5 Mechanistic Controls of Community Assembly and Biodiversity

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CONTENTS

INTRODUCTION

PATTERNS OF DIVERSITY AT LOCAL AND REGIONAL SCALES

The deceptively uniform bilayer structure of longleaf pine (*Pinus palustris*) ecosystems, featuring forests, woodlands, and savannas of canopy longleaf pines and grass-dominated ground cover, belies the exceptional floristic diversity associated with the herbaceous ground cover. Most notably, this ground cover harbors the highest levels of plant species richness in North America and globally rivals other species-rich herbaceous-dominated plant communities (Walker and Peet 1983; Peet and Allard 1993). Not only does high species richness occur at local scales (Table 5.1), but regionally, the species-rich ground cover is also characterized by many species endemic to the southeastern Coastal Plain. In addition, the entire North American Coastal Plain, which encompasses the former range of the longleaf pine, has been proposed as a global biodiversity hotspot (Noss et al. 2015).

Of the 1630 total vascular plant species endemic to the Coastal Plain Floristic Province identified by Sorrie and Weakley (2001), 1000 species are obligate associates of the longleaf pine ecosystem and many of these endemics are restricted to quite narrow subregions. Furthermore, fire-maintained longleaf pine communities provide habitat for numerous rare plant (Hardin and White 1989; Drew et al. 1998; Sorrie and Weakley 2006) and animal species (Earley 2004; Noss et al. 2015).

TABLE 5.1
Mean (and Maximum) Values for Species Richness (Number of Species) per Area in Longleaf Pine Communities of Florida (FL), Georgia (GA), Louisiana (LA), and North Carolina (NC)

Soil Moisture Regime	Community Type	State	Scale (m^2)						References
			0.01	0.10	1.00	10.00	100.00	1000.00	
Wet	Wet savannas	NC	–	–	32.9	–	–	–	Walker and Peet (1983)[a]
			4.4	11.3	22.4	36.0	61.1	94.8	Noss (2013)
		FL	3.1	9.2	18.7 (46)	30.4	54.5	89.8	Noss (2013) and references therein
	Wet-mesic to wet flatwoods	NC	2.3	6.0	11.2	18.7	33.2	54.6	Noss (2013) and references therein
		FL	1.8	5.2	11.7	21.4	40.0	71.2	Noss (2013) and references therein
Mesic	Mesic savannas	NC	–	–	30.5 (50)	–	–	–	Walker and Peet (1983)[a]
		LA	1.9 (4)	–	–	–	–	–	Myers and Harms (2009a)
			–	–	30.8 (50)	–	–	–	Myers (unpublished data)
			–	–	–	–	103.0 (130)	–	Platt et al. (2006)
	Mesic to wet-mesic uplands	NC	2.7	7.5	15.7	27.1	51.7	81.4	Noss (2013) and references therein
		GA		7.9	18.7	33.0	57.9	–	Kirkman et al. (2016)
		FL	2.1	7.1	17.1	32.8	63.7	107.5	Noss (2013) and references therein
Dry	Dry savannas	NC	–	–	23.3	–	–	–	Walker and Peet (1983)[a]
	Sandhills	FL	–	–	18.2 (33)	–	–	–	K. Harms, S. Gagnon, and J. Myers (unpublished data)
		NC	0.5	1.3	3.2	6.6	12.9	22.5	Noss (2013) and references therein
		FL	1.1	3.2	9.5	20.9	42.6	74.1	Noss (2013) and references therein
	Subxeric uplands	NC	0.8	2.7	5.5	10.3	19.1	34.8	Noss (2013) and references therein
		GA	–	5.5	14.1	26.6	49.0	–	Kirkman et al. 2016
		FL	1.1	3.9	11.2	24.4	48.1	84.0	Noss (2013) and references therein

Source: Modified from Noss, R. F., *Forgotten Grasslands of the South: Natural History and Conservation*, Island Press, Washington, DC, 2013.

[a] Mean values of sites with annual and infrequent fire regimes.

Across the southeastern Coastal Plain, large species pools occur not only within individual sites, but they also contribute to a highly diverse regional species pool (Peet 2006). Based on region-wide comparisons of vegetation, Peet et al. (2014) describe a latitudinal increase in plant species richness from the Carolinas southward to the Florida Panhandle—a trend that is particularly apparent in subxeric and sandhill communities. They attributed this trend to a longer growing season and higher average mean temperature of more southerly areas, as well as the biogeographic history of the East Gulf Coastal Plain, which served as species refugia during periods of glaciation (Palmquist et al. 2014; Peet et al. 2014). Further, Carr et al. (2009) described a decrease in species richness of pine woodlands from the Florida Panhandle into Peninsular Florida despite similar soil moisture and fertility conditions. This pattern was probably caused by different biogeographic histories related to the timing of sediment deposition and sea level fluctuations and their effects on species pools (Myers 1990; Carr et al. 2009).

PURPOSE AND ORGANIZATION OF THIS CHAPTER

Understanding the complex feedback mechanisms that create and maintain species diversity within the longleaf pine ecosystem is foundational to guiding conservation strategies for promoting biodiversity, particularly those strategies that guide reassembly and recovery processes during restoration of such species-rich communities. In this chapter we summarize the mechanisms that maintain high plant species diversity in the system; we review the ecological theories that seek to explain community assembly and patterns of diversity at different spatial scales in species-rich plant communities; and we examine the empirical evidence addressing these theories. In particular, we focus on field experiments where ecological processes have been manipulated in ways that help identify how plant community assembly occurs in natural or restored longleaf pine sites. Finally, we summarize what is known and not known about community assembly and diversity, and identify research gaps that would help to inform restoration approaches.

THEORETICAL FRAMEWORK FOR UNDERSTANDING COMMUNITY ASSEMBLY AND SPECIES DIVERSITY IN SPECIES-RICH COMMUNITIES

THE CONTINUUM FROM NICHE-ASSEMBLY TO DISPERSAL-ASSEMBLY THEORIES

Patterns of diversity reflect the interplay of processes at local and regional scales (Ricklefs 1987; Harrison and Cornell 2008). At local scales, the interactions among species and the responses of species to environmental conditions underlie classical coexistence and diversity models (Connell 1978; Tilman and Pacala 1993), which have been built upon extensively since their inception (Chesson 2000; Chase and Leibold 2003; Adler et al. 2007). Under this paradigm, species diversity patterns predominantly reflect a deterministic outcome of species responses to environmental conditions and species interactions, including interspecific competition, predation, and facilitation. In contrast, regional perspectives on community assembly emphasize the importance of the available species pool in determining the diversity of local communities (MacArthur and Wilson 1967; Ricklefs 1987). Under this perspective, patterns of local diversity are primarily determined by the size of the regional species pool, the colonization history, and the rate of immigration into communities. The processes that influence the size of this pool include those that operate at broader spatial and temporal scales, such as climate, dispersal, speciation, and extinction (Ricklefs 1987; Palmquist et al. 2014), as well as processes that operate at finer scales within and among local communities (Mittelbach and Schemske 2015).

Local- and regional-scale perspectives on community assembly can be organized along a continuum bounded at one extreme by niche-assembly theory and at the other extreme by dispersal-assembly theory (Hubbell 2001; Bell 2005; Gravel et al. 2006) (Figure 5.1), each embodying a large

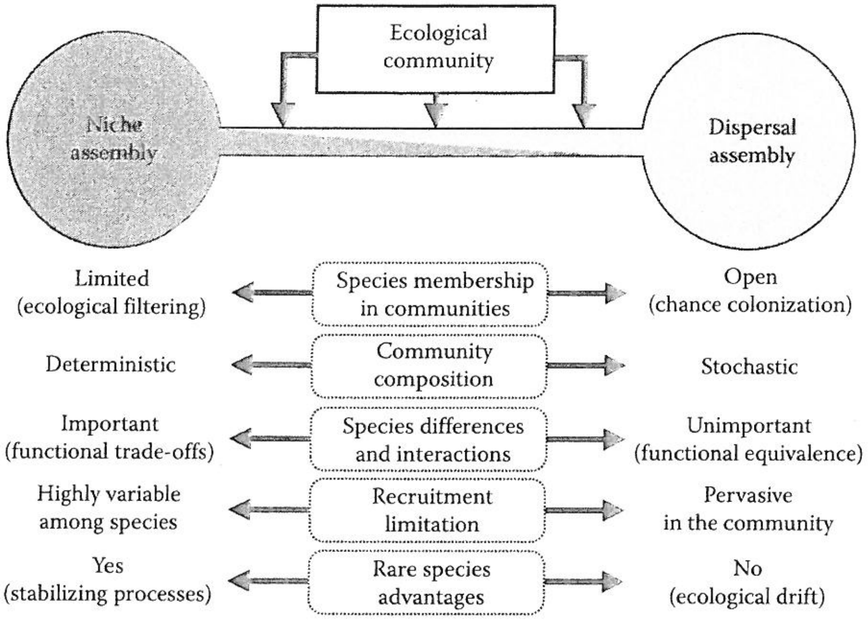


FIGURE 5.1 Schematic illustrating that community-assembly theory can be organized along a continuum, bounded at one end by niche-assembly theory and at the other end by dispersal-assembly theory. Deterministic community composition refers to membership in local communities that is nonrandom with respect to species identity, whereas stochastic community composition refers to species membership that is a random assemblage. An ecological community can be envisaged as falling anywhere along this continuum in space or time, depending on the presence and relative importance of mechanisms involved in community assembly. Note that not all of these mechanisms need to operate simultaneously at any given point on the continuum. (From Myers, J.A. 2010. Ecological assembly of high-diversity plant communities: dispersal, competition, and environmental filtering in longleaf pine savannas, PhD Dissertation. Louisiana State University, Baton Rouge, Louisiana.)

family of more detailed models and hypotheses (Chase and Leibold 2003; McGill et al. 2006; Chase and Myers 2011). These theories provide general—but contrasting—predictions about the principal mechanisms that control community assembly. Here, we focus on predictions based on these theories regarding local species richness (α-diversity) and spatial variation in community composition (β-diversity) (Anderson et al. 2011).

PATTERNS OF SPECIES DIVERSITY IN DISPERSAL- AND NICHE-ASSEMBLED COMMUNITIES

According to dispersal-assembly theory, which was popularized in large part by Hubbell (2001), chance colonization, rates of immigration from the species pool, pervasive recruitment limitation, and/or stochastic births and deaths are the primary ecological mechanisms that influence community assembly (MacArthur and Wilson 1967; Sale 1977; van der Maarel and Sykes 1993; Hubbell 2001; Bell 2005). Hubbell's Unified Neutral Theory of Biodiversity and Biogeography (2001) represents an extreme version of the dispersal-assembly perspective because it assumes that all species within guilds are equivalent with respect to per capita rates of birth, death, and colonization; thus their abundances change randomly through time (ecological drift). Accordingly, local diversity is controlled by the size of the species pool (or metacommunity), the rate of immigration, and the degree of dispersal limitation within local communities.

Dispersal-assembly theory makes at least three predictions about species richness and variations in community composition across sites. First, local communities should have relatively "open-membership" assemblages—meaning that they are open to invasion by most if not all species in the regional species pool. Consequently, species richness should be positively related to the rate of immigration (dispersal) from the species pool (Chase et al. 2005). Second, the theory predicts that local communities with similar environmental conditions should have dissimilar species compositions (high β-diversity), reflecting dispersal limitation, historical contingencies resulting from variation in the arrival order of species into communities (priority effects), or stochastic colonization (Chase 2003; Fukami 2015). Third, in the extreme case of neutral models, where all individuals are assumed to be ecologically equivalent, β-diversity should not change systematically along environmental gradients (Chase and Myers 2011).

Niche-assembly theory, in contrast, proposes that membership in local communities is controlled by biotic and abiotic conditions that deterministically limit local species membership (Chesson 2000; Chase and Leibold 2003; Chase and Myers 2011) (Figure 5.1). In this case, local diversity is determined by species tolerances to local environmental conditions and the outcome of local interactions among species (Keddy 1992; Diaz et al. 1998). This theory makes at least three general predictions. First, local communities should be "limited-membership" assemblages in which α-diversity either saturates or declines as the rate of immigration increases. A decline in α-diversity is predicted when immigration introduces dominant competitors or predators into local communities (Mouquet and Loreau 2003), or when abiotic conditions impose environmental filters on species traits (Weiher et al. 2011). Second, local communities with similar environmental conditions are predicted to have similar species composition (low β-diversity) owing to deterministic filtering of the species pool (Chase 2003; Chase and Myers 2011). Third, β-diversity should change systematically along environmental gradients (Chase and Myers 2011).

Recruitment limitation is a key ingredient in both niche- and dispersal-assembly theory, but its mechanistic role differs between the two theories. Recruitment limitation can result from both the failure of propagules to arrive (for example, "seed limitation") and unsuitable conditions for establishment ("microsite limitation") (Nathan and Muller-Landau 2000). Seed limitation can be further decomposed into "dispersal limitation" and "source" or "fecundity limitation" (Clark et al. 1998). In dispersal-assembly theory, recruitment limitation is often assumed to be pervasive within communities. A fundamental consequence of community-wide recruitment limitation is the establishment of inferior competitors in sites where dominant competitors have failed to colonize, thereby reducing the rate of competitive exclusion (Hurtt and Pacala 1995). In niche-assembly models, recruitment limitation is often nonrandom with respect to species identity (deterministic). A classic example is the competition-colonization trade-off model, whereby populations of competitively dominant species have lower dispersal than populations of less competitive species (Tilman 1994). Evidence of recruitment limitation alone therefore cannot be used to disentangle the relative importance of niche-assembly and dispersal-assembly mechanisms (Adler et al. 2007; Clark 2009; Vellend et al. 2014), but evidence for recruitment limitation leaves open the possibility that both deterministic and stochastic processes contribute to community structure.

The relative roles of dispersal-assembly mechanisms and niche-assembly mechanisms are hypothesized to vary across disturbance and productivity gradients. Species pools are thought to be most important in limiting colonization and species richness in relatively unproductive habitats where competitive exclusion is slow and recruitment microsites are abundant (Grime 1979; Huston 1979, 2014; Huston and DeAngelis 1994; Pärtel et al. 2000; Zobel et al. 2000). However, on sites with higher productivity, competition can become more important in limiting establishment and species richness, regardless of the size of the species pool (Huston 1979; Foster 2001). Frequent fires and other disturbances can decrease species richness by increasing environmental filtering from the species pool (Pausas and Verdú 2008) or by causing stochastic local extinctions (Myers et al. 2015), but they can also increase species richness by decreasing interspecific competition (Burkle et al. 2015). The effect of disturbance on species richness can also vary with productivity (Huston 1979, 2014; Foster 2001). For example, disturbance can increase species richness in productive habitats by decreasing competition, but can also decrease species richness in unproductive habitats where low resource availability decreases birth rates or increases mortality. Interactions between disturbance and productivity can also scale up to influence patterns of β-diversity among communities (Burkle et al. 2015).

High-diversity plant communities have served a prominent role in theoretical and empirical studies of dispersal and niche assembly. Dispersal assembly is hypothesized to play a particularly important role in high-diversity communities that have many rare species and a large potential species pool. Rarity can contribute to dispersal assembly by increasing demographic fluctuations (Barot 2004); limiting pairwise species interactions, resulting in more diffuse competition (Grubb 1986; Hubbell and Foster 1986; Myers and Harms 2009b); and increasing recruitment limitation, thereby reducing the rate of deterministic competitive exclusion (Hurtt and Pacala 1995). Communities assembled from a large species pool are more likely to have higher variation in community composition (higher β-diversity) than communities assembled from a small species pool simply because of a greater probability of random sampling effects (Kraft et al. 2011; Myers et al. 2013) or a stronger influence of immigration history on community composition (Chase 2003).

EVIDENCE OF COMMUNITY ASSEMBLY MECHANISMS IN THE LONGLEAF PINE ECOSYSTEM

Early botanical descriptions as well as recent empirical studies suggest that three pervasive niche-based factors influence community assembly in the longleaf pine ecosystem: fire, soil moisture, and soil texture (as it controls soil fertility). Historical records describing fire effects on southeastern vegetation in regard to the origin of prairies and scrub barrens date back as early as the 1600s and later in the 1700s. Several references to the longleaf pine forest as a fire-maintained vegetation type were chronicled in the 1800s (Garren 1943, and references therein). Subsequent botanists and ecologists described the prevalence of fire in longleaf pine forests and the encroachment of hardwoods in the absence of fire (Harper 1914; Wells 1928; Wells and Shunk 1928; Chapman 1932; Heyward 1939). Others addressed the effects of soil texture and moisture on dominance patterns in longleaf pine and slash pine (*P. elliottii*) woodlands (Harper 1907, 1914, 1943; Gano 1917; Wells and Shunk 1928, 1931; Garren 1943). Although these studies clearly showed that fire is a structuring agent of native vegetation, they were met by considerable scientific opposition based on a perception of fire as a detrimental process that thwarts natural successional processes (Garren 1943; Vogl 1979).

Few studies in the early to mid-1900s specifically focused on the effects of fire on ground cover vegetation or species richness; rather, most studies of fire and pineland vegetation concentrated on the influence of fire on conifer growth, forage yield, or wildlife management (Greene 1935; Stoddard 1935; Wahlenberg et al. 1939). One study, which compared burned sites to unburned sites, identified a greater abundance and richness of legumes in burned sites (Lemon 1949). Although not specifically addressing species richness, later studies found that more species were present in the ground cover of longleaf pine stands when the time-since-fire decreased, and that groups of ground cover species (referred to as "fire followers") increased in abundance or productivity after fire (Lemon 1967). Vogl (1973) described the exceptionally high species richness of longleaf pine grasslands compared to other North American grasslands, and in a fire-exclusion study, reported that the absence of fire resulted in decreased abundance of grasses.

EVIDENCE FOR NICHE-ASSEMBLY MECHANISMS

Fire and Environmental Conditions

Walker and Peet (1983) conducted one of the first studies on how species richness responds to fire frequency and soil moisture in longleaf pine communities. They sampled ground cover composition in 21 island-like grass-dominated sites that occurred on mineral soils within a peatland swamp matrix; the canopy ranged from treeless to 150 stems/ha, and site moisture conditions ranged from well-drained longleaf pine-dominated ridges to poorly drained depressions that were not dominated by longleaf pine-wiregrass (*Aristida stricta*). They reported the highest species richness observed in North American plant communities at fine scales (42 species/0.25 m^2, and 84 species/625 m^2). Species richness was highest in frequently burned sites that were near the middle of the soil moisture gradient. They attributed mechanisms of species co-occurrence to the elimination of woody competition and litter by fire and to phenological differences in biomass production by small- and large-stature species. Although their study gradient was not necessarily restricted to longleaf pine-wiregrass-dominated sites and captured a relatively small range of environmental conditions across the distribution of the longleaf pine ecosystem, they described strong variation in community composition across the environmental gradient. They suggested that the influence of fire is less pronounced at the extremes of the moisture gradient, where vegetation was sparser, presumably because the potential for competitive exclusion was lower.

Results consistent with these observations also indicated that environmental conditions interact with fire frequency to influence species richness. For example, compared to burned sites, flatwood sites that had been fire excluded for four decades had lower herbaceous species richness and higher hardwood abundance (Brockway and Lewis 1997). Evidence from several studies in longleaf pine stands indicated that fine-scale changes in environmental conditions along topographic gradients can contribute to changes in species richness, particularly when the changes are coupled with fire (Platt 1999; Glitzenstein et al. 2003; Carr et al. 2009; Palmquist et al. 2015; Kirkman et al. 2016). Glitzenstein et al. (2003) reported that species richness increased with decreasing fire intervals in wet-mesic sites occurring on Ultisols, as well as in longleaf pine flatwoods occurring on Spodosols. In flatwoods, the increase in species richness with greater fire frequency occurred only at finer scales. Also, a decline in species richness at fine scales was reported across a soil moisture gradient in a decade-long fire-exclusion experiment (Kirkman et al. 2016), as well as in longleaf pine sites that had experienced only a modest reduction in fire frequency (Palmquist et al. 2014). Collectively, these examples highlight the roles of fire history, current fire regimes, and various topographic conditions in maintaining species richness at multiple scales (Kirkman, Goebel, et al. 2004; Peet et al. 2014; Palmquist et al. 2015; Kirkman et al. 2016).

The effects of frequent fire on species richness are linked to alterations in forest structure that promote light penetration to the ground cover. Regardless of soil moisture, when the fire-return interval is lengthened, a midstory of fire-sensitive hardwoods will become rapidly established (Garren 1943; Monk 1968; Veno 1976; Myers 1990; Waldrop et al. 1992; Brockway and Lewis 1997; Haywood 2007; Kirkman et al. 2016). The buildup of leaf litter (herbaceous and hardwood) is also associated with fire exclusion, as is the consequent development of organic soil horizons (Varner et al. 2005; Hiers et al. 2007).

Although both conditions likely contribute to the suppression of ground cover diversity, the relative role of litter buildup versus shading from the midstory appears to depend on site conditions. Hiers et al. (2007) provide evidence that the influence of midstory encroachment on ground cover in xeric sites can differ fundamentally from more mesic sites because of differences in site productivity that govern the degree or rate of canopy closure. In sandhill sites with varying frequency of prescribed fires, they used structural equation modeling to examine the role of forest-floor conditions on species composition and found that forest-floor development (accumulations of litter, duff, and organic horizon development) was positively correlated with reduced fire frequency and was the primary factor explaining decreased richness of functional groups of ground cover species. In contrast, midstory density explained relatively little variation in richness (Hiers et al. 2007). Given that most ground cover species in the longleaf pine ecosystem are perennials that thrive in sunlight and resprout after fire, they suggested that the shade that is produced by litter reduces plant vigor and will inhibit species recovery if fire exclusion continues (see Chapter 6).

Additional supporting evidence came from an examination of ground cover richness in hardwood-encroached sandhill sites after the reintroduction of frequent fire with and without the removal of midstory oaks (Provencher, Herring, et al. 2001). With frequent prescribed burning for 15 years after midstory oak removal, species richness did not differ between the control and the treatment plots (Kirkman et al. 2013). Using structural equation modeling, Veldman et al. (2014)

similarly demonstrated that in extremely xeric sites frequent fire influences ground cover richness primarily by reducing the litter and duff depth, independent of tree abundance.

The fire-frequency interval that results in the highest ground cover species richness appears to vary with site fertility and production of fuels that can carry fire. In a long-term fire-frequency study conducted in mesic to subxeric sites, the highest level of species richness was associated with prescribed fires every 1–3 years (Glitzenstein et al. 2012). Further, no evidence of a decline in ground cover species richness due to overly frequent fire was observed, a finding that has been reported for other fire-influenced savanna and woodland systems (Glitzenstein et al. 2012, and references therein). Glitzenstein et al. (2012) attributed this phenomenon to the unique combination of characteristics of the longleaf pine ecosystem: an evolutionary history of very frequent low-intensity fire, the abundance of perennial herbaceous species that are adapted to survive and resprout after frequent fires, sufficiently productive climate and soil conditions to facilitate the competitive exclusion of fire-adapted species by fire-intolerant species during longer intervals between fires, and the absence of enhanced competitiveness of dominant C_4 grasses when frequently burned.

Soil moisture was the most important factor correlated with ground cover richness based on a large data set of fire-maintained forests and woodlands in the Southeast, regardless of scale (Carr et al. 2009; Peet et al. 2014). Other important factors included soil texture and cation availability. Across a natural edaphic gradient in frequently burned longleaf pine-wiregrass sites, Kirkman et al. (2001) examined the relationship of species richness to productivity as a function of nitrogen mineralization rates and soil moisture. Using the depth to the clayey layer and soil drainage classes, they sorted the sites into xeric, mesic, and wet-mesic conditions along the gradient. Their results showed that highest biomass and highest species richness occurred at the wet-mesic sites and that nitrogen availability was inversely correlated with richness and productivity; hence, percent soil moisture was found to be an important regulator of species richness and community production within the defined gradient of the study.

Competition

Many researchers have suggested that competition from bunchgrasses plays an important role in determining variation in species richness (Walker and Peet 1983; Keddy et al. 2006; Noss 2013; Peet et al. 2014); the assertion being that competitive effects of bunchgrasses are especially important in productive habitats, assuming that size asymmetries among species increase as productivity levels increase. However, little evidence exists to support a negative or unimodal relationship between increased ground cover productivity and species richness within frequently burned longleaf pine ecosystems. Instead, Kirkman et al. (2001) found that the proportional dominance of the ground cover by wiregrass persisted across a productivity and moisture gradient and that the relative abundance of wiregrass was not correlated with species richness. The monotonic relationship of species richness and productivity that they reported indicated that with frequent fire, competitive exclusion by wiregrass does not mechanistically structure variation in species richness along the environmental gradient—and they suggested that the growth form of wiregrass was perhaps a factor. The wiregrass growth form, which is nonrhizomatous (a perennial bunchgrass), results in distinct interstitial spacing between grass clumps. Across this gradient, water was likely a limiting resource to productivity, and stress due to water limitation was a major factor in seedling establishment in sandy soils (Kirkman et al. 2001).

Results from two experimental studies also support the idea that competition from dominant bunchgrasses has little influence on species richness in frequently burned communities. Roth et al. (2008) found that removal of bluestem (*Andropogon* spp.) in both wet and dry sites had no effect on local species richness 2 years after removal. At the same study site, Myers and Harms (2009a) also found no effect when slender bluestem (*Schizachyrium tenerum*) was removed, except at small neighborhood scales (0.1 m^2); they also found no effect on species rank-abundance distributions (Myers and Harms 2009a) or β-diversity (Myers, unpublished data). In contrast, they found a positive effect on species richness, but no effect on species rank-abundance distributions or β-diversity, when gallberry (*Ilex glabra*), a dominant clonal shrub, was removed. They suggested that their results were inconsistent with "peripheral-species" or "fugitive-species" concepts (Horn and MacArthur 1972; Keddy et al. 2006) in which local diversity is considered to reflect the escape of rare, small-stature species from dominant large-stature species in space or time. Further, other studies (Kirkman et al. 2001; Clark et al. 2008) suggest that the co-occurrence of a large number of infrequently occurring species may reflect the ability of small grasses and rosette-forming forbs to tolerate frequent fire and to survive between or under the dense canopy of larger grasses during the transient fire-free period (Walker and Peet 1983; Myers and Harms 2009a; Glitzenstein et al. 2012).

A niche-related factor that influences many legumes is the characteristically nitrogen-poor soils in this ecosystem, a condition exacerbated by frequent fire and volatilization of nitrogen with combustion (Wilson et al. 1999, 2002). In a nitrogen-enrichment study, Kirkman et al. (2016) found that legume richness decreased with the addition of nitrogen. They suggested that this was not necessarily a shift from belowground competition for nutrients to aboveground competition for light, but perhaps the response of legumes to the altered nitrogen-to-phosphorus ratio in the soil. In contrast to other plants, nitrogen-fixing legumes have a higher demand for phosphorus (Dixon and Wheeler 1983), meaning that they cannot compete effectively for very low levels of phosphorus when nitrogen ceases to be the most limiting resource.

EVIDENCE FOR DISPERSAL-ASSEMBLY MECHANISMS

Myers and Harms (2009a, 2011) proposed that the characteristically high number of rare species in longleaf pine ecosystems has important implications for community assembly processes. Rarity increases the importance of demographic stochasticity because it increases the probability of local extinctions. In individual species, rarity also limits the degree of interspecific interactions, such as competition, in turn diminishing the degree that assemblages are shaped by deterministic interactions. Furthermore, populations of rare species are likely to be recruitment limited through reduced dispersal and fecundity (Barot 2004).

Several lines of evidence support the hypothesis that dispersal assembly plays an important role in longleaf pine communities. In one ground cover study, Kirkman, Coffey, et al. (2004) examined the recovery of species richness from prior soil disturbance in a 64-year-old slash pine plantation that was located within close proximity to natural longleaf pine reference sites. They found high floristic overlap between reference and recovery sites. Additionally, similar species richness occurred at broader scales ($\geq 10\ m^2$), indicating that substantial passive vegetation recovery (recovery without active reintroduction of species) had occurred. However, at finer scales, species richness was lower in the recovery site; this suggests that co-occurrence of a high number of species depends on local dispersal and that establishment at fine scales will likely take longer. They also observed that species with low dispersal potential (such as those that depend on gravity and ants) had a lower probability of occurrence than would be expected after 64 years relative to other species, even though source populations were present in the nearby longleaf pine-wiregrass communities (Kirkman, Coffey, et al. 2004). Collectively, these results suggest that dispersal limitation constrains establishment.

Similar correlative evidence suggesting dispersal and establishment limitation was provided in a comparison of paired plots from remnant longleaf pine sites and agricultural sites that had been abandoned in the mid-1900s (Brudvig et al. 2013; Grman et al. 2015). A broad-scale replicated experiment (Brudvig et al. 2009; Damschen and Brudvig 2012) demonstrated that landscape corridors between patches promoted species richness of animal-dispersed plants (including some native longleaf pine-associated species) compared to isolated patches; species richness of wind-dispersed plants increased in response to changes in patch shape created by corridors with higher edge-to-interior ratios (see Chapter 11).

Seed-addition experiments also have demonstrated that species richness is strongly limited by seed arrival from the species pool (Myers and Harms 2009a, b, 2011). Introducing seed of 38 ground cover species to experimental plots with and without two dominant functional groups (bunchgrasses and shrubs) increased species richness on all plots (Myers and Harms 2009a), and decreased β-diversity in shrub-dominated patches (Catano et al. 2017), indicating that high rates of immigration can homogenize community composition in the ground cover. In a companion experiment, Myers and Harms (2011) also found that seed addition of 31 ground cover species increased species richness irrespective of local fire intensity and soil moisture manipulations.

POTENTIAL FOR INTERPLAY BETWEEN NICHE AND DISPERSAL PROCESSES

Experimental studies also indicate that dispersal-assembly processes interact with multiple niche-based processes to structure biodiversity in the ground cover. In particular, the effects of dispersal on community assembly are strongly influenced by two environmental filters—soil resource availability and fire intensity—through space and time (Table 5.2).

Soil Resource Availability and Dispersal

As an initial study within a long-term factorial experiment that included an examination of ground cover responses to resource manipulations (addition of water and nitrogen) across a soil moisture/texture gradient, Iacona et al. (2010) found that the mean number of species naturally recruited was increased by irrigation regardless of the soil moisture conditions of the site. In this short-term study, nitrogen addition did not affect species richness. To determine if establishment is limited by seed supply, Iacona et al. (2010) manipulated seed-addition densities of three species in subxeric and wet-mesic longleaf pine-wiregrass sites with and without water and nitrogen addition. Seedling recruitment increased at the mesic site but not at the subxeric site without additional water. They also found no differences in species richness or seedling density from seed rain samples (germinated in a greenhouse), suggesting that the local seed pools were similar in species richness (but not necessarily in species composition). Although seed limitation was observed across the naturally occurring moisture gradient, its relative importance to establishment depended on moisture availability. Together, these results suggest that water availability is an important driver of species richness in seedling recruits, which could explain the notably high levels of species richness that are observed at the mesic end of the naturally occurring moisture gradient (Figure 5.2). In subxeric sites, environmental conditions at recruitment microsites are rarely optimum for regeneration; at more mesic sites, a higher level of environmental variation (amplitude, frequency, or both) over time and space is more likely to result in optimum regeneration conditions. Seed limitation provides an upper bound on potential recruitment at both ends of the spectrum, but microsite limitation is the primary regulator of recruitment at the subxeric end.

Similarly, Myers and Harms (2011) found that soil moisture altered the relative importance of seed arrival in community assembly in a study that manipulated soil moisture (drought, water addition) and seed arrival (seed addition) of 31 ground cover species. Seed arrival had a weaker positive effect on total species richness in local communities with either drought or irrigation compared to control communities with natural soil moisture, further suggesting that spatial variation in soil moisture or temporal variation in rainfall interacts with dispersal to influence species richness. In contrast, local densities of individual seed-addition species were reduced under experimental drought conditions, but increased by watering. Despite these interactions, enhanced seed arrival increased total species richness regardless of soil moisture, suggesting that species-rich ground cover communities constitute relatively open-membership assemblages.

In contrast, in a 10-year irrigation experiment replicated across a natural soil moisture gradient in wiregrass-dominated communities, Kirkman et al. (2016) found that irrigation increased species richness as well as aboveground net primary production in subxeric sites. Irrigation had no influence on productivity in the mesic site, but increased species richness both for woody ground cover plants in mesic and subxeric sites and for legumes and forbs at the subxeric sites.

TABLE 5.2
Experimental Studies Conducted in Georgia and Louisiana That Tested the Influence of Niche-Assembly or Dispersal-Assembly Mechanisms on Species Richness in Longleaf Pine Ecosystems

		Experimental Manipulations			
Habitat	**Location**	**Niche Assembly**	**Dispersal Assembly**	**Effects on Species Diversity**	**References**
Subxeric uplands	Georgia	Nitrogen addition, water addition	Seed addition	No effect of nitrogen addition on species richness; positive effect of water on species richness; positive effect of seed addition plus water on recruitment	Iacona et al. (2010)
Mesic uplands	Georgia	Nitrogen addition, water addition	Seed addition	No effect of nitrogen addition on species richness; positive effect of water addition on species richness; positive effect of seed addition on recruitment	Iacona et al. (2010)
	Louisiana	Competition from dominant bunchgrasses[a]	None	No effect on species richness	Roth et al. (2008)
		Competition from dominant bunchgrasses[a]	Seed addition	No effect of competition on species richness, community composition, or species evenness; positive effect of seed addition on species richness but no effect of seed addition on β-diversity; no effect or weak interactive effects of competition and seed addition on species richness or β-diversity	Myers and Harms (2009a), J. Myers (unpublished data)
		Competition from dominant shrubs	Seed addition	Negative effect of competition on species richness; no effect of competition on β-diversity or species evenness; positive effect of seed addition on species richness; negative effect of seed addition on β-diversity; no interactive effects of competition and seed addition on species richness or β-diversity	Myers and Harms (2009a), J. Myers (unpublished data)
		Fuel addition (fire intensity)	Seed addition	Negative effect of fuel addition on species richness; no effect or weak negative effect of fuel addition on β-diversity[b]; positive effect of seed addition on speciesrichness; negative effect of seed addition on β-diversity; interactive effects of fuel addition and seed addition on species richness or β-diversity	Myers and Harms (2011), J. Myers (unpublished data)
		Water addition, water removal	Seed addition	Variable effects of water on species richness and community composition; positive effect of seed addition on species richness; interactive effects of water and seed addition on species richness	Myers and Harms (2011)
	Georgia	Facilitation by dominant bunchgrass[a]	Shading, seed addition	No facilitative effect of shading on recruitment	Iacona et al. (2012)

(Continued)

TABLE 5.2 (*Continued*)

Experimental Studies Conducted in Georgia and Louisiana That Tested the Influence of Niche-Assembly or Dispersal-Assembly Mechanisms on Species Richness in Longleaf Pine Ecosystems

		Experimental Manipulations			
Habitat	**Location**	**Niche Assembly**	**Dispersal Assembly**	**Effects on Species Diversity**	**References**
Subxeric uplands	Georgia	Facilitation by dominant bunchgrass[a]	Shading, seed addition	No facilitative effect of shading on recruitment	Iacona et al. (2012)
		Nitrogen addition, water addition, burn exclusion	None	Negative effect of nitrogen addition on species richness; positive effect of water addition on species richness; negative effect of fire exclusion on species richness	Kirkman et al. (2016)
Mesic uplands	Georgia	Nitrogen addition, water addition, prescribed fire	None	Negative effect of nitrogen addition on species richness; no effect of water addition on species richness; negative effect of fire exclusion on species richness	Kirkman et al. (2016)

Studies were conducted at the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia or at Camp Whispering Pines in southeastern Louisiana.

[a] Dominant bunchgrasses: broomsedge bluestem (Roth et al. 2008), slender bluestem (Myers and Harms 2011), and wiregrass (Iacona et al. 2012).

[b] No effect on β-diversity of all species; weak negative effect on β-diversity for seed-addition species.

Although these studies suggest that low soil moisture limits establishment and growth of ground cover species, their conclusions about the effects of irrigation on species richness were inconsistent. These differences could reflect a shift in the relative importance of different environmental filters among sites that vary in soils, water-holding capacity, or the composition of dominant functional groups (such as bunchgrasses). In addition, the contrasting effects of abiotic filters at different life-history stages (such as seed germination, seedling establishment, or adult performance) could, in part, explain some of the differences in results (Kirkman et al. 2016).

Spatial Heterogeneity in Fires and Interactions with Dispersal

Processes occurring at fine spatial scales, such as spatial heterogeneity in fire, influence patterns of community assembly (Thaxton and Platt 2006; Myers and Harms 2011; Gagnon et al. 2012; Wiggers et al. 2013, 2017). In burned landscapes, fine-scale fuel heterogeneity alters fire characteristics (see Chapter 6), which in turn can affect the availability of recruitment microsites, growth and survival of individual plants, and patterns of species composition and diversity (Thaxton and Platt 2006; Hiers et al. 2009; Wenk et al. 2011; Gagnon et al. 2012, 2015; Ellair and Platt 2013; Wiggers et al. 2013, 2017; O'Brien, Loudermilk, Hiers, et al. 2016).

Gagnon et al. (2012) reported differing responses (mortality and tussock size reduction) of two dominant bunchgrasses to fine-scale variation in fuel loads. In a later study, Gagnon et al. (2015) found that an increase in fuel loads resulted in greater duration of fire and soil heating, which in turn substantially reduced vegetation through mortality, damage to belowground perennating organs, and by reducing recruitment from the soil seed bank. They suggested that the localized short-term suppression of vegetation resulting from increased fuels provides episodic opportunities for recruitment. Additional evidence of the effects of fire heterogeneity was provided by Wiggers et al.

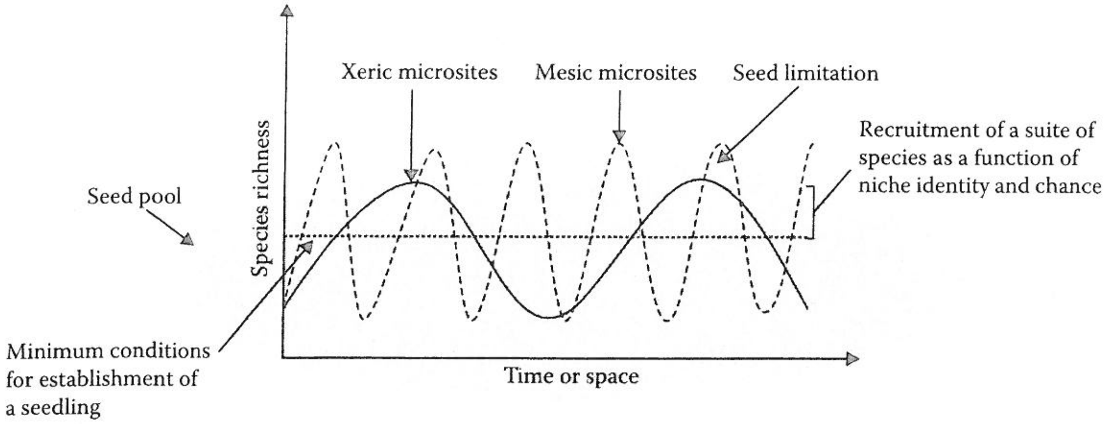


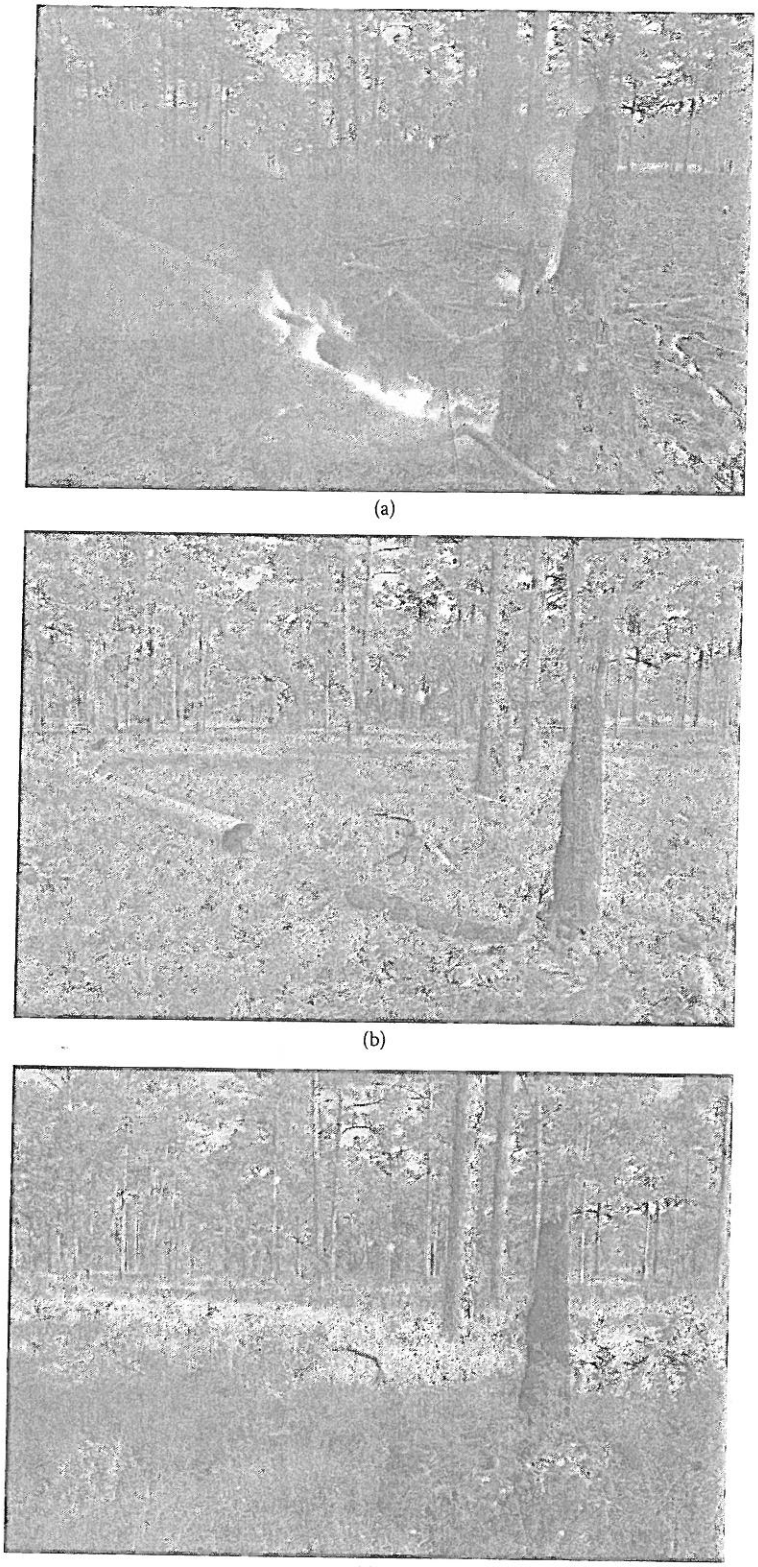
FIGURE 5.2 Conceptual model illustrating episodic recruitment depending on soil water availability. At xeric sites, environmental conditions at recruitment microsites are rarely optimum for regeneration; whereas, at more mesic sites, a higher amplitude and frequency of environmental variation over time and space could result in optimum regeneration conditions more commonly. At both locations, seed limitation provides an upper bound on potential recruitment, but at the xeric location, microsite limitation is the primary regulator of recruitment. (Modified from Iacona, G.D. 2008. Seedling recruitment as a driver of species richness in the understory of the longleaf pine savanna, M.S. thesis. University of Florida, Gainesville, Florida.)

(2013), who found that legume seed mortality increased in the vicinity of smoldering pine cones, but was not affected by increased pine needle fuel loads. They concluded that the prolonged duration of burning associated with coarse woody debris results in death of most seed or bud banks, but temperatures fall into a range that is favorable for germination of hard-coated seeds as depth and lateral distance from a pine cone increases (Wiggers et al. 2013, 2017). Moreover, Hiers et al. (2009) concluded that pine cones and other long-burning fuels are not distributed uniformly throughout longleaf pine stands (see Chapter 6), suggesting that recruitment into open microsites created by the combustion of these fuels exhibits similarly heterogeneous distribution, thus influencing fine-scale patterns of species distributions (Figure 5.3).

Myers and Harms (2011) suggested that local variation in fires may alter the relative importance of dispersal assembly. In a factorial field experiment that combined manipulations of fine fuel (addition of longleaf pine needles) and seed arrival (seed addition) of 31 ground cover species following burning, they found that postfire seed arrival had a stronger positive effect on species richness in local communities that burned under augmented fuel loads compared to those burned under control fuel loads. This finding suggests that fine-scale variation in fuel loads and fire intensity interacts with seed dispersal to create local variation in species richness. They also found a synergistic effect of seed arrival and local fire intensity on β-diversity, where composition was more similar among disturbed communities with high seed arrival compared to disturbed communities with low seed arrival (Catano et al. 2017). Collectively, these results suggest that fine-scale variation in fire intensity creates a mosaic of open microsites that promote the establishment of immigrating species—even within frequently burned landscapes.

SUMMARY

The maintenance of extraordinary numbers of ground cover species in the longleaf pine ecosystem appears to be mediated through a continuum of dispersal-related and environmental filtering factors. Collectively, these factors represent a unique complex of multivariate processes that regulate species richness in longleaf pine woodlands and forests. However, the interplay of various community-assembly processes as they occur at different spatial scales and how they are influenced by temporally fluctuating environmental conditions is largely unknown.



(a)

(b)

(c)

FIGURE 5.3 Fine-scale environmental heterogeneity from smoldering of coarse woody debris in which the prolonged duration of burning creates heterogeneity in the survival of regenerating plants and recruitment niche: (a) Flaming and smoldering snag, (b) a barren scar 6 weeks postfire, (c) recruitment of vegetation (resprout and germination) in the burn scar 6 months postfire. (Photographs courtesy of Richard T. Bryant.)

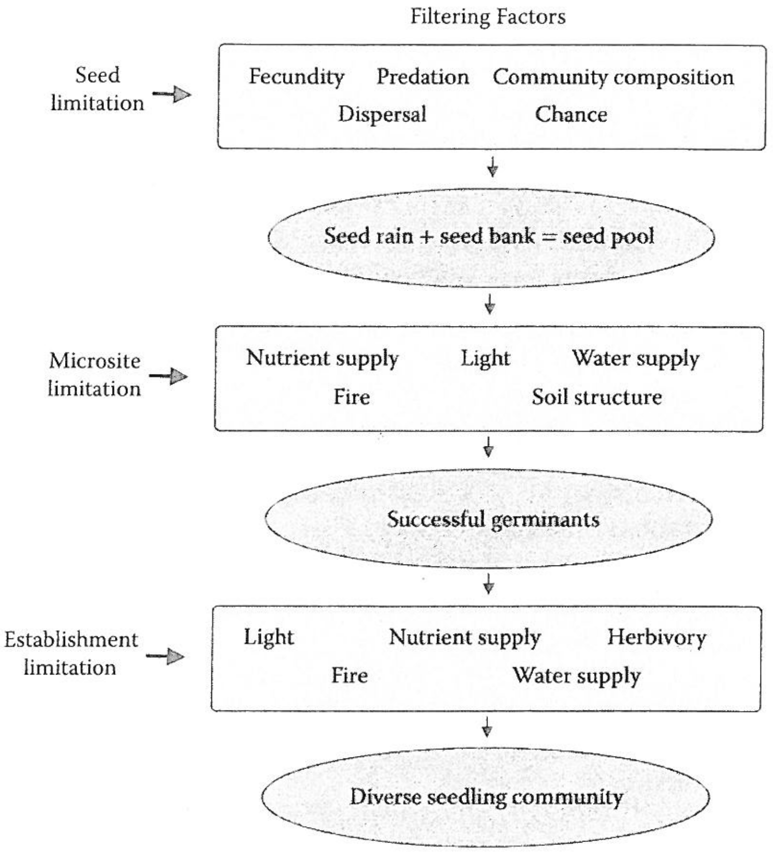


FIGURE 5.4 Conceptual model of seed availability and environmental filtering processes that regulate species richness in a frequently burned longleaf pine ecosystem.

The biogeographic and evolutionary processes that are associated with a history of frequent, low-intensity fires have resulted in large local and regional species pools, each composed of species with adaptations to survive burning and to resprout. This large species pool serves as a lottery-based seed supply that is sorted by various environmental filters imposed by regional habitats and gradients (Figure 5.4). Importantly, a key integrating mechanism that perpetuates high species richness of the longleaf pine ecosystem is an assemblage of dominant grasses that lack the trait of increased competitiveness with frequent fires or with increased resources in most sandy Coastal Plain soils. The abundance of species in frequently burned natural longleaf pine ecosystems at all scales, coupled with the infrequent occurrence of most species, suggests a strong influence of recruitment limitation at multiple levels including dispersal limitation, microsite limitation, and establishment limitation. The relative importance of these factors in regulating community assemblage across soil types has been addressed by only a few studies. At the local level, dispersal is coupled with the episodic availability of appropriate recruitment microsites. Although seed supply may be limited to some degree by dispersal, in some localities soil moisture availability is of paramount importance to species establishment. Interwoven with recruitment microsite availability and establishment is stochasticity associated with mortality of seeds and seedlings that results from fine-scale heterogeneity of fire behavior and intensity. Moreover, local-scale neighborhood interactions among individual plants associated with episodic availability of recruitment sites and seed arrival via seed rain or soil seed bank recruitment and the role of predation remain unexplored in most community types.

Finally, several gaps in empirical studies limit our understanding of diversity-maintenance mechanisms that are fundamental to linking theoretical, conservation, and restoration perspectives of the longleaf pine ecosystem. Future research contributions that would bridge these information gaps will need to focus on a broad range of questions (outlined below). The answers to these and other outstanding questions will play a central role in furthering our understanding of one of the most biologically diverse and relatively understudied ecosystems on the planet.

RESTORATION OF GROUND COVER COMMUNITIES: OUTSTANDING QUESTIONS AND EMPIRICAL GAPS

How Much Intersite Variation in Species Richness and Community Composition Originates from Species-Pool Variation across Landscapes?

Biogeographic and evolutionary processes that shape landscape species pools can strongly influence patterns of biodiversity across spatial scales (Ricklefs 1987; Harrison and Cornell 2008; Kraft et al. 2011; Myers et al. 2013). Cross-site comparisons of landscape-level influences on ground cover biodiversity will help address gaps in understanding the relative importance of landscape- and local-scale controls on community assembly and local biodiversity.

What Are the Mechanistic Roles of Dispersal in Ground Cover Community Assembly?

Dispersal can contribute to both nonrandom and random community assembly (Myers and Harms 2009a; Vellend et al. 2014) and can influence the outcome of restoration efforts (Kirkman, Coffey, et al. 2004). A few studies have examined the natural patterns of seed dispersal in species-rich longleaf pine ground cover communities (Mulligan et al. 2002; Stuble et al. 2010; Cumberland and Kirkman 2013; Chandler et al. 2016). Future studies comparing natural patterns of seed rain and intersite variations among species in seed dispersal and soil seed banking can be used to inform both theoretical models of community assembly and restoration of ground cover communities.

What Is the Relative Importance of Landscape-Scale Environmental Factors and Local-Scale Species Interactions as Determinants of Species Richness and Community Composition? How Do These Processes Vary among Community Types?

Landscape-scale factors such as topography, soil moisture, and soil nutrients strongly influence species diversity and composition in ground cover communities. However, the degree to which community assembly is influenced by landscape-scale factors, local-scale species interactions (such as competition, facilitation, or predation), and the interplay between them is largely unknown, especially in different soil moisture regimes and different community types (for example, uplands versus wet-mesic flatwoods). Although some experiments have examined the effects of competition among species on ground cover biodiversity (Roth et al. 2008; Myers and Harms 2009a), little is known about the effects of facilitation, pathogens, herbivory, seed predation, and other interactions among species.

What Is the Role of Ecological Drift in Creating Patterns of Biodiversity?

Theory suggests that ecological drift has an especially strong influence on the assembly of hyperdiverse communities, but empirical tests of ecological drift are currently lacking in longleaf pine ecosystems. Future experimental and observational studies can address key questions such as: (1) the extent to which ecological drift explains patterns of biodiversity; (2) the extent to which (and timing of) stochastic colonization and extinction dynamics contribute to community assembly; and (3) the extent to which fire frequency influences drift by altering local plant densities (community size).

Does the Relative Importance of Niche Assembly and Dispersal Assembly Vary among Different Functional Groups?

Within functionally diverse communities, the relative importance of niche- and dispersal-assembly processes can vary among different functional groups (such as perennial grasses, legume forbs, or nonlegume forbs). Studies that test assembly mechanisms both within and across functional groups can reveal the extent to which community-wide patterns are driven by differences or similarities in assembly mechanisms across guilds.

What Processes Determine Spatial and Temporal Patterns of Functional Diversity among Plants?

Community-assembly processes can be difficult to infer from patterns of species diversity alone, especially when communities contain large numbers of species with functionally redundant traits (Swenson et al. 2011). Little is known about patterns of functional-trait diversity in the ground cover communities and how they are shaped by different community assembly mechanisms.

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