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Long-term, large-scale experiment reveals the effects of seed limitation, climate, and anthropogenic disturbance on restoration of plant communities in a biodiversity hotspot

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Ecological restoration is essential for maintaining biodiversity in the face of dynamic, global changes in climate, human land use, and disturbance regimes. Effective restoration requires understanding bottlenecks in plant community recovery that exist today, while recognizing that these bottlenecks may relate to complex histories of environmental change. Such understanding has been a challenge because few long-term, well-replicated experiments exist to decipher the demographic processes influencing recovery for numerous species against the backdrop of multiyear variation in climate and management. We address this challenge through a long-term and geographically expansive experiment in longleaf pine savannas, an imperiled ecosystem and biodiversity hotspot in the southeastern United States. Using 48 sites at three locations spanning 480 km, the 8-y experiment manipulated initial seed arrival for 24 herbaceous plant species and presence of competitors to evaluate the impacts of climate variability and management actions (e.g., prescribed burning) on plant establishment and persistence. Adding seeds increased plant establishment of many species. Cool and wet climatic conditions, low tree density, and reduced litter depth also promoted establishment. Once established, most species persisted for the duration of the 8-y experiment. Plant traits were most predictive when tightly coupled to the process of establishment. Our results illustrate how seed additions can restore plant diversity and how interannual climatic variation affects the dynamics of plant communities across a large region. The significant effects of temperature and precipitation inform how future climate may affect restoration and conservation via large-scale changes in the fundamental processes of establishment and persistence.

conservation | diversity | restoration | seed limitation | longleaf pine ecosystem

Significance

A major challenge to global plant restoration is that numerous factors, including land management practices and climate variability, affect plant populations through multiple demographic processes, including establishment and persistence. Few studies have resolved these complexities. Our multiyear, multisite experiment reveals several factors structuring recovery of 24 understory plant species in longleaf pine savannas where past agricultural use has reduced plant diversity. Addition of seeds, cool and wet climatic conditions, low tree density, and reduced litter depth promoted establishment. Once established, most species persisted for the duration of the 8-y study. Our long-term study illustrates the contribution of temporal variation in climate and land management. Our demographic-based approach informs restoration of entire communities, maximizing potential for restoration on former agricultural lands.

Human activities have led to unprecedented rates of species loss, wholesale shifts in community composition, and the alterations of ecosystem functions and services (1–3). In response, conservation and ecological restoration have become global priorities (4–7). Successful restoration, particularly in terrestrial systems, often relies on reinstating plant communities because of their role in supporting higher trophic levels, aspects of ecosystem functioning, ecosystem services, and landscape-scale connectivity across diverse taxa (8, 9). As such, understanding the processes influencing the outcomes of plant restoration is essential for the present United Nations Decade on Ecosystem Restoration to yield guidance that will generate benefits for decades to come (8). The need for durable solutions places immense responsibility on immediate actions of restoration managers (10), who must be equipped with empirically based guidance. Yet, conservation and restoration outcomes are notoriously variable, and this leads to a lack of concrete guidance for many ecosystems (11).

Variation in outcomes of plant biodiversity recovery efforts stem from numerous sources, including differences in site conditions, management approaches, or climate (11). For example, plant establishment following seed additions to restore communities can vary with soil attributes, disturbance regimes, or interannual variation in weather conditions (12, 13). The challenge of unraveling the influence of drivers of variation is further complicated by the fact that drivers may operate in different ways for different species. These influences can play out over the course of years during recovery efforts, over which time climate and other factors may fluctuate. Critically needed, therefore, are studies capable of disentangling influences of putative drivers of recovery outcomes, like management actions and climate variability, conducted over appropriately large temporal and spatial scales to encompass site-to-site and year-to-year variability, thus clarifying their relative roles in shaping the restoration of plant communities (14–16).

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To address this critical need, we must understand two key aspects of plant dynamics: factors that affect the establishment of new individual plants and factors that affect the persistence (i.e., survival) of established plants. Gaining this understanding requires a long-term perspective: establishment and persistence occur within the context of multiyear changes in climate, land use, and management. Large-scale studies are also necessary, as factors that affect plant diversity can vary in space and time: location-specific differences in climate, local management activities (e.g., prescribed fire, timber harvest), and historical activities (e.g., past agricultural land use) can have profound effects on patterns of plant diversity and community composition (17–19). Their specific roles in affecting the demographic processes of establishment and persistence, however, remain poorly resolved.

This lack of long-term, large-scale studies makes it difficult to provide actionable guidance for conservation and restoration in plant communities. For example, ongoing abandonment of agricultural lands (10, 20, 21) provides a global opportunity to restore plant communities (18, 21, 22). However, this opportunity highlights a profound gap in our knowledge and illustrates the importance of temporal dynamics: despite decades or even centuries after agriculture has ended, plant biodiversity often fails to recover (6, 19, 23, 24) and predicting restoration outcomes across variable environments is notoriously difficult (11). As a result, isolating the effects of specific, and potentially interactive, management actions (e.g., adding seeds of restoration species, promoting natural disturbance regimes, reducing tree densities) amid environmental variability is essential for identifying targets for conservation and maximizing restoration success. Fundamental to plant restoration success is understanding whether plant populations are limited by particular demographic bottlenecks, such as the arrival of seeds, the rate at which plants establish from seeds, and the rate at which established plants continue to persist. It is important to understand if one (or more) of these stages is limiting diversity because limitation can happen at any of these bottlenecks (e.g., while establishment is needed for persistence, persistence is never guaranteed) and because different forms of limitation often require different restoration approaches. For example, if plant diversity is only limited by the dispersal of seeds into areas where species have been eliminated by past human land uses (25–28), then adding seeds [or otherwise facilitating long-distance dispersal (29–31)] will ensure restoration success. However, if granivores destroy arriving seeds before they establish (32), then restoration aimed at reducing seed palatability or satiating granivores will be important (e.g., ref. 33). Alternatively, if diversity is limited because few established seedlings persist due to competition with woody plants, then restoration strategies that reduce woody competitors will be required for successful restoration. Importantly, demographic bottlenecks may operate singly or in combination to affect plant recovery during restoration.

Evaluating the importance of limitation due to seed arrival, establishment, and persistence for plant restoration would optimally be undertaken by using long-term studies, since patterns in plant communities can take many years to become apparent. They would also be done at the community level, simultaneously evaluating multiple species of restoration interest to facilitate a comparison of how different species respond to the same management activities and environmental conditions. While numerous studies have evaluated how plant communities respond to seed addition in the short term (25–27), long-term studies that evaluate the relative importance of establishment and persistence within communities are rare (13, 25, 27, 28). Moreover, although previous metaanalyses have been useful for understanding the effects of short-term seed additions (25–27), metaanalyses necessarily combine studies that use different methods, species, and response variables, making it difficult to generate strong inference regarding the relative importance of management activities, climate, and species' traits on establishment and persistence for the scores of species that may be the focus of restoration. Given these knowledge gaps, restoration efforts will be most successful when evidence from long-term, multispecies studies can be used to inform the coupling of environmental conditions and management activities that promote plant establishment and persistence.

With this in mind, we conducted an experiment to understand factors that limit restoration of plant community diversity in postagricultural savanna–woodlands (hereafter "savannas") of the longleaf pine (*Pinus palustris*) ecosystem, a biodiversity hotspot and one of the most species-rich ecosystems in North America (34, 35). We sought to determine how environmental conditions and management activities affect key demographic bottlenecks (i.e., seed limitation, establishment limitation, or persistence) and to evaluate whether some forces are more important than others so that we could create data-driven, prescriptive restoration guidance. Our 8-y experiment spanned three locations in three states and a large portion of the historic range of longleaf pine (Fig. 1*B*). Longleaf pine savannas are among the most imperiled ecosystems in North America: once extending across the southeastern United States, many decades of fire exclusion, logging, urbanization, and agricultural use (17, 18, 36, 37) have left less than 5% of the longleaf pine ecosystem intact (38). Longleaf pine savannas thus provide an optimal system for our study. Similar to other imperiled savanna ecosystems across the globe, these species-rich herbaceous plant communities have been subjected to different forms of human-caused environmental change across multiple spatial and temporal scales (39), including agriculture, fire suppression, and conversion to high-density tree plantations, leading to a persistent loss of plant biodiversity (39, 40).

To disentangle the factors affecting plant establishment and persistence, we conducted a long-term, multilocation replicated experiment that manipulated seed arrival (i.e., seed additions) and plant competition (i.e., preseeding herbicide application), and evaluated the joint impacts of climate, tree densities, prescribed fire regimes, and soil conditions on the establishment and persistence of 24 herbaceous understory plant species (Fig. 1*B*). We also examined whether plant species characteristics (i.e., functional traits) provide insight into which types of species are most likely to respond to particular restoration actions or environmental conditions. This trait-based experimental approach makes it possible to identify whether particular species, specific traits, or both are consistently associated with successful establishment or persistence.

Results and Discussion

Our multisite experiment revealed the importance of seed dispersal, climate variability, and management activities for the long-term restoration of plant communities in a global biodiversity hotspot (Figs. 2 and 3). The long-term nature of our experiment was essential for clarifying the influence of important factors (i.e., climate and management) that change among years and locations: patterns in occupancy of experimental plots by target restoration species were highly variable among years and locations (Fig. 2*B*), and our distributed experiments allow us to estimate variation due to changes in climate and management, rather than be confounded by them. The long-term nature of our

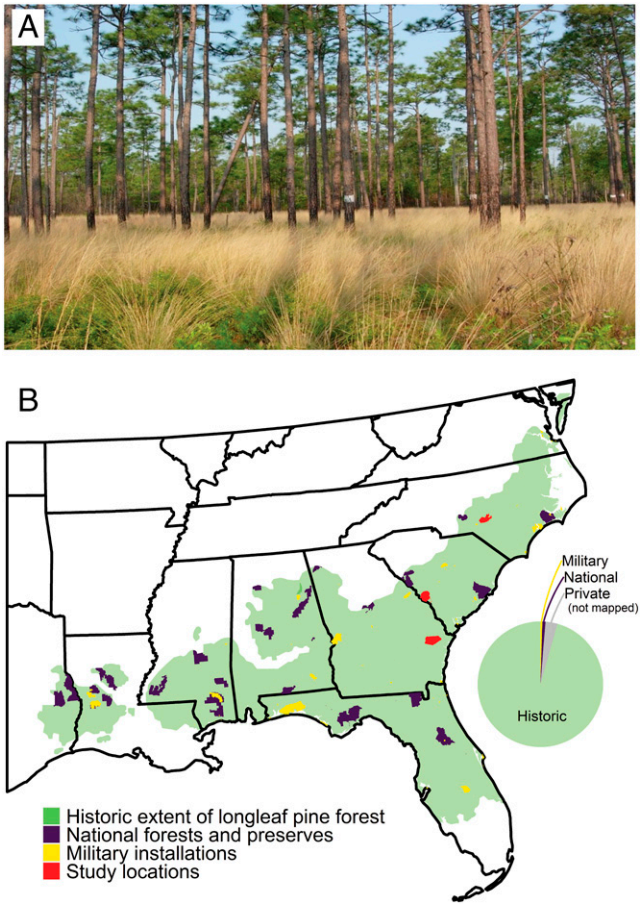

Fig. 1. (*A*) Our study occurs in the longleaf pine ecosystem, a biodiversity hotspot characterized by high understory plant diversity from local to regional scales. (*B*) Although the historical extent of longleaf pine spanned 36.8 million hectares of the southeastern and southern United States (38), less than 5% of the original area remains today (38). Approximately 10.1% of current longleaf pine ecosystems occur on national forests, 10.1% on Department of Defense lands, 16.3% on state forests, and 63.5% on privately owned forests (not shown on map) (38). In this system, ecological restoration is essential to protecting biodiversity. We conducted a distributed experiment to evaluate the role of seed addition, competition reduction, and local management (i.e., differences in canopy tree density) on 24 herbaceous plant species at each of three different locations. Photo credit: W.B.M.; historical range of longleaf pine map layer from Peet et al. (72).

study also enables one of our key findings, that establishment—not persistence—is the primary ecological process consistently limiting plant community diversity under a variety of conditions across broad spatial scales (Fig. 3 *A* and *B*). Our finding reaffirms short-term studies that restoration of plant communities is limited by seed input and advances this understanding to show how, once established, perennial plants are persistent over many years. This result has important and lasting implications for restoration of plant diversity: a single restoration action (addition of seeds) had positive effects on establishment of the most of our focal species, leading to an increase in diversity across three separate geographic locations that remained evident 8 y later (Figs. 3*C* and 4).

A single seed-addition event had significant and lasting effects on the restoration of plant diversity at our study sites (Figs. 2*A* and 3*C*). While seed dispersal is thought to play a key role in the maintenance of biodiversity at small (25–28, 41, 42) and larger scales (30), the degree to which single pulses of dispersal can modify ecological communities at large geographic scales and over extended periods of time remains unexplored in most ecosystems. Adding seeds is a common means of experimentally testing for the role of dispersal in limiting occupancy (27, 43), and the results of our seed-addition experiment demonstrate that the number of plant species in longleaf pine understory communities is limited by the number of seeds that arrive at the site. This result, obtained across 48 sites spanning over 480 km, provides strong evidence to support the generality of earlier studies (25, 26, 44) but also extend previous findings to suggest that, once established, perennial plants persist under a wide range of abiotic and biotic conditions. Our results point to the applied relevance of this fundamental finding. Intentionally adding seeds may be highly effective for slowing rates of biodiversity loss and for promoting active restoration because it can result in novel establishment and persistent occupancy within a community. This pattern was evident for most, but not all, species in our study, and our investigation of establishment and persistence affords further insights into additional management needs (*SI Appendix*, Figs. S3–S7). For example, *Anthenantia villosa* and *Coreopsis major* established poorly, but showed high persistence, suggesting that these species might be best restored using methods other than seeding to achieve establishment, such as transplanting of seedlings. Other species, such as *Liatris* spp. and *Aureolaria pectinata*, exhibited low rates of establishment and relatively low levels of persistence, illustrating species where restoration may be particularly challenging and where novel considerations (e.g., *A. pectinata* is a hemiparasitic species on the roots of woody hosts) and optimal conditions (i.e., cool, wet years in habitats with low canopy tree density and thin litter layers) may be needed to facilitate both establishment and persistence.

In revealing that the arrival of viable seeds can yield long-term increases in diversity, our results suggest that factors affecting the potential for long-distance dispersal of plants will be essential for promoting plant biodiversity under global change (29–31). For example, conservation strategies that increase dispersal via passive means, such as conservation corridors (30), activities that lead to large changes in seed production (e.g., canopy thinning) (44), or changes in the behavior of seed-dispersing animals (29) may have promoted persistent plant populations by increasing rates of establishment. As we describe below, our study indicates seed dispersal is necessary, but not always sufficient: the success of long-distance dispersal events depends not only on seed input, but on postdispersal climatic conditions and site-level management activities. For example, our findings illuminate how understanding the spatial process of long-distance dispersal requires considering the temporal dynamic of interannual variation in climate: the outcome of long-distance dispersal events for plant establishment depends upon whether the long-distance dispersal event happens in a cool, wet year, since those are the years that are associated with increased establishment (Fig. 2). As a result, considering variation in annual climate may be essential for predicting the capacity for plant species to move in response to climate change (45), as well as the utility of single seed-addition events as viable tools for increasing plant restoration and migration.

While our results point to the primacy of dispersal in affecting plant establishment and biodiversity in savanna restoration (30), we also find that many dispersal events are unsuccessful: most species added as seeds had very low establishment success, mirroring findings from other seed-addition studies in longleaf pine savannas (12, 44). Seeds are only likely to establish where local microsite conditions are favorable, providing ample light to fuel photosynthesis and ample soil contact to ensure adequate rooting and water acquisition. Our results reflect this reality and reveal the essential role that management can play in promoting plant diversity. Establishment was higher at sites with lower canopy tree density (i.e., greater light at ground level) and was higher at

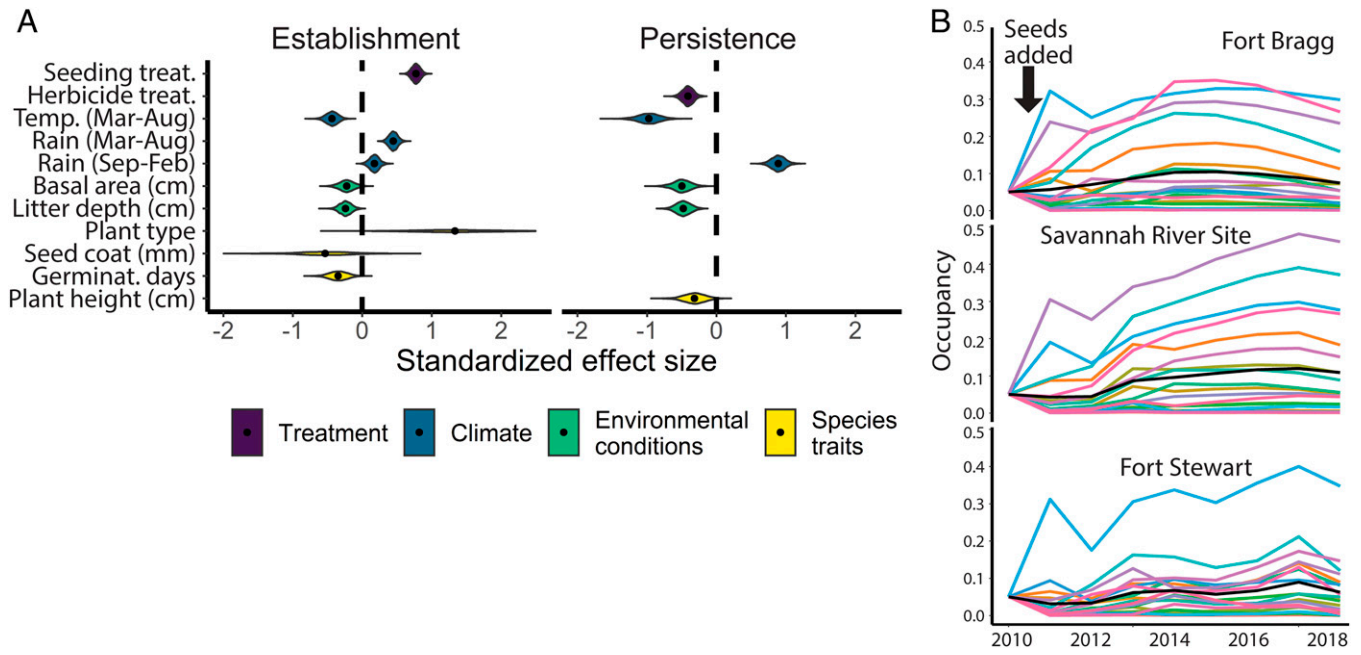

Fig. 2. (*A*) Factors that affect establishment and persistence of 24 plant species in the longleaf pine ecosystem. Factors plotted represent the subset of all factors examined (*SI Appendix*, Fig. S3 and Table S2) that were significantly associated with changes in establishment and persistence. (*B*) Annual estimates of species occupancy demonstrate considerable variation among years and species. Each line color represents 1 of the 24 added species. Information on the identity of individual species is presented in *SI Appendix*, Figs. S4 and S6. The estimate of occupancy in the initial year of the experiment is derived from naive priors that do not yet incorporate knowledge from predictors or the time series. As such, the estimate for year 1 appears nearly identical for all species and approximates the grand estimate of occupancy in year 1 at all sites (*SI Appendix* includes additional details). The value of our long-term study is that our experimental design allows us to use this variation to understand how changes in climate and management lead to annual variation in plant species occupancy, and thus diversity.

sites where management actions, such as frequent prescribed fires (17), prevent the accumulation of litter (Fig. 2*A*). Our results suggest that the scope for local conditions to increase establishment is considerable: establishment is two to three times greater at sites with low tree basal area (i.e., <40 cm) and shallow leaf litter (<2 cm) (Fig. 4). We also found that some management activities have location-specific effects, through their influence on plant establishment and persistence. For example, the long-term benefits of removing preexisting vegetation (via herbicide application) prior to seed addition for the establishment and persistence of seeded species were noticeable at only one of our three geographic locations, Savannah River Site (46). This location-specific effect of herbicide application contrasts strongly with the consistent effect of seed addition, tree density, and litter depth across all three locations, suggesting that timing seed additions to coincide with favorable climatic conditions and implementing management that reduces tree density (via low planting densities or tree thinning) and decreases litter depth (via prescribed fire) are more likely to yield predictable positive effects on restoration of plant diversity.

Our ability to restore and conserve plant populations hinges upon our ability to understand how changes in climate and ecosystem processes (e.g., fire suppression, loss of animals that disperse seeds) affect plant establishment and persistence. Our long-term study shows that regional climate (specifically years with cool, wet conditions), has strong effects on establishment and long-term persistence (Fig. 2*A*), and that the magnitude of these effects is similar to the magnitude observed with our experimental seed additions (Fig. 2*A*). Once species were established, most persisted for the duration of our 8-y study, highlighting how restoration of these plant communities is limited by processes that promote establishment, largely because persistence itself is so high. As such, restoration approaches based on maximizing establishment (i.e., seed addition, possible protection of seeds from granivores) seem very promising. These results also indicate that long-term changes in plant diversity can be heavily influenced by conditions during a particular year (and thus missed in short-term studies), and that the strength of these responses differs depending upon the plant species studied (Figs. 2*B* and 4). In particular, fluctuations in climate can dictate which species initially establish from seed and thus the long-term trajectory of species persistence and community diversity (13, 47), a result that is apparent in our data (Fig. 4).

This finding is especially noteworthy because our study points to the importance of cool, wet years, while empirical data and future climatic projections for the southeastern United States suggest that current trends of warming and increased extreme precipitation will continue (48, 49). Our results provide a means to predict shifts in the success of longleaf pine plant community restoration in future climate scenarios because they provide general (i.e., community-level) guidance but also indicate how particular species or plant groups (e.g., legumes) (Fig. 4) may respond. For example, our data generally suggest that high levels of precipitation are beneficial for plant population establishment and persistence (Fig. 2*A*), but seasonality is important because spring rainfall increases establishment whereas autumn and winter precipitation increases plant persistence (Fig. 2*A*). On the other hand, increased summer temperatures have deleterious effects on both establishment and persistence. Because these effects are pronounced for some species (e.g., establishment of *Aristida purpurascens*, *Sorghastrum* spp., and *Lespedeza hirta* was much higher in cool, wet years), our results help provide prescriptive guidance for species that may benefit the most from conservation and restoration action depending upon expected future climate conditions.

Trait-based approaches are increasingly used to predict ecological responses to global change (50) and also highlight how biotic and abiotic factors affect restoration success (51). Our study

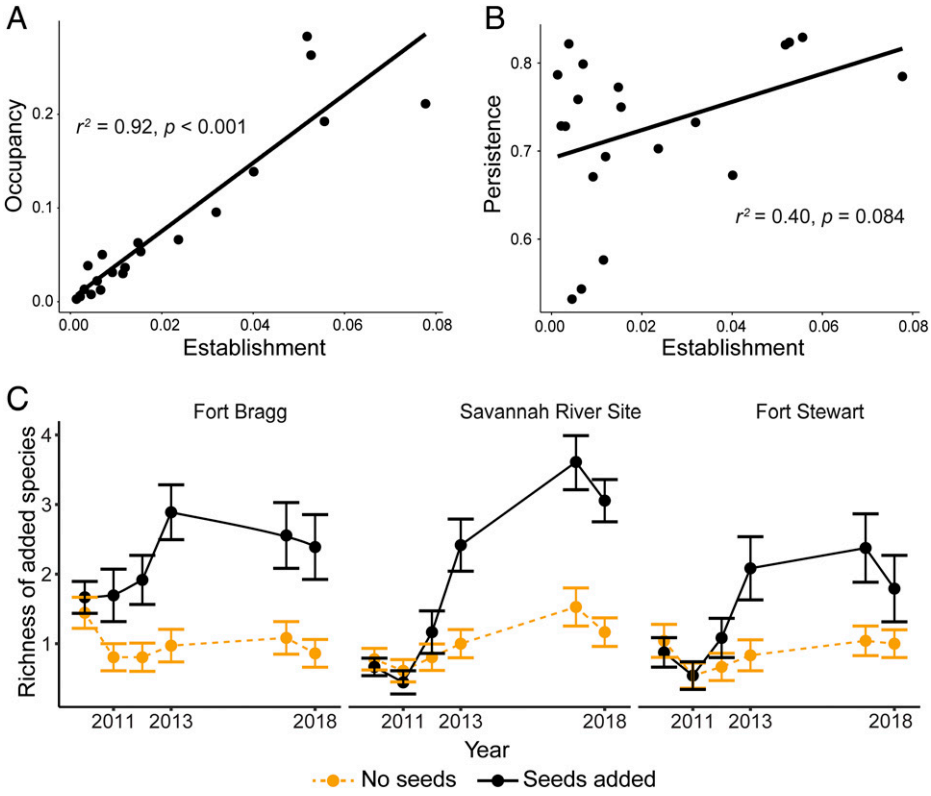

Fig. 3. (*A*) Establishment was the primary process affecting the occupancy of plant species in our study, although persistence also contributed to variation in occupancy (r^2 = 0.51, P = 0.22). Each point represents one study species (species listed in *SI Appendix*, Table S1). (*B*) Once established, persistence were generally quite high (i.e., >0.5); species that established well also tended to persist. (*C*) Because persistence is high once establishment occurs, establishment following a single seed addition produced lasting changes in the diversity of focal plant species.

evaluated several plant traits that are commonly thought to be important predictors of plant population responses to environmental conditions (*SI Appendix*, Table S3) (50, 52). Our findings show that some plant traits may be indicative of establishment and persistence, especially when these traits are closely linked to the ecological process of interest (e.g., seed dormancy characteristics that are associated with establishment) (Fig. 2*A*). Our findings also caution that careful evaluation of multiple traits within the context of specific restoration or conservation goals is essential. For example, establishment was greater for species with thinner seed coats that germinated quickly (Fig. 2*A*), such as *A. purpurascens*, *Pityopsis graminifolia*, *Solidago odora*, and *Sorgahstrum* spp. However, plant type (e.g., whether the species was a legume) (Fig. 4) had a stronger predictive effect on establishment, although legumes have relatively long germination times.

Finally, our study is instructive because many of the traits we examined had little predictive ability. This may have occurred because we did not include the most relevant plant traits in our analysis. Although we selected traits that have been found to be important in a variety of contexts and study systems (*SI Appendix*, Table S3) (50, 52), the strong role of establishment implies that future studies that evaluate traits related to plant establishment and phenotypic variation may be very informative. For example, standardized plant trait measurements are typically taken from adult plants within a narrow range of environmental conditions (52). While this approach can be useful for understanding trait variation across very large (global) spatial scales, it may be less useful at the scale of local sites where community assembly occurs (53–57). Given the importance of establishment we observed, measuring traits during key life stages (e.g., seeds and seedlings) and across a wider range of environmental conditions may be important for understanding the key process of establishment (58, 59) and may more effectively capture the potential for phenotypic plasticity to contribute to meaningful covariance between plant traits and success in a particular environment (60). However, in situations where mean trait-level data on adult plants are all that are available, our results suggest that modeling of multiyear plant population data will be essential for understanding plant population dynamics, because species responses to climate and management, rather than species' traits, are the best determinant of species performance (Figs. 2*A* and 4).

Conclusions. Conservation and restoration of plant communities is a global need in an era of unprecedented global change and biodiversity loss. Our results provide several important messages to assist future restoration and conservation efforts. The potential to recover savanna plant biodiversity is critically dependent on seed arrival and establishment, as demonstrated by the result that a single seed-addition event led to plant reestablishment that persisted for years (Fig. 3*C*). Climate has significant, predictable effects on herbaceous plant diversity, and we can use these predictable effects to optimize timing of our restoration and conservation efforts. Management can play a vital role in fostering success in these arenas: we found that tree harvests and frequent prescribed burns can provide a significant boost to plant establishment and persistence. Given that many of the added species had very low rates of establishment, we suggest that more studies are needed to understand whether trait variation associated with establishment can provide greater cross-species predictive power toward promoting full community restoration.

Our work underscores the importance of collecting long-term data to understand the dynamics that determine plant community diversity, conservation, and restoration. The importance of

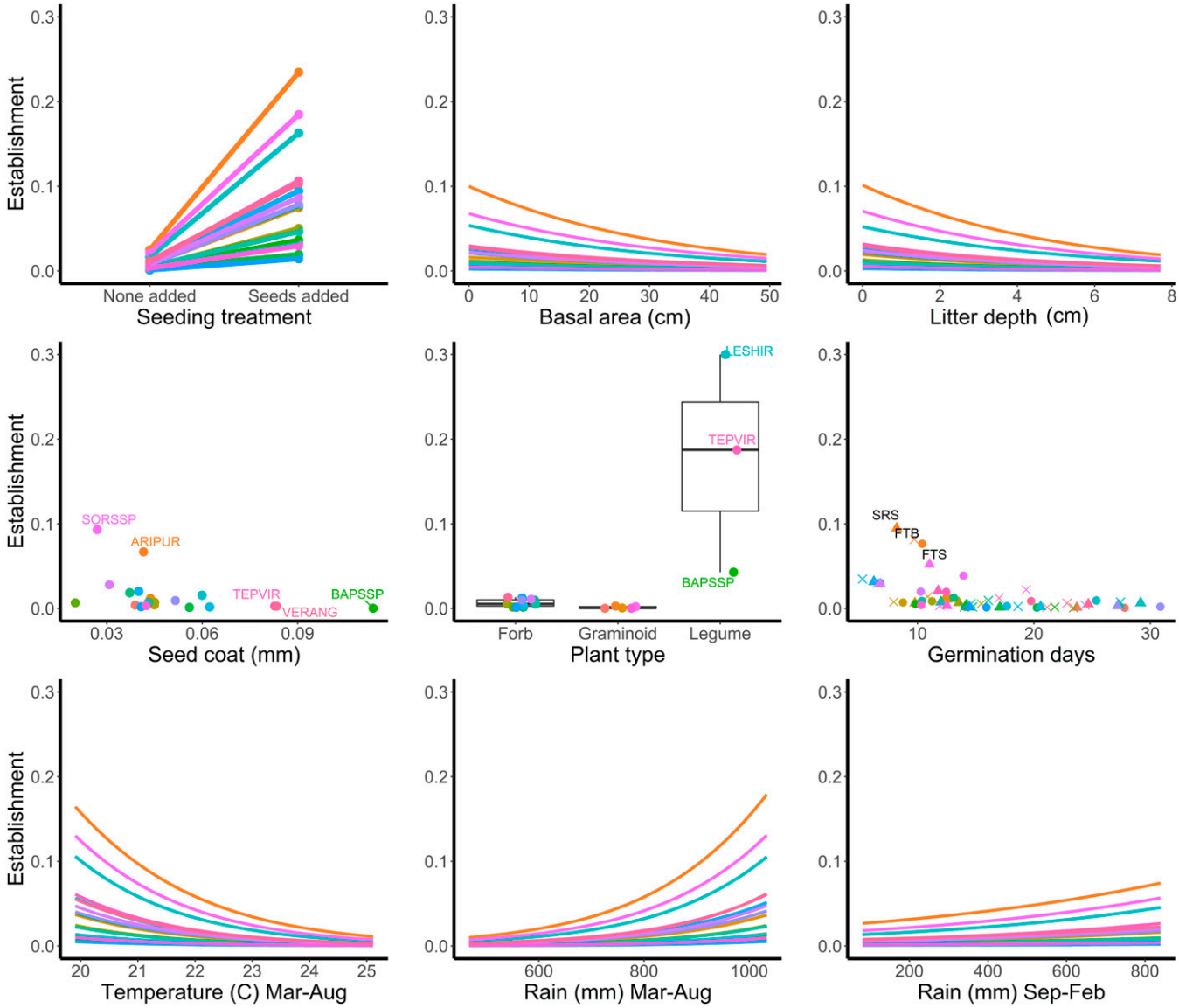

Fig. 4. Species-specific variation in factors that affect plant establishment; values represent standardized relationships between each species and predictor. Each line color represents one of the 24 added species. Information on the identity of individual species is presented in *SI Appendix*, Fig. S6.

seed additions for affecting establishment developed differently across locations, species, and management contexts, requiring several years to become apparent, sometimes unfolding 6 to 7 y after the single seed addition was performed (Fig. 2*B*). Importantly, current and future challenges to biodiversity are complex and unfold along different temporal scales, requiring long-term experiments to disentangle causal mechanisms. Moreover, while many challenges we face in the present can be informed by the past, challenges we face in the future will be increasingly characterized by novel ecological conditions with no past analog that we can look to for insight. Long-term experiments in biodiversity hotspots and those conducted at global scales (61) will be essential to understand threats to biodiversity today and mitigate threats to biodiversity in the future.

Materials and Methods

Study Locations and Field Methods. Long-term experimental sites were selected at three locations: Fort Bragg in North Carolina (18 sites), Savannah River Site in South Carolina (18 sites), and Fort Stewart in Georgia (12 sites) (Fig. 1*B*) (see refs. 46 and 62 for additional information regarding sites and locations). These three locations fall strategically within three of the primary physiographic regions of longleaf pine ecosystems: Fall-line Sandhills, Atlantic Coastal Plain, and Southern Coastal Plain (63, 64), respectively. Sites were selected in upland habitats each ≥1 ha, supported overstory longleaf pines, and lacked firebreaks, drainages, shrubby ecotones, or other features causing abrupt transitions in understory vegetation. Sites had the same land-use history (i.e., intensive agriculture that stopped 70 to 100 y ago), but maximized variation across prescribed fire frequency and overstory tree density (39). At each site, four 7 × 7-m plots were used for long-term evaluation (*SI Appendix* includes additional details). Two experimental treatments were applied in a factorial design at each site: competitor manipulation and seed addition. Competitor presence was manipulated by applying a broad-spectrum herbicide (OneStep, active ingredients: Imazapyr, 8.36% and Glyphosate, 22.13%) at a rate of 9.4 L/ha to half of the plots during August of 2010. In summer and autumn of 2010, we locally collected over 20 million seeds of perennial species that are indicative of high-quality upland longleaf pine savanna communities (65). Seeds were collected locally (i.e., within 10 to 30 km of each site) to ensure use of local genotypes. In March 2011, seeds were added inside 5 × 5-m subplots at half of the plots at each site (62) across the three study locations. Due to nonoverlapping geographic ranges, four species were congeners, resulting in 25 total species across the three locations (*SI Appendix*, Table S1). Note that *Gaylussacia dumosa* was not included in analyses as it was the only suffrutescent

(i.e., woody subshrub) and animal-dispersed species that was added, and was too different in trait values from the other species to provide meaningful comparisons; as such, the total number of species we analyzed was 24.

To quantify the establishment and persistence of seeded species, we recorded the occurrence of these species in the 5 × 5-m center of each experimental plot during 2010 to 2013 and 2017 to 2018 (*SI Appendix*, Fig. S4); this multiyear dataset at each site allowed use to estimate establishment and persistence for each year. Sampling occurred during the mid-late growing season (July to September).

Statistical Analyses. At the plot level, predictors included herbicide treatment (yes or no), seeding treatment (yes or no), measures of soil moisture (percent by mass), soil hardness measured using a cone penetrometer (pounds per square inch), visual estimates of cover of litter (percent), cover of bare ground (percent), and litter depth (centimeter, including duff) (*SI Appendix*, Fig. S5 and Table S2). At the site level, predictors included basal area of overstory trees (total centimeter diameter at breast height), fire frequency described as the total number of fires preceding the experiment (during 1991 to 2009); and, as a categorical measure of fire history, classified as high if a site experienced ≥5 fires during 1991 to 2009, or low otherwise. Current fire regime was defined as the number of years since the last fire occurred during the experiment (2010 to 2018). We evaluated interactions between continuous fire measures and soil moisture assuming the impact of fires on plant communities would differ depending on soil conditions.

At the location level, we also evaluated weather metrics, including mean temperature (°C) and seasonal rainfall (millimeter) for growing (March to August) and dormant (September to February) seasons (*SI Appendix*, Table S2). Functional traits for each species included measures of dispersal ability, defined as their dispersal mode (classified as wind-dispersed, or nonwind dispersed) (*SI Appendix*, Table S3) and classification of plant clonality (i.e., their ability to vegetatively propagate, classified as clonal or not) (*SI Appendix*, Table S3). Traits describing seed characteristics included seed width (millimeter), length (millimeter), depth (millimeter), coat thickness (millimeter), volume (cubic millimeter), sphericity, mass (milligram), and seed-to-dispersule mass ratio (*SI Appendix*, Table S3). Traits describing seed characteristics related to viability and dormancy included the proportion of seeds that germinated in growth-chamber trials, and the average number of days to germination (germination days) (*SI Appendix*, Table S3). Finally, traits describing growth strategies included plant type (classified as graminoid, nonleguminous forb, or legume), plant height (centimeter) defined as distance from ground to tallest photosynthetic structure, specific leaf area (leaf area/dry mass), and leaf tissue chemistry (carbon-to-nitrogen ratio) (*SI Appendix*, Table S3). Further details on how predictors were estimated are provided in the *SI Appendix* and in Orrock et al. (46). We evaluated pairwise correlations among continuous predictors using Pearson's correlation and excluded one of a pair when highly correlated (> 0.7) (*SI Appendix*, Figs. S1 and S2 and Tables S2 and S3). Continuous predictors were standardized by subtracting the mean and dividing by the SD while categorical predictors were scaled within a −1 and 1, which allowed direct comparisons of coefficients as relative effect sizes (66).

We fitted multispecies dynamic occupancy models (*SI Appendix*) using a Bayesian framework, which partitioned occurrence into establishment and persistence, accounted for the unbalanced sampling from sites lost to logging in later years, and provided estimates during unmeasured years (67). We updated posterior distributions of predictors in models using Markov chain Monte-Carlo (MCMC) methods available in the program JAGs (68), which we called from the R program (v3.5.3) using the jagsUI package (v1.5). For each model, we ran three parallel MCMC chains of 25,000 iterations, thinned every fifth iteration, and excluded the first 20,000 as burn-in. We assessed model convergence using MCMC trace-plots and the Gelman–Rubin statistic expected to be <1.1 (69).

We evaluated goodness-of-fit using Bayesian *P* values calculated from deviance residuals, following Broms et al. (70), with values between 0.1 and 0.9 indicating adequate fit; equations and code from Cruz et al. (71). We only used sampled years (excluded 2014 to 2016, 2018) in Bayesian *P* value calculations. Estimates suggested all models had adequate fit (range = 0.116, 0.146). Additional modeling details are available in *SI Appendix*.

Data, Materials, and Software Availability. All study data are included in the main text and supporting information.

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