

Overdispersed Spatial Patterning of Dominant Bunchgrasses in Southeastern Pine Savannas

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Submitted September 12, 2017; Accepted September 22, 2017; Electronically published February 16, 2018

Dryad data: <http://dx.doi.org/10.5061/dryad.20536>.

ABSTRACT: Spatial patterning is a key natural history attribute of sessile organisms that frequently emerges from and dictates potential for interactions among organisms. We tested whether bunchgrasses, the dominant plant functional group in longleaf pine savanna ground-cover communities, are nonrandomly patterned by characterizing the spatial dispersion of three bunchgrass species across six sites in Louisiana and Florida. We mapped bunchgrass tussocks of >5.0 cm basal diameter in three 3 × 3-m plots at each site. We modeled tussocks as two-dimensional objects to analyze their spatial relationships while preserving sizes and shapes of individual tussocks. Tussocks were overdispersed (more regularly spaced than random) for all species and sites at the local interaction scale (<0.3 m). This general pattern likely arises from a tussock-centered, distance-dependent mechanism, for example, intertussock competition. Nonrandom spatial patterns of dominant species have implications for community assembly and ecosystem function in tussock-dominated grasslands and savannas, including those characterized by extreme biodiversity.

Keywords: spatial pattern, overdispersion, grassland, savanna, bunchgrass, Programita.

Introduction

Nonrandom spatial patterns are frequently observed in natural populations (Levin 1992; Rietkerk and van de Koppel 2008; fig. 1). When individual organisms are modeled as either points or shapes, their population-level spatial dispersion pattern is nonrandom when it departs from complete spatial randomness (Wiegand and Moloney 2014). Over-

dispersed (more regularly spaced than random) patterns occur in some plant populations (e.g., van de Koppel and Crain 2006). Overdispersed patterns can be generated by inhibition or scale-dependent feedback mechanisms whose strengths vary as a function of distance from each individual organism, for example, competition or plant-soil feedbacks (Packer and Clay 2000; Kikvidze et al. 2005; Stoll and Bergius 2005; van de Koppel et al. 2012). In contrast to overdispersion, aggregated or clumped patterns—such as those found in biofilms in mudflats and herbaceous vegetation in alpine ecosystems—may be generated by facilitation, limited dispersal, environmental heterogeneity, or clonal propagation (Gibson and Menges 1994; HilleRisLambers et al. 2001; Purves and Law 2002; Gilbert and Lechowicz 2004; Lejeune et al. 2004; Houseman 2013). Facilitation and competition operating in tandem can generate a combination of both small-scale aggregation and larger-scale overdispersion in mussel beds and shrubs in arid ecosystems (Lefever and Lejeune 1997; van de Koppel et al. 2005, 2008; Cipriotti and Aguiar 2015). Competition may also counteract facilitation to generate random patterns (Kikvidze et al. 2005). Accurately characterizing spatial patterns in nature can generate useful insights toward understanding the natural history of sessile organisms and how local ecological pattern-formation processes scale up to influence populations, communities, and ecosystems.

Individuals in a community are often assumed to encounter other individuals, whether conspecifics or heterospecifics, in proportion to their average population densities. This is referred to as the mean-field assumption (Murrell et al. 2001). In communities with species-specific nonrandom spatial patterning and ecological processes (e.g., competition, dispersal, natural enemies) occurring at relatively small spatial scales, the mean-field assumption may not be an accurate reflection of what most individuals experience (Murrell et al. 2001; Milbau et al. 2007; Hart and Marshall

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Figure 1: *Muhlenbergia expansa* bunchgrass tussocks 1 month postburn, June 2009, Lake Ramsay Preserve, LA. (Charred black stems are *Ilex glabra*.) Photo credit: J. A. Myers.

2009). In sessile communities, where individuals are subject to the conditions of their immediate surroundings, the mean-field assumption is especially likely to be violated (Tilman 1994; Barot et al. 1999). If individuals are aggregated by species, they will encounter heterospecifics in lower proportion than predicted by the mean-field assumption, reducing interspecific competition in the community (Stoll and Prati 2001; Hart and Marshall 2009; Raventós et al. 2010). If individuals within a species are overdispersed, they will encounter heterospecifics in higher proportion than predicted by the mean-field assumption, increasing interspecific competition in the community (Hart and Marshall 2009). Furthermore, if individuals within a physically and competitively dominant species are overdispersed, the resulting increase in heterospecific encounters and interspecific competition between dominant and subordinate species may increase the effect of dominant species on community dynamics relative to their abundance.

Many studies of spatial patterns rely on point-pattern analyses (pair-correlation functions, nearest-neighbor distances, or other measures) that treat individuals as points on a map. However, a sessile individual occupies a volume of three-dimensional space and an area of two-dimensional space. When the space an individual occupies is large relative to the scales over which many interactions occur and when there is a size disparity among interacting individuals, treating individuals as dimensionless points may produce inaccurate assessments of pattern (Wiegand et al. 2006).

For example, centroids of the two-dimensional projections of two sessile, nonoverlapping organisms cannot be nearer one another than the summed distance of their radii, whereas in randomized simulations, those centroids as points could occur more closely to one another, thereby biasing the test in favor of finding overdispersion. This bias arises from the fact that the observed nearest-neighbor distances would be skewed toward larger values than the distribution of expected nearest-neighbor distances using a centroid-based approach. Therefore, preserving the sizes and shapes of individuals in many spatial pattern analyses is vital to accurately characterizing the spatial patterns observed in nature.

As in many grasslands and savannas worldwide, bunchgrasses often constitute the majority of aboveground biomass in groundcover plant communities. Longleaf pine savannas are an ideal environment in which to examine spatial patterning given that they have a species-rich groundcover dominated by large-stature C_4 bunchgrasses. Despite high dominance by bunchgrasses, longleaf pine savannas harbor some of the highest levels of small-scale plant species richness worldwide, for example, $30\text{--}40 \cdot 1 \text{ m}^{-2}$ (Walker and Peet 1983; Peet and Allard 1993; Kirkman et al. 2001). Dominant bunchgrasses are foundation species in pine savanna groundcover because they have an oversized influence on community and ecosystem processes due to their abundance (e.g., negative or positive effects on subordinate species, producing fuel that enables fire, etc.; Platt 1999; Ellison et al. 2005; Myers and Harms 2009). The spatial pattern of domi-

nant species is likely to be an especially important determinant of the frequency of pairwise inter- and intraspecific interactions as well as larger-scale ecosystem processes (e.g., resource depletion, fire propagation; Greig-Smith 1979; Barot and Gignoux 2004; Law et al. 2009). Even so, spatial patterns of bunchgrasses have rarely been taken into account in studies of community or ecosystem composition in grasslands or savannas, and we know of no studies of bunchgrass spatial patterning in pine savannas specifically. Since sessile organisms interact mostly with nearby neighbors, the spatial patterning of physically or competitively dominant species can have important consequences for individual performance, population dynamics, community assembly, and ecosystem function.

To better understand the ecological roles played by dominant bunchgrasses, we asked whether bunchgrass tussocks are randomly or nonrandomly arrayed at the small scale of local neighborhoods. If the spatial pattern is nonrandom, is that pattern scale dependent? Furthermore, are nonrandom patterns consistent among species and across sites? We found consistent nonrandom spatial patterning that provides insights into intraspecific interactions among bunchgrass tussocks, dominant-subordinate interactions between bunchgrasses and smaller-stature forbs and grasses, and the characteristics of the bunchgrass functional group as a principal fuel source for grassland and savanna fires.

Methods

Sampling Methods

Between May and August 2013, we characterized the spatial patterning of the dominant bunchgrasses at six longleaf pine savanna sites ranging from central Louisiana to the Florida panhandle (tables 1, A1). All sites are managed with fairly regular 2- to 3-year prescribed fire regimes. At each site, we established three square plots measuring 3×3 m. Plots were selected for minimal shrub cover and were at least 20 m apart. We divided each plot into grid cells measuring 0.1×0.1 m and mapped onto a corresponding grid map the location and shape of the base (where the plant met and was in rooted contact with the ground surface) of each bunchgrass tussock >5.0 cm in basal diameter. We were primarily interested in the largest-diameter tussocks, since they accounted for the majority of biomass in our plots, and we included all tussocks >5.0 cm in basal diameter. Since these bunchgrasses are often rhizomatous, we considered tussocks separated by 3.0 cm of bare ground to be separate individuals. We did not observe any surface-area overlap between any two tussocks. We recorded species identity of each tussock. At each site, one species was considered dominant because of its abundance. We first assessed spatial patterning of the tussocks of only the dominant species in each plot.

Then, for the subset of plots in which additional species in the C_4 bunchgrass guild occurred, we assessed patterning of all tussocks collectively. Dominant bunchgrass species at each site are listed in table 1; second-most-common bunchgrass species are listed in table A1. We also mapped the locations of any shrubs occurring in the plots since they also represent large potential competitors (Myers and Harms 2009).

Data and Statistical Analyses

A tussock that was rooted in $>50\%$ of a cell was considered to be an occupant of that cell. No more than one tussock occupied a single cell. The data matrix for a single plot therefore contained an entry for each 0.1×0.1 -m cell in the plot. Each entry was either a zero (0) or a number code that corresponded to the identity of one of the bunchgrass species or shrub cover (data deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.20536> [Hovanec et al. 2018]).

We used Programita (ver. 2010; see Wiegand et al. 2006) to analyze the spatial patterns of bunchgrass tussocks at multiple spatial scales in each plot. We calculated the univariate L -statistic, $L(r)$, to identify nonrandom spatial patterns in each plot; $L(r)$ is the ratio of the number of individuals that occur within a certain distance of a focal individual to the number of individuals expected to occur within that distance given the plot-wide density of individuals (Wiegand et al. 2006). The $L(r)$ measure was calculated by Programita at 0.1-m increments, ranging from a radius of 0.1 m to 1.5 m around focal tussocks.

Because $L(r)$ is a cumulative measure of spatial dispersion (i.e., data used to determine spatial patterns at small scales are included in measurements of spatial patterns at larger scales), especially strong nonrandom spatial patterns at small scales can mask other spatial patterns at larger scales (Wiegand and Moloney 2004). To accurately pinpoint the scale at which nonrandom spatial patterns occur, we also calculated the univariate O -ring statistic. The O -ring statistic is similar to $L(r)$, but the ring width is fixed. Therefore, as the scale being measured increases, data at smaller scales are excluded from the analysis. For the O -ring analyses, we set the ring width to 0.3 m, which is larger than the individual tussocks (as recommended in the Programita manual), and to accommodate five nonoverlapping ring widths within focal tussocks' 1.5-m $L(r)$ -assessment radii.

We generated a null expectation for $L(r)$ and the O -ring statistics of each plot by rearranging individual tussocks under the assumption of complete spatial randomness for 199 iterations. We constructed 95% confidence envelopes around the null expectation for each plot using the fifth-highest and fifth-lowest values generated by the Monte Carlo simulation (Wiegand and Moloney 2014). The sizes and shapes of indi-

Table 1: Maximum scale of overdispersion for $L(r)$ and O -ring statistics—that is, individual bunchgrass tussocks were overdispersed from 0 m to the value shown in meters—and scale of aggregation when present

Site, dominant species, plot	Tussock density (tussocks · m ⁻²)	Mean tussock diameter ± SD (m)	All bunchgrass species		Dominant species only		Dominant- species-only aggregation (O -ring)
			$L(r)$	O -ring	$L(r)$	O -ring	
Blackwater River State Forest, FL:							
<i>Aristida stricta</i> :							
1	8.11	.12 ± .03	.7	.2	.4	.2	NA
2	6.89	.14 ± .03	.4	.2	.4	.2	NA
3	3.00	.17 ± .06	.9	.4	1.1	.3	NA
Eglin Air Force Base, FL:							
<i>A. stricta</i> :							
1	6.33	.16 ± .06	.4	.2	.4	.2	NA
2	8.56	.15 ± .05	.5	.3	.6	.2	NA
3	5.33	.14 ± .03	.5	.2	.6	.2	NA
Abita Creek Flatwoods Preserve, LA:							
<i>Muhlenbergia expansa</i> :							
1	6.89	.13 ± .03	.4	.2	.4	.2	1.1
2	3.11	.13 ± .04	.4	.3	.4	.2	NA
3	3.66	.16 ± .04	.5	.3	.5	.3	NA
Lake Ramsay Preserve, LA:							
<i>M. expansa</i> :							
1	4.56	.19 ± .08	.9	.3	.9	.3	NA
2	4.44	.16 ± .04	.4	.2	.2	.1	NA
3	8.22	.15 ± .04	.4	.2	.3	.2	NA
Camp Whispering Pines, LA:							
<i>Schizachyrium tenerum</i> :							
1	5.00	.14 ± .03	.5	.2	.2	.1	NA
2	6.22	.14 ± .04	.3	.2	.2	.1	NA
3	4.78	.15 ± .03	.4	.3	.4	.3	.6
Kisatchie National Forest, LA:							
<i>S. tenerum</i> :							
1	6.55	.13 ± .03	.3	.2	.3	.2	.8
2	5.78	.14 ± .04	.4	.2	.3	.2	NA
3	7.67	.13 ± .03	.5	.2	.5	.2	NA

Note: Mean diameter of bunchgrass tussocks ± SD is shown in meters. NA = not applicable.

vidual tussocks were preserved and individual tussocks were not allowed to overlap. We used the toroidal correction to reduce bias away from plot edges. Values of $L(r)$ and O -ring lower than the null expectation indicate overdispersion; $L(r)$ and O -ring values within the null expectation indicate random patterns; $L(r)$ and O -ring values higher than the null expectation indicate aggregation.

To compare our analysis against a point-pattern assessment, we also analyzed the spatial patterns of tussocks as points in Programita, using the centroid of each tussock. We found that using point-pattern analysis without accounting for the shapes and sizes of tussocks consistently overestimated the scale of overdispersion relative to modeling tussocks as two-dimensional shapes. We do not present these results, since point-pattern analysis is inappropriate in this case.

Results

Tussock density of dominant bunchgrass species ranged from 4.56 tussocks · m⁻² at Abita Creek Flatwoods Preserve to 6.74 tussocks · m⁻² at Eglin Air Force Base (table A2). Mean tussock density was lowest when *Muhlenbergia expansa* was the dominant bunchgrass species (5.15 tussocks · m⁻²) and highest when *Aristida stricta* was the dominant bunchgrass species (6.37 tussocks · m⁻²; table A2). Mean tussock diameter did not appreciably differ between species and varied from 0.14 ± 0.03 m to 0.15 ± 0.05 m (table A2). For comparison, we also present tussock densities and diameters for the collection of all bunchgrass species per site in table A3.

Population-level, species-specific bunchgrass tussocks were significantly overdispersed in all sites and across all species. The scale at which $L(r)$ indicated an overdispersed pattern

varied, ranging from a radius of 0.2 to 1.1 m around focal tussocks (table 1), and in no cases did we detect aggregation. The *O*-ring statistic indicated a less variable scale of overdispersion, ranging from a radius of 0.1 to 0.3 m around focal tussocks, 0.67–2.0 times the mean tussock diameter (table 1). In a few cases, the *O*-ring statistic indicated that dominant species were aggregated for a short distance beyond the maximum radius of overdispersion but then transitioned into random patterns at the largest testable radii (table 1). When we analyzed all tussocks collectively, as a functional guild, the results were qualitatively similar to the overdispersed patterns we found for dominant species only, and we found no cases of aggregation (table 1).

By analyzing the tussocks as two-dimensional shapes rather than dimensionless points, our analysis revealed the scale at which the spatial pattern changed from overdispersed to random. The overdispersed pattern was only significant at small scales relative to the sizes of and distances between nearest-neighbor tussocks. In contrast, when the radius was expanded beyond a threshold distance from the focal tussock, the spatial pattern became random (fig. 2), even though in a few cases when the dominant species were analyzed separately, the pattern became aggregated over a very narrow range of radii. Thus, the pattern of bunchgrass overdispersion was scale dependent and likely affected primarily by local biotic interactions.

Discussion

Bunchgrass tussocks were overdispersed at the local neighborhood scale at all sites and for all species. Two possible classes of mechanisms may give rise to overdispersed patterns: abiotic microsite heterogeneity (e.g., an overdispersed distribution of nutrient-rich patches) or a biotic repulsion dependent on distance between individual tussocks (e.g., tussock-tussock competition, apparent competition mediated by natural enemies, or other enemy-related influences). The consistency of the overdispersed pattern renders it unlikely that underlying abiotic microsite heterogeneity (which would likely be structured idiosyncratically among sites) caused the pattern. Rather, our results suggest that a scale-dependent, biotic mechanism is likely responsible for generating the pattern.

Although we cannot infer the specific mechanism responsible for overdispersed spacing of tussocks based solely on the observed pattern, overdispersed patterns are generally caused by scale-dependent mechanisms (van de Koppel et al. 2005, 2012; Rietkerk and van de Koppel 2008). Intraspecific competition, negative distance-dependent interactions between hosts and their natural enemies, and small-scale fire heterogeneity (owing to the fuels produced by the tussocks themselves) are examples of scale-dependent mechanisms that may generate overdispersed patterns. Intraspecific competition (or intertussock competition within the bunchgrass guild) for light, water,

or soil-borne resources could prevent tussocks from growing directly adjacent to each other (Stoll and Bergius 2005; van de Koppel and Crain 2006; Rietkerk and van de Koppel 2008; Wallet 2015). Large tussocks could function as reservoirs for enemies (herbivores, pathogens), making seedlings less likely to successfully establish near them (i.e., a Janzen-Connell mechanism; Janzen 1970; Connell 1971; Bagchi et al. 2010). In fire-driven pine savannas, increased accumulation of flammable biomass where grass blades and culms overlap between large tussocks could lead to greater intertussock soil heating during fires, causing the death of seedlings sprouting in the spaces between tussocks (Gagnon et al. 2015). Each of the proposed mutually compatible mechanisms—alone or in combination—could cause the overdispersed patterning. Even so, the ubiquity of the pattern from plant to plant renders the simplest mechanism the most parsimonious; since intertussock competition for light or soil resources does not require an additional agent (higher-trophic-level enemies or fire), this might be the underlying cause. In any case, further research involving experimental manipulations is needed to identify the mechanisms causing overdispersed spacing of bunchgrass tussocks in pine savannas.

Just as nonrandom spatial patterns of species have consequences for population, community, and ecosystem dynamics in sessile organisms in other ecosystems (Greig-Smith 1979; Amarasekare 2003; Barot and Gignoux 2004; Monzeglio and Stoll 2005; Hart and Marshall 2009; Adler et al. 2010; de Waal et al. 2015), regardless of the causal mechanism that produces the overdispersed spatial patterning of bunchgrasses in longleaf pine savannas, the patterning should have broader consequences. Aggregated patterns of conspecifics increase the frequency of intraspecific interactions relative to interspecific interactions (Hart and Marshall 2009). Conspecific aggregations of dominant competitors also prolong co-occurrence of inferior competitors by reducing interspecific competition (Stoll and Prati 2001; Rejmanek 2002; Idjadi and Karlson 2007). Conversely, species-specific overdispersion reduces the frequency of intraspecific interactions and increases the frequency of interspecific interactions between the overdispersed species and other species. Overdispersed patterns of dominant bunchgrasses could reduce intraguild competition and increase interactions between bunchgrasses and subordinate species. Overdispersed bunchgrass patterns may also limit the frequency of interspecific interactions among subordinate species. Our current working model for these pine savannas proposes that spacing mechanisms among dominant bunchgrasses create overdispersed patterning, which reduces competition among the subordinate species and thereby reduces competitive exclusion among them, fostering co-occurrence, if not coexistence. This model may apply to tussock-dominated ecosystems worldwide.

Besides population- and community-level consequences, nonrandom spatial patterns in nature can also have emer-

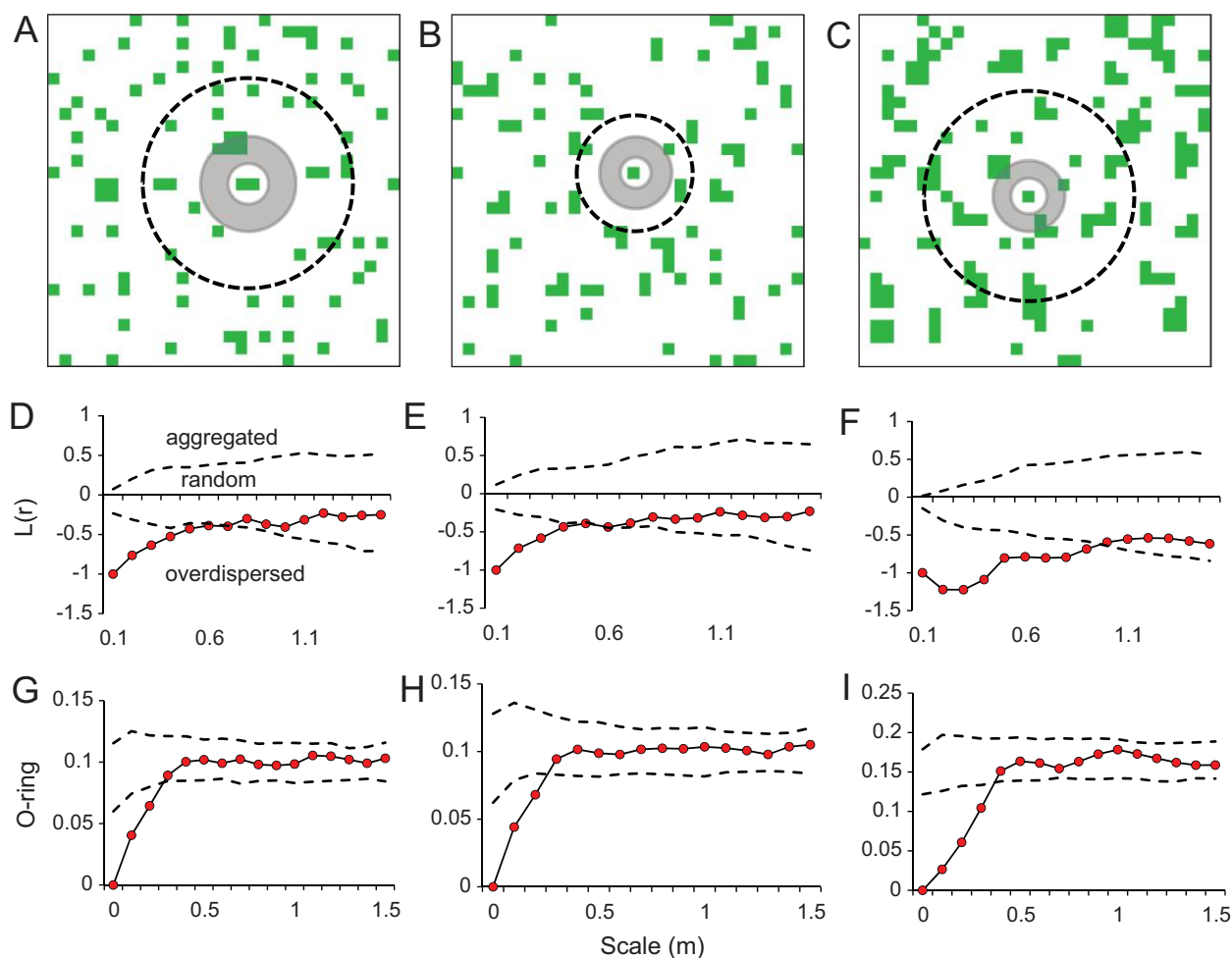


Figure 2: Scale of overdispersion for $L(r)$ and O -ring statistics in three plots. A–C, Actual bunchgrass tussock patterns in one selected plot for each site: Blackwater River State Forest (BRSF, plot 1, dominant species: *Aristida stricta*); Camp Whispering Pines (CWP, plot 1, dominant species: *Schizachyrium tenerum*); and Lake Ramsay Preserve (LRP, plot 1, dominant species: *Muhlenbergia expansa*), respectively. A green cell or a group of contiguous green cells constitutes an individual tussock. The dashed circle in each panel shows the maximum scale of overdispersion using the L -statistic. The shaded ring in each panel shows the maximum scale of overdispersion using the O -ring statistic. In each panel, the dashed circle and shaded ring are centered on a single tussock chosen near the center of the plot for illustration purposes. D–I, Points connected by a solid line indicate the measured statistic ($L(r)$ or O -ring) of the plots in panels A–C; dashed lines represent the upper and lower 95% confidence limits of the null expectations. Areas of each figure where the measured statistic indicates aggregated, random, or overdispersed patterns are denoted in D. D–F, The $L(r)$ statistic over a range of scales for the selected plots in BRSF, CWP, and LRP, respectively. G–I, The O -ring statistic over a range of scales for the selected plots in BRSF, CWP, and LRP, respectively. The $L(r)$ and O -ring statistics were similar for all remaining plots regardless of site or dominant species.

gent effects on ecosystem functions. In desert communities, aggregated shrubs increase water infiltration into the soil near vegetated patches, facilitating plant establishment and growth (HilleRisLambers et al. 2001; Rietkerk et al. 2002). Nonrandom vegetation patterns in arid ecosystems also increase productivity and efficient use of available resources (D’Odorico et al. 2006). Spatial pattern formation in mussel beds and arid ecosystems may increase resilience to disturbance along with enhancing productivity (van de Koppel and Rietkerk 2004; van de Koppel

et al. 2005; Liu et al. 2012). In African savannas, termite mounds function as hotspots for plant and animal abundance; the regular spacing of termite mounds observed in Kenya enhanced abundance and biomass of several trophic levels of consumers relative to randomly distributed termite mounds (Pringle et al. 2010). Bunchgrasses produce fuels that enable natural fire disturbances. The overdispersion of bunchgrass tussocks in pine savanna ground-cover may increase fuel continuity and facilitate the spread of fire.

Such a consistent overdispersed pattern of bunchgrass tussocks regardless of site or dominant species indicates that tussock patterning is an important and general natural history attribute of pine savannas. Further research could determine whether the overdispersed neighbor-to-neighbor patterning extends to larger spatial scales. For example, a larger-scale spectral analysis of digitized aerial images could be employed (Couteron 2002), with images taken after a fire as the bunchgrasses are resprouting but before they have grown sufficiently to obscure the footprints of their bases (as in fig. 1).

An overdispersed pattern is likely to occur in other tussock-dominated herbaceous communities (grasslands, savannas, etc.). Given the effect that nonrandom spatial patterning of sessile organisms can have on population, community, and ecosystem processes, both the causes and consequences of overdispersed tussock patterns in these ecosystems should be fully investigated.

Acknowledgments

We would like to thank the two anonymous reviewers whose comments greatly improved the manuscript. For access to field sites, we thank Latimore Smith and Alex Entrup (The Nature Conservancy); David Moore, Liz Langston, and Craig Iverson (US Forest Service); Jill Pollard, Jason Brown, and Larry Ehrlich (Camp Whispering Pines, Girl Scouts Louisiana East); and Kevin Hiers and Brett Williams (Jackson Guard, Eglin Air Force Base). Additionally, for help in the field, we thank Amanda Briant, Cory Groover, Christina Mahmood, Whitney Walle, and Elizabeth Weltman. For helpful suggestions, we thank Susan Carr, Chris Cate, Marc Cohn, Jim Cronin, Jessica Eberhard, Andrew Flick, Sandra Galeano, Jean Huffman, Metha Klock, Jennie Kluse, Teresa Kurtz, Heather Passmore, Lori Patrick, Richard Stevens, and Thorsten Wiegand. The National Science Foundation provided funding (DEB 1144079, 1144084).

APPENDIX

Additional Field Site Information and Summary Statistics for Bunchgrass Tussock Density and Diameter

Table A1: Dominant bunchgrass species, second-most-common bunchgrass species, and GPS coordinates for all plots

Site, plot	Dominant species	Co-occurring species	North	West
Blackwater River State Forest, FL:				
1	<i>Aristida stricta</i>	<i>Schizachyrium scoparium</i>	30.85445	86.80367
2	<i>A. stricta</i>	NA	30.78275	86.80466
3	<i>A. stricta</i>	<i>S. scoparium</i>	30.86311	86.80368
Eglin Air Force Base, FL:				
1	<i>A. stricta</i>	NA	30.60685	86.22701
2	<i>A. stricta</i>	<i>S. scoparium</i>	30.60929	86.22341
3	<i>A. stricta</i>	<i>S. scoparium</i>	30.60375	86.22321
Abita Creek Flatwoods Preserve, LA:				
1	<i>Muhlenbergia expansa</i>	<i>S. scoparium</i>	30.50848	89.96661
2	<i>M. expansa</i>	<i>S. scoparium</i>	30.51490	89.96961
3	<i>M. expansa</i>	<i>S. scoparium</i>	30.51610	89.96882
Lake Ramsay Preserve, LA:				
1	<i>M. expansa</i>	<i>S. scoparium</i>	30.51548	90.17033
2	<i>M. expansa</i>	<i>S. scoparium</i>	30.51281	90.16222
3	<i>M. expansa</i>	<i>S. scoparium</i>	30.51319	90.16180
Camp Whispering Pines, LA:				
1	<i>Schizachyrium tenerum</i>	<i>S. scoparium</i>	30.67942	90.46650
2	<i>S. tenerum</i>	<i>S. scoparium</i>	30.67940	90.46608
3	<i>S. tenerum</i>	<i>S. scoparium</i>	30.68003	90.46531
Kisatchie National Forest, LA:				
1	<i>S. tenerum</i>	<i>S. scoparium</i>	31.68605	92.47184
2	<i>S. tenerum</i>	<i>S. scoparium</i>	31.68615	92.47222
3	<i>S. tenerum</i>	<i>S. scoparium</i>	31.68584	92.47244

Note: NA = not applicable.

Table A2: Mean tussock density and diameter \pm SD for each site and each dominant bunchgrass species

Site	Mean tussock density \pm SD at site (tussocks \cdot m ⁻²)	Mean tussock diameter at site \pm SD (m)	Dominant species	Mean tussock density \pm SD of dominant species (tussocks \cdot m ⁻²)	Mean tussock diameter of dominant species \pm SD (m)
Blackwater River State Forest, FL	6.00 \pm 2.67	.14 \pm .04	<i>Aristida stricta</i>	6.37 \pm 2.03	.15 \pm .05
Eglin Air Force Base, FL	6.74 \pm 1.65	.15 \pm .05			
Abita Creek Flatwoods Preserve, LA	4.56 \pm 2.04	.14 \pm .04	<i>Muhlenbergia expansa</i>	5.15 \pm 1.98	.15 \pm .05
Lake Ramsay Preserve, LA	5.74 \pm 2.15	.16 \pm .06			
Camp Whispering Pines, LA	5.33 \pm .78	.14 \pm .03	<i>Schizachyrium tenerum</i>	6.00 \pm 1.07	.14 \pm .03
Kisatchie National Forest, LA	6.67 \pm .95	.13 \pm .03			

Table A3: Mean tussock density and diameter \pm SD for each site for all bunchgrass species

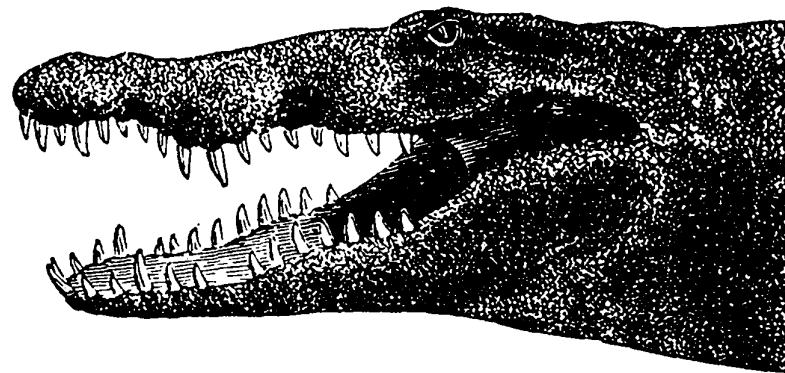
Site	Mean tussock density \pm SD at site (tussocks \cdot m ⁻²)	Mean tussock diameter \pm SD at site (m)	Dominant species	Mean tussock density \pm SD of all bunchgrass species (tussocks \cdot m ⁻²)	Mean tussock diameter \pm SD of all bunchgrass species (m)
Blackwater River State Forest, FL	6.52 \pm 1.92	.14 \pm .04	<i>Aristida stricta</i>	7.17 \pm 2.19	.14 \pm .04
Eglin Air Force Base, FL	7.81 \pm 2.67	.15 \pm .05			
Abita Creek Flatwoods Preserve, LA	7.96 \pm 1.25	.14 \pm .04	<i>Muhlenbergia expansa</i>	8.11 \pm 1.98	.15 \pm .05
Lake Ramsay Preserve, LA	8.26 \pm 2.85	.16 \pm .05			
Camp Whispering Pines, LA	6.22 \pm 1.53	.14 \pm .03	<i>Schizachyrium tenerum</i>	7.20 \pm 1.64	.14 \pm .03
Kisatchie National Forest, LA	8.19 \pm 1.22	.13 \pm .03			

Literature Cited

- Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. *Ecology Letters* 13: 1019–1029.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6:1109–1122.
- Bagchi, R., T. Swinfield, R. E. Gallery, O. T. Lewis, S. Gripenberg, L. Narayan, and R. P. Freckleton. 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters* 13:1262–1269.
- Barot, S., and J. Gignoux. 2004. Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos* 106: 185–192.
- Barot, S., J. Gignoux, and J.-C. Menaut. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology* 80:1987–2005.
- Cipriotti, P. A., and M. R. Aguiar. 2015. Is the balance between competition and facilitation a driver of the patch dynamics in arid vegetation mosaics? *Oikos* 124:139–149.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. Pages 298–312 in P. J. Den Boer and G. Gradwell, eds. *Dynamics of populations*. Center of Agricultural Publication and Documentation, Wageningen, Netherlands.
- Couteron, P. 2002. Quantifying change in patterned semi-arid vegetation by Fourier analysis of digitized aerial photographs. *International Journal of Remote Sensing* 23:3407–3425.
- de Waal, C., B. Anderson, and A. G. Ellis. 2015. Relative density and dispersion pattern of two southern African Asteraceae affect fecundity through heterospecific interference and mate availability, not pollinator visitation rate. *Journal of Ecology* 103:513–525.
- D'Odorico, P., F. Laio, and L. Ridolfi. 2006. Patterns as indicators of productivity enhancement by facilitation and competition in dryland vegetation. *Journal of Geophysical Research* 111:G03010.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486.
- Gagnon, P. R., H. A. Passmore, M. Slocum, J. A. Myers, K. E. Harms, W. J. Platt, and C. E. T. Paine. 2015. Fuels and fires influence vegetation via above- and belowground pathways in a high-diversity plant community. *Journal of Ecology* 103:1009–1019.
- Gibson, D. J., and E. S. Menges. 1994. Population structure and spatial pattern in the dioecious shrub *Ceratiola ericoides*. *Journal of Vegetation Science* 5:337–346.
- Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences of the USA* 101:7651–7656.
- Greig-Smith, P. 1979. Pattern in vegetation. *Journal of Ecology* 67: 755–779.
- Hart, S. P., and D. J. Marshall. 2009. Spatial arrangement affects population dynamics and competition independent of community composition. *Ecology* 90:1485–1491.
- HilleRisLambers, R., M. Rietkerk, F. van den Bosch, H. H. T. Prins, and H. de Kroon. 2001. Vegetation pattern formation in semi-arid grazing systems. *Ecology* 82:50–61.
- Houseman, G. R. 2013. Aggregated seed arrival alters plant diversity in grassland communities. *Journal of Plant Ecology* 7:51–58.
- Hovanes, K. A., K. E. Harms, P. R. Gagnon, J. A. Myers, and B. D. Elderd. 2018. Data from: Overdispersed spatial patterning of dominant bunchgrasses in southeastern pine savannas. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.20536>.
- Idjadi, J. A., and R. H. Karlson. 2007. Spatial arrangement of competitors influences coexistence of reef-building corals. *Ecology* 88: 2449–2454.
- Janzen, D. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Kikvidze, Z., F. I. Pugnaire, R. W. Brooker, P. Choler, C. J. Lortie, R. Michalet, and R. M. Callaway. 2005. Linking patterns and processes in alpine plant communities: a global study. *Ecology* 86: 1395–1400.
- Kirkman, K. L., R. J. Mitchell, R. C. Helton, and M. B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88: 2119–2128.
- Law, R., J. Illian, D. F. R. P. Burslem, G. Gratzler, C. V. S. Gunatilleke, and I. A. U. N. Gunatilleke. 2009. Ecological information from spatial patterns of plants: insights from point process theory. *Journal of Ecology* 97:616–628.
- Lefever, R., and O. Lejeune. 1997. On the origin of tiger bush. *Bulletin of Mathematical Biology* 59:263–294.
- Lejeune, O., M. Tlidi, and R. Lefever. 2004. Vegetative spots and stripes: dissipative structures in arid landscapes. *International Journal of Quantum Chemistry* 98:261–271.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Liu, Q., E. J. Weerman, P. M. J. Herman, H. Olff, and J. van de Koppel. 2012. Alternative mechanisms alter the emergent properties of self-organization in mussel beds. *Proceedings of the Royal Society B* 279:2744–2753.
- Milbau, A., D. Reheul, B. De Cauwer, and I. Nijs. 2007. Factors determining plant-neighbor interactions on different spatial scales in young species-rich grassland communities. *Ecological Research* 22:242–247.
- Monzeglio, U., and P. Stoll. 2005. Spatial patterns and species performances in experimental plant communities. *Oecologia* 145:619–628.
- Murrell, D. J., D. W. Purves, and R. Law. 2001. Uniting pattern and process in plant ecology. *Trends in Ecology and Evolution* 16:529–530.
- Myers, J. A., and K. E. Harms. 2009. Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. *Ecology* 90:2745–2754.
- Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281.
- Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. *Proceedings of the Tall Timbers Fire Ecology Conference* 18:45–81.
- Platt, W. J. 1999. Southeastern pine savannas. Pages 23–51 in R. C. Anderson, J. S. Fralish, and J. M. Baskin, eds. *Savannas, barrens, and rock outcrop plant communities of North America*. Cambridge University Press, New York.
- Pringle, R. M., D. F. Doak, A. K. Brody, R. Jocqué, and T. M. Palmer. 2010. Spatial pattern enhances ecosystem functioning in an African savanna. *PLoS Biology* 8:e1000377.
- Purves, D. W., and R. Law. 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. *Journal of Ecology* 90:121–129.

- Raventós, J., T. Wiegand, and M. De Luis. 2010. Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology* 91:2110–2120.
- Rejmanek, M. 2002. Intraspecific aggregation and species coexistence. *Trends in Ecology and Evolution* 17:209–210.
- Rietkerk, M., M. C. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. van de Koppel, L. Kumar, H. H. T. Prins, and A. M. de Roos. 2002. Self-organization of vegetation in arid ecosystems. *American Naturalist* 160:524–530.
- Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. *Trends in Ecology and Evolution* 23:169–175.
- Stoll, P., and E. Bergius. 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. *Journal of Ecology* 93:395–403.
- Stoll, P., and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82:319–327.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- van de Koppel, J., T. J. Bouma, and P. M. J. Herman. 2012. The influence of local- and landscape-scale processes on spatial self-organization in estuarine ecosystems. *Journal of Experimental Biology* 215:962–967.
- van de Koppel, J., and C. M. Crain. 2006. Scale-dependent inhibition drives regular tussock spacing in a freshwater marsh. *American Naturalist* 168:136–147.
- van de Koppel, J., J. C. Gascoigne, G. Theraulaz, M. Rietkerk, W. M. Mooij, and P. M. J. Herman. 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. *Science* 322:739–742.
- van de Koppel, J., and M. Rietkerk. 2004. Spatial interactions and resilience in arid ecosystems. *American Naturalist* 163:113–121.
- van de Koppel, J., M. Rietkerk, N. Dankers, and P. M. J. Herman. 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. *American Naturalist* 165:66–77.
- Walker, J., and R. K. Peet. 1983. Composition and species-diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55:163–179.
- Wallet, W. 2015. Neighborhood interactions of an understory dominant, *Aristida stricta*, along a soil resource gradient of the longleaf pine ecosystem. MS thesis. Murray State University, Murray, KY.
- Wiegand, T., W. D. Kissling, P. A. Cipriotti, and M. R. Aguiar. 2006. Extending point pattern analysis for objects of finite size and irregular shape. *Journal of Ecology* 94:825–837.
- Wiegand, T., and K. A. Moloney. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104:209–229.
- . 2014. *Handbook of spatial point-pattern analysis in ecology*. CRC Press, New York.

Natural History Editor: Mark A. McPeck



“In the warm, placid waters of tropical streams whose banks are bordered by reedy marshes and forests of perpetual green, is the home of the crocodile. About the middle of the day numbers may be seen lying lazily on the banks enjoying the heat, their polished scales shining in the sunlight, and all looking the very picture of tropical languor and repose.” From “The Crocodile in Florida” by Wm. T. Hornaday (*The American Naturalist*, 1875, 9:498–504).