townsend (1936), several authors have argued for placement in the subfamily Tachininae based on both larval (Thompson 1963) and adult characters (Guimarães 1976; O'Hara and Wood 2004). Indeed, they strongly resemble members of the Leskiini in general appearance, although they lack the strongly protruding lower facial margin characteristic of most Leskiini and the palpi are strongly reduced or absent in Iceliines. Tschorsnig (1985) suggests that the tribe is closely allied with the Tachinini (*sensu lato*), with only minor differences in the structure of the distiphallus.

ACKNOWLEDGEMENTS

We thank the Strategic Environmental Research and Development Program (SERDP) RC-2243 for funding Dell's fire ecology research, as well as the Earthwatch Institute Ignite Program for assistance in the field. Stireman was supported by NSF DEB NSF DEB 1442134.

FIGURE LEGENDS

Figure 1. Map of Eglin Air Force Base (EAFB) located within the panhandle of Florida, USA. The left panel shows the location within EAFB of the burn units where specimen was captured.

Figure 2. Malaise trap erected immediately after a prescribed fire in a longleaf pine forest. Traps were set up seven times in relation to each burn (before, during, immediately after, and then 2,5,10, and 12 months post-burn) to track the effects fire had on insect communities.

Figure 3-6. *Iceliopsis borgmeieri* specimen from Eglin Air Force Base. 3. Dorsal view (note lepidopteran scales covering the specimen from the dry Malaise trap and the apparent lack of black dorsal markings on T1+2 and T3). 4. Left lateral view. 5. View of the posterior surface of the left hind tibia illustrating the median, longitudinal groove thickly lined with inward pointing setae. 6. Left lateral sketch of the genital capsule, illustrating the distinctive knobbed cerci and narrow, elongate surstylus. The distal portions of both structures are partially concealed beneath sternite 5 (St. 5), as indicated by the diagonal fill lines.

FIGURES

Figure 1

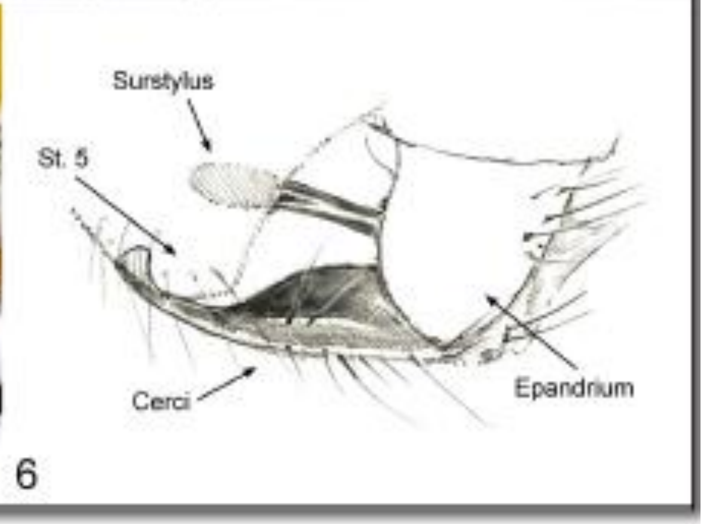
Figure 2

Figures 3-6


3


4


5


6

CHAPTER 6

Scale dependent patterns in interaction diversity maintain resiliency in a frequently disturbed ecosystem*

*Citation: Dell, J.E., Salcido, D.M., Lumpkin, W., Richards, L.A., Pokswinski, S.M., Loudermilk, E.L., O'Brien, J.J., and Dyer, L.A. (2018) Scale dependent patterns in interaction diversity maintain resiliency in a frequently disturbed ecosystem. In review, *Ecology*.

Keywords: interaction diversity; scale-dependency; response diversity; resilience; tri-trophic interaction; *Pinus palustris;* prescribed fire

ABSTRACT

Frequently disturbed ecosystems must be resilient in order to reorganize post-disturbance and maintain ecological function. Longleaf pine ecosystems are characterized by frequent fire disturbance which sustains ecosystem function and biodiversity. We examined how the frequency of fire maintains turnover in the diversity of species interactions, as this community parameter provides a measure of functional redundancy or response diversity of an ecosystem. We found that turnover in interaction diversity at the local scale is best maintained in the most frequently burned stands, conferring immediate resiliency to disturbance by fire. Interactions become more specialized and less resilient as fire frequency decreases. Local scale patterns of interaction diversity contribute to broader scale patterns and confer long-term ecosystem resiliency.

INTRODUCTION

Disturbance regimes are significant features of ecosystems, with frequency and intensity being important variables shaping not only community composition, structure, and function but also serving as selective forces in the evolution of life history strategies, especially in disturbance-prone ecosystems (Seidl et al. 2016, Sousa 1984). Resiliency is a critical feature of these frequently disturbed ecosystems (Larson et al. 2013). Regular disturbance events maintain a diverse and functional ecosystem state in disturbance-dependent systems and represent short-term pulse disturbances. In this context, resiliency is defined as ecosystem recovery to pre-disturbance levels of parameters such as diversity, species abundances, and nutrient cycling immediately post-disturbance. Conversely, a disruption of the disturbance regime, such as reduced occurrence, represents a transformational and longer-term press disturbance where ecosystem structure and function shifts and pushes such systems to unpredictable or unstable, alternative states (Beisner et al. 2003). In this context, removal of disturbance erodes long-term resilience of a disturbance-adapted ecosystem.

Resiliency requires a minimum level of underlying species and functional diversity to allow for multiple pathways towards post-disturbance responses (Seidl et al. 2016). The return to pre-disturbance function due to functional redundancies provided by biological diversity is also known as response diversity. Elmqvist et al. (2003) define response diversity as the diversity of responses to disturbance among different assemblages of species that contribute to equivalent ecosystem functions. However, response diversity is not simply equivalent to species richness for different broad taxa or at different trophic levels, because ecological communities are comprised of interacting species. For instance, a broad diet breadth or shared basal resources provide functional redundancy and are indicative of response diversity and trophic network stability (Pilosof et al. 2017). As such, quantification of response diversity requires easily measured metrics focused on interactions between species, such as interaction diversity.

Critical ecosystem functions, such as pollination, population control of herbivores by natural enemies, and seed dispersal are dependent upon a broad range of biotic interactions, the loss of which can precipitate species extinctions and loss of ecological function (Valiente-Banuet et al. 2015, Kremen et al. 2007). Therefore, it is also important to consider interaction diversity, defined as the richness and relative abundance of species interactions in a community (Dyer et al. 2010), as a primary contributor to ecosystem resilience and a critical component of response diversity. While species richness and potential interactions are necessarily positively correlated, diversity of species and diversity of interactions can have different effects on ecosystem function and stability (Pardikes et al. 2018). Like other diversity metrics, interaction diversity across the landscape has alpha, beta, and gamma components.

As with any metric exploring patterns of biodiversity, concepts of scale are necessary to consider when examining the causes and consequences of the richness and turnover of interactions among interacting species. Patterns observed at larger scales represent the combined processes occurring at smaller scales, but it is not always clear how patterns at nested scales relate to one another. Species richness differs among local and regional scales (Rahbek and Graves 2001, Witman et al. 2004) partly because regional and local diversity are shaped by different processes. For plant-insect networks, regional processes are affected more by large-scale evolutionary and historical factors, such as speciation, dispersal, extinction, and biogeographical history, while local processes include ecological effects such as, biotic interactions, resource availability, and disturbance. Furthermore, interaction networks are not static, and patterns in interaction diversity are unlikely to be constant across the landscape or at different spatial extents. At smaller local scales, trait-distributions, environmental conditions and species abundance will affect the potential of two co-occurring species to interact (Poisot 2015). Regionally, interaction diversity values can change substantially depending on the scale at which they are examined (Pardikes et al. 2018).

In this study we focused on trophic interactions between host plants, arthropod herbivores, and their parasitoid enemies in a frequently disturbed ecosystem across a broad geographic extent. Disturbance by fire has been a part of terrestrial ecosystems since the Silurian Period and is an essential process for maintaining both ecosystem function and biological diversity in fire dependent ecosystems (Pausas and Keeley 2009), such as the frequently burned longleaf pine (*Pinus palustris* Mill., O'Brien et al. 2008, Kirkman et al. 2004, Mitchell et al. 2009). In the absence of fire, competitive advantage is given to faster growing, non-fire dependent broadleaved vegetation, resulting in a closed canopy, extensive habitat degradation, and reductions in plant diversity (Mitchell et al. 2009, Noss et al. 2014). The removal of fire from the landscape initiates a shifting ecosystem trajectory where fire-adapted species are replaced by other species assemblages, yielding an alternative stable state (Beisner et al. 2003).

Our primary objective was to quantify interaction diversity across a time since fire gradient, in order to comparatively assess the effect of longer fire return intervals, (i.e press disturbance) on biotic community interactions in longleaf pine forests. As frequent fire maintains high-levels of plant diversity and ecosystem function, we also predict that large-scale interaction diversity will be higher in frequently burned stands than in stands with longer times since fire. Second, to understand the way interaction diversity varies with scale, we investigated how these patterns vary at both the small, plot-level versus broader, regional-level scales. Many understory plant species have a patchy distribution in longleaf pine because of fine-scale variation in fuel and fire heterogeneity (Dell et al. 2017, Menges and Hawkes, 1998), and diversity of these plants is best quantified at small spatial scales, therefore we expect that interaction diversity will also vary and patterns will change with increasing spatial scale. Furthermore, we posit that resiliency will be greatest in ecosystems where there is functional redundancy, (i.e. high response diversity), and that this functional redundancy is greatest when levels of beta interaction diversity (for multiple scales) are maintained (Figure 1). Due to the connectivity between these spatial scales any such local scale patterns of interaction diversity will contribute to broader scale patterns and confer long-term ecosystem resiliency for the region.

METHODS

Study Area

Research was conducted in longleaf pine forests across the Gulf Coastal Plain during 2013 to 2016. Sites included Eglin Air Force Base and Blackwater River State Forest located in the Florida panhandle and Solon Dixon Forestry Education Center and Conecuh National Forest in southern Alabama. The fire regime in longleaf pine ecosystems is characterized by high-frequency, low-intensity surface fires with return intervals of 1-5 years (Mitchell et al. 2009). Numerous longleaf pine stands within the region are actively managed by prescribed fires with a target of an 18-month to two-year fire return interval (Hiers et al. 2007). However, there exist stands within all management areas that have not experienced burning for longer periods of time including up to several decades. Sampling includes both frequently burned and an alternative stable state (infrequently burned) for longleaf pine as well as a transitional state.

Field Collection

We established sixty-seven, 30-m diameter plots in forested stands that varied in the time since last disturbance by fire (Figure 2). Based on available fire history records and vegetative indicator species associated with known fire return intervals, plots were placed into a burn category; frequently burned (fire return interval (FRI): 1-5 years, n = 49), intermediately burned (FRI: 5-25 years, n = 9), and infrequently burned (FRI: >25 years, n = 9).

Within each plot, lepidopteran larvae were sampled using beat sheets and visual searches in a standardized format moving clockwise around the plot. Within each fire return interval type, we also generally collected caterpillars outside of standardized plots to further expand the trophic network within each fire return interval category. Caterpillars were reared out to adulthood or eclosion of a parasitoid. Host plant associations were based on the vegetation from which the caterpillars were collected on and confirmed through feeding in the laboratory. Host plants and arthropods were identified to species or were assigned a morphotype based on morphological characteristics, behavior, and host plant record following Wagner (2005). Sampled arthropods were deposited into the research collection at the University of Nevada, Reno Museum of Natural History.

Quantification of Diversity

Diversity was estimated for species and interactions at two scales; the plot-level or local scale and the broader, regional-level scale. The regional level is defined as the aggregate of all plots and general collecting sites within each fire return interval category over the entire range of the study. It should be noted that longleaf pine forests in this study may have frequently burned stands adjacent to infrequently burned stands, therefore our use of the term regional does not infer a singular spatial aggregation, but rather a broader level organization. Interaction diversity was based on the richness and abundance of interactions between species, where richness is the number of unique interactions and abundance the total number of each interaction (Dyer et al. 2010). Bipartite interactions were quantified between plants and caterpillars as well as between caterpillars and parasitoids. Additionally, tri-trophic interactions between plants, caterpillars, and parasitoids were included to capture emergent properties on network structure (Pilosof et al. 2017, Dyer et al. 2010; Figure S1). Alpha diversity of species and interaction at the local-level were quantified within each plot with plot means used in statistical analyses. Local beta diversity represents the turnover of species or interactions and was quantified between plots within each fire return interval category. To estimate standard errors around each estimate we performed bootstrapping with the relative proportions of each species/interaction and the total sample size used to construct 100 simulated plots for each burn category following Chao et al. (2008). Regional-level diversity components were estimated within (alpha) and between (beta) each fire return interval category. Diversity estimates are reported using the inverse Simpson diversity index (1/D) and represent independent measures of alpha and beta following Jost (2007). Documented interactions were used to create and visualize trophic networks for all data and for each fire return interval category (Figure S2).

Statistical Analysis

To determine if interaction and species diversity across the burn gradient showed similar patterns within plots we utilized analysis of variance, with fire return interval category as an independent variable, and with alpha and beta diversity parameters as response variables. We performed separate univariate ANOVAs for each diversity component at the local scale. Post-hoc analyses utilizing Tukey's test were performed to identify differences between fire return interval types for each diversity parameter.

To address unequal sampling efforts in terms of number of plots within each fire return interval category, we performed sample-based rarefaction for species and interaction richness. We also calculated nonparametric asymptotic estimators at equal sample coverage levels following Chao et al. (2014) to allow for community comparison across the fire return interval gradient. Discriminant function analyses were conducted to detect differences between species and interactions within fire return interval categories and compositional similarity at the local, plot-level was assessed using non-metric multidimensional (NMDS) ordination techniques. All analyses were performed in R (v.3.2.3, R Development Core Team 2013).

RESULTS

The collective sampling effort resulted in a trophic network between 64 host plant species, 183 caterpillar species, and 47 parasitoid species (Figure S2). Combined, there were 1,415 individual interactions between species comprised of 468 unique interactions. 66% of all interactions were detected only once, and only 2% of interactions occurred over 20 times. Individual plant species tended to have numerous interactions with herbivores, while parasitoid species tended to have a more specialized diet breadth with generally only singular interactions. Within all fire return interval categories, the majority of herbivorous interactions tended to be between one caterpillar and one host plant species and the percentage of caterpillars with more than two host plants had an inverse relationship with time since fire (Table 1). Each fire return interval category, had certain plant species that were involved in a disproportionate number of interactions (Table 1). These highly connected nodes, such as the host plant *Quercus laevis* (turkey oak) connected to 24% of the entire network, are also referred to as network hubs (Figure S2).

Rarefaction analyses illustrated that richness of both species and interactions was highest within infrequently burned plots as compared to intermediately and frequently burned plots. Comparing Chao's asymptotic estimates of species richness at an equal level of coverage of 20 samples, the most species were found within infrequently burned plots ($\text{Chao1}_{\text{infrequent}} = 149$) followed by intermediate ($\text{Chao1}_{\text{intermediate}} = 89$), and frequently burned plots ($\text{Chao1}_{\text{frequent}} = 78$; Fig S3). Interaction richness was also highest in infrequently burned plots compared to intermediately and frequently burned plots in both rarefaction compared at equal sampling effort and comparison of Chao's asymptotic estimates of interaction richness ($\text{Chao1}_{\text{frequent}} = 75$, $\text{Chao1}_{\text{intermediate}} = 110$, and $\text{Chao1}_{\text{infrequent}} = 172$; Figure S3).

Large scale patterns

Dividing the entire network into regions of similar fire return intervals: frequently, intermediately, and infrequently burned yielded variable patterns in both species and interaction diversity (Table 2). At this larger scale, species alpha diversity increased with longer fire return intervals. However, frequently burned areas had the greatest parasitoid and herbivore species diversity. Parasitoids made up 15% of species richness in frequently burned areas while only 8% in the infrequently burned stands (Table 2). The diversity of interactions did not have a clear pattern across the burn gradient with frequent and infrequently burned regions having higher interaction diversity than intermediately burned regions.

Small scale patterns

At the local level, alpha species diversity was significantly higher in intermediately burned plots than in frequently burned plots with infrequently burned plots not significantly different than either ($F_{(2,63)} = 6.48$, $P = 0.003$; Figure S4). Beta species diversity was significantly higher in infrequently burned plots compared to intermediately burned plots but was not different compared to frequently burned plots ($F_{(2,297)} = 202.3$, $P < 0.001$). Interaction richness was greatest within infrequently burned plots, while alpha interaction diversity was significantly greater in intermediate burned plots than in frequently burned plots but did not differ between infrequent plots ($F_{(2,63)} = 5.03$, $P = 0.01$). In contrast, beta interaction diversity, or the turnover of interactions, was significantly higher in frequently burned plots, almost double the beta diversity of plots in intermediately and infrequently burned stands ($F_{(2,297)} = 820.6$, $P < 0.001$).

Patterns in alpha diversity in both species and interactions varied with scale (Table 2, Figure 3). The greatest difference was between frequently burned plots and both infrequent and intermediately burned plots. This pattern was confirmed through the discriminant function analysis where the first discriminant function explained 99% of the variance and differentiated interactions and species in frequently burned forests from intermediate and infrequently burned forests, with an opposite relationship at the local (species: b = 0.75; interactions: b = 0.83) and regional (species: b = -0.72; interactions: b = -0.64) scale. NMDS plots also indicated a differentiation of species along the fire return interval gradient and a separation in the aggregation of interactions between frequently burned stands and those experiencing longer periods between fires (Figure S5).

DISCUSSION

We found that the effect of fire return interval on biodiversity was highly scale dependent for both species and interactions, as measured by richness; as well as alpha and beta diversity components (Table 2). Frequently burned stands were more diverse at a regional-level scale in species and interaction richness as well as interaction alpha diversity. However, these patterns were not consistent when scaling down to the local, plot-level scale. The higher levels of richness among species and interactions, and the higher alpha interaction diversity at local scales in infrequently and intermediately burned stands may be driven by rare species and specialized, single interactions. Shrubby growth forms of hardwood species in longleaf pine forests are maintained by frequent fire, so as fire is removed from the landscape, these species grow and eventually close out the canopy (Hiers et al. 2007). This leads to a depauperate understory of shade tolerant and fire-sensitive plants (Mitchell et al. 2006, Kirkman et al. 2004). As these key plant species are removed due to lack of fire, the increase of fire-sensitive species promotes new interactions.

As frequently burned stands in our study area have more open canopies (Dell et al. 2017), the characteristic vegetation and associated specialist consumers within more closed canopy stands are not found outside of areas that have not burned in decades as indicated by the segregation of species along the fire return interval gradient (Figure S5). While the assemblages of plants, herbivores, and parasitoids are constrained to infrequently burned stands and are characterized by higher richness in comparison to plots that burn more often, interactions between these species are also constrained at the local scale. The lower levels of beta diversity, or the turnover of interactions, within infrequently burned plots are indicative of repeated sampling of the same specialized interactions as well as reduced response diversity.

One of the most interesting patterns of diversity in the longleaf pine system was the high beta diversity of interactions in frequently burned plots compared to other plots. Lower species richness in frequently burned stands might usually predict similar assemblages in any given plot at the local scale, but this was not the case. While species and interactions are fewer than in plots without fire, the increased turnover of interactions between plots reveals that stands that burn more often harbor slightly more generalized consumers, an attribute that confers greater potential resiliency to disturbance with increased response diversity (Elmqvist et al. 2003). Fire maintains high response diversity by keeping the ecosystem in a state dominated by longleaf pine and a species-rich, fire-adapted ground cover. In frequently burned forests 20% of the herbivores had a more generalized diet breadth (i.e. > 2 host plant species, Table 1), which provides functional redundancy. In this case, the decreased local alpha diversity can facilitate increased local beta diversity (Chase and Myers 2006), contributing to greater gamma or regional interaction diversity in frequently burned forests - supporting our predictions of frequent fire positively affecting interaction diversity and varying across scale. Furthermore, interaction surplus, where interactions are redundant and may be substituted, results in sustained ecosystem function (Valiente-Banuet et al. 2015). Higher interaction beta diversity and lower species richness suggest an interaction surplus in frequently burned forests. This high degree of interaction turnover may provide an advantage to species adapted to frequently disturbed longleaf pine ecosystem. For example, more generalized diet breadth can be beneficial for individuals post-fire when there is high variability in local plant species composition (García et al. 2016).

Response diversity depends on examining multiple spatiotemporal scales to assess full resiliency potential, which may not be evident if only one scale is examined. Regional or ecosystem-level networks represent an aggregation of numerous snapshots in space and time. Thus, there are dynamic processes occurring over time in real networks that are not captured in our static presentation of trophic networks in this system. However, application of a multilayer network perspective allows for associative connectivity between individual plots (single layer) and the larger scale (multiple layers) by way of shared species and interactions (Pilosof et al. 2017, Figure S2). Therefore, the information we gain by analyzing diversity of interactions are still informative for assessing the impact of fire return interval on the biotic communities. Specifically, contributions to both immediate and long-term resiliencies are found at local and regional-level scales, respectfully.

The relative ecological importance of connectivity in these longleaf networks becomes more apparent when focusing on dynamics of individual species or management of particular species. The relative connectivity of highly connected species, or hubs, has an inverse relationship with fire return interval (Table 1). For example, turkey oak (*Quercus laevis*), a host plant to many herbivores, was represented in 24% of all network links in frequently burned forests compared to only 12% and 6% in intermediate and infrequently burned forests, respectively. While highly connected networks are more resilient to perturbation, the loss of highly connected nodes would have significant impact on the remaining network and in simulations, eventually leads to network collapse (Bascompte and Jordano 2014). Therefore, maintenance of hub species is an important management consideration. Removal of turkey oak has often been the inappropriate target of intense management in longleaf pine ecosystem (Loudermilk et al. 2016, Hiers et al. 2014). However, our results highlight that the significant contributions of turkey oak to functioning networks in longleaf pine forests.

Conclusion

Disturbances (e.g. fire, insect outbreaks, hurricanes) increase habitat heterogeneity which in turn affects the realization of interactions locally and regionally as a consequence of varying species abundances, trait distributions and local environmental conditions across the landscape due to variation in disturbance frequency, intensity, duration, and extent. Understanding patterns of interaction diversity within disturbance-dependent networks requires clear data on both the scale at which interactions occur and the position along the disturbance gradient. No biological network is static, and large published webs that are assembled from species inventories (Bascompte and Jordano 2014) or that examine interactions over large gradients (Forister et al. 2015, Dyer et al. 2007) are misleading in many ways because identities of interactions often vary across the landscape (Fox and Morrow 1981). At finer scales, such as those examined in our longleaf pine plots, local environmental conditions, community composition, and phenologies differ (Poisot 2015, Garzon-Lopez et al. 2014, Chase and Myers 2006), and the large static network does not exist. Local scale patterns are particularly important in the longleaf pine ecosystem because fine scale heterogeneity in soils, fuels, fire, and dispersal affect plant diversity and community assembly processes (Dell et al. 2017). For example, the processes maintaining assemblages of species and interactions within longleaf pine networks may be deterministic and niche-based at larger (entire ecosystems across the landscape) scales and neutral or stochastic at small (1-10m^2) scales. Such variable processes across spatial scales, as well as along the disturbance gradient suggest that interactions in this system are governed by both niche and neutral processes as described by the continuum hypothesis (Gravel et al. 2006), presenting an exciting opportunity for future research.

ACKNOWLEDGEMENTS

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TABLES

Table 1: Relative connectivity of the most linked plant and herbivore species in each tri-trophic network within each fire return interval category. Individual species (i.e. node) connectivity is measured as the percentage of total network links connected to the node in the network. As a summary of diet breadth for each fire return interval category, the percentage herbivore species that consume 1, 2, or >2 host plants is reported.

Frequent		**Intermediate**		**Infrequent**	
Plant	Connectivity (%)	Plant	Connectivity (%)	Plant	Connectivity (%)
Quercus laevis	24	*Quercus laevis*	12	*Vaccinium arboreum*	7
Diospyros virginiana	12	*Quercus marilandica*	10	*Ilex vomitoria*	6
Quercus incana	8	*Quercus margaretta*	9	*Quercus laevis*	6
Smilax auriculata	4	*Ilex vomitoria*	6	*Vitis rotundifolia*	6
Vaccinium arboreum	4	*Quercus incana*	5	*Vaccinium stamineum*	5
Herbivore	Connectivity (%)	Herbivore	Connectivity (%)	Herbivore	Connectivity (%)
Gelechiidae 8	3	*Gelechiidae 3*	5	*Hypeagyris esther*	3
Hyperstrovia flaviguttata	3	*Gelechiidae 10*	4	*Noctuidae 5*	3
Gelechiidae 3	3	*Anisota stigma*	3	*Geometridae 22*	3
Erebidae 1	2	*Megalopyge crispata*	2	*Thysanopyga intractata*	2
Noctuidae 5	1	*Hyperstrovia flaviguttata*	2	Gelechiidae 4	2
Host plants per species		Host plants per species		Host plants per species	
1	70%	1	80%	1	72%
2	10%	2	11%	2	22%
>2	20%	>2	9%	>2	6%

Table 2: Diversity measures for both species and interactions calculated at the regional and local scales for each fire return interval category. Alpha and beta diversity components were estimated using inverse Simpson's index (1/D). Variance around local beta values estimated by bootstrapping. Regional-level values are calculated from the aggregation of plot and general collection data within each fire return interval category. Bracketed values in regional species richness represent plants (P), herbivores (H), and parasitoids (E), respectively. Local level means are reported (+/- SE). Letters denote significant differences between local fire return interval categories based on Tukey's test at $P < 0.05$.

		Species Diversity			**Interaction Diversity**		
Scale	**Fire Return Interval**	**Richness** [P/H/E]	**α**	**β**	**Richness**	**α**	β
Regional	Frequent	170 [37/108/25]	14.11	2.11	245	29.83	2.80
	Intermediate	115 [30/67/18]	12.28		143	8.93	
	Infrequent	145 [38/95/12]	28.18		158	20.44	
Local	Frequent	6.84^{a} (0.59)	4.39^{a} (0.29)	5.42^{b} (0.63)	5.44^{a} (0.54)	3.97^{a} (0.35)	15.29^{b} (1.39)
	Intermediate	9.33^{ab} (1.45)	7.26^{b} (1.20)	4.27^{a} (0.38)	7.55^{ab} (1.39)	7.13^{b} (1.32)	8.04^{a} (0.44)
	Infrequent	13.57^{b} (2.31)	6.63^{ab} (1.37)	5.57^{b} (0.88)	11.29^{b} (2.61)	5.57^{ab} (1.45)	9.00^{a} (0.21)

FIGURE LEGENDS

Figure 1: (A) The pre-disturbance and post-disturbance metawebs, displaying the full regional pool of species and potential interactions. Here nodes represent individual species of primary producers (circles) and pollinators (squares), while edges (links) represent interactions between species. Post-disturbance, the loss of species and interactions are indicated by dashed edges. In this case the loss of a single species (c1) also results in the loss of an interaction, however ecological function (i.e. pollination of this plant species) is maintained as a redundant interaction occurs with another pollinator species (c2). Conversely, the loss of a specialized interaction may result in the loss of ecological function. In this example, the specialized mutualism between a plant (p3) and pollinator (c4) no longer occurs, reducing functional diversity and eventual loss of partner species (p3-c4). **(B)** The regional meta-network, for which nodes represent plots and edges represent shared interactions between plots. Three plots are enlarged so that we may examine the corresponding local networks of interactions. While α-diversity of species and interactions are calculated within each plot, β-diversity is calculated between plots. Focusing in on shared interactions between three individual plots illustrates the turnover of interactions between local plots (high β-diversity), this β-diversity summarizes variation in post-disturbance responses, which provides ecological resiliency.

Figure 2: Reference map of Southeastern United States with study area highlighted in black rectangle. Within the study area, individual plot locations are indicated by colored dots corresponding to each of the three fire return intervals.

Figure 3: Interaction diversity components calculated from frequently, intermediately, and infrequently burned sites at hierarchical spatial extents. The broader, regional-level alpha diversity (top panel) represents diversity calculated at each fire return interval category. Our use of the term regional does not infer a singular spatial aggregation, but rather a broader level organization. Local level alpha diversity (middle panel) and beta diversity (bottom panel) represent diversity components calculated at the plot level. Solid lines indicate median value and points connected to dashed lines indicate mean value within local level panels. Diversity values are reported in (1/D).

FIGURES

Figure 1

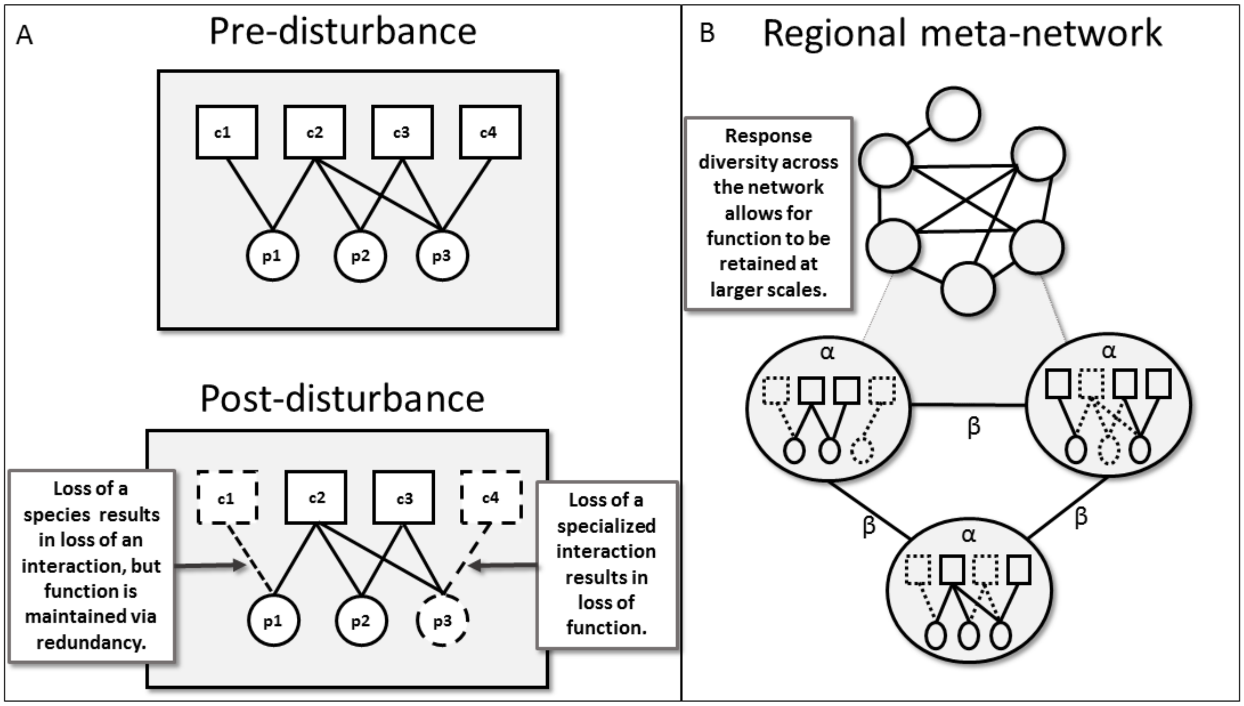
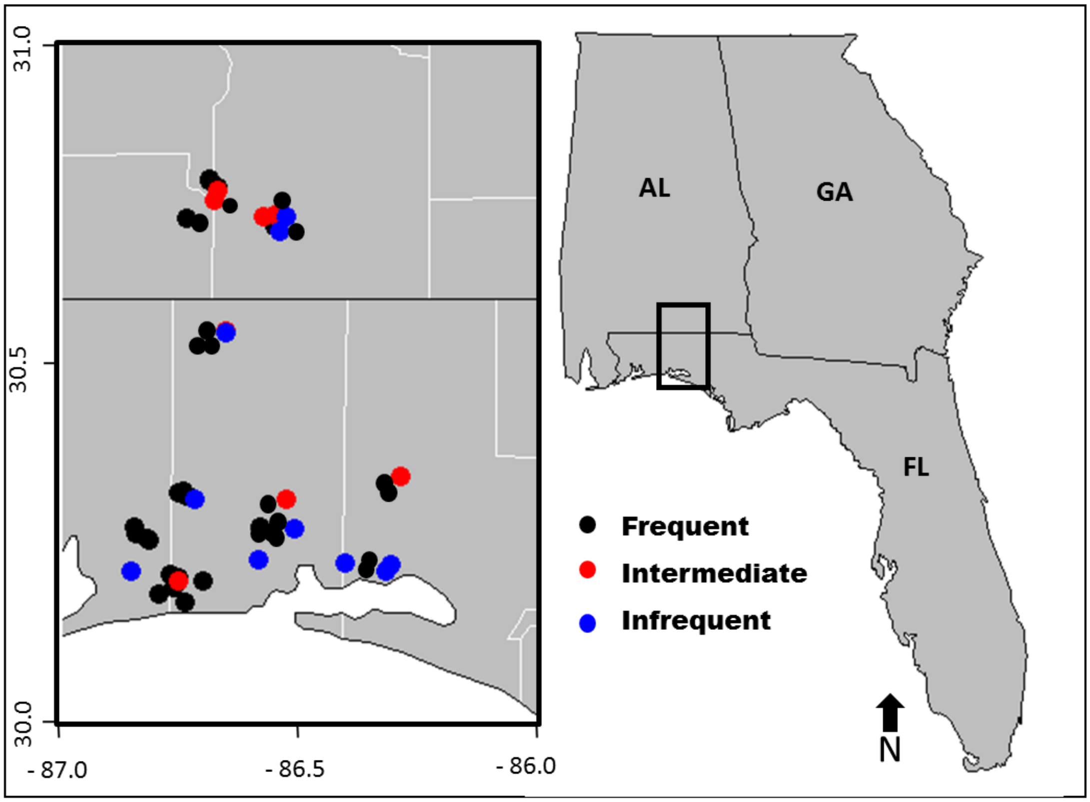


Figure 2


31.0
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- 86.0
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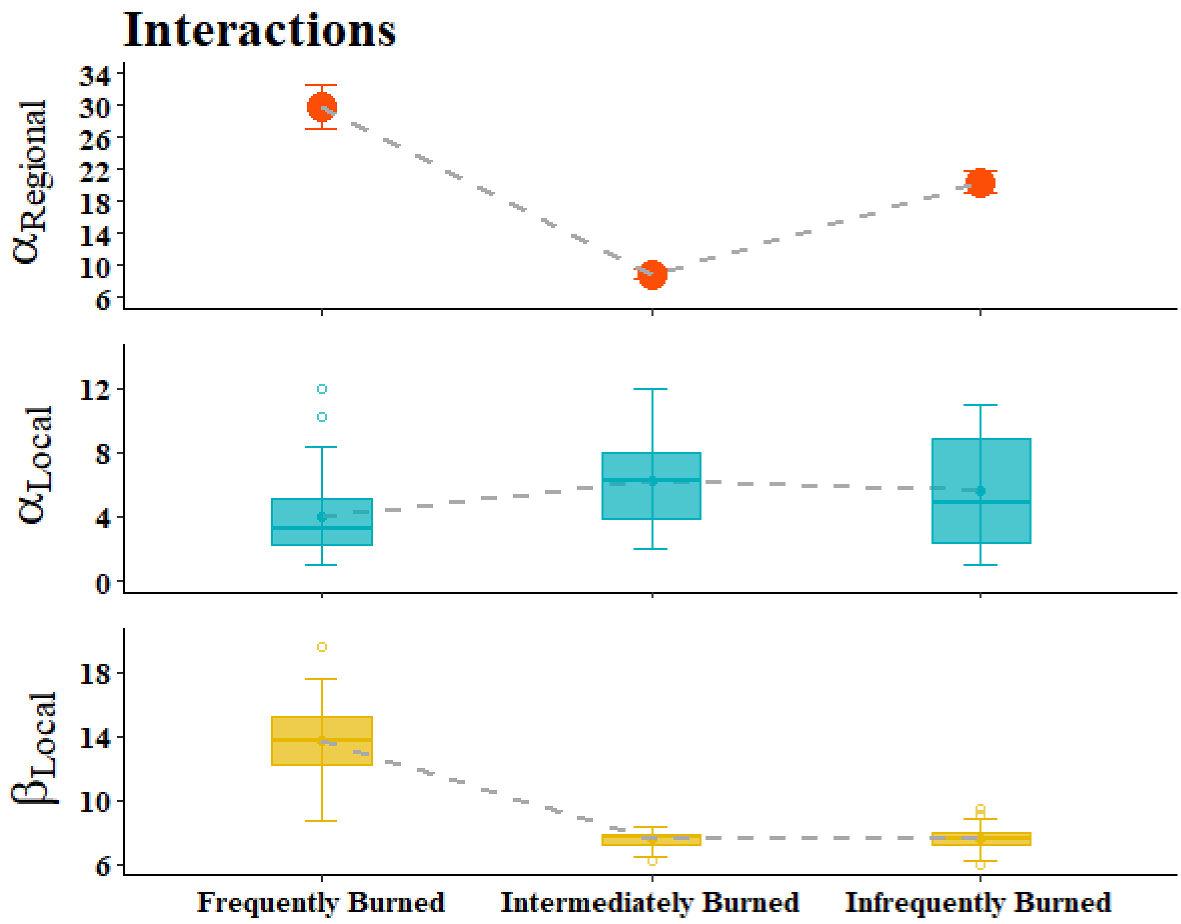
Figure 3


Interactions
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β_{Local}
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10
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Frequently Burned
Intermediately Burned
Infrequently Burned

SUPPLEMENTAL INFORMATION

Supporting Figure Legends

Figure S1: Photo representation of each fire return interval (FRI) category and a sample interaction diversity network found within a single plot in each FRI type. Interactions and their abundances are indicated by solid lines and corresponding numbers, representing interactions between host plants (circles) and herbivores (squares), or between herbivores and parasitoids (triangles), respectively. Each tri-trophic interaction linking a plant, herbivore, and their parasitoid is considered an additional single interaction. Interaction richness and abundance are used to quantify interaction diversity components. Local-scale diversity metrics were calculated with individual plots while regional-scale diversity metrics represent an aggregation of interaction diversity plots and general collections within each FRI category.

Figure S2: 3-D visualization of entire Florida interaction diversity database created using Network 3-D software (Williams 2010, Yoon et al. 2004). The tri-trophic network is comprised of nodes (individual species) and edges (interactions between species). Red nodes represent plants, orange nodes represent herbivores, and yellow nodes represent parasitoid enemies. The pink highlighted plant node represents *Quercus laevis* (turkey oak), a highly-connected network hub.

Figure S3: Rarefaction curves for species (top panel) and interaction (bottom panel) richness. Solid circles and lines represent observed richness in plots within each fire return interval and open circles represent extrapolated Chao estimates. Solid squares indicate an appropriate level of comparison at the blue dotted line following Chao et al. (2014). Shaded regions represent 95% confidence interval.

Figure S4: Species diversity components calculated from frequently and infrequently burned sites at hierarchical spatial extents. The broader, regional-level alpha diversity (top panel) represents diversity calculated at each fire return interval category. Our use of the term regional does not infer a singular spatial aggregation, but rather a broader level organization. Local level alpha diversity (middle panel) and beta diversity (bottom panel) represent diversity components calculated at the plot level. Solid lines indicate median value and points connected to dashed lines indicate mean value within local level panels. Diversity values are reported in (1/D).

Figure S5: Non-metric multidimensional scaling (NMDS) ordinations of local species and interaction assemblages within each fire return interval category. (A) Interacting species aggregate in ordination space along time since fire gradient indicating that each fire return interval type possesses a differing suite of species. (B) Interactions aggregate into two clusters, those occurring in frequently burned stands differing from interactions occurring within intermediate and infrequently burned stands.

Supporting Figures

Figure S1

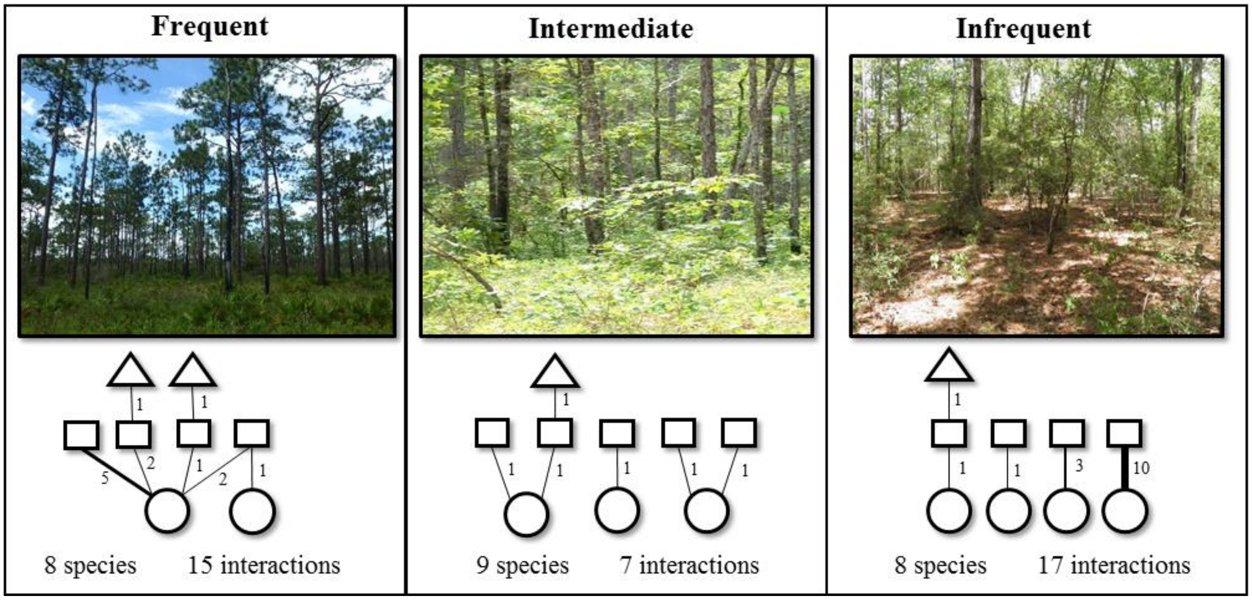

Figure S2

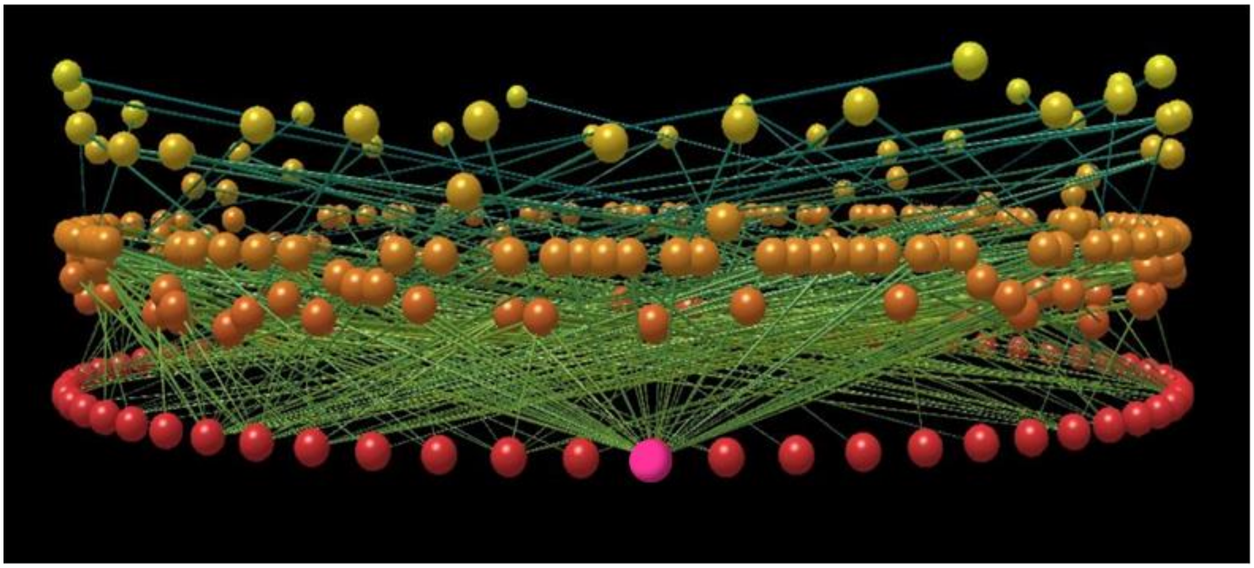

Figure S3

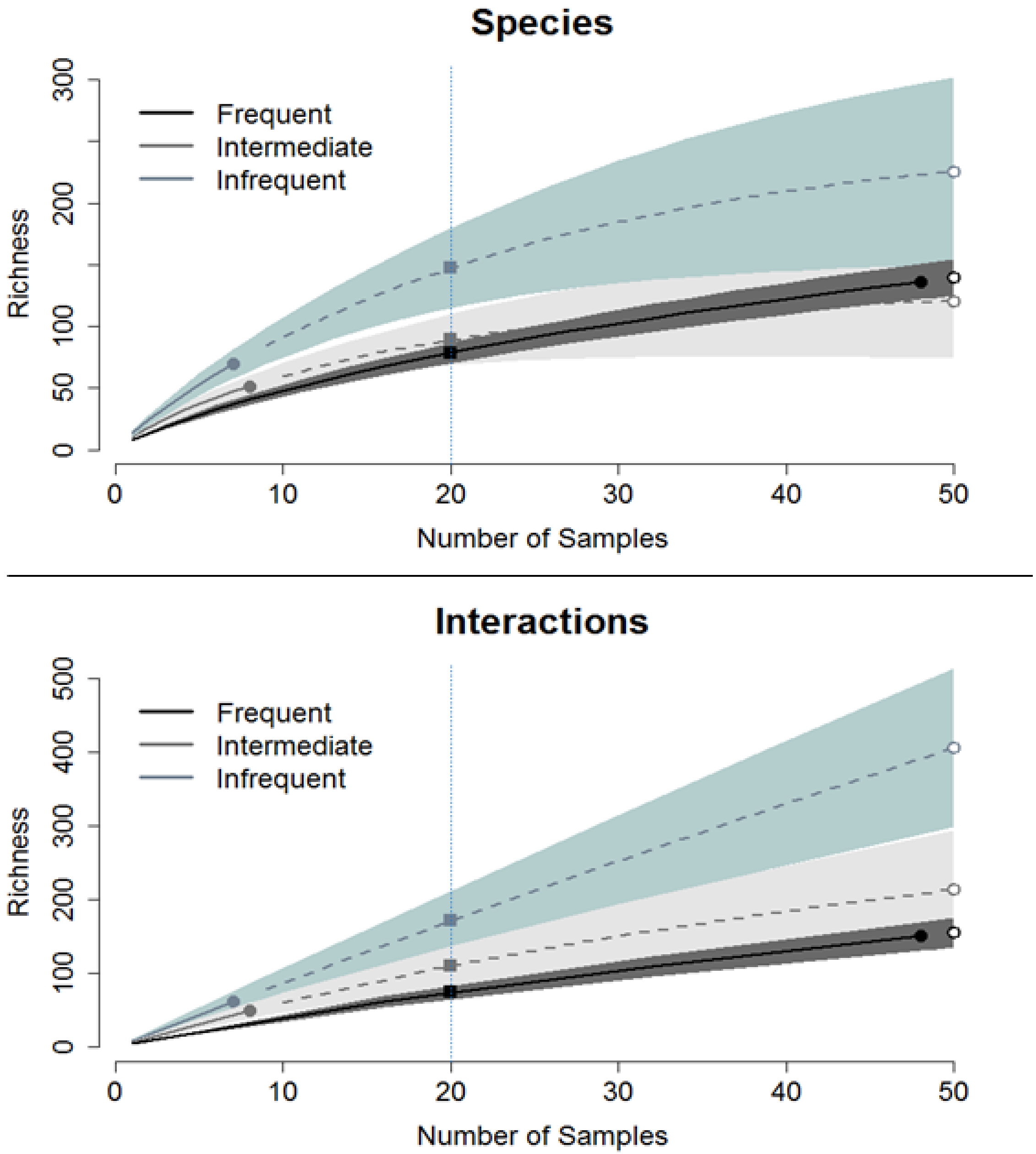
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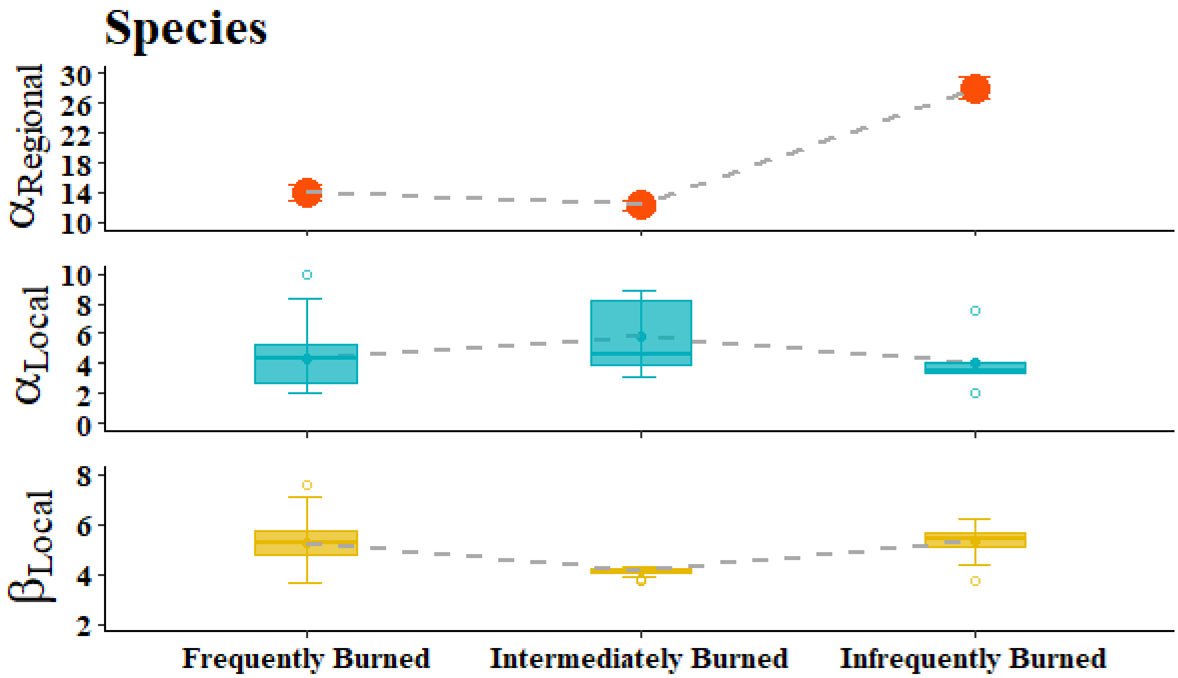
Figure S4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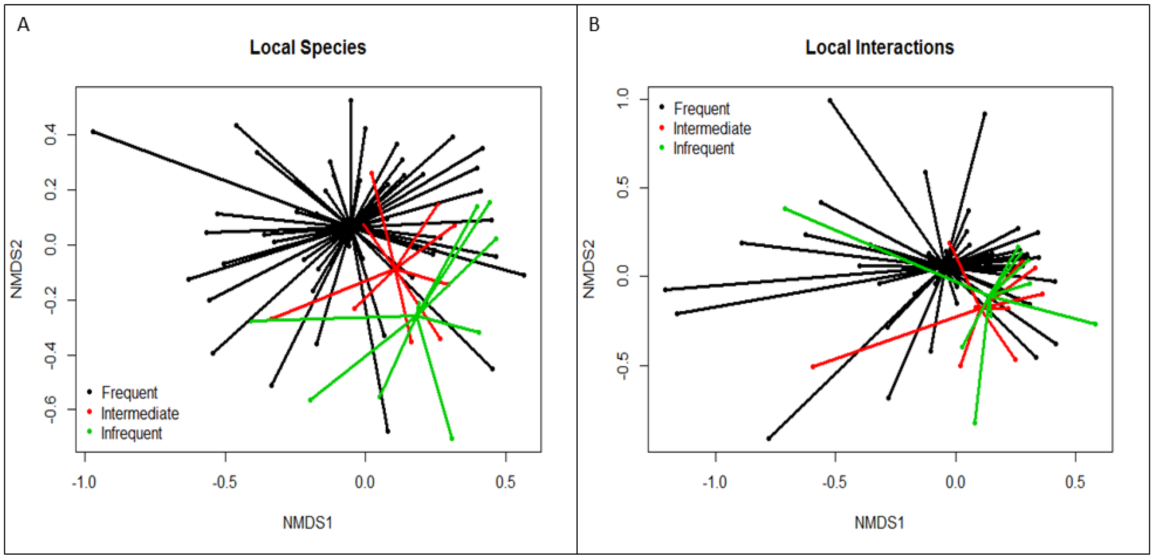
10
8
6
4
2
0
β_{Local}
8
6
4
2
Frequently Burned
Intermediately Burned
Infrequently Burned

Figure S5


A
Local Species
NMDS2
0.4
0.2
0.0
-0.2
-0.4
-0.6
-1.0
-0.5
0.0
0.5
NMDS1
Frequent
Intermediate
Infrequent
B
Local Interactions
NMDS2
1.0
0.5
0.0
-0.5
-1.0
-0.5
0.0
0.5
NMDS1
Frequent
Intermediate
Infrequent

CONCLUSION

Understanding patterns in biodiversity across spatial scales is a key component of efforts to preserve ecosystem functioning and resilience in the face of biodiversity loss. Studies on the scale-dependence and distribution of species diversity have contributed significantly to understanding patterns of biodiversity (Crawley and Harral 2001, Chown and Gaston 2000, Condit et al. 2002, Rahbek 2005) and community structure (Ricklefs & Schluter 1993). Furthermore, while my dissertation has focused on a single ecosystem, many aspects of my approaches and associated findings could be applied to other ecosystems, providing insight especially to those with similar structural components that are influenced by fire.

Patterns of species diversity are dependent upon the scale in which they are examined. Species richness differs among local and regional scales (Rahbek 2001, Witman et al. 2004) indicating that regional and local diversity can be shaped by different processes. Regional processes include large-scale evolutionary and historical effects (e.g. speciation, dispersal, extinction, biogeographical history), while local processes include ecological effects (e.g. biotic interactions, resource availability, disturbance).Using two extensive datasets including both mined historical data and supplemental experimental data, I identified spatial patterns of understory diversity in longleaf pine and investigated the impact of sampling intensity (plot area, distribution) and sampling design on multiple measures of taxonomic diversity. Specifically, I partitioned plant diversity to elucidate hierarchical spatial patterns in species richness, and independent measures of alpha and beta diversity. This analysis allowed me to identify the spatial scale that most effectively captures plant diversity by using measures of species turnover. I found that while species richness and alpha diversity increased with spatial scale, beta diversity began to asymptote at smaller scales, in particular,1m^2 plots. Additionally, I found that sampling effort at this 1 m^2 scale required as few as 60 samples (e.g. plots, quadrats) in order to effectively estimate plant diversity. Thus, the efficiency of monitoring activities that assess effects of management on biodiversity will be maximized when performed at fine-scales.

Furthermore, results that fine-scale beta components of diversity were greater than expected supports previous studies (e.g., Dell et al.2017, Loudermilk et al. in review) showing plant species richness and composition are structured by small-scale processes in frequently burned longleaf pine forests. These processes include fine-scale fuel heterogeneity as well as neutral processes as outlined in the Unified Neutral Theory of Biodiversity (UNTB, Hubbell 2001). UNTB is a null model that assumes individuals among species at an equivalent trophic level are competitively and functionally equivalent and that communities of these species are structured by random demographic processes such as birth, death, and dispersal, and at longer time scales speciation and extinction. Neutrality is likely a process affecting plant community assembly in frequently burned longleaf forests because the high-levels of richness (up to 50 species of vascular plants per m^2) occur at scales too small for niche differentiation in the relatively uniform sandy soils. Therefore, the frequently burned longleaf pine community might be the closest example of a truly neutral community at fine scale.

Frequently burned coniferous forests around the globe often share a similar forest structure with a monospecific overstory of pine, a sparse midstory, and a high diversity understory. My dissertation identifies mechanistic processes contributing to the maintenance of understory diversity in one of these such ecosystems, the longleaf pine forest. I created links between common fuel types, where these fuels originate within the forest structure, and how each fuel type specifically contributes to understory diversity following fire. I found that overstory derived fuels specifically longleaf pine litter and 10-hour woody fuels, increased diversity when burned and provided the greatest contributions to species richness. I also describe connections between remote sensing metrics and the observed fuels and discovered specific contributions of fuels derived from various vertical canopy strata within the forest structure using landscape scale LiDAR data and plot scale ground observations. I found that overstory LiDAR was an effective predictor of longleaf pine litter. This information establishes a linkage between small scale patterns in understory plant diversity and coarser scale stand characteristics.

My results support the ecology of fuels (*sensu* Mitchell et al. 2009), a concept in which forest structure and vegetative composition impact fuel heterogeneity, which in turn affects fire behavior and community responses to fire, including changes in plant diversity and long-term forest structure. This link between fine-scale fuels and landscape-scale properties within the ecology of fuels framework, which I document in this dissertation, can contribute to more cost-effective management models conducted at broader scales.

Fire extent, severity, seasonality, and frequency impact the abundance and diversity of insects across all trophic levels. Fire disrupts ecological processes at a landscape scale in a number of distinctive ways, which may place unique selective pressures on fire-affected communities. Compared to other major landscape-level disturbances, fire alone concurrently alters the abundance and quality of basal resources, causes short- and long-term effects on soil nutrients, temperature, and moisture, as well as transforms habitat structure for the entire biological community. I found that arthropod communities in longleaf pine are regulated by bottom-up forces after fires because plant community recovery defines habitat structure as well as the direct and indirect availability of resources for the entire insect community. For instance, herbivorous species experience concurrent decreases in diversity mirroring plant community compositional alterations when fire is removed from the system.

A recent review by Pausas and Parr (2018) highlighted the importance of increased research on animal adaptation to fire, as studies are lacking in comparison to those focused on plant adaptations. The authors argue that most adaptations might be behavioral, as animals can move away from the fire and are not modular (in opposite to plants). A clear example of behavior adaptation is the escape from fire, in which arthropods can be seen climbing trees (Dell et al. 2017), seeking refugia from fire (Janion-Scheepers et al. 2016), burrowing into the soil (Sensenig et al. 2017), or fleeing the site (Kral et al. 2017). Some arthropods can have morphological adaptations to detect fire, such as using the antennas as a smoke detector (Álvarez et al. 2015) or infrared radiation sensors (Schmitz et al. 2015). These adaptations can be used to locate fire and make use of resources available post-burn as cues for mate attraction and oviposition. Such morphological, physiological and behavioral adaptive traits of arthropods in fire-prone ecosystems confer potential for improved fitness in terms of survivability and enhanced reproductive output.

Animals that are adapted to fire will have benefits post-fire, due to availability of food, mating cues, habitat alteration or species interactions (Pausas and Parr 2018, New 2014). Examples of trophic resources include arthropod herbivores that can feed on sprouting leaves (Lopes and Vasconcellos 2011) and on seeds released due to fire (Setterfield and Andersen 2018), or the high availability of dead wood or animal for saprophytic arthropods (Hammon et al. 2017). Pollinators benefit in terms of increased density of floral resources available post-burn, as well as opening bare ground for ground-nesting species (VanNuland et al. 2013). Indirect benefits are also achieved via reduction of overstory basal area which results in increased herbaceous plant cover as available sources of pollen and nectar (Campbell et al. 2007). Some arthropods can synchronize emergence after fire or swarm towards smoke, presumably to find mates (Millberg et al. 2015). Post-fire habitat alterations immediately benefit some ants due to increased temperature as a result of vegetation removal (Christian and Morton 2011), or benefits can also come from release of predation pressure (Pausas and Parr 2018).

Fire is a natural form of periodic disturbance in many terrestrial ecosystems (Kral et al. 2017, Pausas and Keeley 2009). Global climate change is leading to more common fires due to recent changes in the intensity and frequency of droughts and global patterns of precipitation. In addition to fires becoming more frequent, ecosystems are experiencing changes in the timing, seasonality, extent, duration, and severity of fires (IPCC 2014). These changing fire regimes are likely to affect the composition of biological communities, the strength of biological interactions within them, and the provisioning of ecosystem services (IPCC 2014). Therefore, studies providing linkages between disturbance, corresponding effects on diversity, and ecosystem resilience will provide further insight into mitigating the effects of climate change.

My dissertation presents an interesting and novel quantification of ecological resiliency in a frequently disturbed ecosystem. Here I utilized empirical metrics of interaction diversity to support the idea of response diversity (*sensu* Elmqvist et al. 2003) as it confers redundancy and resiliency in the fire-dependent longleaf pine ecosystem. While the concept of interaction diversity has been discussed for decades, especially in the context of conservation and global change (Burkle and Alarcón 2011), this dissertation is the first to use empirical data to quantify interaction diversity at ecologically relevant scales to examine its role in resiliency. This was accomplished by recording interaction diversity parameters across a time since fire gradient as well as at hierarchical spatial scales.

I found that local scale patterns of interaction diversity are associated with short-term resilience and broader scale patterns confer longer-term resilience. These findings are important, because they demonstrate that fire not only maintains species diversity, but it also maintains interactions that contribute to ecosystem function and services, such as biological control. For instance, parasitoids examined in my trophic webs regulate populations of herbivorous lepidopteran larvae, which left unchecked, may exert tremendous impacts on plant biomass in both natural and applied systems. Global change will continue to alter disturbance cycles and species richness; thus, a continued research priority will be to understand these relationships between disturbance and diversity. As fire regimes continue to shift as a result of climate change (IPCC 2014), arthropods and the ecological communities they inhabit are likely to change as well.

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