

PLANT SPATIAL STRUCTURE IS MORE DEPENDENT ON ENDOGENOUS PROCESSES  
THAN SOIL HETEROGENEITY IN AN ASSEMBLING COMMUNITY

A Thesis by

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The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science, with a major in Biological Sciences.

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Gregory Houseman, Committee Chair

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## ABSTRACT

Within communities, organisms potentially self-organize through endogenous processes that create non-random spatial structure as they interact with one another or modify the abiotic environment. In contrast, exogenous processes such as environmental heterogeneity or variable immigration are thought to be dominant processes controlling these spatial patterns. Although both endogenous and exogenous processes likely occur, their relative importance is still largely unknown because of limited analytical tools and the lack of experimental evidence – particularly those that address exogenous sources of environmental heterogeneity. Here, I used a soil heterogeneity experiment to examine the relative effect of endogenous and exogenous processes on plant spatial structure after five years of community assembly. Soil heterogeneity was manipulated by splitting the vertical soil profile into three soil-types that were randomly assigned to 40x40 cm patches within 2.4x2.4 m plots. Homogeneous plots were created by mixing all soils before filling each patch. Thirty-four grassland species were then sown into all plots and allowed to grow for five years after which the location of all plants were mapped using a 5x5 cm grid. Results from point-pattern spatial analysis indicated that, even in the absence of soil heterogeneity and seed dispersal limitation, spatial structure was primarily generated by endogenous processes. Although soil heterogeneity increased species aggregation at certain scales, most of the spatial structure was created by endogenous processes. These results suggest that endogenous processes are more important than expected for generating spatial structure in grasslands, and these processes are likely important for plant coexistence and species abundance patterns in this ecosystem.

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# CHAPTER 1

## INTRODUCTION

One of the more intriguing ideas in ecology is that organisms may self-organize, creating spatial structure that influences species coexistence and patterns of abundances within communities (Bolker et al. 2003, Barot and Gignoux 2004). These endogenous processes occur as organisms interact with one another through demographic or competitive processes, or by modification of the abiotic environment, generating spatial or temporal heterogeneity in their distributions. For example, limited dispersal of offspring around parents can create aggregations of conspecifics (Chave and Leigh 2002), positive or negative plant-soil feedbacks can lead to measurable changes in soil conditions that subsequently influence con- and hetero-specific success (Temperton et al. 2007, Jiang et al. 2011, Bulleri et al. 2016), or predators accumulating on adults may suppress the establishment of offspring near parents (Janzen 1970). Through these processes, species can potentially modify initially homogeneous conditions creating environmental heterogeneity, or generate non-random patterns in their distributions that leave opportunities for additional species to establish. These spatial patterns may then alter species coexistence and observed patterns of diversity within communities (Barot and Gignoux 2004).

In contrast to endogenous processes, non-random spatial structure can also arise from exogenous processes, where forces work from outside plants themselves. The existence of spatial or temporal environmental heterogeneity provides one exogenous source of spatial structure, where separate niches encourage the growth of different species, leading to aggregations or the separation of species in space (Chesson 2000, Wilson 2011). However, other exogenous forces such as disturbances also influence the spatial patterns of organisms, and limited dispersal between separate communities can create regional-scale differences in species distributions

(Barot and Gignoux 2004). These exogenous processes are thought to be critically important for explaining species coexistence.

Because spatial patterns are likely a combination of exogenous and endogenous processes, teasing the two apart is challenging, but essential to fully understand which processes are most important for generating and maintaining spatial structure (Potts et al. 2004, Cottenie 2005). For example, if soil heterogeneity is created following plant establishment as they grow and reproduce, the process that led to the heterogeneity may no longer be apparent once community assembly is well underway. Additional challenges arise because processes can be both endogenous and exogenous. For example, disturbances may be exogenous if created by fire, flood, or wind events, or endogenous if litter accumulation around certain species is detrimental to heterospecifics (Bascompte and Rodriguez 2000) or when aging trees create treefall gaps that have positive effects on heterospecifics (Grau 2004). Likewise, dispersal can also be either exogenous when organisms disperse unequally between communities, or endogenous when dispersal of sessile organisms occurs over short distances (Pottier and Evette 2011, Lara-Romero et al. 2016).

Distinguishing between exogenous and endogenous processes has also been hampered by a lack of suitable analytical techniques and empirical approaches, as traditional ecological measurements such as species area curves or species abundance distributions cannot differentiate between key processes (Brown et al. 2011, May et al. 2015, Brown et al. 2016). Analysis of spatial patterns themselves is more informative, but has been limited because spatial analysis demands highly intensive data collection to associate each individual with an exact location, and until recently analytical techniques and computation power have been unavailable.

Fortunately, developments in point-pattern spatial analysis that rigorously quantify spatial patterns have begun to foster deeper exploration of ecological processes at work in real communities (Wiegand and Moloney 2014). Generally, studies that utilize point-pattern spatial analysis have been observational, relying on the mapped locations of trees (John et al. 2007, Kubota et al. 2007, Wiegand et al. 2007, Shen et al. 2009, Wang et al. 2010, Nguyen et al. 2016, Song et al. 2017), shrubs (Mureva and Ward 2016), or grassland species (Dickinson and Norton 2011, Pescador et al. 2014, Lara-Romero et al. 2016) to identify the contributions of exogenous and endogenous processes in real communities. While these studies have provided important insights, they have limited ability to distinguish between processes that create similar spatial patterns. For example, the effects of exogenous environmental heterogeneity are often addressed analytically by approximating this heterogeneity from large-scale patterns present in the distribution of individuals. However, this approach relies heavily on observational approaches that ignore the influence of plants on the physical environment. Seed dispersal is also difficult to entirely account for analytically, and spatial patterns created by this process could mask the influence of other endogenous processes that create aggregations.

Experiments that control key processes such as environmental heterogeneity or limited dispersal would provide the necessary, direct evidence for the relative importance of endogenous and exogenous processes in creating spatial structure. However, experiments utilizing point-pattern spatial analysis in complex communities are rare, and to my knowledge are limited to environmentally homogeneous grassland systems, where limited dispersal and competition have been identified as important processes generating spatial patterns (Seabloom et al. 2005, Benot et al. 2013).

To address these shortcomings, I established an experiment that manipulates soil heterogeneity and quantifies plant spatial structure that developed after four years of community assembly. My analyses address three questions: 1) Do endogenous processes create spatial patterns in grassland communities? 2) Does exogenous heterogeneity influence spatial patterns in this same system? 3) What is the relative importance of exogenous and endogenous processes during community assembly?

Specifically, I compared plant spatial structure under homogenous and heterogeneous soils within and among patches of a known scale. Additionally, thirty-four grassland species were sown uniformly across all plots so that any spatial structure that emerged would be the result of either differences in soil heterogeneity or endogenous processes of the species occurring within the plots.

## CHAPTER 2

### MATERIALS AND METHODS

#### *Experimental Set-Up*

The experiment was established in a restored grassland located at Wichita State University's Ninnescah Field Station in south-central Kansas. The site has a mean annual temperature of 14.3 °C, a mean annual precipitation of 782 mm, and soils consisting of sandy loam, clay loam, silt loam, and silty-clay loam families (Houseman et al. 2016). This site had been used in row crop agriculture for several decades prior to restoration which began in 1984 (Houseman et al. 2016). In the summer of 2010, existing plants were removed from plots by applying 9% glyphosate herbicide to an 11x23 m area. Seven weeks after vegetation was removed, ten 2.4 m<sup>2</sup> plots were established in a randomized complete block design, with five blocks containing a pair of homogeneous and heterogonous soil plots. To create heterogeneous soils of a known scale and condition, the natural variation in soil organic matter, pH and texture occurring vertically in the soil profile was used to create patches within the heterogeneous plots. This approach avoided the use of inorganic fertilizers that may disrupt natural plant-soil interactions (Collins and Wein 1998, Bliss et al. 2001). To do this, three 15 cm soil "strata" (Soil Patch Type 1, Soil Patch Type 2, and Soil Patch Type 3) were removed from heterogeneous plots and transferred to separate, large holding containers. A wooden form was placed in the plot once soil was removed. This form consisted of 36, 40x40 cm cells that were 45 cm in depth. Each soil type was mixed within the holding container and then returned to a randomly selected 40x40 cm patch within its plot of origin. Once all three soil types were distributed back into the plot, the wooden form was removed and gaps between patches filled in as the soil settled. Homogeneous soil plots were treated similarly except that all three soil types were mixed together and then

redistributed into the 40x40 cm patches. Because there were only three soil types, often the same soil patch type occurred adjacent to each other, effectively creating larger patches of the same soil type. All plots were then covered with a polypropylene cloth to minimize soil erosion over the winter.

Because the soil types potentially had different seedbanks, plots were re-treated with the glyphosate mixture in the spring following emergence from the seedbank. After die-back, thirty-four native grassland species were sown evenly into each plot, and a biodegradable germination blanket was placed over plots to protect seeds from seed predators and maintain suitable germination conditions. Because of an ongoing drought in the region, plots were watered three times a week for ten weeks using rates equivalent to average spring rainfall for the region (Williams and Houseman 2013). No other droughts occurred in subsequent years, so no additional watering was utilized.

### *Plant Sampling*

After four years of community assembly, the location of individual plants in each plot were mapped using a grid-based approach. Plots were burned in March 2015, consistent with standard grassland management in the region and does not kill the majority of established plants. Following the removal of dead aboveground litter by the fire, a 2.4 m<sup>2</sup> section of welded wire fencing with 10.2x5.1 cm<sup>2</sup> rectangular cells was centered in each plot and laid flush with the soil surface. Plants were allowed to grow for two months through the grid, and then the identity of each individual plant was determined in each half of all cells resulting in a grid cell size of 5.1x5.1 cm<sup>2</sup>. Grid cells were numbered from 1-48 along both axes, and these were used to indicate the approximate location of individual plants within plots. When possible, individuals

were distinguished by assessing whether stems were connected under the soil surface by rhizomes. The number of stems or tillers associated with an individual was also recorded. For species known to grow clonally, individuals were difficult or impossible to distinguish, and were likely larger than single grid cells. Therefore, presence/absence in grid cells was used to create point patterns for *Sorghastrum nutans*, *Andropogon gerardii*, *Schizachyrium scoparium*, and *Monarda fistulosa*, and any spatial patterns detected would therefore indicate the patterns developed by multiple, large individuals. All other species were identified at the individual level.

### *Point-Pattern Spatial Analysis*

The O-ring statistic,  $O(r) = \lambda \frac{dK(r)}{dr} / (2\pi r)$ , was used to quantify spatial patterns that developed in homogenous and heterogeneous soil treatments for the thirteen species that had a sample size greater than 50 individuals in each treatment. This spatial statistic measures the mean density of points at a distance  $r$  away from an average individual point of the pattern (Wiegand and Moloney 2004). In the univariate case,  $O_{11}(r) = \lambda_1 \frac{dK_{11}(r)}{dr} / (2\pi r)$  gives the density of points of Pattern 1 (such as a single species) at distance  $r$  around individual points of Pattern 1, where  $\lambda_1$  is the intensity (density) of Pattern 1 over the entire observation window (plot). The bivariate case,  $O_{12}(r) = \lambda_2 \frac{dK_{12}(r)}{dr} / (2\pi r)$ , gives the density of points of Pattern 2 (such as a single species) at distance  $r$  around individual points of Pattern 1 (such as a soil patch), where  $\lambda_2$  is the intensity of Pattern 2 over the entire observation window. The O-ring statistic was selected over the more common Ripley's K-function,  $K(r)$ , because of the noncumulative nature of  $O(r)$ . The K-function gives the average density of points within a distance  $r$  from the average point in the pattern, making the K-function cumulative. This means that patterns occurring at small scales influence those at larger scales. The O-ring statistic therefore provides greater detail about exact

scales where spatial patterns occur and easier interpretation of multiple spatial patterns occurring at different scales (Wiegand and Moloney 2014).

In order to determine whether deviations of the observed summary statistics differed from hypothesized null models, 95% simulation envelopes were constructed by taking the 5<sup>th</sup> highest and lowest ranked values of calculated  $O(r)$  from 199 simulations of a null model. Deviations of observed summary statistics outside of the simulation envelopes therefore indicated significant departures from the null model expectation (Wiegand and Moloney 2014).

### *Analysis 1: Univariate Plant Patterns*

To determine spatial patterns that developed for individual species between soil treatments, univariate summary statistics,  $O_{11}(r)$  were compared to a null model of complete spatial randomness (CSR) in both homogeneous and heterogeneous soil treatments. Observed values were inspected for deviations outside of simulation envelopes, revealing scales of aggregation if above the envelope, and scales of over-dispersion if below.

### *Analysis 2: Bivariate Species-Soil Interactions*

The relationship between patterns of individual species and soil patch types in the heterogeneous treatment were also examined. Species responding to soil heterogeneity during establishment were predicted to be “attracted” (occurring more frequently than expected by chance) to specific soil patch types and “segregated” (occurring less frequently than expected by chance) from others. In addition, significant relationships are expected to occur at scales correlated with soil patches in the heterogeneous treatment.



The bivariate  $O_{12}(r)$  was calculated for each species and soil patch type pair, then compared to a null model assuming independence of these patterns. Null distributions were constructed by holding patterns of individual soil patch types constant, while shifting patterns of each individual species using a Toroidal shift. Specifically, the species pattern was shifted a random distance outside of the observation window, and portions of the pattern moved outside were placed back inside the observation window using a Torus translation. With this method, univariate patterns of individual species, which include those that have developed by endogenous processes, were preserved, while the pattern is disassociated from soil patch type patterns. Deviations of the observed summary statistic outside of the simulation envelope indicated species attracted or segregated from soil patch type patterns, and the scales where those associations occurred.

#### *Point-Pattern Spatial Analysis Settings*

All spatial statistics were conducted with the software *Programita*, using a grid-based approach and pooling replicate plots to calculate single statistics for each analysis (Wiegand and Moloney 2004, 2014). Smallest scales of analysis were equal to one grid-cell of  $5.1 \times 5.1$  cm<sup>2</sup>. Maximum distance of analysis was equal to half the length of plots,  $r_{\max} = 24$  cells ( $\sim 120$  cm), using a ring width of  $dr = 1$  cell (5.1 cm).

#### *Statistical Analysis of Community Measures*

One-way analysis of variance (ANOVA) with block as a random effect was used to compare species richness between soil treatments and soil patch types, with pairwise t-tests using a Bonferroni adjustment to test for differences between individual soil patch types (R 3.3.1;

Bates et al. 2015, Kuznetsova et al. 2016, R Core Team 2016). To examine how richness accumulated in relation to density across replicates, I calculated a sample-based Coleman rarefaction for the patch-scale measured within homogeneous and heterogeneous treatments (EstimateS 9.0; Colewell 2013). Occurrence of the 13 species used in spatial analysis and bare ground was used to approximate abundance in plots. I used a PERMANOVA with block as a random effect to test of overall differences in species abundance between treatments (Primer v6). Bare ground was not included in this analysis. To test for differences in species abundance and bare ground in soil treatments, I used a two-tailed t-tests with log transformed data (R 3.3.1; R Core Team 2016).

## CHAPTER 3

### RESULTS

I recorded a total of 53,302 individuals representing 70 species across the 10 plots, although only 18 species were present in every plot. Of the 13 species with sufficient abundance for spatial analysis, most had similar rank abundances in both homogeneous and heterogeneous soil treatments (Fig. 1). *Sorghastrum nutans* was the most common species regardless of soil treatment, occurring in an average of 51% of cells in homogeneous treatments and 47% of cells in heterogeneous treatments. *Rudbeckia hirta* occurred in a greater number of cells in homogeneous than heterogeneous treatments, while *Monarda fistulosa* and *Ambrosia psilostachya* had a higher occurrence in heterogeneous than homogeneous treatments. Of the three non-sown species that had sufficient abundance to conduct spatial analysis, *Chamaecrista fasciculata* and *Cirsium altissimum* had no difference in frequency between soil treatments, while *A. psilostachya* had higher frequency in heterogeneous than homogeneous treatments.

Average species richness did not differ between soil treatments at the plot scale, with homogeneous treatments having a richness of 33.6, and heterogeneous treatments a richness of 34.4 ( $df = 1$ ,  $F = 0.516$ ,  $P = 0.51$ ). However, rarefaction curves showed increased richness in heterogeneous over homogeneous soil treatments at a stem count of approximately 11,500 stems (Fig. 2). This count corresponds to an approximate area of 11.7m<sup>2</sup> based on the density-area relationship for heterogeneous plots. There was a significant difference in species richness between soil patch types ( $df = 3$ ,  $F = 3.17$ ,  $P = 0.024$ ), with Soil Patch Type 3 having a significantly higher species richness than the Mixed Soil Patch Type ( $P = 0.028$ ; Table 1). No other patch types had significant differences in richness ( $P > 0.05$ ). PERMANOVA revealed a significant difference in species abundances between soil treatments ( $df = 1$ , pseudo- $F = 5.829$ ,  $P$

= 0.018). However, results of multiple t-tests showed only three species with significant differences in abundance between soil treatments (Table 2).

#### *Univariate Spatial Patterns in Homogeneous Soils*

Of the 13 species analyzed with univariate O-ring analysis within homogeneous plots, 12 (92%) were intraspecifically aggregated (Fig. 3). Only *C. altissimum*, an unsown, weedy species from the sunflower family, showed no deviation from a random expectation. All other species demonstrated some level of fine-scale non-random spatial structure at 5-10 cm, although most species were also aggregated at larger scales. Only *Andropogon gerardii*, *Baptisia australis*, *Echinacea angustifolia*, and *Salvia azurea* were intraspecifically aggregated exclusively within 10 cm around focal plants. Four other species (*Panicum virgatum*, *Schizachyrium scoparium*, *C. fasciculata*, *Lespedeza capitata*) aggregated up to a 50 cm radius around focal individuals, while the remaining four (*S. nutans*, *A. psilostachya*, *R. hirta*, *M. fistulosa*) aggregated at scales larger than 50 cm.

Bare ground was spatially aggregated from 5-65 cm in the homogeneous treatment, which was twice the size as that in heterogeneous plots (Fig. 3). This suggests that there were patches over a meter across where the density of plants was lower in the homogeneous treatment, and such patches were roughly half of that size in the heterogeneous treatment.

#### *Univariate Spatial Patterns in Heterogeneous Soils*

Spatial analysis of the three soil patches comprising the heterogeneous treatment was used to estimate the scale at which plants were expected to respond to soil heterogeneity. If patches of the same type were isolated from one another, the expectation is that soil types would

aggregate at an approximate scale of 20 cm, equivalent to the radius of a 40x40 cm patch.

However, univariate spatial analysis of individual soil patches showed aggregation of the patches to a scale of 35 cm for Upper and Middle Strata, and 40 cm for Lower Stratum. Aggregation of soil patches was larger than 20 cm because there were only three patch types, and it was common to find adjacent patches with the same soil type, effectively creating larger patches of each soil. Plant spatial patterns associated with soil patches were therefore expected to occur at scales from 35-40 cm.

The same 12 species that were intraspecifically aggregated in the homogeneous treatment were also intraspecifically aggregated in the heterogeneous treatment, although the scale often differed (Fig. 3). Three species (23%), *S. nutans*, *S. azurea* and *A. gerardii* had no difference in the scale of aggregation between soil treatments. Five species (38.5%), *R. hirta*, *C. fasciculata*, *S. scoparium*, *B. australis*, and *E. angustifolia*, aggregated in heterogeneous treatments not only at most scales present in homogeneous treatments, but also at additional larger scales only present in heterogeneous treatments (Fig. 3). For four of these species (30.8%), *C. fasciculata*, *S. scoparium*, *B. australis*, and *E. angustifolia*, the additional aggregation occurred from 20-40 cm, roughly corresponding with the scale of soil patches (Fig. 3). One species, *L. capitata* was aggregated at a larger upper scale in homogeneous treatments, but this only occurred at a single scale of 50 cm, contrasted to the presence of continuous aggregation from 0-45 cm in heterogeneous treatments. Three species (23%), *M. fistulosa*, *A. psilostachya*, and *P. virgatum*, and bare ground were aggregated at smaller scales in heterogeneous than homogeneous treatments, with *A. psilostachya* and bare ground the only two restricted by more than 5 cm (Fig. 3).

In addition to individual species' differences, aggregation patterns varied within and between functional groups, with legumes and mints demonstrating the most consistent response to soil heterogeneity within their family (Fig. 3). All three legume species (*L. capitata*, *C. fasciculata*, and *B. australis*) had additional scales of aggregation in heterogeneous but not homogeneous treatments corresponding to the scale of soil patches found in heterogeneous treatments. Aggregation of mints (*M. fistulosa*, *S. azurea*) was essentially consistent between soil treatments, although *M. fistulosa* aggregated at a slightly larger scale in homogeneous treatments. Responses in grasses and sunflowers were more varied. Spatial aggregation for two grasses (*S. nutans*, *A. gerardii*) was consistent between soil treatments, while *S. scoparium* aggregated at a larger scale in heterogeneous than homogeneous treatments corresponding to the scale of soil patches. The one rhizomatous grass, *P. virgatum*, had a slightly smaller scale of aggregation in heterogeneous than homogeneous treatments. Among sown sunflowers, *R. hirta* and *E. angustifolia* had larger scales of aggregation in heterogeneous than homogeneous treatments. For unsown sunflowers, *C. altissimum* did not aggregate in either treatment, while *A. psilostachya* had larger scales of aggregation in homogeneous than heterogeneous treatments.

Cumulative spatial patterns between the two soil treatments also revealed important similarities and differences). Below 15 cm, most of the species analyzed aggregated in homogeneous and heterogeneous treatments (Fig. 4), and the identity of these species was the same (Fig. 3). Cumulative aggregation declined in a roughly linear function beyond 15 cm in both soil treatments, yet nearly 50% of the analyzed species remained spatially aggregated to a radius of 50cm (Fig. 4). Additionally, a spike in cumulative aggregation occurred at 20-35 cm in the heterogeneous treatment, similar to the spatial scale of soil patches in the heterogeneous

treatment. Above 35 cm the linear decline in aggregation was once again roughly the same between treatments.

### *Bivariate Spatial Associations between Species and Soil Patch Type*

Bivariate analysis of individual species patterns with soil patch type patterns can reveal whether species occur more frequently in the neighborhood of certain soil patch types if the relationship is a positive association (attraction), or less frequently if a negative association (segregation), potentially providing further insight into whether species sort into specific soil patches. In heterogeneous plots, 11 of the 13 species as well as bare ground were spatially associated (either attracted or segregated) with at least one soil patch type at scales  $\geq 5$  cm, although the scales differed (Fig. 5). Specifically, ten species (77%) were associated with the Soil Patch Type 1, 7 species (54%) with the Soil Patch Type 2, and 8 species (62%) with the Soil Patch Type 3.

Within soil patches found in heterogeneous plots, the spatial scale of attraction and segregation varied by soil patch type. Attraction to Soil Patch Type 1 occurred exclusively within 50 cm, within 90 cm for Soil Patch Type 3, and at all scales with Soil Patch Type 2 (Fig. 6). Segregation from soil was less common, and occurred below 30 cm and above 55 cm with Soil Patch Type 1, from 40-65 cm in Soil Patch Type 2, and at 10 cm and from 20-45 cm in Soil Patch Type 3 (Fig. 6).

Individual species also differed in their spatial associations with the three soil patch types. Most species were associated with more than one soil patch type, and usually at non-overlapping scales (exceptions being *S. azurea*, *S. nutans*, *B. australis*; Fig. 5). All species that were segregated from one soil patch type at small scales were also attracted to either one or two

other soil patch types at those same scales (*S. azurea*, *B. australis*, *L. capitata*, *E. angustifolia*; Fig. 5). Three of these species, *B. australis*, *L. capitata*, and *E. angustifolia* demonstrated univariate aggregation at larger scales in heterogeneous than homogeneous treatments. However, *C. fasciculata*, which aggregated at larger scales in heterogeneous than homogeneous treatments, was not associated with any soil patch type in the heterogeneous treatment. In addition, several species were associated with soil patch types, but did not have differences in univariate aggregation between soil treatments at the expected scale of soil patches. Cells containing bare ground were attracted to Soil Patch Type 3 at scales of 0-20 cm.



## CHAPTER 4

### DISCUSSION

My results suggest that even when soils and seed arrival were experimentally homogenized, significant species aggregation developed in 12 of 13 most common species after five years of community establishment. With exogenous environmental heterogeneity and seed dispersal effectively removed as drivers of spatial patterns, these results suggest that endogenous processes created spatial structure in this grassland as the plants interacted with their environment.

#### *Endogenous Drivers of Spatial Patterns*

At fine scales, nearly every species developed spatial aggregation under homogeneous seeding and soil conditions, suggesting endogenous mechanisms such as clonal growth and facilitation are common. Not surprisingly, two bunch grasses (*A. gerardii*, *S. scoparium*) aggregated almost exclusively at a distance between 5-10 cm, likely due to their clonal growth strategy (Benot et al. 2013, Semchenko et al. 2013). Yet clonality was not the only mechanism driving fine-scale aggregation, as several forb species (*L. capitata*, *B. australis*, *S. azurea*, *E. angustifolia*), which are weakly clonal if at all, were also aggregated at the 5-10 cm scale. Instead, fine-scale aggregation may occur because of facilitation among conspecifics (Jiang et al. 2011, Punci-Manage et al. 2015). For example, one greenhouse experiment found that competition and facilitation among hetero- and conspecifics extended to scales of 15 cm (Vogt et al. 2010), consistent with the scale of aggregation observed in my experiment. Furthermore, legumes, such as *L. capitata* and *B. australis*, may facilitate conspecifics through enhancement

of mutualists that can be important for nitrogen fixation (Temperton et al. 2007, Roscher et al. 2016).

Perhaps more surprising than fine-scale spatial structure was the frequency of aggregation that extended well beyond the expected plant neighborhood. Typically for sessile organisms, interactions are likely at the interface between root or shoots or neighboring individuals. Yet, I found aggregation at scales from 50-120 cm, which is well beyond the size of individuals (e.g. *S. nutans*, *R. hirta*, and *M. fistulosa*, Fig. 3). Such large-scale patterns might be explained by seed dispersal from outside the community or underlying environmental heterogeneity, but both factors were homogenized in this experiment. One possibility is that these species facilitate establishment or growth of conspecifics driven by plant-soil feedbacks associated with mycorrhizae or other microbes (Callaway 1995, van der Heijden and Horton 2009, Markham et al. 2011), with these benefits passed among individuals at small scales resulting in larger-scale spatial aggregation. Additionally, litter accumulation may reduce heterospecific success near dominant grasses, encouraging aggregation of conspecifics, either in clumps where grasses do not occur, or the aggregation of grasses themselves (Bascompte and Rodriguez 2000). The litter hypothesis is made more likely here because plots were not burned during the first four years, potentially increasing the importance of litter interference during resource acquisition or growth. However, it is impossible to determine how litter influenced patterns with this experiment, as no measurements of accumulated litter were taken. Still, these endogenously-driven mechanisms may be particularly important given that the aforementioned species are the three dominants in the experiment and likely to have cascading effects on spatial patterns for the remaining species.

Although seed dispersal did not generate intraspecific aggregation for most species, some species did disperse into plots from the surrounding grassland or emerged from the seedbank. Additionally, some species were annuals or biennials that likely produced seed over the four years of community establishment. This suggests that limited seed dispersal, which is another endogenous source of spatial structure, may have contributed to aggregation of some species. Specifically, *A. psilostachya* and *C. fasciculata* are both weedy annuals that were not included in the original seed mix that aggregated up to scales of 70 cm and 30 cm, respectively, potentially reflecting short-distance dispersal around parent plants. Among those species purposefully seeded, *R. hirta* is the most likely to have set seed during the course of the experiment, and aggregation of this species would include the influence of local seed dispersal. However, this experiment cannot attribute the relative importance of these different potential sources of endogenously driven spatial structure for these species.

Despite a clear emergence of spatial structure in this community, I found no evidence for the over-dispersion of conspecifics, such as predicted by the Janzen-Connell hypothesis (Janzen 1970) or competition (Murrell and Law 2003). Evidence for Janzen-Connell effects have been found in systems worldwide (Comita et al. 2014), and plant-soil feedback experiments in grasslands suggest that Janzen-Connell processes could contribute to the coexistence of grassland species (Petermann et al. 2008). However, my results suggest that negative plant-soil feedbacks or host-specific pests did not limit establishment of individuals near conspecifics in the early stages of community development. This could reflect the relatively young age of the experiment, as Janzen-Connell processes involve establishment of offspring around adults, with adults aggregating while seedlings do not (Murrell 2009). Most of the species did not set seed by

the time of data collection, suggesting there may not have been time for these processes to influence spatial patterns.

The results presented here contribute to the growing body of evidence that endogenous processes are important to establishing spatial structure in plant communities. Seabloom et al. (2005) found that significant aggregation developed at scales from 1-2 m in a restored grassland with initially homogeneous conditions, reaching scales >4 m in later years, that they attributed to competition between heterospecifics and seed dispersal limitation. Point-pattern spatial analysis in tropical and temperate forests suggest widespread facilitative and competitive interactions between both hetero- and conspecifics that contribute to a wide array of spatial patterns observed in these systems (Wiegand et al. 2007, Wang et al. 2010, Nguyen et al. 2016). However, these studies were all limited in their ability to distinguish between the influence of endogenous and exogenous processes on spatial patterns, as experimental treatments did not completely homogenize soils or include a heterogeneous treatment.

### *Exogenous Drivers of Spatial Patterns*

Here I define exogenous factors as those processes that are not dependent on the resident plant community such as soil heterogeneity prior to plant colonization, immigration from outside the community, or disturbances. Disentangling exogenous from endogenous effects on plant spatial structure is difficult, as both processes can generate similar patterns. For example, John et al. (2007) reported spatial associations between 36-51% of tropical tree species and soil nutrients, and Phillips et al. (2003) found 76.5% of Amazon tree species were significantly related to specific habitats. However, seed dispersal was not controlled in these experiments, and

it is impossible to clearly distinguish whether plants responded to exogenous differences in soil properties or whether established plants altered soil conditions endogenously.

I found that exogenously derived soil heterogeneity had small effects on cumulative aggregation relative to endogenous processes. Seven species aggregated at different scales (>5 cm difference) in heterogeneous than homogenous treatments indicating exogenous soil patchiness influenced spatial patterns. This difference was most clear from approximately 20-40 cm (corresponding with the spatial scale of soil patches in heterogeneous plots), where cumulative interspecific aggregation revealed a peak in aggregation only present in the heterogeneous treatment (Fig. 4). However, cumulative aggregation was relatively consistent at other scales, with similar peaks in aggregation at 5-15 cm for both plot types, and similar trends of decreasing aggregation above 40cm.

While overall community differences in spatial patterns were small, they were restricted to soil patches in heterogeneous plots, suggesting that for some species soil conditions were important in developing spatial aggregation. Five species (*L. capitata*, *C. fasciculata*, *S. scoparium*, *B. australis*, and *E. angustifolia*) had a clear increase in aggregation from small-scales  $\leq 15$  cm in homogeneous plots to approximately 30-40 cm in heterogeneous plots, corresponding with scales of soil patches (Fig. 3). Furthermore, these species were also significantly associated with soil patch types at scales of approximately 40 cm (Fig. 5) suggesting that differences in plant aggregation between treatments were in response to soil patches.

In addition to differences in individual species spatial patterns, bivariate spatial analysis within heterogeneous plots indicated that 11 of 13 species were attracted to at least one soil patch type at scales corresponding with soil patches suggesting these species performed relatively

better in some soil types over others (Fig. 5). This response is consistent with species sorting patterns found after two years of community assembly (Williams and Houseman 2013).

However, species spatially associating with soil patch types did not always correspond with detectable differences in spatial aggregation between soil treatments. In this system, examples of species with consistent patterns were grasses and forbs that are known to spread clonally (*S. nutans*, *M. fistulosa*, and *A. gerardii*). So while bivariate spatial analysis suggests their location in plots may have been influenced by soil patches, consistent univariate patterns between soil treatments indicate aggregation was primarily influenced by some process other than soil patchiness.

Further evidence for the importance of endogenous processes over exogenous processes in this grassland is that no species aggregated exclusively in heterogeneous plots. So while soil heterogeneity appears to have altered the scale of aggregation for some species, it was never the sole driver of spatial patterns. This indicates that endogenous processes created most of the spatial structure in this community, especially over small scales  $\leq 15$  cm, where patterns were nearly identical between treatments in each species.

A final exogenous process that may have influenced spatial patterns in this grassland system was seed dispersal from outside of plots. Two species with large scales of aggregation, *C. fasciculate* and *A. psilostachya*, were not sown into plots, and these large aggregation patterns could indicate a gradient across plots as a result of dispersal from the surrounding grassland (Wiegand and Moloney 2014).

### *Non-Spatial Community Responses*

While some differences exist in the scales of aggregation between species in different soil treatments, there was modest evidence for effects on species abundance and richness. While species richness did differ between Soil Patch Type 3 and the Mixed Soil Patch type, richness did not vary between treatments at the plot scale, suggesting that increased aggregation of conspecifics in heterogeneous plots has not contributed to coexistence of a greater number of species. However, richness was higher in heterogeneous plots after two years (Williams and Houseman 2013), and results of rarefaction also suggest that richness at larger scales is higher in heterogeneous than homogenous plots. This indicates that heterogeneity may influence richness in grasslands, but the importance of heterogeneity may differ depending on community age or spatial scale.

There were significant differences in overall community species composition (PERMANOVA results). Specifically, three species (*R. hirta*, *M. fistulosa*, *A. psilostachya*) differed in abundance depending on soil conditions (Table 2). While few species were impacted by soil heterogeneity in their abundance, *R. hirta* and *M. fistulosa* were two of the most common species in either treatment, and therefore changes in their abundances could have impacts on less common species around them.

The difference in patterns of bare ground between treatments is also interesting, and indicates a difference in overall plant distribution. While total cover of bare ground was the same between treatments, cells of bare ground aggregated at smaller scales in heterogeneous plots and corresponded with the size of soil patches. Bivariate analysis of soil patch type and bare ground indicated attraction of bare ground to Soil Patch Type 3, suggesting plants were less successful or were more widely spaced in this soil patch type.

Whether the differences seen in the distribution of bare ground, species abundances, or patterns of aggregation between treatments would result in longer-term differences in richness or species coexistence will require monitoring this system over longer time periods. In addition, bivariate spatial analysis of the associations between pairs of species in this system could reveal changes to the patterns of species-species interactions. Changes in the types of interactions between species could impact coexistence, and how these interactions have been altered by soil heterogeneity could provide further insight into the dynamics of this community.



## CHAPTER 5

### CONCLUSIONS

My experiment attempted to overcome the limitations of previous studies of fine-scale spatial patterns by experimentally controlling soil heterogeneity and seed dispersal. Processes unrelated to soil heterogeneity and seed dispersal created non-random, aggregated patterns for the majority of common species in an experimental grassland after four years of community establishment. This suggests that endogenous processes such as facilitation and clonal growth were more important in structuring spatial patterns in this community than exogenous heterogeneity. Though research suggests aggregation of conspecifics can lead to increased species richness, my results suggest that greater aggregation of some species in heterogeneous conditions did not lead to higher richness after four years. However, slight differences in rarefaction curves and species abundances suggest differences in aggregation may become increasingly important as community assembly continues to unfold. Though it is not possible in this experiment to determine exactly which processes created specific patterns of aggregation in individual species, overall patterns indicate that endogenous processes are most important for structuring spatial patterns of aggregation in grasslands, and that these processes may contribute most to understanding plant coexistence in this ecosystem.

Table 1. Average species richness in 40x40 cm soil patch types comprising heterogeneous and homogeneous soil treatments (Soil Patch Types 1,2,3 (n=60), Mixed Soil Patch Type (n=180)), and between homogeneous and heterogeneous plots (n=5).

<b>Soil Patch Type</b>	<b>Species Richness</b>	
	<b>Mean</b>	<b>Standard Error</b>
Soil Patch Type 1	10.0	0.25
Soil Patch Type 2	10.2	0.28
Soil Patch Type 3	10.6	0.31
Mixed Soil Patch Type	9.7	0.15
<b>Treatment</b>		
Homogeneous	33.6	0.98
Heterogeneous	34.4	1.03

Table 2. Results of two-tailed t-test with log transformed data, for differences between homogeneous and heterogeneous plots for the most common species (n=5). \* indicates a significant difference between soil treatments ( $p < 0.05$ ).

<b>Species</b>	<b>t-value</b>	<b>p-value</b>
<i>Sorghastrum nutans</i>	-1.005	0.3442
<i>Rudbeckia hirta</i>	-2.497	0.0371*
<i>Monarda fistulosa</i>	3.140	0.0138*
<i>Chamaecrista fasciculata</i>	0.000	1.0000
<i>Schizachyrium scoparium</i>	-0.681	0.5099
<i>Ambrosia psilostachya</i>	4.004	0.0039*
<i>Andropogon gerardii</i>	-0.423	0.6833
<i>Lespedeza capitata</i>	0.999	0.3469
<i>Salvia azurea</i>	1.393	0.2012
<i>Panicum virgatum</i>	-0.394	0.7038
<i>Echinacea angustifolia</i>	0.640	0.5401
<i>Baptisia australis</i>	-0.325	0.7539
<i>Cirsium altissimum</i>	0.396	0.7022
Bare ground	-0.184	0.8588

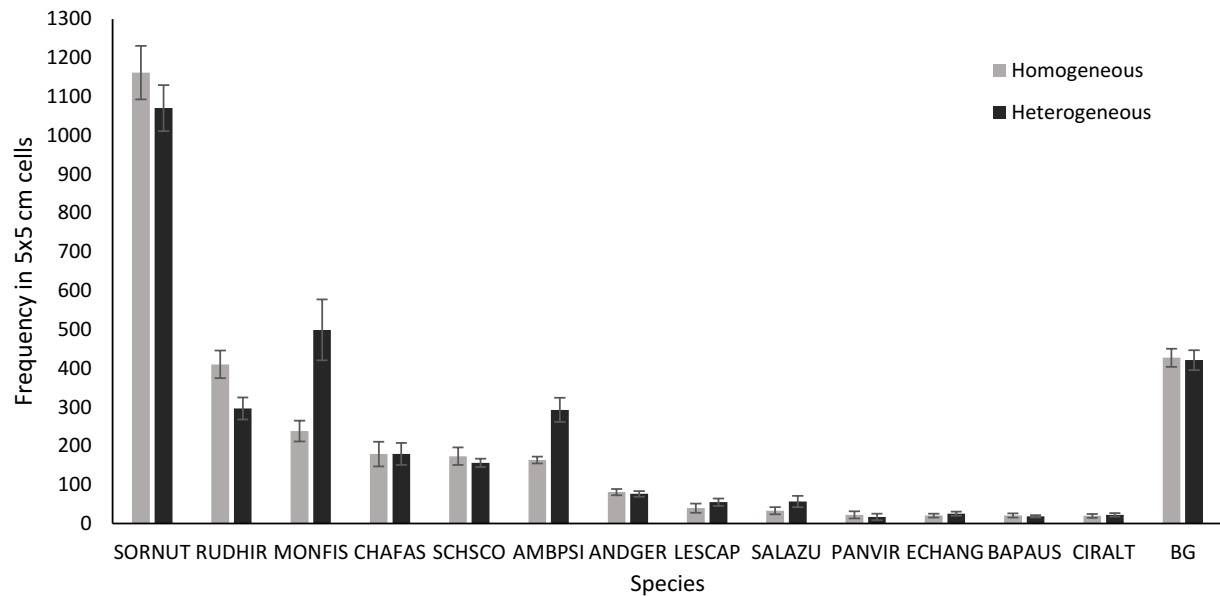


Figure 1. Mean number of 5x5 cm cells within each 2.4x2.4 m plot occupied by 13 most common species (SORNUT = *Sorghastrum nutans*, RUDHIR = *Rudbeckia hirta*, MONFIS = *Monarda fistulosa*, CHAFAS = *Chamaecrista fasciculata*, SCHSCO = *Schizachyrium scoparium*, AMBPSI = *Ambrosia psilostachya*, ANDGER = *Andropogon gerardii*, LESCAP = *Lespedeza capitata*, SALAZU = *Salvia azurea*, PANVIR = *Panicum virgatum*, ECHANG = *Echinacea angustifolia*, BAPAUS = *Baptisia australis*, CIRALT = *Cirsium altissimum*) and bare ground (BG) for homogeneous and heterogeneous soil treatments. n=5. Error bars = 1 SE.

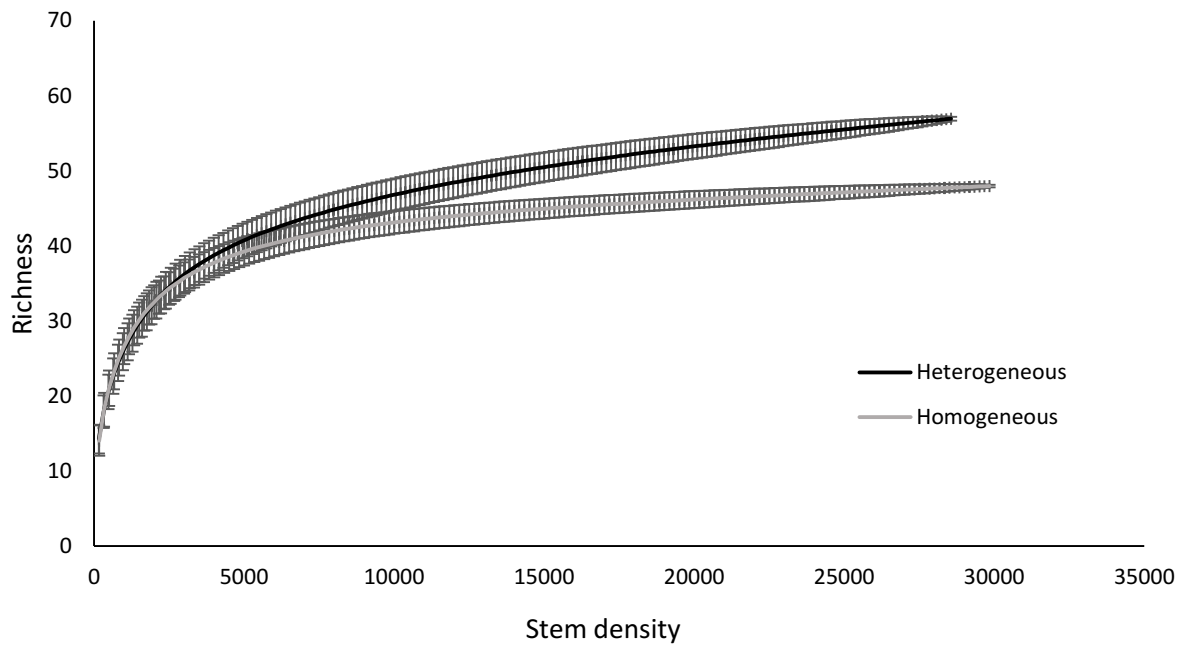


Figure 2. Rarefaction curves estimating accumulated richness as a function of stem density across homogeneous and heterogeneous plots. Estimates based on resampling of stem density and richness within individual patches.

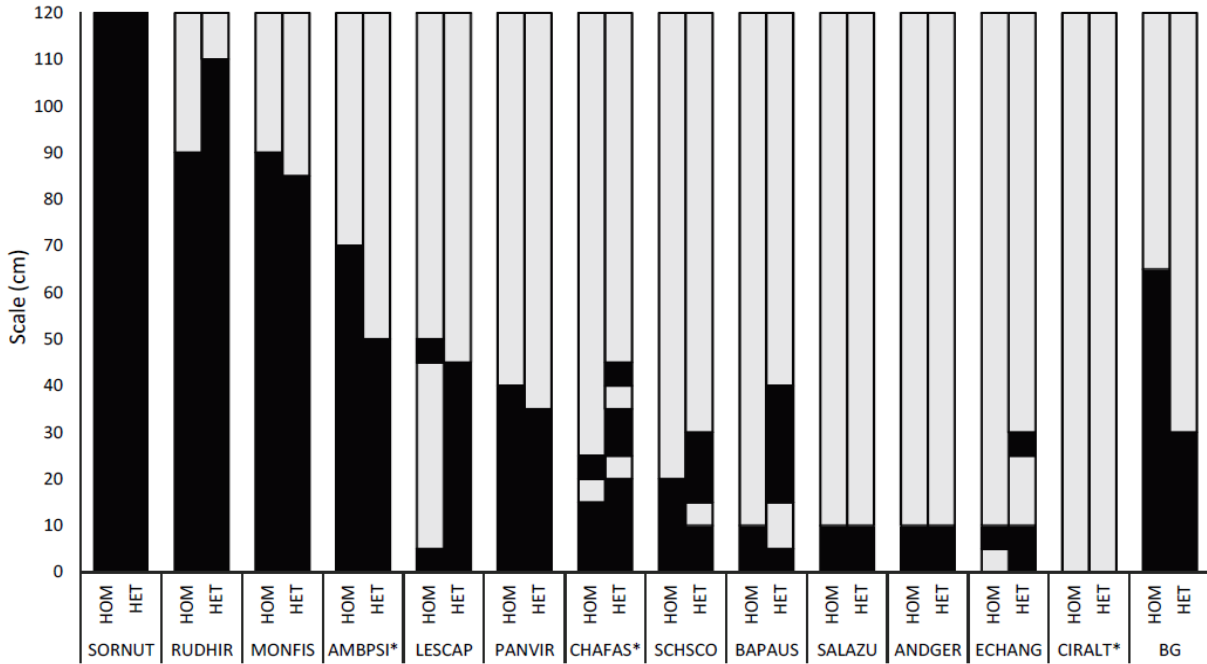


Figure 3. Scale of intraspecific aggregation (black) or random (gray) spatial patterns for the thirteen analyzed species and bare ground (abbreviations follow Fig. 1) in homogeneous and heterogeneous plots. Detection of aggregation based on a test statistic outside the 95% simulation envelopes constructed with a CSR null model. \* indicates species not sown in the original seed mix.

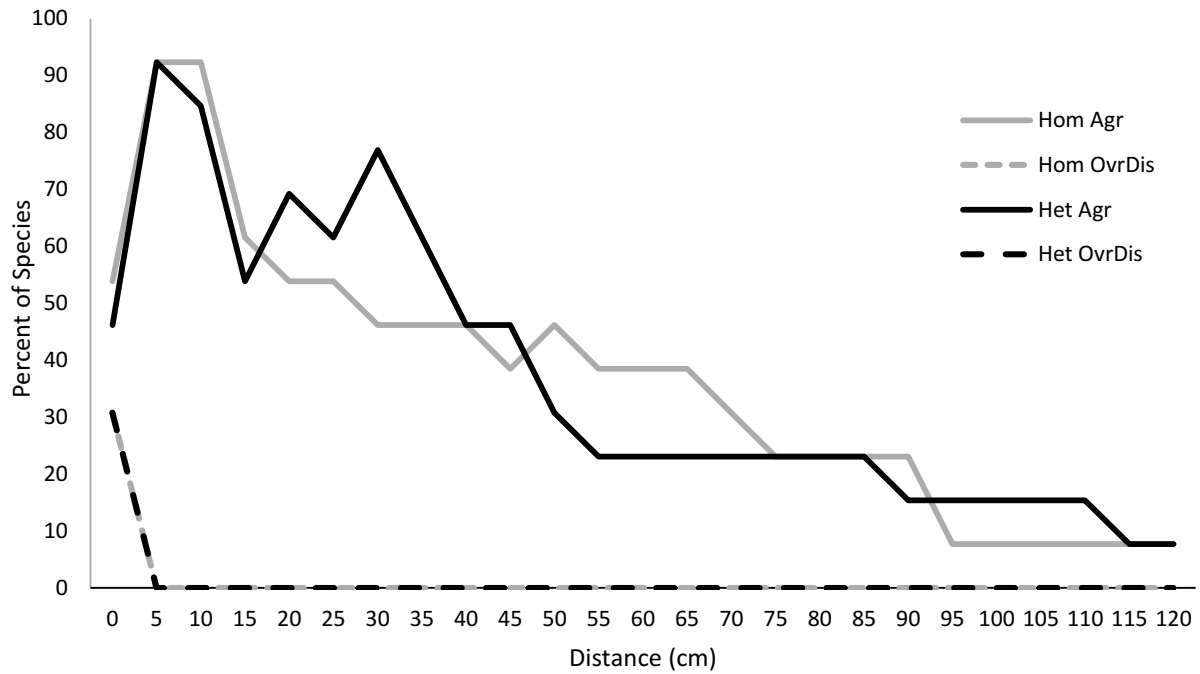


Figure 4. Percentage and type of non-random spatial patterns out of 13 species around focal plants in homogeneous (Hom) and heterogeneous (Het) soil treatments. Agr = aggregation of species' patterns, OvrDis = over dispersion of patterns.

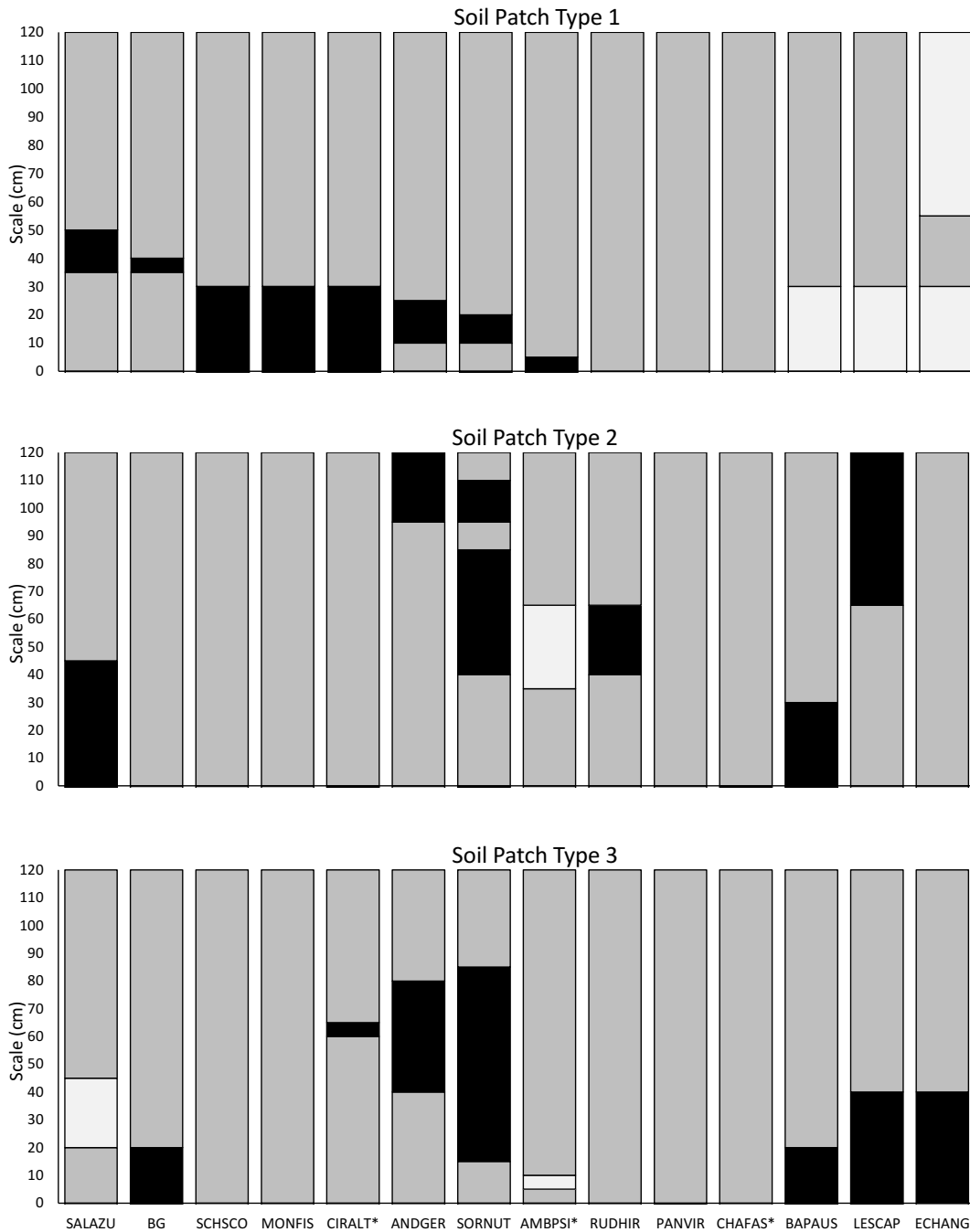


Figure 5. Significant spatial associations between 13 species and bare ground (abbreviations follow Fig. 1) with three separate soil patch types present in heterogeneous plots. Species arranged from left to right based on largest scale of attraction to largest scale of segregation with the Soil Patch Type 1. Black = attraction between patterns, gray = no association between patterns, light gray = segregation of patterns. \* indicates species not sown in the original seed mix. Individual soil patches aggregated at a scale of 40 cm, approximately twice as large as individual patches because patches of the same soil were often adjacent to one another.



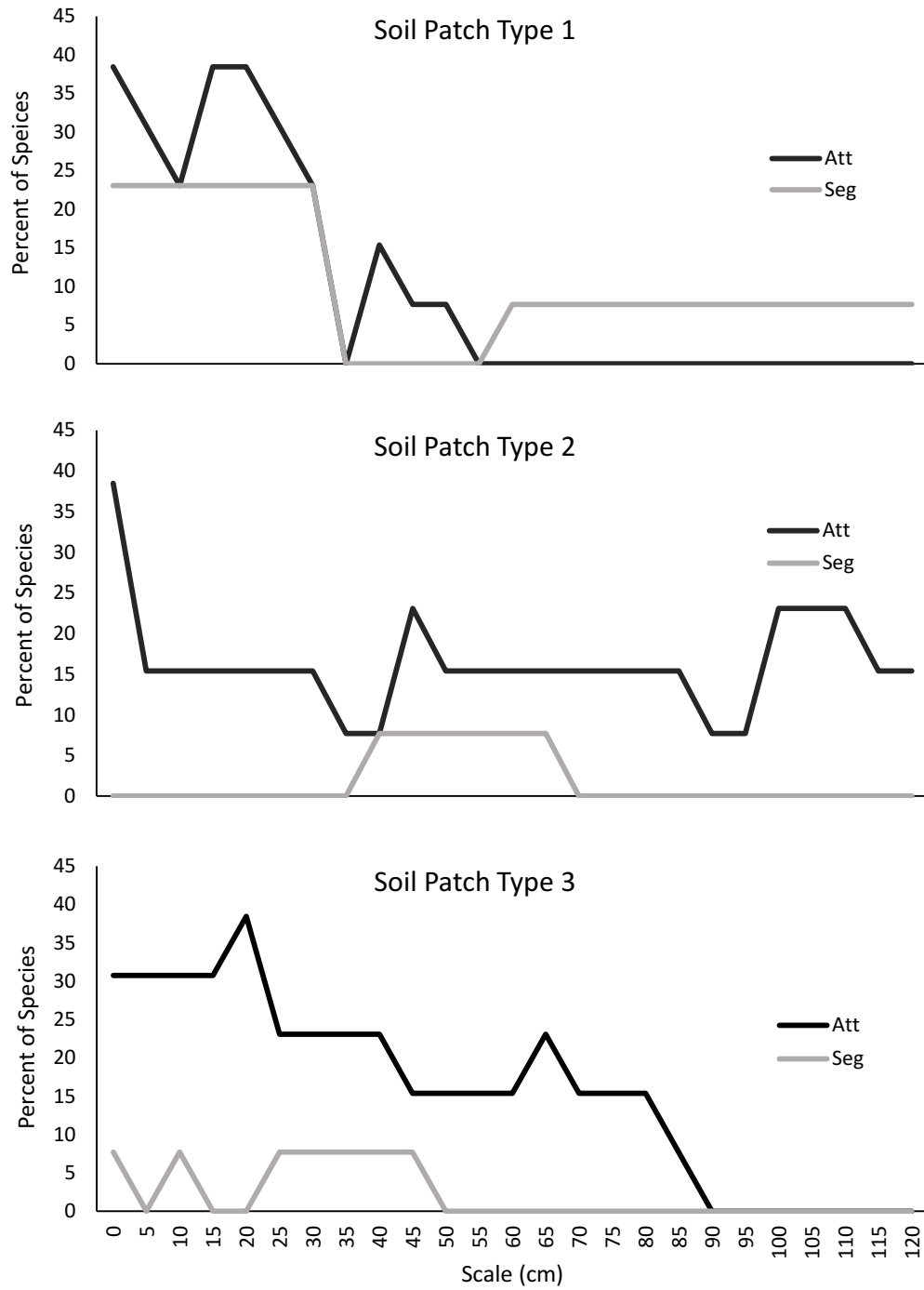


Figure 6. Percentage of species that were spatially attracted (Att) to or segregated (Seg) from each soil patch types in heterogeneous plots.

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