EXECUTIVE SUMMARY

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

SERDP Project RC-2707

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ACRONYMS AND ABBREVIATIONS

CJS	Cormack-Jolly-Seber model
CONUS	Continental United States
DoD	Department of Defense
ESA	Endangered Species Act
GLMM	generalized linear mixed models
LDMC	leaf dry matter content
LiDAR	Light Detection and Ranging
MARPS	Monitoring and Assessment of Rare Plant Species
MIRBI	Mid Infrared Burn Index
RF	Random Forest
SERDP	Strategic Environmental Research and Development Program
SLA	specific leaf area
TES	Threatened and Endangered Species
WUE	water use efficiency

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1.0 INTRODUCTION

Department of Defense (DoD) 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.

Table 1. Objectives and Hypotheses

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

2.0 OBJECTIVES

Text 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 (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 (MARPS) database. Using the first two of these surveys, (Gray et al. 2003) the project team undertook an analysis of population dynamics to test the following hypotheses:

- Prescribed fire reduces population extirpation rates.
- Fire increases population size.
- Populations persistence is positively correlated with population size.
- Plant functional groups differ in their response to fire frequency.

Since this initial analysis, two additional surveys have been undertaken, thereby increasing by three-fold the duration of the study.

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

3.0 TECHNICAL APPROACH

MARPS 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 a 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), the project team modeled the data using a methodology that can estimate detection probabilities while also estimating population persistence.

For each of the four objectives (Table 1), the project team 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 (φ), 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 capture history of "1011."

Characterizing Fire Frequency: To quantify the effect of fire frequency on population persistence, the project team 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. The project team therefore complemented these data with fire histories reconstructed from satellite images.

The project team 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: The project team modeled canopy cover for the years 1991-2014 using LiDAR from 2012, Landsat imagery, and a RF classification model, in a manner similar to the project team's approach to modeling the fire history.

Characterizing Metapopulation Structure: Metapopulation structure was estimated for each species with ≥ 10 populations using the connectivity parameter (S) from the incidence function model (Hanski 1998). Specifically, the project team estimated connectivity for each population using the following formula: $S_i = \sum_{(j \neq i)} \exp(-\alpha d_{ij}) p_j A_j$, where α 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 (m2) of the patch j. The project team arbitrarily set α to 0.01 and did not modify α for individual species.

Characterizing Species Functional Traits: The project team estimated the effects of species' functional traits on population persistence using a subset of seven species for which data were available and have ≥10 populations on Fort Bragg (Ames et al. 2017). The project team examined seven traits that have been associated with plant performance in the project team's 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, the project team implemented a series of increasingly complex CJS models using the Bayesian statistical modeling language STAN (Carpenter et al. 2017). First, the project team fit a model to the data with constant survival (i.e., persistence) and detection probabilities across surveys and species. Next, the project team 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, the project team fit a model to the data that considered species as a random effect and allowed for the inclusion of covariates that the project team hypothesized as being correlated with population persistence (Table 1). For each of the hierarchical models, the project team considered species as a random effect with a varying intercept, but a common slope. Because the project team was fitting the species as a random effect, the project team removed all species with fewer than ten populations in the dataset from this set of analyses. Furthermore, the project team 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. The project team 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 α is the random intercept term for species i, β is the effect of covariate(s) X at time t, and ϵ 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. The project team observed whether the 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.

The project team 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. The project team first analyzed each independent variable (except for species traits) individually in a model (fire, canopy cover, connectivity, area). Next, the project team ran a series of models with combinations of the management-relevant variables both with and without an interaction term (fire + canopy cover and fire + canopy cover + fire:canopy cover). The project team compared the models with and without interaction terms by first calculating the (log) marginal likelihoods for the two competing models. Next, the project team computed the Bayes Factor (Jeffreys 1961) and the posterior model probabilities for each of the alternative models using the package bridge sampling (Gronau et al. 2017). The project team performed all statistical analyses in the R version 3.6 (R Development Core Team 2019).

Finally, the project team explored the additional insights gained via the long-term ecological datasets by comparing the results from the 1991-2014 data 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, the project team was unable to estimate detection probabilities for the 1999 survey. In order to make a fair comparison, the project team 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. The project team compared these results, when detection probabilities were not included, to the results from the project team's CJS models that include all the data (hereafter referred to as the full dataset).

4.0 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 (± 0.01), while the mean detection probability was 0.88 (± 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 (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 ± 0.01) was greater than the nine wetland and ecotonal species (0.81 ± 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 ± 0.01) was greater than the nine wetland and ecotonal species (0.84 ± 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 (Figure S1), 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 0.1 (equivalent to one fire every 10 years). When fire frequency increased to 0.33 (equivalent to 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.

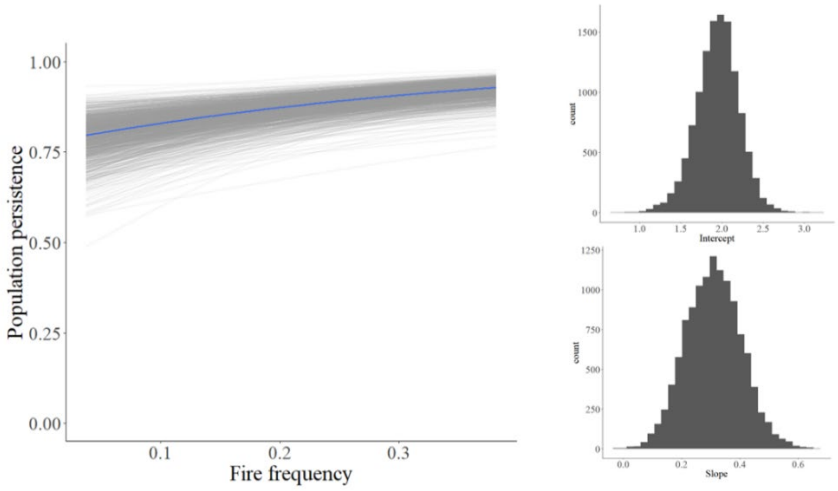

Figure 1. Effect of Fire Frequency on the Probability of Population Persistence Across 720 Populations of 14 Species over Four Surveys Spanning 1991-2014.

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 S2), 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).

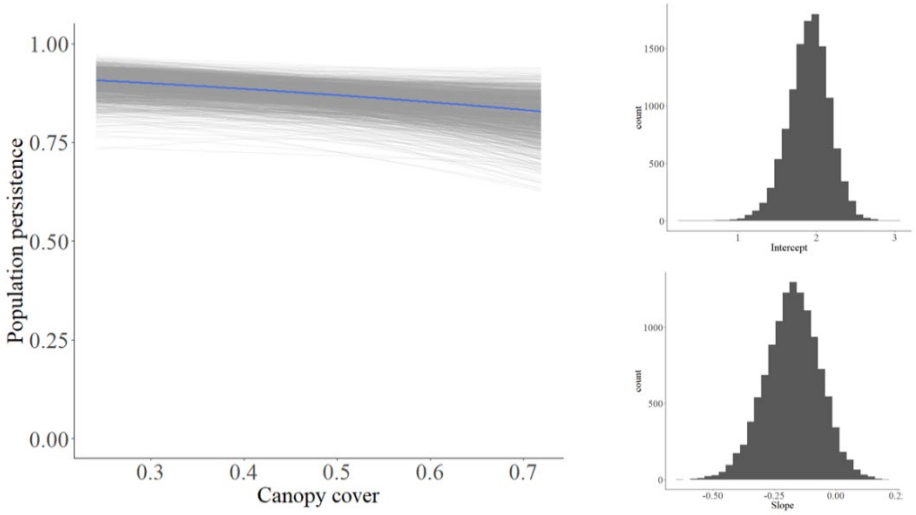

Figure 2. Effect of Canopy Cover (Proportion) on the Probability of Population Persistence Across 723 Populations of 14 Species Over Four Surveys Spanning 1991-2014.

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 S3).

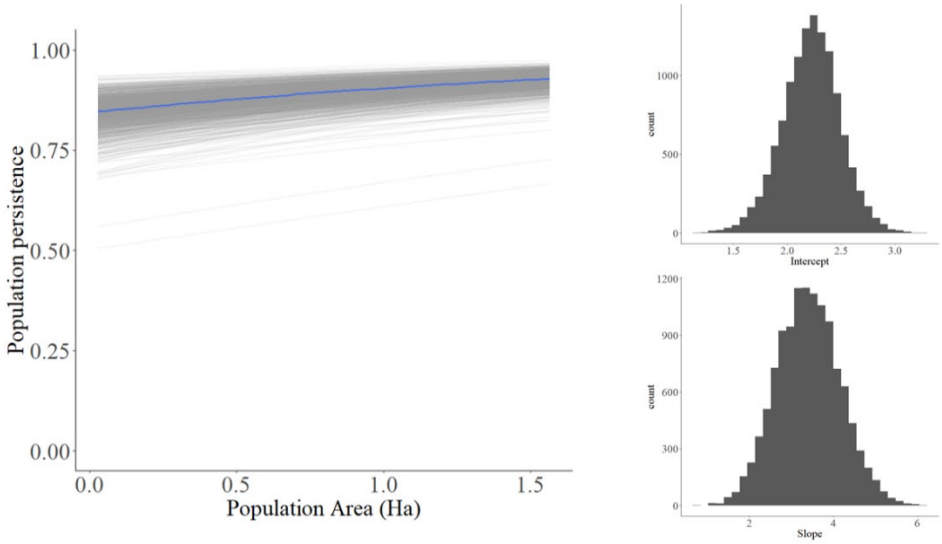

Figure 3. Effect of Population Area on the Probability of Population Persistence Across 723 Populations of 14 Species Over Four Surveys Spanning 1991-2014.

Each thin gray line corresponds to one posterior sample from the Bayesian model analysis, and the thick blue line is the median.

The project team's results demonstrate a correlation between population connectivity, as measured by Hanski's incidence function, and persistence (Figure S4). Isolated populations were more likely to be extirpated relative to more connected populations.

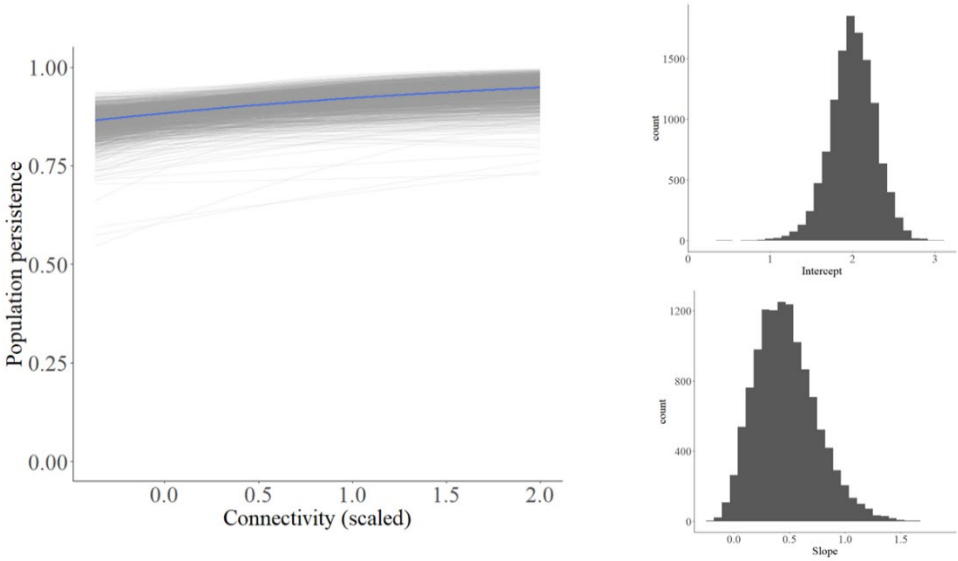

Figure 4. Effects of Patch Connectivity on the Probability of Population Persistence for 14 Species Across 723 Populations on Fort Bragg.

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. The project team 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, the project team 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 ± 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 the project team's 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, the project team's 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 S2).

Gray et al. (2003) found a positive relationship between population persistence and area occupied. The project team's 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, the project team's 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.

5.0 IMPLICATIONS FOR FUTURE RESEARCH AND BENEFITS

The project team's results confirm three of the 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. The project team 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. The project team's final hypothesis was that plant functional traits would be correlated (either positively or negatively) with population persistence. The project team was 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 the project team was able to infer based on multiple surveys. This is clearly demonstrated by comparing the project team's 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, was the project team 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 the project team 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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