

# FINAL REPORT

Understanding Species Persistence in Complex Landscapes with  
a Long-Term Metapopulation Study of Rare Flora

SERDP Project RC-2707

JANUARY 2020

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<b>14. ABSTRACT</b> Management of rare species is limited by an understanding of long-term population dynamics. We investigated factors affecting population persistence of long-lived plant species at Fort Bragg using a 23-year monitoring dataset on 1,396 populations of 41 rare species. Across all study species, populations have higher probabilities of persistence if they experience more frequent fires, occur under lower canopy cover, are more highly connected to other populations, occupy a larger area, or occur in upland habitats. There was substantial diversity in species response to fire and canopy cover, necessitating species-specific management where adequate knowledge is available and additional detailed studies where knowledge is still insufficient to inform management. Fire frequency, canopy cover, and metapopulation structure, three factors found to influence population persistence, represent a continuum of management options in terms of resource investment. Prescribed burning is likely the least costly and would yield the greatest overall benefits. Where tree density exceeds a level where low-intensity fires can effectively control canopy cover, mechanical thinning is the second option. Enhancing metapopulation structure by targeted population reintroduction and augmentation represents the third and most costly management option.					
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## **Acronyms**

CART – classification and regression trees

CJS – Cormack-Jolly-Seber model

DEM – Digital Elevation Model

DoD – Department of Defense

DSM – Digital Surface Model

ESA – Endangered Species Act

ETM+ - Enhanced Thematic Mapper Plus

GIS – Geographic Information System

GPS – Global Positioning System

GLM – generalized linear model

GLMM – generalized linear mixed models

Ha – hectare

LDMC – leaf dry matter content

LiDAR – Light Detection and Ranging

MARPS – Monitoring and Assessment of Rare Plant Species

MIRBI – Mid Infrared Burn Index

NDVI – Normalized Difference Vegetation Index

NIR – near infrared

OLI – Operational Land Imager

OOB – out-of-bag

RF – Random Forest

SLA – specific leaf area

SON – Statement of Need

SWIR – shortwave infrared

TES – Threatened and Endangered Species

TM – Thematic Mapper

WUE – water use efficiency

## **Keywords**

Cormack-Jolly-Seber, Bayesian, fire, longleaf pine, *Pinus palustris*, rare plants, population dynamics

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## Abstract

**Objectives:** Long-term datasets are particularly important in the ecological sciences because they allow for the integration of data collected across variable biotic and abiotic conditions. Our overall objective was to investigate factors affecting population persistence of long-lived plant species using a long-term monitoring dataset. Specifically, we investigated the effects of fire frequency, canopy cover, metapopulation structure, and functional traits on the persistence of 1,396 populations of 41 rare plant species at Fort Bragg over 23 years.

**Technical Approach:** We used the Fort Bragg Monitoring and Assessment of Rare Plant Species (hereafter MARPS) database, which contains over 32,000 population-years of data collected over four surveys from 1991-93, 1998-99, 2005-06, and 2012-14. We modeled population persistence using a Cormack-Jolly-Seber (CJS) mark-recapture model in a Bayesian framework which took into account imperfect detection. We modeled the fire history of each population by classifying atmospherically corrected Landsat images for the time period 1991-2014 with the mid-infrared burn index (MIRBI) and a Random Forest (RF) algorithm. We modeled canopy cover for the years 1991-2014 in a manner similar to our approach to modeling the fire history, using Landsat imagery, LiDAR data collected in 2012, and a RF algorithm. We quantified metapopulation structure for each species with  $\geq 10$  populations using the connectivity parameter ( $S$ ) from Hanski's incidence function model. For a subset of species, we acquired data for seven functional traits that have been associated with plant performance in our study system. We analyzed the relationship between population persistence and fire frequency, canopy cover, metapopulation structure, area, and functional traits using Generalized Linear Mixed Models (GLMMs) with a binomial error structure and a logit link function that was embedded in a CJS model within a Bayesian framework. Finally, we explored the additional insights gained via the long-term dataset by comparing results from 1991-2014 to data collected from 1991-1999.

**Results:** Our results confirm that long-term persistence of rare plant populations in the longleaf pine ecosystem is influenced by fire frequency, canopy cover, population area, population connectivity, and hydrologic position. Across all study species, populations have higher probabilities of persistence if they experience more frequent fires, occur under lower canopy cover, are more highly connected, occupy a larger area, or occur in upland habitats. While no single functional trait was found to be correlated with population persistence, there were interactions between fire frequency and SLA, and canopy cover and onset of flowering.

**Benefits:** Fire frequency, canopy cover, and metapopulation structure, three factors that influence population persistence on Fort Bragg, represent a continuum of management options in terms of resource investment. Burning management units according to a schedule is likely the least costly in terms of resource investment and would likely yield the greatest overall benefits. If management units are not burned on a frequent (i.e. 3-yr) interval and woody vegetation is allowed to escape the fire trap and enter the midstory and canopy, mechanical thinning is the second option. Enhancing metapopulation structure by targeted population reintroduction and augmentation represents the third and most costly management option. While overall trends in the data were strong, the results also identified substantial diversity in species response to fire and canopy cover, necessitating species-specific management where adequate knowledge is available and additional detailed studies where knowledge is still insufficient to inform management. This is especially relevant for federally listed species. Additionally, we have confirmed the value and benefit of long-term data for elucidating important drivers of rare plant population persistence in our study system.

# Executive Summary

## Introduction

Department of Defense lands harbor a higher density of threatened and endangered species (TES) than any other federal agency (Stein et al. 2008), with the majority of these species being plants. Understanding and preventing local extinction of rare species is of great relevance to DoD resource managers as federal listing under the Endangered Species Act (ESA) can increase the cost of species management and reduce access to training lands. The training and testing mission of DoD installations is sustained through prudent, science-driven, long-term management of their natural resources including the threatened, endangered and at-risk species that may be dependent upon this public land base (DoD Instruction 4715.03). However, for many listed and at-risk plants, evaluating local extinction risk is complicated by the long lifespan and slow dynamics of most species. This necessitates taking a more long-term approach to monitoring, as short-term dynamics may not be indicative of a species long-term prospects.

## Objective

Long-term datasets are particularly important in the ecological sciences because they allow for the integration of data collected across variable biotic and abiotic conditions. Unfortunately, most studies are short-term (i.e. less than five years), so many of the inferences drawn from them may be limited to the conditions at the time of the study. Since 1991, the Endangered Species Branch of Fort Bragg has surveyed all known plant populations of federally-listed species and federal species of concern, at intervals of roughly seven years, including 1,396 populations of 41 plant species. This information is collated in a Monitoring and Assessment of Rare Plant Species (hereafter MARPS) database. Using the first two of these surveys, Gray et al. (2003) undertook an analysis of population dynamics to test the following hypotheses: 1) prescribed fire reduces population extirpation rates, 2) fire increases population size, 3) populations persistence is positively correlated with population size, and 4) plant functional groups differ in their response to fire frequency. Since this initial analysis, two additional surveys have been undertaken, thereby increasing by 3-fold the duration of the study.

Our overarching research objective was to investigate factors affecting population persistence of long-lived plant species using this long-term monitoring dataset. To meet our overarching research objective, we investigated the effects of fire frequency, canopy cover, metapopulation structure, and species functional traits on persistence of rare plant populations. Specifically, we explored the four objectives and associated hypotheses listed in Table 1.

**Table 1: Research objectives and hypotheses.**

<b>Objectives and Hypotheses</b>	
<b>Objective 1: Verify the effects of fire management on plant population persistence</b>	
<i>H1: Population persistence is positively correlated with fire frequency.</i>	
<b>Objective 2: Verify the effects of canopy cover on plant population persistence</b>	
<i>H2: Population persistence is negatively correlated with canopy cover.</i>	
<b>Objective 3: Verify the effects of metapopulation structure on plant population persistence</b>	
<i>H3: Population persistence is negatively correlated with population isolation.</i>	
<b>Objective 4: Verify the effects of functional traits on plant population persistence</b>	
<i>H4: Population persistence is correlated with species function traits.</i>	

## **Technical Approach**

*Monitoring and Assessment of Rare Plant Species Database:* For over 20 years, the Endangered Species Branch of Fort Bragg has monitored 1,396 populations of 41 rare plant species, resulting in a unique database that has over 32,000 population-years of data and is putatively the largest, longest, and most comprehensive undertaken on CONUS military lands. This database offers a rich resource for understanding the drivers of local extinction. The Fort Bragg MARPS database consists of four surveys conducted from 1991-93, 1998-99, 2005-06, and 2012-14. For the first survey, a systematic search for rare plant populations was performed by trained field botanists walking transects over the installation and recording the location and extent (i.e. area) of each population. Populations are defined as discrete entities separated by minimum of 0.8 km (Gray et al. 2003). Subsequent surveys revisited these locations to record species' occupancy at each site and record the current population area of occupied sites, in addition to adding new populations encountered elsewhere.

*Estimating Population Detection and Persistence:* Imperfect detection during surveys can lead to biased estimations and erroneous inferences (Kellner and Swihart 2014). This has been well documented in the animal ecology literature, but is usually not accounted for in plant ecological studies (Kéry 2004; Chen et al. 2009). Imperfect detection leads to an increased number of erroneous "0s", or populations that were present, but not detected. Because of the imperfect detection of plant populations during each of the surveys (i.e. failure to detect a population when it was actually present), we modeled the data using a methodology that can estimate detection probabilities while also estimating population persistence.

For each of the four objectives (Table 1), we fit a Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) to the data in order to estimate population survivorship while taking into account imperfect detection. CJS models are usually used to estimate survival ( $\phi$ ), capture probability ( $p$ ), population size ( $N$ ), and new individuals entering the population ( $B$ ) from data on marked individuals within a population over a number of recapture events. After individuals within a population are "marked", the population is revisited repeatedly over a period of time, resulting in a capture history for each marked individual within the population. For example, an individual that was captured at time  $t$ , not seen again at time  $t+1$ , recaptured at time  $t+2$ , and finally observed again at time  $t+3$ , would have a recapture history of 1011.

*Characterizing Fire Frequency:* To quantify the effect of fire frequency on population persistence, we used both recorded burn histories and remotely sensed burn scars. The former comes from a database

of fire records maintained by the Fort Bragg Forestry Branch. The database includes primarily prescribed fires performed in each burn unit, but also contain a small number of unplanned fires. These records, however, do not capture variation at scales smaller than the whole burn unit, and therefore tend to overestimate burn extent, particularly where burning is often incomplete, such as in drainages and other areas with high shrub cover. We therefore complemented these data with fire histories reconstructed from satellite images. We modeled the fire history of rare plant populations by classifying atmospherically corrected Landsat images for the time period 1991-2014 with the mid-infrared burn index (MIRBI) and a Random Forest (RF) algorithm.

*Characterizing Canopy Cover:* We modeled canopy cover for the years 1991-2014 using LiDAR from 2012, Landsat imagery, and a RF classification model, in a manner similar to our approach to modeling the fire history.

*Characterizing Metapopulation Structure:* Metapopulation structure was estimated for each species with  $\geq 10$  populations using the connectivity parameter ( $S$ ) from the incidence function model (Hanski 1998). Specifically, we estimated connectivity for each population using the following formula:  $S_i = \sum_{j \neq i}^R \exp(-\alpha d_{ij}) p_j A_j$ , where  $\alpha$  is a distance decay parameter,  $d$  is the distance (m) from population  $i$  to population  $j$ ,  $p$  is patch occupancy, and  $A$  is the area ( $m^2$ ) of the patch  $j$ . We arbitrarily set  $\alpha$  to 0.01 and did not modify  $\alpha$  for individual species.

*Characterizing Species Functional Traits:* We estimated the effects of species' functional traits on population persistence using a subset of seven species for which data were available and have  $\geq 10$  populations on Fort Bragg (Ames et al. 2017). We examined seven traits that have been associated with plant performance in our study system (Ames et al. 2016), including: specific leaf area (SLA), leaf dry matter content (LDMC), leaf percent nitrogen, leaf percent carbon, the ratio of carbon to nitrogen, water use efficiency (WUE), and date of flowering onset.

*Data Analyses:* For the full data set spanning 1991-2014, we implemented a series of increasingly complex CJS models using the Bayesian statistical modeling language STAN (Carpenter et al. 2017). First, we fit a model to the data with constant survival (i.e. persistence) and detection probabilities across surveys and species. Next, we fit a model that allowed persistence and detection probability to vary across survey periods. While this model is slightly more complex, it did not account for variation between species. The next model estimated persistence and detection probability for each species, with species being considered a fixed effect. Finally, we fit a model to the data that considered species as a random effect and allowed for the inclusion of covariates that we hypothesized as being correlated with population persistence (Table 1). For each of the hierarchical models, we considered species as a random effect with a varying intercept, but a common slope. Because we were fitting the species as a random effect, we removed all species with fewer than ten populations in the dataset from this set of analyses. Furthermore, we excluded species that were not monitored for the entire study period because multiple follow-up surveys are required to fit CJS models. The remaining data set contained 723 populations of 14 species. We used the following generalized linear mixed model (GLMM) for the inclusion of a covariate:  $\text{logit}(\varphi_{i,t}) = \alpha_i + \beta * X_{i,t} + \epsilon_{i,t}$ , where  $\alpha$  is the random intercept term for species  $i$ ,  $\beta$  is the effect of covariate(s)  $X$  at time  $t$ , and  $\epsilon$  is the error. The inclusion of a covariate (e.g., canopy cover) as a predictor of persistence necessitated the modeling of individual heterogeneity for each population. We observed whether our models were able to recover parameters by simulating a dataset using known parameters (e.g., known detection probabilities, persistence, and covariate-

persistence correlations) and using the model to estimate the known parameters from the simulated data.

We analyzed the data in a similar manner for each of the four objectives (Table 1). Analyses relating population persistence to fire frequency, canopy cover, metapopulation structure, area, and functional traits were performed as GLMMs (Breslow and Clayton 1993) with a binomial error structure and a logit link function that was embedded in a CJS model within a Bayesian framework. All predictor variables were scaled by subtracting the mean and dividing by the standard deviation. Species were treated as a random effect. We first analyzed each independent variable (except for species traits) individually in a model (e.g., fire, canopy cover, connectivity, area). Next, we ran a series of models with combinations of the management-relevant variables both with and without an interaction term (e.g. fire + canopy cover and fire + canopy cover + fire:canopy cover). We compared the models with and without interaction terms by first calculating the (log) marginal likelihoods for the two competing models. Next, we computed the Bayes Factor (Jeffreys 1961) and the posterior model probabilities for each of the alternative models using the package *bridgesampling* (Gronau et al. 2017). We performed all statistical analyses in the R version 3.6 (R Development Core Team 2019).

Finally, we explored the additional insights gained via the long-term ecological datasets by comparing the results from the 1991-2014 to data collected from 1991-1999. Because the 1991-1999 time step represents a single observation and does not allow for estimation of detection probabilities, we were unable to estimate detection probabilities for the 1999 survey. In order to make a fair comparison, we fit a GLMM with a binomial error structure, with species as a random effect, to both the 1991-1999 data and the 1991-2014 data. We compared these results, when detection probabilities were not included, to the results from our CJS models that include all the data (hereafter referred to as the full dataset).

## Results and Discussion

*Population Detection and Persistence:* Across the 23-year period, plant populations on Fort Bragg generally exhibited high persistence between surveys. Mean population persistence among the three intervals was 0.92 ( $\pm 0.01$ ), while the mean detection probability was 0.88 ( $\pm 0.01$ ). Here and throughout this document, population persistence will be reported as the probability that the population survived from one survey until the next, with a mean interval of 7 years. These population persistence estimates were higher than persistence estimates that did not account for detection (mean = 0.81).

There were differences in detection probability across the surveys, but no differences in persistence across surveys after accounting for detection probability. The 2006 survey had an estimated detection probability of 78%, lower than both the 1999 and 2014 surveys. A number of factors could be responsible for the difference in detection probabilities among surveys. The most likely explanation is that each of the three follow-up surveys (i.e. 1999, 2006, and 2014) after the initial survey in 1991 were performed by different contractors and this likely contributed to some of the variation in detection probabilities.

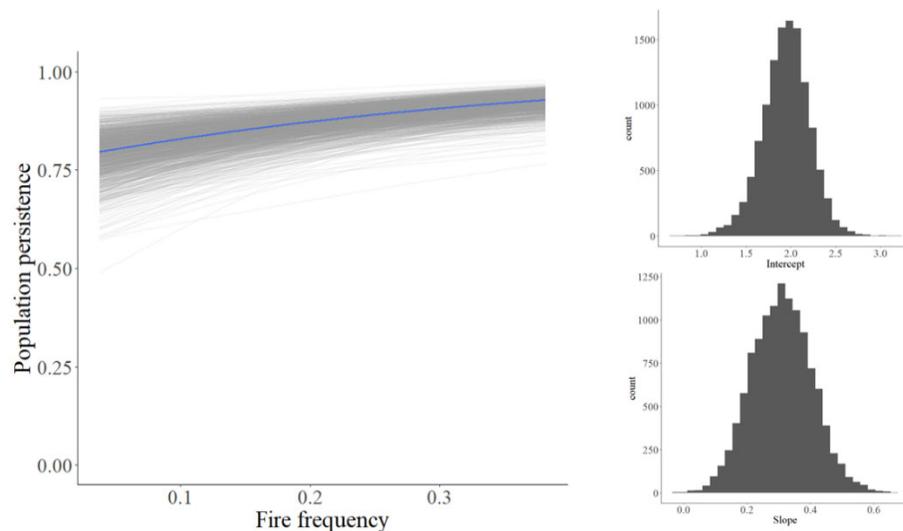
Imperfect detection occurred for all species and detection varied among species and gross habitat categories. The mean detection probability of the five upland species ( $0.89 \pm 0.01$ ) was greater than the nine wetland and ecotonal species ( $0.81 \pm 0.02$ ). This difference is likely due to the sparseness of understory vegetation in upland habitats as compared to the dense vegetation of wetland and ecotonal habitats.

Individual species demonstrated variability in population persistence over the 23-year period, ranging from 0.65 for *L. asperulifolia* to 0.97 for *L. subcoriacea*. The consequences of species-level differences in population persistence for conservation and management are exacerbated because of the differences in the number of initial populations and the number of individuals/stems.

Population persistence varied between hydrological positions, after accounting for detection probability. The mean population persistence for the five upland species ( $0.95 \pm 0.01$ ) was greater than the nine wetland and ecotonal species ( $0.84 \pm 0.01$ ). Mesic drainages and the ecotones between drainages and xeric uplands are particularly susceptible to reduced fire frequency and can quickly become dominated by evergreen shrubs due to feedbacks between vegetation and fire behavior (Just et al. 2016).

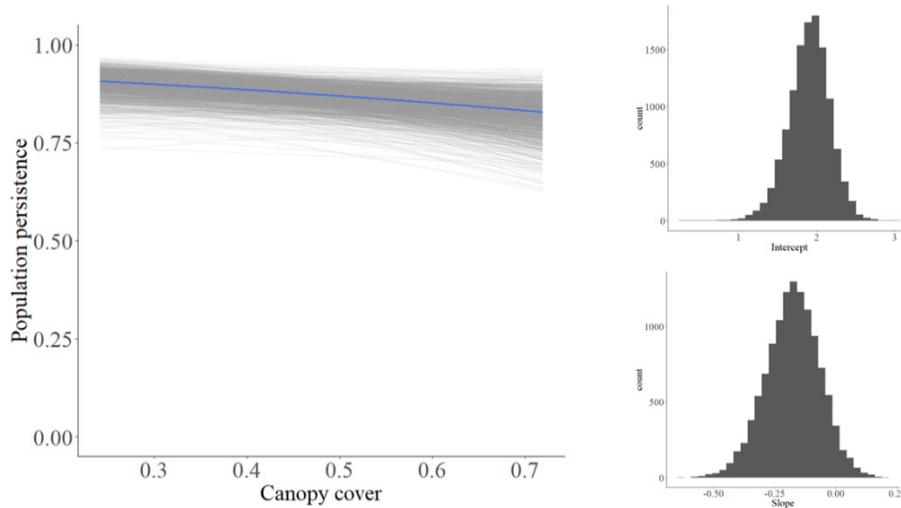
*Effects of Fire Frequency:* Over the entire period, fire frequency estimates across the 723 populations averaged 0.27 based on recorded fire history, but only averaged 0.15 (i.e. one fire every six years) based on the modeled fire history. Although the recorded fire frequency increased after 1999, the modeled fire frequency decreased, resulting in roughly similar frequencies between surveys when averaged across the two data sources.

Population persistence estimates for 14 species across 723 populations were positively correlated with average fire frequency from 1991-2014 (Table 1), consistent with the findings of Gray et al. (2003) for the period 1991-1999. Under a mean fire frequency of 0.21 (approximately equivalent to two fires every 10 years), average population persistence between surveys was 0.88, but decreased to 0.83 when fire frequency decreased to 0.01 (equivalent to one fire every 10 years). When fire frequency increased to 0.33 (three fires every ten years), average population persistence was estimated to increase to 0.91. While the difference between population persistence estimates of 0.83 and 0.91 (representing roughly one standard deviation from the mean for fire frequency) may appear small, for long-lived species with limited recruitment this represents a substantial loss of populations, and may be especially detrimental for species with a small number of initial populations.



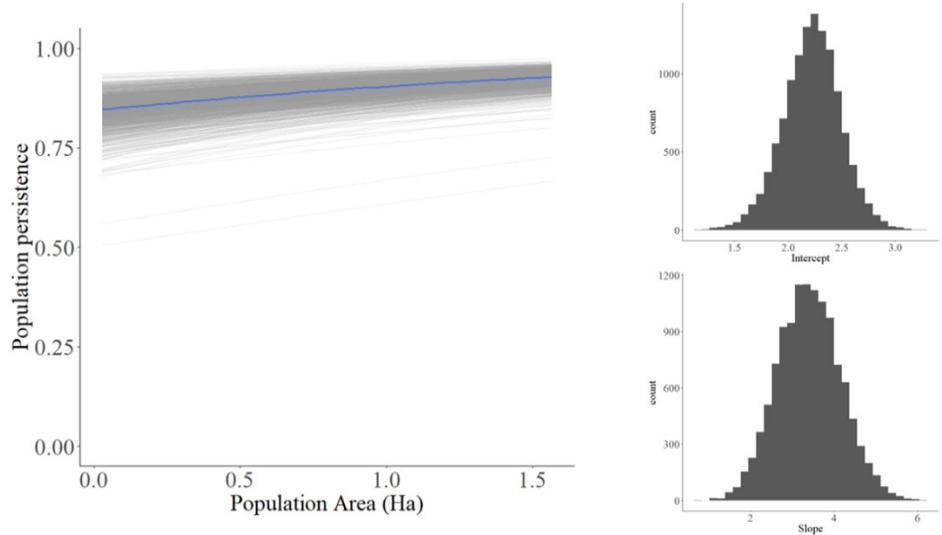
**Figure S1: Effect of fire frequency on the probability of population persistence across 720 populations of 14 species over four surveys spanning 1991-2014. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

*Effects of Canopy Cover:* Overall, higher canopy cover appeared to have a negative effect on population persistence (Figure 12), but the slope estimate for canopy cover did include 0 in the 95% confidence interval (-0.18; CI -0.40 – 0.03). Estimated population persistence at the mean canopy cover estimate (0.48) was 0.88. Population persistence decreased to 0.85 when canopy cover increased to 0.60. In contrast, low canopy cover estimates (e.g., 0.33) lead to increased population persistence (0.90). There was no evidence from the data that population persistence was negatively impacted by an extremely low canopy cover, when examined across species. These results are in alignment with studies that have looked at the effect of canopy cover and biodiversity in longleaf pine ecosystems, which have found that species richness increases with decreased canopy cover (Platt et al. 2006; Veldman et al. 2013).



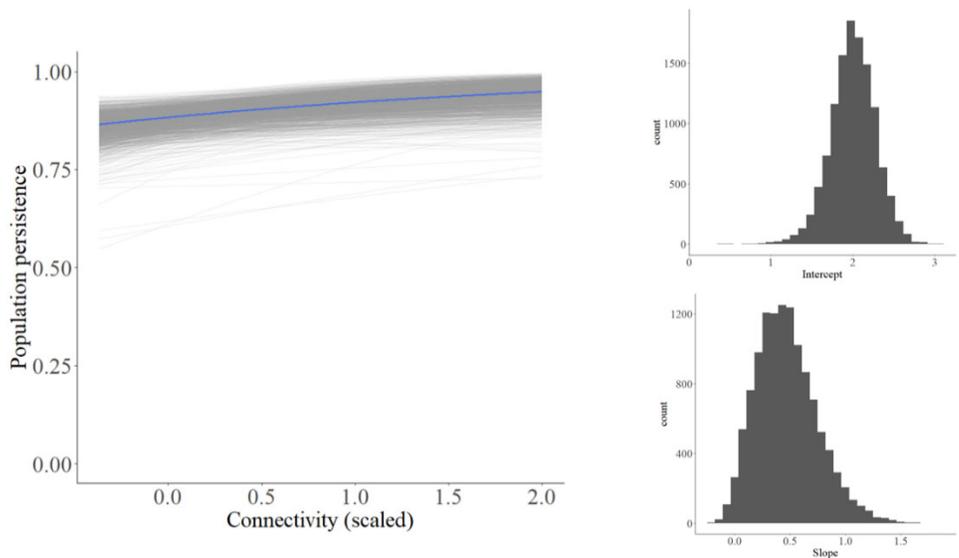
**Figure S2: Effect of canopy cover (proportion) on the probability of population persistence across 723 populations of 14 species over four surveys spanning 1991-2014. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

*Effects of Metapopulation Structure:* The spatial extent (area occupied) of populations was predictive of population persistence, with large populations being more likely to persist relative to smaller populations (Figure 14).



**Figure S3: Effect of population area on the probability of population persistence across 723 populations of 14 species over four surveys spanning 1991-2014. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median.**

Our results demonstrate a correlation between population connectivity, as measured by Hanski’s incidence function, and persistence (Figure 15). Isolated populations were more likely to be extirpated relative to more connected populations.



**Figure S4: Effects of patch connectivity on the probability of population persistence for 14 species across 723 populations on Fort Bragg. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

*Effects of Functional Traits:* Results did not indicate that any of the seven functional traits on their own were particularly predictive of overall population persistence, but two trait-environment interactions

(i.e. fire:SLA and canopy cover:flowering onset) were significant. We had anticipated that the interactions would provide greater predictive information than the trait variables, given that the functional importance of traits is manifest in how they perform under specific environmental conditions.

*Interactions:* There was no evidence for an interaction between fire frequency and canopy cover, with the posterior probability of the model with no interaction term (0.78) being greater than a model that included an interaction term (0.22). This result suggests that the effects of higher fire frequency on population persistence operate across a range of canopy covers. As with fire frequency and canopy cover, there was no evidence of an interaction between fire frequency and population connectivity, with the posterior probabilities being roughly equal (0.42 with an interaction term versus 0.58 without). There was some evidence of an interaction between fire frequency and area (posterior probability of 0.65 with an interaction term versus 0.35 without), with increased fire frequency having a mildly negative effect on small populations. There was some evidence for a negative interaction between canopy cover and connectivity, with the posterior probability of the model that includes an interaction term between canopy cover and connectivity (0.73) being greater than a simpler model with no interaction term (0.27). There was a negative correlation between canopy cover and population persistence for populations with average connectivity, while isolated populations appeared to benefit from canopy cover and exhibited increased persistence under higher canopy cover. Canopy cover had little effect on average and large area populations, but if anything, there was a positive effect of increasing canopy cover on populations with small area. There was some evidence for the persistence of small populations being positively impacted by greater connectivity relative to larger populations, with the posterior probability of a model that includes an interaction term (0.68) being roughly twice as great as a model without an interaction term (0.32). As expected, populations covering a large area persisted between surveys regardless of their level of connectivity, while smaller populations were positively impacted by connectivity.

*Comparisons Between the Long-term and 1991-1999 Datasets:* Contrary to the findings of Gray et al. (2003), estimates of the effects of fire frequency on population persistence from 1991-1999, as analyzed with a GLMM, were not significant. However, we did identify a significant effect of fire frequency on population persistence for the 1991-2014 dataset, with the mean slope being higher than the 1991-1999 parameter estimate. The parameter estimate for the full dataset ( $0.30 \pm 0.09$ ) was similar to the 1991-2014 dataset (that did not account for detection). Thus, expanding analyses over a longer time period, and refining estimates of fire frequency and population persistence appeared to have a substantial impact on our understanding of the relationship between persistence and fire frequency.

Gray et al. (2003) did not explicitly evaluate the effects of canopy cover on population persistence; however, our evaluation of the effects of canopy cover based only on the 1991-1999 dataset identified no significant relationship. Similarly, no significant relationship was found for the long-term dataset when analyzed with a GLMM. This is in contrast to the full model that includes detection probability, where a negative relationship between canopy cover and population persistence was found (Figure 12).

Gray et al. (2003) found a positive relationship between population persistence and area occupied. Our reanalysis of the 1991-1999 and the 1991-2014 dataset revealed a similar positive relationship between population persistence and area occupied, with no marked differences in the shape of the relationship over the short- versus long-term, confirming that area occupied has a significant impact on population persistence.

Gray et al. (2003) did not explicitly evaluate the effects of population connectivity on persistence; however, our evaluation of the effects of connectivity on population persistence based only on the 1991-1999 dataset generated a positive correlation, but no correlation of spatial isolation and population persistence based on the 1991-2014 dataset.

## **Implications for Future Research and Benefits**

Our results confirm three of our four initial hypotheses (Table 1). First, fire frequency is positively correlated with rare plant population persistence on Fort Bragg. This is in alignment with other studies in the longleaf pine ecosystem that have looked at either biodiversity or individual species. Next, there is evidence for a negative correlation between canopy cover and population persistence, with populations under higher canopy cover being less likely to persist relative to populations under low canopy cover. We also found that metapopulation structure, specifically connectivity, was positively correlated with persistence. This is the most surprising result of the study, as most of the species in the MARPS dataset are long-lived species with limited dispersal and/or recruitment. Our final hypothesis was that plant functional traits would be correlated (either positively or negatively) with population persistence. We were unable to confirm this hypothesis. Briefly, the included populations span a range of hydrological conditions and vegetation communities which select for specific functional traits. It is likely that including populations from such a wide range of conditions masked the underlying directionality of the functional traits. Across all study species, populations that experience frequent fires, occur under low canopy cover, are highly connected or occupy a large area, and occur in upland habitats are expected to have higher probabilities of persistence than populations under opposite conditions.

The present study demonstrates the benefits of collecting, in a consistent manner, long-term data from rare species on military installations. Without these efforts, it would be difficult to reach the conclusions that we were able to infer based on multiple surveys. This is clearly demonstrated by comparing our results using mark-recapture models with single survey methods that are not able to estimate detection probabilities. If conclusions were drawn based on just the 1991-1999 data, one would infer that fire and canopy cover had no effect on population persistence. Likewise, conclusions based on the 1991-2014 (and not including population detection) would be that canopy cover and population connectivity had no effect on population persistence. Only with access to the full data set, collected over 23 years and across multiple surveys, were we able to reach the conclusions presented in this study. Furthermore, the long and repeated nature of the MARPS dataset made it possible to apply appropriate analytical tools to avoid biases that arise from imperfect detection of populations. Ignoring imperfect detection results in overestimation of population extirpations, can obscure identification of important environmental drivers of population persistence, and may result in poor management prioritization. Estimation of detection probabilities is only possible with carefully executed, repeated surveys over sufficient timespans.

*Implications for Future Research:* The MARPS database is a unique resource for understanding the dynamics of rare species populations, and its value will continue to grow as future surveys are performed. The additional data generated by future surveys will be invaluable for investigating long-term metapopulation dynamics of rare plants by providing more robust estimates of relationships we elucidated here. Substantial diversity in species response necessitates species-specific management where adequate knowledge is available and additional detailed studies where knowledge is still insufficient to inform management.

*Implications for Management and Recommendations:* Several management implications and recommendations can be made based on the present study. First, the results suggest increasing the fire frequency, with caution because some species might be negatively impacted. Second, reducing canopy cover will benefit rare plant populations on Fort Bragg. Third, metapopulation structure and population connectivity is important, with isolated populations more likely to be extirpated relative to more connected populations. These three factors, fire frequency, canopy cover, and metapopulation structure, represent a continuum of management options in terms of resource investment. Prescribed burning is the least costly in terms of resource investment and would likely yield the greatest benefits. If management units are not burned on a frequent (i.e. 3-yr) interval and woody vegetation escapes the fire trap and enters the midstory and canopy (Hoffmann et al. 2020), thinning is the second option. Manipulating metapopulation structure and population connectivity via population introduction and augmentation may be an option for increasing the probability of population persistence, but protocols have not been developed for most species.

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## Objective

Long-term datasets are particularly important in the ecological sciences because they allow for the integration of data collected across variable biotic and abiotic conditions. Unfortunately, most studies are short-term (i.e. less than five years), so many of the inferences drawn from them may be limited to the conditions at the time of the study. Since 1991, the Endangered Species Branch of Fort Bragg has surveyed all known plant populations of federally-listed species and federal species of concern, at intervals of roughly seven years, including 1,396 populations of 41 plant species. This information is collated in a Monitoring and Assessment of Rare Plant Species (hereafter MARPS) database. Using the first two of these surveys, Gray et al. (2003) undertook an analysis of population dynamics to test the following hypotheses: (1) prescribed fire reduces population extirpation rates, (2) fire increases population size, (3) populations persistence is positively correlated with population size, and 4) plant functional groups differ in their response to fire frequency. Since this initial analysis, two additional surveys have been undertaken, thereby increasing by 3-fold the duration of the study.

Our overarching research objective was to investigate factors affecting population persistence of long-lived plant species using this long-term monitoring dataset. To meet our overarching research objective, we investigated the effects of fire frequency, canopy cover, metapopulation structure, and species functional traits on persistence of rare plant populations. Specifically, we explored the four objectives and associated hypotheses listed in Table 1.

**Table 2: Research objectives and hypotheses.**

Objectives and Hypotheses	
<b>Objective 1: Verify the effects of fire management on plant population persistence</b>	
<i>H1:</i>	<i>Population persistence is positively correlated with fire frequency.</i>
<b>Objective 2: Verify the effects of canopy cover on plant population persistence</b>	
<i>H2:</i>	<i>Population persistence is negatively correlated with canopy cover.</i>
<b>Objective 3: Verify the effects of metapopulation structure on plant population persistence</b>	
<i>H3:</i>	<i>Population persistence is negatively correlated with population isolation.</i>
<b>Objective 4: Verify the effects of functional traits on plant population persistence</b>	
<i>H4:</i>	<i>Population persistence is correlated with species function traits.</i>

This project was proposed against RCSON-17-02: Long-Term Ecological Studies: Testing Previous Hypotheses and Conclusions. It directly meets three of the four research needs outlined in the Statement of Need:

*Need 1. Facilitate confirmation, modification, or abandonment of initial hypotheses and conclusions regarding treatment effects, mechanistic understanding of system processes, or management implications. We sought to confirm or refute the initial hypotheses and conclusions of Gray et al. (2003) regarding drivers of local extinction. This was accomplished by utilizing the current MARPS database, which contains 3-fold greater information than was available at the time of the previous analysis.*

*Need 2. Extend the degree of inference of results from previous studies in statistically relevant ways. We expanded the degree of inference in three ways. First, we utilized generalized linear mixed*

model (GLMM) analyses aimed specifically to quantify the variation among species in their response to the primary drivers of local extinction. By elucidating this variability, we sought to evaluate the extent to which our outcomes can be generalized to other species and locations. Second, we incorporated detection probabilities using a Cormack-Jolly-Seber mark-recapture model in a Bayesian framework into all of our analyses. This not only increased the accuracy of population persistence estimates, it also enhanced our ability to identify the effects of multiple biotic and abiotic variables on population persistence. Third, we incorporated functional trait data to facilitate extrapolation of our results to other species (Objective 4).

*Need 3. Translate findings from additional data collection and analysis into actionable information for DoD resource managers.* Our results are directly translatable into guidelines for assessing risk of local extinction and for remediating this risk. The broadest guidelines originate from analyses performed on the full multi-species dataset. At this scale, insights about the impacts of metapopulation structure (i.e. population size and connectivity) on extinction probability (Objective 3) can guide current and future population reintroduction and augmentation efforts, in addition to habitat management to enhance connectivity. For other factors, such as fire response and canopy cover (Objectives 1 and 2), the most actionable information arose from analyses performed on individual species. For all study species with sample sizes sufficient to detect a significant response to these factors, our results provide species-specific information about changes in fire frequency or targeted management of vegetation that would enhance population persistence.

## **Background**

Department of Defense lands harbor a higher density of threatened and endangered species (TES) than any other federal agency (Stein et al. 2008), with the majority of these species being plants. Understanding and preventing local extinction of rare species is of great relevance to DoD resource managers as federal listing under the Endangered Species Act (ESA) can increase the cost of species management and reduce access to training lands. The training and testing mission of DoD installations is sustained through prudent, science-driven, long-term management of their natural resources including the threatened, endangered and at-risk species that may be dependent upon this public land base (DoD Instruction 4715.03). However, for many listed and at-risk plants, evaluating local extinction risk is complicated by the long lifespan and slow dynamics of most species. This necessitates taking a more long-term approach to monitoring, as short-term dynamics may not be indicative of a species' long-term prospects.

The southeastern United States, and especially the Atlantic and Gulf Coastal Plain Floristic Province, is an area of high plant diversity, with a number of centers of endemism (Sorrie and Weakley 2001). The region is also home to a large number of important military installations. This has led to the situation where southeastern military installations are not only important for training and force projection, but are also caretakers of a significant portion of the nation's natural heritage. Of the many installations in the southeastern United States, four are located in the Fall-line Sandhills, a region that has been previously identified as an area of high endemism (Sorrie and Weakley 2001), with ten species identified as being endemic. The Fall-line Sandhills was historically included under the great longleaf pine (*Pinus palustris*) ecosystem.

The longleaf pine ecosystem once covered over 37 million hectares of the southeastern United States (Frost 1993). However, land use changes, such as conversion to agriculture and residential

development, over the last few centuries have severely reduced the range of longleaf pine and the associated ecosystem, to the extent that it only occupies 3% of its former area (Frost et al. 1986). Remaining areas are fragmented, reduced in size, and in many cases severely degraded due to fire suppression, invasive species, and other factors. While only a small percentage of the original longleaf pine ecosystem remains, the region is still recognized as a globally significant area of endemism and species diversity (Sorrie and Weakley 2001), especially for plant species.

In modern landscapes many natural populations of plants and animals are threatened by their isolation from other populations of the same species (Ellstrand and Elam 1993; Hanski 1998; Fischer and Lindenmayer 2007). Many military lands are exceptions to this trend because they offer large and relatively intact landscapes where multiple populations of a species can persist sufficiently near each other to allow genetic exchange, provide a source of individuals that can rescue declining populations, and permit colonization of suitable, unoccupied habitat. These interactions among interconnected populations, or *metapopulations*, are widely assumed to promote biodiversity and improve the success of rare species (Hanski 1998), and therefore should be particularly important for DoD installations, which have a 3-fold higher density of listed and at-risk species than other federal agency lands (Stein et al. 2008).

*Source-sink* dynamics are a particularly important component of metapopulation dynamics because growing (source) populations can supply new individuals and genetic material for declining (sink) populations (Pulliam 1988). This process can rescue marginal populations from extirpation. However, metapopulation dynamics are particularly slow in many perennial plants because of their immobile nature, long lifespans, limited dispersal, and low recruitment rates (Eriksson 1996). Consequently, colonization and extinction are extremely infrequent events. This emphasizes the need for long-term studies involving large numbers of populations to provide sufficient information for statistically robust conclusions.

A common goal of metapopulation studies is to arrive at a generalizable understanding of interactions among populations that can be translated into robust guidelines for management that are broadly applicable to other species and other regions. This is challenging because metapopulation dynamics are influenced by species characteristics such as dispersal mode, reproductive biology, and life span, all of which vary immensely across species. This is further complicated because metapopulation dynamics are superimposed upon spatial and temporal heterogeneity in the biotic and physical environment. In many cases, these environmental factors may be the ultimate cause of local extinction (Harrison et al. 2015), making it difficult to extrapolate results to species that differ in their response to the environment or to landscapes that differ in their inherent environmental spatial and temporal heterogeneity.

In light of such problems, several authors have made a plea for wider use of comparative approaches for understanding extinction risk (Fisher and Owens 2004; Murray et al. 2014). Most of the studies that have heeded this plea have focused on animals, but several studies have demonstrated that comparative trait-based approaches can achieve a more generalizable understanding of the drivers of range contraction in plants (Piqueray et al. 2011; Saar et al. 2012; Powney et al. 2014). By comparing the dynamics of a large number of species, and relating this to the traits possessed by species, we sought to identify relationships that can predict metapopulation dynamics in across species and offer DoD land managers on multiple installations a more scientifically defensible approach to plant species management that accounts for the possible range of response variation.

## Materials and Methods

### Site Description and Characterization

This study was conducted on Fort Bragg (35°8'21"N, 78°59'57"W), which resides in the Fall-line Sandhills ecoregion, a part of the once extensive fire-dependent longleaf pine (*Pinus palustris*) ecosystem. Since the onset of Fort Bragg's rare plant monitoring program in 1991, the mean monthly temperature ranged from 5.5°C in January to 26.6°C in July, with mean annual precipitation of 1,253.8 ± 178.1 mm. The region is characterized by sandy, well-drained soils overlaying clay subsoils. The sandy, xeric uplands are dominated by longleaf pine/wiregrass (*Aristida stricta*) savanna, while the low-lying, mesic-hydric areas contain a mixed hardwood overstory with a dense layer of evergreen and deciduous shrubs (Figure 5). Many plants in the Fall-line Sandhills experience slow growth rates due to nutrient and/or water limitation (Wells and Shunk 1931; Hatchell and Marx 1987). The flora of Fort Bragg is extremely diverse with over 1,200 recorded vascular plant taxa, including three Federally Endangered Species, six species under review for Federal listing, 15 Federal Species of Concern, and more than 60 species listed as rare by the state (Gray et al. 2003; Sorrie et al. 2006; Gadd and Finnegan 2012).

Natural fires are believed to have occurred in this region every three years on average (Frost 1998; Stambaugh et al. 2011). To mimic this disturbance history, Fort Bragg is partitioned by fire breaks into >1,000 burn units (mean area = 45 hectares), which have been managed with prescribed fire primarily early in the growing season on a roughly 3-year rotation since 1991. These prescribed fires are implemented using low-intensity backing fires to maximize control and minimize damage to the mature longleaf pines. While the use of backing fires may mimic the historical fire frequency in the upland areas, fire is less likely to burn into the wetland areas and result in a reduced fire frequency in these areas, relative to the historical fire frequency.



**Figure 5: Upland longleaf pine savanna (left) and ecotone between savanna and wetland showing where fire stopped (right).**

### Monitoring and Assessment of Rare Plant Species Database

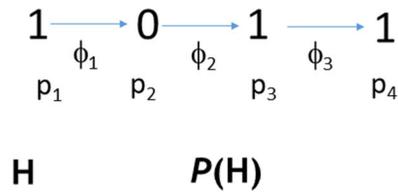
For over 20 years, the Endangered Species Branch of Fort Bragg has monitored 1,396 populations of 41 rare plant species, resulting in a unique database that has over 32,000 population-years of data and is putatively the largest, longest, and most comprehensive undertaken on CONUS military lands. This database offers a rich resource for understanding the drivers of local extinction. The Fort Bragg MARPS

database consists of four surveys conducted from 1991-93, 1998-99, 2005-06, and 2012-14. For the first survey, a systematic search for rare plant populations was performed by trained field botanists walking transects over the installation and recording the location and extent (i.e. area) of each population. Populations are defined as discrete entities separated by minimum of 0.8 km (Gray et al. 2003). Subsequent surveys revisited these locations to record species' occupancy at each site and record the current population area of occupied sites, in addition to adding new populations encountered elsewhere. The 1991-1993 survey manually recorded population area and locations on aerial photographs that were later digitized and input into a GIS database, but subsequent surveys recorded location and population area using GPS. The dataset allows for testing of the effect of biotic and abiotic factors on population persistence during the interval between surveys for populations that were surveyed at least twice.

### **Estimating Population Detection and Persistence**

Imperfect detection during surveys can lead to biased estimations and erroneous inferences (Kellner and Swihart 2014). This has been well documented in the animal ecology literature, but is usually not accounted for in plant ecological studies (Kéry 2004; Chen et al. 2009). Imperfect detection leads to an increased number of erroneous "0s", or populations that were present, but not detected. Because of the imperfect detection of plant populations during each of the surveys (i.e. failure to detect a population when it was actually present), we modeled the data using a methodology that can estimate detection probabilities while also estimating population persistence.

For each of the four objectives (Table 2), we fit a Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) to the data in order to estimate population survivorship while taking into account imperfect detection. CJS models are usually used to estimate survival ( $\phi$ ), capture probability ( $p$ ), population size ( $N$ ), and new individuals entering the population ( $B$ ) from data on marked individuals within a population over a number of recapture events. After individuals within a population are "marked", the population is revisited repeatedly over a period of time, resulting in a capture history for each marked individual within the population. For example, an individual that was captured at time  $t$ , not seen again at time  $t+1$ , recaptured at time  $t+2$ , and finally observed again at time  $t+3$ , would have a recapture history of 1011 (Figure 6).



1111	$\phi_1 p_2 \phi_2 p_3 \phi_3 p_4$
1110	$\phi_1 p_2 \phi_2 p_3 [\phi_3(1 - p_4) + (1 - \phi_1)]$
1101	$\phi_1 p_2 \phi_2 (1 - p_3) \phi_3 p_4$
1100	$\phi_1 p_2 \{ \phi_2 (1 - p_3) [\phi_3 (1 - p_4) + (1 - \phi_3)] + (1 - \phi_3) \}$
1011	$\phi_1 (1 - p_2) \phi_2 p_3 \phi_3 p_4$
1001	$\phi_1 (1 - p_2) \phi_2 (1 - p_3) \phi_3 p_4$
1010	$\phi_1 (1 - p_2) \phi_2 p_3 [\phi_3 (1 - p_4) + (1 - \phi_1)]$
1000	

**Figure 6: Mark-recapture example for three time steps, with an initial capture (1) and a recapture history 011. This results in a recapture history of 1011. The table illustrates how the likelihood off each capture history scenario is calculated.**

For our analyses, we considered populations as “marked individuals”. The MARPS dataset meets most of the assumptions of CJS models, which were initially designed to work with individuals. The first assumption is met; the populations represent a random sample of the available populations and there is no evidence of spatial bias. The initial survey was a systematic survey of the installation. Secondly, the number of releases (located populations) is known, as all populations located in the initial survey were recorded. The marking of the populations can be considered accurate, as each population was georeferenced at the initial survey. This criterion is more of an issue with mobile individuals. A fourth criterion is that the fate of individuals are independent of each other. This again is likely to be true, unless large-scale disturbances (e.g., forest thinning operations) affected multiple populations in the study. A fifth criterion is that the parameter estimates are based on a good model. One assumption is violated. CJS models assume that all releases are made within a relatively short period of time. The first survey did span multiple years, but we would argue that, because of the high persistence of individual plant populations, this does not bias the data in a substantial way.

### Characterizing Fire Frequency

To quantify the effect of fire frequency on population persistence, we used both recorded burn histories and remotely sensed burn scars. The former comes from a database of fire records maintained by the Fort Bragg Forestry Branch. The database includes primarily prescribed fires performed in each burn unit, but also contain a small number of unplanned fires. These records, however, do not capture variation at scales smaller than the whole burn unit, and therefore tend to overestimate burn extent, particularly where burning is often incomplete, such as in drainages and other areas with high shrub

cover. We therefore complemented these data with fire histories reconstructed from satellite images, as described below.

We downloaded all atmospherically corrected Landsat images covering Fort Bragg for the time period 1991-2014 using a custom python script in Google Earth Engine (Gorelick et al. 2017). For the time period 1991-2011, we used images collected from the Landsat 5 Thematic Mapper (TM) sensor. For 2012, we used the Landsat 7 Enhanced Thematic Mapper Plus (ETM+), and the 2013-2014 images were collected from the Landsat 8 Operational Land Imager (OLI) sensor. We filtered the image collection to only include images with less than 10% cloud cover, resulting in a total of 171 images for the 24 year period (mean 7 images per year). Clouds were masked based on the pixel quality assurance band included with each Landsat image. For each image, we calculated several indices that were used as features in both the fire frequency and canopy cover model construction. Normalized difference vegetation index (NDVI) provides a measure of the density of live green vegetation and is strongly correlated with a number of vegetation properties (leaf area index biomass, chlorophyll concentration of leaves, plant productivity, fractional vegetation cover, etc.). We calculated NDVI using the standard formula  $Band4 - Band3 / Band4 + Band3$ , where Band4 represents the near-infrared band in the Landsat TM+ imagery and Band 3 represents the red band. We performed a tasseled cap transformation on each of the Landsat images to generate brightness, greenness, and wetness bands (Kauth and Thomas 1976). Because we were using surface reflectance Landsat values, we used the coefficients identified by DeVries et al. (2016), rather than the standard coefficients used for top-of-atmosphere images.

We utilized the mid-infrared burn index (MIRBI), which has been successfully used to identify fires in savanna ecosystems (Trigg and Flasse 2001), to delineate burned areas in acquired satellite imagery. The MIRBI uses Landsat bands 5 and 7 and is calculated using the following formula:  $MIRBI = B7 * 10 - (B5 * 9.8 + 2)$ . We scaled the resulting MIRBI values of the Landsat image by subtracting the mean and dividing by the standard deviation. We classified the resulting scaled MIRBI raster cells (900 m<sup>2</sup>) as burned if they were greater than one standard deviation from the mean. Burned cells were assigned a value of 1 and unburned cells were assigned a value of 0. Because we were not able to ground truth historical burns, we selected a Landsat 4 image (27 February, 1991) with no cloud cover for delineating burned areas. Fortunately, we were able to visually identify burns from the satellite imagery using a combination of the following Landsat bands: short-wave infrared (SWIR), near-infrared (NIR) and the blue band. We compared the classified image to the original Landsat image and the burn records collected by Fort Bragg personnel.

After classification of an image using the MIRBI, burned areas were further delineated using a Random Forest (RF) to construct a classification model for the probability that raster cells were burned in a given year (Liaw and Wiener 2002) in R (R Development Core Team 2019). Random Forest, a machine learning algorithm (Breiman 2001), is an ensemble learning method that can be used for either regression or classification. It is basically an extension of classification and regression tree (CART) methods (Breiman et al. 1984), whereby a user-specified number of decision trees are generated by randomly sampling the data. At each decision node, a random sample of the predictors is selected. For each decision tree, the out-of-bag (OOB) error rate is calculated by predicting the value of the unsampled data and comparing to the known values. Benefits of using RF are that it is relatively robust to overfitting as compared to CART and does not require data standardization or normalization, since it is insensitive to the value range of the predictors.

We generated 10,000 random points and extracted the burned (1) or unburned (0) values from the classified MIRBI layer. From the 27 February 1991 Landsat image, we extracted bands 1-7, as well as the MIRBI and the NDVI values at each of the same 10,000 points to be used as features in the RF model. We then divided the data for these 10,000 points into a training set (75% of the data) and a testing set (remaining 25%). We tuned the RF algorithm by comparing the results using varying numbers of trees (1,000, 1,500, and 2,000) and random predictors at each node (3, 4, 5, 7, 9, and 10). After constructing an RF model using the identified tuning parameters, we predicted the values of the testing set. Finally, we used the constructed RF model to predict whether the probability that a cell was burned or not for each of the Landsat images from 1991-2014. For each of the resulting probability rasters, we set a threshold of 0.75 to identify cells that were presumably burned: cells with values < 0.75 were classified as unburned; cells with values  $\geq 0.75$  were classified as burned. To filter out errant, small burns in the data set, we set a minimum burn patch size of 2.25 Ha. Any identified burns that were smaller than 2.25 Ha were classified as unburned. For each of the years 1991-2014, we combined the individual Landsat images to create a composite burn classification image. We then extracted the burn status for each of the populations for each year and calculated the *cumulative* fire frequency for each of the surveys. In other words, for the 1999 survey, we calculated the fire frequency from 1991-1999, while for the 2006 survey, we calculated the cumulative fire frequency from 1991-2006.

Burn histories estimated from the satellite imagery likely underestimate burn frequency, because low-intensity surface fires are sometimes undetected where canopy cover is high. On the other hand, the available ground-based, observational fire history tends to overestimate burn frequency. We therefore considered these two data sources to represent endpoints in the range of possible burn frequencies.

## Characterizing Canopy Cover

Airborne Light Detection and ranging (LiDAR) data were acquired from several flights flown between 20-27 December, 2012 by Magnolia River Inc. (Huntsville, AL). A Cessna Stationaire 206/G carrying an Optech ALTM 310 LiDAR system was used to acquire the LiDAR data. Accuracy was within 10 cm for the flights. LiDAR points were processed and classified using Applanix POSPac 6.0 software. The classified LiDAR point cloud was used to generate a canopy cover model for Fort Bragg using a custom script in ArcGIS Pro 2.0 (ESRI Inc.). After creating a classified LiDAR dataset by combining the separate point cloud data files, we generated a 1 meter resolution Digital Elevation Model (DEM) by selecting only the ground returns. In a similar manner, we created a Digital Surface Model (DSM) by selecting the non-ground returns from the classified LiDAR dataset. Canopy height was estimated by subtracting the DEM from DSM, with resulting negative values set to 0. We estimated canopy cover by first converting the LiDAR dataset into a raster image with a cell size of 25 m<sup>2</sup>. For each cell, we counted the number of above ground (AG) points and the number of bare earth (BE) points within the cell and estimated canopy cover using the following formula:  $\frac{AG}{AG+BE}$ . We did not explicitly ground truth the generated canopy cover and canopy height layers, but we did visually compare the resulting images to high resolution aerial images to assess model performance.

We used the canopy cover layer generated from the 2012 LiDAR data to model canopy cover for the years 1991-2014 using a RF classification model and Landsat imagery, in a manner similar to our approach to modeling the fire history. We first selected two Landsat images that were temporally close to the LiDAR data acquisition date. The Landsat images were acquired in May and September, 2013. For each image, we generated 10,000 random points and extracted the Landsat band data at each of the

points, as well as NDVI and the tasseled cap indices. In addition, we extracted the canopy cover estimates from the LiDAR canopy cover map at each of the 10,000 points. We used an RF model to predict annual canopy cover estimates for the years 1991-2014. Because the Landsat 5 imagery did not produce satisfactory results (based on visual inspection of the images), we constructed a separate RF model for the Landsat 5 images (years 1991-2011) using the same process.

## Characterizing Metapopulation Structure

Metapopulation structure was estimated for each species with  $\geq 10$  populations using the connectivity parameter ( $S$ ) from the incidence function model (Hanski 1998). Specifically, we estimated connectivity for each population using the following formula:  $S_i = \sum_{j \neq i}^R \exp(-\alpha d_{ij}) p_j A_j$ , where  $\alpha$  is a distance decay parameter,  $d$  is the distance (m) from population  $i$  to population  $j$ ,  $p$  is patch occupancy, and  $A$  is the area ( $m^2$ ) of the patch  $j$ . We arbitrarily set  $\alpha$  to 0.01 and did not modify  $\alpha$  for individual species.

## Characterizing Species Functional Traits

We estimated the effects of species' functional traits on population persistence using a subset of seven species for which data were available and have  $\geq 10$  populations on Fort Bragg (Ames et al. 2017). We examined seven traits that have been associated with plant performance in our study system (Ames et al. 2016). Specific leaf area (SLA) is the leaf area per unit of dry mass and is correlated with plant relative growth rate (Hunt and Cornelissen 1997). Leaf dry matter content (LDMC) is also correlated with relative growth rate (Ryser and Aeschlimann 1999), as well as flammability (Perez-Harguindeguy et al. 2016) and post-fire regeneration strategy (Saura-Mas and Lloret 2007; Saura-Mas et al. 2009) in pyrogenic systems. Leaf percent nitrogen is positively correlated with photosynthetic rates (Wright et al. 2004), while percentage carbon is associated with leaf palatability (Chapin III 2003). The ratio of carbon to nitrogen (C:N) is correlated with plant productivity (Craine et al. 2002). Water use efficiency (WUE), was assessed by measuring the fractionation of C isotopes ( $\delta^{13}C$ ) in leaf samples from the seven species (Smedley et al. 1991; Stewart et al. 1995; Dawson et al. 2002). Finally, date of flowering onset has been shown to influence post-fire flowering response of species in longleaf pine plant communities (Platt et al. 1988). Trait data (Table 3) were collected in 2015 (Ames et al. 2016; Ames et al. 2017 for sampling protocols).

**Table 3: Mean trait values for seven species included in trait analyses. Traits included specific leaf area (SLA), leaf dry matter content (LDMC), percentage nitrogen, percentage carbon,  $\delta^{13}C$ , the ratio of carbon to nitrogen, and date of flowering onset.**

Scientific name	Family	SLA ( $cm^2 g^{-1}$ )	LDMC ( $gg^{-1}$ )	N (%)	C (%)	$\delta^{13}C$	C:N	Flowering onset (Julian date)
<i>Amorpha georgiana</i>	Fabaceae	156.84	0.45	1.99	50.08	-28.16	25.97	122
<i>Astragalus michauxii</i>	Fabaceae	124.49	0.26	3.74	47.15	-29.93	12.70	92
<i>Eupatorium resinosum</i>	Asteraceae	146.51	0.31	1.79	52.95	-31.53	30.46	214
<i>Lindera subcoriacea</i>	Lauraceae	159.68	0.34	1.86	51.96	-30.95	29.35	61
<i>Lysimachia asperulifolia</i>	Primulaceae	254.54	0.28	1.63	51.95	-32.29	32.71	122
<i>Solidago verna</i>	Asteraceae	207.58	0.26	1.61	49.51	-31.88	32.34	122
<i>Stylisma pickeringii</i>	Convolvulaceae	202.37	0.23	2.74	48.90	-30.21	18.81	153

## Data Analyses

For the full data set spanning 1991-2014, we implemented a series of increasingly complex CJS models using the Bayesian statistical modeling language STAN (Carpenter et al. 2017). First, we fit a model to the data with constant survival (i.e. persistence) and detection probabilities across surveys and species. Next, we fit a model that allowed persistence and detection probability to vary across survey periods. While this model is slightly more complex, it did not account for variation between species. The next model estimated persistence and detection probability for each species, with species being considered a fixed effect. Finally, we fit a model to the data that considered species as a random effect and allowed for the inclusion of covariates that we hypothesized as being correlated with population persistence (Table 2). For each of the hierarchical models, we considered species as a random effect with a varying intercept, but a common slope. Because we were fitting the species as a random effect, we removed all species with fewer than ten populations in the dataset from this set of analyses. Furthermore, we excluded species that were not monitored for the entire study period because multiple follow-up surveys are required to fit CJS models. The remaining data set contained 723 populations of 14 species. We used the following generalized linear mixed model (GLMM) for the inclusion of a covariate:  $\text{logit}(\varphi_{i,t}) = \alpha_i + \beta * X_{i,t} + \epsilon_{i,t}$ , where  $\alpha$  is the random intercept term for species  $i$ ,  $\beta$  is the effect of covariate(s)  $X$  at time  $t$ , and  $\epsilon$  is the error. The inclusion of a covariate (e.g., canopy cover) as a predictor of persistence necessitated the modeling of individual heterogeneity for each population. We observed whether our models were able to recover parameters by simulating a dataset using known parameters (e.g., known detection probabilities, persistence, and covariate-persistence correlations) and using the model to estimate the known parameters from the simulated data.

We analyzed the data in a similar manner for each of the four objectives (Table 2). Analyses relating population persistence to fire frequency, canopy cover, metapopulation structure, area, and functional traits were performed as GLMMs (Breslow and Clayton 1993) with a binomial error structure and a logit link function that was embedded in a CJS model within a Bayesian framework. All predictor variables were scaled by subtracting the mean and dividing by the standard deviation. Species were treated as a random effect. We first analyzed each independent variable (except for species traits) individually in a model (e.g., fire, canopy cover, connectivity, area). Next, we ran a series of models with combinations of the management-relevant variables both with and without an interaction term (e.g. fire + canopy cover and fire + canopy cover + fire:canopy cover). We compared the models with and without interaction terms by first calculating the (log) marginal likelihoods for the two competing models. Next, we computed the Bayes Factor (Jeffreys 1961) and the posterior model probabilities for each of the alternative models using the package `bridgesampling` (Gronau et al. 2017). We performed all statistical analyses in the R version 3.6 (R Development Core Team 2019).

Finally, we explored the additional insights gained via the long-term ecological datasets by comparing the results from the 1991-2014 to data collected from 1991-1999. Because the 1991-1999 time step represents a single observation and does not allow for estimation of detection probabilities, we were unable to estimate detection probabilities for the 1999 survey. In order to make a fair comparison, we fit a GLMM with a binomial error structure, with species as a random effect, to both the 1991-1999 data and the 1991-2014 data. We compared these results, when detection probabilities were not included, to the results from our CJS models that include all the data (hereafter referred to as the full dataset).

## Results and Discussion

### Population Detection and Persistence

Across the 23-year period, plant populations on Fort Bragg generally exhibited high persistence between surveys. Mean population persistence among the three intervals was 0.92 ( $\pm$  0.01), while the mean detection probability was 0.88 ( $\pm$  0.01). Here and throughout this document, population persistence will be reported as the probability that the population survived from one survey until the next, with a mean interval of 7 years. These population persistence estimates were higher than persistence estimates that did not account for detection (mean = 0.81).

There were differences in detection probability across the surveys, but no differences in persistence across surveys after accounting for detection probability (Table 4). The 2006 survey had an estimated detection probability of 78%, lower than both the 1999 and 2014 surveys. A number of factors could be responsible for the difference in detection probabilities among surveys. The most likely explanation is that each of the three follow-up surveys (1999, 2006, and 2014) after the initial survey in 1991 were performed by different contractors and this likely contributed to some of the variation in detection probabilities. The initial survey was performed by The Nature Conservancy and consisted of teams of observers. The 1999, 2006, and 2014 surveys were performed by contractors that consisted of 1-2 individuals performing the surveys.

**Table 4: Mean persistence ( $\phi$ ), detection probability ( $\rho$ ) and their 95% confidence intervals across three survey periods.**

Parameter	Mean	SD	Confidence intervals	
			2.5%	97.5%
$\phi$ [1991-1999]	0.90	0.01	0.88	0.92
$\phi$ [1991-2006]	0.92	0.01	0.89	0.92
$\phi$ [1991-2014]	0.92	0.05	0.84	0.99
$\rho$ [1999]	0.95	0.01	0.93	0.97
$\rho$ [2006]	0.78	0.02	0.75	0.82
$\rho$ [2014]	0.92	0.05	0.84	0.99

Imperfect detection occurred for all species and detection varied among species and gross habitat categories (Table 5). The mean detection probability of the five upland species ( $0.89 \pm 0.01$ ) was greater than the nine wetland and ecotonal species ( $0.81 \pm 0.02$ ). This difference is likely due to the sparseness of understory vegetation in upland habitats as compared to the dense vegetation of wetland and ecotonal habitats. It is well known in the animal literature that ignoring imperfect detection results in overestimation of the deaths of individuals, but detection is not usually accounted for in plant studies (Kéry and Gregg 2003). This has the potential to obscure important environmental drivers of population persistence and may result in poor management prioritization. In this particular study, ignoring detection probabilities would have led to the conclusion that species occupying wetland habitats had higher levels of extirpation than were actually estimated after accounting for detection (see below).

**Table 5: Species detection and persistence probabilities. Wetland Status indicates whether species classified as wetland (0) or upland (1).**

Species	Code	Wetland Status	Persistence		Detection	
			Mean	SD	Mean	SD
<i>Amorpha georgiana</i>	AMGE	0	0.94	0.03	0.88	0.04
<i>Astragalus michauxii</i>	ASMI	0	0.93	0.02	0.83	0.03
<i>Danthonia sericea</i>	DASE	1	0.89	0.07	0.69	0.10
<i>Eupatorium resinosum</i>	EURE	1	0.82	0.03	0.85	0.03
<i>Lindera subcoriacea</i>	LISU	1	0.97	0.02	0.73	0.04
<i>Lysimachia asperulifolia</i>	LYAS	1	0.65	0.08	0.86	0.09
<i>Pyxidantha brevifolia</i>	PYBR	0	0.96	0.01	0.94	0.01
<i>Rhynchospora crinipes</i>	RHCR	1	0.75	0.11	0.69	0.13
<i>Schoenoplectus etuberculatus</i>	SCET	1	0.88	0.04	0.90	0.04
<i>Schoenoplectus subterminalis</i>	SCSU	1	0.91	0.04	0.91	0.05
<i>Solidago verna</i>	SOVE	1	0.89	0.05	0.90	0.05
<i>Stylisma pickeringii</i>	STPI	0	0.93	0.02	0.93	0.03
<i>Xyris chapmanii</i>	XYCH	1	0.82	0.07	0.79	0.09
<i>Xyris scabrifolia</i>	XYSC	1	0.81	0.07	0.76	0.09

Individual species demonstrated variability in population persistence over the 23-year period, ranging from 0.65 for *L. asperulifolia* to 0.97 for *L. subcoriacea* (Table 5). The consequences of species-level differences in population persistence for conservation and management are exacerbated because of the differences in the number of initial populations and the number of individuals/stems. For example, both *Eupatorium resinosum* and *Pyxidantha brevifolia* occurred in more than 130 populations in 1991, while *Dionea muscipula*, *L. asperulifolia* and *R. michauxii* each had fewer than ten populations (Gray et al. 2003). Both *L. pyrophyllum* and *L. asperulifolia* occur in very small populations of typically fewer than 10 individuals on Fort Bragg, while *Stylisma pickeringii* populations contained more than 280 individuals on average in 1991 (Figure 7). Consequently, management efforts identified in this report should consider these important differences.

Population persistence varied between hydrological positions, after accounting for detection probability (Table 5). The mean population persistence for the five upland species ( $0.95 \pm 0.01$ ) was greater than the nine wetland and ecotonal species ( $0.84 \pm 0.01$ ). Mesic drainages and the ecotones between drainages and xeric uplands are particularly susceptible to reduced fire frequency and can quickly become dominated by evergreen shrubs due to feedbacks between vegetation and fire behavior (Just et al. 2016). When maintained as a mix of herbaceous and woody vegetation, ecotones have both high biodiversity (Kirkman et al. 2004) and high numbers of rare plant species (Sorrie et al. 2006). Therefore, if one's objective is the conservation of rare plant populations, particular attention should be given to the fire frequency and vegetation structure in the wetland and ecotonal areas.

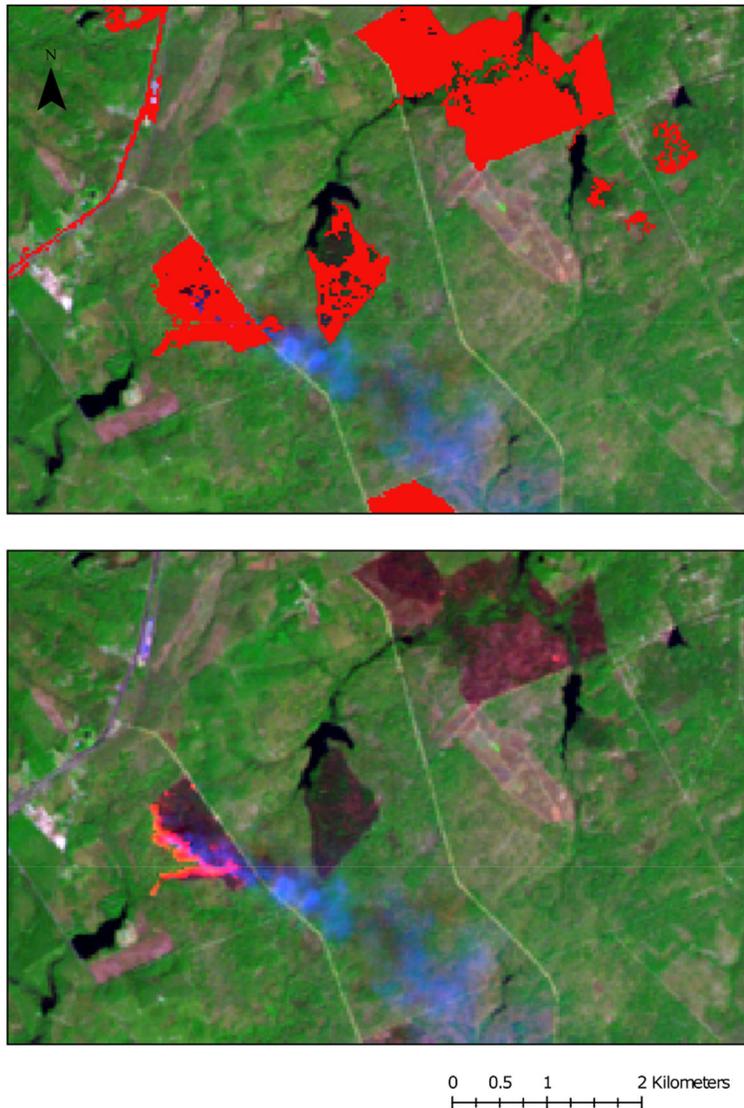


**Figure 7: The impact of population persistence on species conservation status varies due to differences in initial numbers of populations and population size. For example, there are more than 250 *Pyxidantha brevifolia* (upper left) populations on the installation, but only a few *Lysimachia asperulifolia* (upper right) populations. Populations of *Stylisma pickeringii* (lower left) typically contain hundreds of individuals, while *Lilium pyrophilum* (lower right) populations often contain just a few.**

### **Effects of Fire Frequency**

Results from modeling the prescribed fire history using Landsat imagery and the MIRBI indicated the model provided a satisfactory fit and was able to delineate burns in the landscape (Figure 8). Because installation personnel record the burn history at Fort Bragg at the burn block level, burn variation within a burn block is not recorded and thus ground-truthing of our model would need to occur, we were not able to explicitly estimate percent accuracy of our burn model. However, visual inspection of the results across the years 1991-2014 indicated that (1) the fire model was able to capture the burn compartments

accurately, (2) wetland areas that do not burn as frequently as upland areas were identified as unburned in many of the images, and (3) there was limited identification of burns that were not visible in the Landsat imagery. Fire frequency estimates, as recorded by installation personnel, were higher than the estimates from satellite imagery (Table 6). Over the entire period, fire frequency estimates across the 723 populations averaged 0.27 based on recorded fire history, but only averaged 0.15 (i.e. one fire every six years) based on the modeled fire history. Although the recorded fire frequency increased after 1999, the modeled fire frequency decreased, resulting in roughly similar frequencies between surveys when averaged across the two data sources (Table 6).



**Figure 8: Burn classification (top image, in red) of fires on Camp Mackall from 22 March, 2010 (bottom image). The use of the mid infrared burn index (MIRBI) and the Random Forest algorithm was able to satisfactorily capture burn history on Fort Bragg.**

**Table 6: Mean fire frequency across all populations over three cumulative time periods as recorded by installation personnel, estimated using satellite imagery and a Random Forest model, and averaged across the two fire frequency data sources.**

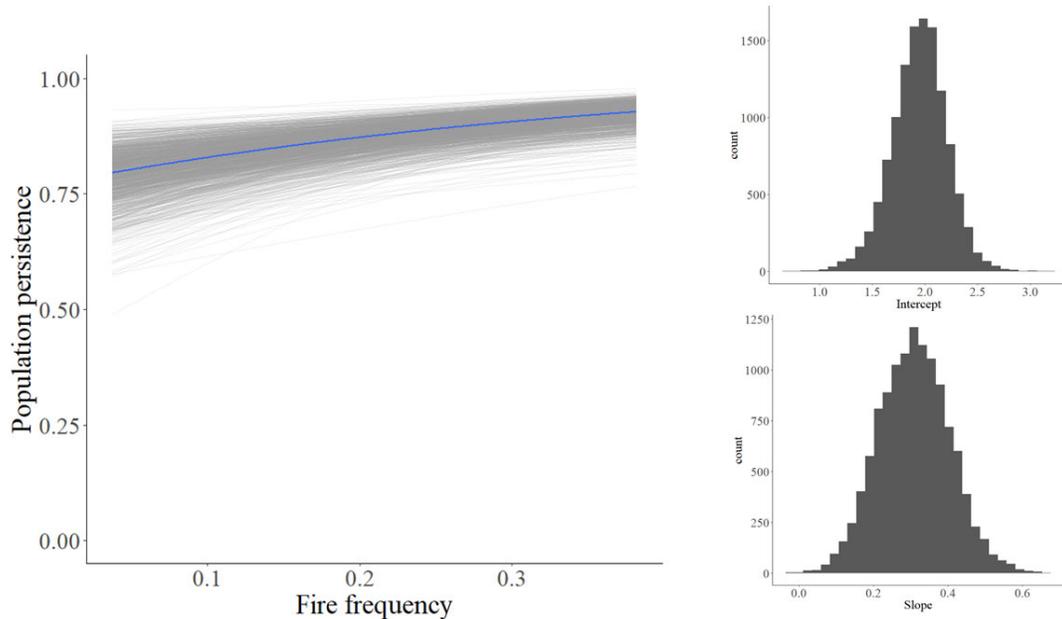
<b>Time period</b>	<b>Mean (<math>\pm</math>SD) recorded frequency</b>	<b>Mean (<math>\pm</math>SD) modeled frequency</b>	<b>Mean (<math>\pm</math>SD) of recorded and modeled frequencies</b>
1991-1999	0.23 (0.13)	0.17 (0.13)	0.20 (0.10)
1991-2006	0.29 (0.09)	0.15 (0.11)	0.22 (0.07)
1991-2014	0.28 (0.08)	0.13 (0.11)	0.21 (0.08)

Population persistence estimates for 14 species across 723 populations were positively correlated with average fire frequency from 1991-2014 (Figure 9), consistent with the findings of Gray et al. (2003) for the period 1991-1999. Under a mean fire frequency of 0.21 (approximately equivalent to two fires every 10 years), average population persistence between surveys was 0.88, but decreased to 0.83 when fire frequency decreased to 0.01 (equivalent to one fire every 10 years). When fire frequency increased to 0.33 (three fires every 10 years), average population persistence was estimated to increase to 0.91. While the difference between population persistence estimates of 0.83 and 0.91 (representing roughly one standard deviation from the mean for fire frequency) may appear small, for long-lived species with limited recruitment this represents a substantial loss of populations, and may be especially detrimental for species with a small number of initial populations.

Persistence of a species in a landscape is a delicate balance between extinction and recruitment of new subpopulations. Thus, the difference between subpopulation persistence estimates of 0.83 and 0.91 might be the difference between an extinction spiral versus long-term stability. These differences in persistence are particularly alarming when we consider the compounded losses over multiple intervals. Over the three intervals totaling 22 years, persistences of 0.83 and 0.91 are compounded to 0.57 and 0.75 for the low fire frequency and high fire frequency, respectively. While several years of fire suppression may be tolerable for most populations in this system, when compounded over time would have severe effects.

Prescribed fires at Fort Bragg are ignited primarily along road margins and often fail to burn throughout the entire burn unit, so populations near roads are expected, on average, to experience more frequent fire than those that are distant from roads. Therefore we examined whether distance to road has a detectable effect on population persistence, but found no evidence of a relationship (slope parameter = 0.01, standard error = 0.8, confidence interval = -0.14 to 0.18).

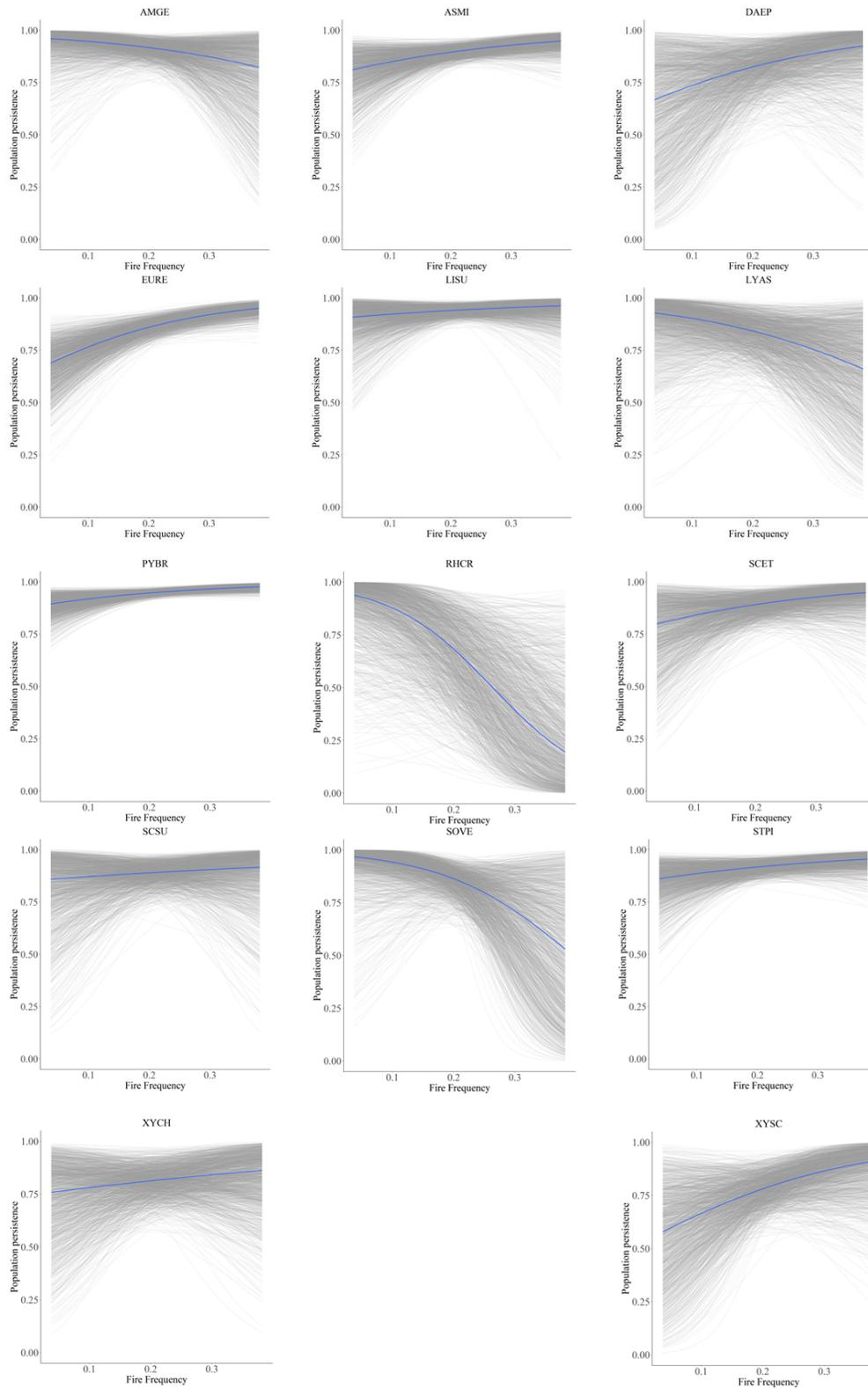
Stream margins are less likely to burn on average due to wetter fuels and greater woody plant cover so we also tested whether distance to stream is a significant predictor of population persistence. We found no evidence of an effect of distance to stream (slope parameter = -0.05, standard error = 0.10, confidence interval = -0.24 to 0.16).



**Figure 9: Effect of fire frequency on the probability of population persistence across 720 populations of 14 species over four surveys spanning 1991-2014. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

While the overall trend was for higher probability of population persistence with increased fire frequency, individual species exhibited differential responses to fire frequency (Figure 10). *Eupatorium resinosum* and *Pyxidantha brevifolia* exhibited the clearest responses to fire frequency, which is likely attributable to the large sample sizes for these two species (111 and 252 populations, respectively). In contrast, the two woody species in the study (*Amorpha georgiana* and *Lindera subcoriacea*) showed little to no response to increased fire frequency. Several species (e.g. *L. asperulifolia*, *Rhynchospora crinita*, and *Solidago verna*) appeared to exhibit decreased population persistence with increased fire frequency. However each individual species should be analyzed with all available data before management decisions are made, as there may be other explanations for a negative response to increased fire frequency. For example, fire suppression over the course of decades could have forced *L. asperulifolia* populations into higher (and drier) areas of the ecotone, thus placing them under unfavorable conditions. Prescribed fires could thus be acting on populations in suboptimal conditions.

A habitat- or ecosystem-based approach to conservation is often advocated in the absence of autecological information, a common problem for rare taxa. However, our analyses of individual species' responses to fire frequency revealed that a one-size-fits-all approach can fall short for some species. This metapopulation-scale insight mirrors findings conducted at finer ecological scales in our study system. For example, using matrix models Wall et al. (2012) showed that *A. michauxii* and *P. brevifolia* achieved their greatest population growth rates under a 4 year fire-return interval, which is a lower frequency than the 1-3 year interval suggested for longleaf pine restoration efforts (Glitzenstein et al. 2003).

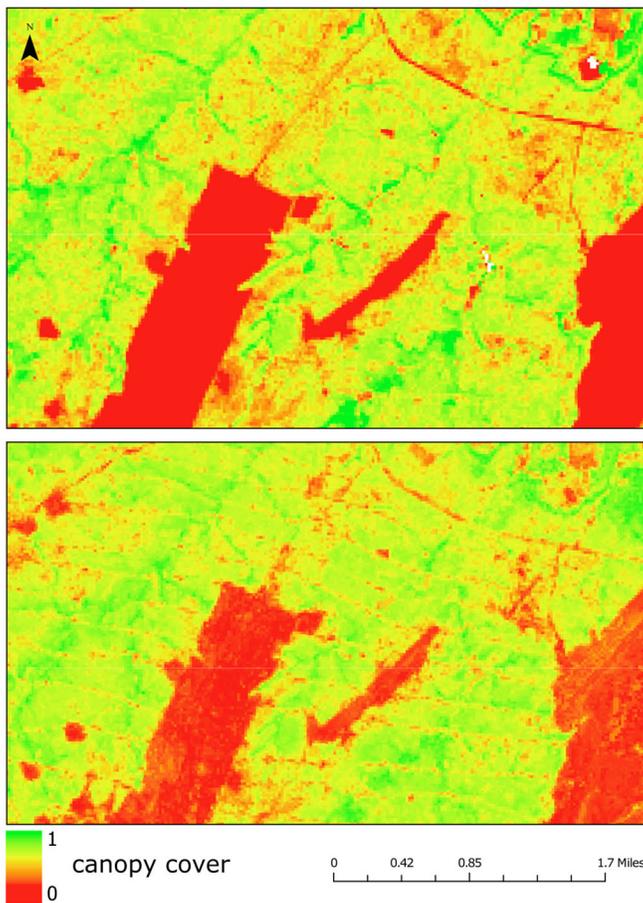


**Figure 10: Relationship between fire frequency and probability of population persistence for 14 species on Fort Bragg. Each thin gray line corresponds to one posterior sample from the Bayesian**

model analysis, and the thick blue line is the median of these samples. Species codes are provided in Table 4.

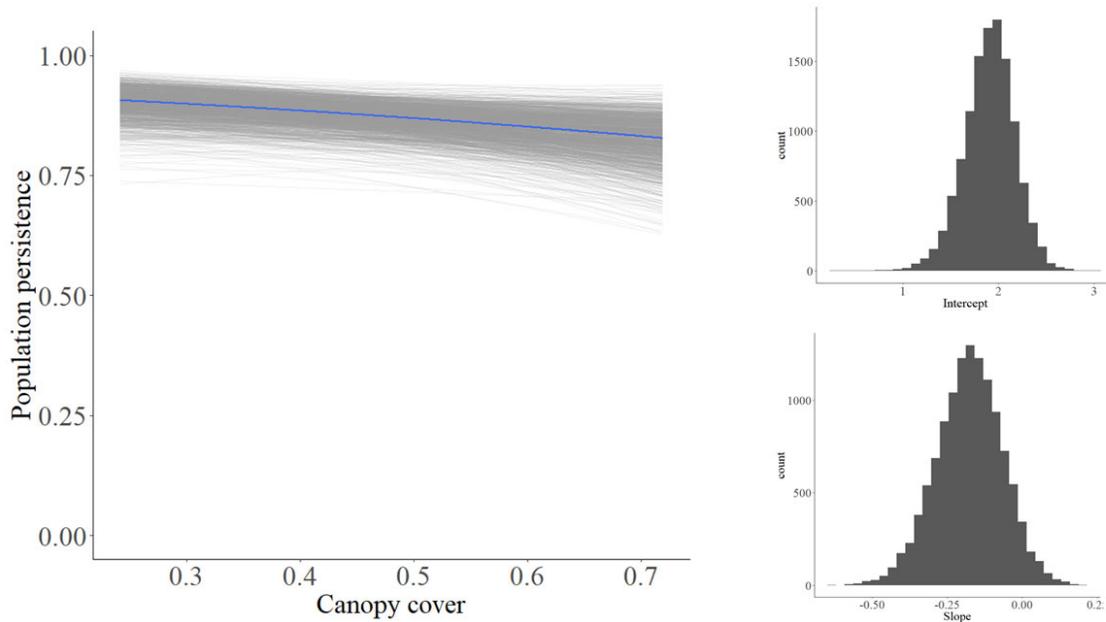
### Effects of Canopy Cover

Modeling canopy cover with Landsat imagery and a Random Forest algorithm appeared to capture canopy cover as estimated from the 2012 LiDAR data (Figure 11). The correlation between LiDAR derived canopy cover and our model was 0.81. This is remarkable since Landsat imagery is at a much coarser resolution (900 m<sup>2</sup>) relative to the collected LiDAR data. Across the three survey intervals (1991-1999, 1991-2006, 1991-2014), mean canopy cover estimates at rare plant populations were roughly the same for each of the three survey periods (0.46, 0.48, 0.49, respectively). This is an interesting result in that the Forestry Branch on Fort Bragg has done extensive canopy thinning and prescribed burning across the installation in the past few decades. The lack of an observed change in tree cover at these sites may reflect the tendency for rare species to occur predominantly in high-quality sites with sparse, mature longleaf pines, where thinning is unnecessary and burning is likely to have little effect on tree cover. Alternatively, thinning activities may be followed by infilling by crowns of surrounding large trees, which expand into the unoccupied space. Fire management activities on Fort Bragg have likely precluded hardwoods from reaching the midstory and canopy (Hoffmann et al. 2020).



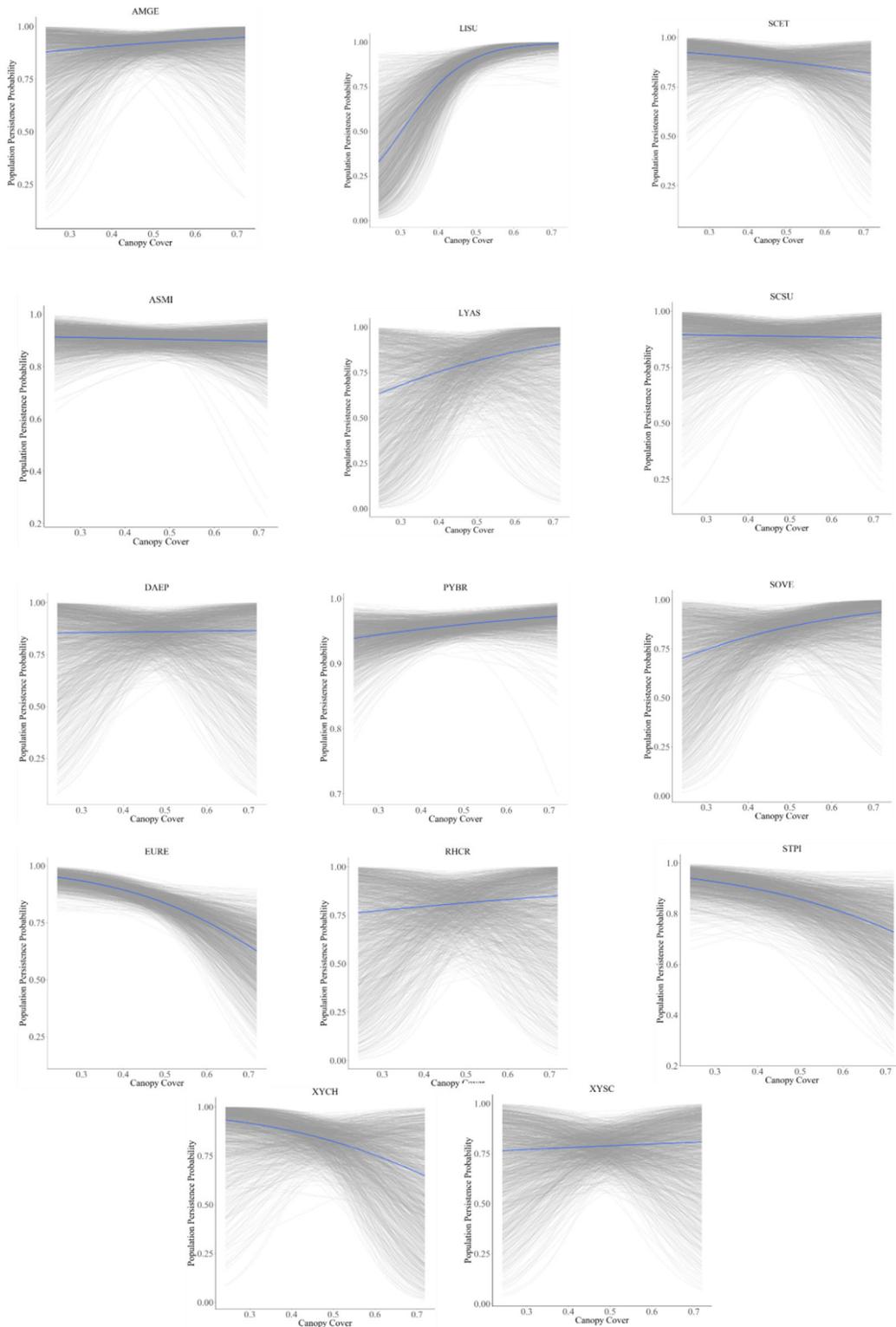
**Figure 11: Example of canopy cover (proportion) estimated from LiDAR flown 22 March 2013 (top), and canopy cover modeled using Landsat imagery and a Random Forest algorithm (bottom).**

Overall, higher canopy cover appeared to have a negative effect on population persistence (Figure 12), but the slope estimate for canopy cover did include 0 in the 95% confidence interval (-0.18; CI -0.40 – 0.03). Estimated population persistence at the mean canopy cover estimate (0.48) was 0.88. Population persistence decreased to 0.85 when canopy cover increased to 0.60. In contrast, low canopy cover estimates (e.g., 0.33) lead to increased population persistence (0.90). There was no evidence from the data that population persistence was negatively impacted by an extremely low canopy cover, when examined across species. These results are in alignment with studies that have looked at the effect of canopy cover and biodiversity in longleaf pine ecosystems, which have found that species richness increases with decreased canopy cover (Platt et al. 2006; Veldman et al. 2013). There are also suggestions in the literature that canopy cover up to a threshold of 70% does not affect understory biodiversity (Hiers et al. 2014). However, biodiversity may not be an appropriate surrogate for understanding rare plant population dynamics and making management decisions, and we must caution that species richness does not necessarily equate to rare plant species, as increases in species richness can be driven by increases in the number of ruderal or invasive species. In addition, our results suggest that population persistence decreases with increasing canopy cover at all canopy cover estimates and that there is no identifiable threshold where population persistence is not affected by increasing canopy cover.



**Figure 12: Effect of canopy cover (proportion) on the probability of population persistence across 723 populations of 14 species over four surveys spanning 1991-2014. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

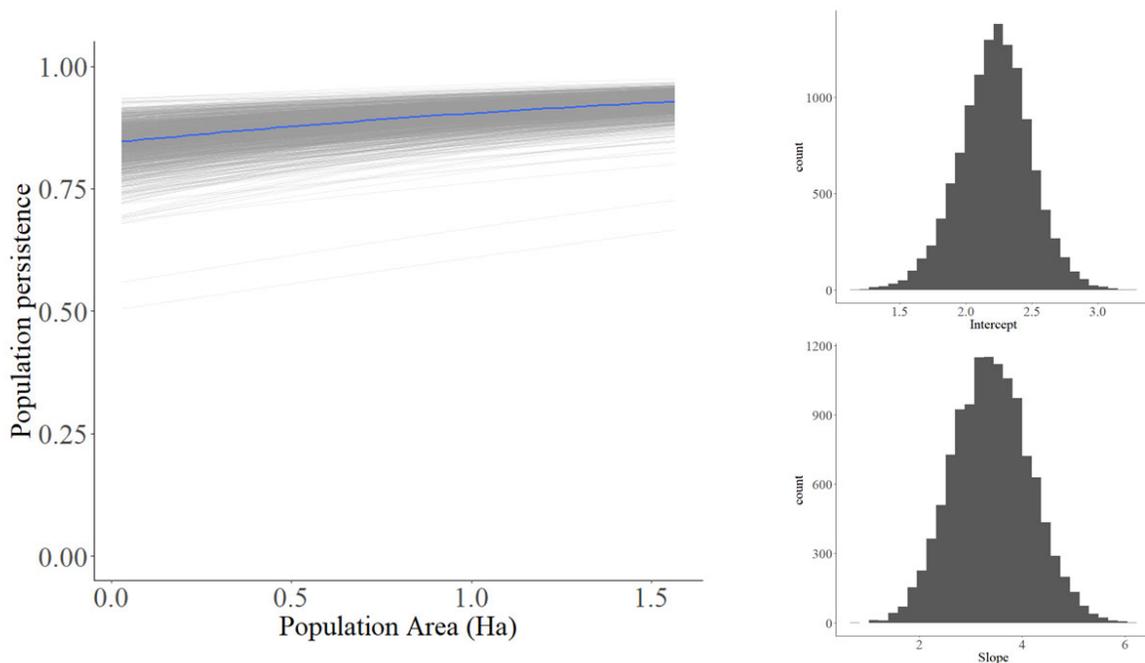
As expected, individual species demonstrated different responses to canopy cover (Figure 13). For example, *Lindera subcoriacea* exhibited a strongly positive relationship to increases in canopy cover, while population persistence in *Eupatorium resinosum* and *Stylisma pickeringii* was negatively correlated with canopy cover. As we pointed out earlier, one needs to be careful in concluding that canopy cover is either negative or positive for individual species without including all available data. In the case of *Stylisma pickeringii*, it is known that the species performs better in areas of reduced biomass, both in the ground layer, and in the midstory and canopy. However, the results for other species may be more complicated. *Lindera subcoriacea* is found in a several different habitat types with varying canopy cover (Wall et al. 2013). An alternate explanation for *L. subcoriacea* demonstrating reduced population persistence in habitats with lower canopy cover is that these habitats are spatially restricted and thus population sizes in these habitats are naturally smaller and less likely to persist due to limitations in habitat size.



**Figure 13: Relationship between canopy cover (proportion) and the probability of population persistence for 14 species on Fort Bragg. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples. Species codes are provided in Table 4.**

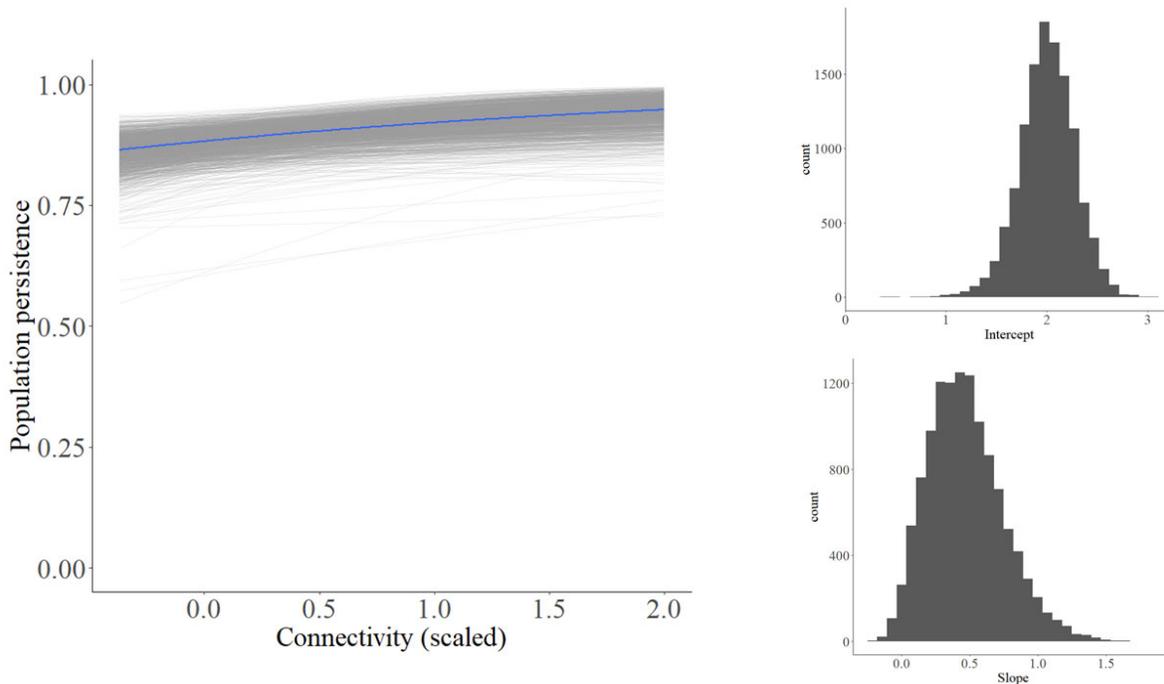
## Effects of Metapopulation Structure

The spatial extent (area occupied) of populations was predictive of population persistence, with large populations being more likely to persist relative to smaller populations (Figure 14). The median area occupied by populations across the surveys was 0.08 ha. Populations occupying this area were predicted to have a probability of persistence of 0.85. Populations with an average area of 0.35 ha had a probability of persistence of 0.87, while populations larger than 1.00 ha had an estimated persistence of 0.91. These results mirror the results of the influence of fire and canopy cover, in that most populations persist over multiple decades, even those occupying small spatial areas. We consider spatial extent to be a surrogate for the number of individuals in a population, although the relationship between population spatial extent and number of individuals is not perfect, owing to variation in population density across populations.



**Figure 14: Effect of population area on the probability of population persistence across 723 populations of 14 species over four surveys spanning 1991-2014. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

Our results demonstrate a correlation between population connectivity, as measured by Hanski's incidence function, and persistence (Figure 15). Isolated populations were more likely to be extirpated relative to more connected populations. These positive relationships between population persistence, connectivity, and area are anticipated based on metapopulation theory (Levins 1969) and the dynamic theory of island biogeography (MacArthur and Wilson 1963; MacArthur and Wilson 1967; Hanski 2001). Still, it is surprising that long-lived species that likely have limited reliance on new individuals to maintain populations also exhibit a correlation between population connectivity and persistence.



**Figure 15: Effects of patch connectivity on the probability of population persistence for 14 species across 723 populations on Fort Bragg. Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median of these samples.**

Although demographic data are only available for a small subset of species, the continued persistence of small populations of rare species is mostly likely contingent on the survival of long-lived individuals. Long-term observations suggest rates of recruitment for most species are low, which implies rates of survival are high and individual life spans exceed a decade or longer (Franco and Silvertown 2004). For example, we have documented survivorship of large individuals over four or more years to be 0.99, 0.98, 0.79, and 0.99 for *A. georgiana*, *A. michauxii*, *L. pyrophilum*, and *P. brevifolia*, respectively (Wall et al. 2012; Hohmann and Wall 2018).

### Effects of Functional Traits

Results did not indicate that any of the seven functional traits on their own were particularly predictive of overall population persistence (Table 7), but two trait-environment interactions (fire:SLA and canopy cover:flowering onset) were significant. We had anticipated that the interactions would provide greater predictive information than the trait variables, given that the functional importance of traits is manifest in how they perform under specific environmental conditions. For example, the negative effect of increased fire frequency on population persistence of species with high SLA (i.e. low mass per unit area), which is generally associated with rapid growth in resource rich sites, is potentially attributable to reductions in the soil nutrient profile that do not favor high SLA after repeated fires (de Souza et al. 2016).

Previous studies in this system have also shown that (1) fire and its interactions with soil moisture availability drive community-weighted mean (CWM) functional traits (Ames et al. 2016), (2) multiple

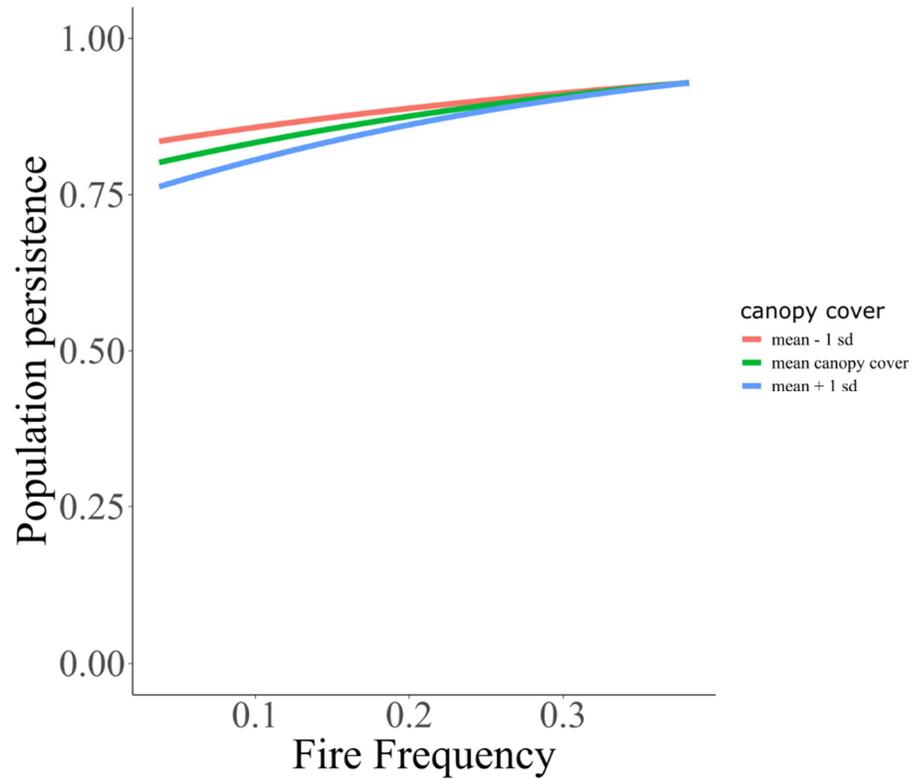
functional traits associated with flowering, flammability and leaf tissue chemistry differ between 19 rare and 134 co-occurring common species (Ames et al. 2017), and (3) functional traits are relevant for predicting individual survival during rare plant reintroductions (Ames et al. 2020). Specifically, rare species had a shorter flowering duration, later onset of flowering, higher flammability, higher leaf percent N, and lower C:N relative to more common species. Higher functional similarity between reintroduced individuals of four species (*A. georgiana*, *A. michauxii*, *L. pyrophilum*, and *L. asperulifolia*) and the local community, as measured by differences between their multivariate functional traits and the community weighted mean traits of their immediate neighbors, enhanced survival and was a stronger predictor of survival than local variation in abiotic variables (e.g., canopy cover, soil moisture, number of fires

**Table 7: Mean parameter estimates and 95% confidence intervals for population persistence models that include fire or canopy cover, species traits, and interactions. Traits include specific leaf area (SLA), leaf dry matter content (LDMC), N (%), C (%), C:N,  $\delta^{13}C$ , and date of flowering onset. Parameter estimates that don't contain 0 within the 2.5%-97.5% confidence interval are in bold.**

Variable	Trait	Parameter	Mean	SD	Confidence interval	
					2.5%	97.5%
fire	SLA	trait	-0.10	0.41	-0.85	0.81
<b>fire</b>	<b>SLA</b>	<b>fire:trait</b>	<b>-0.24</b>	<b>0.11</b>	<b>-0.45</b>	<b>-0.03</b>
fire	LDMC	trait	0.29	0.42	-0.57	1.11
fire	LDMC	fire:trait	0.06	0.18	-0.29	0.43
fire	N (%)	trait	0.10	0.51	-0.97	1.09
fire	N (%)	fire:trait	0.09	0.13	-0.15	0.35
fire	C (%)	trait	-0.36	0.51	-1.35	0.71
fire	C (%)	fire:trait	0.00	0.12	-0.23	0.24
fire	C:N	trait	-0.19	0.49	-1.11	0.84
fire	C:N	fire:trait	-0.09	0.13	-0.34	0.16
fire	$\delta^{13}C$	trait	0.53	0.32	-0.17	1.12
fire	$\delta^{13}C$	fire:trait	0.15	0.14	-0.12	0.43
fire	flowering onset	trait	-0.89	0.61	-2.08	0.32
fire	flowering onset	fire:trait	0.17	0.23	-0.26	0.64
canopy cover	SLA	trait	-0.11	0.39	-0.81	0.76
canopy cover	SLA	canopy cover:trait	-0.06	0.15	-0.34	0.25
canopy cover	LDMC	trait	0.31	0.38	-0.47	1.06
canopy cover	LDMC	canopy cover:trait	0.01	0.19	-0.38	0.38
canopy cover	N (%)	trait	0.06	0.52	-1.01	1.05
canopy cover	N (%)	canopy cover:trait	0.14	0.13	-0.13	0.40
canopy cover	C (%)	trait	-0.35	0.52	-1.37	0.76
canopy cover	C (%)	canopy cover:trait	-0.17	0.12	-0.41	0.07
canopy cover	C:N	trait	-0.17	0.49	-1.09	0.83
canopy cover	C:N	canopy cover:trait	-0.14	0.13	-0.39	0.11
canopy cover	$\delta^{13}C$	trait	0.39	0.33	-0.31	0.99
canopy cover	$\delta^{13}C$	canopy cover:trait	0.17	0.16	-0.14	0.47
canopy cover	flowering onset	trait	-0.87	0.59	-2.03	0.33
<b>canopy cover</b>	<b>flowering onset</b>	<b>canopy cover:trait</b>	<b>-0.61</b>	<b>0.25</b>	<b>-1.10</b>	<b>-0.13</b>

## Interactions

There was no evidence for an interaction between fire frequency and canopy cover, with the posterior probability of the model with no interaction term (0.78) being greater than a model that included an interaction term (0.22) (Figure 16, Table 7). This result suggests that the effects of higher fire frequency on population persistence operates across a range of canopy covers.

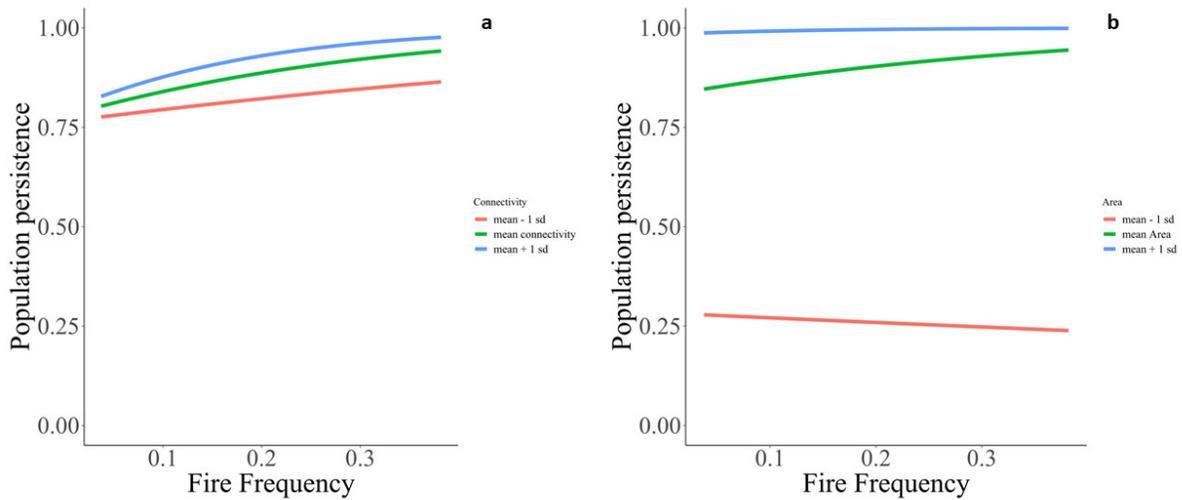


**Figure 16: Effect of the interaction between fire frequency (X axis) and canopy cover on the probability of population persistence.**

**Table 8: Mean parameter estimates and 95% confidence intervals for population persistence models that include two variables and an interaction term. Parameter estimates that don't contain 0 within the 2.5%-97.5% confidence interval are in bold.**

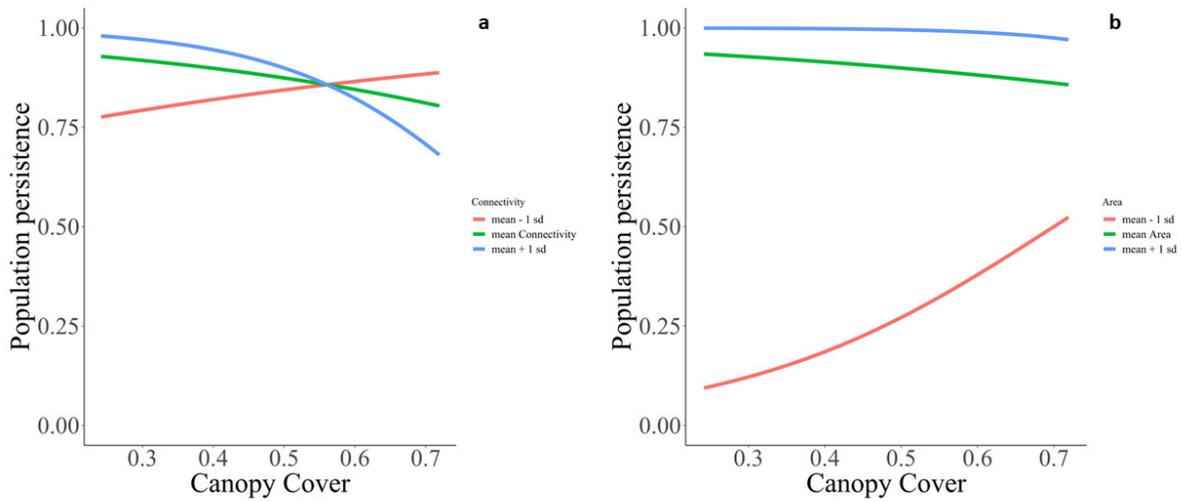
Model	Parameter	Mean	SD	2.50%	97.50%
<b>fire and canopy cover</b>	<b>fire</b>	<b>0.29</b>	<b>0.1</b>	<b>0.11</b>	<b>0.48</b>
fire and canopy cover	canopy cover	-0.11	0.11	-0.34	0.1
fire and canopy cover	interaction	0.06	0.08	-0.11	0.21
<b>fire and connectivity</b>	<b>fire</b>	<b>0.35</b>	<b>0.11</b>	<b>0.14</b>	<b>0.58</b>
<b>fire and connectivity</b>	<b>connectivity</b>	<b>0.55</b>	<b>0.28</b>	<b>0.06</b>	<b>1.18</b>
fire and connectivity	interaction	0.19	0.25	-0.24	0.72
<b>fire and area</b>	<b>fire</b>	<b>0.28</b>	<b>0.12</b>	<b>0.05</b>	<b>0.53</b>
<b>fire and area</b>	<b>area</b>	<b>3.32</b>	<b>0.79</b>	<b>1.82</b>	<b>4.92</b>
fire and area	interaction	0.33	0.7	-0.86	1.8
<b>canopy cover and connectivity</b>	<b>canopy cover</b>	<b>-0.28</b>	<b>0.14</b>	<b>-0.58</b>	<b>-0.02</b>
canopy cover and connectivity	connectivity	0.33	0.25	-0.04	0.93
canopy cover and connectivity	interaction	-0.49	0.31	-1.16	0.09
canopy cover and area	fire	-0.22	0.13	-0.49	0.04
<b>canopy cover and area</b>	<b>canopy cover</b>	<b>3.31</b>	<b>0.78</b>	<b>1.82</b>	<b>4.85</b>
canopy cover and area	interaction	-0.8	0.74	-2.31	0.59

As with fire frequency and canopy cover, there was no evidence of an interaction between fire frequency and population connectivity, with the posterior probabilities being roughly equal (0.42 with an interaction term versus 0.58 without). This is illustrated by examining the slopes under different connectivity scenarios (Figure 17a). These results suggest that there is no additional benefit of fire for isolated populations versus connected populations; the effects of fire are similar regardless of spatial isolation. There was some evidence of an interaction between fire frequency and area (posterior probability of 0.65 with an interaction term versus 0.35 without), with increased fire frequency having a mildly negative effect on small populations (Figure 17b).



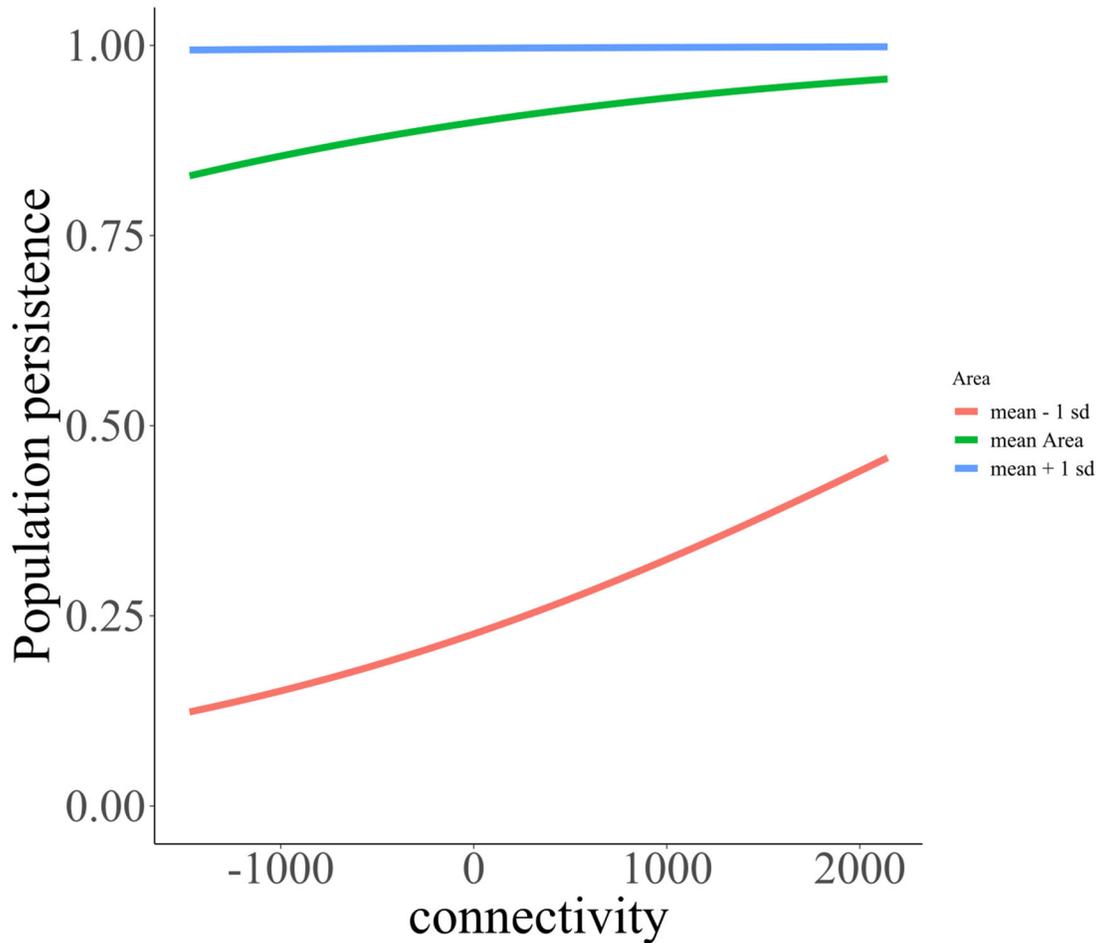
**Figure 17: Effect of the interaction between fire frequency (X axis) and connectivity (a) and population area (b) on the probability of population persistence.**

There was some evidence for a negative interaction between canopy cover and connectivity, with the posterior probability of the model that includes an interaction term between canopy cover and connectivity (0.73) being greater than a simpler model with no interaction term (0.27). There was a negative correlation between canopy cover and population persistence for population with average connectivity, while isolated populations appeared to benefit from canopy cover and exhibited increased population persistence under higher canopy cover (Figure 18a). Canopy cover had little effect on average and large area populations, but if anything, there was a positive effect of increasing canopy cover on populations with small area (Figure 18b).



**Figure 18: Effect of the interaction between canopy cover (X axis) and connectivity (a) and population area (b) on the probability of population persistence.**

There was some evidence for the persistence of small populations being positively impacted by greater connectivity relative to larger populations (Figure 19), with the posterior probability of a model that includes an interaction term (0.68) being roughly twice as great as a model without an interaction term (0.32). As expected, populations covering a large area persisted between surveys regardless of their level of connectivity, while smaller populations were positively impacted by connectivity.



**Figure 19: Effect of the interaction between population connectivity (X axis) and population area on the probability of population persistence.**

### Comparisons Between the Long-term and 1991-1999 Datasets

To address the research needs outlined in the SON, we confirmed or refuted the initial hypotheses and conclusions of Gray et al. (2003) regarding drivers of local extinction by comparing results obtained from analyses of the 1991-1999 dataset and results from the entire long-term dataset (1991-2014).

Contrary to the findings of Gray et al. (2003), estimates of the effects of fire frequency on population persistence from 1991-1999, as analyzed with a GLMM, were not significant. However, we did identify a significant effect of fire frequency on population persistence for the 1991-2014 dataset, with the mean slope being higher than the 1991-1999 parameter estimate (**Error! Not a valid bookmark self-reference.**). The parameter estimate for the full dataset ( $0.30 \pm 0.09$ ) was similar to the 1991-2014 dataset (that did not account for detection). Thus, expanding analyses over a longer time period, and refining estimates of fire frequency and population persistence (by accounting for detection probability) appeared to have a substantial impact on our understanding of the relationship between persistence and fire frequency. There are likely two reasons for the differences between the initial analyses of Gray et al (2003) and the results presented here. First, we modeled the data with a random species effect, which increases the variance. Secondly, the analyses presented in this report did not include all the

populations that were included in Gray et al (2003). The reason for this is that monitoring of several species was suspended after 1999 due to updated conservation status of the species.

Gray et al. (2003) did not explicitly evaluate the effects of canopy cover on population persistence; however, our evaluation of the effects of canopy cover based only on the 1991-1999 dataset identified no significant relationship (**Error! Not a valid bookmark self-reference.**). Similarly, no significant relationship was found for the long-term dataset when analyzed with a GLMM. This is in contrast to the full model that includes detection probability, where a negative relationship between canopy cover and population persistence was found (Figure 13).

Gray et al. (2003) found a positive relationship between population persistence and area occupied. Our reanalysis of the 1991-1999 and the 1991-2014 dataset revealed a similar positive relationship between population persistence and area occupied, with no marked differences in the shape of the relationship over the short- versus long-term (**Error! Not a valid bookmark self-reference.**), confirming that area occupied has a significant impact on population persistence.

Gray et al. (2003) did not explicitly evaluate the effects of population connectivity on persistence; however, our evaluation of the effects of connectivity on population persistence based only on the 1991-1999 dataset generated a positive correlation, but no correlation of spatial isolation and population persistence based on the 1991-2014 dataset (**Error! Not a valid bookmark self-reference.**). These results are interesting, in the fact that the results suggest that, through time, the correlation between spatial isolation and population persistence is decreasing.

**Table 9: Slope estimates for the relationship between population persistence and fire frequency, canopy cover, area, and spatial isolation over the two time periods 1991-1999 and 1991-2014. Parameter estimates that do not contain 0 within the 2.5%-97.5% confidence interval are in bold.**

Parameter [period]	Mean	SD	Confidence intervals	
			2.50%	97.50%
fire [1991-1999]	0.11	0.10	-0.09	0.31
<b>fire [1991-2014]</b>	<b>0.27</b>	<b>0.10</b>	<b>0.06</b>	<b>0.47</b>
canopy cover [1991-1999]	-0.13	0.12	-0.35	0.10
canopy cover [1991-2014]	0.08	0.10	-0.11	0.27
<b>area [1991-1999]</b>	<b>1.07</b>	<b>0.17</b>	<b>0.75</b>	<b>1.42</b>
<b>area [1991-2014]</b>	<b>0.68</b>	<b>0.11</b>	<b>0.47</b>	<b>0.90</b>
<b>spatial isolation [1991-1999]</b>	<b>1.23</b>	<b>0.80</b>	<b>0.06</b>	<b>3.18</b>
spatial isolation [1991-2014]	0.01	0.18	-0.30	0.38

## Conclusions and Implications for Future Research/Implementation

Our results confirm three of our four initial hypotheses during the course of this study (Table 2). First, fire frequency is positively correlated with rare plant population persistence on Fort Bragg. This is in alignment with other studies in the longleaf pine ecosystem that have looked at either biodiversity or individual species. Next, there is evidence for a negative correlation between canopy cover and population persistence, with populations under higher canopy cover being less likely to persist relative to populations under low canopy cover. We also found that metapopulation structure, specifically

population connectivity, was positively correlated with persistence. This is the most surprising result of the study, as most of the species in the MARPS dataset are long-lived species with limited dispersal and/or recruitment. Our final hypothesis was that plant functional traits would be correlated (either positively or negatively) with population persistence. We were unable to confirm this hypothesis, but in the results and discussion we suggest several reasons for this result. Briefly, the included populations span a range of hydrological conditions and vegetation communities which select for specific functional traits. It is likely that by including populations from such a wide range of conditions masked the underlying directionality of the functional traits. Across all study species, populations that experience frequent fires, occur under low canopy cover, are highly connected or occupy a large area, and occur in upland habitats are expected to have higher probabilities of persistence than populations under opposite conditions

The present study demonstrates the benefits of collecting, in a consistent manner, long-term data from rare species on military installations. Without these efforts, it would be difficult to reach the conclusions that we were able to infer based on multiple surveys. This is clearly demonstrated by comparing our results using mark-recapture models with single survey methods that are not able to estimate detection probabilities (**Error! Reference source not found.**). If conclusions were drawn based on just the 1991-1999 data, one would infer that fire and canopy cover had no effect on population persistence. Likewise, conclusions based on the 1991-2014 (and not including population detection) would be that canopy cover and population connectivity had no effect on population persistence. Only with access to the full data set, collected over 23 years and across multiple surveys, were we able to reach the conclusions presented in this study. Furthermore, the long and repeated nature of the MARPS data set made it possible to apply appropriate analytical tools to avoid biases that arise from imperfect detection of populations. Ignoring imperfect detection results in overestimation of population extirpations, can obscure identification of important environmental drivers of population persistence, and may result in poor management prioritization. Estimation of detection probabilities is only possible with carefully executed, repeated surveys over sufficient timespans.

The trends in the data are strong, even when species identity is ignored, providing valuable evaluation of generalized management strategies. However the results also reveal substantial diversity in species response to fire and canopy cover, necessitating species-specific management where adequate knowledge is available and additional detailed studies where knowledge is still insufficient to inform management. In general, ecosystem approaches may be appropriate as initial solutions in the absence of autecological information, but they are unlikely to generate long-term benefits for all species when multiple species of conservation concern are relevant. The benefits of species-specific data, as compared to biodiversity indices (e.g., species richness or evenness metrics) were demonstrated in the present study. Without this information, we would not have been able to demonstrate the differential species responses to abiotic factors such as fire frequency and canopy cover. While we did not, in the current study, investigate individual species beyond identifying differences, these data can generate hypotheses in their own way. We were also only able to investigate our hypotheses for a subset of the rare species on Fort Bragg, due to data limitations. For the species not included in our analyses, the relationship between population persistence and environmental drivers remains unknown. Consequently, additional detailed studies are needed to inform the conservation management of rare species on Fort Bragg.

When examined across all species, the effect of canopy cover on population persistence was not as strong as other factors, however individual species exhibited a strong response. These species-specific

responses can be used to inform management. For example, the continuous, installation-wide, high resolution, historical, canopy cover estimates generated for our analyses will allow explicit identification of the long- and near-term canopy conditions to which populations have been exposed. With this information, populations exposed to unsuitably high canopy cover can be prioritized for management. Importantly, prior to our modelling effort, no information about canopy cover was available to inform management. This is especially relevant when a particular species is listed, or being considered for listing, under the Endangered Species Act. Additionally, we have confirmed the value and benefit of long-term data for elucidating important drivers of rare plant population persistence in our study system.

### **Implications for Future Research**

The MARPS database is a unique resource for understanding the dynamics of rare species populations, and its value will continue to grow as future surveys are performed. In fact a new survey is currently underway. The additional data generated by future surveys will be invaluable for investigating long-term metapopulation dynamics of rare plants by providing more robust estimates of relationships we elucidated here.

The results revealed substantial interspecific variation in plant response to environmental factors. While this result is quite robust, the details of the responses of individual species are not, particularly for the rarest species. While continued monitoring would gradually allow for improved parameter estimates, it is important that long-term population monitoring be complemented with detailed demographic studies of those species most at risk.

### **Implications for Management and Recommendations**

In regards to specific management recommendations, there are a number of management implications and recommendations based on the present study. First, the results suggest a general benefit of increasing the fire frequency, though it is important to acknowledge that some species would likely be negatively affected, so continued careful monitoring of impact would be important. While Fort Bragg is nominally on a three year burn cycle, it is clear from our results that the actual fire frequency is lower for a subset of the populations. This is especially true for species of wetlands and their ecotones, which often fail to burn when prescribed fire is applied to adjacent uplands. These species are in a tenuous position, as many of them require wet conditions but relatively open habitat (e.g., *Eupatorium resinotum*). Wetland habitats are more dynamic than upland habitats with regard to vegetation cover, as fire plays a larger role in determining vegetation structure over shorter time scales. Under long fire-return intervals, clonal shrubs and other woody species can dominate wetland and ecotonal areas on Fort Bragg. This situation can set up a positive feedback that precludes future fires from entering the wetland areas.

We recommend increasing the fire frequency, which, if implemented appropriately, could lead to the reduction in woody vegetation in ecotonal areas that are the most susceptible to woody encroachment. An increase in frequency should be accompanied with careful monitoring because not all species are expected to benefit from additional burning. For species that are negatively impacted by frequent burning, such as those that need a longer fire-free window for successful recruitment, introduction of variation in fire interval may mitigate the effects of frequent burning. The recent trend on Fort Bragg toward longer fire return intervals may be problematic, especially given the continued

extirpation of populations. The results of the present study can be used by installation personnel to identify populations that may warrant targeted prescribed burning. In addition, we recommend extending our remote-sensing approach to estimating fire history on other public and private lands to inform management of rare plant populations. This could be especially relevant for public and private lands surrounding Fort Bragg. Considering the strong influence of population connectivity that we observed here, the success of rare plant populations will bring benefits to the persistence of these species on Fort Bragg, and vice versa.

The second management implication of the present study is that reduced canopy cover has an overall beneficial effect on rare plant populations on Fort Bragg. While the results of the effects of canopy cover were not as conclusive as fire frequency, we are still able to conclude that it has an effect on population persistence. Canopy cover was not investigated in the original study of Gray et al. (2003), though our analyses in the current study suggest that it would have been difficult to identify canopy cover as a factor influencing population persistence using a single time step, whether from 1991-1999 or 1991-2014. However, utilizing our innovative approach to estimating canopy cover allowed us to demonstrate the negative influence of high canopy cover has on rare plant populations on Fort Bragg. This is supported not only by the results presented here, but also by personal observations and anecdotal evidence as well. Installation personnel and the current authors have observed a number of species and plant populations on Fort Bragg that have benefitted from reduced canopy cover. The plant populations on Fort Bragg have benefitted from forest thinning operations related to the listing of the red-cockaded woodpecker in the 1990s. With the future conservation status of the red-cockaded woodpecker is uncertain, continued canopy thinning operations are recommended if the persistence of rare plant populations is one of the installation's management goals.

A third important management implication from the current study is that metapopulation structure and population connectivity is important, with isolated populations more likely to be extirpated relative to more connected populations. These results become especially important for species that have a limited number of populations that experience a high degree of separation (e.g., *Lilium pyrophilum*). These populations are more likely to experience extirpation, and so manipulating metapopulation structure and population connectivity via population reintroduction and augmentation is one of the solutions to increasing the probability of population persistence (e.g., Hohmann and Wall 2018). Connectivity is characterized by both population size and separation distance, which inherently provides two options on which to focus management attention. However, population reintroduction and augmentation have a number of drawbacks relative to manipulating fire frequency and canopy cover. First, reintroduction success can be determined by a number of factors and can have a relatively high failure rate. Second, the cost of a reintroduction project is likely more than prescribed burns and canopy thinning. Understandably, there may be some reservations about introducing rare plant populations into certain locations to increase connectivity due to potential conflict with training land use should a species be federally listed. Increasing the size of existing populations via augmentation or habitat management may alternately enhance metapopulation structure and population persistence with fewer conflicts on training land use.

These three factors, fire frequency, canopy cover, and metapopulation structure, represent a continuum of management options in terms of resource investment. Burning management units at a frequent (i.e. 3-yr) interval is likely the least costly in terms of resource investment and would likely yield the greatest benefits. If management units are not burned frequently and woody vegetation is allowed to escape the fire trap and enter the midstory and canopy, thinning is the second option. However, canopy thinning can lead to unintended negative consequences such as ground disturbance and impacts

to native vegetation, including rare plant populations. Reduced fire frequency and the eventual increase in canopy cover would lead to, based on our results, reduced population connectivity, as small populations are lost. Thus the reduction in fire frequency would exacerbate these other threats to rare plant species on Fort Bragg.

Natural resource managers in the Southeast have a limited number of management tools they can efficiently employ to achieve conservation goals. Although rare plant species and the native plant communities in which they occur have historically been, and continue to be, impacted by a diversity of threats (e.g., invasive species, hydrological alteration, habitat fragmentation, and wholesale land-use and cover change), one of the most pervasive pressures is woody encroachment due to fire suppression. Woody encroachment reduces light availability in the ground layer, eliminating the high light conditions needed by many of the rare plants in the region. Where woody encroachment has not yet altered fire dynamics, application of prescribed fire is the most effective and cost-efficient tool land managers have for maintaining and restoring longleaf ecosystems.

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