

FINAL REPORT

Using Long-Term Data to Optimize Recovery of Understory Plant
Communities: Identifying the Management Contexts and Species Traits
that Maximize the Likelihood of Sustained Persistence and Spread of
Plant Populations
SERDP Project RC-2705

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List of Acronyms

BA: Basal area of overstory trees
BCI: Bayesian 95 % Credible Interval
CI: 95 % Confidence interval
DBH: Diameter at breast height
DoD: US Department of Defense
DOE: US Department of Energy
ESTCP: Environmental Security Technology Certification Program
FTB: Fort Bragg
FTS: Fort Stewart
GA: Georgia, USA
GIS: Geographic Information System
MCMC: Markov-Chain Monte-Carlo
NC: North Carolina, USA
PCA: Principal Component Analysis
SERDP: Strategic Environmental Research and Development Program
SC: South Carolina, USA
SLA: Specific Leaf Area
SON: Statement of Need
SRS: Savannah River Site
SSVS: Stochastic Search Variable Selection
USA: United States of America
USDA: United States Department of Agriculture
WAIC: Watanabe-Akaike Information Criterion

Keywords

Agriculture
Assessment framework
Bayesian variable selection
Degradation
Dispersal kernel
Effective dispersal
Ecological reference model
Ecosystem recovery
Establishment
Fire
Functional traits
Herbicide application
Land-use legacies
Longleaf pine savanna
Long-term recovery
Multi-species dynamic occupancy model
Plant community ecology
Persistence
Recovery
Restoration ecology
Seeding treatment
Spread
Weather

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1. Abstract

Objectives. We evaluated the combined long-term impacts of management, site characteristics, climate, and species traits on the on the **long-term, local and outward recovery** of understory plant communities in longleaf pine savannas through three complementary technical objectives. **First**, we evaluated **if short-term recovery led to long-term recovery**, as defined by species initial establishment and ongoing persistence. **Second**, we evaluated whether the understory species that established locally, **spread outwardly**. **Third** we **identified whether trait characteristics** were related to species' establishment, persistence, and spread.

Technical Approach. We used three complementary approaches during 2017-2018. First, we resampled presence of 25 species, within 192 plots (half seeded in 2011, originally sampled 2010-2013) from 18 sites at Fort Bragg (DoD, NC), 12 sites at Fort Stewart (DoD, GA), and 18 sites at Savannah River Site (DOE, SC). Second, we quantified the spread of each seeded species (up to 9 m) away from the 48 sites. Third, we collected trait data on the 25 seeded species. We evaluated establishment and persistence using multi-species dynamic occupancy models. We evaluated spatial spread using multi-species Weibull-kernel based models.

Results. The greatest limitation to successful local recovery (**Objective 1**) was the ability of a species to establish (i.e., for a species to successfully colonize a site where it had not previously been found). Once established, all seeded species had high probabilities of persisting across all years spanned by our study. After establishing, most species also exhibited spatial spread beyond the area where they were initially seeded (**Objective 2**), highlighting the potential for self-perpetuating recovery once populations are established. The greatest determinant of establishment was the addition of seeds of understory species in our initial experiment in early 2011. Sites with lower total basal area of canopy trees and shallow leaf litter had greater establishment as well as persistence. We found that annual climatic conditions were also important. Persistence for all species was greater with higher levels of winter precipitation, whereas precipitation had species-specific effects on establishment. Establishment and persistence of all species was associated with cooler temperatures during the spring and summer.

Differences in functional traits explained some variation in establishment and spread, but not persistence (**Objectives 1, 2, 3**). Species with taller adult plants and smaller seed/dispersule ratios established better. Wind-dispersed species with smaller SLA, slower germination rates and higher probabilities of germination spread at higher rates. For non-wind-dispersed species, spread was greater for taller species and those with greater SLA and faster germination.

Benefits. DoD and DOE are faced with the challenge of promoting successful recovery of understory plant communities in a way that allows continued execution of mission-related activities. Achieving this goal requires understanding how to maximize the establishment, persistence, and spatial spread that are the hallmarks of recovery. Through long-term sampling of a large-scale experiment, we find that seed additions are a primary means DoD/DOE managers can use to promote establishment, persistence, and subsequent species spread. These findings further benefit DoD/DOE goals by revealing that some management activities (e.g., prescribed burn regimes, low-density canopy trees) can also be particularly helpful. Our results also benefit recovery efforts by revealing a strong link between climatic conditions (e.g., temperature and precipitation) and establishment and persistence. This knowledge will help DoD/DOE plan optimal recovery efforts under current climatic conditions, and also highlights how it will be important to understand the role of future non-stationary climate on establishment, persistence, and spread in order to promote continued long-term recovery.

2. Executive Summary

2.1 Introduction

DoD is tasked with the maintenance of biodiversity and persistence of threatened, endangered, and at-risk (TER) species on lands that it manages (Benton et al. 2008). Because perennial understory plants are key components of biodiversity and include many TER species (Noss 2012, Díaz et al. 2019), management strategies that promote large-scale, persistent recovery of perennial plant species is a valuable tool for ensuring that DoD facilities maintain the continued capacity for training and readiness. Our research expanded on four years of existing data (one pre-treatment, three post-treatment) from 192 plots within 48 sites at 3 installations to experimentally determine which recovery strategies and site conditions contributed to (or limited) longer-term and outward recovery of perennial understory plant species. We investigated local-scale establishment (from absence to presence), persistence (ongoing presence) and spatial spread (dispersal away from established populations, and survival to seedling/adult stage). Our previous data illustrated that understory plant species can be successfully reestablished from seed at small scales, but this pattern was not immediately apparent (took years to play out), substantial variation in short-term recovery existed among species, and recovery depended on the conditions at a particular site (Orrock et al. 2015).

Despite the importance of plant communities for ecosystem health, managers attempting to promote recovery of plant communities face several major challenges. First, because studies rarely track persistence and spread of plants at time scales relevant to the longer-term dynamics of perennial plants that can take many years to reach reproductive maturity (Kirkman et al. 2004, Peet 2006, Brudvig et al. 2015), **it is unknown whether short-term establishment translates into long-term persistence (Fig. 2.1.1)**. This is exemplified by 93% of ecological studies reporting results based on less than five years of data even though many impacts take a decade or longer to manifest (Tilman 1989). Second, although landscape scales are typically the focus of recovery plans, management actions to recover degraded or destroyed plant communities often focus on local scales (Brudvig 2011). In many cases, this is due to the cost of intensive recovery actions, like the sowing of native seeds. **A better understanding of the constraints to spatial spread of locally-recovered communities would provide a cost-effective bridge from local implementation to large-scale recovery.** Because plant communities can be degraded by multiple, interacting factors (e.g., past land use, canopy tree density, altered fire regimes; Brudvig and Damschen 2011, Brudvig et al. 2014, Brudvig et al. 2015, Hahn and Orrock 2015a), **the ecological conditions that maximize long-term demographic performance can depend upon the environmental and management context, but these are poorly understood. This makes it difficult for managers to implement informed strategies to maximize population establishment, persistence and spread.** Third, although managers have to contend with highly diverse plant communities that vary in space (1000+ plant species in the southeastern U.S.), **we know little regarding the identity or characteristics (i.e., traits) of species that are indicative of maximum long-term recovery potential.** As a result, it is difficult to generalize whether a species that catalyzes recovery in one region is indicative of recovery in another region. Our objectives fully addressed the research needs described in the Statement of Need (SON). As with our original SERDP study, and the Roadmap to Recovery handbook for managers that we produced, our research group is committed to **translating the additional data and analyses into actionable information for DoD resource managers.**

The ecological questions we consider are of current relevance to DoD resource managers.

Our objectives met the specific requirements for study areas and ecological questions described in the SON. Previous data collection occurred on DoD lands (Fort Stewart and Fort Bragg) as well as a DOE facility (Savannah River Site) and consisted of over 80,000 observations on 900+ species over four years (one year of pre-treatment data, three years of post-treatment data), providing a robust foundation for comparison with data collected in this study.

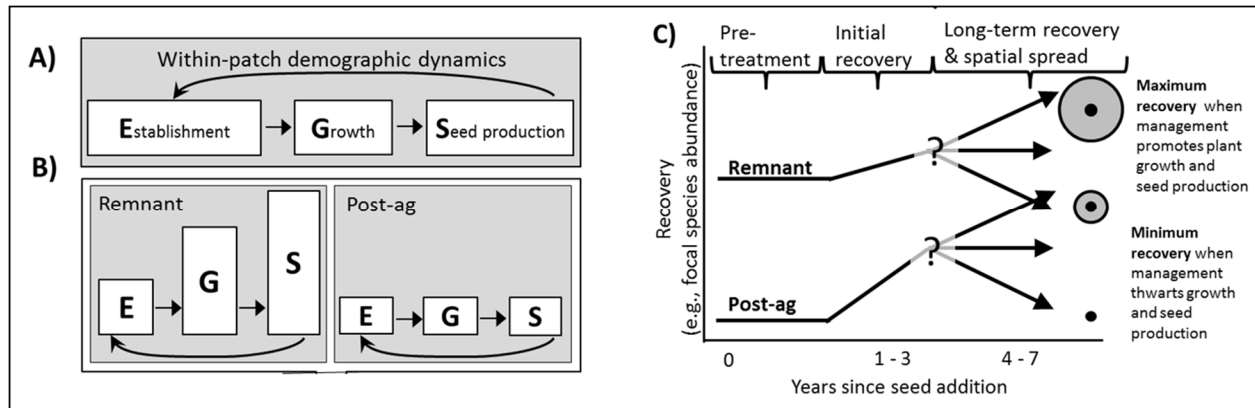


Fig. 2.1.1 Conceptual model of long-term recovery and outward community recovery (i.e., spatial spread) following seed additions to sites that differ in degradation and management due to past land use, fire regime, and tree density. Key considerations are: A) the dynamics of local recovery and spread are contingent upon local Establishment, Growth, and Seed production. B) The speed and magnitude of these demographic dynamics are likely a function of past activities (e.g., history of land use) and contemporary management (e.g., fire frequency). C) Long-lived perennial plants may take many years to reproduce and demography is linked to management thus, understanding long-term and outward recovery requires understanding the interplay between management and demographic dynamics.

2.2 Objectives

We evaluated the combined long-term impacts of management, site characteristics, climate, and species traits through three complementary technical objectives. First, we evaluated **if short-term results led to long-term recovery**. Second, we evaluated whether the understory **plant species that established locally spread, thereby facilitating their recovery over larger spatial scales**. Third, we **identified whether trait characteristics** facilitated species' establishment, persistence, and spread. Working at 48 sites that span a range of fire frequencies and tree densities across three installations supporting longleaf pine ecosystems, we evaluated how plant establishment and persistence, climate variation, fire, logging regimes, and traits contributed to plant community recovery.

2.3 Technical Approach

This research evaluated which management practices, site characteristics, weather conditions, and species traits facilitated long-term recovery and spread of longleaf pine (*Pinus palustris*) understory plant species on Department of Defense (DoD) installations by combining three complementary monitoring approaches that addressed our three technical objectives. During 2010-2013 and 2017-2018, we resampled annual occurrence of the 25 added species within 192 plots belonging to the large-scale experiment we conducted in 2010 within 18 sites at Fort Bragg (DoD, North Carolina), 12 sites at Fort Stewart (DoD, Georgia), and 18 sites at Savannah River Site (DOE, South Carolina). We expanded existing short-term (1-4 years) results to new long-term findings (6-10 years) to determine if early success was indicative of long-term recovery. Sites were selected to be post-agricultural and to maximize variation in key factors of

plant community degradation (Orrock et al. 2015): fire frequency and density of overstory trees (Brudvig et al. 2014) (Fig. 2.3.1).



Fig. 2.3.1. Location of installations used in the study and experimental design highlighting three levels of spatial complexity. Seed addition and herbicide treatments were applied in a factorial design to plots within sites that were subject to varied fire and basal area treatments. Weather varied among installations and during the study period of 2010 to 2018.

Plot Design: At each of the 48 sites, we re-established four 7×7m plots, where competitor presence, and dispersal limitation had been manipulated in 2010 as part of the original experiment, resulting in four factorial treatment combinations per site (i.e., all treatment combinations plus a control, Fig. 2.3.1). Competitor presence was manipulated by applying a broad spectrum herbicide across the 7×7m area within plots in August, 2010. The dispersal-limitation treatment was applied by adding locally collected seeds in March 2011 that represented indicators of reference upland longleaf pine savannas (Orrock et al. 2015) to the center 5×5m of plots. A total of 21 species were added to each seed addition plot within each of the three study locations; due to non-overlapping ranges, four species were congener substitutions resulting in 25 total species across the three installations.

Field Sampling: We previously quantified the identity and abundance of understory vegetation, woody plants in the sub-canopy (i.e., shrubs), and overstory trees (Orrock et al. 2015). Vegetation sampling for our current work consisted of three complementary sampling efforts that addressed our three technical objectives. First, we resurveyed the 48 sites in 2017 and 2018 to understand the long-term changes in local persistence of the species added by seed within each of our study plots (**Objective 1, local recovery**). Second, to evaluate spread (**Objective 2, outward recovery**) we counted the number of individuals of each added species that recruited outside of the experimental plots at 1 m intervals, up to 9 m away, at the same 48 sites in 2018 (Fig. 2.3.2). Because all of our sites had four 7x7 plots where seeds were added, this approach allowed us to assess if, and how rapidly, plants moved from the original area of

introduction. Third, we obtained plant functional traits (i.e., species characteristics) that are commonly associated with key ecological processes such as establishment, competitiveness, dispersal, and stress tolerance (Lavorel and Garnier 2002, Wright et al. 2004, Westoby and Wright 2006) using standardized protocols, to determine if they predicted establishment, persistence and spread (**Objective 3, Functional traits**).

Statistical analysis: We evaluated how annual changes in initial establishment (absent the previous year, present in current year) and ongoing persistence (present previous year, continued to be present in current year) for each of the 25 seeded species were influenced by the experimental treatments (e.g., seed addition and herbicide treatment), changing site conditions (e.g. fire frequency, basal area), weather (e.g. rainfall, temperature) and species functional traits (e.g., seed measures, leaf chemistry, plant height, dispersal mode) (**Objectives 1 and 3**). We used multi-species dynamic models using a Bayesian framework, which allowed us to evaluate community-level and species-specific responses at the same time, and to rigorously discriminate among the large number of potential factors impacting local recovery. We also evaluated how spread distances and rates of spread varied amongst seeded species and linked these patterns to site conditions and species traits using multi-species Weibull Dispersal Kernels, which assessed species effective dispersal (**Objectives 2 and 3**). Effective dispersal is a better measure of outward recovery because it accounts for a seed's movement from the experimental plots, and their effective arrival, survival and growth to the seedling/adult stage, to become a recruit.

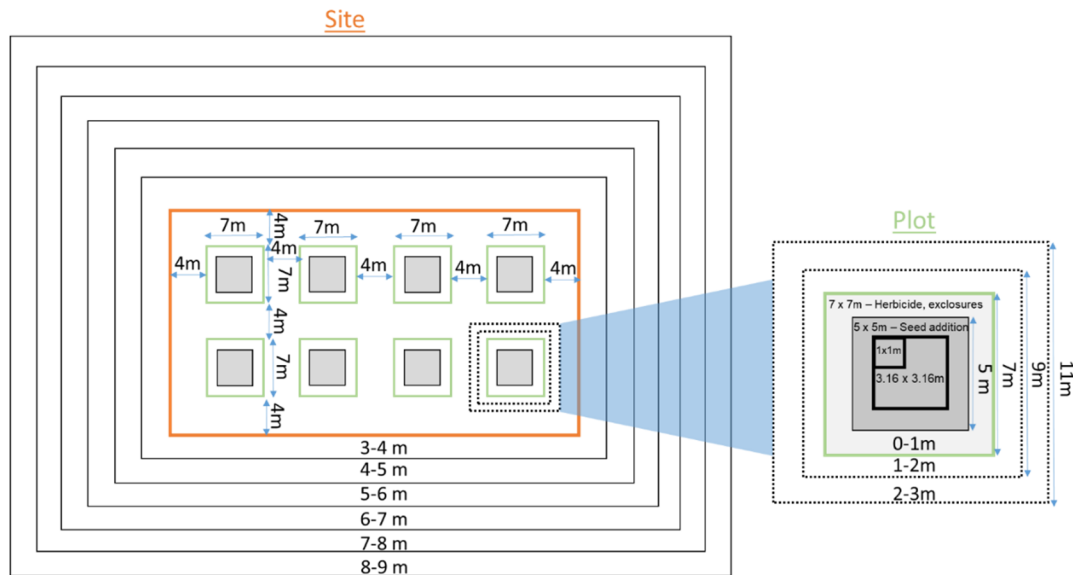


Fig. 2.3.2. Spread sampling design at each site. Plot-rings (0-1, 1-2, 2-3 m) and site-rings (3-4, 4-5, 5-6, 6-7, 7-8, 8-9 m) were used to evaluate spread of seeded species away from experimental plots. Blue arrows indicate distances.

2.4 Results and Discussion

The greatest limitation in successful local recovery (**Objective 1**) of most species was their initial ability to establish (Figs. 2.4.1 and 2.4.2). Once established, all species added as part of the seeding treatment had a high probability of persisting (Fig. 2.4.1), suggesting that the community of species chosen was a good target group for local recovery efforts. In addition, most species that established were also able to spread (**Objective 2**) over short to medium distances (up to 9 m) highlighting their potential for continued outward recovery once source populations are established (Figs. 2.4.2 and 2.4.3). Differences in functional traits (**Objective 3**)

explained some of the differences in species potential to establish and spread, but not to persist, likely because persistence was consistently high among all species.

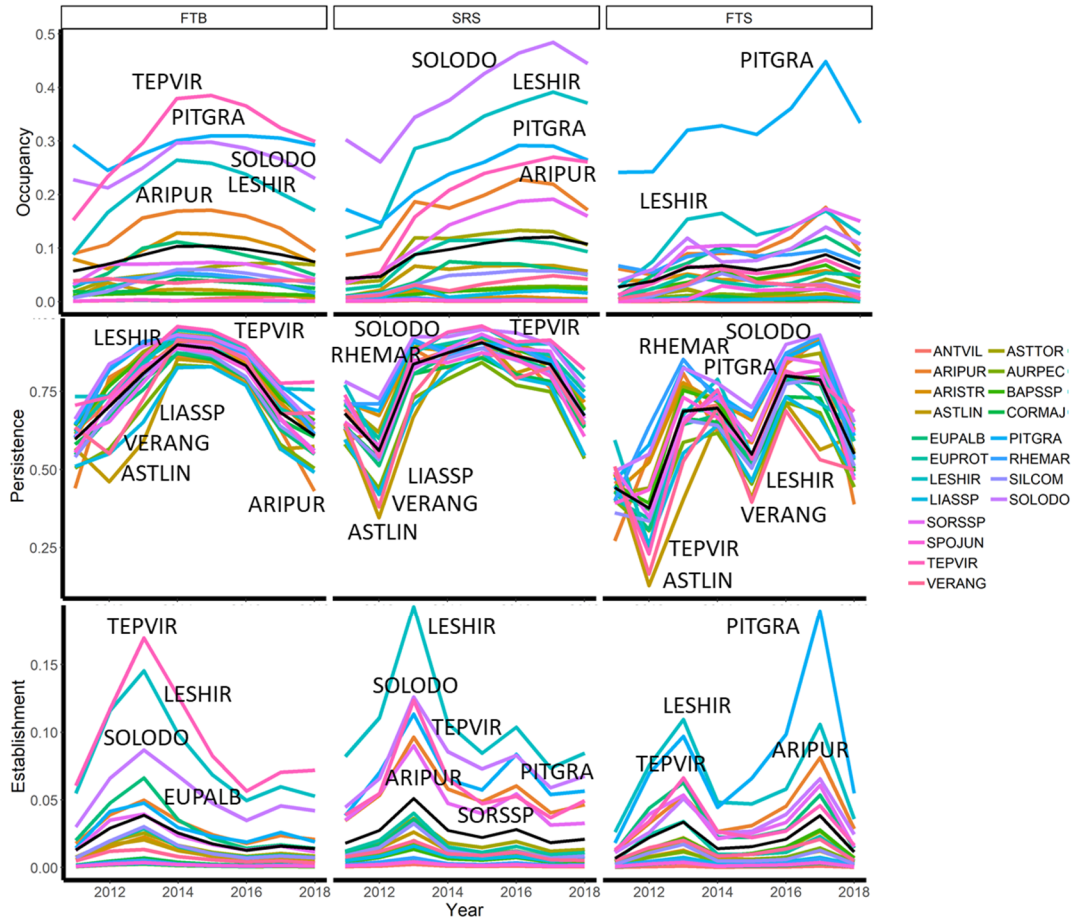


Fig 2.4.1. Species-specific estimates of mean establishment (bottom), persistence (middle) and occupancy (top) at Fort Bragg (FTB), Savannah River (SRS) and Fort Stewart (FTS) installations during the study period (2010-2018). The black lines represent community-level mean responses. Note the much lower probabilities of establishment compared to persistence.

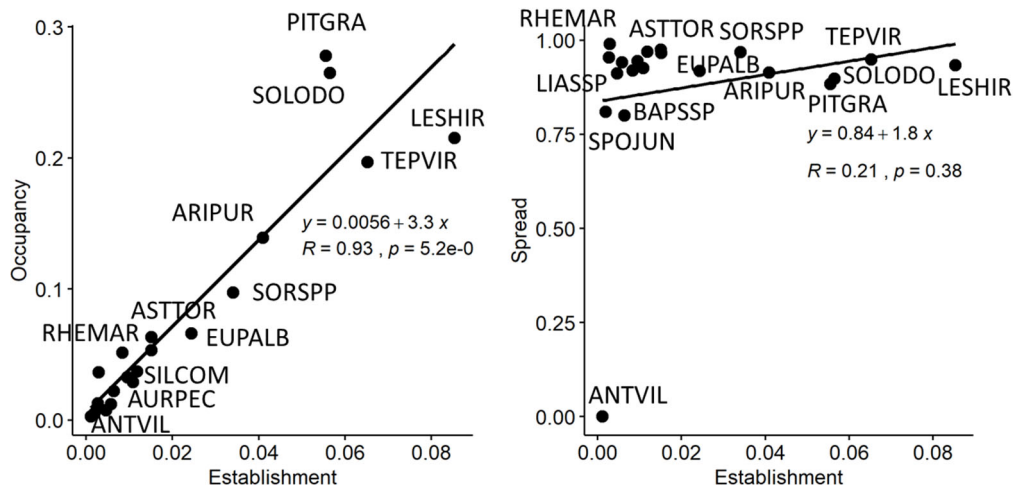


Fig. 2.4.2. Univariate relationships between mean probability estimates for establishment and occupancy (left) or spread (right) for seeded species.

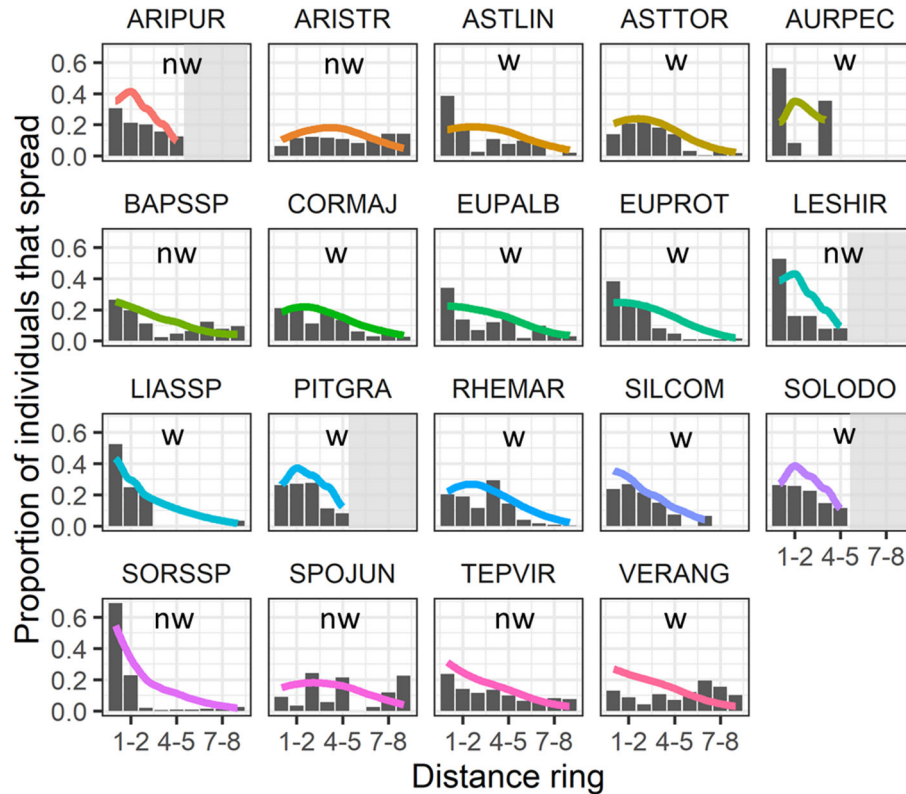


Fig. 2.4.3. Raw (histograms) and estimated (lines) spread rate for seeded species that spread beyond the experimental plots. Grey areas represent rings that were not surveyed for those species (i.e. beyond 5m). w = wind-dispersed species and nw = non-wind-dispersed (including adhesive, ballistic and unassisted) species.

The strongest predictor of successful establishment (**local recovery, objective 1**) was the seed-addition treatment (Figs. 2.4.4 and 2.4.5), demonstrating the long-term utility of seed additions for promoting recovery of longleaf understory plant communities and confirming previous findings that understory community recovery in areas with a history of agricultural land use can take decades (or longer) without direct addition of seeds or seedlings (Brudvig et al. 2013). Strong differences among species in response to the seeding treatment were also apparent, with *Lespedeza hirta* (LESHIR), *Tephrosia virginiana* (TEPVIR), *Sorghastrum nutans* and *Sorghastrum secundum* (collectively SORSPP), and *Eupatorium album* (EUPALB) experiencing the greatest benefits of seeding for their establishment and occupancy (Fig. 2.4.6). Strong and opposing differences among species in response to the herbicide treatment influenced their establishment at treated plots compared to untreated plots. The opposing, species-specific effects of the herbicide treatment suggests that it is not the ideal approach for improving community-level recovery. Unless the species that benefited were the main target of recovery efforts, we do not recommend wide implementation of this approach.

Community-level establishment (**Objective 1**) changed little in response to other management interventions examined including fire frequency, years since last fire and herbicide

treatment (Fig. 2.4.4). Conversely, increased fire frequency (> 3 prescribed fires between 1991 and year when sampling occurred) appeared to benefit persistence (**Objective 1**) but slightly hindered dispersal for the species that are not dispersed by wind (**Objective 2**) (Figs. 2.4.4 and 2.4.7). Environmental conditions including open areas and weather affected local and outward recovery of some key species (**Objectives 1 & 2**). *Pityopsis graminifolia* (PITGRA), *Aristida purpurascens* (ARIPUR), *Eupatorium album* (EUPALB), and *Tephrosia virginiana* (TEPVIR), had higher establishment in more open areas, with lower basal areas and shallower litter. More open sites, with lower basal areas and shallower litter, also increased persistence of all seeded species (Figs. 2.4.4 and 2.4.5). Sites with lower tree basal area also had higher spread (**Objective 2**) of wind-dispersed species (Fig. 2.4.7). Cooler summers promoted community establishment (Fig. 2.4.4 and 2.4.5). Seeded species persistence also benefited from cooler summers (Figs. 2.4.4 and 2.4.5), but the benefits of rain in the summer months differed among species, ranging from negative to inconsequential to beneficial. The same species that established better in more open areas also benefited more strongly from cooler and wetter summers. Rainfall in winter had a strong and consistent benefit for all seeded species' persistence (Figs. 2.4.4 and 2.4.5).

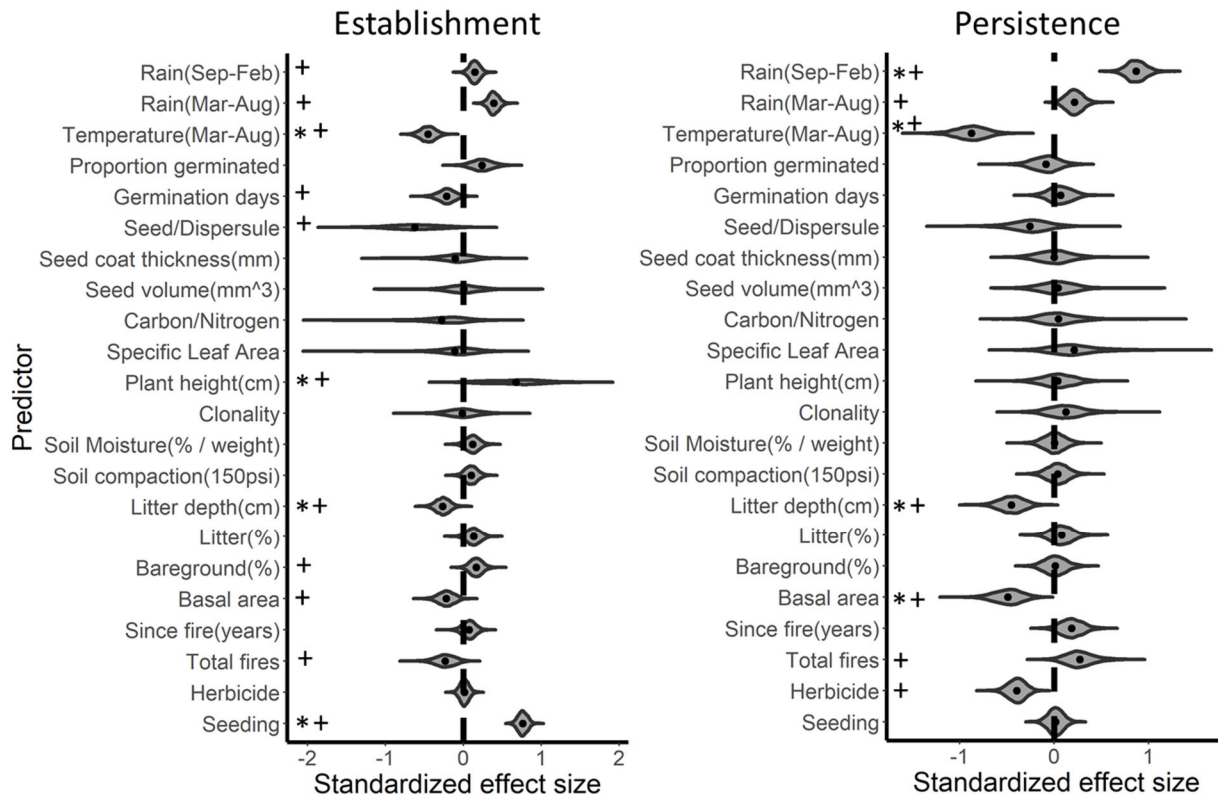


Fig. 2.4.4. Coefficient means and 95% Credible Intervals (CIs) estimated for predictors related to establishment (left panel) and persistence (right panel). Predictors classified as important as part of the Bayesian variable selection approach that accounts for their contribution towards improving model fit are marked with an asterisk. Predictors classified as potentially important based on their 95 % CIs not-overlapping zero are marked with a plus sign.

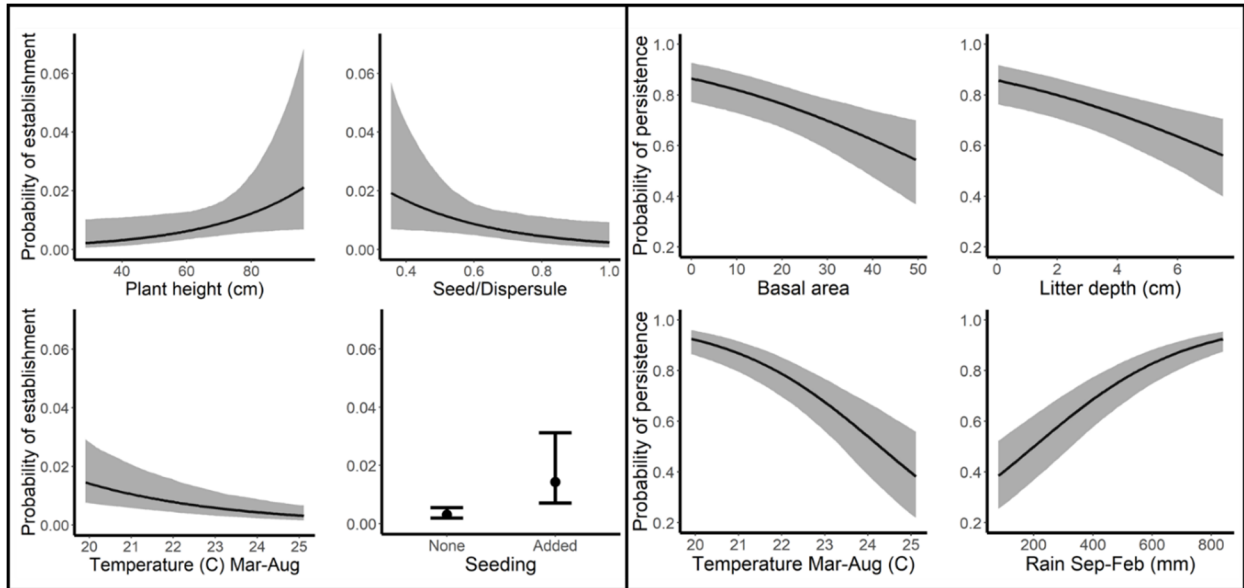


Fig. 2.4.5. Estimated relationships (partial prediction plots) between important predictors for community-level establishment (left panel) and persistence (right panel). Bold lines indicate mean relationships and grey bands the 95 % Credible Intervals. Relationships were estimated from the top model (model 5), while keeping all other predictors at their mean values.

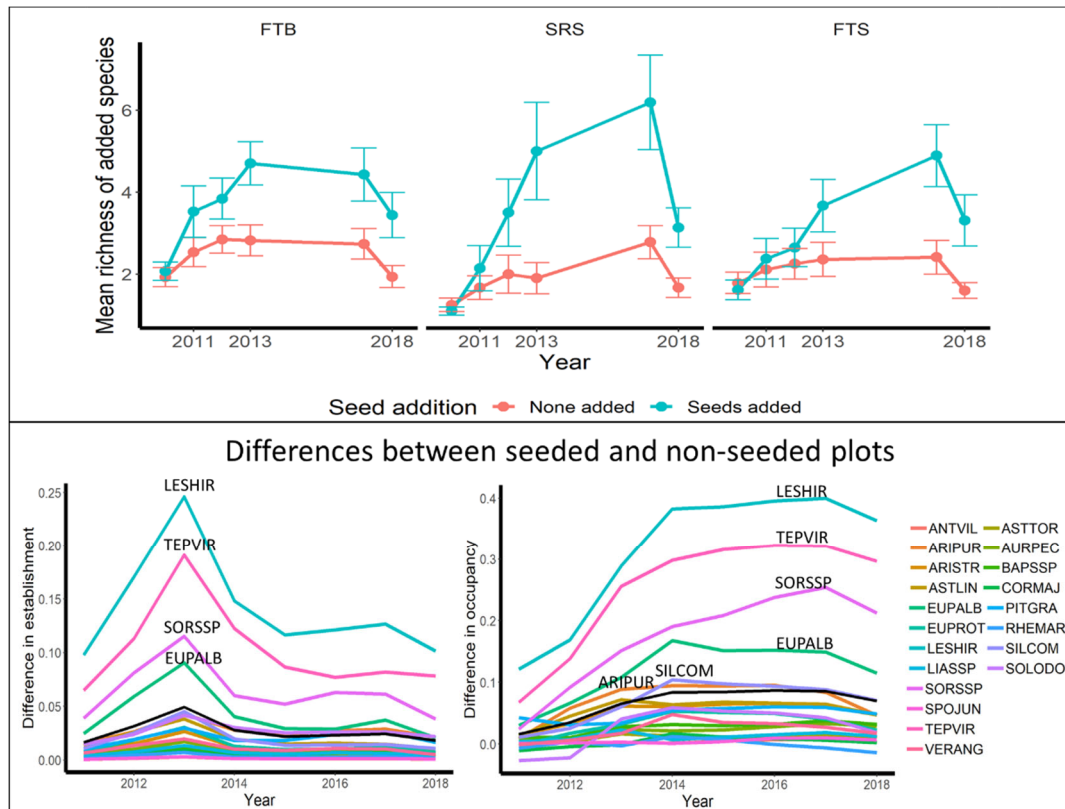


Fig. 2.4.6. Top panel: Changes in annual richness of seeded species within 3x3m subplots for plots treated with seed addition (red) and without (aqua) at each installation. Bottom panel: Differences between plots treated with seed addition and untreated plots in annual estimates of mean probability of establishment (left) and of occupancy (right) for each seeded species. The black lines are the average differences in probabilities between seeded and non-seeded plots at the community-level.

Differences in species' functional traits helped to explain variation in establishment and spread (local and outward stages of recovery); persistence was uniformly high and was not related to any traits we examined (**Objectives 1, 2, and 3**). Height of adult plants appeared to benefit a species ability to establish and increased spread for species not dispersed by wind (Fig. 2.4.5 and 2.4.7). For species not dispersed by wind, higher specific leaf area (SLA) lead to faster rates of spread (e.g., *Aristida purpurascens* ARIPUR, *Tephrosia virginiana* TEPVIR; Fig. 2.4.7). Higher establishment occurred for species that germinate quickly (e.g., *Pityopsis graminifolia*, PITGRA [wind-dispersed], *Aristida purpurascens* ARIPUR [non-wind-dispersed] and *Solidago odora* SOLODO [wind-dispersed]). Spread rate was higher for species that are not dispersed by wind and germinate quickly (e.g., *Aristida purpurascens* ARIPUR) and also for wind-dispersed species that germinate more slowly (e.g., *Silphium compositum* SILCOM, *Vernonia angustifolia* VERANG) (Fig. 2.4.7).

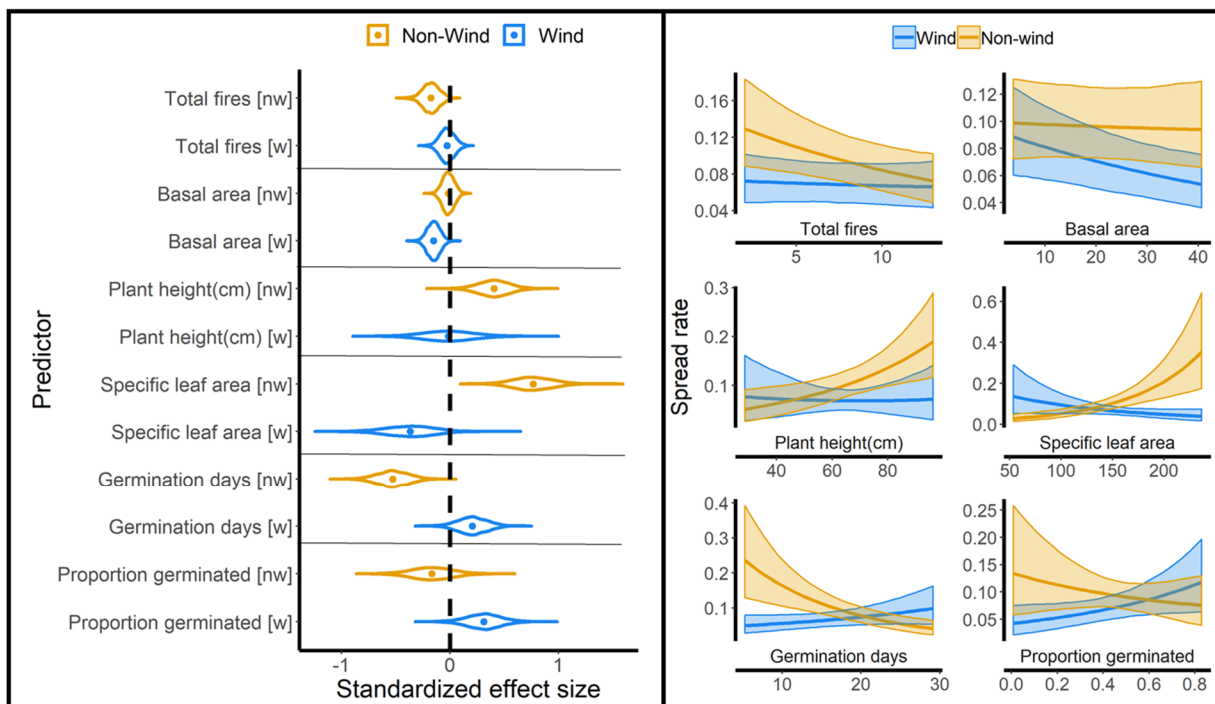


Fig. 2.4.7. Group-specific coefficients (left panel) and partial predicted relationships (right panel) between spread rate of species dispersed by wind or non-wind (including adhesive, ballistic and unassisted) in relation to management conditions and species traits.

2.5 Implications for Future Research and Benefits

Our work revealed that the greatest obstacle to recovery of longleaf pine understory plant species at two DoD and one DOE installation was the ability to establish. Once established, most species exhibited high rates of persistence, followed by spatial spread away from the site of establishment. These results, spanning 8 years, **suggest that a single seed addition (in 2010) can lead to long-term recovery and generate populations that spread outwards, continuing to foster recovery in the absence of additional intervention.** Seeding and maintenance of open habitats (through litter and canopy removal) provided clear benefits to all stages of restoration for some key species. Weather also played an important role, with cooler summers facilitating establishment and persistence, while wetter winters benefited community persistence. Functional traits were linked to how species established and spread. Species that are taller as adults,

germinate quickly as seeds and with small seed mass/dispersule mass ratios also generally established better. The relationships between quantitative traits and spread were complex and depended on the species dispersal mode (Fig. 2.4.7).

One important finding, made possible because our work spans many years, is that establishment and persistence exhibit considerable annual variation (Fig. 2.4.1), and the dynamics of plant community establishment, persistence, and spatial spread are strongly linked to annual variation in climate (Fig. 2.4.3, Fig. 2.4.6). This finding is especially noteworthy because empirical data and future climatic projections for the southeastern U.S. suggest that non-stationary climate will be an important management challenge on DoD and DOE installations. In particular, the frequency of warmer temperatures and extreme precipitation events has increased and is expected to continue to do so (Carter et al. 2018). Although future climatic events may be more extreme than those encountered in our study, our work provides important insights into how future climate may affect plant establishment, persistence, and spread. Specifically, our community-level results suggest that, increased precipitation may have benefits for both establishment and persistence of many species, serving to foster spread via the strong link between establishment and spread. On the other hand, increasing temperatures in the spring and summer are expected to have negative effects on both establishment and persistence. Yet, despite the role of climate revealed by this project, it is not clear whether extreme climatic events (e.g., increasing frequency and severity of hurricanes) that are increasing in prevalence in the Southeast will alter the trajectory of recovery. Moreover, we have little capacity to predict species responses or the most effective management strategies under these novel conditions, because there are no clear, science-based guidelines for maximizing the success of future recovery efforts amidst different climatic scenarios. Future studies that help elucidate the role of extreme climatic events in affecting plant community recovery and spread by using experiments that mimic extreme events (e.g., water-addition or rain-out shelter experiments) would be useful to explicitly link extreme climatic events to plant community recovery and provide further capability for managers of DoD installations to promote plant community recovery and resilience and maintain mission-related activities.

3. Objective

Our objective was to evaluate whether factors that promote short-term plant establishment and recovery (e.g., management strategies, site conditions, and species characteristics) leads to long-term recovery and outward recovery (spatial spread of individuals into new areas). This objective fully addressed the research needs described in the Statement of Need (SON) by facilitating confirmation, modification, or abandonment of initial hypotheses and conclusions regarding treatment effects, mechanistic understanding of system processes, and of management implications. Our work built upon our existing multi-year dataset, allowing us to extend inference from previous studies in ways that were both statistically and ecologically relevant. We collected long-term data regarding the role of management actions, site characteristics, and species traits on long-term recovery and spread, providing a critical link between management, site characteristics, and persistent, large-scale, community recovery. By evaluating how the identity and traits of species can serve as indicators of long-term recovery, we also informed reduced-form datasets from more complex studies that enable effective and cost-efficient monitoring of treatment effects and management implications by DoD resource managers. As with our previous SERDP study (Orrock et al. 2015), and the Roadmap to Recovery handbook for managers that we produced, our research group is committed to translating data and analyses into actionable information for DoD resource managers.

Our objectives also met the specific requirements for study areas and ecological questions described in the SON. Previous data collection occurred on DoD lands (Fort Stewart and Fort Bragg) as well as a DOE facility (Savannah River Site). As the primary investigators on the previous project, we had access to all necessary existing datasets, methodological approaches, and study plots. The previously collected data consisted of over 80,000 observations on 900+ species over four years (one year of pretreatment data, three years of post-treatment data), providing a robust foundation for comparing and complementing our current dataset containing over 21,000 observations collected from 2 years. Prior experimental treatment and monitoring activities were completed in 2013, and our current monitoring occurred during 2017 and 2018. The ecological questions we addressed about how to maximize the long-term recovery and large-scale spread of diverse plant communities are of current relevance to DoD resource managers.

3.1 Technical Objectives

Understory plant species play key roles in many ecosystems by enhancing biodiversity, promoting critical ecosystem processes (e.g., fire-carrying bunchgrasses), and providing resources and habitat for higher trophic levels (e.g., TER species such as the Red-cockaded woodpecker, St. Francis Satyr, and Gopher tortoise). Understory plants are also among the most endangered and threatened species in many ecosystems, including in the Southeast (Noss 2012). As a result, successful recovery of degraded plant communities is a primary focus of many managers on DoD facilities.

Despite the importance of plant communities for meeting biodiversity goals and for ecosystem health, managers attempting to promote recovery of plant communities face several major challenges. First, it is unknown whether short-term establishment translates into long-term persistence because studies rarely track persistence and dispersal of plants at time scales relevant to the longer-term dynamics of perennial plants, which can take many years to reach reproductive maturity (Fig. 2.1; Kirkman et al. 2004, Peet 2006, Brudvig et al. 2015). This is exemplified by the ecological literature where 93% of studies report results based on less than

five years of data even though many impacts take a decade or longer to manifest (Tilman 1989). Second, although large, landscape scales are typically the focus of recovery plans, management actions to recover degraded or destroyed plant communities often focus on relatively small, local scales (Brudvig 2011). In many cases, this is due to the cost of intensive recovery actions, like the sowing of native seeds. A better understanding of the constraints to the natural spread of locally-recovered populations would provide a cost-effective bridge from local implementation to large-scale recovery. Third, because plant communities can be degraded by multiple, interacting factors, e.g., past land use, canopy tree density, altered fire regimes (Brudvig and Damschen 2011, Brudvig et al. 2014, Brudvig et al. 2015, Hahn and Orrock 2015b), the ecological conditions that maximize long-term demographic performance are likely to depend upon the environmental and management context, and are currently not known, making it impossible for managers to implement informed strategies to maximize population persistence and spread. Finally, although managers have to contend with highly diverse plant communities that vary in space (1000+ plant species in the southeastern U.S.), there is no way to provide guidance to managers regarding the identity or characteristics (i.e., traits) of species that are indicative of maximum long-term recovery potential. As a result, it is difficult to generalize whether a species that catalyzes recovery in one region is indicative of recovery in another region.

We used a species-specific, follow-up study of a multi-level, large-scale experiment conducted across an established gradient of management and disturbance regimes to overcome these challenges. From 2008-2013, we implemented a factorial experiment at 108 sites at three DoD/DOE facilities in three different states in the southeastern U.S. This novel experiment (the largest, best replicated experiment of its kind that we are aware of) provided the first robust evidence of the context-specific nature of plant community recovery in longleaf ecosystems (Mattingly and Orrock 2013, Veldman et al. 2013, Brudvig et al. 2014, Veldman et al. 2014, Hahn and Orrock 2015a, b), and provided management guidelines to maximize the initial establishment of longleaf pine understory plant species at local scales (i.e., our “Roadmap to Recovery” guide for managers, available on the SERDP/ESTCP website). As part of this work, we permanently marked and georeferenced each of our plots, making it possible to precisely relocate each of the 964 experimental plots in our 108-site study and build upon the >80,000 observations of plant communities in our existing 4-year, 900-species dataset.

By conducting additional intensive field sampling in the context of a factorial experiment involving seed additions, prescribed fire, and canopy density, our goal was to provide a decadal understanding of the conditions under which long-term recovery of plant communities is maximized on post-agricultural sites – locations where species reintroductions through seed addition are typically important to recovery.

This study had three complementary technical objectives:

3.1.1 Technical Objective 1: Evaluate whether establishment over short time scales is indicative of persistence over longer time scales.

Task 1. Determine which management activities result in continued persistence of species once established

Rationale: The time scale for perennial plants to establish from seed and grow large enough to become reproductive is 2-10 years within the longleaf pine ecosystem, and management (e.g., burn frequency) plays a large role in the time necessary for plants to reach reproductive size and affects the degree of seed production. Our initial study was long enough to document significant changes in recovery due to initial establishment (Fig. 2.2), as well as to demonstrate how the dynamics of recovery are only apparent after several years (e.g., note that, averaged across all the three DoD/DOE installations, significant differences in recovery only became clearly apparent in the third year after seeds were added; Fig. 2.2). However, our initial study was too short to conclude whether established plants are persisting long enough to lead to continued recovery. Moreover, our initial study was too short to capture the potential demographic inertia that could arise if management promotes maximum growth and reproduction over longer time scales (Fig. 2.1), making the current research critical for providing management recommendations for long-term recovery. In addition, natural variability in climate and fire regimes operate over multi-year time scales that likely extend beyond the duration of our initial study, potentially resulting in greater impacts of our experimental treatments over time. For example, greater precipitation in a particular single year of our initial study led to increased recruitment of seeds sown two years earlier. Furthermore, the ecological processes that we manipulated with our experimental treatments may operate at different temporal scales such that interactions among treatments may change over time. All of these temporally dependent impacts suggest that the effects of our treatments and the differences among them may become amplified or altered over longer time scales.

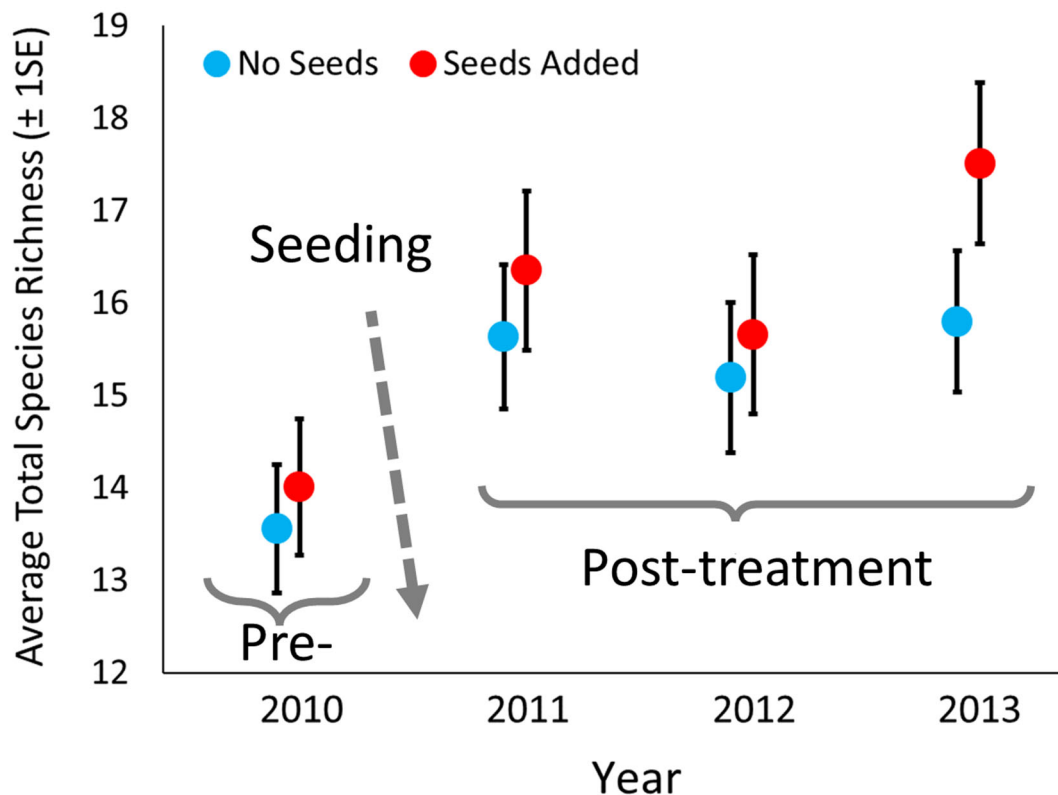


Fig. 2.1.2. Average total species richness (±1 SE) across years of our initial study.

3.1.2 Technical Objective 2: Evaluate whether species that have been established by recovery efforts are now spreading throughout sites, and whether particular site conditions maximize this spread.

Task 2: Determine which management activities optimize spread of populations

Rationale: Our initial study focused on local scale recruitment of species indicative of recovery within their first 1-3 years of growth. Given that we expect perennial plants to mature and become reproductively active over longer time scales, we are only now able to move beyond initial, local scale recruitment from sown seeds to evaluate the dispersal and subsequent spread of plants from our initial study manipulations. Determining cumulative impacts of recovery activities on the surrounding landscape will give new evidence-based insight into the long-term, and spatial effectiveness of management actions, especially given evidence that site conditions affect the growth and reproduction of plant species indicative of recovery. In addition, we evaluated whether particular environmental conditions and management activities impact the spread of our founder populations. The possibility of self-sustaining population spread is often considered the “holy grail” of management and recovery activities because it presumably allows community recovery to continue with increasing effectiveness and decreased effort and expense from managers over time.

3.1.3 Technical Objective 3: Identify species and their characteristic traits that indicate their potential for long-term recovery and spread under particular site conditions.

Task 3: Link species’ identities and functional traits to long-term recovery success and the capacity for spread

Rationale: In our initial study, we focused on the identities of species indicative of short-term recovery to assess how site quality and appropriate management actions initiate reestablishment of these species. However, given that recovery trajectories may diverge over longer time scales and that some species may take longer to establish, the indicator species associated with long-term impacts may be different than those previously identified. Furthermore, because it will be the characteristics (i.e., traits) of species, not their botanical names *per se*, that influence long-term recovery potential, a species-specific evaluation of recovery based on plant traits (e.g., competitive ability, dispersal ability) will provide mechanistic insight into the processes that led to their success or failure. Accomplishing this objective will not only provide managers with the ability to rapidly determine long-term impacts of recovery activities within particular site histories and conditions, but also enhance transferability of our findings to new locations where the identities of species are different, but their traits are the same.

4. Background

Plant communities are an essential part of terrestrial ecosystems, comprising substantial amounts of biodiversity and providing habitat and resources for higher trophic levels. Here, we focus on longleaf pine ecosystems, which is a North American biodiversity hotspot that supports more plant species per square-meter than the tropics (Noss 2012, Noss et al. 2015). These plant communities include a rich assemblage of native legumes, sedges, grasses, and composites as well as many TER plant species (Walker 1993, Sorrie et al. 2006) and several TER vertebrate species, such as the Gopher Tortoise, Red-Cockaded Woodpecker, the Eastern Indigo Snake, and the Carolina Gopher Frog (Frost 1993, 2006, Peet 2006). The geographical extent of longleaf pine ecosystems historically extended from Texas to Virginia. Today, less than 3% of this original ecosystem remains across the southeast (Frost 2006), including over 20 DoD and DOE facilities (15 that are >5000 ha.). Because of high levels of biodiversity, a history of degradation, and the importance for TER species, the recovery of degraded longleaf pine plant communities is a top management priority for DoD (Benton et al. 2008) and across the Southeast (Jose et al. 2006). Successful recovery requires accurate site assessments, clearly defined recovery goals, appropriate recovery strategies and species selection, and the ability to measure progress towards recovery objectives (Suding et al. 2004, Jose et al. 2006).

Scale is a critical consideration in ecology (Levin 1992). Our work sought to investigate different temporal, spatial, and measurement scales than what are more traditional in the literature. Previously, we studied a short temporal scale to consider establishment. Currently, to study whether or not the effects of our efforts persisted, we considered a longer temporal scale, which also allowed us to incorporate inter-annual variability. The majority of empirical studies focus on short term changes in communities (but see: Turkington et al., 1998; White et al., 1997). When studying community changes for long-lived species, such as perennial plants, it is important to determine if the short-term outcomes predict long-term outcomes.

Challenge 1: It is unknown whether short-term establishment is indicative of longer-term persistence. Long-term recovery success hinges upon short-term success, but short-term success does not guarantee long-term recovery. Managers often invest significant time and resources into actions known to promote recovery in the short term (e.g., adding seeds of rare plant species, conducting prescribed burns, applying herbicide to weedy plants), yet it often remains unclear whether these activities continue to yield long-term success. This issue is not unique to managers of longleaf ecosystems: studies that assess the long-term success of recovery efforts are rare (Bernhardt et al. 2005, Gomez-Aparico 2009, Damschen et al. 2019) and, when conducted, can provide surprising insights (Damschen et al. 2008, Matthews and Spyreas 2010, Damschen et al. 2019). Long-term data informing recovery may be most critical for ecosystems, like longleaf pine savannas, which are dominated by long-lived perennial plant species: these species may take many years to establish and achieve a size where continued survival is high and where rates of seed production are high enough to foster outward recovery via dispersal and subsequent spatial spread. For perennial plants in longleaf ecosystems, the time required to enter the reproductive stage can be 2-8 years (or more) and depend on the management regime (Brudvig et al. 2015). As a result, determining which management techniques are optimal to a particular situation (e.g., a site affected by former agricultural or fire exclusion) hinges upon data collected over many years.

Previous research by our group has shown that recovery of longleaf pine plant communities is context-specific: plant communities degraded by past agricultural land use

respond differently to seed additions than those that are primarily degraded by fire exclusion (Orrock et al. 2015). For example, the relative efficacy of seed addition depends upon both past land use and the amount of time that has passed since seeds were added. Moreover, we have found that seeds of indicator species rarely emerge from the soil following long-term storage, i.e., there is no persistent seed bank for these species (Orrock et al. 2015). As a result, the dispersal of indicator species and recovery of plant communities requires maximizing seed production and reproduction by mature plants. Because our work has shown that management activities (e.g., canopy thinning, fire regime) and land-use history may also interact to affect growth, flower production, and production of seed-bearing structures, understanding the capacity for seed production in post-agricultural habitats requires long-term studies with the ability to evaluate seed production and plant dispersal within the context of these management activities.

Achieving these goals is challenging because the processes that govern recovery occur over different temporal and spatial scales, are influenced by other DoD and DOE priorities, and are affected by land use (e.g., military training, past agricultural history), management activities (e.g., fire frequency, canopy thinning), environmental characteristics (e.g., soils, moisture availability, weather), species traits, and biotic interactions (e.g., competition with invasive/ruderal species, composition of the seed bank). A critical realization is that all of these factors are likely to interact (Brudvig 2011), making it difficult to provide general recommendations for recovery based upon studies of only one or a few of these processes over relatively short time scales. For example, fire exclusion can lead to the loss of herbaceous forbs and grasses in the ground layer, depleting local species in the soil seed bank (Cohen et al. 2004). Once fire regimes are restored, these sites may still be unlikely to recover because of limited seed dispersal (Brudvig and Damschen 2011, Alstad et al. 2016), or because canopy density and fire interact to alter the capacity for plant seed production.

Challenge 2: Moving beyond local recovery: management to optimize spread. Optimal recovery requires more than short-term establishment of desired plant species at local-scales. To maximize the often-large initial investments in local establishment, recovery must result in long-term persistence and in the spread of populations across larger spatial scales. Moreover, successfully prioritizing management activities across sites requires knowing which actions and environmental conditions will promote establishment, reproduction, and dispersal of long-lived perennial plant species.

In some areas it may be difficult to establish a source population, but once that initial population establishes, it could produce and disperse seeds into additional available areas. Native species have limited capacity for natural dispersal from remnant habitats into areas with agricultural land-use history even 60 years after agricultural abandonment (Turley et al., 2017). Yet, when dispersal limitation is reduced (e.g., by sowing seeds of desirable species), species indicative of high quality longleaf pine stands can recover, even highly degraded post-agricultural sites, leading to the establishment of new populations and setting the stage for population spread (Orrock et al. 2015, Turley et al. 2017, Barker et al. 2019). If any of the methods used in our original project increase the probability of population spread it will be important to identify those methods and provide management recommendations that would promote spread through the establishment, persistence, and dispersal of species indicative of longleaf pine savannas. To further consider the spatial benefits of our efforts, we determined whether our restoration efforts showed signs of initial spread.

Challenge 3: Identifying species and traits indicative of establishment, persistence, and

dispersal. A suite of simple summary metrics that accurately reflect larger, more complex community patterns are paramount for assessing the impacts and progress of recovery actions given the large amount of time involved with intensively surveying communities. One approach is to determine species that are indicative of these larger patterns (e.g., indicator species), which we successfully implemented in our previous study. However, species associated with recovery may change over the long-term, depending on the stage of recovery (e.g., establishment vs dispersal), management intervention, and site and environmental conditions. Furthermore, species composition differs amongst installations, making it difficult to translate findings using particular species' identities across the broader suite of southeastern installations. This challenge requires using indicators of recovery that relate to species attributes (e.g., functional traits) so that findings can be generalized and applied to other installations with different species identities.

Functional traits are characteristics of an organism that correspond with their life history strategy and response to environmental conditions and how they interact with other species (Lavorel and Garnier 2002, Wright et al. 2004, Shipley et al. 2016). Traits can be morphological, physiological, or phenological and can be quantified using categorical or using continuous, quantitative data. Plant functional traits can provide explanation as to which species are in a particular area with various disturbances, but can also help predict what species may exist there under changing conditions (Gondard et al., 2003). For example, Gondard et al. (2003) presents functional response type groups for logging and grazing along with a list of species that match the attributes of each functional response group. Recent studies have reignited interest in grouping organisms by their functional traits rather than focusing on species identity (for a review see Funk et al., 2017). Functional traits may, therefore, be a useful tool for predicting how species respond to different land-use histories or restoration techniques, the process of community assembly, and subsequent spatial spread (Mayfield et al., 2010). To understand the mechanisms underpinning our restoration efforts and allow predictions beyond our specific sites and species, we measured species traits and determined whether and how they predicted establishment and spread over the long-term.

5. Materials and Methods

5.1 Field Methods

5.1.1 Study Locations

The geographical extent of longleaf pine savannas encompasses a large portion of the southeast (Frost 1993, 2006) and contains over 20 DoD and DOE facilities, 15 of which are greater than 5000 hectares. Our experiment was conducted at three installations (Fort Bragg (NC), Savannah River Site (SC), and Fort Stewart (GA)) that span a range of degradation conditions that are common at DoD bases in the southeast and a range of climatic conditions similar to other DoD locations (Fig. 5.1.1). The three installations fall strategically within three of the primary physiographic regions of longleaf savannas: Atlantic Coastal Plain, Fall-line Sandhills, and Southern Coastal Plain. These physiographic regions encompass longleaf communities that stretch from Virginia to Alabama. Our results are thus intended to transfer to most of the Fall-line and Atlantic and Southern Coastal Plain longleaf associations, with the exception of very wet associations (e.g., pocosins and seeps). At each of these installations, we used existing experimental sites (48 total sites: 18 sites at Fort Bragg, 12 sites at Fort Stewart, and 18 sites at Savannah River Site) from our original study. Four soils orders were found at our study sites, which characterize the primary substrates for longleaf pine communities (Peet 2006): Ultisols, Entisols, Spodosols, and Inceptisols. Sites were each ≥ 1 ha, supported overstory longleaf pines, and lacked firebreaks, drainages, or other features causing abrupt transitions in understory vegetation. Sites had the same land-use history (i.e., they were once used for agriculture), but maximized variation across two key factors of plant community degradation (Orrock et al. 2015): fire frequency and density of overstory trees (Brudvig et al. 2014).

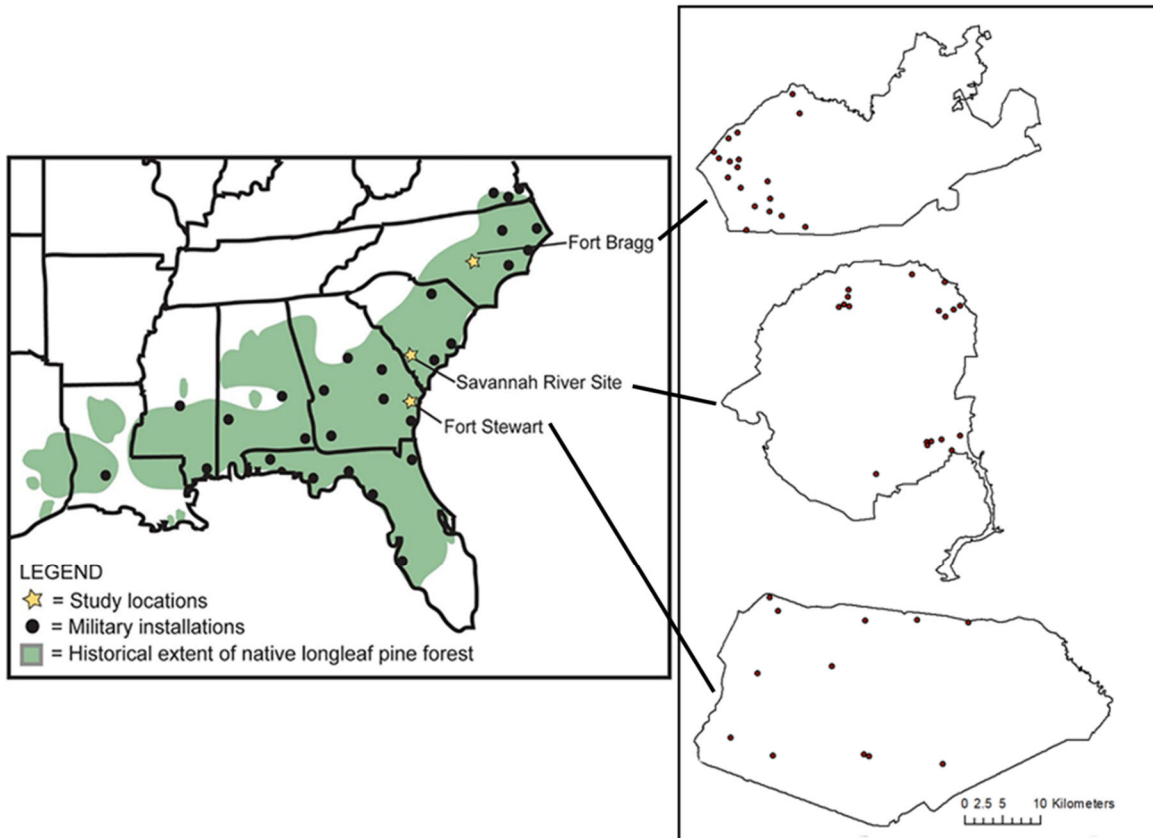


Fig. 5.1.1 Map indicating the widespread historical extent of longleaf pine, the large number of DoD facilities in the longleaf pine ecosystem, and our three study locations.

5.1.1.1 Fort Bragg

Fort Bragg Military Reservation (FTB; 73,000 ha, elevation: 43-176 m, mean annual precipitation: 1270 mm, mean annual temperature: 16°C) contains longleaf pine savanna within the Sandhills region of North Carolina (Sorrie et al. 2006). The sandy, infertile soils of the region largely limited the scale and intensity of agricultural practices in the uplands. Agriculture was abandoned around the time the military reservation was established in 1918, at which point only 7% of the landscape was under cultivation (Aragon 2004). Land abandonment and subsequent reforestation has since yielded post-agricultural sites that have been timbered for nearly a century. Prior to 1989, upland habitat was burned once every 5 years, but since 1990 the prescribed fire program has increased the frequency of burns to a 3-year return interval (Cantrell et al. 1995). Chronically fire-suppressed upland longleaf pine savanna is uncommon at Fort Bragg.

5.1.1.2 Savannah River Site

The Savannah River Site (SRS; 77,000 ha, elevation: 20-130 m, MAP: 1225 mm, MAT: 18°C), a National Environmental Research Park in South Carolina, contains longleaf pine savanna within the Atlantic Coastal Plains region (Peet 2006). Although longleaf pine covered nearly 80% of the uplands at SRS prior to European settlement (Frost 2006), the majority of upland habitat was under intensive agricultural production by the time SRS was acquired by the Department of Energy in 1951 (Kilgo and Blake 2005). Following site acquisition, management efforts focused on reforesting abandoned agricultural fields, and much of SRS is now managed for either

longleaf pine or loblolly pine timber (Kilgo and Blake 2005). From 1951 until the 1980s, wildfires were suppressed and prescribed fires were rare. For the past ~30 years, SRS has re-introduced prescribed fires, including to manage habitat for the endangered Red-Cockaded Woodpecker. The total area burned each year has increased from 1980 through 2000, but infrequently or long-unburned areas remain at SRS.

5.1.1.3 Fort Stewart

Fort Stewart Military Reservation (FTS; 114,000 ha, elevation: 2-56 m, MAP: 1220 mm, MAT: 19°C) is located in southeastern Georgia 35 km from the coast, covers of xeric and mesic pine savannas interspersed with mesic and hydric hardwood forests, cypress wetlands, and riparian habitats. Prior to the establishment of the military reservation in 1940, land use included intensive agriculture, livestock grazing, logging, and turpentine extraction (Armstrong 1984). Like SRS, pine stands on former agricultural sites at Ft. Stewart are younger than those at Fort Bragg. Due to frequent accidental fires from military ignitions, historic fire-suppression at Fort Stewart was not nearly as severe as compared to SRS. In recent decades, Fort Stewart managers have used growing season burns, tree thinning, and wiregrass planting to maintain and restore longleaf pine savannas and to improve habitat for the Red-Cockaded Woodpecker and other threatened animals (Mitchell et al. 1999, Stevenson et al. 2003).

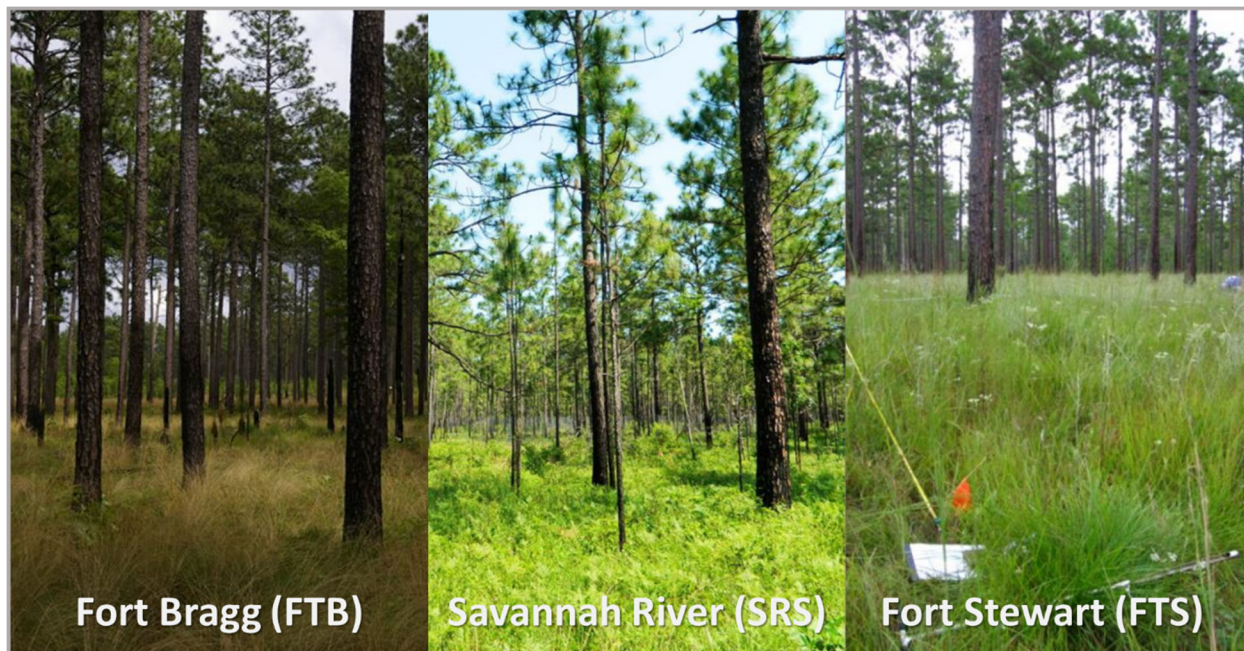


Fig. 5.1.2. Photographs displaying high-quality undegraded understory plant communities at each of the three installations used in this study.

5.1.2 Plot Design and experimental treatments

At each of the 48 sites (6 sites at Fort Stewart had reduced sampling effort due to mechanical manipulation), we re-established four 7×7 m plots, where competitor presence, and dispersal limitation had been manipulated in 2010 as part of the original experiment, resulting in four factorial treatment combinations per site (i.e., all treatment combinations plus a control).

The four plots that had been fenced to exclude herbivores were not included in this study because fences were removed from 2 installations at the conclusion of our last SERDP-funded project in 2013.

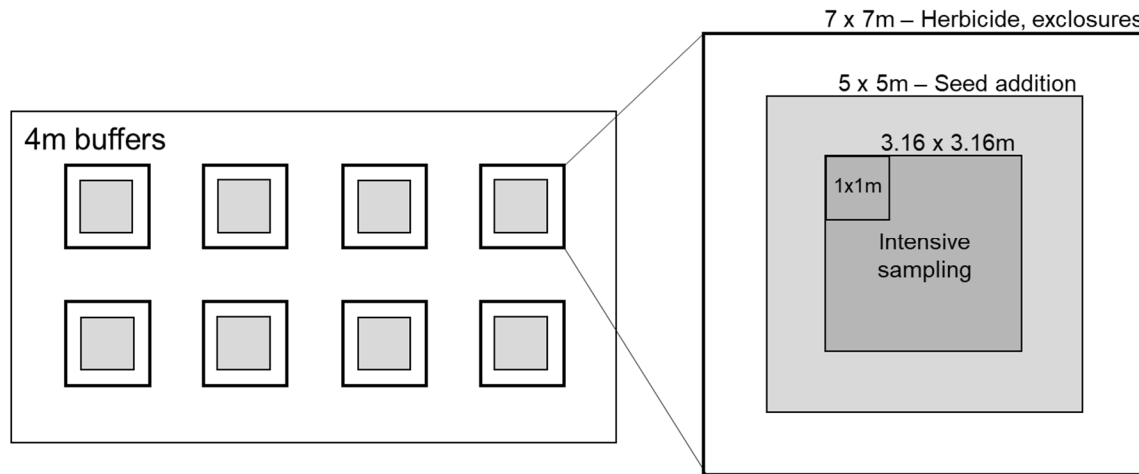


Fig. 5.1.3. Sampling design for each site (left panel). Bold squares indicate plot locations within each site. The area where experimental treatments were applied at the plot-level, and the various scales of vegetation sampling are described on the right panel. Note that only four plots (with no herbivore-exclusion fences) were resampled.

Competitor presence was manipulated by applying a broad spectrum herbicide (OneStep, active ingredients: Imazapyr, 8.36% and Glyphosate, 22.13%) at a rate of 1 gallon per acre to half of the 7×7m plots during August of 2010. Dispersal limitation was counteracted by adding locally collected seeds that represent reference indicators of upland longleaf pine savannas (Orrock et al. 2015). A total of 21 species were added to each seed addition plot within each of the three study locations; due to non-overlapping ranges, four species were congener substitutions resulting in 25 total species across the three installations (Table 4.1.1). Seeds were collected onsite at each location between November 2010 and February 2011 and added to the center 5×5m of half of the plots in March, 2011 after all other manipulations were completed. Note that GAYDUM (*Gaylussacia dumosa*) was not used in analyses reported here as it was the only woody and animal-dispersed species that was added, and was therefore thought to be too different from the other species to provide meaningful comparisons. It was the only species that failed to germinate in any of the viability assays we conducted prior to adding seeds in original experiment (0 of 749 seeds tested failed to germinate; Orrock et al. 2015). We suspect that this lack of apparent viability may have been because animal-dispersed seeds often require some form of scarification or acid treatment (to mimic passage through an animal gut). It is also possible that all of the seeds we collected for this species were not viable, although this seems less likely. For managers specifically interested in *Gaylussacia dumosa*, we note that it has low probability of establishment (~0.1) but high probability of persistence, particularly in plots that did not receive herbicide treatment (> 0.8). *Gaylussacia dumosa* also appeared to spread well, particularly in the 0-5 m range.

Table 5.1.1. Species codes and scientific names for species added in experimental plots. Details of which congeners were added at each installation and of functional traits describing dispersal mode, clonality and plant type. GAYDUM was not included in further analyses.

Code	Added to FTB	Added to SRS	Added to FTS	Family	Dispersal mode	Clonality	Plant type
ANTVIL	<i>Anthraenantia villosa</i>	<i>Anthraenantia villosa</i>	<i>Anthraenantia villosa</i>	Poaceae	Unassisted	Clonal phalanx	Graminoid
ARIPUR	<i>Aristida purpurascens</i>	<i>Aristida purpurascens</i>	<i>Aristida purpurascens</i> <i>Aristida stricta</i>	Poaceae	Adhesive	Clonal phalanx	Graminoid
ARISTR	<i>Aristida stricta</i>	<i>Aristida beyrichiana</i>		Poaceae	Adhesive	Clonal phalanx	Graminoid
ASTLIN	<i>Aster linariifolius</i>	<i>Aster linariifolius</i>	<i>Aster linariifolius</i>	Asteraceae	Wind	Clonal phalanx	Forb
ASTTOR	<i>Aster tortifolius</i>	<i>Aster tortifolius</i>	<i>Aster tortifolius</i>	Asteraceae	Wind	Non-clonal	Forb
AURPEC	<i>Aureolaria pectinata</i>	<i>Aureolaria pectinata</i>	<i>Aureolaria pectinata</i>	Scrophulariaceae	Wind	Non-clonal	Forb
BAPSSP	<i>Baptisia cinerea</i>	<i>Baptisia perfoliata</i>	<i>Baptisia perfoliata</i>	Fabaceae	Ballistic / Tumbling	Clonal phalanx	Legume
CORMAJ	<i>Coreopsis major</i>	<i>Coreopsis major</i>	<i>Coreopsis major</i>	Asteraceae	Wind	Clonal guerrilla	Forb
EUPALB	<i>Eupatorium album</i>	<i>Eupatorium album</i>	<i>Eupatorium album</i>	Asteraceae	Wind	Clonal phalanx	Forb
EUPROT	<i>Eupatorium rotundifolium</i>	<i>Eupatorium rotundifolium</i>	<i>Eupatorium rotundifolium</i>	Asteraceae	Wind	Clonal phalanx	Forb
LESHIR	<i>Lespedeza hirta</i>	<i>Lespedeza hirta</i>	<i>Lespedeza hirta</i>	Fabaceae	Unassisted	Clonal phalanx	Legume
LIASSP	<i>Liatris squarrosa</i>	<i>Liatris secunda</i>	<i>Liatris secunda</i>	Asteraceae	Wind	Clonal phalanx	Forb
PITGRA	<i>Pityopsis graminifolia</i>	<i>Pityopsis graminifolia</i>	<i>Pityopsis graminifolia</i>	Asteraceae	Wind	Clonal phalanx	Forb
RHEMAR	<i>Rhexia mariana</i>	<i>Rhexia mariana</i>	<i>Rhexia mariana</i>	Melastomataceae	Wind	Clonal guerrilla	Forb
SILCOM	<i>Silphium compositum</i>	<i>Silphium compositum</i>	<i>Silphium compositum</i>	Asteraceae	Wind	Non-clonal	Forb
SOLODO	<i>Solidago odora</i>	<i>Solidago odora</i>	<i>Solidago odora</i>	Asteraceae	Wind	Clonal phalanx	Forb
SORSSP	<i>Sorghastrum nutans</i>	<i>Sorghastrum secundum</i>	<i>Sorghastrum secundum</i>	Poaceae	Unassisted/ Wind	Clonal phalanx	Graminoid
SPOJUN	<i>Sporobolus junceus</i>	<i>Sporobolus junceus</i>	<i>Sporobolus junceus</i>	Poaceae	Unassisted	Non-clonal	Graminoid
TEPVIR	<i>Tephrosia virginiana</i>	<i>Tephrosia virginiana</i>	<i>Tephrosia virginiana</i>	Fabaceae	Ballistic	Non-clonal	Legume
VERANG	<i>Vernonia angustifolia</i>	<i>Vernonia angustifolia</i>	<i>Vernonia angustifolia</i>	Asteraceae	Wind	Non-clonal	Forb
GAYDUM	<i>Gaylussacia dumosa</i>	<i>Gaylussacia dumosa</i>	<i>Gaylussacia dumosa</i>	Asteraceae	Animal	Clonal guerrilla	Woody

5.1.3 Environmental Conditions

We collected 8 soil cores (2.5cm diameter by 15cm deep) 50 cm outside each 3x3 plot (two per side) in 2011 and composited these cores to make one sample per plot. Each composited soil sample was analyzed for soil water holding capacity following Salter and Williams (1967), because soil moisture availability correlates with longleaf pine understory diversity and productivity (Kirkman et al. 2001); soil water-holding capacity is also significantly positively correlated with the amount of organic material in the soil at these sites (Orrock et al. 2015). We placed a subsample of soil from each plot into a 5 cm tall by 6.5 cm wide soil tin, with 15 drilled holes in the bottom (1 mm wide) and lined with filter paper to prevent soil loss. We saturated soil subsamples by placing the tins in a shallow pan with tap water for 24 h, draining them on a wire rack until they stopped dripping (~30 s), collecting their wet weight, drying them at 105 °C for 72 h, and collecting dry weight. Soil water holding capacity was calculated as the proportional difference between wet and dry weight ($[\text{wet weight} - \text{dry weight}] / \text{wet weight}$), accounting for the weight of the filter paper. Within each 3x3m plot, soil compaction was quantified by taking the mean of four measurements from a cone penetrometer (Dickey-John Soil Compaction Tester, Dickey-John Corporation, Auburn, IL, USA) positioned at the midpoint along each side of the plot. At each position, we recorded the depth (cm) at which 2 MPa was attained using both 150 and 300 PSI (pounds of force per square inch of area). Plant performance can be negatively affected when soil compaction levels approach and exceed 2 MPa (Bassett et al. 2005).

We visually estimated the percent area covered by leaf litter and bare ground within one 1x1 m plot within each 3x3m experimental plot during 2010-2013 and 2017. We also measured and averaged litter depth (cm) at the four corners of each 1x1m plot during 2010-2013 and 2017. To estimate values for the unmeasured years (2014-2016, 2018) for bare ground (%), litter (%) and litter depth (cm), we calculated separate mean annual changes in each measure for sites that experienced fire or not in a given year at each installation. This was meant to account for the expected impacts of fire on the changes in the amount of litter on the ground (which was expected to impact all three measures). We then added the appropriate expected annual change to the unmeasured years, based on the plot's location (which installation it was part of) and fire regime (if a fire had occurred at that site that year), rounding to 0 or 100 % when it dropped below or above that measure, respectively. We tested the validity of our estimates by estimating values for 2017 with the approach described and comparing them to the observed values sampled that year (Fig. 5.1.4).

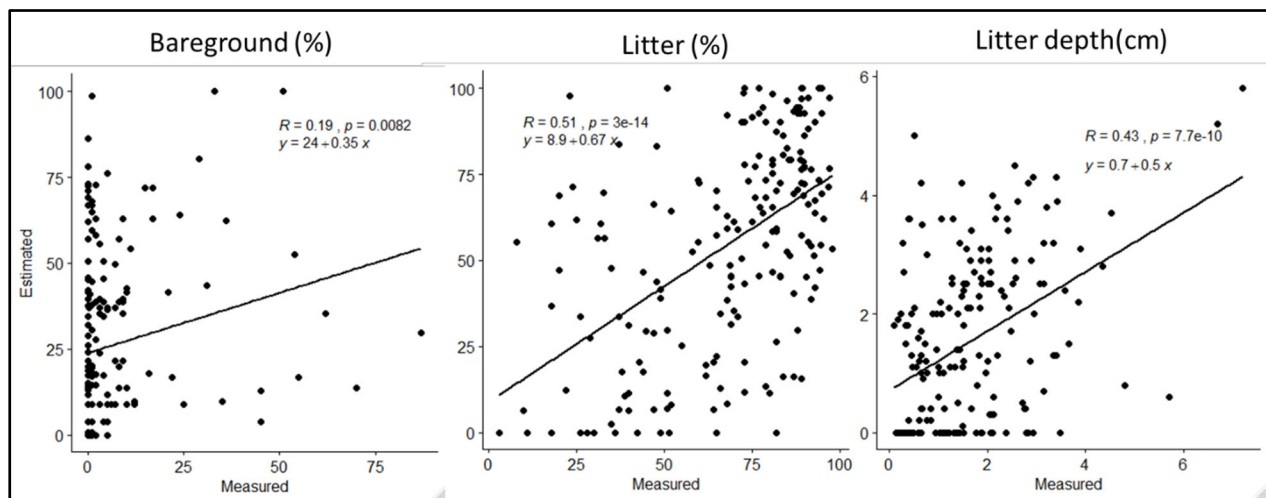


Fig. 5.1.4. Comparison between estimated and measured bare ground (%), litter (%) and litter depth (cm) for all plots during 2017.

We calculated basal area for each experimental plot by measuring diameter at 1.4m height of all woody stems rooted > 50 % within each 7×7 m experimental plot during 2010-2013, and again in 2017. Basal area was not measured in 2018 as it was not expected to change from 2017 for most sites so we used 2017 values for 2018. For the unmeasured years (2014-2016), we estimated basal area as the expected incremental annual change based on differences observed at each site between 2013 and 2017. For example, if a site had basal area of 20 in 2013 and 16 in 2017, the expected annual change added each year was $((16 - 20) / 4) = -1$. We updated annual records of fire regimes for the 48 study sites in collaboration with our manager partners at each installation. We summarized fire records in two ways: as the total number of prescribed fires at a site since 1991, and as the number of years since the last prescribed fire occurred at a site. We defined years since fire as the maximum number of years from the year of sampling until 1991 to keep the spread of values consistent with the other sites and to minimize outliers.

We obtained monthly weather records for each of the three installations from nearby weather-stations (<https://gis.ncdc.noaa.gov/maps/ncei/summaries/monthly>) and summarized average temperature and total rainfall for the growing (Mar-Aug) and non-growing (Sep-Feb) seasons from 2009 to 2018.

Table 5.1.2 Environmental conditions and management treatments considered as factors that could influence either establishment, persistence or spread of the 20 seeded species.

Predictor	Spatial Resolution	Temporal resolution	Description
Seeding	Plot	March, 2011	Whether the plot received the experimental treatment in March, 2011 consisting of addition of seeds from each of 21 species (see Table 4.1) to the center 5 x 5m of each plot.
Herbicide	Plot	August, 2010	Whether the plot received the experimental treatment in August, 2010 consisting of the application of a broad spectrum herbicide across the 7×7m plots.
Soil moisture (% by mass)	Plot	2011	Soil moisture content at field capacity measured from homogenized samples from eight, 20-cm soil cores collected 50 cm away from the 3x3m plot. Calculated from the proportional difference between wet and dry weights.
Soil compaction (150 PSI)	Plot	2011	Soil compaction measured as the mean depth at which 2 MPa was attained using 150 PSI of pressure; four measurements taken, one along each of the four outside edges of the 3x3m plot).
Soil compaction (300 PSI)	Plot	2011	Soil compaction measured as the mean depth at which 2 MPa was attained using either a 300 PSI of pressure; four measurements taken, one along each of the four outside edges of the 3x3m plot).
Bare ground (%)	Plot	2010-2013, 2017	Estimated visually as the percent area covered by bare ground in 1x1 m quadrats within each 3x3m plot.
Litter (%)	Plot	2010-2013, 2017	Estimated visually as the percent area covered by leaf litter in 1x1 m quadrats within each 3x3m plot.
Litter depth (cm)	Plot	2010-2013, 2017	Depth of litter on the ground measured at the four corners of each 1x1m quadrat within each 3x3m plot.
Basal area	Site	2010-2013, 2017	Overstory basal area by recording diameter of all woody stems > 2.5 cm at 1.37 m height.
Total fires	Site	2010-2018	Number of prescribed fires that occurred at a site between 1991 and the year of sampling.
Since fire (years)	Site	2010-2018	Number of years since last fire occurred at a site.
Mean temperature (°C) Mar-Aug	Site	Mar-Aug of 2009-2018	Mean daily temperature averaged over the growing season including spring and summer months.
Total rain (mm) Mar-Aug	Site	Mar-Aug of 2009-2018	Total rainfall over the growing season including spring and summer months.
Mean temperature (°C) Sep-Feb	Site	Sep-Feb of 2009-2018	Mean daily temperature averaged over the non-growing season including autumn and winter months.
Total rain (mm) Sep-Feb	Site	Sep-Feb of 2009-2018	Total rainfall over the non-growing season including autumn and winter months.

5.1.4 Plant functional traits

We used existing categorical and quantitative plant traits and also collected new functional trait data in 2018 to obtain information for all seeded species at each installation (Table 4.1.3). We used standardized methods to measure functional traits for the seeded species (Pérez-Harguindeguy et al. 2016). We measured plant functional traits that describe characteristics of species that are commonly associated with key ecological processes such as establishment, competitiveness, dispersal, and stress tolerance (Lavorel and Garnier 2002,

Wright et al. 2004, Westoby and Wright 2006), to determine if they predicted responses across species. Specifically, we captured dispersal ability as their dispersal mode (classified as wind-dispersed, or other-dispersed, when dispersed by an alternative mechanism including: tumbling, animal, adhesive, or unknown); and their ability to propagate by vegetative means (i.e., clonality, classified as clonal or not), which were categorical traits. We also measured seed characteristics (seed volume, seed width, seed length, seed depth, seed mass, the seed-to-dispersule mass ratio, seed coat thickness, and seed falling velocity for wind-dispersed species) as continuous, quantitative traits. To capture species' establishment strategies, we measured germination characteristics (the proportion of seeds that germinated, the average number of days to germination) as continuous quantitative traits. Lastly, to capture species growth strategies, we assigned each species to a plant type or life form (either Forb, Graminoid, or Legume) as a categorical trait, and measured adult plant height (distance from ground to tallest photosynthetic structure), specific leaf area (leaf area/dry mass), and leaf tissue chemistry (carbon-to-nitrogen ratio) as continuous quantitative traits.

We determined dispersal modes by first searching the Kew Garden Seed Information Database (Royal Botanic Gardens 2019). If species were not in the database, we searched the primary literature with ISI Web of Science for papers that described dispersal for the species and/or genus. In some cases, we also searched reliable plant natural history websites to cross-reference obtained information. We also determined species clonality from searches of primary literature. If species descriptions or primary papers described the species as having rhizomes or stolons or other vegetative parts geared for dispersal, we assigned it as a "clonal" species. We further, subclassified clonal as guerrilla to reflect at one extreme, species that infiltrate the surrounding vegetation, maximizing interspecific contacts and bearing widely-spaced ramets, and as phalanx, to reflect at the other extreme, species that form tight-packed advancing front of ramets that exclude other plants from the clonal territory. The 'guerilla' species follows an opportunistic strategy of rapid dispersal and 'sampling' of the environment, whereas the 'phalanx' strategy is a conservative one of consolidation and slower radial dispersal. All categorical trait designations were independently reviewed by two plant ecologists within our southeastern plant ecology research team (E. Damschen, L. Brudvig, M. Burt, C. Warneke, Q. Sorenson). Any conflicting or missing designations were discussed and decided by this entire team based on morphological and field observations (~10% for each characteristic).

All quantitative, continuous traits were measured from multiple individuals (10-15) from each of 1-5 populations. For each population, dispersule and seed size measures were carried out on 15 seeds (five dispersules from at least three individuals per population) from three populations. Seed mass was determined from an average weight of 15 seeds. Seed dimensions (length, width, depth) were measured for each seed with its dispersal structure (i.e., a dispersule) and without its dispersal structure (i.e., a seed) using a micrometer. Plant height measures (height from ground to highest photosynthetic material) were obtained for 10 individuals per population for each species. Specific leaf area (SLA) was measured from one leaf per individual for each of 10 individuals per population as the average leaf area (cm²) divided by leaf dry mass (g). Leaf tissue chemistry information was obtained from homogenized, dried tissue from 10 leaves taken from each individual within a population. Samples were analyzed for carbon and nitrogen content by the Stable Isotope Ecology Laboratory at the University of Georgia, Center for Applied Isotope Studies (Athens, GA).

We also used results from a seed germination experiment conducted in 2011 to inform species-specific seed viability (Orrock et al. 2015). We evaluated 750 seeds from each species

from each site for a period of two weeks to determine viability rates. Seeds were grown in petri dishes with 25 seeds from a single species and site per dish. Blotter paper was placed at the bottom of each dish, and watered as needed throughout the course of the germination trial. All dishes were placed in a growth chamber, which was set to mimic climate norms in South Carolina for May (29.5 °C during the 13.5 hour day, with nighttime temperatures of 14.2 °C). When present, fungal growth was treated with a 5% bleach solution applied directly to the affected area. Throughout the two week trial, seeds were checked daily for germination. After a seed germinated, it was removed from the petri dish. At the end of the trial, we calculated the proportion of viable seeds of each species, as well as the average number of days before germination occurred (as a measure of the amount of time a seed has to be saturated with water before it germinates).

Table 5.1.3 Candidate list of functional traits that could influence establishment, persistence and dispersal for the 20 seeded species.

Trait	Description
Clonality	Classified as clonal or non-clonal.
Dispersal mode	Classified as either wind-dispersed or non-wind-dispersed (including adhesive, ballistic and unassisted)
Family	Taxonomic family
Plant type	Classified as either forb, graminoid or legume
Height (cm)	Average height from 10-30 individuals measured from the base of plant to the tallest photosynthetic structure
Specific Leaf Area (SLA)	Specific leaf area measured from 10-30 leaves
C/N	Average percent Carbon / Nitrogen content from 10-30 leaves
Seed volume (mm ³)	Average from 15-45 individual seeds
Seed coat thickness (mm)	Average from 15-45 individual seeds
Seed depth (mm)	Average from 15-45 individual seeds
Seed length (mm)	Average from 15-45 individual seeds
Seed width (mm)	Average from 15-45 individual seeds
Seed mass (mg)	Average of 15-45 seeds
Seed / Dispersule (mg)	Seed mass divided by dispersule mass
Terminal velocity (m/s)	Average terminal falling velocity for wind-dispersed species in m/s
Germination days (days)	Mean number of days that 25 seeds for each species took to germinate under laboratory conditions
Proportion germinated	Proportion of 25 seeds for each species that germinated under laboratory conditions

5.1.5 Vegetation Sampling

Our previous work created a comprehensive dataset quantifying the identity and abundance of understory vegetation, woody plants in the sub-canopy (i.e., shrubs), and overstory trees (Orrock et al. 2015). Vegetation sampling for our current work consisted of three complementary sampling efforts. First, we resurveyed the 48 sites in 2017 and 2018 to understand the long-term changes in local persistence of the species added by seed within each of our study plots. Second, we evaluated dispersal by conducting surveys along transects that extended from our sites in 2017 and within 1-meter wide rings (up to 9 m away) surrounding each site in 2018 (see Section 4 below). Third, we collated available categorical and quantitative traits, and supplemented these with additional measures from samples collected in the field in 2018, and from previous germination experiments carried out by the principal investigators to obtain estimates for the 25 seeded species.

To quantify the establishment and persistence of seeded species, we first recorded the presence of species added as seed in the 5×5m center of each experimental plot. We then estimated the percent ground cover of each seeded species present in the 3.16×3.16m center of each plot, to quantify local abundance. We completed these measurements during summer 2017 and 2018, building on the data we had previously collected by the same methods during the summers of 2010 (pre-treatment), 2011, 2012, and 2013 to assess short-term effects.

5.1.6 Sampling spatial spread

We evaluated spread away from experimental plots for seeded species that were part of our original seeding treatment. Potential recruits for the seeded species were located at each of the 48 sites from the 3 installations within 1-m wide search rings over short to medium distances (up to 9 m away from the plots). Plot-level rings were placed at 1-m distance increments surrounding the eight 5 x 5 m plots within a site, up to 3 m away (at 0-1, 1-2, 2-3 m distances). Site-level rings were placed surrounding the entire 8-7x7m plot array, at 4-5 m distances (from the plots) in 2017, and extending to 5-6, 6-7, 7-8, and 8-9 m distances away from the plots in 2018 (Fig.4.1.5). However, *Aristida purpurascens* ARIPUR, *Lespedeza hirta* LESHIR, *Pityopsis graminifolia* PITGRA, and *Solidago odora* SOLODO were not sampled in the outer site rings (5-6m, 6-7m, 7-8m, 8-9m) as they were found to be widespread (cosmopolitan) and counting individuals in those rings proved to be prohibitive due to time constraints. The geometry of the plots and sites meant that the area differed amongst rings, and this was accounted for in our analyses.

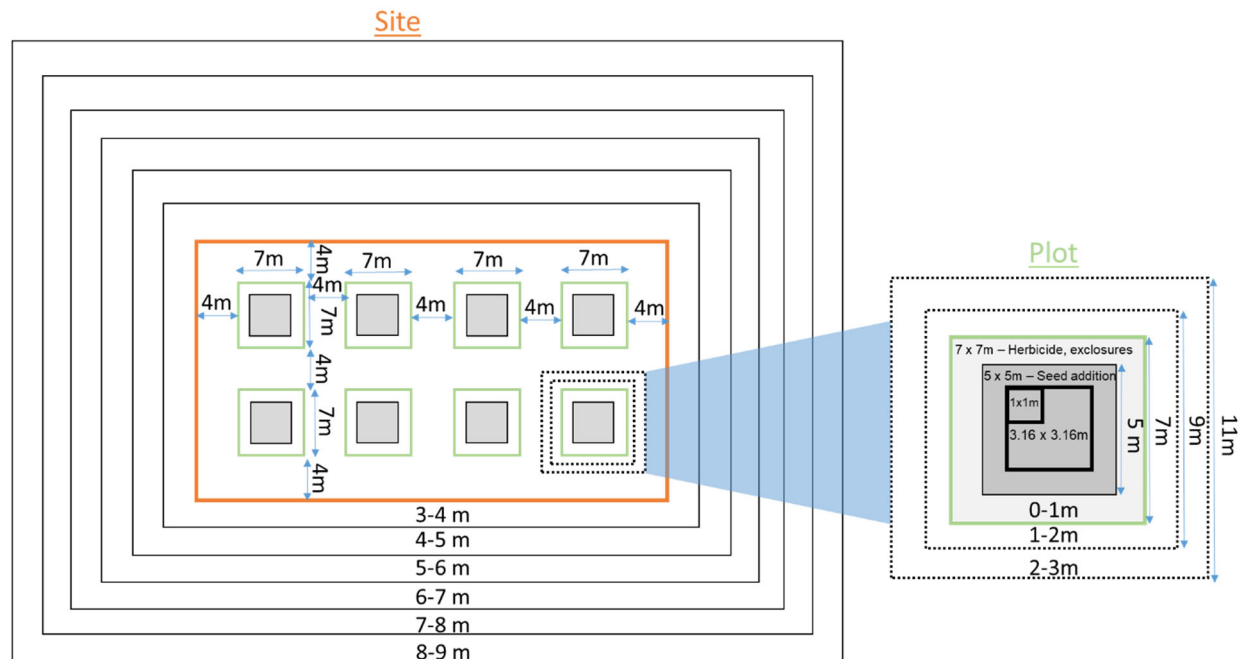


Fig. 5.1.5. Spread sampling design at each site. Plot-rings (0-1, 1-2, 2-3 m) and site-rings (3-4, 4-5, 5-6, 6-7, 7-8, 8-9 m) were used to evaluate spread of seeded species away from experimental plots. Blue arrows indicate distances.

In 2017, we also searched for individuals of the seeded species in four, 2 x 40 m transects extending away from each 7x7 m plot, but we found such small number of individuals that we concentrated efforts on the rings in 2018. All recruits found in each ring were identified to species and assigned to the pool of potential recruits that effectively spread (i.e. dispersed, germinated and survived until 2017 or 2018). Some seeded species were found at some sites in 2010, prior to the seeding treatment. To avoid misclassifying individuals found in the dispersal rings as recruits when they were potentially already present, we removed records from those sites for those species and only focused our analyses on recruits from species that had been previously undetected at each site in 2010. This ensured that all recruits were the product of effective spread from the experimental plots. Because of the differences in field methodologies between 2017 and 2018 we evaluated differences in spread patterns at the rings between years (Fig 4.1.6). The patterns of spread were very similar for both years so we focused further analyses on 2018 data only, as this also included spread beyond 5 m.

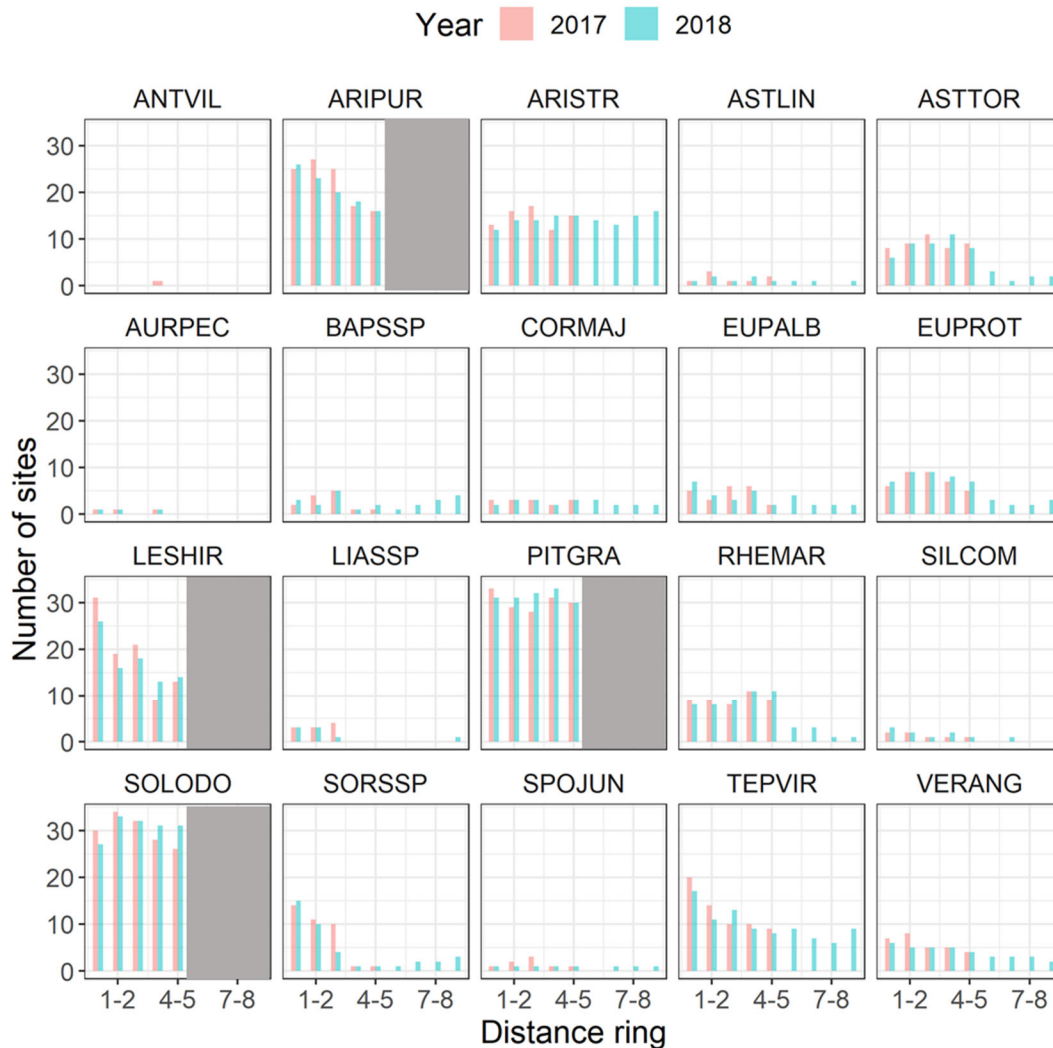


Fig. 5.1.6. Number of sites where each seeded species spread along sampled rings between both sampling years of 2017 and 2018. Note that sampling only occurred up to 4-5 m distance ring in 2017, and was extended to 8-9 m distance ring in 2018. Spread in rings up to 5m away was similar amongst years. ANTUIL was only detected at one site in 2017. Grey areas represent rings that were not surveyed for those species (i.e. beyond 5m).

5.1.7 Combining predictors

The use of collinear predictors in the same model can result in nonsensical model estimates. We evaluated correlation amongst continuous predictors including environmental conditions, management interventions, weather, and species traits (Fig. 4.1.7), using Pearson's correlation tests and derived final predictor sets (Table 4.1.4) that only included non-correlated predictors (< 0.7 , Dormann et al. 2013). For all analyses, we standardized all continuous predictors by subtracting their means and dividing by two standard deviations, while categorical predictors were scaled within the -1 to 1 range (Gelman 2008).

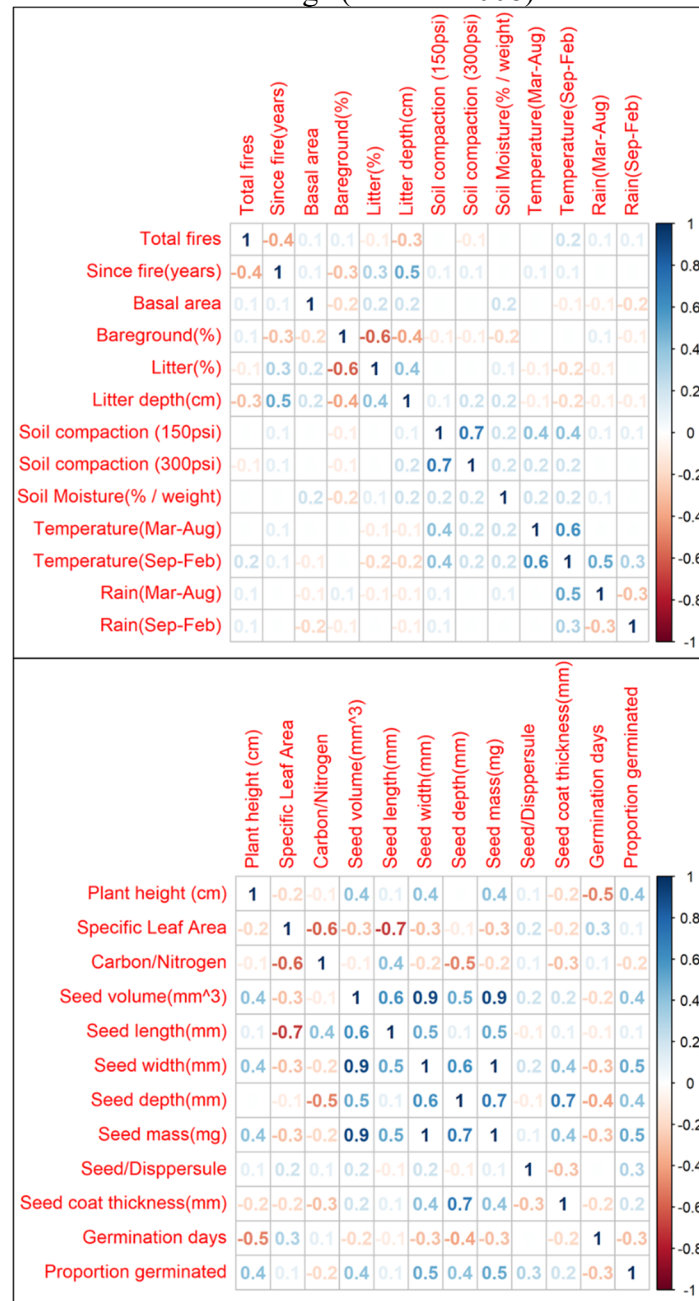


Fig 5.1.7 Correlation plot among environmental conditions (top) and species mean functional traits (bottom). Correlations were evaluated using Pearson correlation tests at the species by plot by year level.

Table 5.1.4. Final predictor list for analyses evaluating local, long-term recovery (using multi-species, multi-year occupancy models decomposed as establishment and persistence) and outward recovery (using multi-species spread kernels during 2018).

Predictor	Used in occupancy analyses (2010-2018)	Used in spread analyses (2018)
Seeding	Yes	No
Herbicide	Yes	No
Soil moisture (% by mass)	Yes	No
Soil depth (150 PSI)	Yes	No
Bare ground (%)	Yes	No
Litter (%)	Yes	No
Litter depth (cm)	Yes	No
Basal area	Yes	Yes (averaged over sampling years)
Total fires	Yes	Yes (for 2018)
Since fire (years)	Yes	Yes (averaged over sampling years)
Mean temperature (°C) Mar-Aug	Yes	No
Total rain (mm) Mar-Aug	Yes	No
Total rain (mm) Sep-Feb	Yes	No
Height (cm)	Yes	Yes
SLA	Yes	Yes
Carbon/Nitrogen	Yes	Yes
Seed volume	Yes	No
Seed length	No	No
Seed width	No	Yes
Seed depth	No	No
Seed mass	No	No
Seed / Dispersule	Yes	Yes
Seed coat	Yes	Yes
Germination days	Yes	Yes
Proportion germinated	Yes	Yes
Clonality	Yes	Yes
Dispersal mode	No	Yes

5.2 Statistical approaches to evaluate local recovery

5.2.1 Multi-species occupancy modelling

We fitted a multi-species dynamic occupancy model using a Bayesian framework to presence data of seeded species, which allowed us to account for the unbalanced design arising from sites lost to logging in the later years of sampling, and to estimate occupancy during unmeasured years (Dorazio et al. 2010). Imperfect detection was assumed to be negligible, given the size of the plots and observer experience in identifying added species. In the first year, when seed and herbicide addition treatments were implemented, we modelled observed occurrence for species s , plot j , year $k=1$, as a simple Bernoulli process driven by the probability of occupancy that year, $z_{s,j,1} \sim \text{Bern}(\psi_{s,j,1})$, with a prior for occupancy defined as: $\psi_{s,j,1} \sim \text{Bern}(0.5)$. From the second sampling year onwards, the dynamic occupancy model took advantage of observations of annual occurrence for species s , plot j , year k , $z_{s,j,k}$, to estimate occupancy probability, $\psi_{s,j,k}$, as the result of two ecological processes:

1) establishment of species s , at plot j , in year k , given that it was not present in the previous year ($k-1$), $\gamma_{s,j,k}$, and

2) ongoing persistence from year to year, if the species was already present at the plot in the previous year ($k-1$), $\phi_{s,j,k}$. So,

$$z_{s,j,k} | z_{s,j,k-1} \sim \text{Bern}(\psi_{s,j,k})$$

$$\psi_{s,j,k} = z_{s,j,k-1} * \phi_{s,j,k} + z_{s,j,k-1} * \gamma_{s,j,k}$$

Species establishment, $\gamma_{s,j,k}$, and persistence, $\phi_{s,j,k}$, were in turn related to $Q = 22$

predictors, $X_{\gamma,q}$ and $X_{\phi,q}$, describing either site-level, m , management, plot-level, j , experimental treatments, location-level, l , weather, and species-level, s , traits (Table 4.4). These sub-models included fixed intercepts, $\beta_{\gamma,0}$ and $\beta_{\phi,0}$, and random intercepts for each species, $\varepsilon_{\gamma,s}$ and $\varepsilon_{\phi,s}$, which facilitate estimates for rare species by sharing information amongst species (Dorazio et al. 2010). Random intercepts for M sites, $\varepsilon_{\gamma,m}$ and $\varepsilon_{\phi,m}$, accounted for the remaining spatial autocorrelation related to the split-plot design.

$$\begin{aligned} \text{logit}(\gamma_{s,j,k}) &= \beta_{\gamma,0} + \varepsilon_{\gamma,s} + \varepsilon_{\gamma,m} + \sum_{q=1}^Q \beta_{\gamma,q} * X_{\gamma,q} \\ \text{logit}(\phi_{s,j,k}) &= \beta_{\phi,0} + \varepsilon_{\phi,s} + \varepsilon_{\phi,m} + \sum_{q=1}^Q \beta_{\phi,q} * X_{\phi,q} \end{aligned}$$

The number of predictors was large relative to our sample size, so we relied on stochastic search variable selection (SSVS) to assess their importance (George and McCulloch 1993). SSVS is easy to use and robust compared to alternative Bayesian variable selection techniques (O'Hara and Sillanpää 2009, Hooten and Hobbs 2015). Predictor coefficients, β_q , were included in a global model and given modified priors that were a mixture of two normal distributions and linked to indicator variables, δ_q , drawn from 'indifference' Bernoulli priors $\delta_q \sim \text{Bern}(0.5)$ (George and McCulloch 1993). So:

$$\beta_q | \delta_q \sim (1 - \delta_q) N(0, \tau^2) + \delta_q N(0, c^2 \tau^2)$$

During each MCMC iteration, predictors with associated $\delta = 0$ indicators, had priors with small variances, $\beta \sim N(0, \tau^2)$, (termed a spike prior), resulting in β estimates that were effectively zero. Conversely, predictors with associated $\delta = 1$ indicators, had 'slab' priors with wide variances, $\beta \sim N(0, c^2 \tau^2)$, resulting in non-zero β estimates (Malsiner-Walli and Wagner 2011). We deemed predictors as significant, if the posterior means of their corresponding indicators were $\delta > 0.7$ (Weiser et al. 2018). The choices of the variance parameters c^2 and τ^2 can affect estimates of δ_q and β_q , as well as the mixing of the MCMC chains and so require tuning (Link and Barker 2006, Hooten and Hobbs 2015). We did this via a sensitivity analysis that compared models with alternative variance combinations ($\tau^2 = 0.02, 0.05$, and $c^2 = 10, 50, 100$) using within-sample model selection measures following Broms et al. (2016), and Cruz et al. (2019). We compared models using the WAIC (Watanabe-Akaike information criterion, Watanabe 2010) with lower values indicating better fit. Formulas used to calculate WAIC are included as a supplement in Cruz et al. (2019). Note that we only used sampled years (excluded 2014-2016, 2018) in WAIC calculations.

5.2.2 Evaluating species differences in their response to important predictors

The SSVS approach described above allowed us to define predictors that were important at the community-level. However, although some predictors may not be important while averaged across the community of species added to the experimental treatments, they may be influential to specific species. The complete list of predictors was too large to allow incorporation of species-specific responses to all of them (via random slopes). We therefore narrowed the predictor list from the top model chosen in the community-level analyses described in section 4.2.1 by focusing on two options:

- 1) Adding species-specific responses to only those predictors that were important at the community level, and
- 2) Adding species-specific responses to potentially important predictors, assessed based on whether their 95 % Credible Intervals did not overlap zero.

We used these reduced predictor sets to build two models with added random slopes to allow assessments of species-specific responses. The establishment and persistence sub-models of each model choice were modified as follows:

$$\begin{aligned} \text{logit}(\gamma_{s,j,k}) &= \beta_{\gamma,0} + \varepsilon_{\gamma,s} + \varepsilon_{\gamma,m} + \sum_{\substack{q=1 \\ Qr\gamma}}^{Qr\gamma} (\beta_{\gamma,q} + \zeta_{\gamma,s,q}) * X_{\gamma,q} \\ \text{logit}(\phi_{s,j,k}) &= \beta_{\phi,0} + \varepsilon_{\phi,s} + \varepsilon_{\phi,m} + \sum_{\substack{q=1 \\ Qr\phi}}^{Qr\phi} (\beta_{\phi,q} + \zeta_{\phi,s,q}) * X_{\phi,q} \end{aligned}$$

where $\zeta_{\gamma,s,q}$ and $\zeta_{\phi,s,q}$ represent the random slopes associated with each predictor in the reduced predictor sets for establishment, $Qr\gamma$, and persistence, $Qr\phi$, respectively (See Fig. 5.2.3 for the list of predictors chosen in each model). We compared the two model options using WAIC and chose the one with the lowest value for further inference of species-specific responses.

5.2.3 Model evaluation and fit

We updated posterior distributions of predictors in the models using Markov-Chain Monte-Carlo (MCMC) methods available in program JAGs (Plummer 2003), which we called from the R program (version 3.5.3) using the jagsUI package (version 1.5). For each model, we ran three parallel MCMC chains of 25,000 iterations, thinned every 5th iteration, and excluded the first 20,000 and as burn-in. We assessed model convergence using the MCMC trace-plots and the Gelman–Rubin statistic expected to be <1.1 (Gelman and Rubin 1992).

Model goodness-of-fit was also evaluated using a posterior predictive check using Bayesian p values based on deviance residuals, following Broms et al. (2016), with values between 0.1 and 0.9 considered as good fit (equations and link to online code available from Cruz et al. (2019). Note that we only used sampled years (excluded 2014-2016) in Bayesian p value calculations.

5.3 Statistical approaches to evaluate outward recovery

5.3.1 Multi-species Weibull Dispersal Kernels

We aimed to evaluate effective spread of each seeded species at short to medium distances (up to 9 m) to evaluate their potential for outward recovery away from the treatment plots. We used the recorded distances dispersed by recruits of each species that were found within the plot and site rings at each study site during 2018. Effective spread is a better measure of outward recovery because it accounts for a seed's movement from the experimental plots, and their effective dispersal, survival and growth to the seedling stage to become a recruit. For each recruit r of species i that spread effectively, we modelled its spread distance d (as a discrete function based on the dispersal ring it was found at) at site j , as a Weibull distribution:

$$d_r \sim \text{Weibull}(v_i, \lambda_{i,j})$$

where v_i represents the shape parameter for species i , which was given a gamma prior $v_i \sim \text{Gamma}(0.01, 0.01)$. The $\lambda_{i,j}$ represents the rate of dispersal for species i at site j and was related to environmental and functional trait predictors as:

$$\log(\lambda_{i,j}) = \beta_{0[g]} + \sum_{p=1}^P \beta_{p[g]} X_p$$

where $\beta_{0[g]}$ represent intercepts for a categorical trait (either dispersal mode or plant type), and $\beta_{p[g]}$ represent coefficients for each group, g , which were assigned uninformative priors, $\beta_{p[g]} \sim \text{Normal}(0, 10)$ and related to $P = 13$ predictors, X_p describing either site-level management and species-level traits (listed in Table 4.1.4). Intercepts and slopes differed by group to allow species with different dispersal or life-form strategies to respond differently to site management practices and species traits.

The Weibull distribution extends the traditional exponential function to allow greater flexibility in how species i spread via species-specific, shape parameters v_i , which modify the spread rate to increase with distance when $v_i > 1$, decrease when $v_i < 1$, or remain constant when $v_i = 1$, the last makes it equal to the exponential function (Medina-Romero et al. 2019). We did not assess alternative kernel shapes (e.g. log-Normal) as Greene et al. (2004) found indistinguishable differences over shorter distances of less than 20 m.

Categorical traits included dispersal mode classified as wind-dispersed, or other-dispersed, when dispersed by an alternative mechanism including tumbling, animal, adhesive, or unknown; and plant type classified as graminoid, forb, or legume. We created alternative full models with each option of categorical functional trait (dispersal mode or plant type) and all continuous predictors. We also attempted models with each option of categorical functional trait (dispersal mode or plant type), but we replaced the continuous functional traits with the four main dimensions of a principal component analysis (PCA), which aimed to combine species using their mean continuous traits to meaningful dimensions (described in detail in Section 4.4 below). We aimed to assess whether combining correlated continuous traits with a PCA provided a better link to spread, compared to using only uncorrelated continuous traits. We reduced the full models by removing those continuous predictors where both group-coefficients overlapped zero (suggesting no effect regardless of grouping). We evaluated which predictor combination better described the observed spread patterns by comparing alternative models using WAIC. We used the model with the lowest WAIC for further inference and plotted partial predicted

relationships between spread rate and either site management or species traits by keeping all other model predictors at their mean values.

For the top model, we also estimated the probability that recruit r spread to distance d is the spread kernel, k_r , which was derived from the density function of the Weibull corrected for the area searched at each distance band:

$$k_r = \frac{v_i * \lambda_{i,j} * d^{v_i-1} * \exp(-\lambda_{i,j} * d^{v_i})}{Area_d / \max(Area_d)}$$

We plotted the estimated spread kernel for each species, averaged across sites, k_i , to the proportion of individuals that spread within each distance ring, also averaged across sites, to visually assess how well the model estimates of spread resembled observed spread for each species.

We also calculated the overall probability, $p(D_{i,j})$, that species i spread at site j , within the search area (0-9 m away) as the area under the curve over the distances surveyed:

$$p(D_{i,j}) = 1 - \exp(-\lambda_{i,j} dmax^{v_i})$$

where $dmax = 9$ m, was the maximum distance surveyed.

5.4 Statistical approaches to evaluating trait correlations among seeded species

Species traits are often correlated within and among species and can describe life history strategies and tradeoffs (Wright et al. 2004, Laughlin 2014, Díaz et al. 2016). To evaluate the extent to which traits co-vary in multidimensional space and interpret our results in light of these potential correlations, we conducted a principal component analysis (PCA) of all traits for all species, with the *prcomp()* function in R (Crawley 2012). We assessed contributions of each dimension or principal component by plotting the scree plot, a bar-graph showing the percentage contribution of each component to the total variation in the data. For those components that contributed most, we also extracted the contributions (i.e., loadings) that each functional trait made to them. We plotted the respective species and trait contribution to each of the three main components using biplots, where the arrow lengths represent the loading of each trait to each dimension, and the species coordinates represent their loadings to each component displayed in the axes. This allowed us to evaluate how functional traits and species with similar profiles are grouped together. We also displayed species loadings (coordinates) along the first two principal components and color-coded species by their categorical traits to evaluate whether the relationship in the contributions of each species to these two components could be grouped naturally based on their trait categories. Lastly, we used the four main components instead of functional traits in the spread analyses outlined above in section 5.3.1 to determine if they were better predictors of models evaluating observed patterns of species spread.

6. Results and Discussion

6.1 Predictors used

There was a wide range of basal area at each of the three installations (Fig. 6.1.1). Fire frequency consisted generally of five to six fires during the 1991-2018 period, with most sites burned one to two years prior (Fig. 6.1.1). At the plot level, the majority had small amounts of bare ground exposed (< 10 %), while most plots at Fort Bragg contained high levels (> 50 %) of litter (Fig 5.1.1). Nonetheless, litter depth was generally shallow (< 3 cm) at the three installations (Fig.

6.1.1). Soil moisture at most plots ranged between 30 and 40 % per weight, and soils were generally least compacted at Fort Bragg, followed by Savannah River, and were most compacted at Fort Stewart (Fig. 6.1.1). The three installations experienced similar broad weather patterns, with some noticeable differences. In particular, Fort Bragg experienced higher than average rainfall in July and also wetter falls, with higher than average monthly rainfall in September, October and December (Fig. 6.1.2). Savannah River had higher rainfall in August and September, while Fort Stewart experienced wetter summers, with higher than average rainfalls in April, June and July (Fig. 6.1.2). Fort Bragg, Savannah River and Fort Stewart experienced warmer winters, with higher than average December and February months (Fig. 6.1.2). Temperatures, unlike rainfall, were consistent among installations (Fig. 6.1.2).

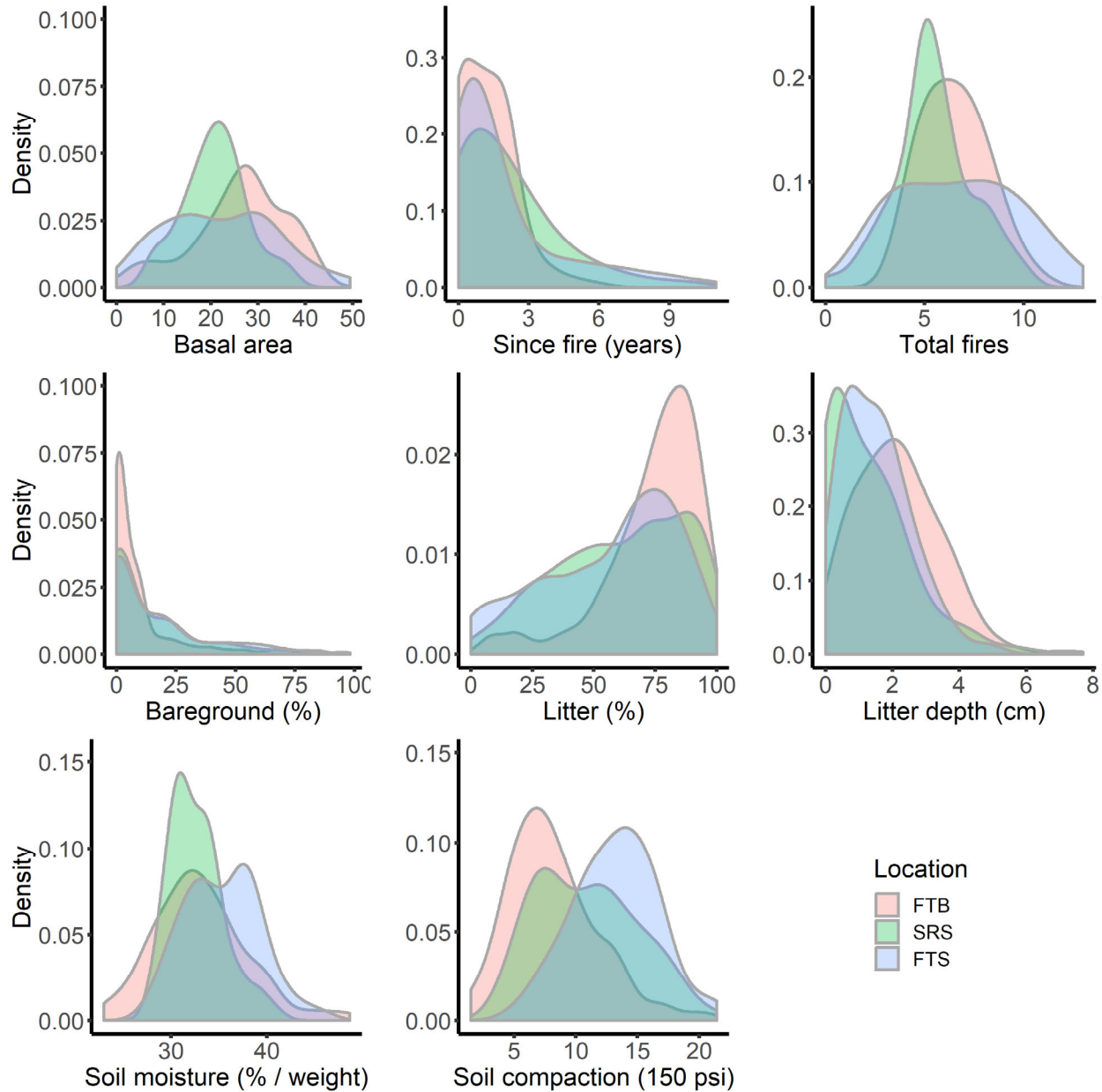


Fig. 6.1.1. Density plots showing distribution of values for environmental predictors used to assess local recovery and spread of seeded species at three installations. Note the different scales for the y axes. Soil moisture and compaction were measured in 2010 while other predictors were measured during 2010-2013, and 2017.

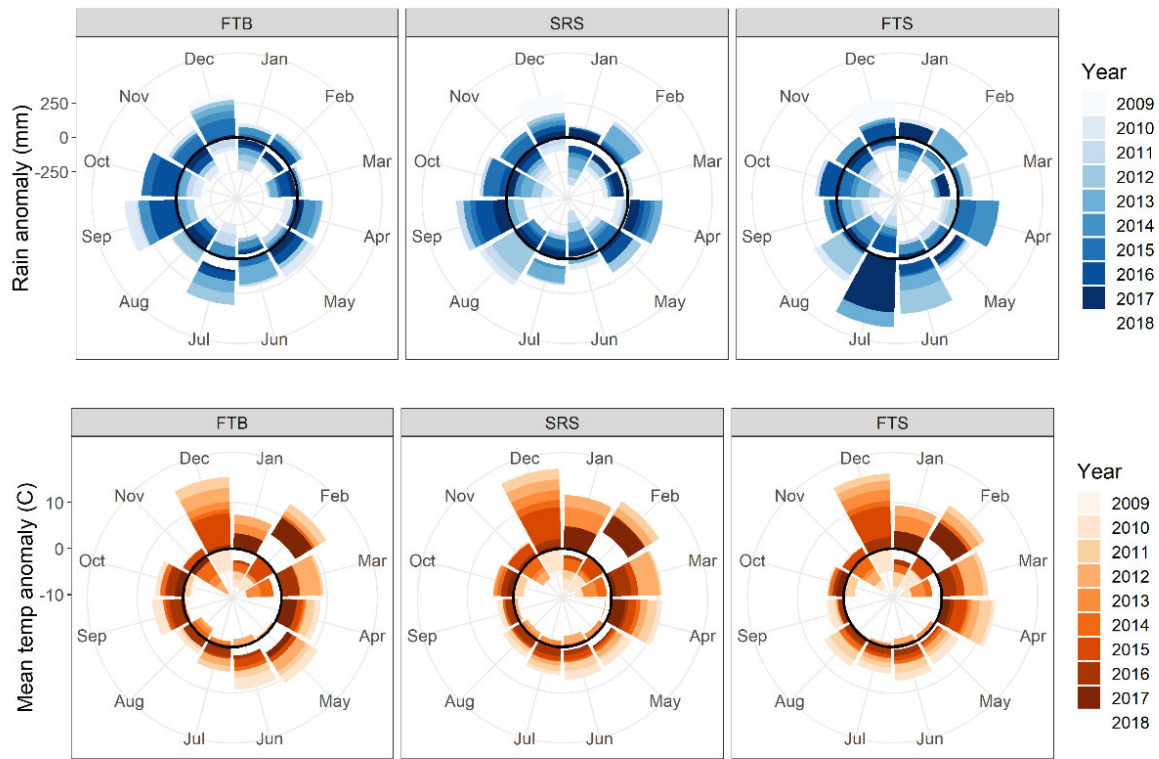


Fig. 6.1.2. Monthly anomalies for total monthly rainfall and mean daily temperatures experienced at the three installations during the study period (2009-2018). The taller sections highlight those months and years when weather was largely different from normal conditions (based on 30 year averages).

Species that were added as part of the seeding treatment showed wide diversity in the traits examined (Fig. 6.1.3). However, similarity among congener species, provided support for our approach that pooled them in analyses of establishment, persistence and spread. A few species stood out in some of the traits examined. For example, *Anthraenantia villosa* (ANTVIL), *Aureolaria pectinata* (AURPEC), and *Rhexia mariana* (RHEMAR) had the largest specific leaf areas (SLA) (Fig. 6.1.3). *Aristida stricta* and *Aristida beyrichiana* (collectively, ARISTR) had the largest Carbon to Nitrogen content ratio (Fig. 5.1.3). *Silphium compositum* (SILICOM) was a distinct outlier regarding seed volume, mass and width (Fig. 6.1.3). *Baptisia cinerea* and *Baptisia perfoliata* (collectively, BAPSSP) were also large in mass (Fig. 6.1.3). The majority of the seeds of (SORNUT) examined in laboratory conditions did not germinate. The large intra-specific variability (Fig. 6.1.3) suggests that evaluation of individual-specific differences in future studies may provide further insights.

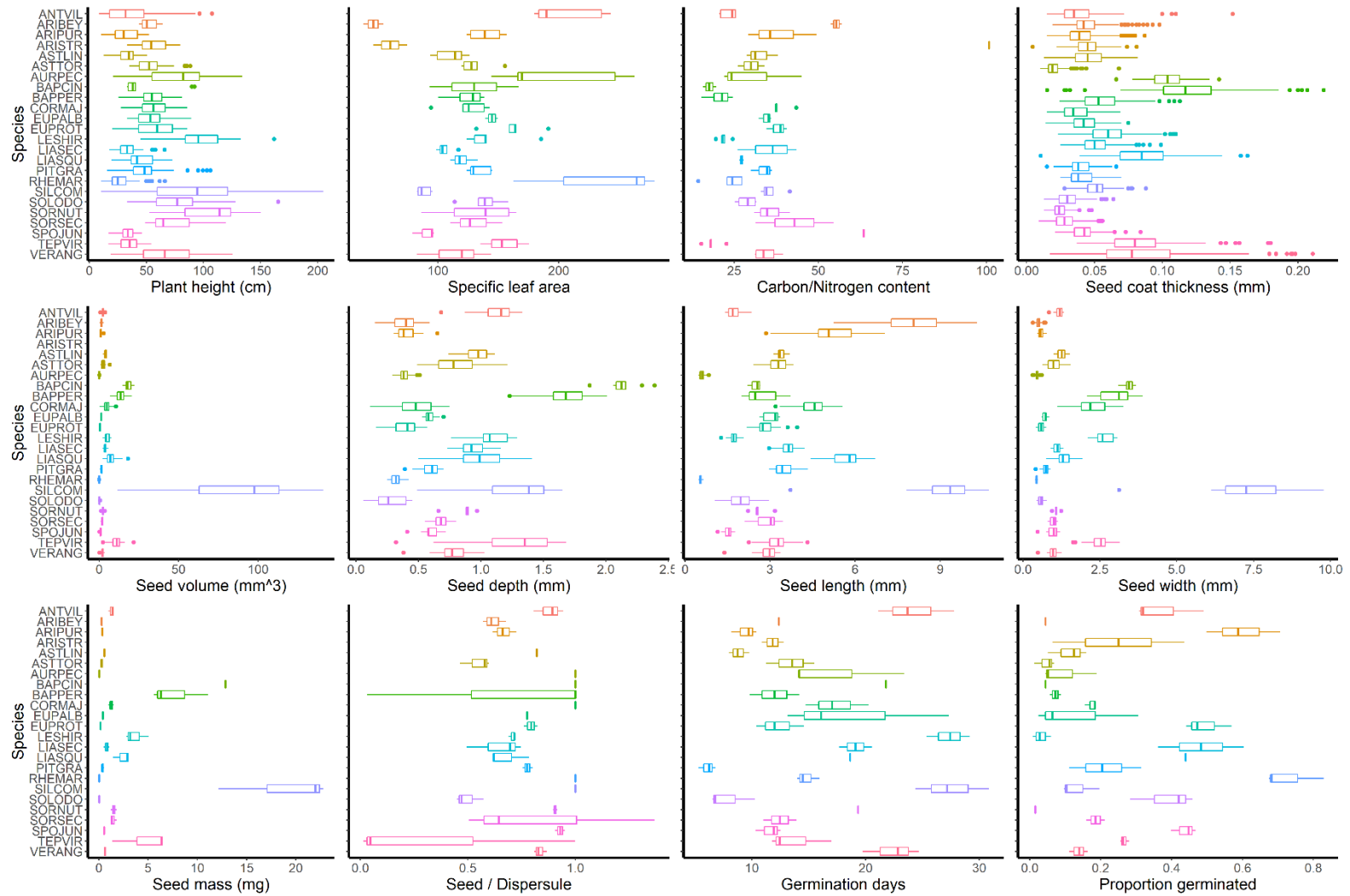


Fig 6.1.3. Variation in continuous traits among species. Note that congeners (see Table 4.1.1) are displayed separately to highlight that their similarities made pooling them appropriate, except for ARIPUR (*Aristida stricta*, *Aristida beyrichiana*) which did not have species-specific data.

6.2 Local, long-term recovery

6.2.1 Community-level establishment, persistence, and occupancy

Our evaluation of establishment (i.e., absent the previous year and present that year) and persistence (i.e., present the previous and current year) of the seeded community first required a sensitivity assessment of which variance values optimized our selection for predictors that were most important to the seeded community. The effects of changing the variances on the inclusion of a predictor as important (based on the posterior of its delta indicator exceeding 0.5) are highlighted in Fig. 6.2.1. Most predictors were insensitive to variance choices and their delta posteriors were well below 0.5, suggesting that they did not contribute to improving model fit (i.e., they did not help explain community-level establishment and persistence). Some predictors clearly improved model fit and were consistently selected as important regardless of variance choice (always above 0.5, Fig. 6.2.1). However, the contributions of some predictors were not clear-cut (Fig. 6.2.1), suggesting that their effects on establishment and persistence were not strong, consistent, or both. Overall, results from this sensitivity analyses suggested that the combined variances of 2.5 in model 5 (indicated by vertical dotted line, Fig. 6.2.1) provided the best fit (lowest WAIC) from the variance choices evaluated (model 5, Table 6.1.1). The Bayesian p value for model 5 suggested adequate fit of model predictions to the data (Fig. 6.2.2). Estimates from model 5 are thus used for further inference on community-level recovery.

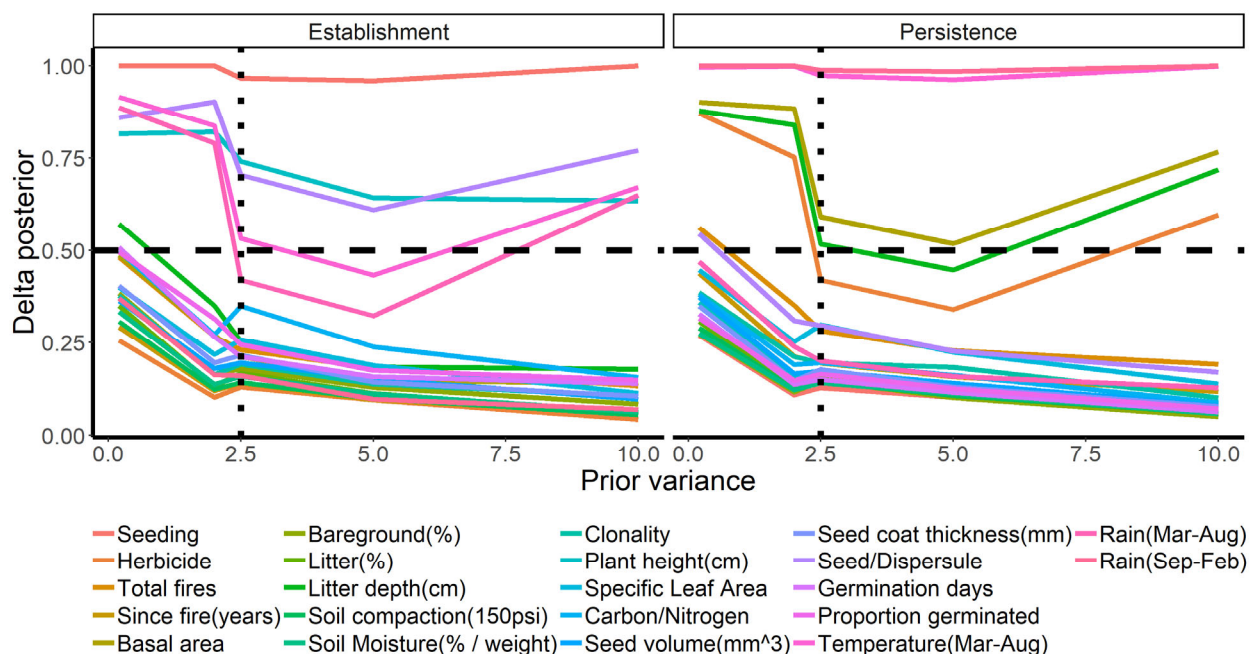


Fig. 6.2.1 Sensitivity analyses results showing changes in the indicator variables as a result of the variance choices. The model with prior variance ($c^2 * \tau^2$) of 2.5 (model 5) provided the best fit based on WAIC, and was used for further inference. The horizontal dashed line indicates the cutoff of 0.5 used to decide if a predictor was important at the community-level. The dotted vertical line indicates the results for the top model.

Table 6.2.1 Results of sensitivity analysis showing model 5 provided the best fit. Bayesian p values indicate adequate fit for all models tested

Model	Prior variance	WAIC	Bayesian p value
1	5	6227	0.105
2	2	6240	0.113
3	0.2	6233	0.095
4	10	6244	0.122
5	2.5	6224	0.109

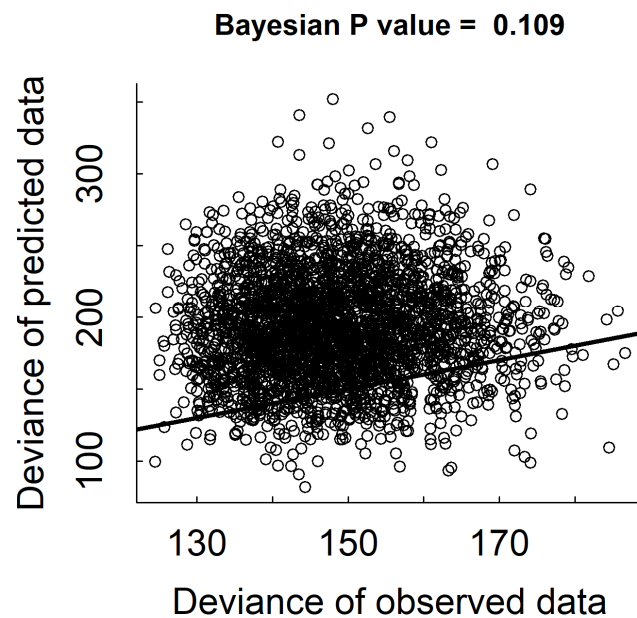


Fig. 6.2.2 Bayesian *p* values for the top model from the SSVS analyses (model 5 in Table 6.1) evaluating which predictors were most important in influencing establishment and persistence at the community level for the 20 added species.

Estimates of community-level responses (means and 95 % CIs of coefficients) for each predictor in relation to establishment and persistence are shown in Fig 6.2.3. Predictors evaluated as important through the SSVS approach (* in Fig 6.2.3) the seeding treatment had the strongest positive benefit on establishment of the community of seeded species (Fig. 6.2.4, left panel). Species with taller adult plants, and species with lower ratios of seed/dispersule mass also had higher probabilities of establishment (Fig. 6.2.4., left panel). Lastly, community-level establishment was higher in cooler years, with lower summer temperatures (Fig. 6.2.4., left panel). Community-level persistence (ongoing survival from year to year) appeared to be higher in more open sites with lower basal areas, and in plots with lower litter depths (Fig. 6.2.4 Right panel). Past work has shown a negative relationship between tree density and understory plant diversity, mediated by litter accumulation, in longleaf pine savannas (Hiers et al. 2007, Veldman et al. 2014) and our finding suggests a mechanism of reduced plant survival for these past results.

Similar to establishment, persistence was also higher in years of lower summer temperatures (Fig. 6.2.4 Right panel). Overly hot summers, therefore appear to limit the ability of seeded species to both establish and persist. Higher rainfall during Sep-Feb also improved community level persistence (Fig. 6.2.4 Right panel), presumably because it extends the growing season at the tail months of September and February. Overall, persistence at the community-level appeared most limited by climatic conditions, with the lowest persistence estimated to have occurred when summers were too hot or winters were too dry.

Results from the model estimating community-level establishment and persistence were supported by additional summaries plotting the effects of the seed addition and herbicide treatments on average richness and average percent cover of the seeded species. Seed addition benefited seeded species richness at the three installations, and percent cover particularly Fort Bragg (FTB) and Savannah River (SRS) (Fig. 6.2.5), a finding reinforcing findings of additional emerging seed-addition studies in longleaf pine (Turley et al. 2017, Barker et al. 2019). At Savannah River in particular, cover and richness of seeded species continued to increase (2017) seven years after initial seeding treatment. At Fort Bragg and Fort Stewart cover and richness were maintained over the long-term (2017) to similar levels observed in 2013 (Fig. 5.2.5). Short-term recovery (2-3 years) post-seeding treatment therefore was indicative of long-term (~7 years) recovery at the community-level. This suggests that initial assessments of the success of restoration efforts can provide robust guidelines to long-term success. Conversely, the long-term benefits of herbicide treatment on the cover and richness of seeded species were noticeable at Savannah River Site but only appeared to benefit plots at Fort Bragg during early recovery, and were equivocal at Fort Stewart (Fig. 6.2.6). This finding suggests that competition with pre-existing vegetation may have been relatively important for plants establishing from seed addition at SRS and support the potential use of herbicide coupled with seed addition for ground layer recovery on post-agricultural locations at this site. Conversely, competition with understory vegetation may not have played as important a role for establishment from seed at Fort Stewart, though this result may also simply reflect the overall lower rates of establishment for seeded species at this location. At Fort Bragg, the transient effect of herbicide application may have been due to recolonization by herbicided species or different effects of non-seed addition species during the establishment vs. persistence phases of groundlayer recover from seed.

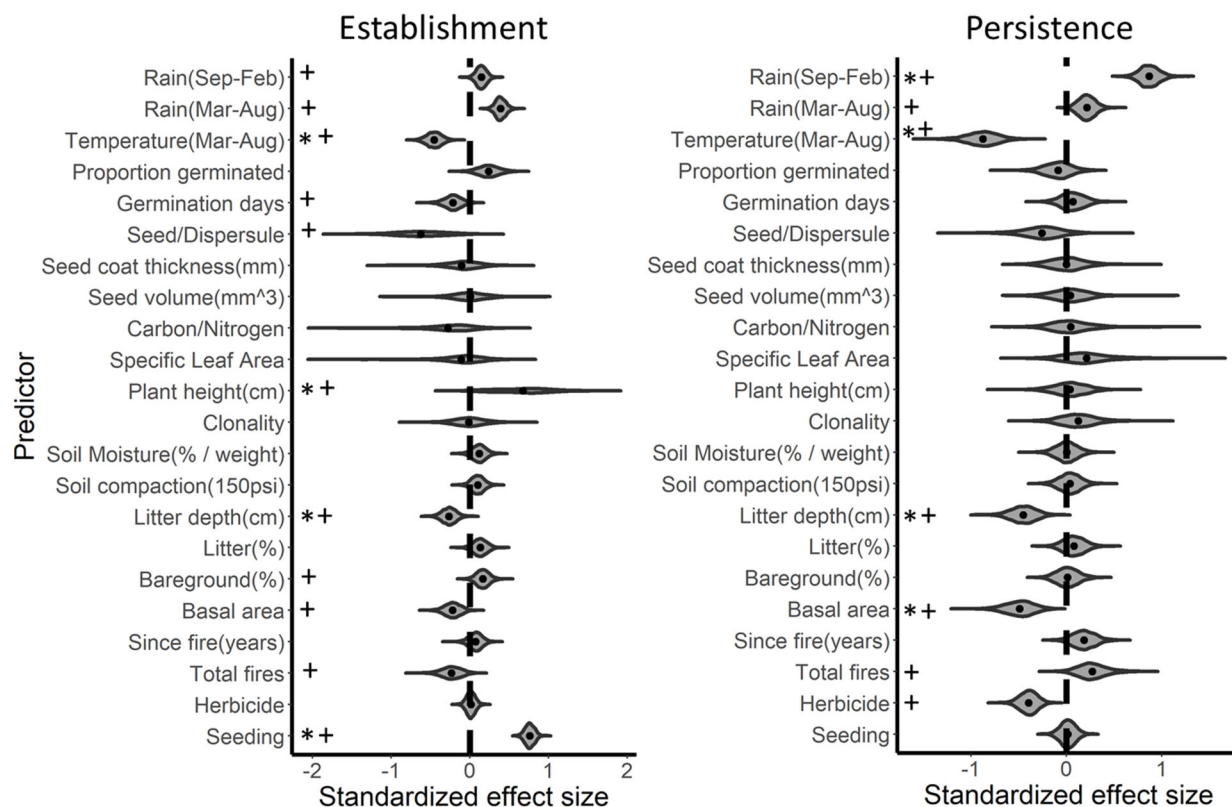


Fig. 6.2.3 Coefficient means and 95% Credible Intervals (CIs) estimated for predictors related to establishment (left panel) and persistence (right panel). Predictors classified as important as part of the Bayesian variable selection approach that accounts for their contribution towards improving model fit are marked with an asterisk. Predictors classified as potentially important based on their 95 % CIs not overlapping zero are marked with a plus sign.

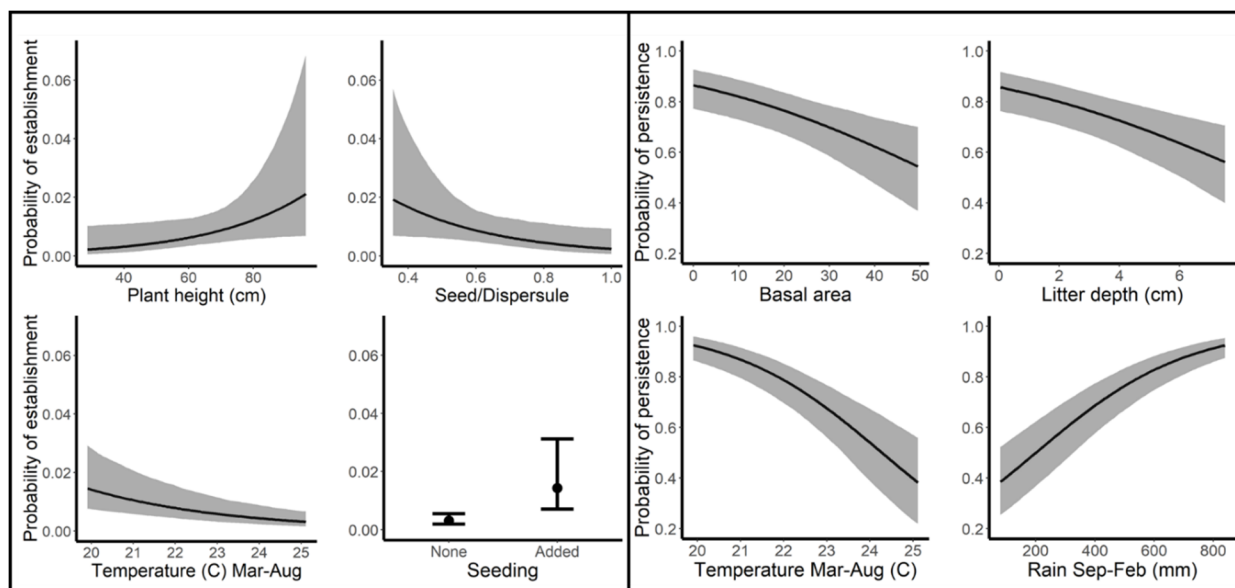


Fig. 6.2.4. Estimated relationships (partial prediction plots) between important predictors for community-level establishment (left panel) and persistence (right panel). Bold lines indicate mean relationships and grey bands the 95 % Credible Intervals. Relationships were estimated from the top model (model 5), while keeping all other predictors at their mean values.

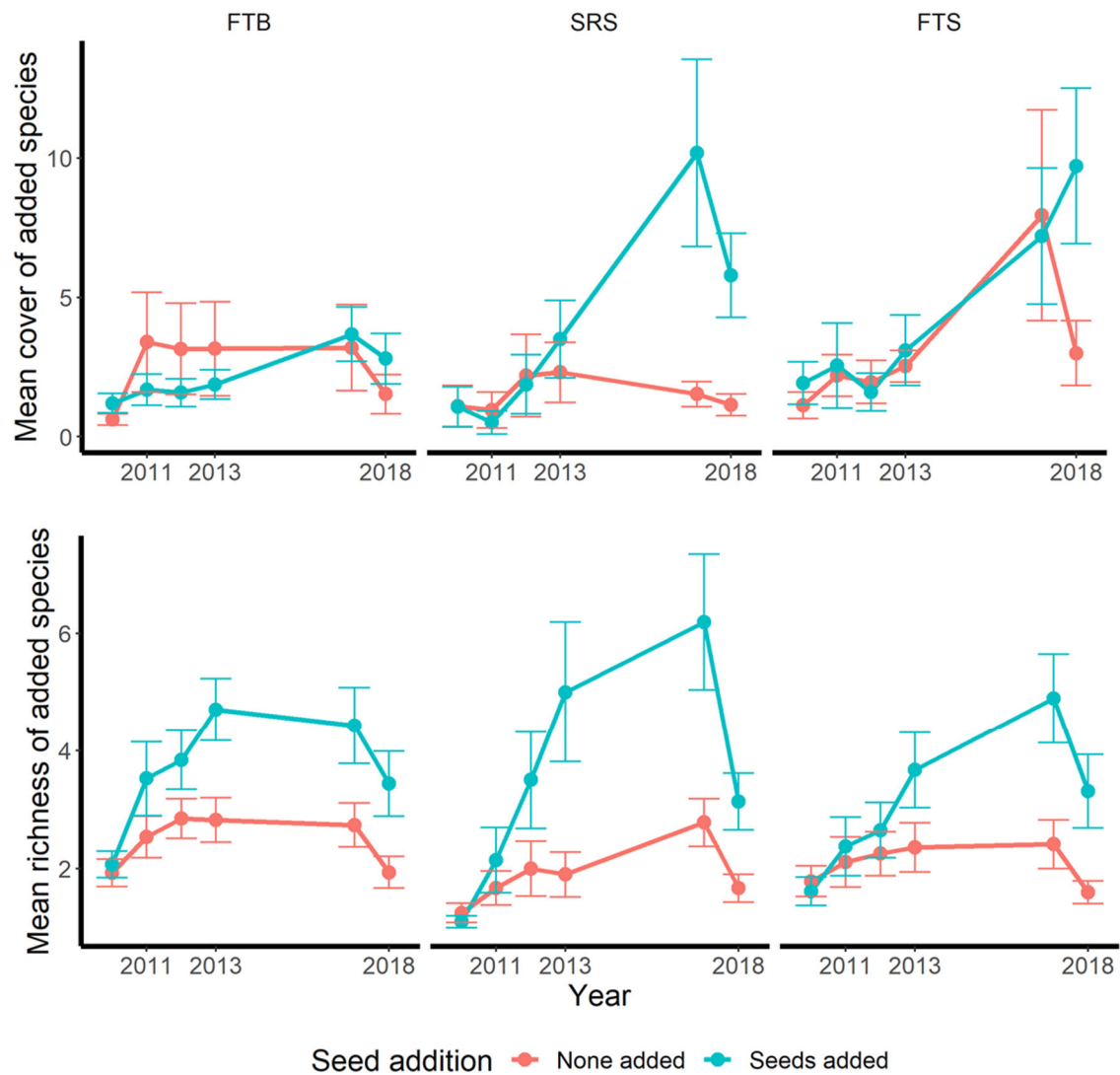


Fig. 6.2.5 Mean percent cover (top) and mean richness (bottom) of added species within 3x3m plots across years and by seed addition treatment at each installation.

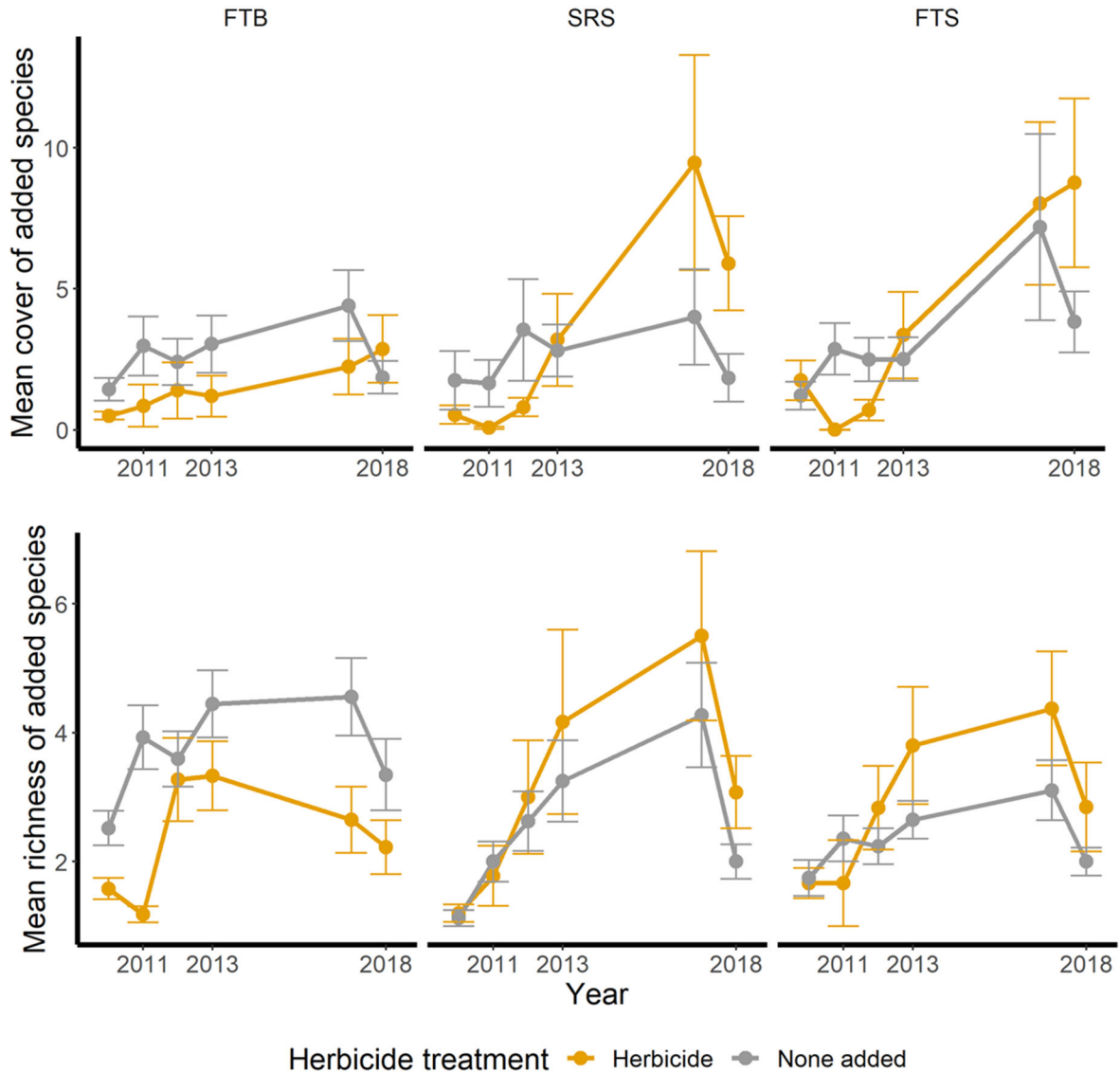


Fig. 6.2.6. Mean percent cover (top) and mean richness (bottom) within 3x3m plots attributable to seeded species across years and by herbicide treatment at each installation.

6.2.2 Species-specific recovery

Accounting for species-specific responses via the addition of random slopes to predictors that were potentially important at the community level based on their 95 % CIs non-overlapping zero (+ in Fig. 5.2.3) improved model fit (WAIC = 5840) compared to only accounting for species-specific responses for predictors chosen to be important at the community level based on SSVS variable selection (WAIC = 6101). We thus use the first random-slopes model for further inference on species-specific responses.

Plots of annual estimates of mean establishment (absent the previous year and present the current), persistence (continued presence from the previous year), and occupancy (present regardless of status the previous year) highlight the main differences among installations, years and species (Fig. 5.2.7). Most seeded species had very low establishment success, mirroring

findings from other seed addition studies in longleaf pine savannas showing low rates of establishment from seed (Barker et al. 2019). We note, however, that typical rates of seed addition (which typically involve adding thousands or hundreds of thousands of seeds) should be sufficient to promote establishment. Success in establishment was dominated by a handful of species at each installation. *Lespedeza hirta* (LESHIR), *Pityopsis graminifolia* (PITGRA) and *Tephrosia virginiana* (TEPVIR) established well across installations, while *Solidago odora* (SOLODO) and *Eupatorium album* (EUPALB) established well at Fort Bragg and Fort Stewart, *Aristida purpurascens* (ARIPUR) established well at Savannah River Site and Fort Stewart, with *Sorghastrum secundum* (SORSSP) also doing well at Savannah River Site (Fig. 6.2.7). Initial establishment was not immediate for these species after the seeding treatment, with an increasing trend in establishment peaking in 2013 (Fig. 6.2.7). This highlights the importance of longer term monitoring in evaluations of species-specific success from restoration efforts. Short-term assessments would have missed increasing establishment in the early study (2010-2013). Lastly, *Pityopsis graminifolia* (PITGRA) experienced its highest establishment at Fort Stewart during 2017 (Fig. 6.2.7), confirming our initial thoughts that long-term monitoring for some species is required to evaluate their recovery success. These results also suggest particular sets of species that might be prioritized for seed additions at each respective location, based on high rates of establishment at that particular location and due to establishment being the main bottleneck for long-term occupancy (see below).

Once species established, they had a high probability of persisting, which highlights that species are most vulnerable during the initial stages of recovery when they are seeds and small seedlings. Establishment was estimated to have peaked during 2014-2015 for all species, which showed similar trends at Fort Stewart and Savannah River Site (Fig. 6.2.7). Persistence of species further south, at Fort Stewart, was more staggered, with incremental increases in 2013-2014, and then in 2016-2017 (Fig. 6.2.7). Overall, differences in occupancy (presence in the current year regardless of outcome in the previous year) among species were driven by their establishment success, with the same species groups that had higher establishment, also showing higher occupancy. Conversely, persistence appeared consistent amongst species, with differences in persistence driven mainly by differences among installations and years.

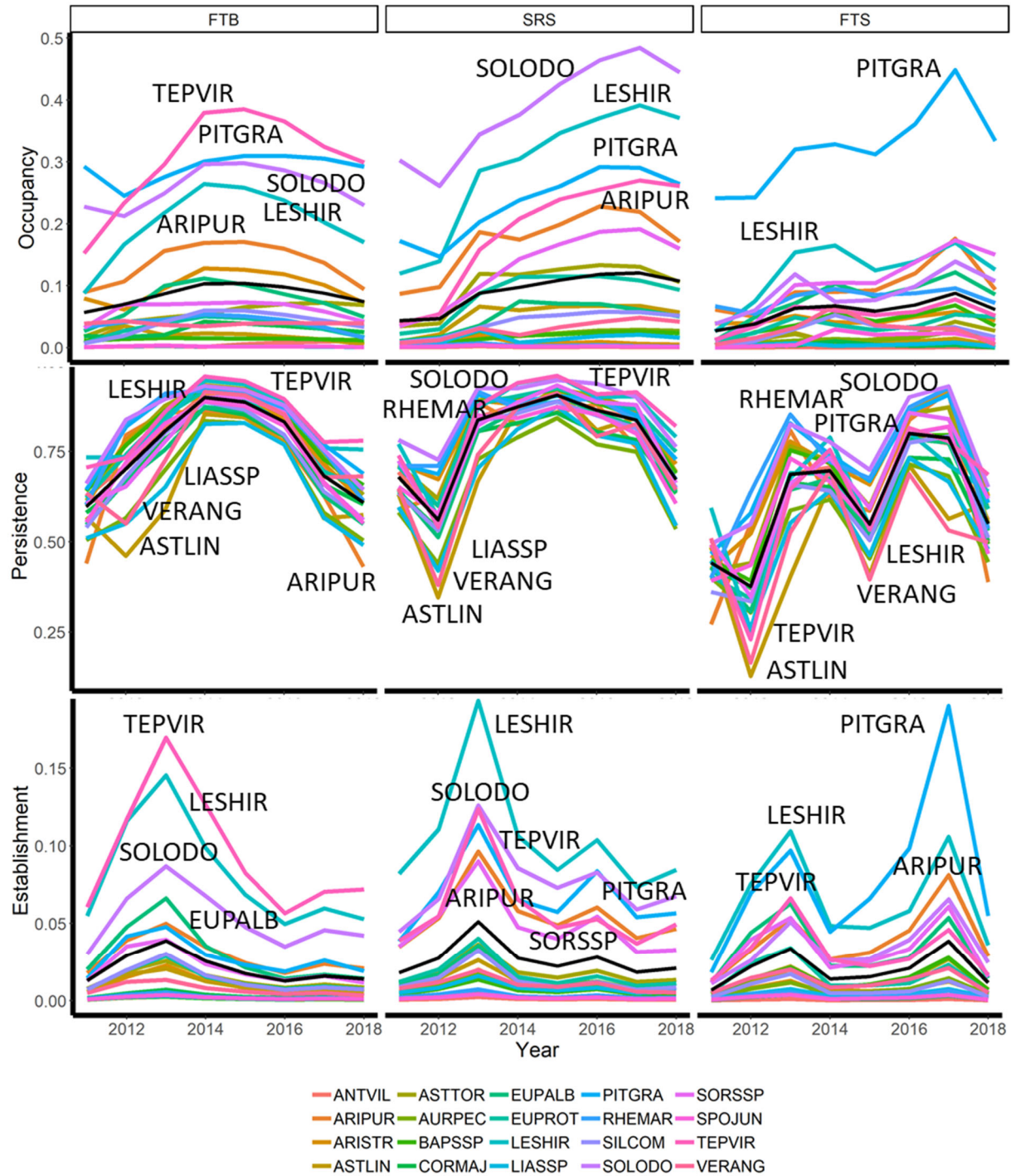


Fig 6.2.7 Species-specific estimates of mean establishment (bottom), persistence (middle) and occupancy (top) at Fort Bragg (FTB), Savannah River Site (SRS) and Fort Stewart (FTS) installations during the study period (2010-2018). The black lines represent community-level mean responses.

Strong differences among species in response to the seeding treatment were apparent, with *Lespedeza hirta* (LESHIR), *Tephrosia virginiana* (TEPVIR), *Sorghastrum nutans*, *Sorghastrum secundum* (SORSSP), and *Eupatorium album* (EUPALB) experiencing the greatest

increase in establishment, and thus greatest increase in occupancy when seeds were added (Fig. 6.2.8). Differences among species in establishment in relation to environmental predictors were relatively smaller and predominantly due to the magnitude, rather than the direction, of their response (Fig. 6.2.8). In particular, *Pityopsis graminifolia* (PITGRA), *Aristida purpurascens* (ARIPUR), and *Eupatorium album* (EUPALB) showed the strongest responses to more open site conditions (lower basal areas and shallower litter depth), increased rainfall and cooler summer temperatures, while the remaining species showed mainly very slight changes in their establishment (Fig. 6.2.8). *Eupatorium album* (EUPALB) was the main species to benefit somewhat from low fire frequencies for establishment, but not for persistence (Figs. 6.2.9 and 6.2.12). The establishment of most species was not affected by the number of total fires at a site, although a smaller number appeared to benefit slightly when <3 fires had occurred between 1991 and the time of our study (Fig. 6.2.9). However, because only 3 sites in our study had extreme fire suppression (i.e., less than 3 prescribed burns in the 29+ years), our inference regarding establishment in heavily fire-suppressed settings is inherently limited by a very limited number of sites, and may be due to stochastic variation among those three sites (two at Savannah River Site and one at Fort Stewart). The safest conclusion that can be drawn is that establishment was not reduced for sites where fire frequency ranged between three and 13 fires (i.e., 93% of the sites used in this study). However, additional studies that target heavily fire-suppressed sites would be necessary to make strong inference regarding the role of high levels of fire suppression on plant establishment. Responses to the amount of bare ground and winter rainfall were very small for all species, suggesting that these were also unimportant environmental conditions associated with establishment (Fig. 6.2.8). Overall, changes in establishment in response to environmental conditions were modest for most species, and driven predominantly by responses from *Pityopsis graminifolia* (PITGRA), *Aristida purpurascens* (ARIPUR), *Eupatorium album* (EUPALB), and *Tephrosia virginiana* (TEPVIR) to lower basal areas and shallower litter. These same species were also the species that responded most strongly to climatic conditions.

Three species traits were related to mean establishment of a species. Mean establishment was greater for species that had greater heights of adult plants, establishment was greater for species that germinated quickly (i.e., fewer days to germinate), and establishment was greater for species with lower seed / dispersule ratios (Fig. 6.2.10). The relationship between adult plant height and establishment was driven by several species, including *Lespedeza hirta* (LESHIR), *Sorghastrum nutans* and *Sorghastrum secundum* (collectively, SORSPP), and *Silphium compositum* (SILCOM) driving most of the observed trend (Fig. 6.2.10, top left). Some species that germinated quickly also had higher establishment, particularly *Pityopsis graminifolia* (PITGRA) and *Aristida purpurescens* (ARIPUR) (Fig. 6.2.10, top right). *Tephrosia virginiana* (TEPVIR) had the smallest seed to dispersule ratio and an order of magnitude higher establishment relative to the mean establishment of the remaining species (Fig. 6.2.10, bottom right). Nonetheless the trend remained when we considered the relationship for the remaining species only, taking away *Tephrosia virginiana* TEPVIR (Fig. 6.2.10, bottom left).

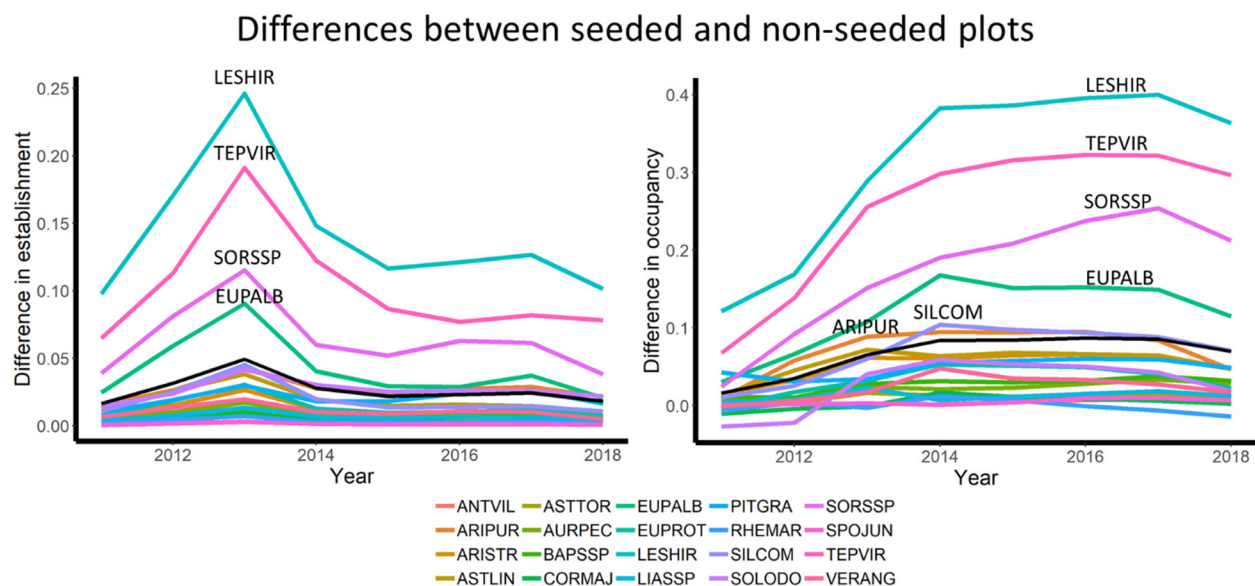


Fig 6.2.8 Differences between seeded and non-seeded plot in annual estimates of mean establishment (left) and occupancy (right) for each seeded species. The black lines are the average differences between seeded and non-seeded plots at the community-level.

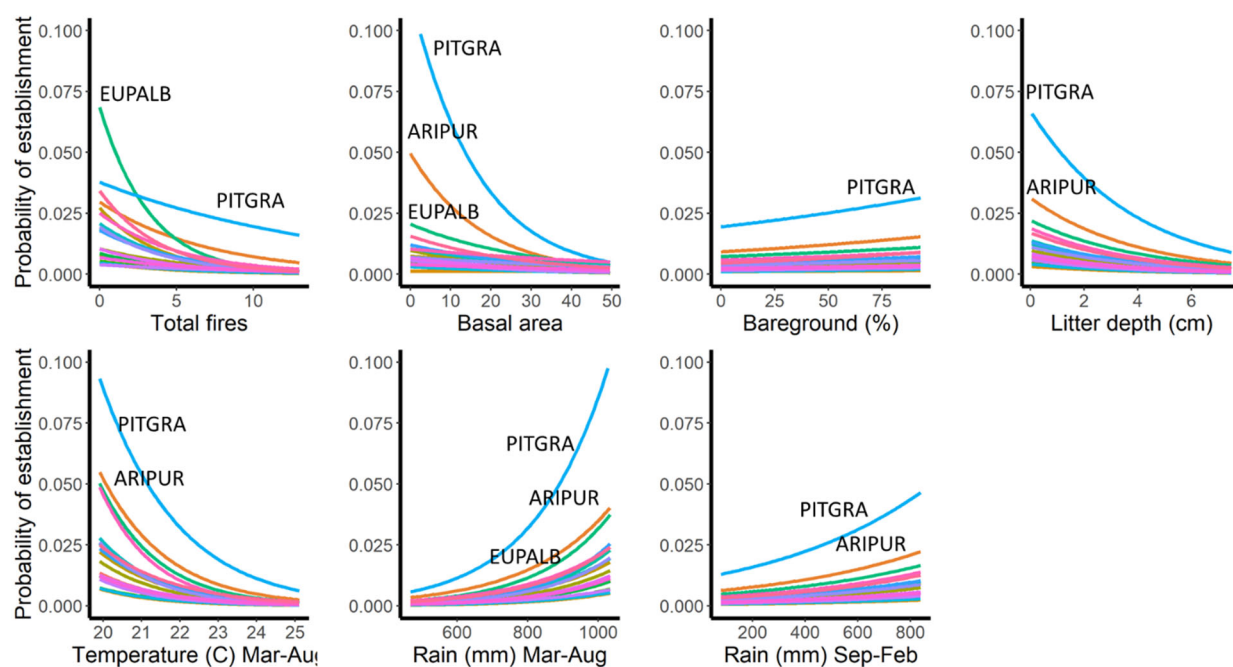


Fig 6.2.9 Species-specific establishment in response to predictors that were potentially important at the community level.

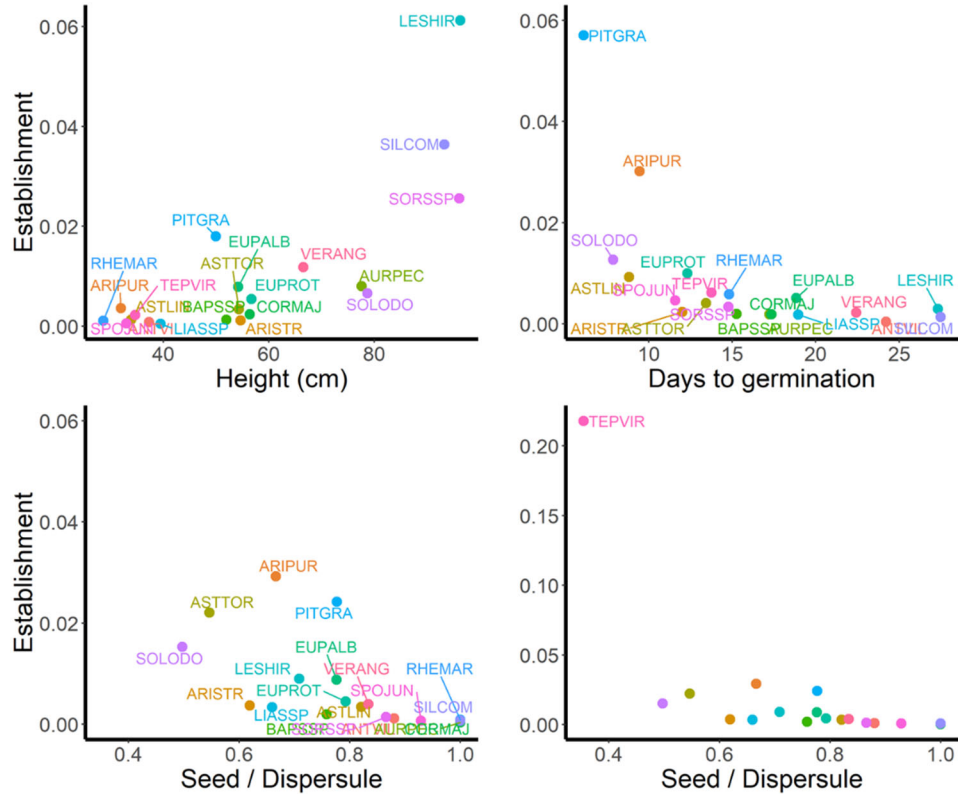


Fig 6.2.10 Species-specific mean establishment in association with their mean plant height (top, left), days to germination (top, right), and seed / dispersule ratio (bottom). Note that TEPVIR is an outlier in terms of seed/dispersule ratio. The panel on the bottom left shows the data without TEPVIR, while the panel on the bottom right shows the data with TEPVIR (note change in y-axis scale).

Strong and opposing differences among species in response to the herbicide treatment influenced their establishment at treated plots compared to untreated plots (Fig. 6.2.11). Species that benefited from herbicide application included *Aristida purpurascens* (AURPEC), *Liatris squarrosa*, *Liatris secunda* (LIASSP), *Eupatorium album* (EUPALB), *Sorghastrum nutans*, and *Sorghastrum secundum* (SORSSP). Conversely, *Coreopsis major* (CORMAJ), *Pityopsis graminifolia* (PITGRA), *Solidago odora* (SOLODO), *Rhexia mariana* (RHEMAR), *Aristida stricta* and *Aristida beyrichiana* (ARISTR) were all negatively affected by the application of herbicide, exhibiting lower persistence and occupancy in treated versus untreated plots (Fig. 6.2.11). Species responded similarly in their persistence in response to the environmental conditions examined except for summer rainfall (Fig. 6.2.12). In particular, *Aster linariifolius* (ASTLIN), *Lespedeza hirta* (LESHIR), *Tephrosia virginiana* (TEPVIR), and *Vernonia angustifolia* (VERANG) showed lower persistence with increased summer rains, while persistence of *Aristida purpurascens* (ARIPUR) decreased strongly with lower summer rain (Fig. 6.2.12). The opposing effect of the herbicide treatment suggests that it is not the ideal approach for improving community-level recovery. Unless the species that benefited were the main target of recovery efforts, we do not recommend wide implementation of this approach.

Species responded similarly (i.e., same slope direction) in their persistence to the environmental and weather conditions examined, except for summer rainfall (Fig. 6.2.12). The impacts of the environmental conditions examined in this top species-specific model were strong

for persistence, unlike those observed for establishment. Opposing responses were observed for summer rains. *Aster linariifolius* (ASTLIN), *Lespedeza hirta* (LESHIR), *Tephrosia virginiana* (TEPVIR), and *Vernonia angustifolia* (VERANG) showed decreases in persistence with increased summer rains, while persistence of *Aristida purpurascens* (ARIPUR) decreased strongly with lower summer rain (Fig. 6.2.12). Consistently for all species, the strongest benefits from weather on persistence came from cooler summers and wetter winters (Fig.6.2.12). Prescribed burns had community-level benefits for persistence, as all species exhibited greater persistence as the number of total fires increased (Fig. 6.2.12). However, the main environmental conditions benefiting persistence were more open sites, with lower basal areas and shallower litter depths (Fig. 6.2.12). These open characteristics also benefited establishment for some species (Fig. 6.2.9), suggesting that managers may use selective tree harvesting to reduce canopy-tree density and promote recovery of longleaf understory plant communities.

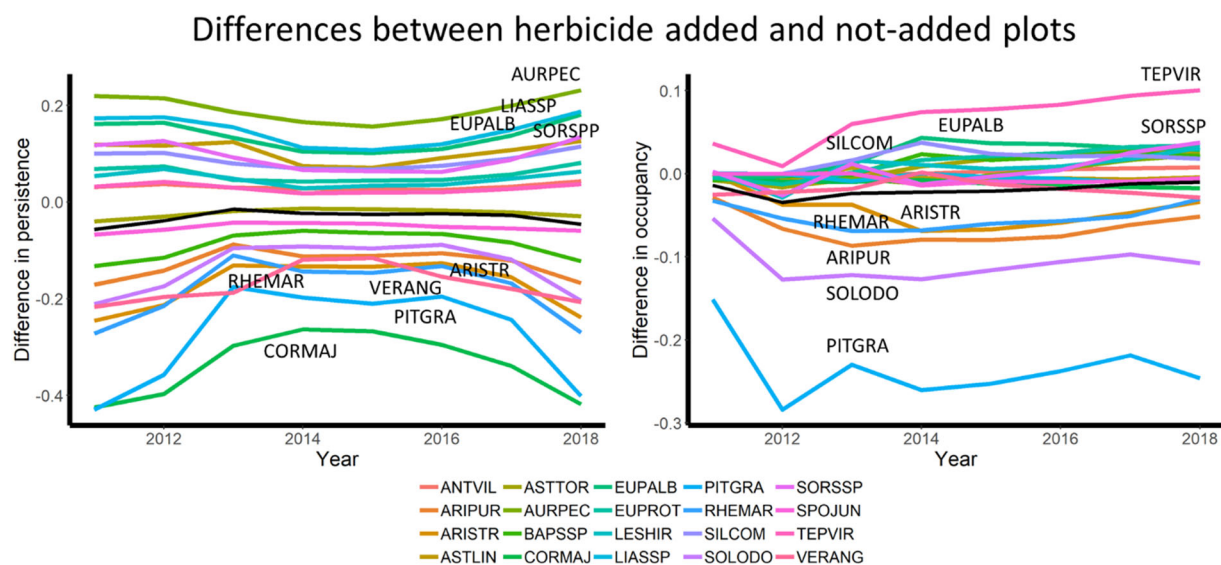


Fig 6.2.11 Differences between plots treated with herbicide and untreated plots in annual estimates of mean establishment (left) and occupancy (right) for each seeded species. The black lines are the average differences between treated and untreated plots at the community-level.

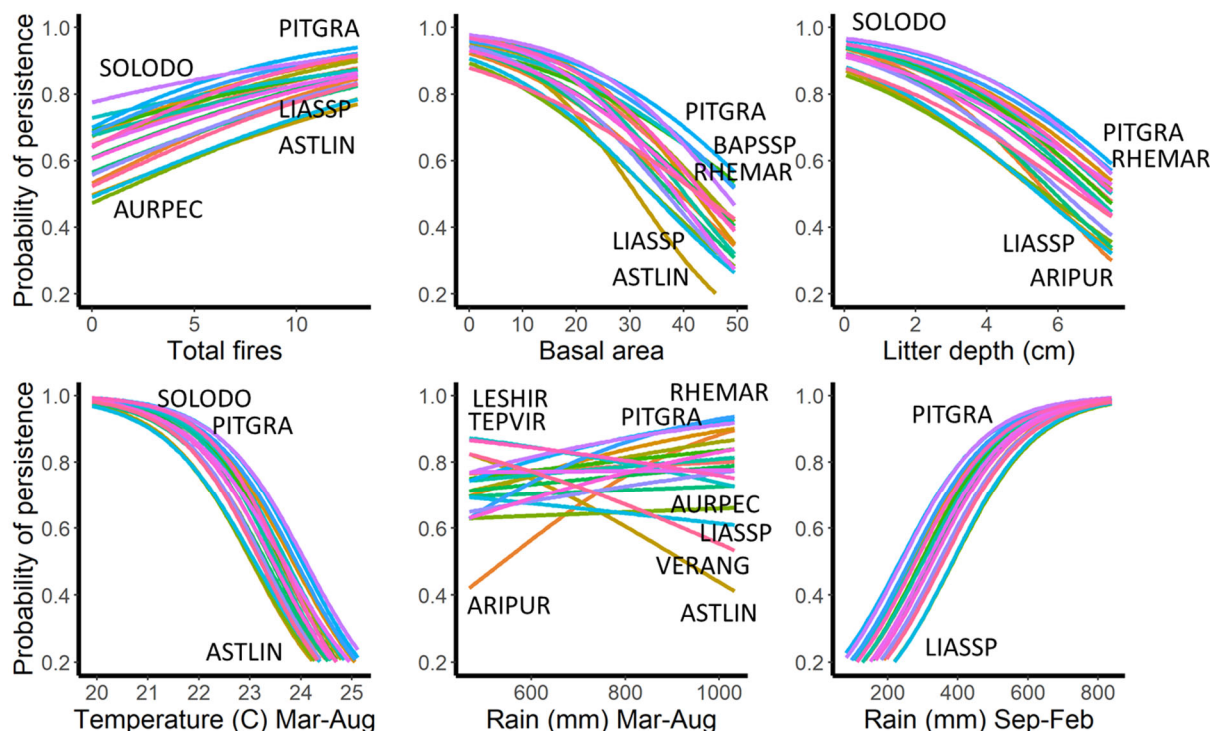


Fig 6.2.12 Species-specific persistence in response to predictors that were potentially important at the community-level.

We also explored univariate relationships between mean estimates of the probability of establishment, persistence, occupancy, and spread (detailed results in section 6.3 below) for each seeded species. For the relationships between establishment or persistence and occupancy we also evaluated whether categorical traits grouped these species according to these relationships. These were assessed using univariate relationships and so are only meant to be descriptive and provide avenues for further exploration, and are not indicative of causation. Occupancy was tightly and positively correlated with establishment more so than to persistence, suggesting that it is the bigger driver of successful local recovery (Fig. 6.2.13, top). Species with higher probability of establishing also high higher probability of occupying more plots (Fig. 6.2.13, bottom left). Conversely, higher probability of persistence did not necessarily result in higher occupancy for some species (Fig. 6.2.13 top right). All species spread with high probabilities once established except for *Anthraenantia villosa* (ANTVIL) (Fig. 6.2.13, bottom right). Of important note is that wind-dispersed species with higher probability of establishment appear to lead to higher occupancy success compared to other-dispersed species (Fig 6.2.14, top, far left panel). Clonality and dispersal mode resulted in indistinguishable relationships between persistence and occupancy (Fig 6.2.14, bottom, far left and far right panels). Family group and life form (plant type) both resulted in similar patterns in the relationships between occupancy and either establishment or persistence (Fig. 6.2.14, middle panels). This suggests that there were not enough differences among species based in these two categorical traits to evaluate differences between the two.

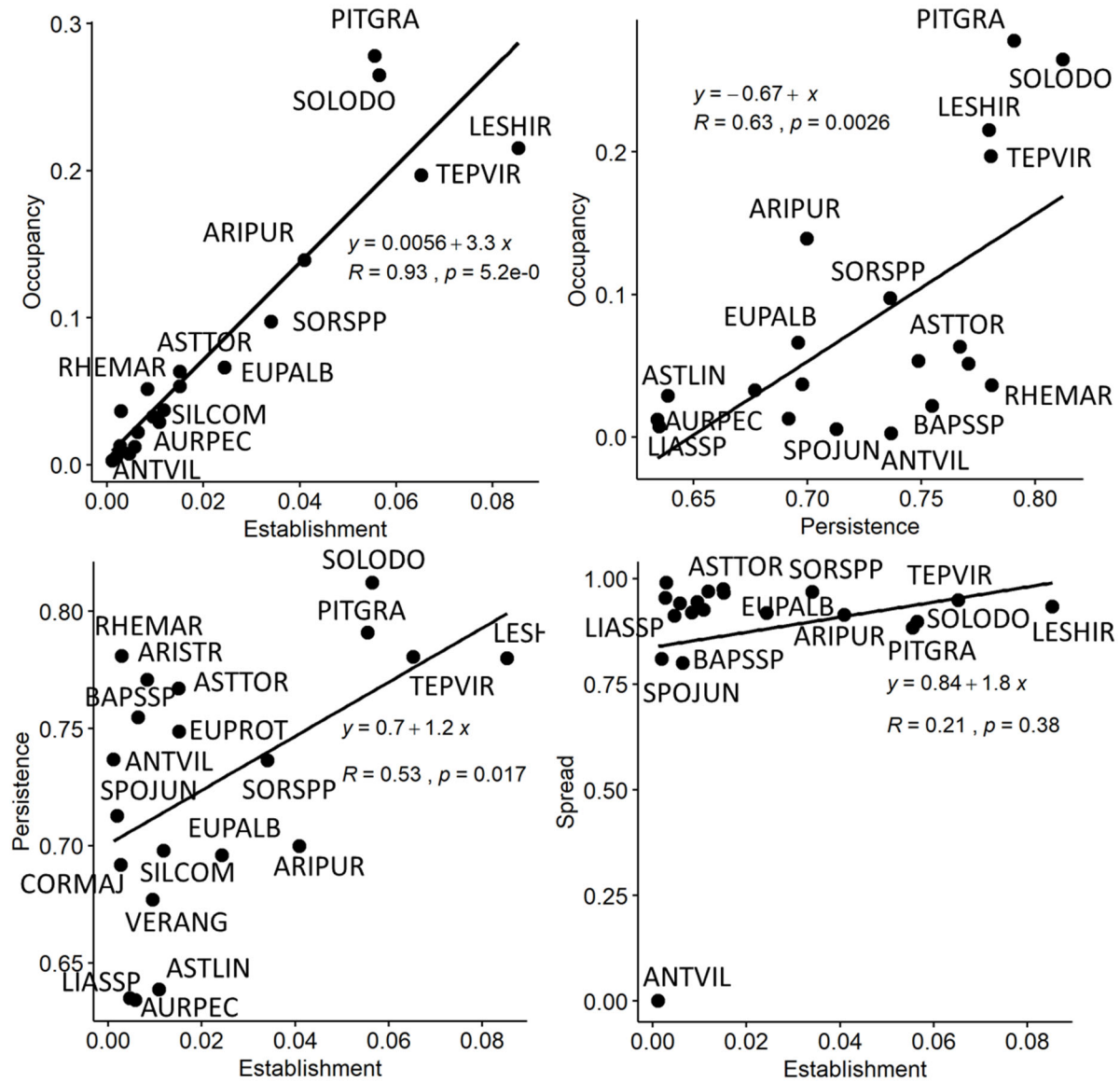


Fig. 6.2.13. Univariate relationships among mean probability estimates for establishment, persistence, occupancy and spread for seeded species. Estimates were derived from (1) a multi-species dynamic occupancy model with random intercepts and slopes for each species, and (2) for spread, from a multi-species Weibull dispersal kernel.

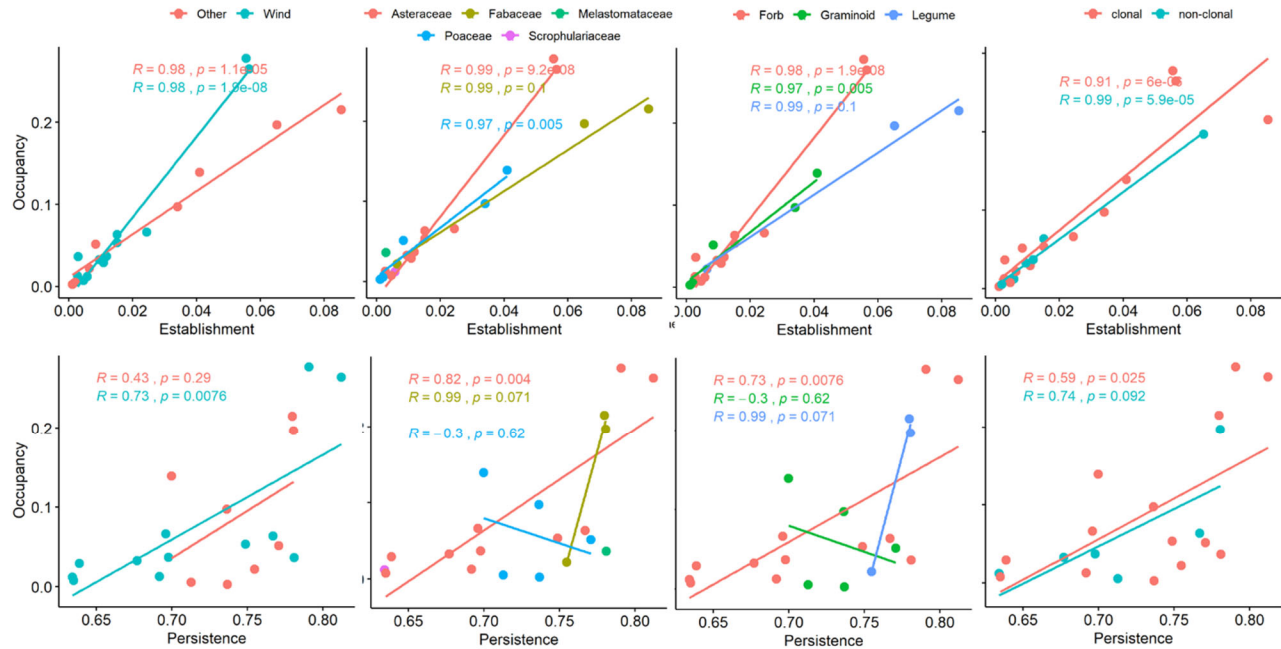


Fig. 6.2.14. Univariate relationships among mean probability estimates for occupancy with either establishment or persistence for seeded species, grouped by their categorical functional traits including dispersal mode (far left), family (center left), plant type (center right) and clonality (far right).

6.3 Outward recovery – spatial spread

The reduced model including dispersal mode as a group, and the raw continuous traits instead of PCA dimensions provided the best fit and is used for further inference (Table 6.3.1). Note that the use of plant type as a grouping failed to produce results, likely because of the low number of species in some of the groups. The top model did a good job at estimating the rate of spread observed with the spread kernels for each species (Fig. 6.3.1). Most spread occurred in the first three meters for most species, but some including *Aristida stricta*, *Aristida beyrichiana* (ARISTR), *Baptisia cinerea*, *Baptisia perfoliata* (BAPSSP), *Coreopsis major* (CORMAJ), *Sporobolus junceus* (SPOJUN), *Tephrosia virginiana* (TEPVIR), and *Vernonia angustifolia* (VERANG) spread at similar rates out to 9 m (Fig. 6.3.1). Species that spread most (based on number of individuals found at the spread rings) were *Aristida purpurascens* ARIPUR (3239 individuals spread), *Aristida stricta* and *Aristida beyrichiana* ARISTR (2675 individuals), *Tephrosia virginiana* TEPVIR (2638 individuals), *Lespedeza hirta* LESHIR (2196 individuals), and *Solidago odora* SOLODO (1909 individuals). Those that exhibited less (or no) spread included *Anthraenantia villosa* ANTVIL (0 individuals), *Aureolaira pectinata* AURPEC (56 individuals), *Liatris squarrosa*, *Liatris secunda* LIASSP (250 individuals), and *Coreopsis major* CORMAJ (265 individuals).

An increased number of total fires had a negative effect on the spread rate of other-dispersed species, while more open sites (with lower basal area) benefited spread by species dispersed by wind (Fig. 6.3.2). Non-wind-dispersed (i.e., other) species spread at a greater rate when their plants were taller (e.g. *Lespedeza hirta* LESHIR) and had greater SLA (e.g., *Aristida purpurascens* ARIPUR, *Tephrosia virginiana* TEPVIR) (Fig. 6.3.2). Interestingly, the species with the greatest SLA values from our seeded group (*Anthraenantia villosa* ANTVIL, *Aureolaira*

pectinata AURPEC, *Rhexia mariana* RHEMAR) were wind-dispersed. *Anthraenantia villosa* ANTVIL was the only species not to disperse, and only few (56) individuals of *Aureolaira pectinata* AURPEC were found in the spread-rings. Species that were not wind dispersed spread at greater rates when they germinated early (e.g., *Aristida purpurascens* ARIPUR), and counterintuitively, those non-wind-dispersed species that germinated better in the laboratory, appeared to spread at a slower rate in the field (Fig. 6.3.2.). Wind-dispersed species that germinated later (e.g., *Silphium compositum* SILCOM, *Vernonia angustifolia* VERANG) spread at higher rates, as well as those wind-dispersed species that germinated better under laboratory conditions (Fig. 6.3.2).

Table 6.3.1. Full and reduced set of models evaluated for species-specific spread kernels. Models were fitted to evaluate whether the role of a particular variable (e.g., basal area) differed depending upon plant species dispersal mode (wind-dispersed or non-wind-dispersed). The top model (with lowest WAIC) is presented in bold. Models with plant type as a group failed to converge and are not shown.

Parameters associated with dispersal rate	Model type	WAIC
Intercept[disp. mode] + Since fire[disp. mode] + Total fires[disp. mode] + Basal area[disp. mode] + Height[disp. mode] + SLA[disp. mode] + Seed width[disp. mode] + Seed/dispersule[disp. mode] + Seed coat[disp. Mode] + Clonality[disp. mode] + Germination days[disp. mode] + Proportion germinated[disp. mode]	Full, raw traits	2463
Intercept[disp. mode] + Total fires[disp. mode] + Basal area[disp. mode] + Height[disp. mode] + SLA[group] + Germination days[disp. mode] + Proportion germinated[disp. mode]	Full, raw traits	2451
Intercept[disp. mode] + Since fire[disp. mode] + Total fires[disp. mode] + Basal area[disp. mode] + PCA1[disp. mode] + PCA2[disp. mode] + PCA3[disp. mode] + PCA4[disp. mode]	Full, PCA	2468
Intercept[disp. mode] + Total fires[disp. mode] + Basal area[disp. mode] + PCA1[disp. mode] + PCA2[disp. mode]	Reduced, PCA	2468

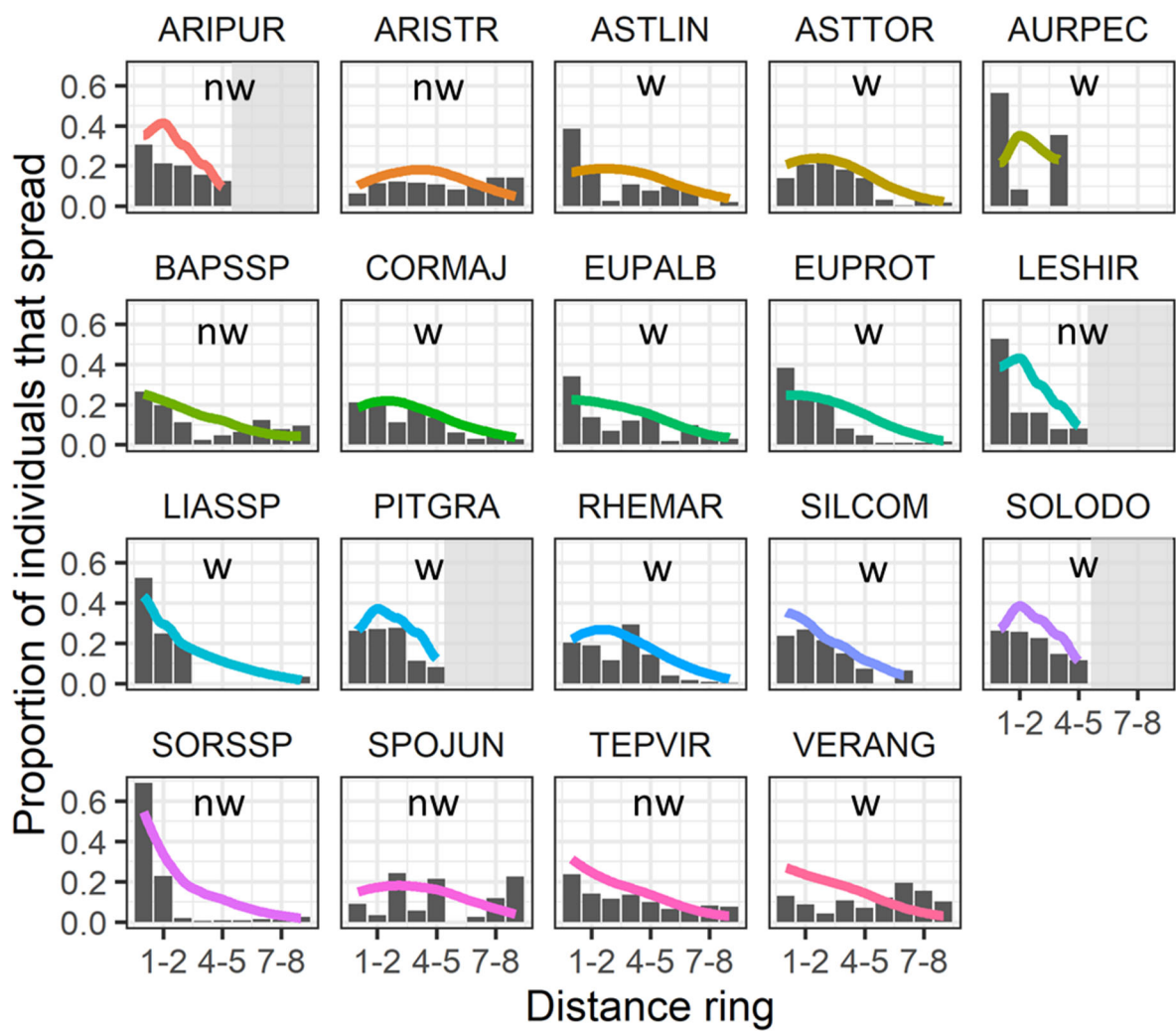


Fig. 6.3.1. Raw (histograms) and estimated (lines) dispersal rate for each seeded species that spread beyond the experimental plots. Grey areas represent rings that were not surveyed for those species (i.e. beyond 5m). w: wind-dispersed species and nw: non-wind dispersed.

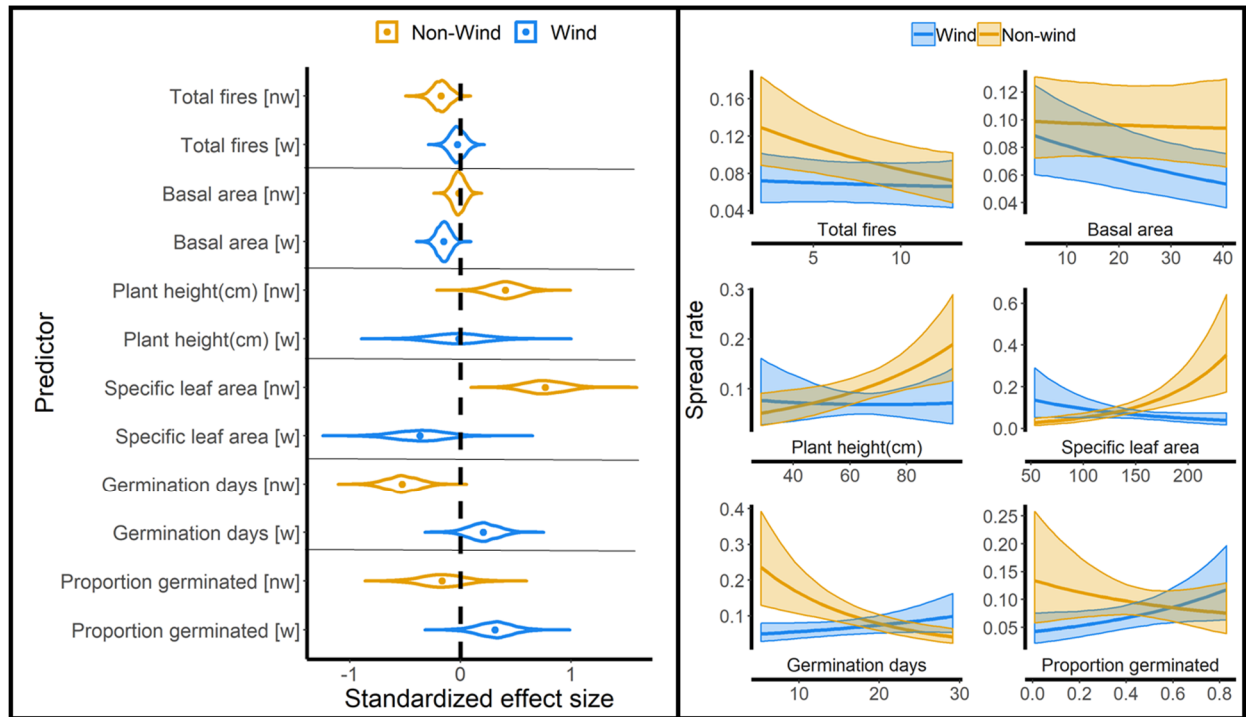


Fig 6.3.2. Group-specific coefficients (left panel) and partial predicted relationships (right panel) between spread rate of species dispersed by wind or non-wind (including adhesive, ballistic and unassisted) in relation to management conditions and species traits.

6.4. Functional similarities in seeded community

The four first components explained most (84 %) of the variation in the data (Fig. 6.4.1 Top, left panel). The first component (PC1) predominantly captured seed traits (Fig. 6.4.1 Bottom, left panel). The second component (PC2) capture leaf traits including carbon to nitrogen content (C/N) and specific leaf area (SLA), as well as seed length (Fig. 6.4.1 Bottom, left panel). Note that SLA and seed length traits were highly correlated (> 0.7) so SLA was chosen instead of length in evaluation of species establishment, persistence, and spread (Fig. 5.1.7). The third component (PC3) described the ratio of seed to dispersule mass, seed coat and adult plant height (Fig. 6.4.1 Bottom, left panel), while the fourth component (PC4) also captured adult plant height but also the germination potential, as described by the proportion of seeds that germinated in laboratory conditions (Fig. 6.4.1 Bottom, left panel). The right panel of Fig. 6.4.1 highlights the pairwise correlations of these contributing traits with each of the principal components (i.e., dimensions).

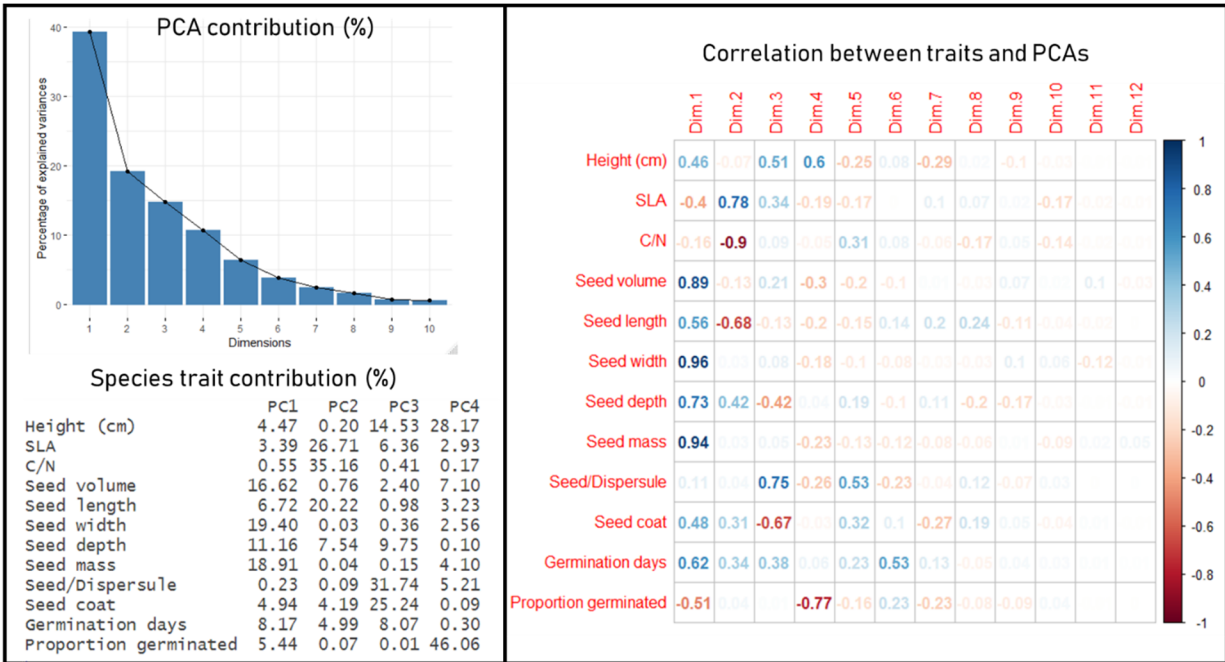


Fig 6.4.1. Results from the principle component analysis (PCA) showing the contribution of each dimension (i.e., principal component) to the overall variance explained (top, left); the contribution of each functional trait to the main four principal components (bottom, left); and the pairwise correlations between each functional trait and all the principal components (right).

Biplots allowed us to visualize how individual species contributed to each trait. For example, *Aristida stricta* and *Aristida beyrichiana* (collectively, ARISTR) had the largest Carbon to Nitrogen content of all species examined, while *Silphium compositum* (SILCOM) had the largest values for seed size traits (Fig. 6.4.2 and Fig. 6.1.3). *Anthraenantia villosa* (ANTVIL), *Aureolaira pectinate* (AURPEC) and *Rhexia mariana* (RHEMAR) had the largest SLA values. *Baptisia cinerea* and *Baptisia perfoliata* (collectively, BAPSPP) had the largest seed depth and coat values (Fig. 6.4.2 and Fig. 6.1.3). We can also see that some of these species group in a multi-dimensional space according to their categorical traits. For example members of the Asteraceae family, forbs and wind-dispersed species appear to group well together (Fig 6.4.3). No clear patterns are seen based on clonality (Fig. 6.4.3).

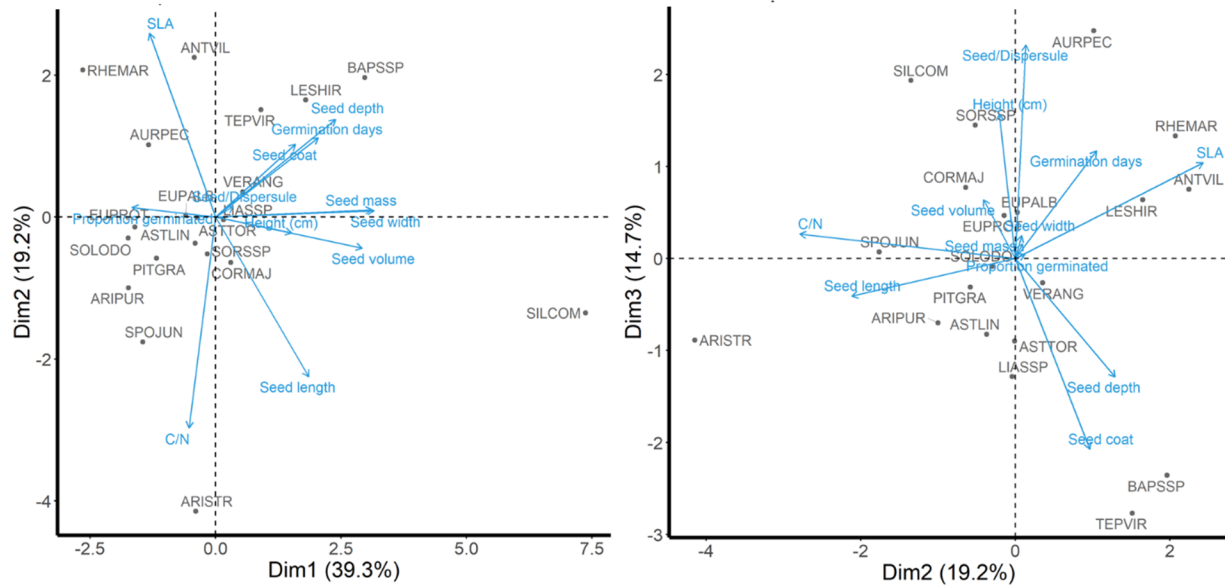


Fig 6.4.2. Biplots showing the contribution of traits and species to principal components one and two (left) and two and three (right).

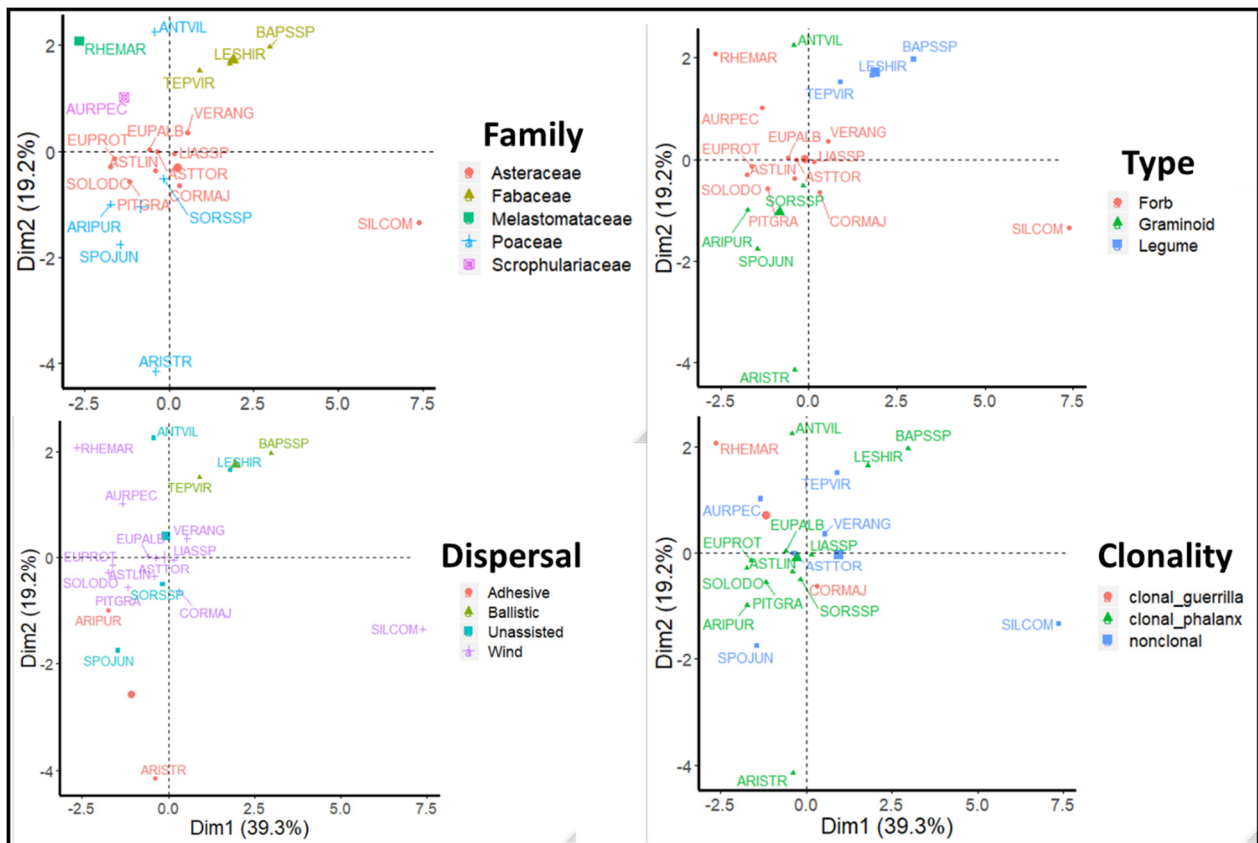


Fig 6.4.3. Grouping of species among the main principal component dimensions based on categorical functional groups including family, plant type, dispersal mode and clonality.

7. Conclusions and Implications for Future Research/Implementation

DoD is tasked with the maintenance of biodiversity and persistence of threatened, endangered, and at-risk (TER) species on lands that it manages (Benton et al. 2008). Because perennial understory plants are key components of biodiversity and include many TER species (Noss 2012, Noss et al. 2015), management strategies that promote large-scale, persistent recovery of perennial plant species can be a valuable tool for ensuring that DoD facilities maintain the continued capacity for training and readiness. Our current project successfully expanded on four years of existing data (one pre-treatment, three post-treatment) from 48 sites at 3 DoD/DOE installations to a dataset spanning 8 years. We collected long-term data on multiple stages of recovery, environmental conditions, and species traits that complemented and built upon our original large-scale factorial experiment.

Our sophisticated species-specific analytical approaches evaluated the long-term impacts of multiple interacting factors at multiple stages of recovery jointly for each species, and for the community, at three different DoD/DOE installations. **Our work demonstrates that adding seeds of understory plant species is a primary means that managers can promote establishment.** While seed addition worked well in an array of different conditions, it worked best in forests that were managed with lower canopy-tree densities, i.e., those approximating the savanna-like conditions present in historical longleaf pine ecosystems. Importantly, **once species established, they persisted locally at very high rates and often spread beyond the initial site of establishment over the course of years.** Although the spread rates we observed were modest in terms of distances moved, spread rates were **uniformly high** with probability of spread being greater than 0.75 for 24 of the 25 species in our study. Because persistence and spread were typically high, our results confirm that, across 48 sites at three separate DoD/DOE installations that **initial establishment of species at degraded sites is the primary constraint to persistence, spatial spread, and recovery.** Given that our results suggest that spread is very likely following establishment, a single seed addition (e.g., in 2011) may be sufficient to create persistent, spreading communities that drive recovery over large spatial areas over the course of decades. This single result has an important management implication: **catalyzing profound, self-sustaining recovery in the plant communities of many DoD installations in the southeastern U.S. may be greatly facilitated by conducting seed additions of understory plant species.**

In addition to documenting the essential importance of establishment for fueling long-term plant population persistence, recovery, and spread, our work also demonstrates an essential role for site-level factors (e.g., timber density, fire frequency), helping provide guidance to DoD and DOE personnel staffed with managing these areas. For example, litter depth can be modified by prescribed fire or raking, and litter depth had significant effects on establishment and persistence. Management activities were also significant affecting spatial spread, as wind-dispersed species exhibited greater spread in sites with lower basal area of canopy trees. By linking these outcomes with plant species' traits, our work provides a transferrable means of predicting how additional species (i.e., those not in our study) might benefit from particular management approaches (e.g., seed sowing, changes in fire regime or tree density).

A clear example in how our species-specific analyses provide richer knowledge than would have been achieved is provided by looking at the effects of the experimental treatments. The effects of seeding treatment were consistently in the same direction for all species. As a result, while some species benefitted greatly from seed addition while others exhibited a more

modest response, the benefit still scaled up to the plant community, leading to increased diversity in sites with seeds added (moreover, this diversity increase is still apparent 8 years later, suggesting that it is permanent). In strong contrast, the effect of herbicide treatment were opposite and strong for multiple species resulting in what was clearly observed as equivocal community-level benefits. The effects of herbicide treatment also generally declined with time, while **seed additions provided long-lasting benefits that yielded additional dividends by fostering spatial spread.**

By evaluating how functional traits influenced the three key processes of recovery: establishment, persistence and spread, while still maintaining a species-specific framework, we were able to identify groups of species with similar traits that responded similarly. Our analyses allowed us to determine that those species that germinated quickly (e.g., *Pityopsis graminifolia*, [wind-dispersed], *Aristida purpurascens* [non-wind-dispersed] and *Solidago odora* [wind-dispersed]) generally had higher establishment. Rates of species-specific spatial spread were highly variable and related with species functional traits in complex ways. Generally, non-wind-dispersed species that germinated fast (e.g., *Aristida purpurascens*) and wind-dispersed species that germinated late (e.g., *Silphium compositum*, *Vernonia angustifolia*), spread at higher rates.

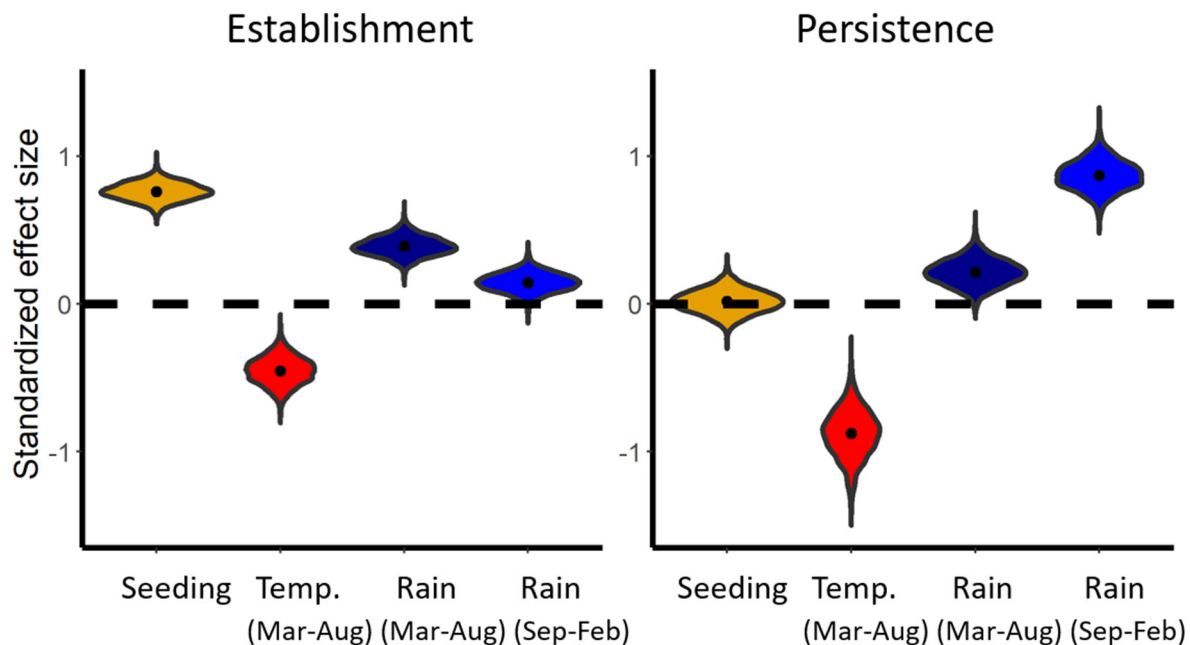


Fig. 7.1. Mean coefficients and associated 95% Credible Intervals (CIs) estimated for seeding treatment and climate in relation to community-level probabilities of establishment (left panel) and persistence (right panel).

One important finding, made possible because our work spans many years, is that the dynamics of plant community recovery and spread are **strongly linked to annual variation in climate (Fig. 7.1)**. This finding is especially noteworthy because empirical data and future climatic projections for the southeastern U.S. suggest that non-stationary climate will be an important management challenge on DoD and DOE installations (DoD 2019). In particular, the frequency of extreme temperature and precipitation events has increased and is expected to continue to do so (Fig. 7.2; USGCRP 2017, Carter et al. 2018, Moore et al. 2019). These events

may be particularly important for the recovery of plant communities in longleaf ecosystems: as the results of our current project have shown a clear link between temperature and precipitation and plant establishment (Fig. 7.1, Fig. 2.4.3), persistence (Fig. 7.1, Fig. 2.4.3), and thus spatial spread (Fig. 6.2.13). Importantly, despite the clear role of climate revealed by this project, it is not clear, however, whether extreme climatic events (e.g., Hurricane Florence) that are increasing in prevalence in the Southeast (Fig. 7.1) will alter the trajectory of recovery (Fig. 7.2). Although future climatic extremes may be of greater magnitude and/or frequency than the climate observed during our study, our long-term study provides a foundation for considering how plant communities may respond to future scenarios. For example, our data generally suggest that high levels of precipitation are beneficial for community-level establishment and persistence. However, seasonality may be important, as spring and summer precipitation was most beneficial for establishment, while fall and winter rainfall had the greatest benefit for persistence. These results may help guide management efforts in several ways. For example, managers may opt to perform seed additions in years when spring and summer temperatures are expected to be low, which should maximize establishment and subsequent persistence. Species-specific results may be useful for producing seed mixes that are most effective in particular years, depending upon projected climate. For example, our species-specific results caution that some species (e.g., *Aster linariifolius*, *Lespedeza hirta*, *Tephrosia virginiana*, and *Vernonia angustifolia*) exhibit lower persistence with high levels of spring and summer rain. Managers may want to perform seed additions of these species in years following heavy spring and summer rain because precipitation promotes establishment and high levels of establishment help offset reduced persistence (thus possibly maintaining population viability). Future work that evaluates how extreme climates (i.e., those beyond the conditions in our study) affect establishment, persistence, and spread will be highly informative for helping further optimize the diversity and sustainability of plant communities in longleaf ecosystems.

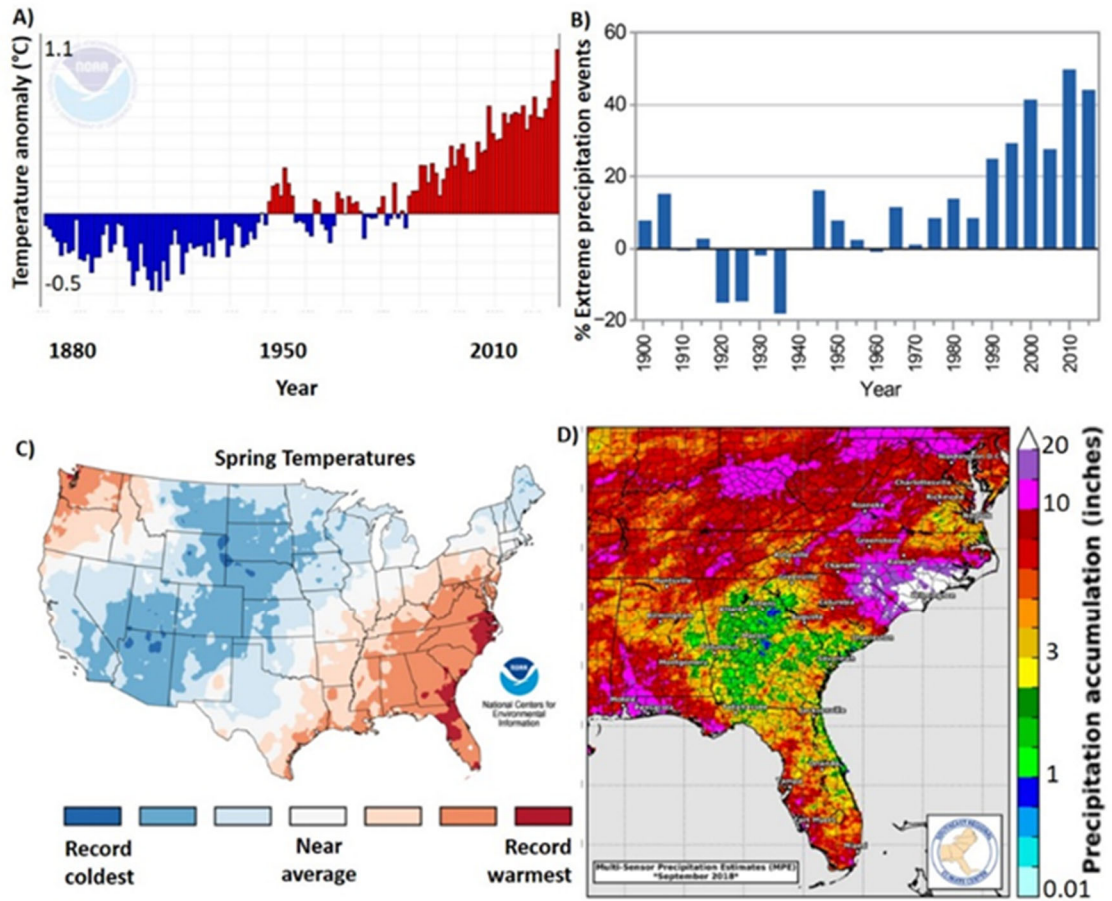


Fig. 7.2. Observed climate change in the US. **A)** Mean temperature anomalies have increased (NOAA). **B)** The percentage increase in extreme precipitation events (2-day events exceeding the 5-year return interval) over time (USGCRP 2017). **C)** Spring temperatures are increasing in the southeastern US (Moore et al. 2019; NOAA). **D)** Extreme precipitation events like Hurricane Florence result in large amounts of rain (20 in, 500 mm) within 2-5 days.

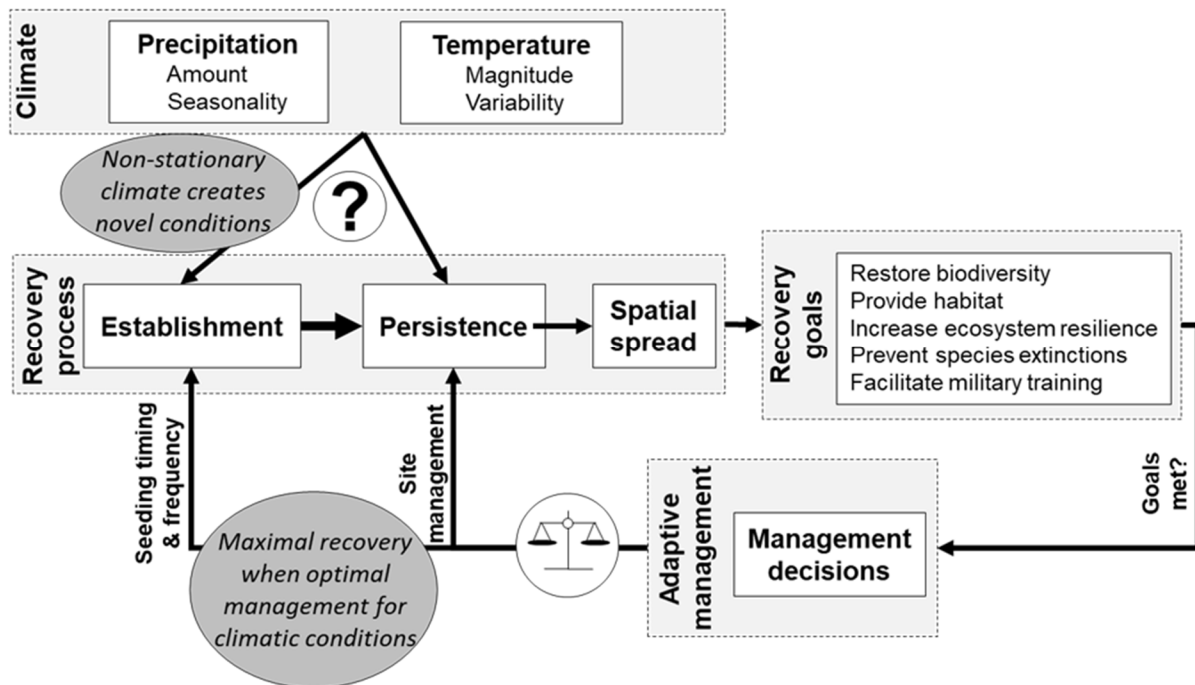


Fig. 7.3. Conceptual model of how climate, recovery, and adaptive management are linked. The proposed research fills key knowledge gaps created by non-stationary climate, facilitating effective decisions to optimize management and recovery.

Our findings (e.g., Fig. 7.1) highlight the integral role of climate and management in affecting the establishment, persistence, and spread that characterize successful recovery. However, despite the importance of plant community recovery for DoD's mission as well as for understanding the basic ecology of plant communities, several fundamental challenges remain. These challenges arise from the linkages between climate, management, establishment, and recovery (Fig. 7.3). We summarize three critical challenges suggested by the results of our current research below.

Future Challenge 1: It is unknown how climatic variability affects long-term establishment, persistence, and spatial spread in intact communities

Successful, sustained recovery of plant communities hinges upon the establishment of new individual plants (Fig. 7.2), a process that is necessary for persistence and a key predictor of subsequent spread (and hence continued recovery; Fig. 7.2). Although data from our study suggest that climatic variation can have an important effect on establishment (Fig. 7.1), and can be used to provide important management recommendations, it is unknown whether the effect of incremental shifts in climate can be used to predict the effect of increasingly frequent extreme climatic events (Fig. 7.2, Fig. 7.3). This lacuna exists because long-term community-level data on recovery are rare (Gomez-Aparico 2009), and such data are necessary to understand the effect of climatic variation (which necessarily plays out over many successive years). Long-term data informing recovery may be most critical for ecosystems, like longleaf ecosystems, that are dominated by long-lived perennial plant species: these species may take many years to establish and achieve a size where continued survival is high and where rates of seed production are high enough to foster spatial spread of recovery (Brudvig et al. 2015, Caughlin et al. 2019).

Future Challenge 2: There are no clear, science-based guidelines for maximizing the success of future recovery efforts amidst different climate scenarios

Past studies, such as ours, can be incredibly useful for understanding how past climatic conditions affected the success of recovery efforts. However, future climatic scenarios are likely to be characterized by conditions that are beyond those examined in past studies (i.e., novel or "no-analog" conditions; Radeloff et al. 2015). Theoretical expectations and extensive empirical data both suggest that the response to future climatic conditions may not be readily predictable from extrapolating based on past events (Radeloff et al. 2015). This challenge is exacerbated because forecasts are typically made on multi-decadal time scales using general scenarios while managers seeking to maximize community recovery require daily to decadal predictions initialized with data that also allow decision alternatives to be evaluated (Dietze et al. 2018). A key for successfully predicting recovery efforts and effective management outcomes is evaluating how plant establishment is affected by current and future climatic conditions (Fig. 7.3).

Future Challenge 3: Identifying which species are most affected by climatic variation and how generalizable these responses are across environments

Given the importance of maximizing the efficacy of recovery efforts amidst non-stationary climate, it would be ideal to know whether particular species are more (or less) robust to the effects of climatic variation. Moreover, because individual DoD installations in the southeast can have highly diverse plant communities with hundreds of plant species, it would be ideal to know if particular plant traits, not just particular plant species, are reliably associated with susceptibility to climatic variation (Fig. 7.3), as this provides a means to make predictions and recommendations to other plant species as well as to other DoD installations, maximizing transferability. The measurement of species characteristics that allow such generalizable predictions are almost always measured on adult plants, which may have little relevance for the two stages we have identified as most critical for plant recovery: seed and seedling establishment (Henn and Damschen In review).

Because of the above challenges, our knowledge of plant community recovery is incomplete, and attempts to predict long-term recovery outcomes and to guide recovery efforts in non-stationary climates may be ineffective or even misguided. Future work could overcome these impediments via three complementary research approaches to understand how species and communities have responded to past climate events, what mechanisms are responsible for these changes, and how future climate scenarios may alter these trajectories. This could be accomplished by first using a long-term, distributed experiment (such as the one in this report) to determine the impacts of climate on the establishment, persistence, and spread of intact plant communities that are actively undergoing recovery in realistic field settings. Data from the long-term experiment could then be integrated with new manipulative field experiments that mimic extreme precipitation events and studies of plant functional traits to understand the mechanisms underpinning these observed patterns and to anticipate how climate extremes will affect species establishment and persistence and the resilience of communities into the future.

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9. Appendices

- A. Supporting Data: We provide a comprehensive overview of our methods, data, datasets, and results in the report. As a result, no additional refined data warrant archiving in this report. Raw data used for analyses will be archived when these results are published in peer-reviewed scientific publications.

- B. Additional figures summarizing cover and richness for added species in relation to total species sampled within the 1x1m plots. Note that total cover was not sampled in 2018 and hence summaries in the main document come from added species only sampled at the 3x3m plots.

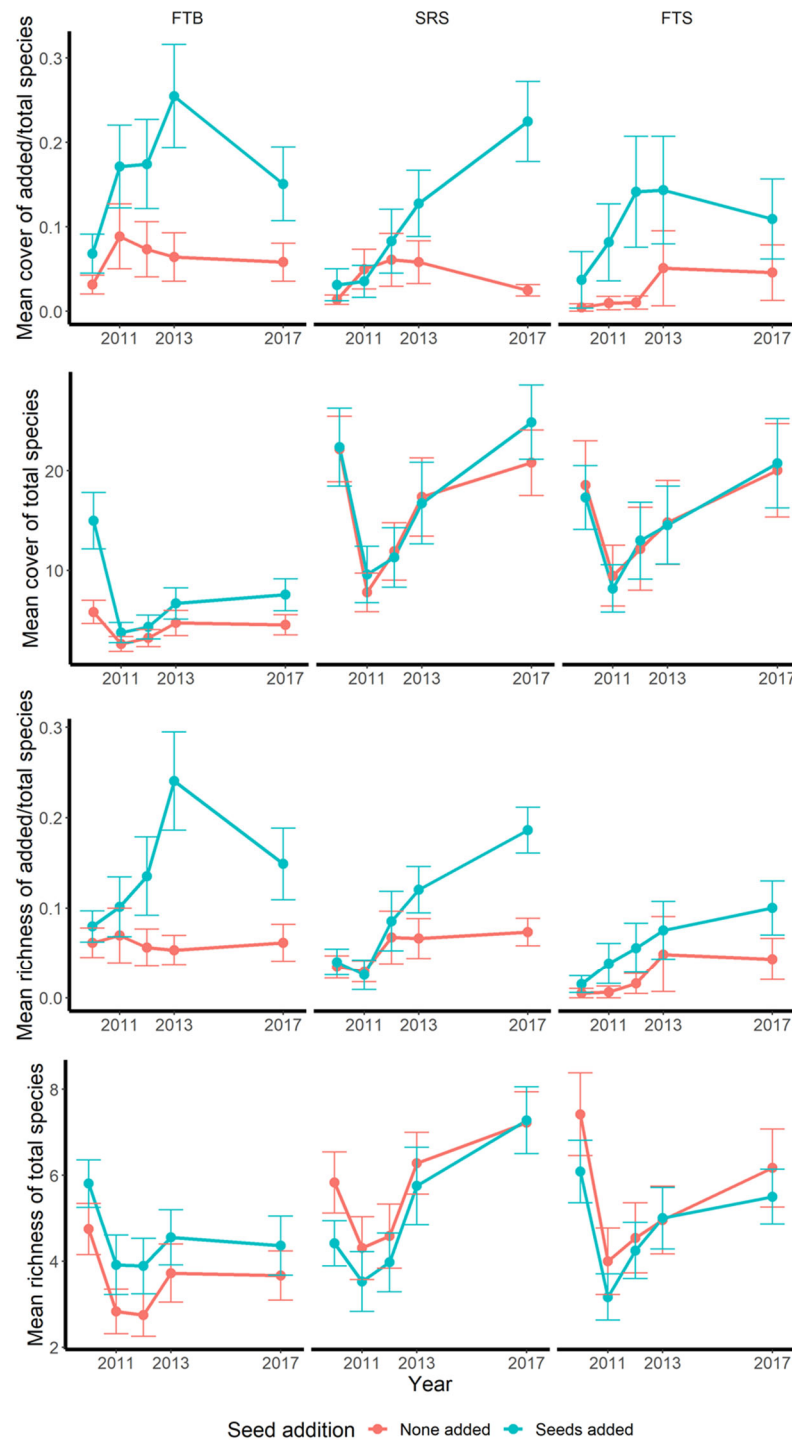


Fig. 6.2.5 Ratios of added species over total amount within 1x1m plots for mean percent cover (top) and mean richness (bottom) across years and by seed addition treatment at each installation. Average of total number of species recorded for cover and richness are also presented for reference.

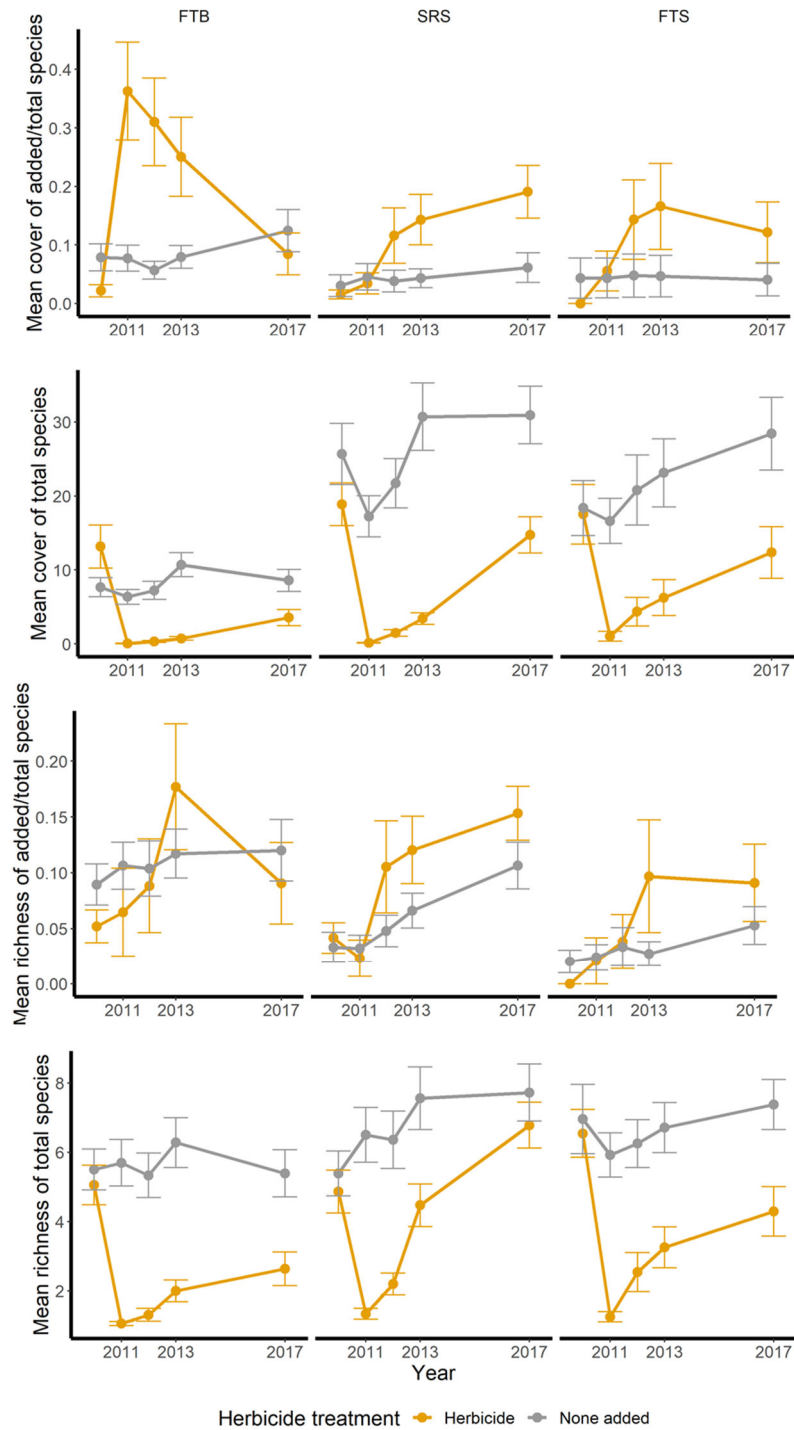


Fig. 6.2.6. Proportion of cover (top) and richness (bottom) within 1x1m plots attributable to the species added in the seed addition as a function of the herbicide treatment. Mean richness across years and by herbicide treatment at each installation. Average of total number of species recorded for cover and richness are also presented for reference.