Patterns and Processes: Monitoring and Understanding Plant Diversity in Frequently Burned Longleaf Pine Landscapes

Final Technical Report
SERDP Project RC-2243

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Acronyms:
ALS: Airborne Laser Scanning
BA: basal area
CA: Cellular Automata
CHM: Canopy Height Model
EAFB: Eglin Air Force Base
FAST: Fourier Amplitude Sensitivity Test
FLIR: Forward Looking Infrared
FRE: Fire Radiative Energy
FRED: Fire Radiative Energy Density
FRFD: Fire Radiative Flux Density
FRI: Fire Return Interval
GPS: Global Positioning System
LiDAR: Light Detection and Ranging
LWIR: Long-Wave Infrared
NMDS: Non-metric Multidimensional Scaling
TLS: Terrestrial Laser Scanning
SEM: Structural Equation Model
UAV: Unmanned Aerial Vehicle
UNTB: Unified Neutral Theory of Biodiversity

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Patterns of biodiversity and the mechanisms driving them must be thoroughly understood to guide an effective monitoring and resource management program. In addition, other dimensions of biodiversity along with new diversity metrics, such as interaction diversity, can act as more sensitive indicators of how ecological communities respond to management activities, disturbances, or global change parameters. These detailed measures of diversity, combined with knowledge of theoretical and mechanistic underpinnings of diversity, then must be made relevant for managers of natural resources.

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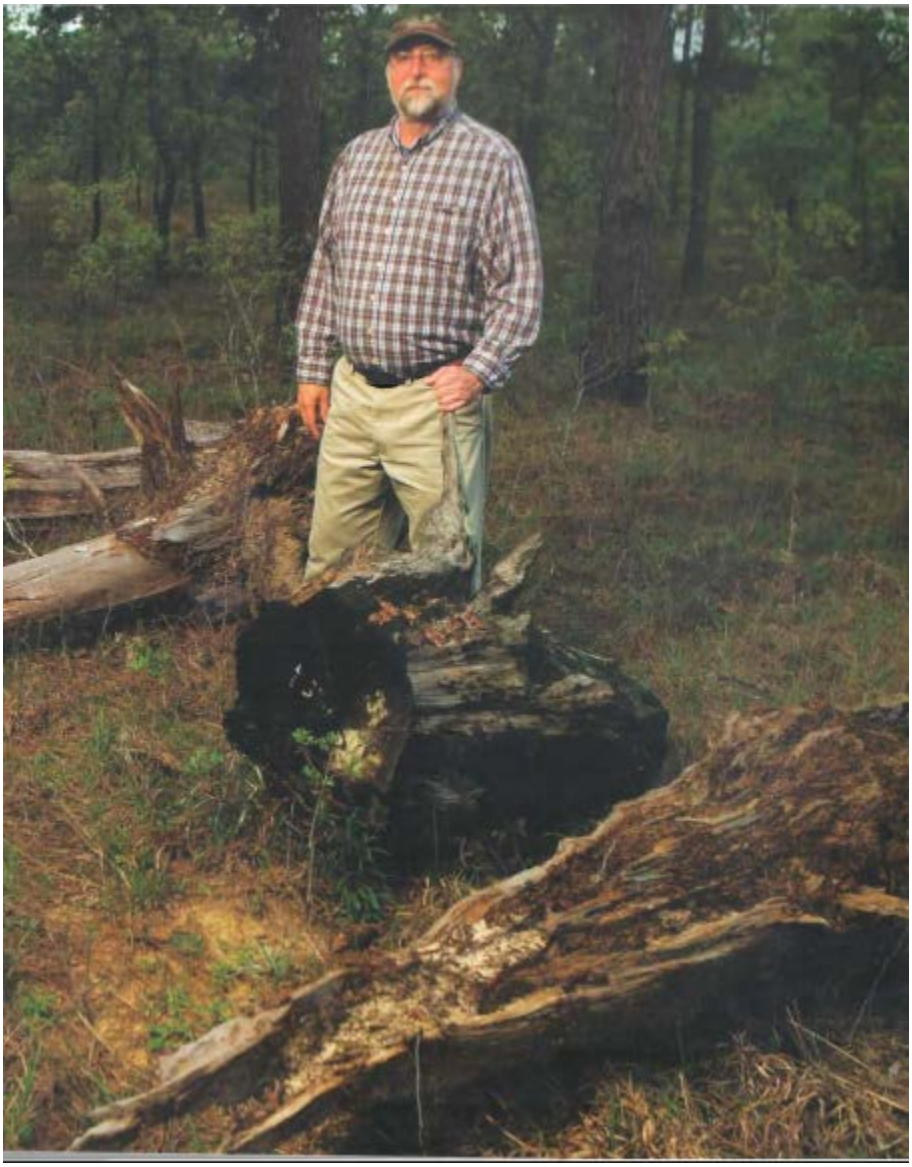

Dedication

We lost our dear friend and colleague, Dr. Robert Mitchell, in 2013 while the project was just beginning. Bob was one of the original principal investigators and his insights and intellect were instrumental in the development of the concepts and research we report here.

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Overview

Patterns of biodiversity and the mechanisms driving them must be thoroughly understood to guide an effective monitoring and resource management program. In addition, other dimensions of biodiversity along with new diversity metrics, such as interaction diversity, can act as more sensitive indicators of how ecological communities respond to management activities, disturbances, or global change parameters. These detailed measures of diversity, combined with knowledge of theoretical and mechanistic underpinnings of diversity, then must be made relevant for managers of natural resources. This combination of diversity pattern, process, and management has been the overarching theme of our SERDP funded research. The strategy outlined below shows how we have divided our activities into three sub-themes (**Fig. 1**): 1) cross-scale spatial and temporal patterns of diversity (**Fig. 1**, yellow boxes); 2) fine-scale examination of the role of fire in driving patterns of diversity (**Fig. 1**, green boxes); and 3) coarser-scale linkages useful for expanding mechanistic understanding to landscape and management relevant scales (**Fig. 1**, blue boxes).

These themes both framed our research and were tactical; the project was large and complex and it was an efficient and effective strategy for guiding our research activities. We adopted this framework for the final report not because we executed three independent projects, but rather because each topic area was crucial for understanding the 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. We have completed all our planned activities and broadened the project in three important areas: fuel and fire behavior spatial dynamics and fuelbed modeling without adding any additional costs. While we have completed all promised analyses and syntheses, the work reported here will form the foundation for several new avenues of research we are actively pursuing. We were also mindful that the focus of the research was to produce management applications. We saw our challenge as generating applied knowledge and tools that have a solid mechanistic and theoretical foundation (**Table 1**).

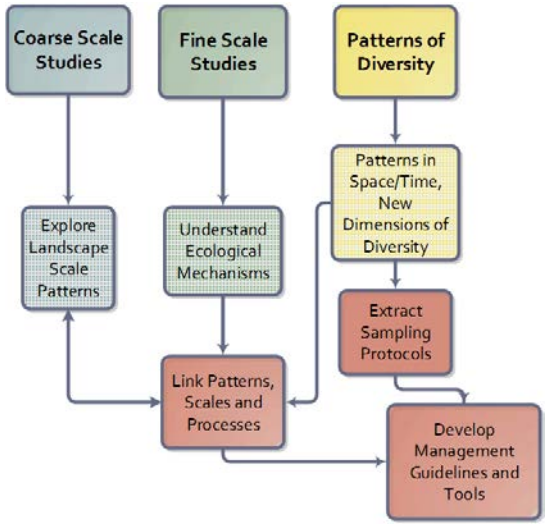

Figure 1. The three themes (blue, green, yellow boxes) of RC-2243, the red boxes indicate the final synthesis phase of the project.

Table 1. Examples of how the project has generated both basic and applied knowledge for science and management. Some of these topics were cited in the original proposal, others are new areas we are still pursuing and will continue to pursue.

Project Activity	**Knowledge Gained**	**Application**	**Future Utility**
Aerial LiDAR	Generate landscape-scale forest structure models; & coupled with terrestrial LiDAR	Stand structural information at management relevant scales; scenario testing	Technique broadly applicable to other forested ecosystems
Cellular Automata model	Identify mechanisms driving patterns of diversity/community assembly; Identified neutral processes.	Community responses to fire management; scenario testing	Applicable to other systems once appropriate model rules are determined; test with other (soil, canopy) disturbances
In-fire Infrared Thermography	Spatial and temporal patterns of fire behavior	Link fire behavior to fire effects at relevant scales	Calibration/validation of fire behavior models
3D Fuel Rendering	Create virtual surface fuels with real estimates of volume and biomass; Link canopy structure and surface fuels	Create landscape-scale surface fuel models	Develop better fuel characterization for fire behavior models; applicable in other systems
Demographic Data (plants & arthropods)	Advance theoretical foundations of community ecology	Define appropriate type/scales for sampling diversity	Identify key transition points where management intervention might be most successful
Interaction Diversity	Identify new dimensions of diversity currently unexplored in most ecosystems.	Provides more robust metrics of diversity that can guide management decisions and helps to quantify actual ecosystem services provided by biodiversity	Allows for more effective calculations of the billions of dollars of ecosystem services provided by biodiversity on any DoD land
Unified Model	Identification and linking of cross scale mechanisms driving patterns of diversity and ecosystem function	Explicitly designed for management to test various interventions (e.g., logging, fire application) scenarios	Modular nature of the model facilitates the inclusion of other parameters (e.g., fire spread, smoke)

Therefore, one major focus of our current project was aimed at identifying the mechanisms driving the relationship between fire and fine-scale patterns of diversity. We have hypothesized *and have empirical evidence* to support that at one end of the fire frequency spectrum, the high plant diversity found at very fine scales is driven by stochastic community assembly processes. This was not because we are joining the more than 5000 studies that have cited Hubbell's influential 2001 book on the unified theory of biodiversity and biogeography (or the 20,000+ publications on neutral theory), but because we hypothesized that the mechanisms that ecologists have identified as neutral processes (e.g., random mortality and recruitment limitation) are *the actual drivers* of the patterns of biodiversity that we have observed. These processes affect more than just a simple number count of species, they affect multiple dimensions of diversity, including genetic, taxonomic, functional, and interaction biodiversity. Understanding these mechanisms will allow us to make realistic predictions on the impacts of management on biodiversity. Because we have developed new ways to measure spatial and temporal patterns of fire energy release, we believe we have identified the mechanistic key to understanding how so many species coexist in such proximity in a nearly uniform substrate. Fuels such as grasses and pine needles dominate fire spread in frequently burned longleaf ecosystems and most plant species survive exposure to the burning of these fuels; the longleaf flora is dominated by perennial species and species composition post fire on the whole generally mirrors what was present prior to fire. However, fuels that burn for longer periods such as pine cones and tree branches release considerably more energy concentrated in a small area. This energy release represents the agent of random mortality key to neutral community dynamics. We also know that when fire is excluded, diversity declines and this process *is not random*, but predictable as certain species are released (e.g. woody plants) and competitively exclude other species. This represents a clear deviation from neutrality. Reconciling these processes has been described as the "Continuum Hypothesis" (Gravel et al. 2006, **Fig. 2**), which posits that different disturbance regimes or scales, allow for both neutral processes and significant deviations from neutrality to affect diversity.

Figure 2. Graphic of the Continuum Hypothesis as influenced by fire return interval and influences on diversity scaling. The arrow points towards longer periods between fires and coarser scales of diversity. The boxes indicate positions on the spectrum of fire return intervals where ecological processes shift from neutral toward deterministic. Understanding the nature of the transition could identify tipping points and be useful for guiding restoration.

Whereas the examples of the Continuum Hypothesis typically involve comparisons of different landscapes, we hypothesized *and have empirical evidence* that in systems dependent on frequent fire, the continuum can occur within a single landscape. A further discovery was that the shift from

neutral to deterministic processes occurs very rapidly, with as few as two missed fire entries, and the transition itself is complex and dynamic. This conceptual framework was one of the foundations of our project and was clearly the correct approach. While Gravel et al. 2006 were attempting to reconcile the theories, we argue that our study shows they are indeed discrete processes separated by the presence or absence of fire. The validity of our approach was also supported by our neutral modeling results. This approach was useful not only for teasing out the relative roles of competing ecological theories on community assembly, but also in providing a framework for testing how forest disturbances affect diversity at large scales. Because we used a spatially explicit rule-based modeling approach (Cellular Automata (CA) model, in 'Fine-Scale Studies' section) to test our ecological hypotheses, this allowed us to seamlessly integrate it with the landscape-scale portion of our project ('Coarse-Scale Studies' section) and the investigations into patterns of diversity. Plant diversity at scales larger than our 1m x 3m plots, including long-term data collection at EAFB were utilized to understand diversity at coarser spatial and temporal scales ('Patterns of Diversity' section). By sampling arthropod diversity and creating linkages to plant diversity at multiple spatial and temporal scales, we could better understand how both plant and animal communities, as well as their interactions, are organized with respect to presence or absence of fire. Our measures of multiple dimensions of diversity reflect the current focus of biodiversity researchers in both basic and applied realms, and 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.

For clarity throughout this report, "diversity" refers to the multiple measures of diversity that we quantify, including the following: species richness = the number of species; species density = the number of species estimated per unit area (Gotelli and Colwell 2001); diversity = measures of entropy that include evenness and relative abundance, such as Shannon or Simpson diversity indices; effective number of species = indices converted from an entropy measure to the equally-common species required to give a particular value of the index - for example, the transformed inverse Simpson index (1/D) is used as the effective species number, and allows for meaningful ecological comparisons (with species as the unit) across samples or studies (Jost 2007). The Simpson species equivalents are better for the ecological comparisons in our studies than rarefaction techniques (e.g., see Lande et al. 2000). In addition, we examine multiple dimensions of diversity, including "interaction diversity," which we define as the richness and relative abundance of trophic interactions linking species into dynamic biotic communities (Dyer et al. 2010, Forister et al. 2015). This measure of diversity is very important for understanding the relationship between economically valuable ecosystem services (e.g., predation, parasitism, pollination) and biodiversity, since these services depend on a diversity of natural interactions (Dyer et al. 2010).

Sampling Design

This section briefly describes the project's sampling design performed at coarse scales (A), fine scales (B), and approaches to data mining and other sampling approaches (C).

A. Coarse-Scale Sampling Design

Expectations at the earlier stages of the project that high-density Buckeye LiDAR would be flown over all or significant portions of Eglin Air Force Base (EAFB), and delivered, never materialized.

As an alternative, we are using publicly available low density (1 to 2 points m^{-2}) LiDAR flown from 2006-2008 across all of EAFB. These data have been downloaded for processing into predictive LiDAR metrics at a 30 m resolution. We have supplemented this low density data with high density (7 points m^{-2}) where available.

B. Fine-Scale Sampling Design

Our overall experimental plan was a two-way randomized block design. Burn units were the blocking variable, site productivity (sandhills, flatwoods) and overstory density (three levels), were the two factors. We established our plots within existing EAFB monitoring plots classified as being in reference condition and used the monitoring tree maps to stratify the overstory as follows: In each habitat type, five replicate burn units had 1m x 3m plots installed in open, single-tree, and clumped canopy conditions for a total of 30 plots (two habitat types x three treatments x five blocks). To stratify the overstory, we used a stem map and created four meter circular buffers around each tree. Open plots could only be located outside buffers, single-tree plots could only be located in a single buffer that did not intersect other buffers and clumped plots could only be placed in areas where at least three buffers overlapped. The locations of the plots were randomly selected within the strata. Arthropod sampling is conducted in proximity to the 30 monitoring plots (see 'Patterns of Diversity' section). We also established three separate replicates of fire exclusion plots in sandhills near each experimental block in areas that could be protected from fire. Operation constraints as determined by EAFB fire managers prevented installation of plots in flatwoods. All plot locations at EAFB associated with this study are shown in **Fig 3.**

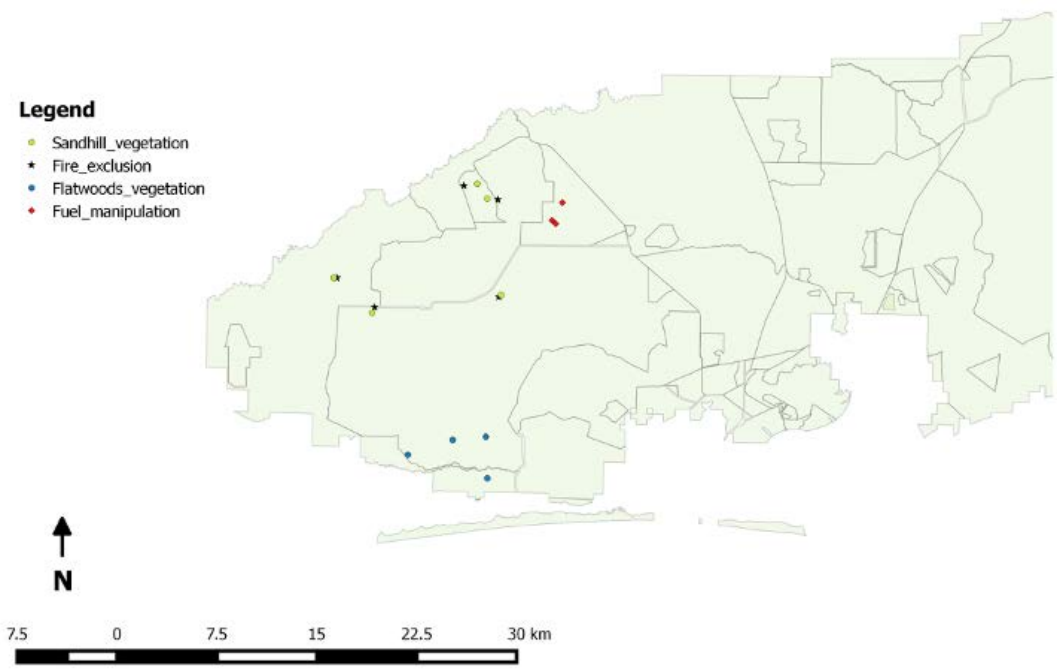

Figure 3. Map of fine-scale vegetation plot locations across EAFB for this study. Arthropod sampling is conducted in close proximity to these vegetation plots. This map includes the plots created specifically for this project, and not the EAFB long-term 1-ha vegetation monitoring plots and sampling done across the FL panhandle. Each symbol represents 3 replicate plots.

In addition to these 30 plots, we created nine additional fine-scale fuel manipulation plots in fall of 2013 within sandhills of EAFB. This was requested by the SERDP board for supplementing our

original design to explicitly test effects of particular fuels types on fire intensity and plant demography. Here, we distributed 0, 5, and 10 pine cones within each $1m^2$ quadrat of the nine 1m x 3m plots. They were placed so as to not overlap or touch each other or extend out from the plot edge, but otherwise randomly distributed within the respective $1m^2$ area. Spatial plant monitoring for these plots started in fall 2013.

C. Data Mining & Other Sampling

For management applicability and linking to other aspects of diversity (i.e., interaction diversity, in 'Patterns of Diversity' section), we used additional data from nineteen reference monitoring plots in the EAFB vegetation monitoring program collected from 2001-2012. After 2012, the EAFB monitoring program shifted focus from diversity to indicator species and no longer collects diversity data. Methods for collecting data in the EAFB monitoring program is detailed in Hiers et al. (2007). The monitoring plots have a hierarchical spatial structure that lends itself to examining patterns of diversity. A large dataset from the longleaf reference project data was originally collected in 1996-1998 (Provencher et al. 2001), then sampled again in the SERDP project RC-1696 in 2010 (Kirkman et al. 2013). Methods for collecting data in the longleaf reference project are detailed in Provencher et al. (2001) and Kirkman et al. (2013). In addition, fine resolution spatial scale sampling using 5 m radius sampling plots were installed to allow us greater insight into species density, species richness, diversity, and effective number of species. **Table 2** illustrates all data collected and other datasets used in this study.

Table 2. Datasets used to calculate plant diversity across EAFB. This table is relevant to sections on 'Fine-Scale Studies' and 'Patterns of Diversity'. The data summarized here are being used in individual-based as well as sample-based analyses of diversity (sensu Gotelli and Colwell 2001).

Dataset	Spatial scale	Temporal Scale	Diversity sampling	Description
lidar AFB vegetation monitoring	$1m^2$, 40 m^2	2001-2012	Abundance and richness at $8m^2$ scale, richness at $40m^2$ scale	152 abundance and richness quadrats, 19 richness plots sampled after each management treatment during the time scale.
Sandhill and Flatwoods vegetation plots	$3m^2$	2012 to present	Richness	15 Sandhill plots and 15 flatwoods plots sampled in the fall of every year and spring in years not burned
Provencher et al. (2001) and RC-1696	$1m^2$, 400 m^2	1996-1998 and 2010	Abundance and richness at $1m^2$ scale, richness at $400m^2$ scale	320 abundance and richness quadrats, 80 richness plots sampled during both time scales.
Spatial scale 5m radius sampling plots	$0.785m^2$ - $78.54m^2$	2014-present	Abundance and richness	7 plots variable spatial scale plots sampled Summer 2014 with more to be added Summer 2015

Coarse-Scale Studies

Abstract
An operating assumption in our project is that fine-scale (sub-meter) patterns in surface fuels and plant diversity are related to fine-scale fire patterns through mutual feedbacks. As detailed elsewhere in this report, O'Brien et al. (2016a, b) provide strong evidence for the causal link between surface fire and surface fuels, and Bright et al. (2016) between surface fuels and understory plant diversity, characterizing the exceptionally high plant diversity observed at sub-meter spatial scales.

Another assumption in our project is that these observed fine scale patterns in understory plant diversity, surface fuels, and fire are related to forest overstory canopy structure that varies at larger scales ranging from individual tree crowns to forest stands, which in our project we equated with the 425 land management blocks distributed across Eglin AFB. The distribution of tree crowns affects the light and moisture microenvironment, providing a constraint on understory fuel structure and plant species composition. That gaps in the longleaf pine forest tend to be shrubbier (e.g., turkey oaks) is evidence of this overstory influence (Mitchell et al. 2006, 2009). Conversely, needle litter beneath the longleaf pine provides a more homogeneous fuel bed that is more conducive to fire spread, thus limiting shrub establishment.

Objectives
For the coarse-scale study portion of the project, our objectives were to map tree density and other canopy metrics (height, basal area, stem volume), across EAFB from freely available low density LiDAR and evaluate these landscape values with EAFB's long-term ecological monitoring data (n=200) as well as this project's field data. Another objective was to examine relationships between LiDAR-based canopy estimates to EAFB's fire regime and surface fuels and species characteristics. We also used terrestrial LiDAR scanners combined with airborne scanners to examine their relationships and combined attributes for landscape surface fuel estimation.

Technical Approach

A. <u>Tree Density and Fuels from aerial LiDAR</u>

We had two LiDAR datasets available for use in this project: High density LiDAR (> 6 pulses m^{-2}) across a select few and considerably smaller extent of Eglin's management blocks or stands (Hudak et al. 2016a) and low density LiDAR (< 2 pulse m^{-2}), which was available across the entire study area. The lidar points within a 3-m radius from the center of 1m x 1m destructive clip plot surface fuel samples were reduced to statistical metrics indicate of surface fuel density, height mean, mode, standard deviation, coefficient of variation, skewness, and kurtosis. These lidar metrics were then considered as candidate variables for predicting surface fuel loads from lidar; nine metrics were selected as significant predictors in a multiple linear regression model (**Table 3**) that explained one third of the variation in fuel load (**Fig. 4**). The predictive model was subsequently applied to the full, high-density lidar collections, in which the lidar points were binned at a 5m x 5m resolution that were comparable in size to the 3m radius areas around the clip plot locations, used to train the model (**Fig. 5**). From the high density LiDAR, Hudak et al. (2016a) demonstrated that surface fuel loads can be predicted with high accuracy (**Fig. 5**), but our goal was to map canopy characteristics across the entire study area.

Table 3. Multiple linear regression model predicting surface fuel loads (ln-transformed) from nine selected LiDAR metrics.

Lidar predictor	Estimate	Std. Error	t value	Pr (>|t|)	Significance
(Intercept)	2.141	0.315	6.789	4.96e-11	***
Mean (0–2 m)	-1.767	0.780	-2.266	0.024	*
Kurtosis (0–2 m)	0.003	0.001	2.261	0.024	*
Mode (0–0.05 m)	-4.772	2.327	-2.051	0.041	*
Proportion (0–0.05 m)	-1.779	0.242	-7.355	1.41e-12	***
Proportion (0.05–0.15 m)	-1.777	0.308	-5.763	1.84e-08	***
Std Dev (0.05–0.15 m)	23.838	8.616	2.767	0.006	**
CV (0.15–0.50 m)	0.575	0.210	2.743	0.006	**
Std Dev (0.5–1m)	1.507	0.677	2.225	0.027	*
Std Dev (1–2m)	0.988	0.368	2.687	0.008	**
Model statistics:					
R^2 = 0.456; Adj. R^2 = 0.442	df = 344	RSE = 0.566	F = 32.07	p <0.0001	***

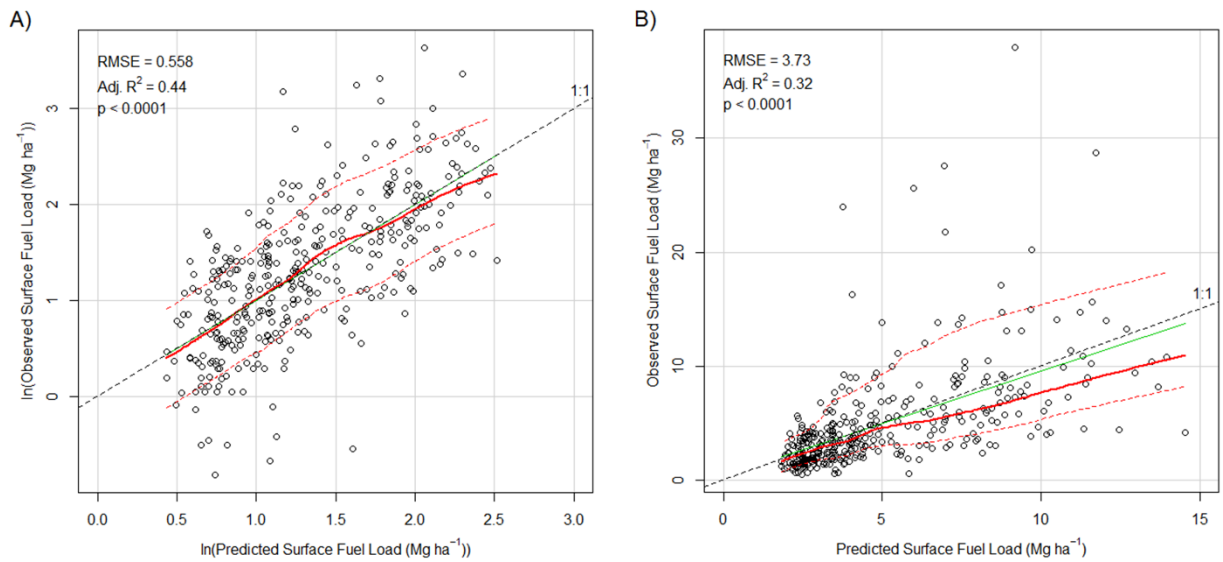

Figure 4. Multiple linear regression models predicting a) pre-fire surface fuel load (ln-transformed) from nine airborne lidar metrics (**Table 3**). Backtransformation with bias correction yielded the predicted vs. observed relationships for surface fuel load in b). On both graphs, the line of best fit is shown in green, and the nonparametric regression with loess smoothing is shown in red, with the solid line indicating the mean fit and the dashed lines indicating the square root of the squared positive and negative residuals above and below the mean.

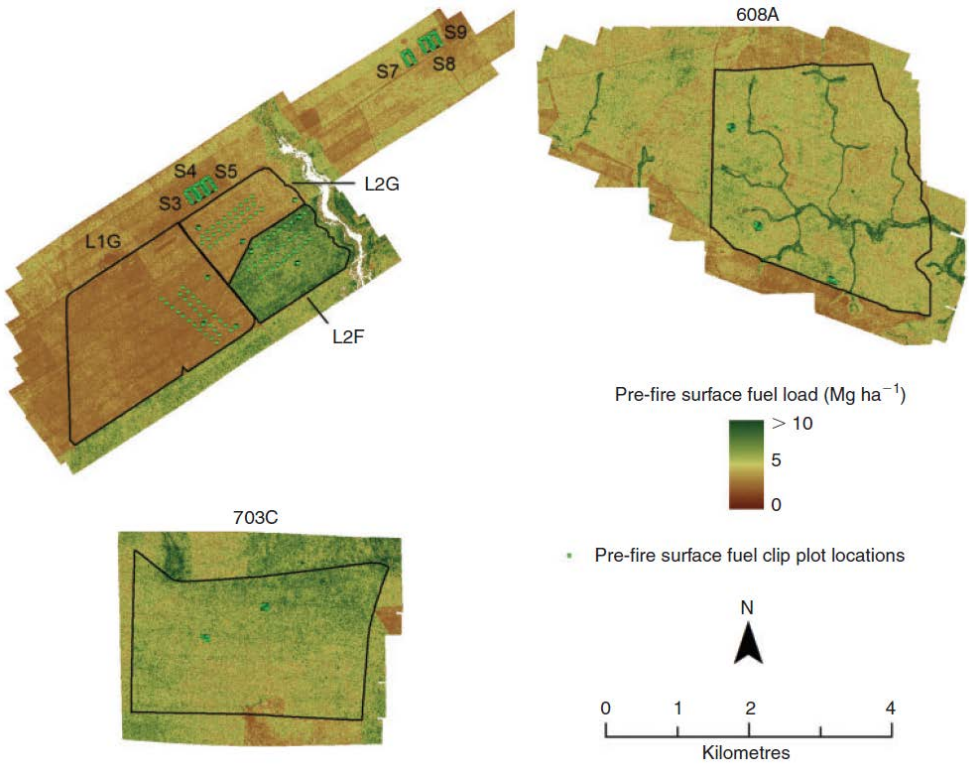

Figure 5. Pre-fire surface fuels mapped across the extent of 2011 and 2012 high density airborne lidar collections (from Hudak et al. 2016a).

We aimed to develop methods for using the low density airborne LiDAR to map tree canopy attributes and link the canopy metrics to understory characteristics across EAFB. As such, utilizing Eglin's environmental monitoring plot data and low density lidar Hudak et al. (2016b) explicitly linked plant species richness and surface fuel measures to overstory structure, as well as the frequent fire management regime. Because understory plant species richness and surface fuel loads are at best only weakly detectable with airborne LiDAR, particularly low density LiDAR, we used an imputation modeling strategy to predict these attributes In this study, the monitoring plot having the most similar structural signal to a given, unsampled location on the landscape based on the lidar data, was imputed to that location, thus "filling in" plot observations at unsampled locations where only lidar data were available. Plant species richness and surface fuel loads. **Fig. 6** shows the models developed to impute tree density and basal area, along with precision and accuracy statistics. Random Forests (RF), a machine-learning algorithm developed by Breiman (2001) and broadly applied for predictive modeling, was the method used to assign the model weights for imputation. A Ripley's L statistical point pattern analysis (Clark and Evans 1954) applied to the plot-level tree stems mapped in 'reference' and 'restoration' stands revealed that longleaf pine trees at Eglin AFB (and likely more broadly) have a clumped distribution that can be captured at a resolution of 30 m (**Fig. 7**). These LiDAR points were binned at a 30m x 30m resolution for imputing tree density, basal area, and dominant tree species estimates measured at 195

environmental monitoring plots. The most similar plot was imputed to every 30m x 30m cell across Eglin based on the canopy structure signal captured by the LiDAR.

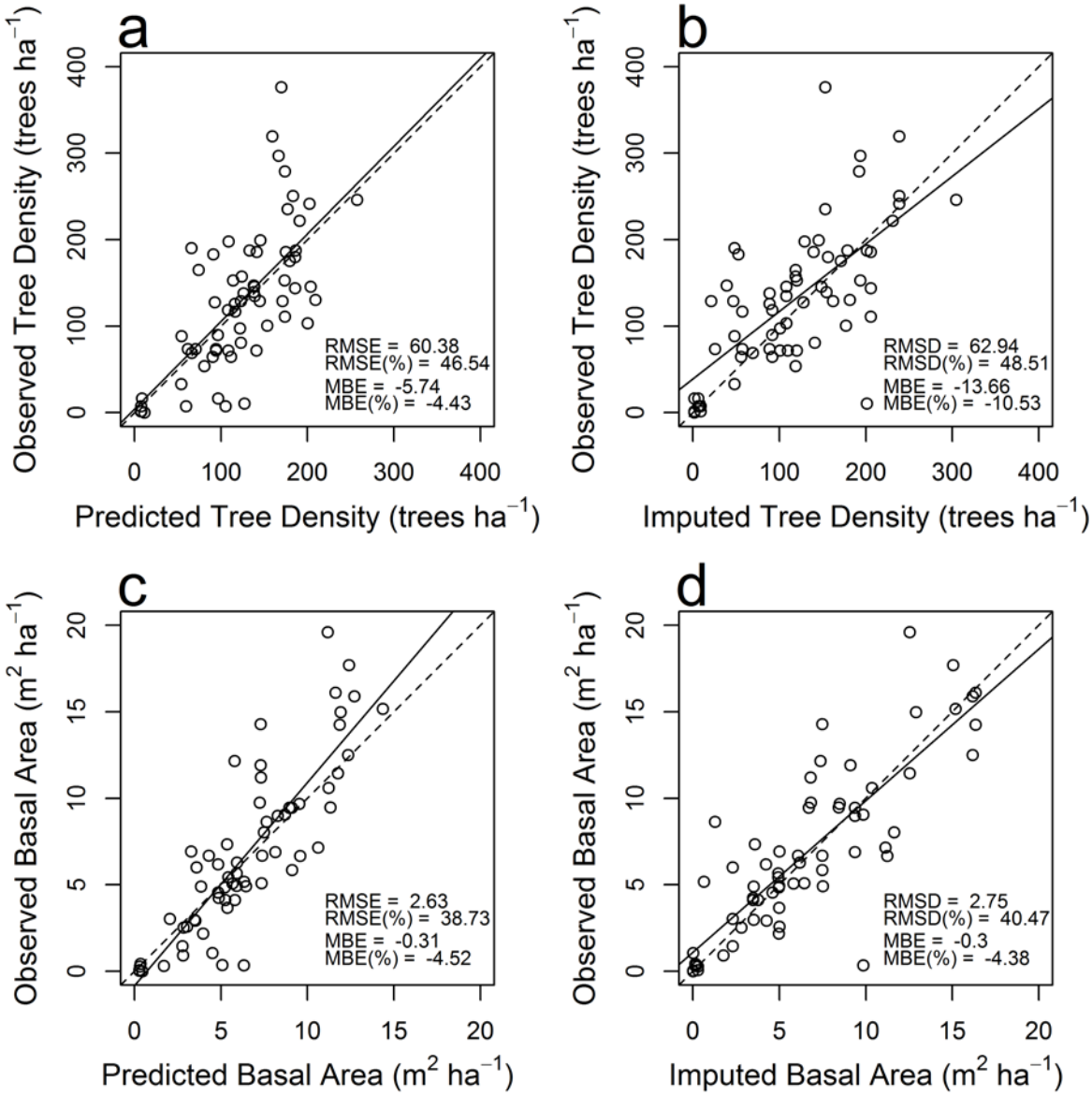

Figure 6. Predicted versus observed results using RF models to predict TPH (a, b) or BA (c, d) as either a univariate response in regression mode (a, c) or via multivariate k-NN imputation (b, d). Models were trained with a random selection of 2/3 of the plot data (n = 130) and tested with the remaining 1/3 of the plot data (n = 65); these graphs illustrate the testing results. The same ten predictor variables (**Table 3**) were used in all models. Solid lines in each graph indicate best linear fit; dashed lines indicate 1:1.

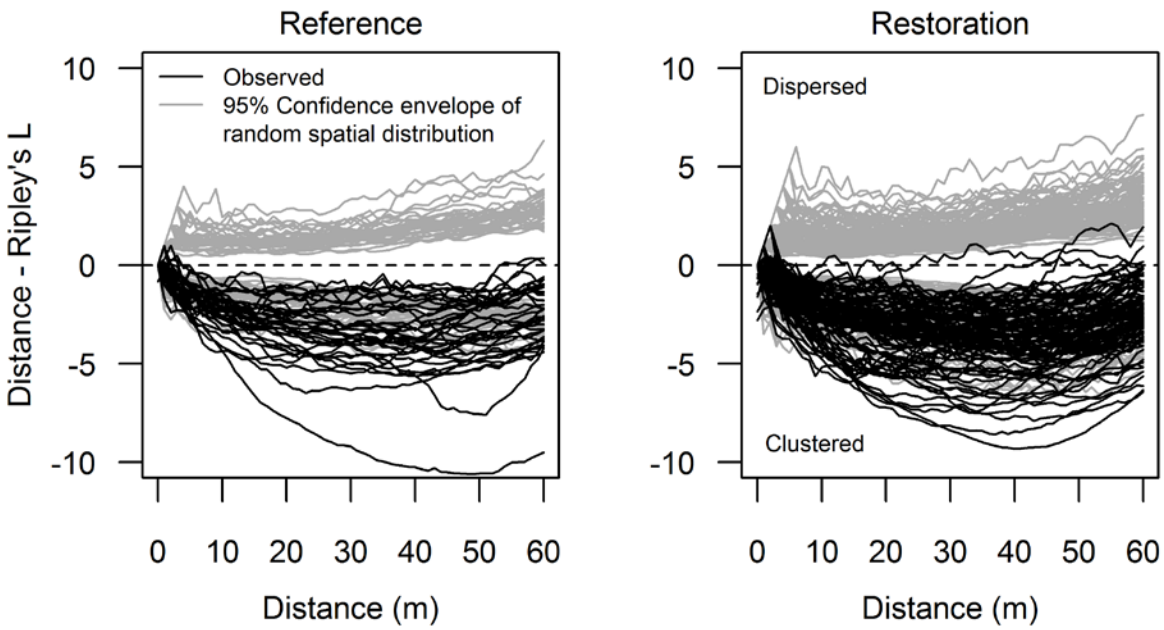

Figure 7. Ripley's L summarizing the spatial pattern of trees from 61-m x 106-m (0.65 ha) plots randomly placed within longleaf pine stands classified by Eglin AFB managers as representing reference (left, n=35) or restoration (right, n=93) conditions. Only plots with a minimum of 20 trees are included (from Hudak et al. 2016b).

B. Imputation of individual tree attributes from field and LiDAR data

The goal was to predict individual-tree height (m), basal area (m^2), and stem volume (m^3) attributes, imputing Random Forest k-nearest neighbour and individual-tree-level-based metrics extracted from a LiDAR-derived canopy height model in longleaf pine stands. All trees were measured for diameter at breast height using calipers (two measurements at right angles, averaged) or a steel diameter tape, and for height using a LaserTech Impulse 200. We also geo-located them using a GPS with <2.5 m accuracy. The mean longleaf pine tree height and diameter at breast height measured in our study area was 22.95 (±4.88) m and 32.87 (±13.30) cm, respectively, and the number of trees per hectare was approximately 147 (±29) trees. The outside-bark stem volume was obtained via a longleaf pine allometric equation according to Gonzalez-Benecke et al. (2014), The equation has a coefficient of determination (R^2) of 0.78 and absolute and relative root-mean-square error of 0.17 m3 and 38.21%, respectively. Individual tree detection was performed in R (R Development Core Team 2015) using the FindTreesCHM function from the rLiDAR package (Silva et al. 2015). The FindTreesCHM function uses a local maximum algorithm to search for treetops in the canopy height model trough a moving window with a fixed treetop window size (Wulder, et al. 2000). A total of 15 test subplots (30 m x 30 m) were randomly situated within each of the 15 plots (1 subplot per plot), and the number of trees detected per subplot from LiDAR were manually compared with field-based data and evaluated in terms of true positive (correct detection), false negative (omission error) and false positive (commission error). The accuracy of the detection was further evaluated for recall, precision and F-score according to Li et al. (2012), using the equations from (Goutte and Gaussier, 2005; Sokolova et al., 2006).

Tree crown delineation was performed in R using the ForestCAS function from the rLiDAR package (Silva et al. 2015). Inputs to this process were the smoothed canopy height model in

addition to the tree location outputs. The algorithm implemented in the ForestCAS function is based on the Voronoi Tessellation (Aurenhammer and Klein, 1999). Initially, it starts by applying a variable radius crown buffer to delimit the initial tree crown area. The variable radius was calculated for each tree by multiplying the LiDAR–derived tree height by 0.6, because preliminary field observation revealed that the tree crown radius typically was not larger than 60% of the LiDAR–derived tree height. After determining the merged tree polygon using the first area delimitation, we then split the data using the centroidal voronoi tessellation approach to isolate each individual tree polygon. After isolating each tree polygon, we clipped them from the canopy height model, and excluded the grid cells with values below 30% of the maximum height in each specific detected tree to eliminate the low-lying noise. Finally, the tree crown delineation and crown area (m^2) were computed by delimiting the boundary of grid cells belonging to each tree. Accuracy of the imputation model was assessed by calculating the absolute and relative root mean square distance and bias between imputations and observations (Stage and Crookston 2007).

C. LiDAR derived crown metrics: Comparison of terrestrial vs. airborne scanners

Airborne Laser Scanners and Terrestrial Laser Scanners are two LiDAR systems currently being used for remote sensing of forested ecosystems. As an added deliverable to this project, we compared crown metrics derived from terrestrial and airborne data for describing forest structure at Eglin Air Force Base, where the longleaf pine forest has an open canopy structure. Lidar data were collected over the study area, and represented by four (7854 m^2) plots with coincident terrestrial and airborne scans. Canopy height models were created from both sets of point clouds separately, and by combining them. Individual trees were detected from the canopy height models and crown metrics, such as crown height, crown projected area and crown volume were computed for each tree using the rLiDAR package. In this study, forest structure was assessed by the number of trees and distribution of crown metrics derived from both instruments. We used the results of the combination of these instruments as the reference, and Kolmogorov-Smirnov tests were applied to compare crown metrics between terrestrial, airborne, and the combined data.

D. Integration of terrestrial and airborne laser scanning for fuels mapping

The fuel cell concept (Hiers et al 2009) describes variability in fire behavior at sub-meter scales for southeastern fuels, indicating fuels and fire effects in this system operate at fine-scales. There has generally been limited ability to collect observed data at these scales as opportunity costs between comprehensiveness and spatial distribution of these data are time and cost intensive. As detailed elsewhere in this report, Hudak et al. (2016) provide an excellent frame work for estimating surface fuel loading using multiple-linear regression models between airborne laser scanning and observed fuel load (dry weighed biomass). However, the limited number of samples taken *in situ* and the relatively large grain size of scanner-based metrics ($25m^2$) only provide a coarse estimate of fuels. To begin bridging between scales, the use of terrestrial scanning to estimate total fuel load, estimation of post-fire consumption from terrestrial scanning derived pre- and –post-fire mass and the use of these terrestrial scanning derived estimates as a surrogate for *in situ* observations to refine predictions from airborne scanning derived metrics were conducted as part of this project.

E. Pinecone density maps from airborne LiDAR

We created a 3-m resolution canopy height model across EAFB using LAStools, using the process outline in **Fig. 8**. A resolution of 3-m was chosen because the canopy height model resolution (9

m^2) were comparable to 8.4 m^2, the mean crown area of 373 longleaf pines measured in our study plots, and because the LiDAR was of relatively low resolution (<2 pulses m^{-2}).

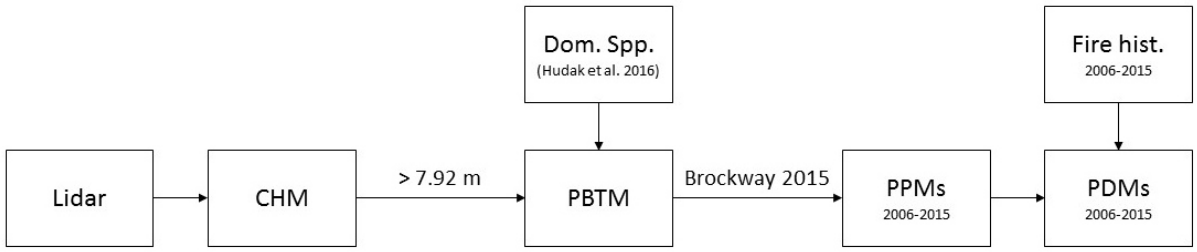

Figure 8. Flowchart describing the creation of pinecone production maps (PPMs) and pinecone density maps (PDMs) from LiDAR and ancillary information. CHM: canopy height model, PBTM: pinecone bearing tree model (PBTM).

The minimum tree height of 218 cone-bearing longleaf pines across EAFB is 7.92 m (26 feet), as measured in the site's long-term ecological monitoring plots, so areas with heights < 7.92 m were eliminated from the analysis. Only areas where the dominant tree species (product of Hudak et al. 2016b) were slash or longleaf pine were included. The pinecone bearing tree model was then multiplied by the annual cone production measurements of Brockway (2015) (**Fig. 9**) to create annual pinecone production maps across EAFB for 2006-2015. A start year of 2006 was chosen to coincide with the beginning year of the LiDAR acquisition, 2006. Annual fire history polygons were rasterized and integrated with pinecone production maps to create pinecone density maps.

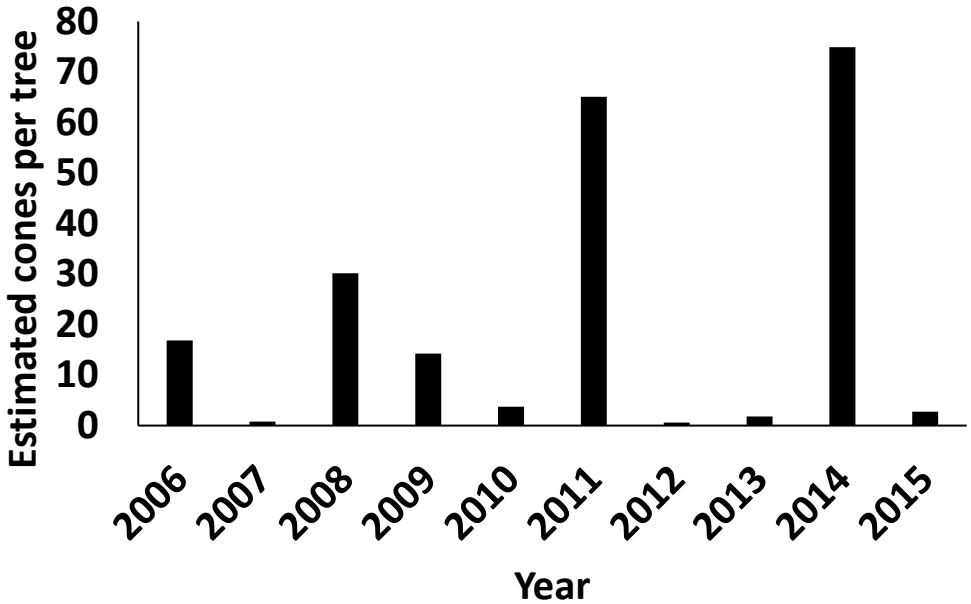

Figure 9. Mean pinecone production per tree estimates for EAFB from Brockway (2015).

Results & Discussion

A. Tree Density and Fuels from aerial LiDAR

Based on the map of nearest neighbor plot IDs, plot-level measures of the surface fuel and plant species richness attributes were also mapped across Eglin AFB (**Fig. 10**). **Fig. 11** shows maps of two of the many attributes mapped via this imputation strategy. When these pixel-level predictions and those of 14 other surface fuel attributes were aggregated to the 425 management blocks and compared to the overstory response variables, and to fire history variables compiled from 1972-2012 Eglin AFB burn records, the Spearman rank correlations were nearly all significant (**Table 4**). That virtually all of these correlations are significant suggests that these fine scale plant diversity and surface fuel attributes relate to overstory structure, a hypothesis we have posed to better understand the underlying ecological mechanisms of this community.

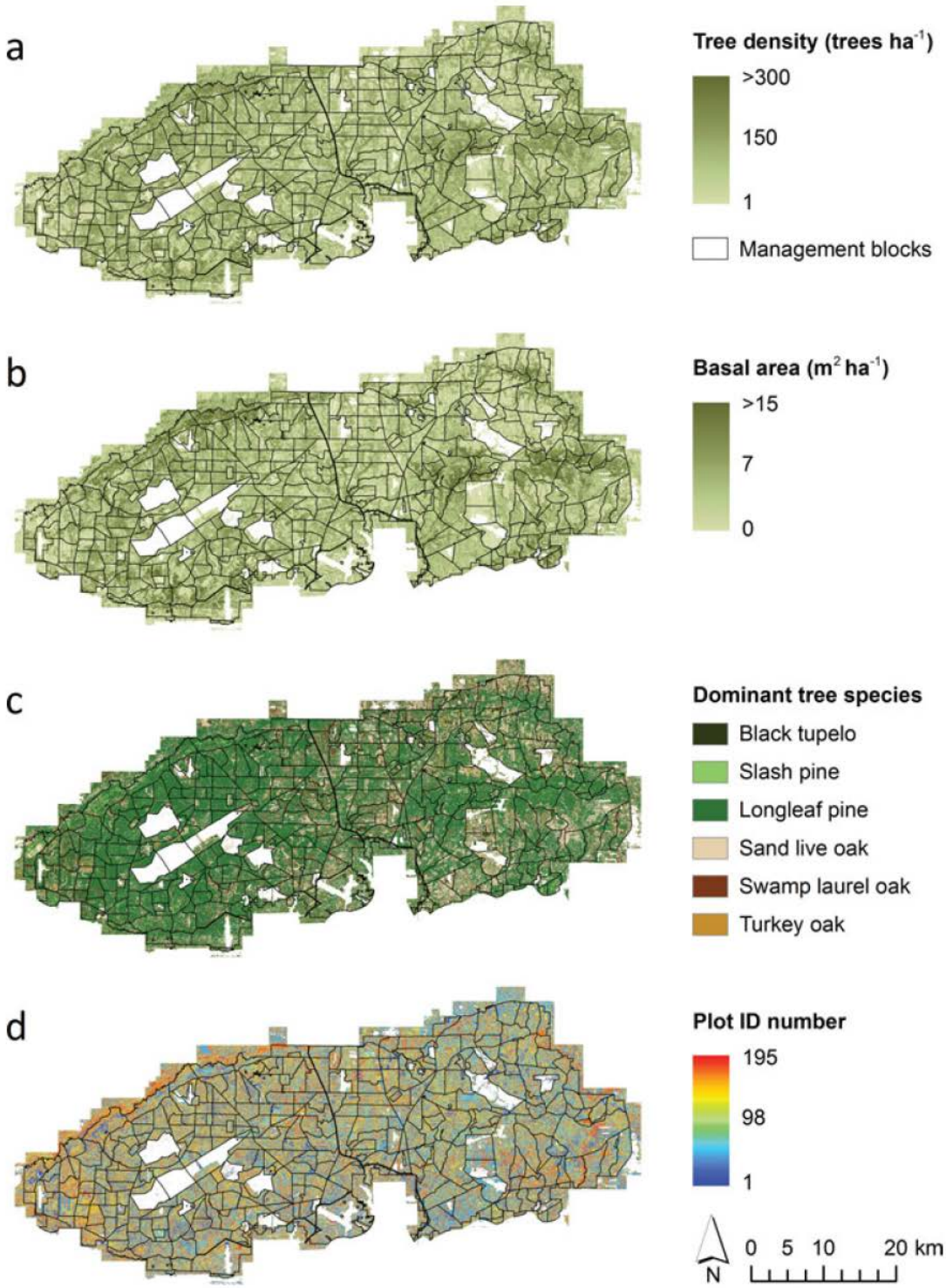

Figure 10. Imputations of (a) TPH, (b) BA, and (c) DomSpp from airborne LiDAR across Eglin AFB, and (d) Plot ID imputed as an ancillary variable (from Hudak et al. 2016b).

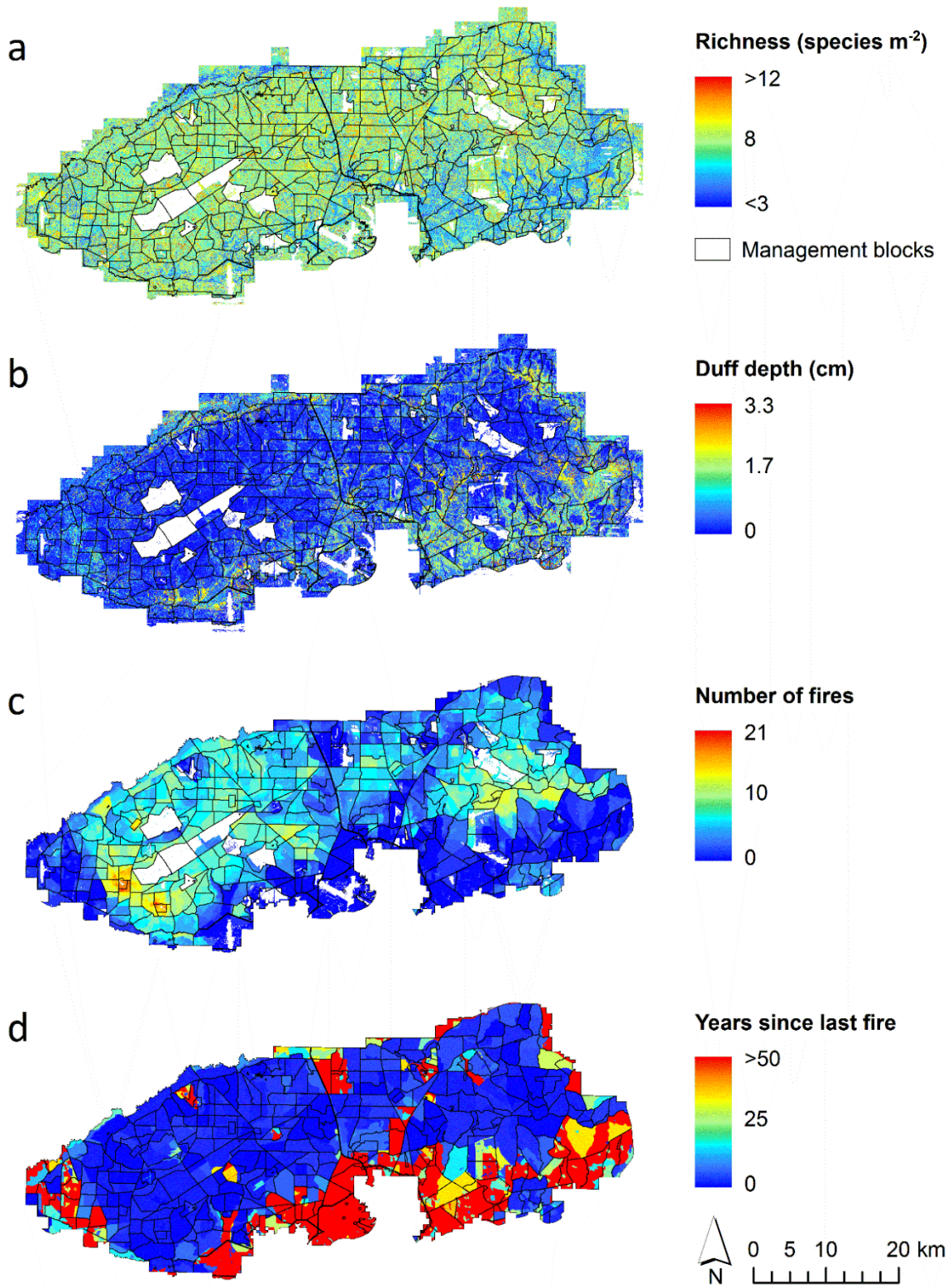

Figure 11. (a) Plant-species richness and (b) duff depth related to the imputed overstory responses via plot ID (**Fig. 10.**), along with (c) number of recorded fires and (d) years since last recorded fire (from Hudak et al. 2016b).

Table 4. Spearman rank correlations between mapped overstory responses or fire history variables and surface fuel and plant species richness measures associated with the Plot ID map (Fig. 3d) and aggregated within Eglin AFB land management blocks (n=425); significant ($P < 0.05$) correlations indicated in boldface (from Hudak et al. 2016b).

Attributes	Tree density (trees ha^{-1})	Basal area (m^2 ha^{-1})	Number of Fires	Years Since Last Fire
1-hr (counts)	**0.27**	**0.28**	**-0.50**	**0.43**
10-hr (counts)	**0.37**	**0.37**	**-0.28**	**0.25**
100-hr (counts)	**0.46**	**0.49**	**-0.09**	**0.14**
1000-hr (counts)	**0.41**	**0.44**	**-0.36**	**0.35**
Litter depth (cm)	**0.58**	**0.64**	**-0.15**	**0.18**
Duff depth (cm)	**0.49**	**0.52**	**-0.42**	**0.38**
Fuelbed depth (cm)	**-0.45**	**-0.42**	**0.08**	**-0.09**
Oak litter cover (%)	**0.14**	**0.12**	**-0.55**	**0.46**
Long-needle conifer litter cover (%)	**0.62**	**0.61**	**0.69**	**-0.60**
Short-needle conifer litter cover (%)	**-0.11**	**-0.11**	**-0.65**	**0.56**
Grass litter cover (%)	**-0.14**	**-0.13**	**0.61**	**-0.52**
Forb litter cover (%)	0.02	-0.01	**0.64**	**-0.57**
Shrub litter cover (%)	**-0.57**	**-0.54**	-0.03	0.03
Saw palmetto litter cover (%)	**0.35**	**0.35**	**-0.41**	**0.31**
Mineral soil cover (%)	**-0.47**	**-0.48**	**0.44**	**-0.39**
Plant species richness (species m^{-2})	**-0.55**	**-0.59**	**0.31**	**-0.32**

From a management perspective, the maps we generated and shared with Eglin AFB managers at the April 2017 workshop were well received and will be used to better inform decisions relating to forest, fuel, and fire management.

B. Imputation of individual tree attributes from field and LiDAR data

We developed a new framework (**Fig. 12**) for modeling tree-level forest attributes that comprise 3 steps: (i) individual tree detection, crown delineation, and tree-level-based metrics computation from LiDAR-derived canopy height model; (ii) automatic matching of LiDAR-derived trees and field-based trees for a regression modeling step using a novel algorithm; and (iii) Random Forest k-nearest neighbour imputation modeling for estimating tree-level height, basal area, and stem volume and subsequent summarization of these metrics at the plot and stand levels. Root-mean-square deviations for tree-level height, basal area, and stem volume were 2.96%, 58.62%, and 8.19%, respectively. Although basal area estimation accuracy was poor because of the longleaf pine growth habitat, individual-tree locations, height, and volume were estimated with high accuracy, especially in low-canopy-cover conditions. Future efforts based on the findings could help improve the estimation accuracy of individual-tree-level attributes, such as basal area.

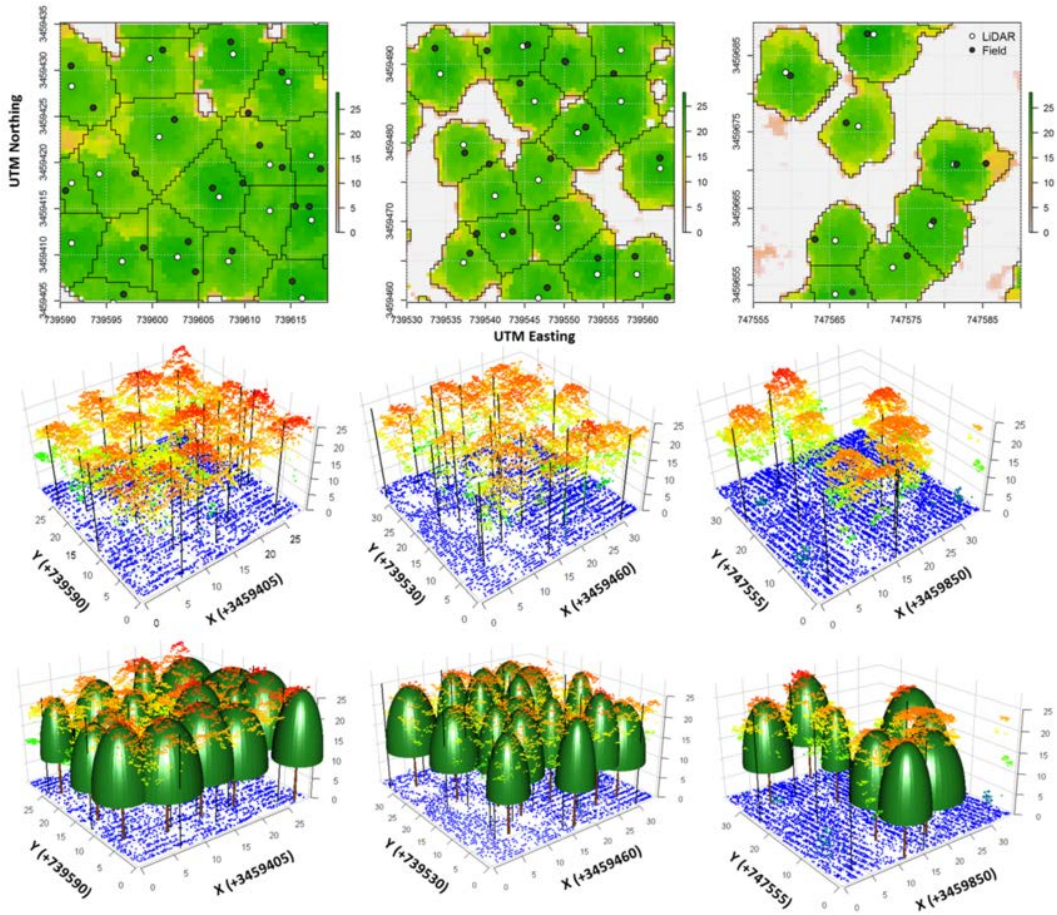

Figure 12. Illustration of individual tree detection and crown delineation under different COV conditions. (1) COV = 90.96%; (2) COV = 76.79%, and (3) COV = 58.66%. (A) 2D visualization of the tree location and crown delineation over the CHM. (B) 3D visualization of the LiDAR point cloud and reference trees measured in the field. (C) 3D visualization of the LiDAR virtual forest, and the reference tree locations.

C. <u>LiDAR derived crown metrics: Comparison of terrestrial and airborne scanners</u>

Terrestrial and airborne laser scanners detected fewer trees when processed individually compared to when the data are combined (**Fig. 13**). The relative difference for the number of individual trees detected between terrestrial and airborne scanners compared to them combined were -2.68 and -23.08%. The mean of crown height, crown area, and crown volume were 7.06 m, 3.65 m^2 and 15.37 m^3 for terrestrial; 7.32 m, 6.13 m^2 and 20.87 m^3 for airborne, and 7.64 m, 9.08 m^2 and 33.33 m^3 for them combined. Kolmogorov-Smirnov tests showed that crown height, crown area, and crown volume computed individually from terrestrial and airborne differed significantly (p-value < 0.05) from them combined. This confirmed our hypothesis that combining the points from these two instruments would produce a higher level of accuracy, as it provides a denser point cloud from which to identify trees and derive crown metrics.

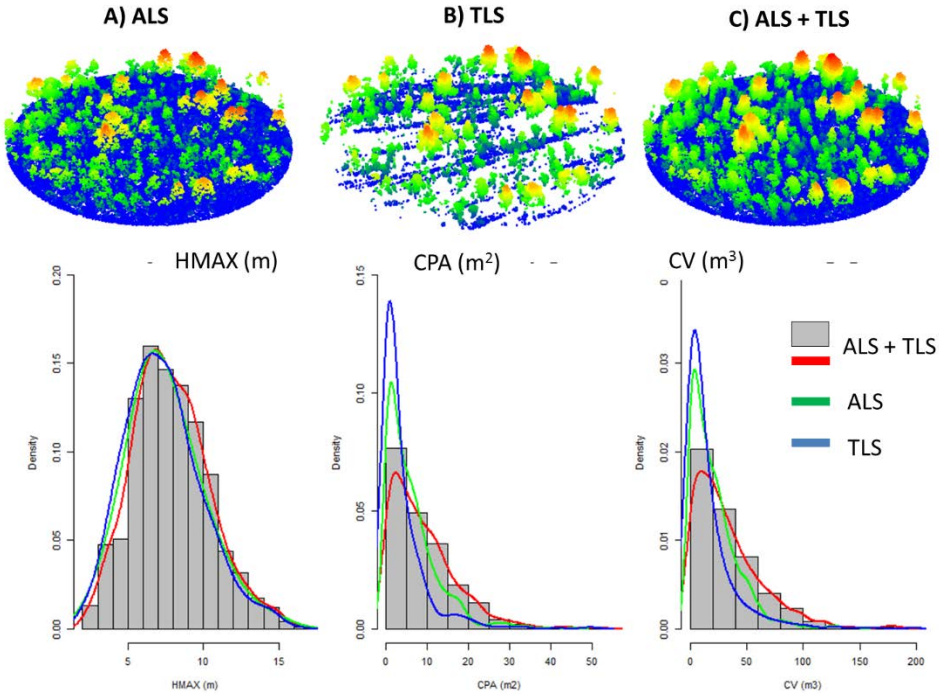

Figure 13. Crown metrics distribution in Airborne Laser Scanning (ALS) A) Terrestrial Laser Scanning (TLS) B) and ALS + TLS C) derived 3d point cloud. HMAX is the crown height; CPA is the crow projected area, and CV is the crown volume.

D. <u>Integration of terrestrial and airborne laser scanning for fuels mapping</u>

Employing voxel (three dimensional pixels) analysis, occupied volume estimates of the fuelbed were used to predict fuel mass for units representing a grass\shrub and forested fuel matrices at Eglin AFB. Terrestrial scanner data is collected at scales of 1 point per mm, providing incredible dense and accurate datasets. Voxel domains were determined to be a 100cm^3 volume that represents if a cell is occupied. Results using leave-one-out-cross validation linear regression modeling outline successful estimation of both pre-and post-fire aboveground biomass for the forested and grass\shrub units (**Fig. 14**). Separate models were used to predict pre- and post-fire estimates from comparison with observed data. Estimates of consumption compared favorably with observed estimated from plot averages. These estimates were used to predict fuel mass across 400m^2 plot that provides a first known attempt at obtaining a spatially explicit total fuel loading (**Fig. 15**).

Terrestrial scanner derived estimates of above-ground biomass were used as independent data to predict large-scale estimates of fuel mass across the high resolution airborne laser scanner dataset described in Hudak et al. (2016). Total above-ground biomass was summed for coincident 25m^2 cells of airborne laser derived height metrics. Using a similar approach to Hudak et al. (2016), a linear model was used to produce a spatially explicit map of surface fuels from the airborne laser scanner (Fig. 3). The results describe improvements of fuel estimation using the terrestrial scanner derived above-ground biomass as an independent variable, improving the coefficient of variation by 30% over using plot data as the independent variable.

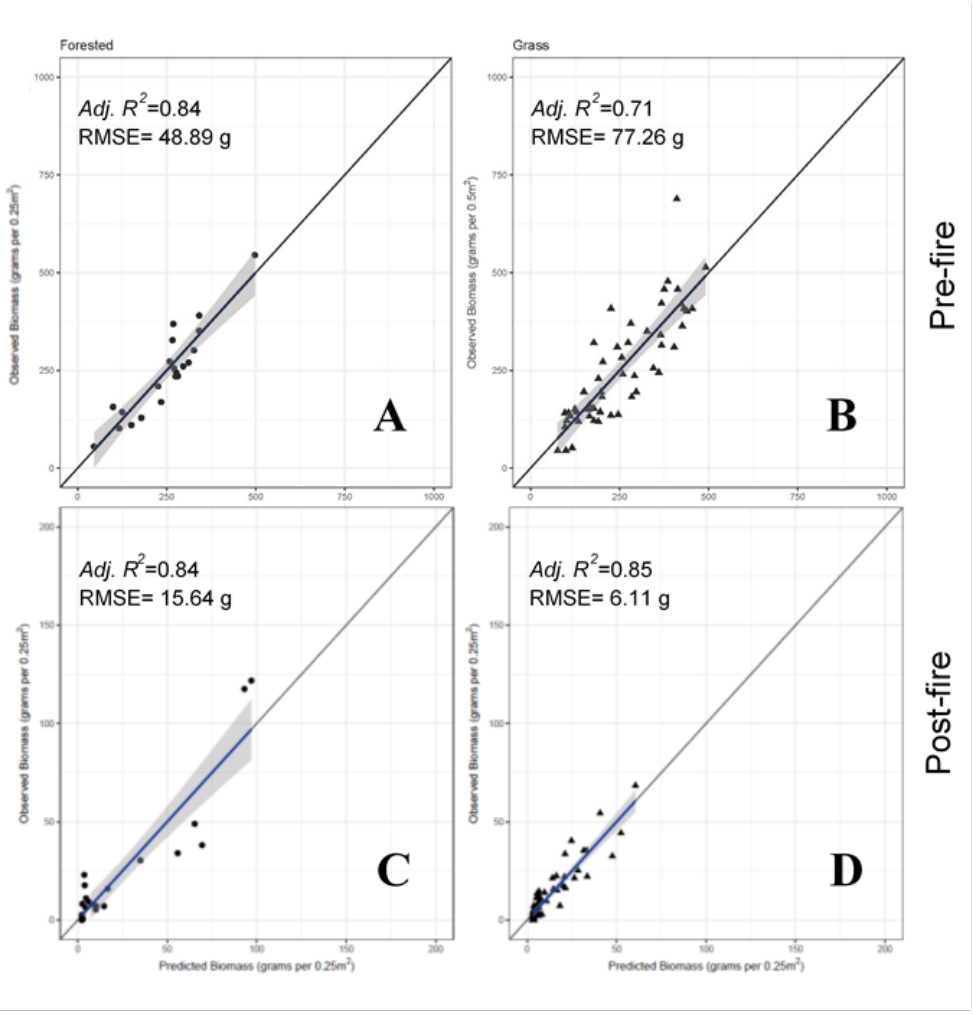

Figure 14. Linear regression models predicting A) forested pre-fire and B) grass\shrub pre-fire above-ground biomass from voxel estimated occupied volume. A separate model is used to estimate C) forested pre-fire and D) grass\shrub post-fire residual above-ground biomass.

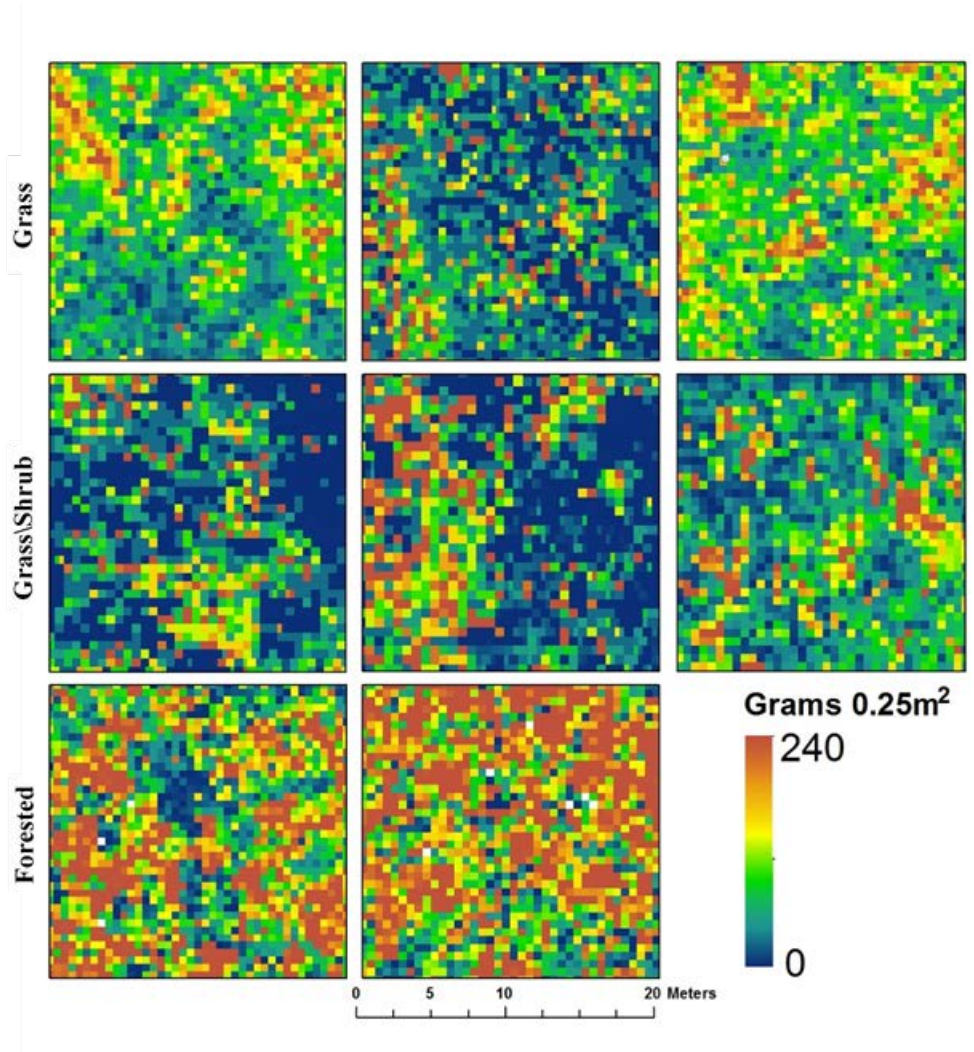

Figure 15. Aboveg-ground biomass is mapped for each of the plots demonstrates the variability and distribution of mass across the plots based off the forested and grass\shrub predictive models.

a. rLiDAR and Web-LiDAR tools

Tools to map individual trees and extract crown attributes from the aerial LiDAR points were developed to support LiDAR-based forest inventory and management at Eglin Air Force Base, Florida, USA (**Fig. 16**). These tools, however, are general applicable to other forests in other ecosystems, and we encourage users to test it broadly. Both of these tools were developed from the ground up by our team, and they are available online for interactive analyses at the plot-level (Web-LIDAR, https://carlosasilva.shinyapps.io/LiDARTreeTop/), or in a downloadable, freely available R package (rLiDAR, http://cran.r-project.org/web/packages/rLiDAR/index.html) for processing LiDAR datasets at the stand or landscape levels. Preliminary results show R^2 = 0.80-0.95 for accurately estimating the number of trees per large plot, which corresponds in size to the 30 m x 30 m map units in the tree density map.

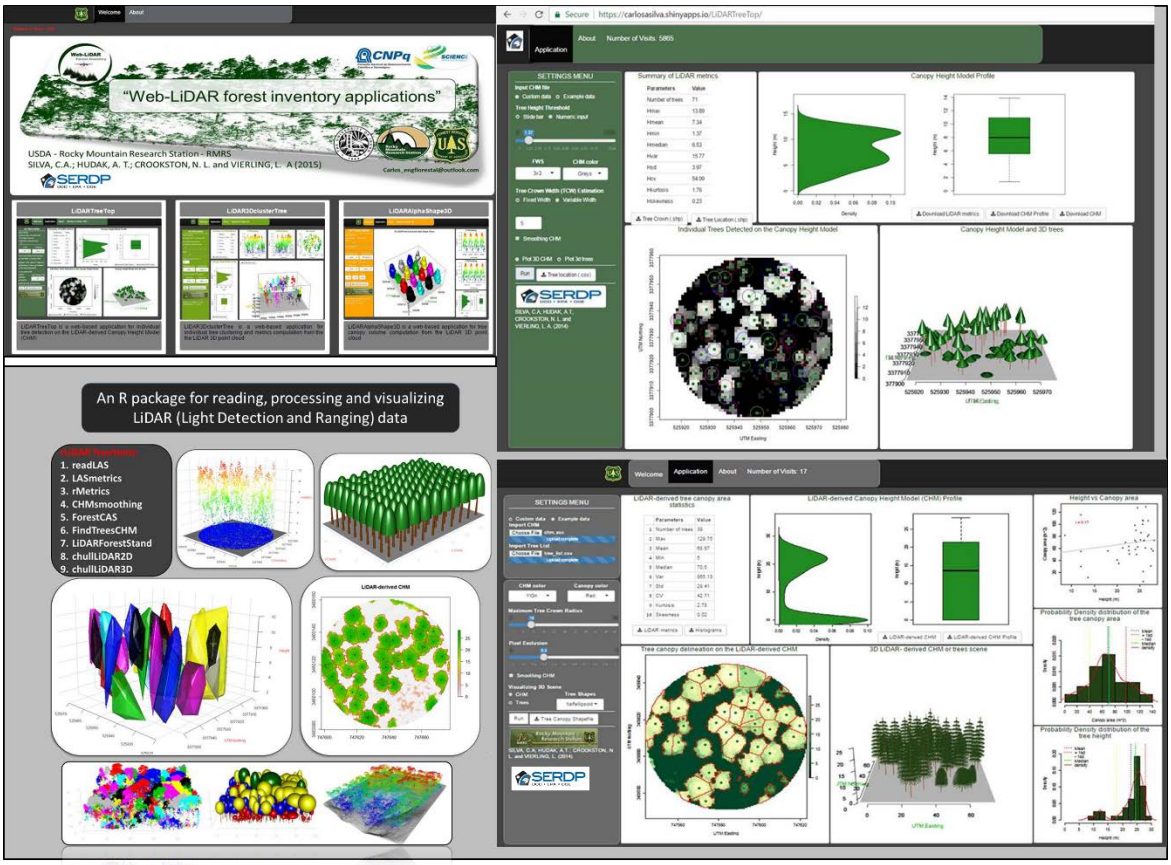

Figure 16. Example of the rLIDAR and Web-LiDAR tools that are freely available and developed from the ground-up by our team.

E. <u>Pinecone density maps from airborne LiDAR</u>

Pinecone density maps were successfully created using LiDAR coupled with field measurements (**Fig. 17**). From our analysis, we found that 10-hr fuels measured in fuel transects from the sites' long-term ecological monitoring plots were weakly, yet significantly positively correlated with predicted pinecone density (Spearman's $\rho = 0.15$, $p = 0.03$). Agreement was better between pinecone weights measured in this study's clip plots versus extracted values from the pinecone density maps Pearson's ($r=0.79$, $p=0.06$, $n=6$), especially considering the small number (6) of clip plots that had pine cones. The limitation of this approach is that the LiDAR is only from one timeframe (2006, 2008) and the farther away we get from this time frame, the more likely canopy cover changes are likely to occur, particularly at the stand level.

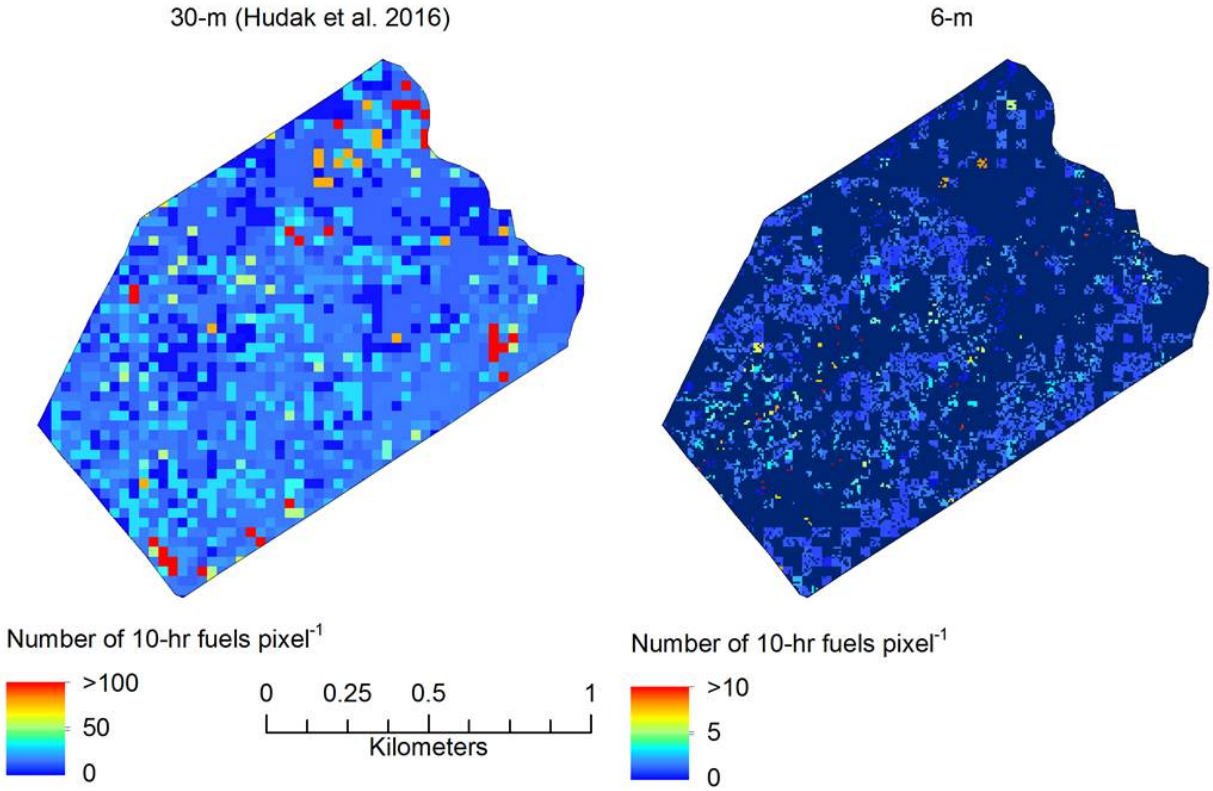

Figure 17. Pine cone density map (10-hour fuel here) of one section of Eglin AFB (block L2F) at the 30 m x 30 m and 6 m x 6 m cell resolution. These datasets were derived from airborne LiDAR data coupled with field measurements of pine cone production.

Fine-Scale Studies

Abstract
Our principal hypothesis that fire maintains diversity through neutral processes hinges on the existence of a random agent of mortality that kills plants regardless of their morphology. We further hypothesized that these consisted of woody canopy derived fuels, especially cones. In order to test whether these fuels release sufficient energy to behave in this manner and to understand the many interactions among fuels, fire, and plant demography in the understory, measurements of must be performed at the appropriate scale. We found this to be at the individual plant scale, which we found to be approximately 100 cm^2. For this portion of the study, we examined these multiple interacting properties in a spatially and temporally explicit manner within our 1m x 3m plots (300 100 cm^2 cells) by using infrared thermography, 3D modeling, and plant monitoring techniques. These data were both analyzed to examine their relationships, e.g. how fire energy impacts plant mortality, whether traits predict mortality, and used to develop a CA model of spatial plant demography. This model was used to examine individual cell plant change in response to fire, as well as to simulate or project changes in plant community dynamics in response to fire intensity and frequency across these plots of varying overstory structure. Finally, we used state-of-the-art rendering to generate fine scale fuel beds with realistic properties useful for advancing fire behavior modeling.

Objectives
For the fine-scale studies portion of the study, our objectives were to:

1) Use infrared thermography to measure cm-scale fire radiative energy of surface fires within each 1m x 3m plot. Use the data to capture the energy release from specific fuel types.
2) Monitor understory plant demography at the 10cm^2 scale pre- and post- experimental burns to track spatial and temporal plant change.
3) Use remote sensing and 3D modeling techniques to characterize the fine-scale fuelbed.
4) Use 1-3 to develop a Cellular Automata model of fire and fuel effects on understory plant demography. This model will be used to test theories of plant community dynamics and project plant change in response to fire frequency and intensity through space and time.
5) Examine the deviation from neutrality when fire is excluded and examine the role of plant traits on predicting competitive outcomes.

Technical Approach
The fine scale measurements we conducted in the 30 monitoring plots, 9 fire exclusion plots and 9 fuel manipulation plots and are reported here in three sub-sections: A) fine scale fire intensity measurements, B) fuel measurements and modeling, and C) plant demography sampling and CA modeling.

A. <u>Linking Fine-Scale Fire Intensity & Fuel Measurements to Plant Demography</u>

As of June 2017, all experimental burns planned for this project are complete, reported in **Table 5**. One set of replicates (3 plots) in the sandhill habitat were burned by a wildfire in 2014, and was unable to be burned in 2015 due to logistical constraints. Also, two sandhill fire exclusion plots were incidentally burned off schedule, however in both cases we continued to collect demography data which was still useful. For each burn, we used three long-wave infrared camera systems developed during this project to record spatio-temporal fire intensity. These data provided total fire radiative energy emitted in high resolution (~ 1 cm^2 scale) imagery that was important for relating individual and community plant change occurring in the understory. One was deployed in

each of three 1m x 3m plots located within a burn unit. This system represents an innovation in the collection of spatially explicit fire behavior measurements (O'Brien et al. 2016).

Table 5. Burn schedule and plant demography monitoring schedule according to fine-scale plots. Grey areas represent future sampling schedule for this project. 'Yes' indicates successful monitoring of plant demography plots. 'Burn' indicates season of experimental burns and no plant monitoring was done. 'NA' indicates no burn and no monitoring. Monitoring in nine fuel manipulation plots started in fall of 2013. All scheduled burns are complete for this project.

	2012	**2013**		**2014**		**2015**		**2016**	
Plots	**Fall**	**Spring**	**Fall**	**Spring**	**Fall**	**Spring**	**Fall**	**Spring**	**Fall**
Stratified 1m x 3m plots (n=30)	Yes	Burn	Yes	Yes	Yes	Burn	Yes	Yes	Yes
1m x 3m fire exclusion plots (n=15)	Yes	NA	Yes	Yes	Yes	NA	Yes	Yes	Yes
1m x 3m fuel manipulation plots (n=9)	NA	NA	Yes	Burn	Yes	NA	Yes	Yes	Yes

Fine-Scale Fuel Measurements & Modeling

Fuels were sampled both non-destructively within each 1m x 3m plot as well as destructively nearby each plot. Fuel characteristics were physically mapped within each 1m x 3m plot using point-intercept sampling in a 10 cm x 10 cm grid (300 points per plot). This was done just prior to each experimental burn. We recorded height and percent cover by plant functional category (e.g. wiregrass, other grasses, herbaceous, deciduous and evergreen shrubs, pine and shrub litter and bare soil), including pine cones and woody fuels as distinct fuel categories within each grid cell. In spring 2015, four additional 0.25 m^2 subplots 5 m away from plot center in the 60°, 120°, 240°, 300° directions from plot center were destructively sampled. Samples have been sorted, oven dried, and weighed for estimations of fuel loading. Photographs and point-intercept sampling were done for each 0.25 m^2 subplot. Photographs were also taken of each plot prior to each burn. Using these photographs, we have developed a novel photogrammetry technique to model the understory fuel bed (Bright et al. 2016). The technique produces a dense surface model, similar to LiDAR, specifically terrestrial laser scanning (Loudermilk et al. 2009). Two or more overlapping digital photographs are spatially referenced to create a 3D surface. The combined 3D spatial point clouds and color information from the photogrammetry provides information on spatial location, structure, texture, and clustering (heterogeneity) of fuels for identifying fuel types and their configuration within the fuelbed.

For the photogrammetry portion, we introduced a novel methodology for fine-scale 3D characterization of understory plants and fuels. We compared products derived from close-range photogrammetry to field measurements of understory plants and fuels, and evaluated the use of close-range photogrammetry for distinguishing understory plants and fuels. Point-intercept measurements of plants and fuels within each 10x10 cm cell were gathered for nine plots that were 1x3 m in size. Fuel measurements for each 10x10 cm cell included presence/absence of the following: litter depth, fuel depth, 1-,10-,1000-hr fuels, perched pine litter, perched oak litter,

grass, shrubs, volatile shrubs, forbs and forb litter, bare soil, deciduous oak litter, longleaf pine litter, and pinecone. Following Hiers et al. (2009), we summarized the above presence/absence measurements by defining fuel types via cluster analysis.

For these same nine plots, close-range photogrammetry was used to create 3D point clouds. Using PhotoModeler Scanner software, stereo pairs were created from two photographs of each plot, and 3D points were extracted from stereo models so that resulting point clouds had densities of roughly 10,000 points per square meter. Points were classified as ground or nonground, nonground point heights were normalized to heights above ground, and metrics were created for each 10x10 cm cell coincident with fuel and plant point-intercept measurements. Statistical tests were used to evaluate how well photogrammetry metrics could distinguish understory species, plant types, and fuel types. Height distributions of field-measured and photogrammetry-derived fuelbed depth were also compared.

3D rendering technique

The two methods described previously using terrestrial laser scanner ($0.25m^2$) and airborne laser scanners ($25m^2$) data are part of a larger gradient of scales that include high resolution 3-D simulations (mm^2). Simulated fuelbeds, using methods developed for three-dimensional models for gaming and animation, create high resolution spatial (**Fig. 18**) data that cannot be achieved through remote sensing or direct observation. Rowell et al (2016) describe a method of using the meshed surface area of the simulation per fuel element (e.g. needle, leaf, grass surface area), where simple assumptions of biomass per unit area (mm^2) produce robust estimates of total and specific biomass. Correlations with observed height and simulated height also demonstrated a strong relationship. These models were developed independently of observed biomass data and models were developed to directly compare with observed biomass, significant relationships were found for litter and grass fuel types. Comparisons with terrestrial scanner point clouds and using the vertices of the simulations as a proxy for simulated point clouds demonstrated that terrestrial scanner data under represents the lowest strata of the fuelbeds (e.g. needle litter) which is characteristic of the highest loads of fuel mass (**Fig. 19**). These findings open avenues for distributing fuels by type using simulations to inform terrestrial scanner derived estimates of fuel load.

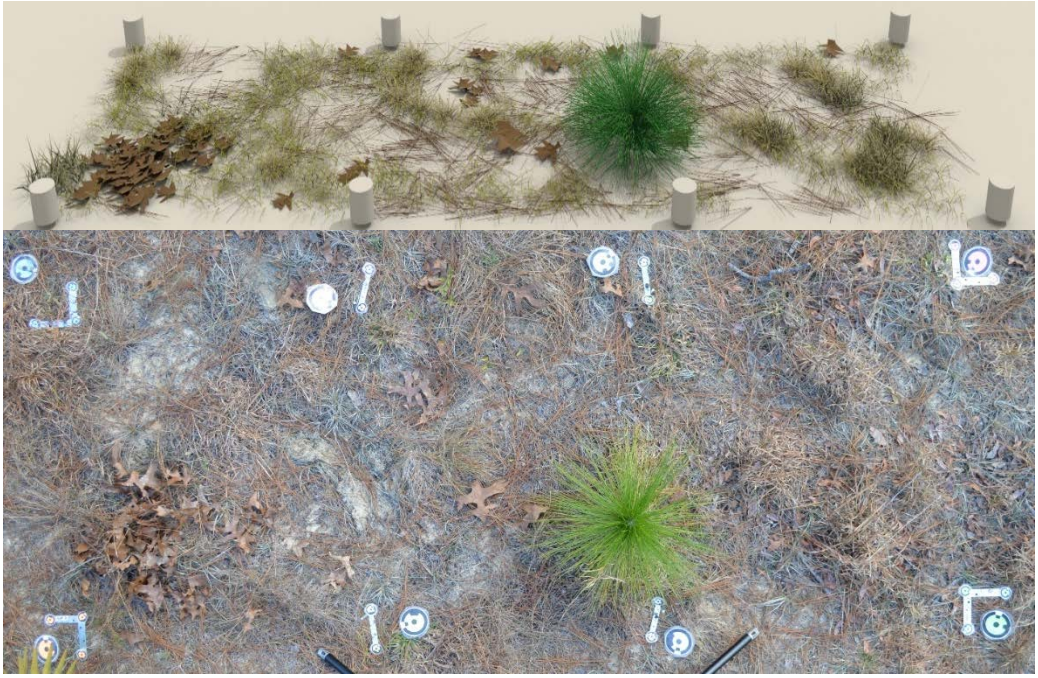

Figure 18. Pre-fire fuelbed simulation compared with nadir photography captured at Eglin AFB.

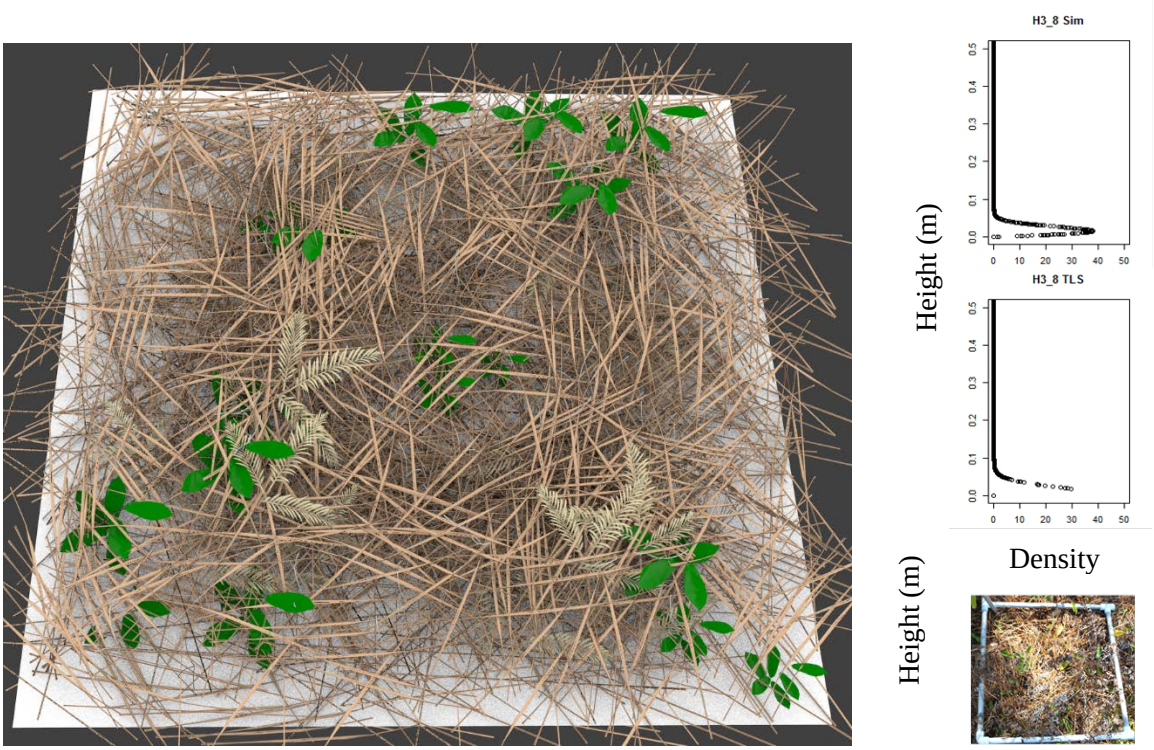

Figure 19. Pre-fire fuelbed simulation for a needle litter dominated plot collected in a managed longleaf pine stand at Eglin AFB. Weibull distributions for the simulated and TLS point clouds demonstrate substantial under representation of mass by the TLS data in the first 10cm of the fuelbed (from Rowell et al. 2016).

Density

B. Fine-Scale Plant Demography for Cellular Automata Modeling

For the cellular automata modeling portion of the study, we focused on incorporating the assumptions of the Unified Neutral Theory of Biodiversity (UNTB), developed originally by Hubbell in 2001. Research on ecological community assembly and biodiversity was invigorated by the UNTB (Hubbell 2001, Chave 2004, Matthews and Whittaker 2014, Missa et al. 2016). The theory stimulated discussion on the relative roles of stochastic processes versus competitive exclusion and niche differentiation in driving patterns of species richness and community assembly, particularly for plants, in different ecosystems. 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. The frequently burned longleaf pine community might be the closest example of a truly neutral community. The assumption of neutrality for longleaf pine ecosystems requires frequent fire, which provides both the required element of randomness, particularly mortality (Wiggers et al. 2013, O'Brien et al. 2016) and keeps competition in check (Barnett 1999, McGuire et al. 2001).

We hypothesized that neutral processes (Hubbell 2001) can explain ground cover community dynamics at high fire frequencies. To test this, we developed a simple autonomous agent model with probability based parameters to examine neutral processes of species richness in longleaf pine ground cover communities found at EAFB. We used our fine-scale plant monitoring data from 2012 to 2016 for model parameterization. Since our parameters were variable across years, yet there was no statistical relationship to species traits (see Trait Analysis section above), we used the Fourier Amplitude Sensitivity Test to examine parameter sensitivity; the first order effects of mortality, birth, dispersal limitation as well as exogenous effects (size of areas, number of areas) on simulated species richness were quantified. To examine the effects of scale and dispersal processes on parameter sensitivity, we examined these first order effects across five scales of input species frequency distributions, employing both spatial and non-spatial dispersal processes. The examination of both endogenous and exogenous parameter sensitivity across scales and dispersal assumptions provides an in-depth look at multiple interacting processes of community dynamics, stochasticity, and scale in a fine-scale plant community, which has not been done before.

Our fine-scale plant monitoring data at the 100 cm^2 grid scale were used to estimate mortality, recruitment (birth), and immigration rates within and across cells and plots. Mortality was determined by individual plant species that died with or without replacement. Similarly, recruitment was determined by new individual plants found in an empty cell or replacing another plant in a cell. We created species frequency distributions from our fine-scale monitoring data, which was used to create the five different scales of input data. The model has been developed with an object-oriented design using the Python programming language.

We used the Fourier Amplitude Sensitivity Test (FAST) (Saltelli et al. 1999) and applied in the python library SALib (v.1.0.2) to examine the first order effects of the five model parameters (birth, mortality, immigration, size of area, number of areas simulated) on simulated species richness. FAST quantifies the sensitivity of multiple parameters simultaneously by oscillating across a range of possible input parameter values (determined by empirical data) at different frequencies. As such, a unique set of input parameter values is created for each model run. A flow chart and description is found in **Fig. 20**. We applied a scenario approach to run the FAST input

parameter sets. First, input parameter sets for five model parameters were created. These parameter sets were run using five scaled input frequency distributions for both the spatial and non-spatial dispersal model. This resulted in 10 scenarios total (5 scales of inputs x 2 models) replicated three times.

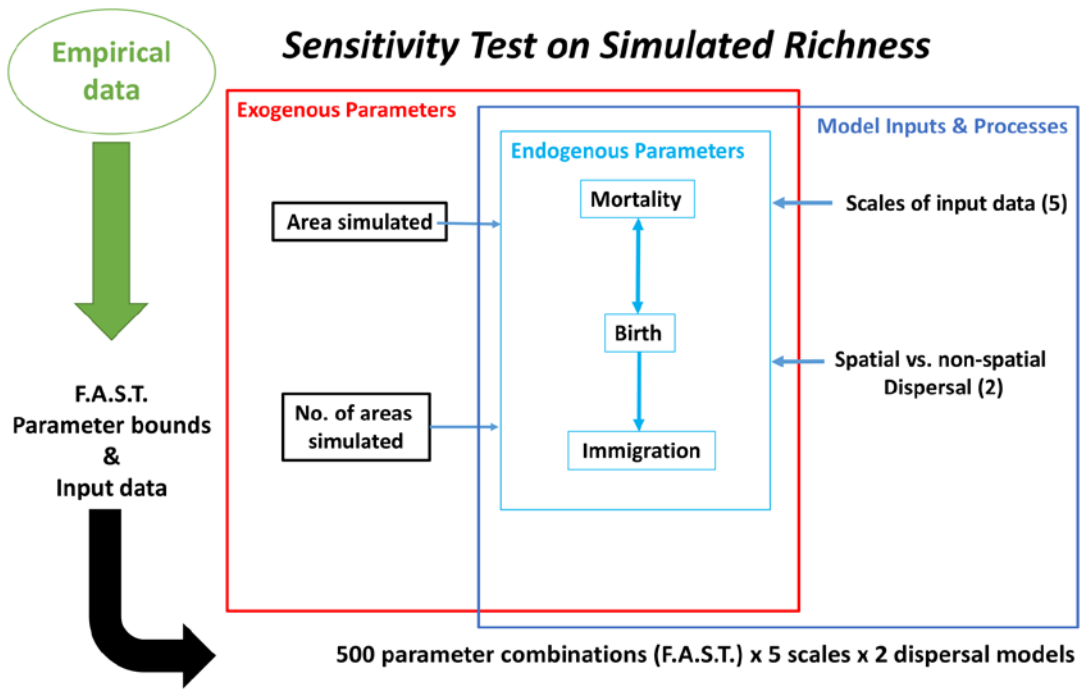

Figure 20. Flow chart of model development and analysis for simulating groundcover richness. Our empirical data on plant monitoring was used to develop the range of parameter values for mortality, birth, and immigration, as well as area simulated and number of areas simulated that were used to run the neutral cellular model. In addition, the species frequency distributions were also from the monitoring data and used to create the five different scales of input data. These values were used in the Fourier Amplitude Sensitivity Test (FAST) where parameters were simultaneously varied (creating 500 parameter combinations) using the five scales of input data and spatial and non-spatial dispersal assumptions for the model. All simulations were replicated three times.

Results & Discussion

A. Linking Fine-Scale Fire Intensity & Fuel Measurements to Plant Demography

The link between fire energy release and plant demography

We used three of the experimental burns conducted on May 23-25, 2014 to examine the impact of fire energy release of specific fuels on plant demography. The three burns were 6 ha, 62ha and 260 ha in extent. All three burns consisted of ground ignition prescribed fires as part of regular fire management operations at Eglin AFB. Target fuel moisture and fire weather conditions were monitored up to the test fire to ensure fire behavior would allow for ignition of pine cones and achieve complete consumption. The fire rate of spread and to a lesser extent, type varied in the plots (**Table 6**).

Table 6. Date of ignition, rate of spread and fire type in the experimental plots. Rate of spread was measured as the time the fire took to travel 1 m perpendicular to the fire front while in a plot. Fire type refers to head fire (fire moving parallel to the wind direction) and flanking fire (fire moving perpendicular to the wind direction).

Unit	Plot	Ignition Date	Type	Wind Speed cm s^{-1}
F-22	1	23-May-14	Head	11.1
	2		Head	9.1
	3		Head	28.2
F-18	4	24-May-14	Head	10.1
	5		Flanking	1.2
	6		Head	3.5
F-19	7	25-May-14	Head	16.7
	8		Head	11.1
	9		Head	4.2

The burns were ignited on three consecutive days with similar ignition times (approximately 1500 UTC). Weather conditions during the burns were comparable: the temperature ranged from 31° C to 32° C and relative humidity ranged from 44% to 54%. While *in-situ* fuel loading was not destructively collected, fuels types within plots were estimated in all the 300 grid cells indirectly using photogrammetry and 3D rendering techniques (see Bright et al. 2016, Rowell et al. 2016).

High resolution LWIR thermography (**Fig. 21**) was collected for each plot using three thermal imaging systems from FLIR Inc.: an SC660 and two A655SC. Both models of FLIR systems have a focal plane array of 640 x 480 pixels, a spatial resolution of 1.3 mRad, a sensitivity of 0.03°C and a thermal accuracy of ± 2%. The temperature range selected for data collection during the fires was 300 - 1500°C at a measurement rate of 1 Hz. The imaging systems provided a nadir view of the plots using an 8.2m tall tripod system (see Loudermilk et al. 2014, O'Brien et al. 2016) which positions the camera optics 7.7m directly above the center of the 1 m x 3 m plots. Having the camera optics 7.7 m above the target resulted in a pixel resolution of ≈ 1 cm^2.

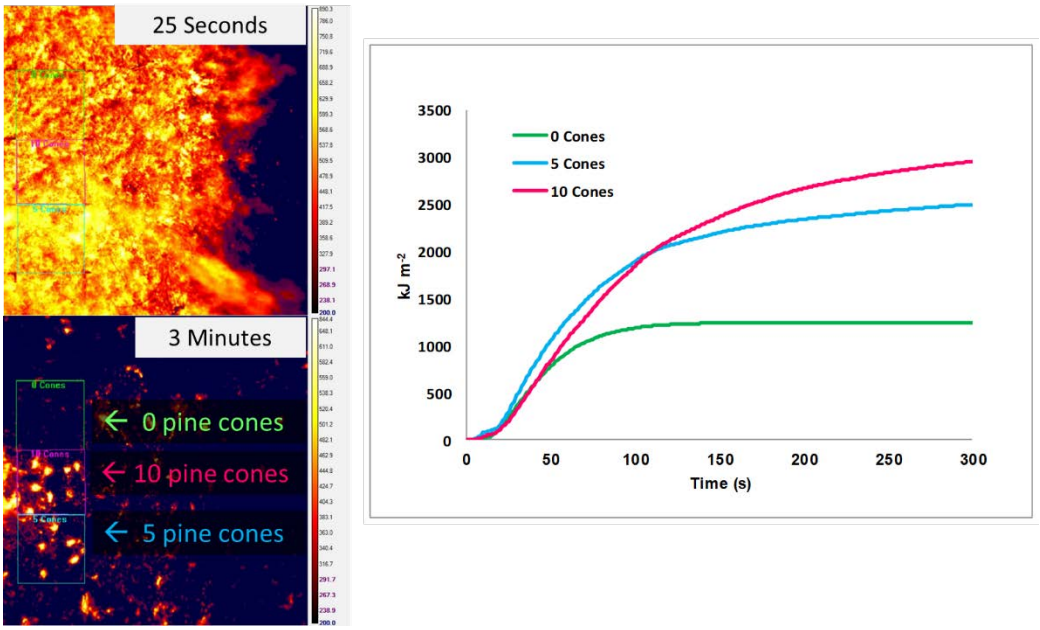

Figure 21. Fire intensity measured with the LWIR illustrating the difference in cumulative radiative power, i.e., fire radiative energy, in 1m2 areas influenced by the cone density treatments (0, 5, 10). As the fire enters the plots (top image) grasses, shrubs, and leaf litter carry the fire, while three minutes after the fire, pine cones and other coarse woody debris are still releasing radiant heat above 300° C.

The initial step of the LWIR imagery used the proprietary FLIR software ExaminIR Pro where plot boundary coordinates were identified and local conditions that impact IR measurements specified (emissivity, air temperature, relative humidity, and distance to target) for proper calibration of the image files. The files were then exported as an ASCII array of temperatures in °C with rows and columns representing pixel positions. The identified plot boundary coordinates were used to extract the region of interest and then converted into another ASCII file of three columns where x, y, z = pixel row, pixel column, and temperature using the Python 2.7 processing language. Temperatures were then converted to degrees Kelvin and the Stefan-Boltzmann equation for a gray body emitter with an emissivity of 0.98 (typical of plant material and soils) was used to convert temperatures into fire radiant flux density, FRFD, Wm^{-2}, (O'Brien et al. 2016). The LWIR data was aggregated to the 10cm x 10cm scale to be comparable to the scale of the plant demography data. This was accomplished by integrating the FRFD in each 10 cm x 10 cm area over time (**Fig. 21**). When integrated over time, FRFD is converted to fire radiative energy density (FRED, J m^{-2}). FRFD from 18 pine cones (two randomly chosen from each plot) were also extracted from the LWIR imagery and integrated over time to give fire radiative energy density (FRED, kJ m^{-2}) released from this particular fuel type for use in further analysis (see below). A mask consisting of the original perimeter of the cone was created and all pixels within this mask were extracted and the FRFD and FRED calculated as described above. We used a blocked split-plot experimental design to examine the additional energy released by cones compared to background fuels. The three individual fire management units were treated as blocks each having three plots (total plots = 9), and cone treatments split within the plots (cones versus cones removed). A general linear mixed effect model was run using STATISTICA (data analysis software system), version 12, StatSoft, Inc. (2013) where the cone treatment and burn blocks were fixed effects and the plots were treated as random effects. We applied a Tukey's HSD *post-hoc*

means test. We measured the magnitude and significance of spatial autocorrelation of fire intensity using the Moran's I analysis within the ''ape'' package (Paradis et al. 2004) in R (R Core Team 2013). To assess the range of spatial correlation and magnitude of spatial variability between the cone density sub-plots, we modeled the semivariance (spatial autocorrelation function) within treatments using the "geoR" package in R (Ribeiro Jr and Diggle 2001). For each group of cone-density sub-plots, an isotropic exponential autocorrelation function (Goovaerts 1997) was fit to the empirical semivariance. All semivariance parameters were the same between groups (lags=10, lag separation distance=5 cm, nugget=0, range ~20 cm), except for the sill (sill~900, 11,000, 22,000 for 0, 5, 10 cone densities, respectively).

We assessed the impact of fine-scale fire intensity, i.e., the "hot spots" created by burning pine cones on understory plant mortality patterns using a logistic regression with mortality as the dependent variable and FRED as the independent variable. We calculated a binary fire intensity metric by using cone FRED as determined by the LWIR imagery as a threshold for a high (1) and low (0) FRED. The mean (standard deviation) FRED of 18 pine cones (2 per plot) was 7730 (3154) kJ m^{-2}. We calculated the threshold value for a high FRED (4576 kJ m^{-2}) as the mean cone FRED minus one standard deviation. We used this threshold to separate areas within the plots that were influenced by cones or other woody fuels from areas of sparse fuels or other quick burning fuels such as grasses and pine litter.

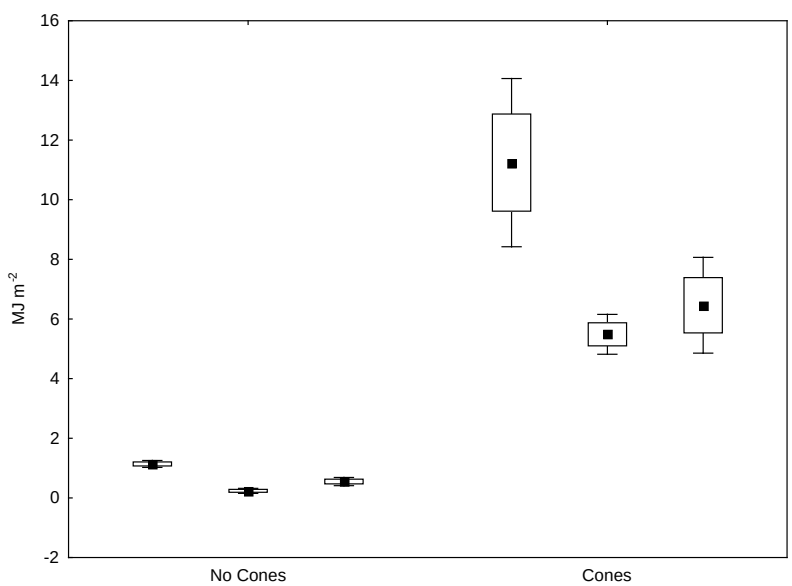

Figure 12. Box plots of background fuel and cone Fire Radiative Energy Density.

The results from the linear mixed effect model illustrated that there was a significant difference between FRED among the burn units and cone treatment, but no interaction between burn unit and plots (**Table 7**, **Fig.s 22**). From the *post hoc* test, cones released significantly more energy than background fuels. The plots in fire management unit F-22 released significantly more energy than F-18 and F-19 which did not differ.

Table 7. Results of analysis of variance.

Effect	*Effect (F/R)*	*df*	*SS*	*MS*	*F*	*p*
Intercept	Fixed	1	315.47	315.47	82.12	>0.001
Block	Fixed	2	37.441	18.721	4.871	0.041
Cones	Fixed	1	226.121	226.121	58.861	>0.001
*Plot*Block*	Random	6	12.1	2.01	0.525	0.775
Error		8	30.73	3.84		
Total			306.41			

The Moran's I test illustrated that there was significant spatial autocorrelation for all three cone density treatments (MI = 0.78, $p < 0.0001$ for all treatments). From the semivariance analysis, we found that the range (distance) of spatial autocorrelation was similar (~17 cm) for all cone densities, but the inclusion of more dense fuel at fine-scales (pine cones) created significantly higher magnitude of spatial variability (sill). The spatial heterogeneity in fuelbed heights and FRE is apparent at these fine scales, where in this study one fuel type (pine cones) drive the FRE release (**Fig. 22**).

The logistic regression results showed that higher mortality rates occurred in areas of high fire intensity (**Table 8**). The results showed that cells with high FRED were 2.78 times more likely to experience mortality than areas with lower FRED.

Table 8. Results of the logistic regression on plant mortality versus high or low FRED.

	D.F.	*Wald Statistic*	*p value*	*Odds Ratio*	*Lower 95% CI*	*Upper 95% CI*
High-Low FRED	1	5.101	0.023	2.78	2.34	3.22

The goal of this portion of the study was to examine the spatial heterogeneity of within-fire energy release, its relationship to type of fuel and link this information to fire effects, particularly vascular plant mortality. The heterogeneity in FRED did vary at fine spatial scales; observations of FRED were spatially dependent at less than 17 cm, similar scales to the individual herbs and grass clumps consumed in the fire (Hiers et al. 2009, Loudermilk et al 2014). Woody fuels (pine cones) increased the magnitude of spatial variability and also resulted in more than twice the energy release. We were successful in showing that areas with higher FRED were related to fuel type, in this case pine cones, and this higher FRED though very local (<17 cm, **Fig. 22**), resulted in nearly 2.5 times greater probability of mortality of vascular plants. These fuels also had a much higher radiative energy density that background fuels; cones released approximately eight times more energy (**Fig. 22**). The connection of fuels to post-fire mortality in this study documents a key prerequisite for a neutral model of plant community dynamics in frequently burned longleaf pines: a random agent of mortality. While the distribution of cones is certainly not random at larger spatial scales since cone density is linked to tree location we argue that at the fine scales relevant to individual plants, the final position of a cone falling from a tree to the ground could be considered random. We can also exploit this correlation by being able to link a fine scale process to landscape scale patterns of tree density (Coarse Scale Study, Hudak et al. 2016) and episodic cone production common in these systems (Boyer 1998). We recognize random processes are not the only mechanisms at work

in longleaf community dynamics. For example, deterministic processes such as facilitation (Espeleta et al. 2004, Loudermilk et al. 2016) and competition (McGuire et al. 2001, Pecot et al. 2007) are well known elements of community ecology in longleaf woodlands, but these mechanisms also require highly resolved LWIR data to elucidate microsites and niche space in frequently burned ecosystems (Loudermilk et al. 2016). Competition becomes especially relevant when fire return intervals lengthen or fire is excluded (Wahlenberg 1946). Nonetheless, with frequent fire, we argue that the mechanism we have identified, mortality driven by fine scale variation in fire behavior, could prove to be a key component of community assembly among the high diversity understory plant community. While further analysis of resulting patterns in plant demography will be needed to fully test a neutral model, our results are a critical first step. Nonetheless, these results highlight the critical importance of understanding spatial patterns of within-fire spatial heterogeneity at fine scales when studying ecological fire effects.

There were also differences across the EAFB landscape in total FRED likely driven by management legacies. Unit F-22 had nearly double the FRED of Units F-18 and F-19. F-22 also had been treated with hexazinone herbicide approximately 10 years before the experiment and this could have resulted in higher loading of fine fuels (Addington et al. 2012) and subsequent higher fire intensity. Plots in F-22 also likely burned with higher intensity due to fireline geometry. We observed two head fires were ignited on either side of the plot and the fireline interactions increased fire intensity as the fire moved across the plot. The higher intensity would have resulted in greater fuel consumption at total higher FRED. Regardless of the differences observed between blocks, the cones still burned with higher intensity within all the burn blocks.

The availability of portable thermal imagers has allowed for the capture of quantitative data on spatial and temporal heat transfer at ecologically relevant scales (O'Brien et al. 2015). This has enabled the mechanistic linkage of fuel structure to fire behavior in ways not possible in the recent past. For example, Hiers et al. (2009) and Loudermilk et al. (2009, 2012) were able to link fuel structure to fire behavior at the 0.25 m^2 scale, though they recognized that their analysis would not detect the influence of point-like fuels such as cones. We show here that even finer scale processes related to cones or other compact high energy releasing fuels (**Fig. 21, 22**) can have a major impact on plant mortality through fine scale, long duration smoldering. While the technology itself is more than a decade old, the application of thermal imagery to fine scale fire behavior measurements still represents a new direction for fire ecology (Hiers et al. 2009).

While the application of this technology deployed here within the fire environment is at fine scales, such spatially and temporally resolved data may prove critical at larger scale fires (10-1000 ha) (O'Brien et al 2016). There currently remains a technology gap for such scale to resolve nadir perspective between airborne and group based sensors (Hudak et al. 2016, Dickinson et al. 2016). Airborne sensors often produce gaps in data due to turn around times and operational constraints on airspace around fires (Hudak et al. 2016). UAVs (Kiefer et al. 2012, Zajkowski et al. 2016) offer promise to bridge this spatial scale. Nonetheless, attenuation of LWIR signals by canopies remains a challenge (Hudak et al. 2016, O'Brien et al. 2016), and may require a combination of sensors and platforms across scales to overcome these issues.

LWIR thermal imagery provides high resolution quantitative measurements of in-fire energy transfer with complete spatial coverage at scales relevant to many ecological processes, such as

plant mortality and stem or soil heating. These measurements are also useful for directly linking spatial fuelbed metrics to fire behavior that should prove useful in better understanding mechanisms driving fire spread.

Trait analysis and departure from neutrality with fire exclusion

The continuum hypothesis predicts a gradient in community assembly dynamics from stochastic to deterministic. In our case we predicted the lack of fire would move plant community assembly from neutral to a pattern driven by competitive exclusion. The results of the analysis of the plant demography monitoring and cellular automata modeling (section) indicated that indeed, with frequent fire, assembly can be predicted by simple demographic parameters because of the random fire driven mortality described above. Interestingly, the departure from neutrality begins almost immediately as was demonstrated by the analysis of the net migration rate parameter of the UNTB (see next section) where there was a marked reduction in community dynamics in only a year following a fire. This pattern continued with longer periods of fire exclusion. To explicitly examine these processes, we analyzed the plot data from both burned and unburned plots using a vector analysis on non-metric multidimensional scaling (NMDS) scores. A vector analysis explicitly tests the relationship between an explanatory variable and the community composition. In our case we tested how fire influenced the patterns of species (**Fig. 23**). The vectors representing time since fire or the number of burns were parallel but pointed in opposite directions. In the plot of the scores, NMDS axis 1 was nearly parallel to the fire vectors indicating that the spread of species along this axis was likely responsive to fire frequency. This observation is supported by the locations species associated with a lack of fire such as *Pinus clausa* and fire dependent species such as longleaf pine at opposite ends of axis 1. The spread of species along Axis 2 shows no obvious pattern and could reflect the ubiquitous high diversity found in the reference plots that is a legacy of regular burning.

We further explored the shift in species composition with a plot of successional trajectory between the first census and last census. The results indicated that the change in species composition in the unburned plots was moving in a similar direction though each had different initial conditions. Conversely, the movement of plots in species space showed no obvious pattern in the burned plots, reflecting the stochastic nature of neutral community assembly. We used indicator species analysis (Dufrêne and Legendre 1997) to identify which species were representative of the burned and unburned plots (**Table 9**).

Table 9. Results of the indicator species analysis showing taxa significantly associated with whether a plot had been burned and unburned. The letter to the right of the species indicates form: G=graminoid, F=forb, W=woody.

Burned		**Unburned**	
Andropogon virginicus	G	*Bulbostylis ciliatifolia*	G
Dichanthelium ovale	G	*Commelina erecta*	F
Schizachyrium scoparium	G	*Galactia regularis*	F
		Paspalum praecox	G
		Pinus clausa	W
		Pityopsis graminofolia	F
		Ruellia caroliniana	F

Interestingly, while one of the species associated with the lack of fire were expected (*P. clausa*), others are used as indicators of frequently burned reference stands. To examine whether there was a trend through time, we then plotted the successional trajectory of the plot scores from the first census to the last census. Finally, we examined the distribution of traits in burned and unburned plots to see if there were particulate guilds of plants that had a competitive advantage. We used a combination of morphological and reproductive traits and analyzed their distribution using a G test. The test was significant ($P<0.0001$) and we examined the pattern of trait change using pairwise comparisons with a Bonferonni correction. The results are shown in **Fig. 23**. The analysis showed that small herbaceous plants decreased in the unburned plots and woody plants with large storage organs increased in frequency. The change in trait distribution through time did not change in the burned plots with the exception of an increase in plants with long distance dispersal in both burned and unburned plots. We hypothesize that a nearby soil disturbance increased the propagule load from weeds profiliferating there.

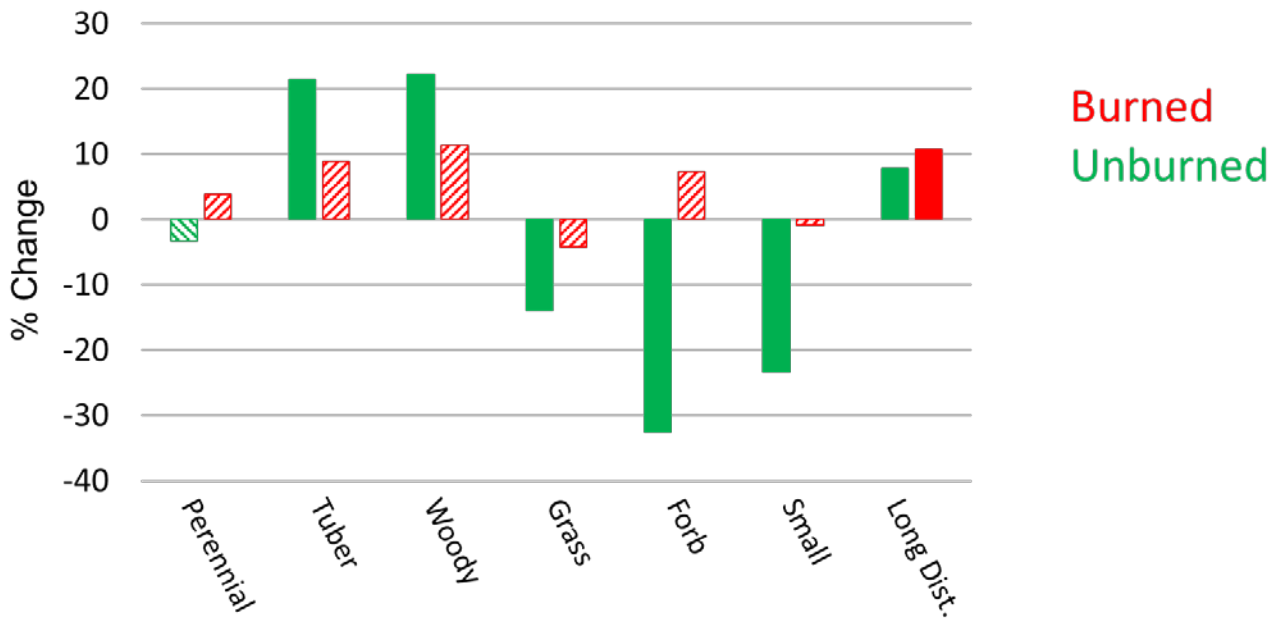

Figure 23. Change in trait occurrence in burned and unburned plots between the 2012 and 2016 census. Filled bars are significantly different after a Bonferroni correction (critical value $\alpha=0.0071$). Hatched bars were not different.

The results showed that the switch between stochastic and deterministic community assembly occurs very rapidly; after missing two burn rotations, new patterns in trait frequency began to emerge. These results support previous work (e.g. Kirkman et al. 2004) that linked the highes diversity with the highest fire frequency and suggests that variable fire return intervals will not augment diversity, on the contrary, consistently frequent fires would be required to maintain the highest plant diversity through suppressing competition. Competition seems the likely mechanism since the smallest plants disappeared first, replaced by more robust and woody plants. Another important result form this analysis is that there appears to be differences between short term responses and long term responses. In the short term, herbaceous species still remain common,

though after longer periods, woody plants eventually dominate. While our study did not encompass the time scale required to capture this further transition, our results are the first to demonstrate the rapid shift in community assembly dynamics.

Fuel metrics from photogrammetry & in-situ data

For the photogrammetry analysis, fifty-seven different species were observed, and cluster analysis resulted in the definition of 13 different fuel types. Point cloud height distributions approximated field-measured height distributions (**Fig. 24, Fig. 25**), and point cloud metrics varied significantly between plant species, plant types, and fuel types 41, 54, and 44% of the time, respectively. We concluded that close-range photogrammetry can provide 3D height information comparable to point intercept techniques.

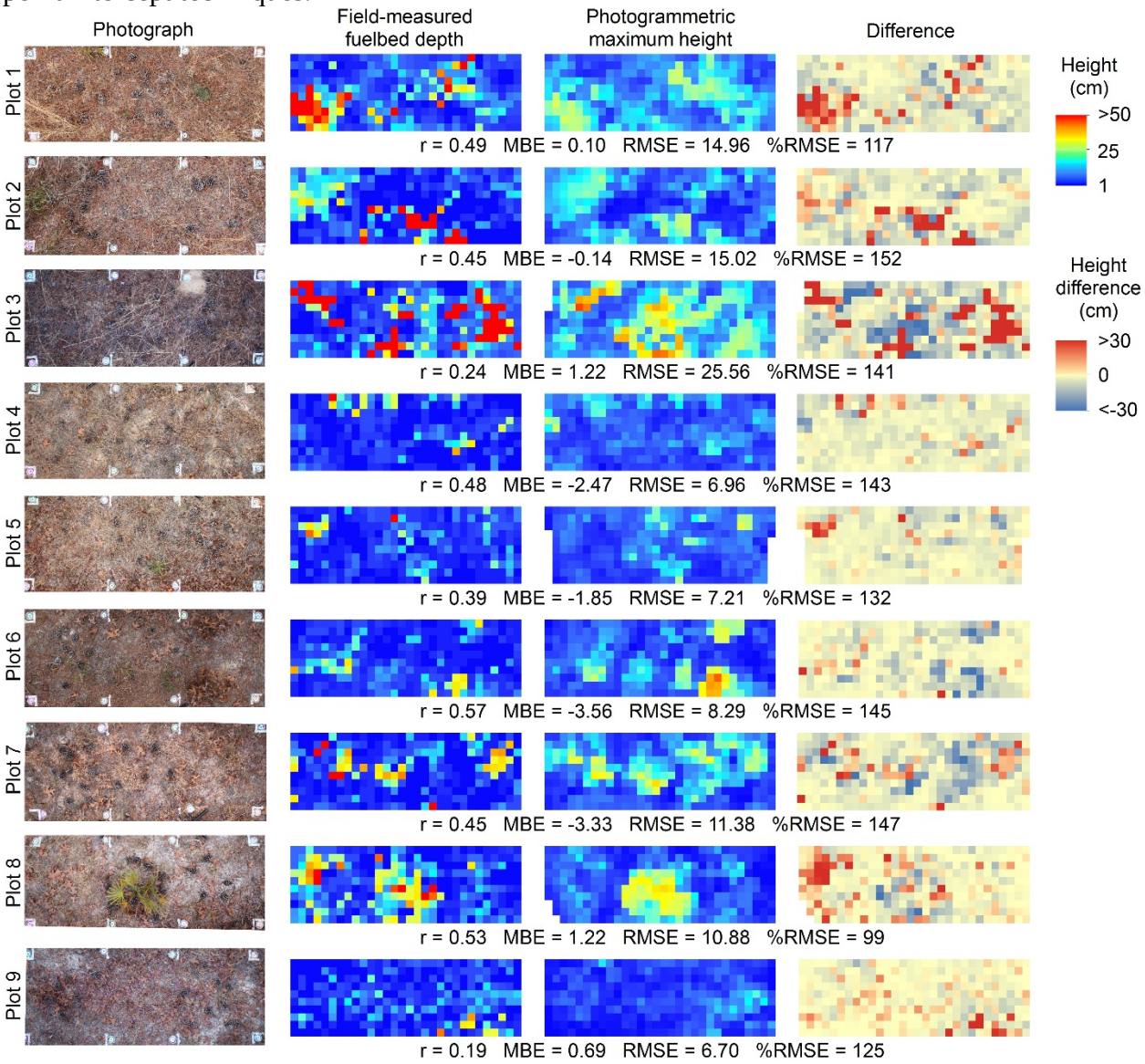

Figure 24. Comparison of field-measured fuelbed depth and photogrammetry-derived maximum height. Grid cells are 10x10 cm in size. From Bright et al. 2016, Canadian Journal of Remote Sensing.

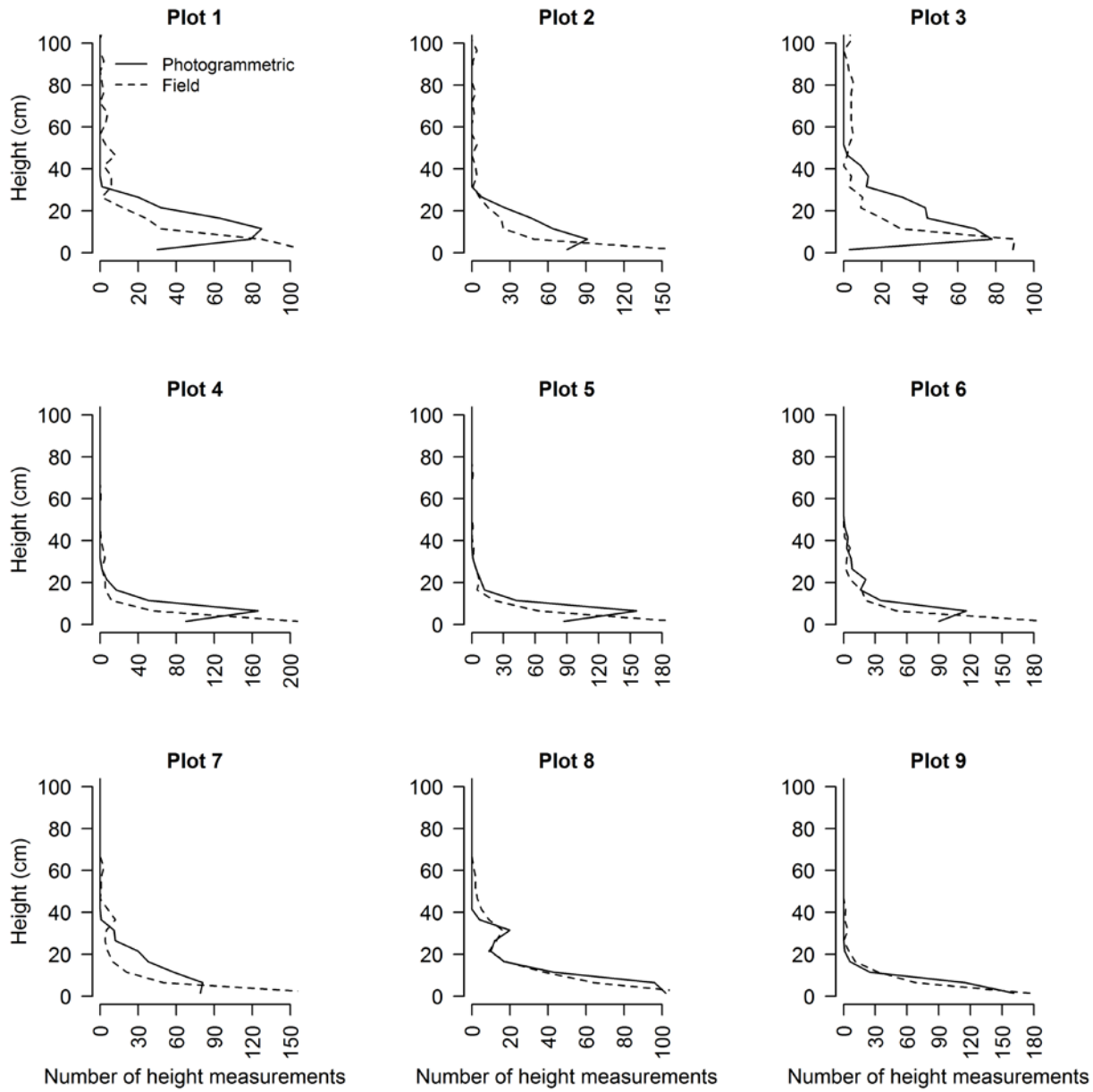

Figure 25. Comparison of distributions of field-measured fuelbed depth and photogrammetry-derived maximum height for each of the nine 1x3 m plots.

A. Fine-Scale Plant Demography for Cellular Automata Modeling

Fire intensity data with plant change

From the empirical data on fire and plants, we compared the net migration rate of individual plants with FRE (fire radiative energy) from surface fires. The migration rate was calculated as the net migration of individuals, regardless of species, in each 10 cm^2 cell within each plot. The spatial location of individual plants and fire was critical, as this rate was dependent on whether an individual previously occupied the cell, there was individual gone (mortality) with or without replacement by another, or a new individual was found (spread into an empty cell). **Fig. 26**

illustrates the relationship between mean cell FRE and total FRE with mean net migration rate across plots.

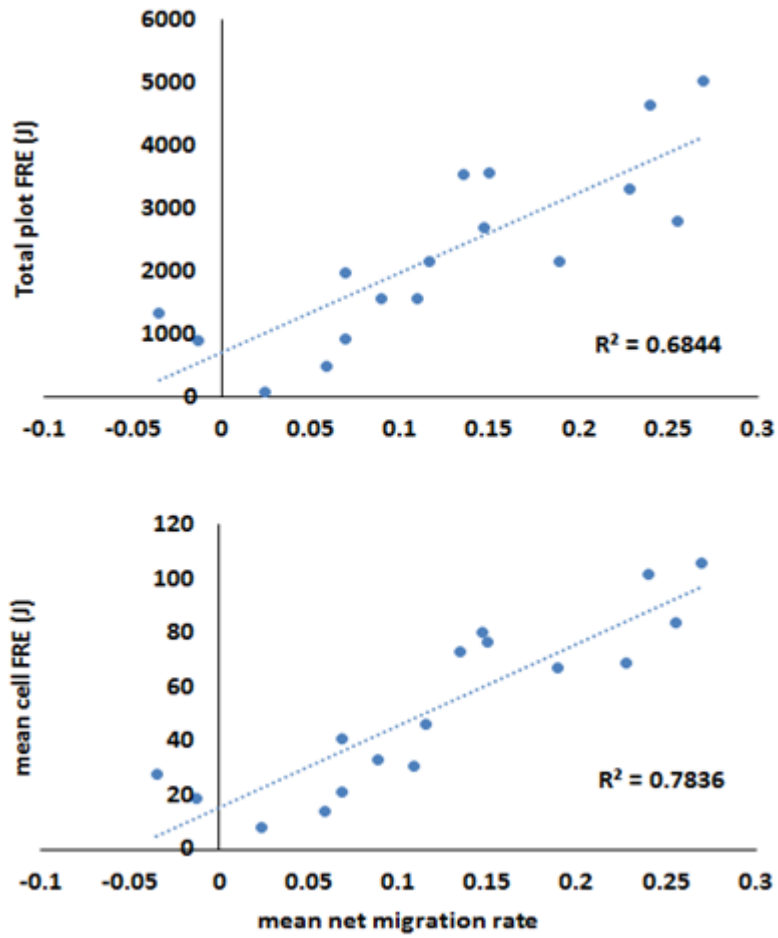

Figure 26. Results illustrating plot level relationships between plant change and fire intensity. Both regressions had a $p < 0.001$. Net migration rate was calculated within each 10 cm^2 cell (plant change between fall 2012 and fall 2013) and averaged across the plot to get the mean net migration rate within each plot. FRE (fire radiative energy) was calculated at the plot level from the spring 2013 burns (IR cameras). Total plot FRE (top graph) is the total FRE within each plot. Mean cell FRE (bottom graph) is the average cell (or pixel) FRE within each plot.

Cellular Automata modeling

Species richness distributions were successfully simulated in a frequently burned longleaf pine ground cover plant community (**Fig. 27**) using simple probability functions, representative of the Unified Neutral Theory of Biodiversity (UNTB). Furthermore, a broad range of estimates for mortality and birth (values from 0.2 to 0.6) were successful in simulating richness; combined, these two parameters accounted for less than 5% of the variance through direct effects. This suggests that general values of recruitment and death rates for the entire community, rather than individual species, produce robust outputs and large efforts to estimate these values may be unnecessary. Immigration on the other hand, was the most sensitivity of the parameters (up to 20%, depending on input scale). This illustrates the importance of quantifying accurate immigration rates (or understanding community level dispersal) when modeling fine-scale community richness. The

importance of immigration and the assumptions about this parameter are similar to other UNTB simulated systems (Girdler and Barrie 2008, Lowe and McPeek 2014).

The two exogenous variables had a larger effect on the model than mortality and birth, but comparable to immigration depending on scale of input data (**Fig. 28**). Number of plots and area simulated (extent) had considerable effects on normalized species richness, ranging from 9-19% and 12-18%, respectively. In the model, the number of areas directly affects the number of local communities, while area simulated affects *size* of the local community pool within areas being simulated. We found that the more plots or larger the area simulated, the more stable the community and likelihood for rarer species to exist through time. We did not see a large effect from the type of dispersal (spatial dispersal vs. non-spatial dispersal, **Fig. 27**) on species richness. And although this would suggest that deciding between spatial vs. non-spatial dispersal processes may be generally irrelevant for modeling species richness, restricting recruitment in the local community (spatial model) creates a modeling environment conducive to more realistic dispersal patterns of these small plants. Population structure, or the scale of input frequency distribution, was significant in terms of influencing parameter sensitivity (**Fig. 28**) and output species richness (**Fig. 27**).

The overall effects of scale on species richness are relatively clear (**Fig. 27**); species richness patterns can successfully be simulated using UNTB assumptions at all scales, although at coarser scales, all species are more evenly represented in the input frequency distributions and create more stable outputs. The effects of scale on individual parameters is more complex. At the finest scales of input frequency distributions (**Fig. 28**), immigration rate had the largest individual parameter sensitivity on normalized richness of any parameter, where rarer species depended more on immigration from the metacommunity using the finer scaled inputs. At coarser scales, the input frequency data were less skewed, i.e., rare species were no longer comparatively rare and richness was more stable than using finer scale data. The same effect of scale was found for birth rate, but with lower individual sensitivities. Here, rarer species depended more on effective recruitment at finer scales. Effects of scale on mortality rates was minor, with little variability across scales of input data, and low overall individual parameter sensitivity. Scale had significant effects on both exogenous variables, where in general, as the input scale coarsened, the individual parameter sensitivity increased, rather than decreased, as seen with the endogenous parameters. These results illustrate how scale and population structure can influence a simulated community determined by neutral processes.

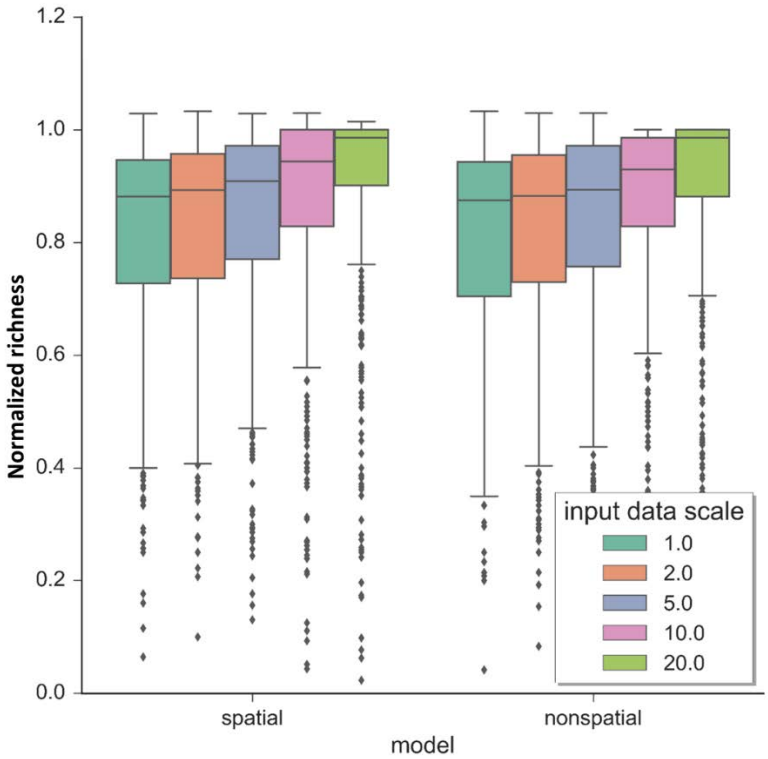

Figure 27. Normalized groundcover species richness as simulated using the neutral CA model, using the 500 F.A.S.T. parameter combinations, five input scales of frequency distributions, and the spatial and non-spatial dispersal assumptions. Each boxplot is the output from 500 model runs using the 500 F.A.S.T. parameter combinations. The legend illustrates the scale in which the data were created from the empirical data, including the original resolution of the data (1.0: 10 cm x 10 cm, etc.). Normalized species richness is the species richness change from time zero compared to last time step (50) of each model run. This was created to analyze simulated richness among simulations of varying size areas and number of areas simulated.

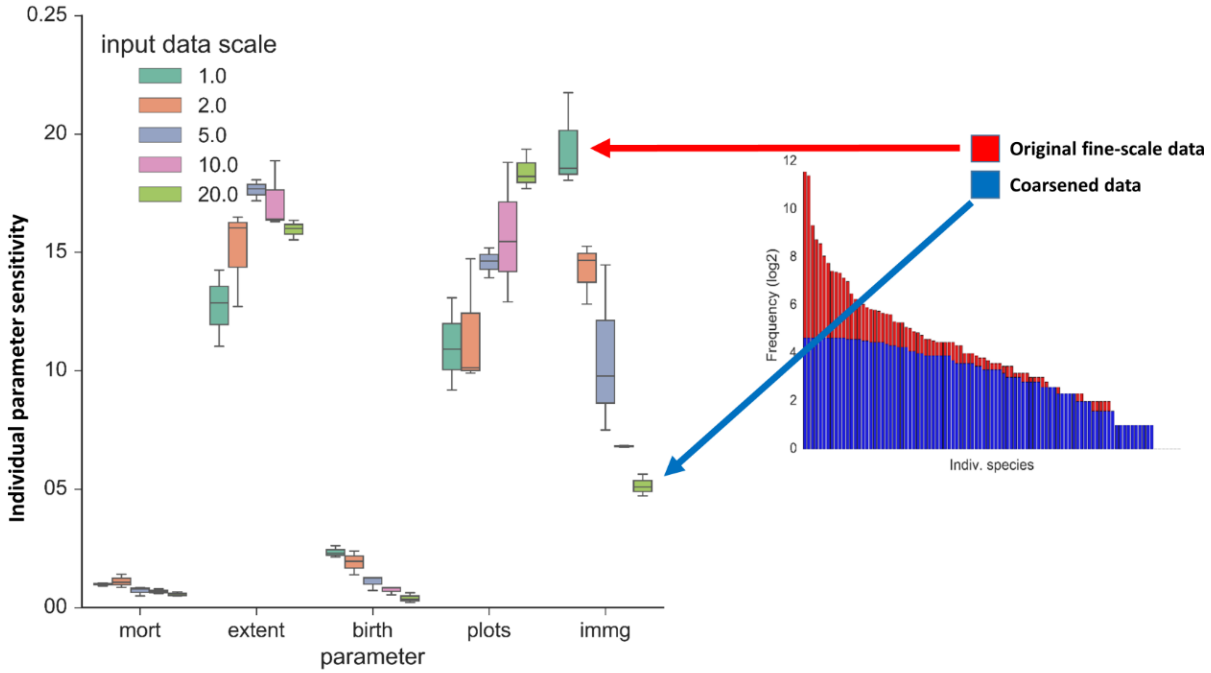

Figure 28. First order effects or individual parameter sensitivity (%) of the three endogenous parameters (mortality, birth, and immigration) and exogenous parameters [extent (size of area) and number of areas (plots)] on simulated normalized richness. The legend illustrates the resolution (in dm) in which the data was created from the empirical data, including the original resolution of the data (1.0: 10 cm x 10 cm). Boxplots represent variance across three replicates of model runs using the 500 FAST parameter combinations. The graph on the right illustrates the difference in input frequency distributions when they are scaled. The arrows illustrate which frequency distributions (scale of data) were used as input for the given boxplot.

The CA model was also successful at illustrating changes in species richness during small intervals of fire exclusion. As we have found that species richness decreases in as little as two years without fire (**Fig. 29**), we assumed a large probability (0.8) of mortality during short time periods without fire. We ran the CA model assuming continuous fire (timestep in model = 2 years), and used a 0.2 probability of experiencing fire exclusion. The results illustrate the temporal "dips" in species richness during years without fire, and the increase thereafter when fires are included again (**Fig. 30**). This illustrates strong decreases in species richness during the time of fire exclusion and smaller (yet significant) reductions in species richness over the course of the simulation.

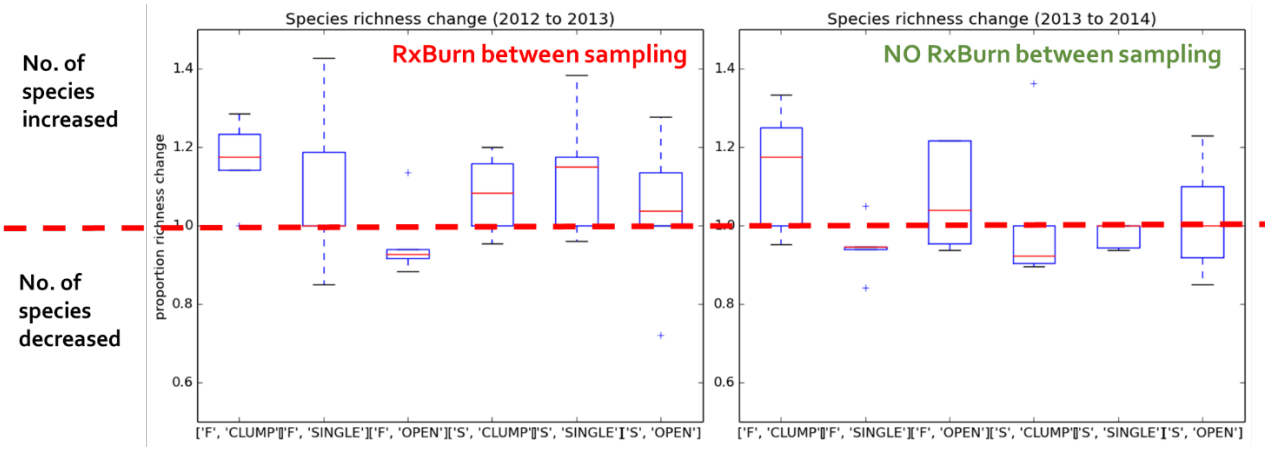

Fig. 29. Species richness change between years of prescribed burning (left) and no prescribed burning (right). The number of species begin to decrease with two years since the last burn in these Flatwoods areas.

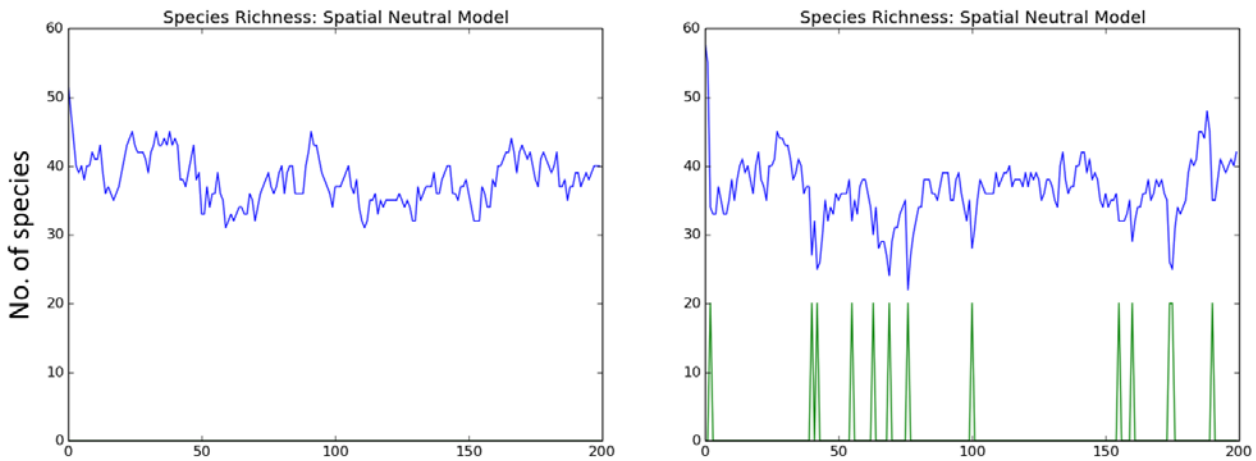

Fig. 30. Illustration of species richness change through time simulated with the neutral CA model when fires are continuous through time (left) and when there are short intervals of fire removal (right) from the system. This illustrates 10, 1 m^2 plots. The x-axis is timesteps, which equal 2-year intervals. The green spikes represent when fire was removed from the model.

Patterns of Diversity

Abstract
In addition to the coarse- and fine-scale vegetation studies, we are coupling data mining and field monitoring to examine how fire effects on plant diversity cascade up to the arthropod community, which can in turn modify fire-plant diversity associations. We are using several arthropod monitoring techniques at varying spatial scales to examine method bias, species area relationships, and functional diversity metrics. By sampling arthropod diversity and creating linkages to plant diversity, we will be able to better understand how both plant and animal communities, as well as their interactions, respond to fire. To quantify trophic interaction diversity, and to model the effects of fire on multiple dimensions of diversity, we are building on a long-term Lepidopteran rearing dataset associated with the long-term monitoring vegetation data.

Objectives
We used the fine scale vegetation plot data and other diversity datasets (**Table 10**) to examine species area relationships, species density, sampling issues, and spatial patterns of diversity across EAFB, between forest types, and across a gradient along the Florida panhandle. For example, we utilized semivariograms of the plot data along with kriging to derive optimal estimates of diversity across the landscape.

Technical Approach

A. Scaling study

To examine spatial patterns of diversity we established a series of nested circular plots in reference longleaf pine sandhills throughout EAFB during summer 2014. A 5 m radius circle was divided into quarters with total stem counts tallied for all species in a quarter arc at each 1m radius increment. Variable spatial scales ranging from a single 1m arc (0.785 m^2) to the entire 5 m radius circle (78.54 m^2) and anything in between can be compared. More scale sampling plots will be sampled during the period May-August, 2015.

We are examining associations between sampling area and means and variances in diversity estimates calculated via bootstrapping (Pla 2004), jackknifing (Smith and van Belle 1984, Colwell and Coddington 1994, also see the approach of Butturi-Gomes et al. 2014 for Tsallis entropy), and similar techniques. We are using nonlinear regression and other standard components of generalized linear models to examine associations between our different methods, scales, and diversity measures with the goal of testing hypotheses about optimal scales and metrics for measuring biodiversity in longleaf pine systems. For some of our diversity comparisons, problems of uneven sample sizes for diversity (based on different spatial or temporal scales) are being corrected using rarefaction, entropies, and additive partitioning (Heck et al. 1975, Lande 1996, Gotelli and Colwell 2001, Lande et al. 2001, Crist and Veech 2006). More importantly, we are utilizing Hierarchical Bayesian statistics (e.g., Ogle and Barber 2008) to test ecological hypotheses at multiple scales via merging data from multiple plots within the spatial hierarchy or merging data with other empirical data (e.g., Hiers et al. 2007, Dyer et al. 2010).

B. Arthropod diversity

To examine the utility of arthropod functional groups as practical indices of management efficacy, we utilized a series of six malaise traps to sample before, during, and four periods post-fire. Sampling was done in conjunction with the fires conducted as part of the fuel manipulations burns

in late May 2014. Specimens were organized by morphospecies, identified at minimum to family, and assigned to a functional trophic guild of herbivore, detritivore, parasitoid, or predator. Abundance and richness of morphospecies were used to calculate Shannon and Simpson diversity indices with the inverse Simpson diversity index (1/D) used for analyses. As described by Jost (2007), the inverse Simpson gives the effective species numbers instead of a measure of entropy given by the untransformed and often used Shannon or Simpson indices. Therefore, this makes for allowable and informative comparisons across studies. Additional malaise sampling will take place during the late spring and throughout the summer of 2015 to address patterns of seasonal variation.

C. Interaction diversity

Here and elsewhere, we define interaction diversity as the number of interactions linking species together into dynamic biotic communities (Dyer et al. 2010, Dattilo and Dyer 2014), and for this and other studies, we focus on trophic interaction diversity. For this metric of diversity, the calculation of richness, diversity indices, and rarefaction diversity is based on trophic links between interacting species rather than species alone. Interaction diversity is affected by taxonomic, genetic, and functional diversity, and our quantitative measure of interaction diversity provides novel insight into debates about neutrality and correlations between diversity, stability, productivity, and ecosystem services (e.g., Forister et al. 2015). For our new measure of interaction diversity (Dyer et al. 2010), which can be used as a proxy for functional and overall species diversity, we established nine 30 m diameter plant-arthropod sampling plots centered on the fine scale monitoring plots. Arthropods were sampled using a sweep-net and walking around the plot in concentric circles working from the outside towards the center. Using beat sheets and visual searches, we collected caterpillars on host plants in the plot and rear them to adult or parasitoid. We recorded plant stem and leaf counts within the plots to estimate the leaf area searched and plant diversity. These plots were sampled at least three times per year, and we will continue collecting these data throughout the duration of the project. During the summer of 2015, additional interaction diversity sampling will take place at the 30m diameter plot scale along a time-since-fire gradient.

To help determine the most effective sampling techniques for quantifying interaction diversity, we compared sweep net sampling with vacuum sampling. We also compared sweep net samples across plots with diameters of 5m, 10m, 30m and 50m. All arthropod samples were sorted, identified, curated and are currently stored at the University of Nevada, Reno Museum of Natural History.

Results & Discussion

A. Scaling study

Additive Partitioning of plant species diversity across EAFB

To best describe the patterns of diversity found in understory plant communities of longleaf pine ecosystems, we analyzed an extensive data set including both mined historical data (Hiers et al. 2007, Provencher et al. 2001) and supplemental experimental data. In addition, we utilized an additive partitioning of plant diversity (Tello et al. 2015, Chandy et al. 2006) to elucidate the hierarchical spatial patterns of diversity including species richness, and independent measures of alpha and beta diversity (Tuisomo 2010, Jost 2007). Datasets included species abundance and richness measures from various timeframes and spatial extents including over 200 monitoring plots

representing a decade of sampling within hierarchically arranged plots (Hiers et al. 2007), (Fig. 1), and dynamic reference stand data (Provencher et al. 2001).

Sampling scales ranged from 0.785 m^2 to 400 m^2 (**Table 10**) among the studies and allowed for aggregation up to the management scale of 5 ha. Data were collected over the time period from 1995 to 2015 in both the spring and fall seasons by crews from The Nature Conservancy, Department of Defense natural resource technicians, and professional botanists. Additionally, fire history records were available for the majority of plots extending over the entire sampling time period.

Table 10: Datasets used in additive partitioning analysis of understory vegetation within Eglin AFB. Abundance (A) and Richness (R) measurements taken as indicated in data description

Dataset	Spatial scale	Temporal Scale	Diversity sampling	Description
Eglin AFB vegetation monitoring	1 m^2, 40 m^2	2001-2012	Abundance and richness at 8 m^2 scale, richness at 40 m^2 scale	152 (A, R) quadrats, 19 (R) plots sampled after each management treatment during the time scale.
Neutral theory vegetation plots	3 m^2	2012 to 2016	Richness	15 sandhill quadrats and 15 flatwoods quadrats sampled in the Fall of every year and Spring in years not burned
Longleaf restoration and Dynamic reference projects	1 m^2, 400 m^2	1996-1998 and 2010	Abundance and richness at 1 m2 scale, richness at 400 m2 scale	320 (A, R) quadrats, 80 (R) plots sampled during both time scales.
Spatial scale 5 m radius sampling plots	0.785 m^2 - 78.54 m^2	2014-2015	Abundance and richness	9 plots variable spatial scale plots sampled Summer

We defined and calculated diversity components in an additive manner: regional diversity represented the sum of alpha and beta diversity (Tuisomo 2010, Jost 2007). At each spatial scale within each dataset, alpha diversity was calculated as the mean diversity within the sampling unit and beta diversity was calculated between sampling units. This differed from Whittaker's multiplicative relationship and allowed us to addititively partition the total diversity across Eglin AFB into scale-specific diversity components.

As expected, richness and alpha diversity increase with area (**Table 11**), but a more relevant metric for managers interested in monitoring biodiversity is beta diversity. Beta diversity is a measure of compositional difference between sampling sites, with high levels of beta diversity indicating greater amounts of species turnover. Beta diversity begins to reach an asymptote amongst 1m^2 plots with increases in spatial extent surveyed adding little to compositional difference in the understory community. This analysis allowed us to identify the spatial scale that most effectively captures diversity and in turn, the extent to efficiently monitor plant diversity. We found that while species richness and alpha diversity increased with spatial scale, beta diversity asymptotes at smaller (1 m^2) scales. Further analysis by rarefaction based on over 1,800 1m^2 reference plots, indicated mean slope began to asymptote at 50 samples. This indicates an effective level of sampling intensity to achieve an accurate measure of plant species richness

Table 11: Results from additive partitioning analysis on different components of diversity at increasing spatial scale. While alpha diversity (H') increases with scale, beta diversity reaches an asymptote among 1m^2 plots indicating sampling larger spatial extents adds little to community composition.

Partition	Scale (m^2)	Change in Richness	Alpha (H')	Beta (H')
α	1	9.24	3.29	4.94
β1	1	18.27	5.44	6.66
β2	3	3.20	10.76	2.65
β3	13	2.79	12.94	2.41
β4	~5 x 10^6	8.00	7.61	2.17

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

We analyzed long term data sets to elucidate 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 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 woody fuels, had the greatest positive impact on diversity in 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.

We found that the overstory-derived fuels in stands maintained by frequent fire, provided a significant contribution to species richness, particularly in flatwoods (**Fig. 31**). 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. 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. 2016). 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). Additionally, variations in the amount of pine litter had significant impacts on fire behavior and fire effects, which in turn alters forest structure by determining the prevalence of midstory hardwood species (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). Woody debris burns at high intensity, releasing 12 times the radiative energy as fine fuels (O'Brien et al. 2016) 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. 2016). 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).

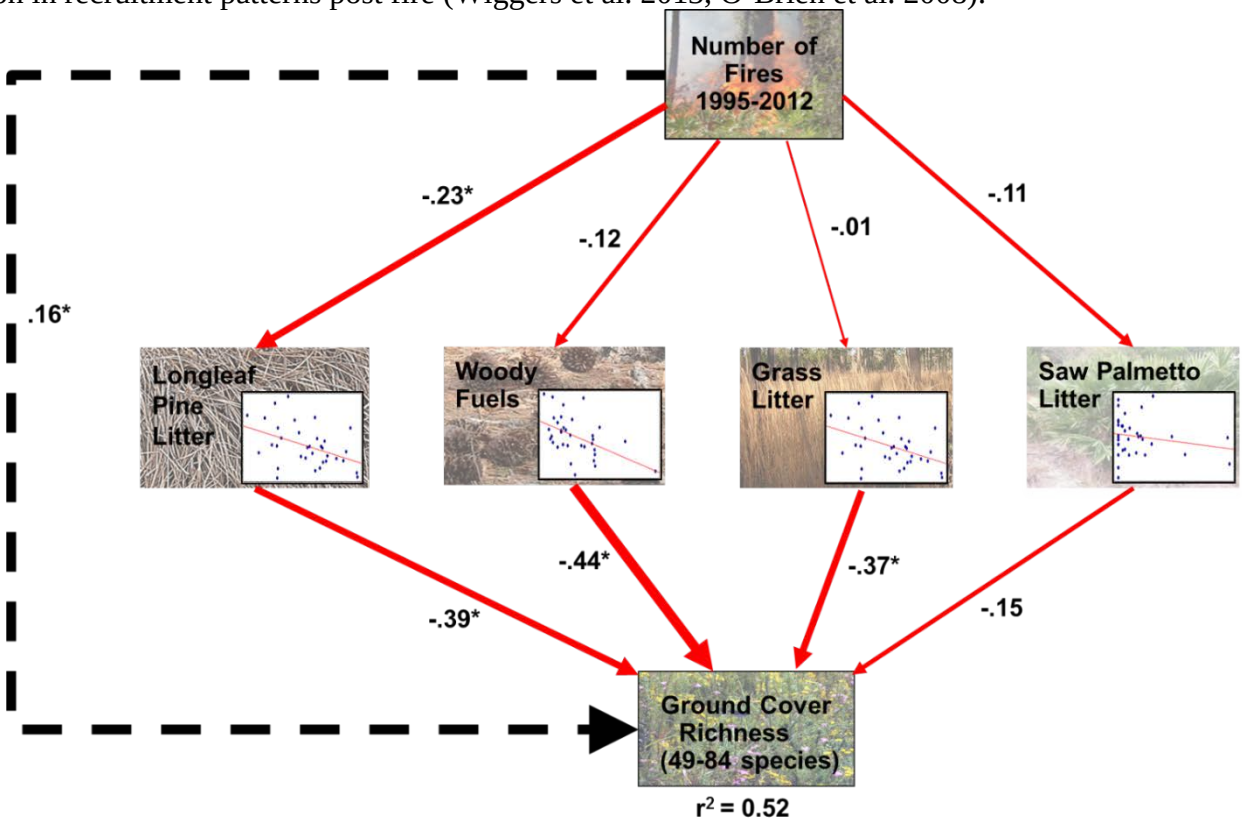

Figure 31. Structural equation model including hypothesized causal relationships between the burning of individual fuel categories and plant diversity in longleaf pine reference stands. In fire dependent ecosystems such as the longleaf pine forest, greater numbers of fires have positive effects on ground 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 12**. 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.

When fire is removed from the landscape, litter and woody fuels accumulate on the forest floor contributing to an O horizon, which is also described as duff or forest floor (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. This was not the case, however, with the consumption of woody fuels. When fire is reintroduced, the increased fire intensity and radiative energy released by woody fuels (O'Brien et al. 2016), 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. This potentially high contribution to diversity by woody debris consumption in flatwoods and pine plantations 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).

Table 12: Indirect effects of fire on diversity for each fuel type in 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. 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**

B. Arthropod diversity

While we know fire is a crucial element in 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. Furthermore, 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. In the numerous studies investigating the effects of fire on arthropod communities there are no clear patterns in the response of arthropods to fire (Pryke and Samways 2012, Whelan 1995, Swengel 2001). Results from such studies are highly variable due to differences in weather, burn intensity, focal taxa studied, and season of burn. 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).

We investigated the diversity of arthropod communities in longleaf forests before, during, and five times post burn. Sampling with malaise traps over an entire year showed fire effects were taxa specific with most orders dropping in diversity after the fire, followed by diversity recovery one-year post burn (**Fig. 32**). 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. Trophic diversity response indicates that bottom-up regulation is resulting in decreased predator diversity and latent recoveries in parasitoids and detritivores.

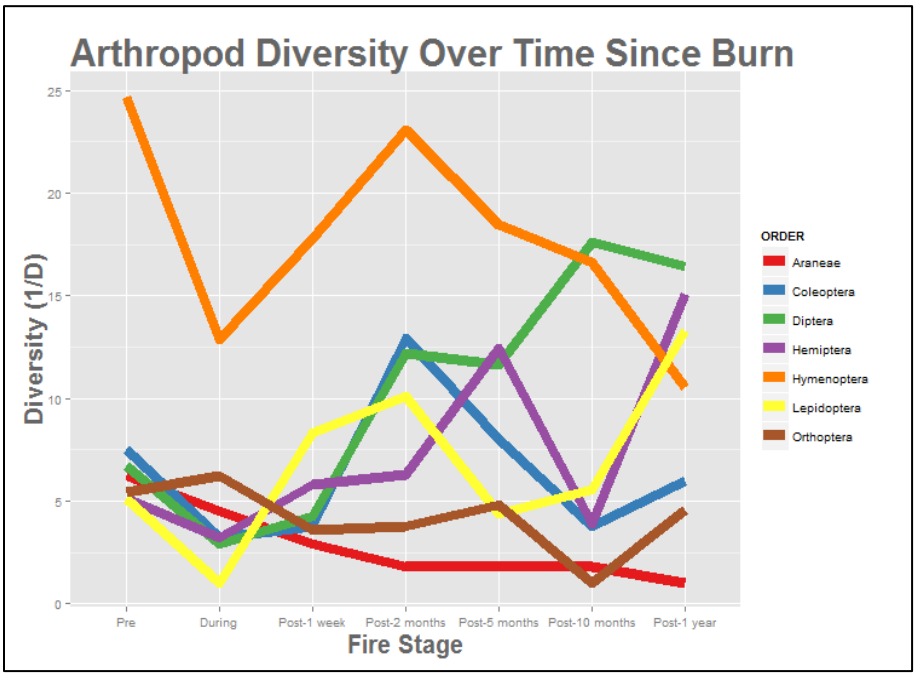

Figure 32: Patterns in the diversity of arthropods calculated at various stages in relation to time since fire. Each line represents a unique taxonomic order.

Arthropods were also sampled with sweepnets along a time since fire gradient represented by plots located within frequently burned stands (fire return interval (FRI): 1-5 years), intermediately burned stands (FRI: 5-20 years), and infrequently burned (FRI: >20). Alpha diversity of the arthropod community was highest in frequently burned plots, followed by infrequently burned plots, and lowest in intermediately burned plots. Furthermore, as time since fire increased, the overall diversity of both herbivores and parasitoids declined. Coupled with the significantly higher levels of beta diversity found between frequently burned plots, results indicated that arthropod communities are most diverse in stands that burn regularly.

We also examined what happened to those taxa that are not as readily mobile by erecting a series of sticky traps within burn units on prescribed fires. Results indicate a significant dispersal response by non-flying juvenile arthropods via vertical dispersal (Dell et al. 2017, **Fig. 33**). The cooler temperatures and reduced combustion in the canopy during low-intensity surface fires in the longleaf pine ecosystem confers increased potential for survival and subsequently recolonization post-burn.

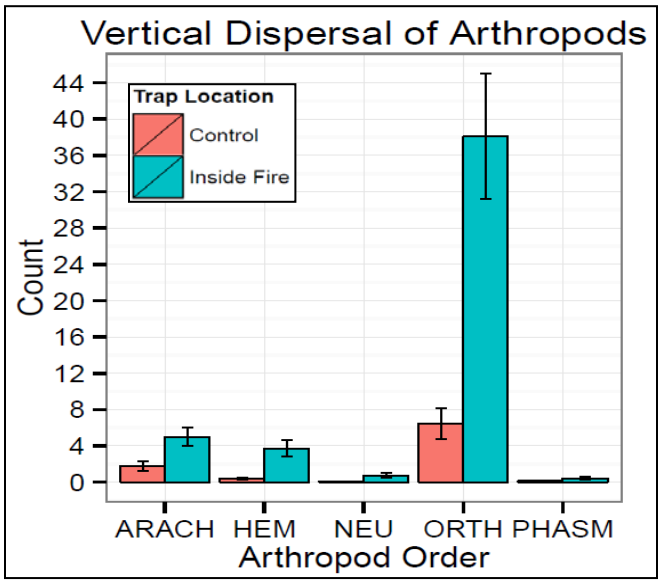

Figure 33. Five arthropods orders collected per sticky trap during fires. Traps were located within burn units and at adjacent control sites away from fire.

Our results indicate that arthropod communities are re-assembling in patterns that suggest bottom-up regulation, since longleaf pine ecosystems are fire-adapted and plants readily resprout quickly after fire, often in a matter of days. As the vegetation returns the arthropod community also returns as habitat is restored and diversity increases as the vegetative community becomes more complex. Subsequent decreases in overall diversity follow as plants enter senescence. However, over the course of one year, communities become compositionally similar to pre-burn assemblages. This is not surprising as the fire return interval in healthy longleaf pine forests can be as short as 1 year. 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.

C. Interaction diversity

In this study, we focused on trophic interaction diversity and have categorized arthropod species into trophic guilds to examine the diversity of trophic interactions per unit area between host plants, herbivores, and their natural parasitoid enemies. We have quantified interaction diversity based on replicated 30 m diameter plots at Eglin and across the Gulf coastal plain. Results of the model have allowed us to frame relevant hypotheses about how interaction diversity is related to species diversity, fire, and ecosystem stability at Eglin. We used plant and arthropod richness, measured at 4 different scales at Eglin ($1m^2$, $25m^2$, $100m^2$, $900m^2$, all of Eglin), along with levels of consumer-resource specialization to parameterize our models and estimate interaction diversity at Eglin. Preliminary model results have been verified with empirical data (**Fig. 34**) – for example, the estimated interaction diversity at Eglin based on diet breadth of known herbivores (from our sampling plots) matches model predictions. We continue to develop our measure of interaction diversity as a useful measure of functional diversity and an important correlate of community resilience and ecosystem function.

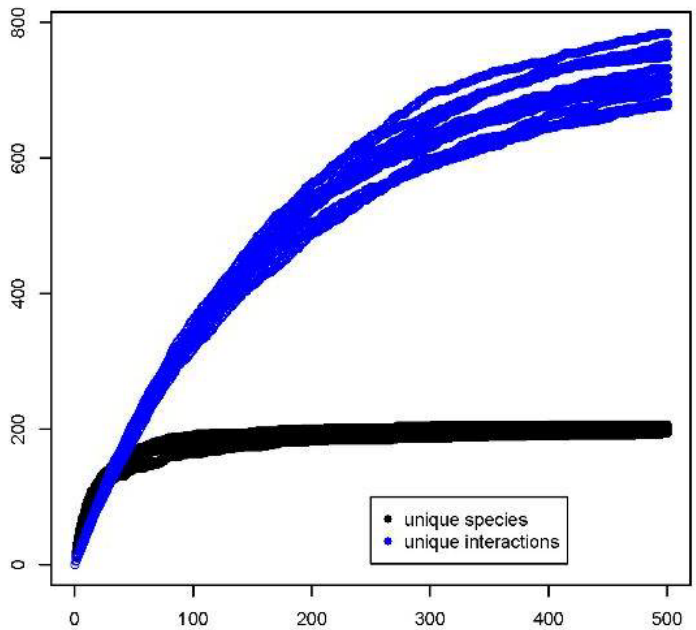

Figure 34: Predictions of species richness and interaction richness from a simulation model (50 runs of the model are depicted here) parameterized with plots at EAFB. For a 1 km2 area, at least 500 plots would be necessary to estimate global interaction richness. Species richness asymptotes at an order of magnitude fewer plots. At smaller scales (1 m^2 to 700 m^2), which are more relevant for plant interactions with insect herbivores and predators, both species and interaction diversity can reach an asymptote within 10 samples, and interactions reach an asymptote before species.

The primary objective of the empirical component was to quantify interaction diversity across a time since fire gradient, to comparatively assess the effect of longer fire return intervals on biotic community interactions and network parameters in longleaf pine forests. The burn gradient was comprised of frequently burned plots (fire return interval (FRI): 1-5 years), intermediately burned plots (FRI: 5-25 years), and infrequently burned plots (FRI: >25 years). Interaction diversity was calculated based on the richness and abundance of links between interacting species (Dyer et al. 2010). Secondly, we investigated how these patterns varied over increasing spatial extents. Diversity was quantified at various hierarchical levels including the local plot level, and at the regional level (plots and general collecting) and aggregated to create a network comprised of all tri-trophic interactions (**Fig 35**).

Regionally, frequently burned plots had greater interaction richness and overall species diversity. In addition, a focus on trophic guilds showed frequently burned plots had greater parasitoid and herbivore species diversity. Parasitoids make up about 15% of the species richness while only 8% in the infrequently burned. This indicates that frequently burned forests have greater biological control with greater parasitoid richness. Furthermore, in a comparison of network parameters, connectance- which is a measure of standardized species interactions, was higher in frequent than in infrequently burned plots. This has ecological relevance as interaction networks with greater connectivity are characterized by higher levels of functional stability within an ecosystem (Thyliankis et al. 2010).

When looking at the plot level scale, alpha interaction diversity was actually greatest in infrequently burned plots; in contrast, beta interaction diversity (turnover of interactions) was highest in frequently burned plots. Taken together, the high degree of interaction turnover is what contributes to greater gamma or regional interaction diversity in frequently burned forests.

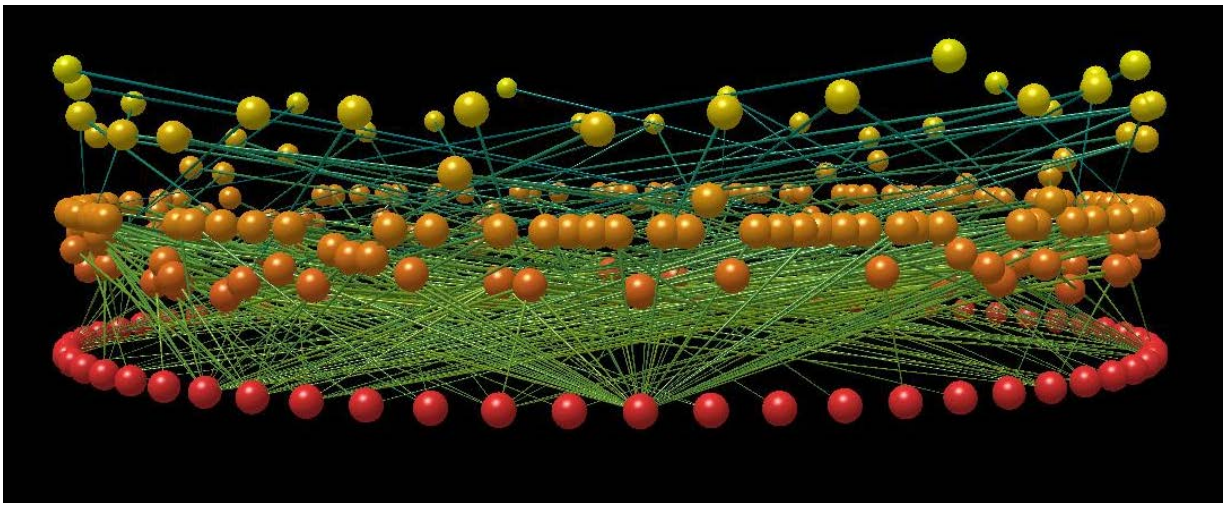

Figure 35: 3-D visualization of entire Florida interaction diversity empirical database. Red nodes represent plants, orange nodes represent herbivores, and yellow nodes represent parasitoid enemies. The colored edges linking nodes together represent bi-trophic (plant-herbivore, herbivore-enemy) and tri-trophic (plant-herbivore-enemy) interactions. Network represents collections compiled from standardized plots and general collecting.

Streamlining Biodiversity Monitoring

We developed a streamlined biodiversity monitoring program at Eglin Air Force Base with efficiency gains and improved methodology to an already existing biodiversity monitoring program. Using existing data, we found spatial and temporal targets in which monitoring efforts are maximized, as well as, recommendations for sampling stratification (location) and intensity plot size and number of samples, **Figs. 36, 37**).

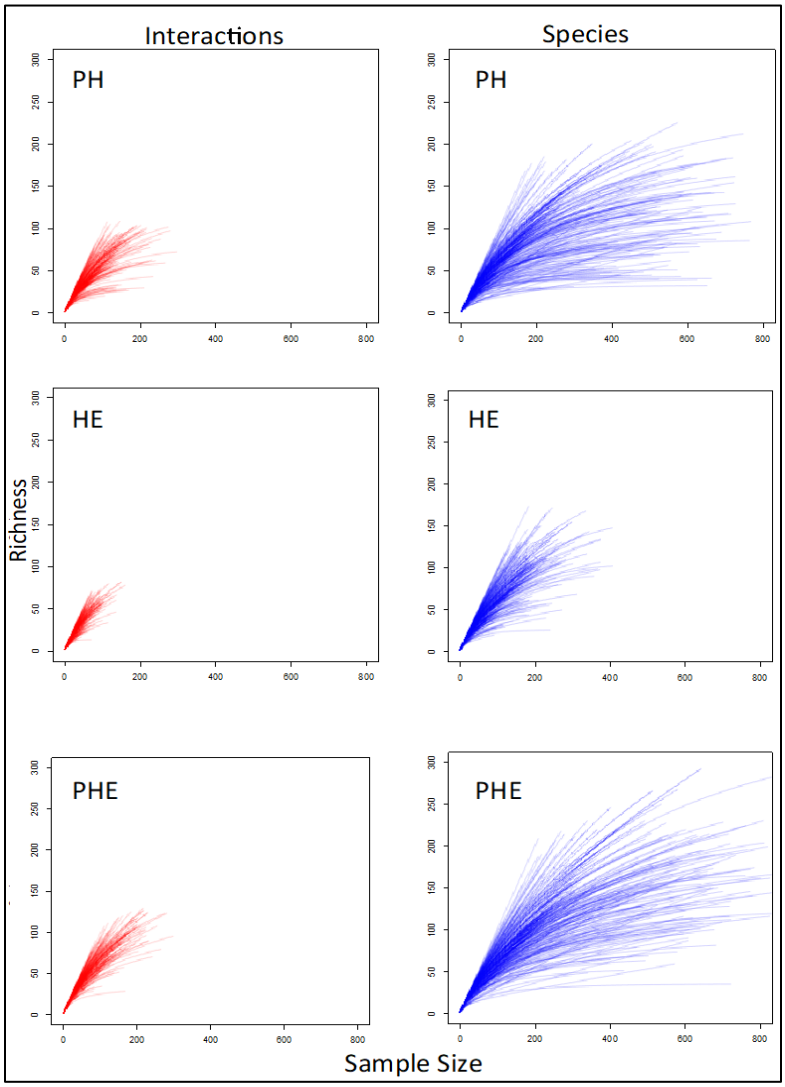

Figure 36: Number of plots to sample for accurate diversity measures. Rarefaction curves are displayed for interactions and species for 500 plant-herbivore-predator communities simulated based on plot data from EAFB. Rarefaction curves were generated for all three networks within each communities: Plant-Herbivore (PH), Herbivore-Enemy (HE), and Plant-Herbivore-Enemy (PHE). PHE networks include all PH and PHE interactions. For a 1 km2 area, at least 500 plots would be necessary to estimate global interaction richness, while species richness asymptotes at an order of magnitude fewer plots. At smaller scales (1 m^2 to 700 m^2), which are more relevant for plant interactions with insect herbivores and predators, both species and interaction diversity can reach an asymptote within 10 samples, and interactions reach an asymptote before species.

Our monitoring program also utilized simulation models parameterized with plot data collected in longleaf pine forests to examine the effectiveness of different sampling methods. Using taxonomic measures of diversity as well as, interactions between plants, herbivores, and natural enemies (Dyer et al. 2010), we calculated diversity indices based on the number of species or interactions and their relative abundance. These indices were transformed into unbiased diversity equivalents, measuring the effective number of species or interactions in samples (Jost 2007). We then performed rarefaction analyses to remove correlations between sample size and measures of

diversity. At smaller scales (1 m^2 to 700 m^2), which are more relevant for plant interactions with insect herbivores and predators, both species and interaction diversity can reach an asymptote within 10 samples, indicating the appropriate number of plots to sample for an accurate measure of diversity (**Fig. 36**).

We also used transformed indices of beta diversity, measuring compositional difference in plant communities between sampling sites. High-levels of beta diversity indicate greater amount of species turnover. Results from our additive partitioning analysis on different components of diversity at increasing spatial scale showed alpha diversity (H') increased with scale, while beta diversity reached an asymptote among 1m^2 plots indicating sampling larger spatial extents adds little to community composition. Therefore, monitoring efficiency will be maximized at the spatial extent where beta diversity begins to reach an asymptote. This point indicates the grain size that best captures representative diversity and can then be used for management objectives such as monitoring programs. Previous to this result, monitoring was being conducted at the 1ha scale, and was highly redundant in terms of diversity representation.

Monitoring at Eglin AFB is typically scheduled the season following management peturbations, such as fire, herbicide application, and timber harvest. We surveyed individual plants within 1m^2 quadrats on a weekly basis post operational prescribed fires in two separate sandhill communities. This chronosequence study indicates that a there should be a minimum of 8 weeks between fire and sampling to accurately measure diversity (**Fig. 37**). In addition, future monitoring frequency will be dependent on the season in which the management event occurred and historical practices.

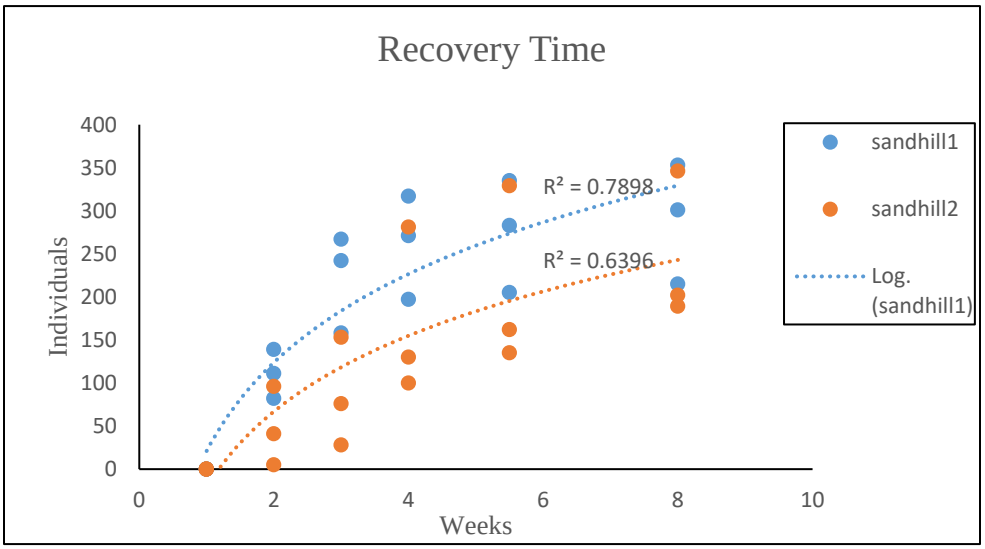

Figure 37: When to sample in relation to disturbances.Monitoring at Eglin AFB is scheduled the season following management. Chronosequence shows that a there should be 8 weeks minimum between fire and sampling to accurately measure diversity.

Conclusions

It is well known that fire is required to maintain healthy longleaf pine ecosystem function, and that frequent fire promotes high plant, arthropod, and functional diversity. Quantifying the spatial pattern of fire-induced mortality is critical for understanding the processes structuring vegetative communities post fire. (Alonso et al. 2006) identified three requirements for explaining the distribution, abundance and diversity of species in a biogeographical (scale-independent) context that are fulfilled by UNTB (Hubbell 2001): first, the plant community must define the random dynamics of species over time, second, one must have a spatial formulation and third, one must consider the fates of discrete individuals which allows the empirical testing of the theory. Our strategy of combining spatially explicit and fine scale fire, fuels and demography measurements with coarser scale measurements of forest structure across the landscape not only allowed us to identify and test mechanisms driving community dynamics, but gave us the framework to make our results relevant to management. These results when coupled with the detailed examination of patterns of diversity through time and space has given us a comprehensive understanding of mechanisms driving diversity, how diversity is distributed and best monitored, and identified new metrics of diversity that should provide sensitive indicators to disturbance and management. We have identified the scales at which patterns of diversity emerge, and thus the appropriate scale for sampling and monitoring of various kinds and dimensions of diversity. We have also identified the mechanisms driving these patterns, namely stochastic demographic dynamics at high fire frequency, and competition as fire becomes less frequent. It is also known that plant diversity, fuel structure, and fire dynamics operate at scales that are too fine to practically guide management of large areas. Management decisions are most often made at the scale of large land blocks. Our coarse-scale study has demonstrated how existing low density LiDAR and high resolution image datasets can be effectively leveraged to improve management of longleaf pine stands at management-relevant scales. We are using our results to build a cross-scale modeling framework that will allow managers to better understand how their actions will affect multiple metrics of diversity. For example, we have been able to link woody fuel distribution, a critical driver of diversity maintenance, to LiDAR derived tree maps. These tree maps could be used to predict how silvicultural treatments will interact with fuels and impact plant diversity. Finally, the inherent flexibility of the spatially explicit rule based core of our model system makes is likely to be useful in other ecosystems given appropriate parameters and initial data. We have met all and in many cases exceeded our objectives as promised in the proposal. Our results also showed that our conceptual framework was appropriate; that is, in the burn plots, neutral dynamics appear to be operative, whereas in fire exclusion plots, deterministic patterns, specifically competitive exclusion of small herbaceous plants occurred. It was surprising how rapidly this process emerged, as soon as the year following fire. We have successfully developed the framework and code of the CA model and have tested hypotheses on community assembly mechanisms. This will provide the foundation for exploration of other disturbance and management impacts. We also used theory to generate not only basic understanding of how diversity is structured over the entire region, but also identified critical elements for accurately measuring and monitoring diversity. We feel the overall success of the project resulted from not just the work of a talented team, but also our approach to organizing and integrating the research activities of such a comprehensive study. What follows are conclusions relevant to the three study areas.

Coarse Scale Studies

We met our original objectives by illustrating the link between canopy structure, the fire regime, and understory vegetation characteristics. Low density aerial LiDAR was a heavily used dataset in this study, where maps were produced that represent landscape-level estimates of tree density, tree heights, basal area, dominant tree species, crown metrics, and stem volume. Furthermore, LiDAR estimates of canopy height distributions were linked to both the long-term ecological monitoring data and Eglin's fire database, as well as our study plots of fuels and groundcover plants. The correlations were successfully used to produce maps of fine fuels, including pine and oak litter, shrubs, and grasses; and coarse woody fuels, including pine cones, which relate to fine-scale mortality; as well as plant species richness. As such, we have illustrated the link between fine-scale fuels and diversity to landscape canopy structure.

We exceeded our objectives by 1) examining two airborne LiDAR datasets of very different resolutions (1 vs. 10 pulses m^{-2}) to provide a large variety of results (individual tree mapping to fine-scale fuel mapping), 2) exploring terrestrial LiDAR approaches to estimating surface fuels and how that information can be combined and compared with aerial platforms, and 3) creating two freely available tools, one web-based (LiDARTreeTop) and one R package (rLIDAR), to run algorithms on input LiDAR data to map individual trees and provide canopy metrics; this was produced using the high density LiDAR provided for only a subset of the area within EAFB.

Fine-Scale Studies

From the fine-scale portion of the study, we met as well as exceeded all our objectives. We captured fine-scale fire radiative energy, and both related that information to specific fuel types, particular those coarse woody fuels (pine cones) that cause individual plant mortality. Plant demography was successfully captured using our $100cm^2$ monitoring protocol within 1 m x 3 m plots, and this was critical for analyzing the relevance of species traits and provide neutral parameters and inputs to the CA model. We captured the fine-scale fuelbed characterisitcs using both field and photogrammetry techniques, and this was linked to the plant monitoring data and 3D fuel rendering. We illustrated that plant community dynamics of 270+ groundcover species can be modeled using neutral-based assumptions. Species richness distributions were successfully simulated in this frequently burned longleaf pine groundcover plant community using simple probability functions, representative of the UNTB. This was done by using four years of fine-scale (10 cm x 10 cm grid) sampling of the groundcover community and across two years of experimental burns. Sampling at this spatial scale represented the scale at which community dynamics occurred and the time-frame of sampling was necessary to quantify the parameters for the neutral CA model. The most difficult parameter to measure and estimate was "immigration" (Lowe and McPeek 2014, Chen 2015). Immigration is characterized by defining the restriction or limitation of dispersal from the species population pool as a whole or metacommunity, e.g. habitat or site of interest. This parameter is particularly important when the species frequency distribution is highly skewed, where there are many rare species. The conundrum of parameterizing immigration can likely be alleviated by simply simulating a large local community, i.e. a large landscape, at a fine resolution. This is supported by the results of the scale effects on size and number of areas simulated; these parameters are generally less sensitive using finer-scaled data.

We exceeded our objectives by 1) developing photogrammetric models of fuels and vegetation to predict groundcover plant diversity, 2) developed a new technique of 3D rendering to create models of individual fuel types and complex fuelbeds.

Patterns of Diversity

From the patterns of diversity portion of the study, we met as well as exceeded all of our objectives. We have identified patterns in numerous measures of diversity across multiple scales, including taxonomic, functional and interactions between plants, arthropods, and their natural enemies. We have optimized the spatial scales that are important to survey alpha and beta diversity for plant and arthropod communities as well as the interactions between them, allowing for identification of the grain size and sampling effort at which to maximize efficiency in monitoring diversity. We found that the optimal plot size for plant diversity was at a fine-scale ($1m^2$), while arthropod and interaction diversity require sampling over a larger spatial extent (30 m diameter, ~700 m^2). This was further supported by combining simulation models and empirical data. We have also documented temporal changes in diversity - for example, we found very different arthropod communities before and after a burn and fire-stage specific effects on trophic diversity**.** In addition, we analyzed 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, which generated informative patterns about the relationship between disturbance and biodiversity.

We exceeded our objectives by 1) finding linkages between small scale patterns in understory plant diversity and coarser scale stand characteristics by identifying a mechanism where overstory derived fuels contribute to plant species richness, 2) developing a framework for maximizing efficiency in biodiversity monitoring, and 3) documenting a novel arthropod adaptation to survival with frequent disturbance.

Implications for Future Research

There are aspects of this work that if continued will contribute substantively to both basic ecological theory and very practical guidance for management of DoD forests. The unified neutral theory of biodiversity has never been tested as effectively and thoroughly as we have done for diversity of all plants and as we are doing for total ecosystem plant-insect diversity. Additionally, the chemical ecology of fire has never been fully explored by collaborations between chemists and ecologists. Our funded work yielded data to examine the null models that comprise neutral theory and to demonstrate how deviations from neutrality are structured by moving away in space and time from fire. This work also provides unprecedented insight into the spatial and temporal scales needed to assess the impact of fire management on maintaining sustainable levels of biodiversity. Our work also laid the ground work for future chemical ecology research to examine how variation in longleaf pine chemistry and variation in plant chemistry across longleaf pine understory plants can contribute to fire intensity and maintenance of plant-insect biodiversity. These are exciting areas of research for fire ecology and for understanding effective management of diverse and interesting ecosystems managed by the Department of Defense

Our study focused on understanding mechanisms driving diversity and community dynamics in pristine habitats. This was crucial for understanding how a fully functioning, intact ecosystem operated. This approach was successful in clarifying how these systems function but also identified topics that could be of interest to DoD land managers. For example, our approach could be used to model the impact of military training on changes in fire behavior and fuels, but would need

further work to incorporate the impact of soil disturbance and vegetation disturbance that occur at multiple scales.

As the scales of disturbance and tree mortality increase, the probability of recruitment for an individual species in the understory will be more influenced by life history traits. Species capable of longer distance dispersal, such as many ruderal species, will likely have a higher probability of recruitment in larger patches of disturbance or mortality (e.g., large canopy gap openings). On the other end of the spectrum, when the disturbance is sufficiently small and irregular (e.g., mortality from smoldering pine cones), the recruitment process is dominated by the surrounding neighborhood of surviving individuals and dispersal syndrome plays a lesser role and random (neutral) dynamics occur more frequently. In the middle of the spectrum, where disturbance is moderate (from e.g. tank tracks) the outcomes are less clear and likely affected by the quality of the very nearby habitat (abundance of herbaceous species) and local fire regime. And, although military training activities represent a range of possible disturbances, experience teaches that these can be large-scale and profound. Soil disturbances that disrupt soil profiles and alter soil structure and topography by compacting and churning mineral soils (e.g., entrenchments, craters, tracks) would likely alter patterns of fire behavior and plant recruitment, which is currently an unexplored area of research. In longleaf pine stands, recruitment and recovery of the groundcover vegetation would depend on unknown interactions determined by plant traits. Community dynamics would be moving in the opposite direction of the Continuum (**Fig. 2**) in which we modeled, from random to deterministic processes. Identifying how these patterns change along this gradient, which operates across time and space, could help guide and possibly speed restoration of disturbed areas. Additional sampling guided by the mechanistic processes we have identified would be necessary and important for demonstrating these technique on multiples sites, as well as assessing their performance and applicability.

We have the foundation for a cross-scale modeling framework that would allow managers to better understand how their actions will affect multiple metrics of diversity. For example, we have been able to link woody fuels distributed on the ground, a critical driver of diversity maintenance, to understory plant species diversity at sub-meter scales, as well as overstory trees at coarser (6-30m) scales, as mapped from LiDAR across EAFB. These tree maps could be used to predict how a silvicultural treatment will interact with fuels and impact plant diversity.

Furthermore, we have the capability to demonstrate a streamlined biodiversity monitoring protocol that can maximize efficiency and ensure the collection of the most relevant data for monitoring longleaf pine diversity. Future validation of these methods at other longleaf pine research sites would be required to develop models that 1) characterize the spatial and temporal patterns of plant diversity at multiple scales; 2) quantify linkages between longleaf pine overstory and understory diversity; and 3) clarify the relationship between fire, fuels and understory composition. The result would be the development of how-to guides for both starting a biodiversity monitoring program from scratch and working with existing programs to leverage long term data sets while improving and streamlining future data collection.

Many aspects of our approach and associated findings, specifically the nested spatial scales of the modeling could be applied to other fundamentally different ecosystems, ranging from grasslands to deserts, after finding appropriate rules and parameter estimates. We have high confidence that

our approach would work in other fire influenced ecosystems. We are interested in expanding our research to examining the impacts of other disturbances on community dynamics; particularly those that could be relevant to DoD land managers, such as timber harvests, hurricane or wind damage, forest pests, as well as fine to coarse scale military training activities. We have developed a template for the development of a modular but unified cross-scale and cross-model (**Fig. 38**) that we are close to completing for longleaf pine at Eglin, but could also be developed with different components.

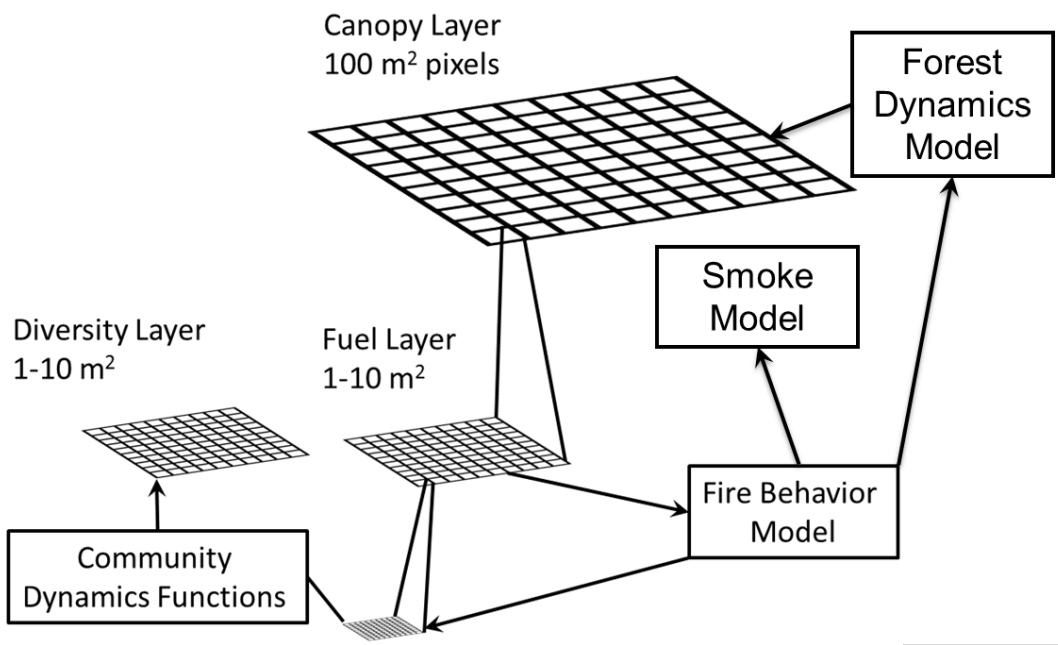

Figure 38. Conceptual model of the "Grand Unification Model" for prescribed fire. The goal is to link in a modeling environment, the coarse-scale to fine-scale processes of the forest (canopy to groundcover) to fuels, fire behavior and smoke modeling. RC-2243 has provided the essential framework (canopy, fuel and diversity layers) but work remains to link process models outside the domain of our study.

We could further expand our framework to include fire behavior, forest stand dynamics, and smoke dynamic models to build a "Grand Unification Model" for prescribed fire (**Fig. 38**). This could act as both a planning and operational tool and would unify interests of fire and timber management. The completion of this model requires the inclusion components beyond our immediate control such as a spatial coupled fire-atmosphere fire behavior model, and smoke and climate models to make a truly unified model, but we are working towards that aim. We are confident that SERDP's investment will continue to provide inspiration and the foundation for new mechanistic understanding of fire, diversity and forest structure that will advance not only basic understanding of the complex theoretical interactions driving these processes, but aid in providing concrete management recommendations for DoD managers.

Literature Cited

Addington, R. N., T. A. Greene, M. L. Elmore, C. E. Prior, and W. C. Harrison. 2012. Influence of herbicide site preparation on longleaf pine ecosystem development and fire management. Southern Journal of Applied Forestry 36:173-180.

Aurenhammer, F., and Klein, R. 1999. Voronoi diagrams. In Handbook on Computational Geometry, edited by J.R. Sack and G. Urrutia, pp. 201–290. Amsterdam: Elsevier.

Chandy, S., Gibson, D. J. and Robertson, P. A. 2006. Additive partitioning of diversity across hierarchical spatial scales in a forested landscape. Journal of Applied Ecology, 43: 792–801.

Barnett, J. P. 1999. Longleaf pine ecosystem restoration: the role of fire. Journal of Sustainable Forestry 9:89-96.

Boyer, W. D. 1998. Long-term changes in flowering and cone production by longleaf pine. Ninth biennial southern silvicultural research conference. USDA Forest Service, Southern Research Station, Clemson, SC.

Butturi-Gomes, D., Petreri, M., Jr., Giacomini, H.C., and P. De Marco, Jr. 2014. Computer intensive methods for controlling bias in a generalized species diversity index. Ecological Indicators 37:90-98.

Breiman, L. 2001. Random forests. Machine Learning, 45: 5–32.

Brockway. 2015. Longleaf Pine Cone Prospects. Available at https://www.srs.fs.usda.gov/longleaf/research/silviculture/longleaf-pine-2015-report.pdf.

Bright, B., E. L. Loudermilk, S. Pokswinski, A. Hudak, and J. J. O'Brien. 2016. Introducing close-range photogrammetry for characterizing forest understory plant diversity and surface fuel structure at fine scales. Canadian Journal of Remote Sensing 42:460-472.

Chave, J. 2004. Neutral theory and community ecology. Ecology letters 7:241-253.

Colwell, R.K., and J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society B: Biological Sciences: 345: 101-118.

Clark, P.J. and Evans, F.C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, 35: 445-453.

Dáttilo, W., and L.A. Dyer. 2014. Canopy Openness Enhances Diversity of Ant–Plant Interactions in the Brazilian Amazon Rain Forest. Biotropica 46: 712-719.

Dell, JE, O'Brien, JJ, Doan, L, Richards, LA, and Dyer, LA. 2017. An arthropod survival strategy in a frequently burned forest. Ecology. doi:10.1002/ecy.1939

Dickinson, M. B., A. T. Hudak, T. Zajkowski, E. L. Loudermilk, W. Schroeder, L. Ellison, R. L. Kremens, W. Holley, O. Martinez, and A. Paxton. 2016. Measuring radiant emissions from entire prescribed fires with ground, airborne and satellite sensors–RxCADRE 2012. International Journal of Wildland Fire 25:48-61.

Drakare, S., Lennon, J.J. and H. Hillebrand. 2006. The imprint of geographical, evolutionary and ecological context on species–area relationships. Ecology Letters 9:215–227.

Dutilleul, P., D. S. Jason, D. Frigon, and P. Legendre. 2000. The Mantel Test versus Pearson's Correlation Analysis: Assessment of the Differences for Biological and Environmental Studies. Journal of Agricultural, Biological, and Environmental Statistics 5:131-150.

Dyer, L.A., Walla, T.R., Greeney, H.F., Stireman III, J.O., and R.F. Hazen. 2010. Diversity of interactions: A metric for studies of biodiversity. Biotropica 42: 281-289

Ellair, D. P., and Platt, W. J. 2013. Fuel composition influences fire characteristics and understorey hardwoods in pine savanna. J Ecol, 101: 192-201.

Espeleta, J., J. West, and L. Donovan. 2004. Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community. Oecologia 138: 341-349.

Fonda, R.W., and Varner, J.M. 2004 Burning characteristics of cones from eight pine species. Northwest Sci. 78: 322–333.

Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., Cizek, L., Coley, P. D., Dem, F., Diniz, I. R., Drozd, P., Fox, M., Glassmire, A., Hazen, R., Hrcek, J., Jahner, J. P., Kama, O., Kozubowski, T. J., Kursar, T. A., Lewis, O. T., Lill, J., Marquis, R. J., Miller, S. E., Morais, H. C., Murakami, M., Nickel, H., Pardikes, N., Ricklefs, R. E., Singer, M. S., Smilanich, A. M., Stireman, J. O., Villamarín-Cortez, S., Vodka, S., Volf, M., Wagner, D. L., Walla, T., Weiblen, G. D., and L.A. Dyer. 2015. Global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences 112: 442-447.

Goovaerts, P. 1997. Geostatistics for Natural Resources Evaluation. Oxford University Press, Inc., New York, NY.

Gonzalez-Benecke, C.A., Gezan, S.A., Samuelson, L.J., Cropper,W.P., Leduc, D.L., andMartin, T.A. 2014. Estimating Pinus palustris tree diameter and stem volume from tree height, crown area and standlevel parameters. Journal of Forestry Research, 25(1): 43–52.

Glitzenstein, J. S., Streng, D. R., and D.D. Wade. 2003. Fire Frequency Effects on Longleaf Pine (Pinus palustris P. Miller) Vegetation in South Carolina and Northeast Florida, USA. Natural Areas Journal 23: 22-37.

Gravel, D., Canham, C. D., Beaudet, M., and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9: 399-409.

Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.

Goutte, C., and Gaussier, E. 2005. A probabilistic interpretation of precision, recall and F-score, with implication for evaluation. Advances in Information Retrieval, Vol. 3408: 345–359.

Heck, Jr., K.L., van Belle, G. and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459-1461.

Hiers, J.K., O'Brien, J.J., Mitchell, R.J., Loudermilk, E.L., and J.M. Grego. 2009. The fuel cell concept: characterizing fine-scale variation in frequently burned longleaf pine forests. International Journal of Wildland Fire 18: 315-325.

Hiers, J.K, O'Brien, J.J., Will, R. and R.J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric Pinus palustris ecosystems. Ecological Applications 17: 806-814.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography (MPB-32). Princeton University Press.

Hudak, A.T., Lefsky, M.A., Cohen, W.B.and M. Berterretche. 2002. Integration of LiDAR and Landsat ETM+ data for estimating and mapping forest canopy height. Remote Sensing of Environment 82: 397-416.

Hudak, A. T., M. B. Dickinson, B. C. Bright, R. L. Kremens, E. L. Loudermilk, J. J. O'Brien, B. S. Hornsby, and R. D. Ottmar. 2016. Measurements relating fire radiative energy density and surface fuel consumption–RxCADRE 2011 and 2012. International Journal of Wildland Fire 25: 25-37.

Hudak, A., B. Bright, S. Pokswinski, E. L. Loudermilk, J. O'Brien, B. Hornsby, C. Klauberg, and C. Silva. 2016. Mapping forest structure and composition from low density lidar for informed forest, fuel, and fire management across Eglin Air Force Base, Florida, USA. Canadian Journal of Remote Sensing 42: 411-427.

Hudak, A.T., Evans, J.S. and A.M.S. Smith. 2009. Review: LiDAR utility for natural resource managers. Remote Sensing 1: 934-951.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

Kiefer, C. M., C. B. Clements, and B. E. Potter. 2012. Application of a mini unmanned aircraft system for in situ monitoring of fire plume thermodynamic properties. Journal of Atmospheric and Oceanic Technology 29: 309-315.

Kirkman, L.K., Barnett, A., Williams, B., Hiers, J.K., Pokswinski, S.M., and R.J. Mitchell. 2013. A dynamic reference model: a framework for assessing biodiversity restoration goals in a fire-dependent ecosystem. Ecological Applications 23: 1574-1587.

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

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5–13.

Lande R, DeVries PJ, and T.R. Walla. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. Oikos 89: 601–605.

Li,W., Guo, Q., Jakubowski,M.K. and Kelly,M. 2012. A new method for segmenting individual trees from the LiDAR point cloud. Photogrammetric Engineering & Remote Sensing, 78(1): 75–84.

Loudermilk, E. L., J. K. Hiers, J. J. O'Brien, R. J. Mitchell, A. Singhania, J. C. Fernandez, W. P. Cropper, and K. C. Slatton. 2009. Ground-based LIDAR: a novel approach to quantify fine-scale fuelbed characteristics. International Journal of Wildland Fire 18: 676-685.

Loudermilk, E. L., J. J. O'Brien, R. J. Mitchell, W. P. Cropper, J. K. Hiers, S. Grunwald, J. Grego, and J. C. Fernandez-Diaz. 2012. Linking complex forest fuel structure and fire behaviour at fine scales. International Journal of Wildland Fire 21: 882-893.

Loudermilk, E. L., G. L. Achtemeier, J. J. O'Brien, J. K. Hiers, and B. S. Hornsby. 2014. High-resolution observations of combustion in heterogeneous surface fuels. International Journal of Wildland Fire 23: 1016-1026.

Loudermilk, E.L., J. Kevin Hiers, S. Pokswinski, J. J. O'Brien, A. Barnett, and R. J. Mitchell. 2016. The path back: oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere 7: 1-14.

Malaeb Z. A., Summers J. K., and B.H. Pugesek. 2000. Using structural equation modeling to investigate relationships among ecological variables. Environmental and Ecological Statistics 7: 93–111.

Matthews, T. J. and R. J. Whittaker. 2014. Neutral theory and the species abundance distribution: recent developments and prospects for unifying niche and neutral perspectives. Ecology and Evolution. 4: 2263-2277.

McGuire, J. P., R. J. Mitchell, E. B. Moser, S. D. Pecot, D. H. Gjerstad, and C. W. Hedman. 2001. Gaps in a gappy forest: Plant resources, longleaf pine regeneration, understory response to tree removal in longleaf pine savannas. Canadian Journal of Forest Research 31:765-778.

Missa, O., C. Dytham, and H. Morlon. 2016. Understanding how biodiversity unfolds through time under neutral theory. Phil. Trans. R. Soc. B 371:20150226.

Mitchell, R. J., J. K. Hiers, J. J. O'Brien, S. B. Jack, and R. T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Canadian Journal of Forest Research 36:2724-2736.

Mitchell, R. J., J. K. Hiers, J. O'Brien, and G. Starr. 2009. Ecological Forestry in the Southeast: Understanding the Ecology of Fuels. Journal of Forestry 107:391-397.

O'Brien, J. J., J. K. Hiers, M. A. Callaham, R. J. Mitchell, and S. B. Jack. 2008. Interactions among overstory structure, seedling life-history traits, and fire in frequently burned neotropical pine forests. AMBIO: A Journal of the Human Environment 37:542-547.

O'Brien, J. J., E. L. Loudermilk, J. K. Hiers, B. Hornsby, S. Pokswinski, A. T. Hudak, D. Strother, E. Rowell, and B. Bright. 2016. Canopy derived fuels drive patterns of in-fire energy release and understory plant mortality in a longleaf pine (*Pinus palustris*) sandhill in Northwest FL, USA. Canadian Journal of Remote Sensing 42:489-500.

O'Brien, J. J., E. L. Loudermilk, B. Hornsby, A. T. Hudak, B. C. Bright, M. B. Dickinson, J. K. Hiers, C. Teske, and R. D. Ottmar. 2016. High-resolution infrared thermography for capturing wildland fire behaviour: RxCADRE 2012. International Journal of Wildland Fire 25:62-75.

Ogle, K., and J.J. Barber. 2008. Bayesian data-model integration in plant physiological and ecosystem ecology. Progress in Botany 69: 281–311.

Olszewski, T.D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos 104:377–387.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289-290.

Pecot, S. D., R. J. Mitchell, B. J. Palik, E. B. Moser, and J. Â K. Hiers. 2007. Competitive responses of seedlings and understory plants in longleaf pine woodlands: Separating canopy influences above and below ground. Canadian Journal of Forest Research 37:634-648.

Pla, L. 2004. Bootstrap confidence intervals for the Shannon biodiversity index: a simulation study. Journal of Agricultural, Biological and Environmental Statistics 9: 42–56

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Tanner, G.W., Hardesty, J.L., Brennan, L.A., and A.R. Litt. 2001. Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. Forest Ecology and Management 148: 63-77.

Pryke, J.S. and Samways, M.J. 2012. Importance of using many taxa and having adequate controls for monitoring impact of fire for arthropod conservation. Journal of Insect Conservation, 16: 177-185.

Rebertus, A.J., Williamson, G.B. & Moser, E.B. 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. Ecology. 70: 60–70.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, accessed Oct. 15 2015, <http://www.R-project.org≥.

Reynoldson, T.B., Norris, R.H., Resh, V.H., Day, K.E., and D.M. Rosenberg. 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. Journal of the North American Benthological Society 16: 833-852.

Ribeiro Jr, P. J. and P. J. Diggle. 2001. geoR: a package for geostatistical analysis R-NEWS. R-NEWS 1:15-18.

Rosenberg, D.K. and K.S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63: 1028–1038.

Rowell, E., E. L. Loudermilk, C. Seielstad, and J. J. O'Brien. 2016. Using simulated 3D surface fuelbeds and terrestrial laser scan data to develop inputs to fire behavior models. Canadian Journal of Remote Sensing 42:443-459.

Silva, C.A., Crookston, N.L., Hudak, A.T., and Vierling, L.A. 2015. rLiDAR: An R package for reading, processing and visualizing LiDAR (Light Detection and Ranging) data, version 0.1, accessed Oct. 15 2015, < http://cran.rproject.org/web/packages/rLiDAR/index.html>.

Silva, C. A., A. T. Hudak, L. A. Vierling, E. L. Loudermilk, J. J. O'Brien, J. K. Hiers, S. B. Jack, C. Gonzalez-Benecke, H. Lee, M. J. Falkowski, and A. Khosravipour. 2016. Imputation of

Individual Longleaf Pine (*Pinus palustris* Mill.) Tree Attributes from Field and LiDAR Data. Canadian Journal of Remote Sensing 42:1712-7971.

Sokolova,M., Japkowicz, N., and Szpakowicz, S. 2006. Beyond accuracy, F-score andROC:Afamily of discriminant measures for performance evaluation. In Advances in Artificial Intelligence, edited by A. Sattar and B.H. Kang, pp. 1015–102. Berlin/Heidelberg: Springer.

Smith, E.P. and G. van Belle. 1984. Nonparametric estimation of species richness. Biometrics, 40: 119-129.

Stage, A.R., and Crookston, N.L. 2007. Partitioning error components for accuracy-assessment of near neighbor methods of imputation. Forest Science, 53(1): 62–72.

Strand, E.K., Robinson, A.P., and S.C. Bunting. 2007. Spatial patterns on the sagebrush steppe/Western juniper ecotone. Plant Ecology 190: 159-173.

Swengel, A.B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity and Conservation. 10:1141-1169.

Tallamy, D.W. 2004. Do alien plants reduce insect biomass? Conservation Biology, 18:1689-92.

Tello, J., Myers, J., Macia, M., Fuentes, A., Cayola, L., Arellano, G., and Jorgensen, P. 2015. Elevational gradients in beta-diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. Plos One, 10(3), e0121458.

Thyliankis, J.M., Laliberte, E., Nielsen, A. and Bascompte, J. 2010. Conservation of species interaction networks. Biological Conservation, 143: 2270-2279

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography, 33, 2-22.

Wahlenberg, W. G. 1946. Longleaf pine: Its use, ecology, regeneration, protection, growth, and management. Charles Lathrop Pack Forestry Foundation, Washington, D.C.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press, United Kingdom.

Wiggers, M. S., L. K. Kirkman, R. S. Boyd, and J. K. Hiers. 2013. Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem. Forest Ecology and Management 310:54-63.

Weisser, WW and Siemann, E. (eds.) 2004. Insects and Ecosystem Function. Springer Publishing, Berlin.

Wulder, M., Niemann, K.O., and Goodenough, D.G. 2000. Local maximum filtering for the extraction of tree locations and basal area from high spatial resolution imagery. Remote Sensing of Environment, 73(1): 103–114.

Zajkowski, T. J., M. B. Dickinson, J. K. Hiers, W. Holley, B. W. Williams, A. Paxton, O. Martinez, and G. W. Walker. 2016. Evaluation and use of remotely-piloted aircraft systems for operations and research—RxCADRE 2012. . International Journal of Wildland Fire.

Appendix A

Peer Reviewed Publications

Butler, B., C. Teske, D. Jimenez, J. O'Brien, P. Sopko, C. Wold, M. Vosburgh, B. Hornsby, and E. L. Loudermilk. 2016. Observations of energy transport and rate of spreads from low-intensity fires in longleaf pine habitat-RxCADRE 2012.

Bright, B., E. L. Loudermilk, S. Pokswinski, A. Hudak, and J. J. O'Brien. 2016. Introducing close-range photogrammetry for characterizing forest understory pland diversity and surface fuel structure at fine scales. Canadian Journal of Remote Sensing 42: 460-472.

Cannon, J. B., J. J. O'Brien, E. L. Loudermilk, M. B. Dickinson, and C. J. Peterson. 2014. The influence of experimental wind disturbance on forest fuels and fire characteristics. Forest Ecology and Management 330:294-303.

Dickinson, M. B., A. T. Hudak, T. Zajkowski, E. L. Loudermilk, W. Schroeder, L. Ellison, R. L. Kremens, W. Holley, O. Martinez, and A. Paxton. 2016. Measuring radiant emissions from entire prescribed fires with ground, airborne and satellite sensors–RxCADRE 2012. International Journal of Wildland Fire 25:48-61.

Dell, JE, O'Brien, JJ, Doan, L, Richards, La, and Dyer, LA. (2017) An arthropod survival strategy in a frequently burned forest. Ecology. DOI:10.1002/ecy.1939.

Dell, JE, Richards, LA, O'Brien, JJ, Loudermilk, EL, Hudak, AT, Pokswinski, SM, Bright, BB, and Dyer, LA. (2017). Fire, Fuels, and Diversity – Overstory Derived Surface Fuels Mediate Plant Species Diversity in Frequently Burned Longleaf Pine Forests. Ecosphere. DOI:10.1002/ecs2.1964.

Dyer, L.A. and D.K. Letourneau. 2013. Can Climate Change Trigger Massive Diversity Cascades in Terrestrial Ecosystems? Diversity 5:1-35.

Hudak, A., B. Bright, S. Pokswinski, E. L. Loudermilk, J. O'Brien, B. Hornsby, C. Klauberg, and C. Silva. 2016. Mapping forest structure and composition from low density lidar for informed forest, fuel, and fire management across Eglin Air Force Base, Florida, USA. Canadian Journal of Remote Sensing 42: 411-427.

Hudak, A. T., M. B. Dickinson, B. C. Bright, R. L. Kremens, E. L. Loudermilk, J. J. O'Brien, B. S. Hornsby, and R. D. Ottmar. 2015. Measurements relating fire radiative energy density and surface fuel consumption – RxCADRE 2011 and 2012. International Journal of Wildland Fire. 25: 25-37.

Hudak, A.T., E.L. Loudermilk and J.C. White. (2016) Introduction to special issue on remote sensing for advanced forest inventory. Canadian Journal of Remote Sensing 42(5): 397-399.

Loudermilk, E.L., J. Kevin Hiers, S. Pokswinski, J. J. O'Brien, A. Barnett, and R. J. Mitchell. 2016. The path back: oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere 7:1-14.

Loudermilk, E.L., Achtemeier, G.L., O'Brien, J.J., Hiers, J.K. 2014. High-resolution observations of combustion in heterogeneous surface fuels. International Journal of Wildland Fire. 23:1016-1026.

Loudermilk, E. L., G. L. Achtemeier, J. J. O'Brien, J. K. Hiers, and B. S. Hornsby. 2014. High-resolution observations of combustion in heterogeneous surface fuels. International Journal of Wildland Fire 23:1016-1026.

O'Brien, J. J., E. L. Loudermilk, J. K. Hiers, B. Hornsby, S. Pokswinski, A. T. Hudak, D. Strother, E. Rowell, and B. Bright. 2016. Canopy derived fuels drive patterns of in-fire energy release and understory plant mortality in a longleaf pine (*Pinus palustris*) sandhill in Northwest FL, USA. Canadian Journal of Remote Sensing. 42: 489-500.

O'Brien, J.J., Loudermilk, E.L., Hornsby, B., Hudak, A.T., Bright, B.C., Dickinson, M.B., Hiers, J.K., Teske, C. and Ottmar, R.D. 2016. High-resolution infrared thermography for capturing wildland fire behavior – RxCADRE 2012. International Journal of Wildland Fire, Special Issue. 25: 62-75.

Rowell, E., E. L. Loudermilk, C. Seielstad, and J. J. O'Brien. 2016. Using simulated 3D surface fuelbeds and terrestrial laser scan data to develop inputs to fire behavior models. Canadian Journal of Remote Sensing 42: 443-459.

Silva, C.A., A.T. Hudak, L.A. Vierling, E.L. Loudermilk, J.J. O'Brien, J.K. Hiers, S.B. Jack, C. Gonzalez-Benecke, H. Lee, M.J. Falkowski and A. Khosravipour. (2016) Imputation of individual longleaf pine (*Pinus palustris* Mill.) tree attributes from field and LiDAR data. Canadian Journal of Remote Sensing 42(5): 554-573.

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

Publications *In Preparation*

Dell, JE, Pokswinski, SM, Richards, LA, and Dyer, LA (2017) Additive partitioning of understory diversity in a longleaf pine forest. Manuscript in preparation.

Dell, JE, Richards, LA, and Dyer, LA. (2017) Quantifying the effects of burning on the diversity of arthropods in a fire-adapted longleaf pine (*Pinus palustris*) forest. Manuscript in preparation.

Loudermilk, Dyer, O'Brien, Pokswinski, Hudak, Hornsby, Dell, Richards, Goodrick, Hiers. Fine-scale neutral dynamics in longleaf pine ground cover. Manuscript in preparation.

Lumpkin, W, Pardikes, N, and L.A. Dyer, LA. Trophic interaction diversity maintained by disturbance: a simulation model parameterized by ecosystems along disturbance and species diversity gradients. Manuscript in preparation.

O'Brien, JJ, Hiers, JK, Loudermilk, EL, Dell, JE, Richards, LA, Dyer, LA, and Cutts, R. (2017) Exorcising natural fire management. Manuscript in preparation.

O'Brien, Hornsby, Loudermilk, Pokswinski. Variation in fire intensity as driven by within-stand overstory structure. Manuscript in preparation.

O'Brien, Loudermilk, Dyer, Pokswinski, Richards. The interaction of fire, the lack of fire and plant life history traits in affecting community assembly in a pine forest dependent on frequent fire. Manuscript in preparation.

Presentations, Workshops, & Software Tools

PI O'Brien and collaborator Loudermilk co-organized an ***Organized Oral Session*** *at the 2017* ***Ecological Society of America*** *conference in Portland, OR. This session, entitled "Linking Fire, Fuels, and Biological Diversity" was designed exclusively to present results associated with this SERDP project. Following are the ten presentation citations for this OOS:*

Dell, J., Richards, L.A., O'Brien, J.J., Loudermilk, E.L., Pokswinski, S., Hudak, A., Bright, B., Hiers, J.K., Williams, B.W., Dyer, L.A., Understanding the contribution of litter type to ground cover plant diversity in a frequently burned forest. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Hornsby, J.J., O'Brien, J.J., Loudermilk, E.L., Pokswinski, S. Ecologicaly relevant measurements of fire behavior for understanding fire effects. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Hudak, A., Bright, B., Pokswinski, S., Loudermilk, E.L., O'Brien, J.J., Hornsby, B.S, Klauberg, C., Silva, C. Longleaf pine overstory structure constrains fine-scale dynamics in fuels, fire, and plant species diversity. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Loudermilk, E.L., O'Brien, J.J., Dyer, L.A., Pokswinski, S., Hornsby, B.S., Hudak, A., Richards, L.A., Dell. J. Neutral plant community assembly in a frequently burned ecosystem: A spatial simulation approach. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

O'Brien, J.J., Loudermilk, E.L., Dyer, L.A., Pokswinski, S., Hornsby, B.S., Richards, L.A., Dell. J., Hudak, A. The interaction of fire, the lack of fire and plant life history traits in affecting community assembly in a pine forest dependent on frequent fire. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Pokswinski, S., Hiers, J.K., Loudermilk, E.L., O'Brien, J.J., Dyer, L.A., Dell, J., Richards, L., Hudak, A., Hornsby, B., Bright, B. Ecological concepts informing management decisions: A case study on how multi-decadal datasets can cause management paradigm shifts. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Richards, LA. Bugs and fire: Patterns of arthropod diversity in frequently burned longleaf pine. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Rowell, E., Seielstad, C., Loudermilk, E.L., O'Brien, J.J., Hiers., J.K. Characterization of fine-scale fuelbeds using terrestrial laser scanning and 3D simulation to link tree stand structure and biodiversity. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Salcido, D, Dyer, LA, Richards, LA and Dell, JE Chemically mediated tri-trophic interaction diversity along a time since fire gradient. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Silva, C., Hudak, A., Rowell, E., Seielstad, C., Klauberg, C., Bright, B., Loudermilk, E.L., O'Brien, JJ. Comparison of terrestrial and airborne LiDAR derived crown metrics for describing forest structure at Eglin Air Force Base, Florida, USA. Organized Oral Session: Linking Fire, Fuels, and Biological Diversity. Ecological Society of America Conference, Portland, OR. August 2017. (oral presentation, published abstract)

Additional presentations & workshops:

Bright B.C., Hudak, A.T., Loudermilk, E.L., Pokswinski, S.M., O'Brien, J.J. 2016. Moderate and fine scale measurement of vegetation and fuels in a longleaf pine forest using 3D point cloud data. University of Idaho Geography Seminar, Moscow, ID.

Bright, B., Loudermilk, E.L., Pokswinski, S., Hudak, A., O'Brien. J. Characterizing fine-scale understory plant diversity and fuels from three-dimensional photogrammetry points. Organized Oral Session: 3D Characterization of Canopy Structure using LiDAR and New Technologies. June 2015. Canadian Symposium of Remote Sensing, St. John's, Newfoundland and Labrador, Canada.

Dell, J.E., L.A. Richards, and L.A. Dyer. Quantifying the effects of burning on the diversity of arthropods in a fire-adapted longleaf pine forest. Association for Fire Ecology's 6th International Fire Ecology and Management Congress, San Antonio, Texas, 16-20, Nov 2015. (poster presentation, published abstract)

Dell, J.E., L.A. Richards, and L.A. Dyer. Quantifying the effects of burning on the diversity of arthropods in a fire-adapted longleaf pine (*Pinus palustris*) forest. Ecological Society of America's 100th Annual Meeting, Baltimore, Maryland, 9-14 Aug 2015. (poster presentation, published abstract)

Dickinson, M. B., Hudak, A. Zajkowski, T., Loudermilk, E. L., Schroeder, W., Ellison, L., Kremens, R. L., Holley, W., Martinez, O., Paxton, A., Bright, B., O'Brien, J. J., Hornsby, B., Ichoku, C., Faulring, J., Gerace, A., Peterson, D., Mauseri, J. 2014. Ground, Airborne, and Satellite Measurements of Fire Radiative Power - Cross-Scale Evaluation with RxCADRE DataAFE/IAWF Conference on Large Wildland Fires, Missoula, Montana, 19-23. May 2014. (poster presentation, published abstract).

Hudak, A.T., B.C. Bright, A. Kato, Y. Hayakawa, E.M. Rowell, R.D. Ottmar, E.L. Loudermilk, J.J. O'Brien and L.M. Moskal. Spatially explicit estimation of fuel consumption from pre- and post-fire traditional and point cloud measurements of fuels. Symposium on Systems Analysis in Forest Resources (SSAFR), Suquamish, Washington, 28-30 Aug 2017. (oral presentation, published abstract).

Hudak, A.T., B.C. Bright, S.M. Pokswinski, E.L. Loudermilk, J.J. O'Brien, B.S. Hornsby, C. Klauberg and C.A. Silva. Mapping forest structure and composition from low density lidar for informed forest, fuel, and fire management at Eglin Air Force Base, Florida, USA.

Eglin Biodiversity Monitoring Workshop, Jackson Guard, Eglin Air Force Base, Niceville, Florida, 4 Apr 2017. (oral presentation).

Hudak, A.T., Bright, B.B., Pokswinski, S.M., Loudermilk. E.L., O'Brien. Longleaf pine forest overstory, understory, and surface vegetation structure as characterized from airborne LiDAR and field plot data. International Association of Landscape Ecology – U.S. Chapter, Asheville, NC. April 2016. (oral presentation)

Hudak, A.T., C.A. Silva, B.C. Bright, E.L. Loudermilk, E. Rowell, A. Kato, J.J. O'Brien and L.A. Vierling. Research: Multi-scale relationships between vegetation, fuels, and fire. 3rd International Workshop on LiDAR Tools for Forestry Applications, Graduate School of Horticulture, Chiba University, Matsudo, Japan, 3 Dec 2015. (oral presentation).

Hudak, A.T., C.A. Silva, B.C. Bright, E.L. Loudermilk, A. Kato, J.J. O'Brien and L.A. Vierling. Lidar tools and techniques for 3D vegetation structure characterization at multiple scales. 23rd Center for Environmental Remote Sensing International Symposium, Chiba University, Chiba, Japan, 1-2 Dec 2015. (oral presentation, published abstract).

Hudak, A.T. Bright, B., Loudermilk, E.L., O'Brien, J.J., Silva, C., Vierling, L., Upscaling tree density measures from environmental monitoring plots across Eglin Air Force Base using low density lidar. Organized Oral Session: 3D Characterization of Canopy Structure using LiDAR and New Technologies. June 2015. Canadian Symposium of Remote Sensing, St. John's, Newfoundland and Labrador, Canada.

Hudak, A.T., M. Dickinson, R. Kremens, B. Bright, E.L. Loudermilk, B. Hornsby, J. O'Brien, R. Ottmar, K. Satterberg, E. Strand. 2014. Landscape-level relationship of fire radiative energy density to surface fuel loads. AFE/IAWF Conference on Large Wildland Fires, Missoula, Montana, 19-23 May 2014. (oral presentation, published abstract).

Hudak, A.T., K. Satterberg, M. Dickinson, R. Kremens, B. Bright, E.L. Loudermilk, J. O'Brien, E. Strand, R. Ottmar. 2013. Fire radiative power and fire radiative energy estimated from multi-temporal airborne WASP thermal infrared images of active fire at Eglin Air Force Base, Florida. American Geophysical Union Fall Meeting, San Francisco, CA. (poster presentation, published abstract)

Hudak, A.T., R.D. Ottmar, R.E. Vihnanek and C.S. Wright. (2013) Relationship of post-fire ground cover to surface fue Hudak, A.T., R.D. Ottmar, R.E. Vihnanek and C.S. Wright. (2013) Relationship of post-fire ground cover to surface fuel loads and consumption in longleaf pine ecosystems. *Proceedings of the 4th Fire Behavior and Fuels Conference*, Raleigh, North Carolina, 6 p.l loads and consumption in longleaf pine ecosystems. Proceedings of the 4th Fire Behavior and Fuels Conference, Raleigh, North Carolina, 6 p.

Hudak, A.T., C.A. Silva, B.C. Bright, E.L. Loudermilk, E. Rowell, A. Kato, J.J. O'Brien and L.A. Vierling. Research: Multi-scale relationships between vegetation, fuels, and fire. 3rd International Workshop on LiDAR Tools for Forestry Applications, Graduate School of Horticulture, Chiba University, Matsudo, Japan, 3 Dec 2015. (oral presentation).

Hudak, A.T., C.A. Silva, B.C. Bright, E.L. Loudermilk, A. Kato, J.J. O'Brien and L.A. Vierling. Lidar tools and techniques for 3D vegetation structure characterization at multiple scales. 23rd Center for Environmental Remote Sensing International Symposium, Chiba University, Chiba, Japan, 1-2 Dec 2015. (oral presentation, published abstract).

Keough, B., C.A. Silva, A.T. Hudak, V. Liesenberg, E. Rowell, C. Seielstad and L.A. Vierling. Comparison of individual tree counts from both airborne and terrestrial lidar systems analyzed individually and combined in a Web-LiDAR environment. Brazilian Symposium on Remote Sensing, João Pessoa, Paraíba, Brazil, 25-29 Apr 2015. (oral presentation, published abstract).

Loudermilk, E.L. Remote sensing for fire and fire effects. Course lecture in: Rx510, Advanced Fire Effects. January, 2017. (oral presentation)

Loudermilk, E.L. Fire ecology in longleaf pine. Lecture for Earthwatch group at Solon Dixon Forestry Education Center, Andalusia, AL. October 2016. (oral presentation)

Loudermilk, E.L. Remote sensing for fire and fire effects. Course lecture in: Rx510, Advanced Fire Effects. January, 2016. (oral presentation)

Loudermilk. E.L., O'Brien, J.J., Hudak, A.T., Dyer, L, Pokswinski, S.M. Landscape patterns of fine-scale plant diversity: Linking overstory structure and site characteristics to the understory community. International Association of Landscape Ecology – U.S. Chapter, Asheville, NC. April 2016. (oral presentation)

Loudermilk. E.L., O'Brien, J.J., Dyer, L, Pokswinski, S.M., Hudak, A.T., Hornsby, B. Does fire behavior drive community assembly through neutral processes in frequently burned ecosystems? Association for Fire Ecology, San Antonio, TX. November 2015. (oral presentation)

Loudermilk, E.L., Rowell, E., Hudak, A., O'Brien, J.J., Seilestad, C., Pokswinski, S., Lee, D. 3D modeling of understory fuels determined by overstory structure. Organized Oral Session: 3D Characterization of Canopy Structure using LiDAR and New Technologies. June 2015. Canadian Symposium of Remote Sensing, St. John's, Newfoundland and Labrador, Canada. (oral presentation)

Loudermilk. E.L., O'Brien, J.J., Dyer, L, Pokswinski, S.M., Hudak, A.T., Hornsby, B. Does fire behavior drive community assembly through neutral processes in frequently burned ecosystems? Association for Fire Ecology, San Antonio, TX. November 2015. (oral presentation)

Loudermilk, E.L., O'Brien, J.J. 2013. Bringing Fire Science into the 21st Century: Using Advanced Technology to Understand Fire Behavior and Fire Effects at Relevant Scales. Forest Service Seminar. USDA Forest Service, Southern Research Station, Athens, GA.

O'Brien, J.J. Fire: Past, Present, Future. University of Georgia Odum School Conservation Seminar. September 13, 2017

O'Brien,J.J. The Ecology of Fuels. Northeastern Fire Exchange Webinar, July 12, 2017

O'Brien,J.J. The Ecology of Fuels. Northeastern Fire Exchange Webinar, May , 2016

O'Brien. Why Frequently Burned Pine Ecosystems are Susceptible to Catastrophic Shifts in Ecological Regimes. Association for Fire Ecology, San Antonio, TX. November 2015. (oral presentation)

O'Brien, J.J., Loudermilk, E.L. Hornsby, B., Hudak, A., Bright, B., Dyer, L., and Pokswinski, S. Canopy derived fuels drive patterns of in-fire energy release and plant community assembly in longleaf pine (*Pinus palustris*) woodlands. Organized Oral Session: 3D

Characterization of Canopy Structure using LiDAR and New Technologies. June 2015. Canadian Symposium of Remote Sensing, St. John's, Newfoundland and Labrador, Canada. (oral presentation)

O'Brien, J.J., Hornsby, B., Loudermilk, E.L. 2013. RxCADRE: Fine-Scale Spatially Explicit Fire Measurements. 4th Fire Behavior and Fuels Conference. Raleigh, NC. (oral presentation, published abstract).

O'Brien, J.J., Dell, J.E., Richards, L., Hudak, A., Silva, C., Loudermilk, E.L., Pokswinski, S. 2017. Patterns and Processes: Fire and Diversity in Longleaf at Eglin AFB. April 4, Jackson Guard, FL.

Ottmar, R.D., R.E. Vihnanek, C.S. Wright and A.T. Hudak. (2013) Ground measurements of fuel and fuel consumption from experimental and operational prescribed fires at Eglin Air Force Base, Florida. Proceedings of the 4th Fire Behavior and Fuels Conference, Raleigh, North Carolina, 8 p.

Rowell, E., Seielstad, C., Loudermilk, E.L., O'Brien, J.J., Seilestad, C., Pokswinski, S., Lee, D. Modeling 3D understory structure for use in physics-based fire behavior simulations. Organized Oral Session: 3D Characterization of Canopy Structure using LiDAR and New Technologies. June 2015. Canadian Symposium of Remote Sensing, St. John's, Newfoundland and Labrador, Canada. (oral presentation)

Silva, C.A., A.T. Hudak and L.A. Vierling. Use of airborne and terrestrial lidar for mapping individual tree attributes. Eglin Biodiversity Monitoring Workshop, Jackson Guard, Eglin Air Force Base, Niceville, Florida, 4 Apr 2017. (oral presentation).

Silva, C.A., A.T.. Hudak, L.A. Vierling, E.L. Loudermilk, J.J. O'Brien, A. Poznanovic, M.A. Falkowski, C.A. Gonzalez-Benecke, S. Jack and H. Lee. Individual tree detection from LiDAR-derived canopy height models (CHM) in longleaf pine forest. 36th Canadian Symposium on Remote Sensing, St. John's, Newfoundland, Canada, 8-11 Jun 2015. (oral presentation, published abstract).

Silva, C.A., A.T. Hudak, L.A. Vierling, E.L. Loudermilk and J.J. O'Brien. Web-based applications for LiDAR data processing and visualizing trees at the plot level. 36th Canadian Symposium on Remote Sensing, St. John's, Newfoundland, Canada, 8-11 Jun 2015. (poster, published abstract).

Silva, C.A., A.T. Hudak, N.L. Crookston, C.K. Silva and V. Liesenberg. Extracting individual trees and lidar metrics using a web-lidar forest inventory application. Part 3: The 3D Clustertree Tool. XI Seminários de Atualização de Sensoriamento Remoto e Sistemas de Informações Geográficas Aplicados à Engenharia Florestal, Curitiba, Paraná, Brazil, 14-16 Oct 2014. (poster, published abstract).

Silva, C.A., A.T. Hudak, N.L. Crookston, C.K. Silva and V. Liesenberg. Visualizing and generating lidar metrics using a web-lidar forest inventory application. Part 2: The Lasmetrics Tool. XI Seminários de Atualização de Sensoriamento Remoto e Sistemas de Informações Geográficas Aplicados à Engenharia Florestal, Curitiba, Paraná, Brazil, 14-16 Oct 2014. (poster, published abstract).

Silva, C.A., A.T. Hudak, N.L. Crookston, C.K. Silva and V. Liesenberg. Detecting individual trees using a web-lidar forest inventory application. Part 1: The Treetop Tool. XI Seminários de

Atualização de Sensoriamento Remoto e Sistemas de Informações Geográficas Aplicados à Engenharia Florestal, Curitiba, Paraná, Brazil, 14-16 Oct 2014. (poster, published abstract).

Silva, C.A., A. Hudak, R. Liebermann, K. Satterberg and L.C.E. Rodriguez. LiDAR remote sensing for individual tree processing: A comparison between high and low pulse density in Florida, USA. Brazilian Remote Sensing Symposium, Foz do Iguaçu, Paraná, Brazil, 13-18 Apr 2013. (poster, published abstract).

Silva, C.A., A. Hudak, R. Liebermann, K. Satterberg and L.C.E. Rodriguez. Evaluation of digital elevation models (DEMs) from high and low pulse density in LiDAR data. Brazilian Remote Sensing Symposium, Foz do Iguaçu, Paraná, Brazil, 13-18 Apr 2013. (poster, published abstract).

Sponsored workshops:

Eglin Biodiversity Monitoring Workshop (with contributions from Jane Dell, Scott Pokswinski, Lora Richards, Carlos Silva, Ben Hornsby, Joe O'Brien, Louise Loudermilk) at Jackson Guard, Eglin Air Force Base, Niceville, Florida, sponsored by a Strategic Environmental Research and Development Program grant, 4 Apr 2017.

Workshop: Web-LiDAR and rLiDAR tools to estimate individual tree attributes (with contributions from C.A. Silva, N.L. Crookston, L.A. Vierling, E.L. Loudermilk, J.J. O'Brien and A. Kato), 3rd International Workshop on LiDAR Tools for Forestry Applications, Graduate School of Horticulture, Chiba University, Matsudo, Japan, sponsored by the Japanese Environmental Research and Technology Development Fund, 3 Dec 2015.

Predictive Modeling of Biomass and other Forest Structure Attributes from Field Data and LiDAR Metrics (with contributions from Carlos A. Silva and Michael M. Keller), EMBRAPA-CNPM, Campinas, São Paulo, Brazil, 4-5 May 2015.

LiDAR Data Processing Workshop for Fuel Applications, Joint AFE/IAWF Conference on Large Wildland Fires, Missoula, Montana (co-taught with Dr. Nancy Glenn), co-sponsored by a NSF Geoinformatics Program grant, 19 May 2014.

Software Tools:

20 Apr 2014. rLiDAR. University of Idaho PhD student Carlos Silva, with help from Nick Crookston and under Hudak's direction, developed an R package to detect tree locations from a canopy height model for stem mapping, height estimation, and tree crown delineation, along with utilities such as estimation of projected crown area, crown volume, generation of crown metrics, and related visualization tools (http://cran.r-project.org/web/packages/rLiDAR/index.html/).

4 Mar 2014. Web-LiDAR. International Programs intern Carlos Silva, with help from Nick Crookston and under Hudak's supervision, developed an interactive, web-based tool for users to process lidar point cloud data to identify tree locations for stem mapping, as well as other tree-level processing and visualization tools (http://forest.moscowfsl.wsu.edu:3838/Web-LiDAR/).

Textbook or Book Chapters

Bigelow, S.W, Stambaugh, M.C., O'Brien, J.J., Larson, A.J., and Battaglia, M.A. 2017. Longleaf Pine Restoration in Context: Comparisons of Frequent-Fire Forests. *In:* Ecological Restoration of Longleaf Pine. Editors: K. Kirkman, S. Jack. CRC Press.

Dyer, L.A., T.J. Massad, and M.L. Forister. 2014. The question of scale in trophic ecology. Chapter 13 *In:* Trophic Ecology: Bottom-Up and Top-Down Interactions across Aquatic and Terrestrial Systems. Editors: T. Hanley, K. La Pierre. Cambridge University Press, Cambridge, MA.

Loudermilk, E.L., J. Kevin Hiers, and J. J. O'Brien. 2017. The role of fuels for understanding fire behavior and fire effects in longleaf pine ecosystems. *In:* Ecological Restoration of Longleaf Pine. Editors: K. Kirkman, S. Jack. CRC Press.