

RESEARCH ARTICLE

Spatial patterns of stand structure and canopy disturbance in a fire-maintained *Pinus palustris* woodland

David L. Phillips  | J. Davis Goode  | Justin L. Hart 

Department of Geography, University of Alabama, Tuscaloosa, Alabama, USA

Correspondence

David L. Phillips, Department of Geography, University of Alabama, Tuscaloosa, AL, USA.
Email: dlphillips1@crimson.ua.edu

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Abstract

Question: Stand structural complexity is increasingly valued by forest managers to promote resilience, and quantitative spatial data from reference stands can help achieve these goals. We questioned how stand structural elements were spatially distributed across a *Pinus palustris* woodland. Specifically, we sought to quantify patterns of individual trees, tree clumps, openings, and canopy disturbance and examine spatial relationships between *P. palustris* saplings and *P. palustris* and *Quercus* spp. trees.

Location: Fall Line Hills, Alabama, USA (32°56'12" N, 87°25'37" W).

Methods: We recorded tree species, diameter, age, and location of all trees, and reconstructed canopy disturbance events across a 1-ha site in a *P. palustris* woodland. We used global point pattern analysis ($g(r)$ function) and a local spatial classification method (individuals, clumps, and openings) to examine the distribution of stand structural elements and canopy disturbance.

Results: Trees were generally clustered by taxa and diameter. *Pinus palustris* saplings exhibited no spatial relationship with *P. palustris* trees, but were clustered around *Quercus* trees at variable distances. Approximately half of the trees in the stand occurred in large clumps, and ca. 10% of trees occurred as individuals that did not touch crowns with neighbors. For three of the five disturbance periods, canopy disturbances were clustered in space at various distances.

Conclusions: Spatial randomness and clustering of structural elements and canopy disturbance events were evident across the reference site. The spatial patterns of stand structure quantified here, in conjunction with data from other georeferenced studies, can be used to develop silvicultural guidelines to enhance structural complexity and promote resilience.

KEYWORDS

canopy gap, point pattern analysis, regeneration, scale, silviculture, spatial complexity

1 | INTRODUCTION

Anticipated shifts in forest disturbance regimes driven by global change have prompted widespread interest in managing for forest ecosystem resilience (Turner, 2010; Seidl et al., 2016). Ecosystem resilience is defined by the capacity of a disturbed ecosystem to maintain its intrinsic structures, feedbacks, and functions (Holling, 1973). Resilience is assessed by the rates and trajectories of ecosystem recovery (Angeler & Allen, 2016). The resilience of a forest ecosystem to perturbations and stresses is dictated in part by forest structure and accordingly, structural complexity is being prioritized in forest management plans (Keeton, 2006; O'Hara, 2014; Peck et al., 2014). Forest structure is the vertical and horizontal distribution of tree biomass within a stand (Zenner & Hibbs, 2000; Franklin & van Pelt, 2004). Stands that exhibit a wide range of individual structures and a heterogeneous distribution of those structures contain the breadth of conditions required to sustain high species and functional diversity (Seidel et al., 2019; Palik et al., 2021).

Stand structure has traditionally been quantified and assessed by mean stand-wide metrics that ignore spatially-explicit structural patterns within stands. This has in part resulted in considerable homogeneity in many managed systems (Puettmann et al., 2009; Palik et al., 2021). Silvicultural treatments applied uniformly (i.e., those that fail to recognize spatial dimensions of structure) typically produce homogenous stand structures that inherently lack structural complexity and consequently have lower adaptation potential than structurally heterogeneous stands. Although elements of stand structure have long been recognized in silvicultural systems, increased emphasis has recently been focused on the spatial arrangement of trees within stands (Sanchez Meador et al., 2011; Churchill et al., 2013; Lydersen et al., 2013). Despite increasing appreciation for the spatial aspects of stand structure, spatially-explicit data are still required to develop silvicultural systems that incorporate spatial dimensions of stand structure into management (Churchill et al., 2013). Thus, spatial information on stand structure from reference stands is essential for managers who wish to enhance structural complexity, which is a central tenant of ecological silviculture (Palik et al., 2021).

In forest ecosystems in which tree species diversity is low, stand structural complexity is an especially critical component of ecological resilience (Neumann & Starlinger, 2001). *Pinus palustris* woodlands of the southeastern USA exemplify this phenomenon (Sharma et al., 2020). Although these ecosystems are noted for high plant diversity of the ground flora (Walker & Silletti, 2006; Dell et al., 2017), tree species richness in the canopy stratum is considerably low because *P. palustris* often occurs in nearly pure stands. Once covering ca. 37 million hectares of the southeastern USA, *P. palustris* forests have been reduced to occupy less than 5% of their former distribution (Frost, 1993; Gilliam & Platt, 1999; Jose et al., 2007). Consequently, *P. palustris* ecosystems have been considered among the most endangered in the USA (Noss et al., 1995). Remnant *P. palustris* stands that lack structural complexity are at increased risk of transitioning to alternative states from disturbance or other stresses (Beckage et al., 2006; Ojha et al., 2021). Intentional enhancement of

structural complexity via silvicultural intervention is hypothesized to increase resilience and ecosystem adaptation potential in *P. palustris* and other monospecific, or largely monospecific, forest ecosystems (O'Hara, 2014; Nagel et al., 2017; Puettmann et al., 2009).

Contrary to many forest types, in *P. palustris* stands, spatial patterns have long been recognized and even successfully incorporated into management (i.e., the Stoddard-Neel method; Jack et al., 2006; Neel et al., 2010). However, the existing silvicultural approach has been criticized because it does not translate well into quantifiable treatment guidelines and has been difficult to teach to timber markers (Way, 2006; O'Hara, 2014). A variety of methods exist to translate natural stand-level spatial variability of structure into tree-marking guidelines, and the individuals, clumps, and openings (ICO) approach is one such method. ICO is based on conceptualizing and quantifying stand-level spatial structure in terms of widely spaced individual trees, variably sized clumps of trees (tree patches), and openings (tree-less patches; Larson & Churchill, 2012; Churchill et al., 2013). Trees are categorized as individuals (their crown does not touch that of a neighbor) or grouped into clumps (their crown touches that of at least one neighboring tree). Traditionally, a single crown width is used for every tree in the stand (based on field measurements for canopy widths of mature trees in the target stand). Silvicultural prescriptions derived from the ICO approach are based on established targets for individual trees, clumps, and openings developed from reference stands. This method has been used successfully to set spatial structure guidelines in frequent-fire forests of the western USA, and we suggest that this approach is applicable to *P. palustris* woodlands in the southeastern USA as well. The overarching goal of our study was to quantify spatial patterns of stand structure and composition in a fire-maintained *P. palustris* woodland to provide initial spatially-explicit reference conditions that can be used to build a more comprehensive understanding of spatial variability in *P. palustris* ecosystems that will ultimately inform silvicultural systems. Specifically, we sought to: (a) quantify the intrastand distribution of trees by species and diameter and reconstructed canopy disturbance; (b) document the local patterns of individuals, clumps, and openings (i.e., ICO); and (c) examine spatial relationships between *P. palustris* saplings and *P. palustris* and *Quercus* trees.

2 | METHODS

2.1 | Study area

This study was conducted on the Oakmulgee Ranger District of Talladega National Forest, Alabama, USA. Our reference site occurred within the Fall Line Hills ecoregion (Griffith et al., 2001) and the *Quercus-Pinus* forest region of Braun (1950). The Fall Line Hills are a physiographic transition zone at the intersection of the Appalachian Highlands and the Gulf Coastal Plain (Fenneman, 1938). Plant species richness in this region is relatively high because plant assemblages often contain taxa characteristic of both the Appalachian Highlands and the Coastal Plain (Shankman & Hart,

2007; Kleinman & Hart, 2018). Our study site was located within what Harper (1943) classified as the central *Pinus palustris* region. Here, *P. palustris*-dominated woodlands occur on fire-maintained ridgetops, upper slopes, and south-to-west facing mid-slope positions. On more mesic sites, *Quercus* and other hardwood species co-dominate with *Pinus taeda* (Beckett & Golden, 1982; Cox & Hart, 2015; Kleinman & Hart, 2018).

Soils in this region are of the Maubila–Smithdale complex. The Maubila series is moderately well-drained and consists of a 5-cm deep, flaggy loam A horizon, with clay Bt and C horizons. The Smithdale series is well-drained and consists of a sandy loam Ap and E horizons to 33 cm depth, with a sandy clay loam Bt1 horizon and sandy loam Bt2 horizon (USDA NRCS, 2020). The topography of the area is undulating and strongly dissected with steep slopes that commonly range from 30% to 35% (Boyer & Bledsoe, 1975), and elevation in the study area ranges from 90 to 160 m a.s.l. The climate of the region is humid mesothermal, characterized by long, hot summers and no distinct dry season (Thorntwaite, 1948). Mean temperature is 17.2°C, with mean January and July temperatures of 6.6°C and 26.9°C, respectively (PRISM, 2020). Mean annual precipitation is 1,376 mm (PRISM, 2020). The frost-free period is ca. 230 days from March to November (USDA NRCS, 2008).

2.2 | Field methods

We subjectively established a 1-ha permanent inventory site in a *P. palustris* stand that was identified by USDA Forest Service staff as exhibiting desired structural conditions (multiple age classes of canopy *P. palustris* and presence of *P. palustris* advance reproduction) and species composition for *P. palustris* woodlands on the Oakmulgee Ranger District. The stand was multi-aged and under a 2–4-year prescribed fire rotation. Prior silvicultural treatments included a timber stand improvement entry in 1979, a midstory removal in 1990, and a thinning from below in 1997. Within the reference stand, we established a 100 m × 100 m contiguous permanent site. The site was subdivided into 100 quadrats (10 m × 10 m each). We also established a 10-m buffer around the permanent site to account for edge effects.

We documented species, diameter at breast height (DBH, 1.37 m above the earth surface), and crown class for all trees (considered as live stems ≥5 cm DBH) on the 1-ha site (394 total trees). Crown class was based on the amount and direction of intercepted light (assessed visually), and classified as dominant, co-dominant, intermediate, or overtopped (Oliver & Larson, 1996). In addition, we documented all *P. palustris* stems ≥1 m height and <5 cm DBH and considered these individuals to be saplings on the 1-ha site. Only *P. palustris* saplings were analyzed in this study. From the southwest corner of each quadrat, we measured the distance using a hypsometer and transponder, and the azimuth using a sighting compass of all trees regardless of species and all *P. palustris* saplings to georeference stems across the permanent site. For the 10-m buffer zone, we documented species, DBH, and geographic location for all trees.

To quantify age structure and reconstruct canopy disturbance history, tree core samples were extracted from all tree-sized stems on the 1-ha site using an increment borer. We extracted a single core from each tree at a height ca. 50 cm above the earth surface. Each tree core sample was collected parallel to the slope to avoid reaction wood in the sample.

2.3 | Analytical methods

We used radial growth patterns to reconstruct canopy disturbance events. Tree-ring samples were processed based on the methods outlined in Stokes and Smiley (1996). Cores were air dried, mounted with cells vertically aligned, and sanded to reveal cellular structure. Tree rings were then dated to the calendar year of formation with the aid of a stereo zoom macroscope. When samples included substantial ring curvature but lacked pith, pith estimators were used to estimate tree age based on visible ring curvature (Villalba & Velben, 1997). After dating each radial growth ring to the year of formation, we used a Velmex measuring stage (Velmex Inc, 2009; Bloomfield, NY, USA) interfaced with Measure J2X software (version 4.2; VoorTech Consulting, 2008, Holderness, NH, USA) to measure raw ring width to the nearest 0.001 mm for all canopy dominant and co-dominant *Pinus* trees. COFECHA software (Version 6.06; Holmes, 1983) was used to test dating accuracy using segmented time-series (50-year segments with a 25-year overlap) correlation analysis. Segments below a pre-determined threshold ($r = 0.32$, $p > 0.01$) were flagged by the program, manually inspected for errors, and adjusted for dating if needed.

Once we were confident that each annual growth ring had been dated to the correct calendar year of formation, we used standard dendroecological techniques to quantify the occurrence of canopy disturbances based on statistically-defined release events for individual trees. To identify release events in radial growth trends, we used the 10-year running mean method (Nowacki & Abrams, 1997) in which releases had to be at least 25% greater than the mean of the 10 years preceding and succeeding and sustained for a minimum of 3 years (Hart & Grissino-Mayer, 2008; Hart et al., 2008, 2012, 2015). The location of all detected release events in the radial growth trends was mapped across the study site based on tree location, and the year of release initiation was recorded. To group reconstructed canopy disturbance events in time, we used the Jenks optimization method (Jenks, 1967). The resulting canopy disturbance periods were 1927–1950, 1952–1962, 1967–1977, 1981–1993, and 1994–2005.

To quantify the horizontal patterns of trees and canopy disturbances across the 1-ha site, we used point pattern analysis techniques (Baddeley et al., 2015). Specifically, we used the pair correlation function $g(r)$, which is a variation of Ripley's K function, the two most commonly used spatial descriptors in ecology (Velázquez et al., 2016; Ben-Said et al., 2020, 2022; Cannon et al., 2022). The pair correlation function uses discrete distance annuli (Wiegand & Moloney, 2004) to test the density of observed points

at multiple distances (r) against the expected density at distance (r). If the observed density is greater than expected ($g(r) > 1$), the points are considered clustered at distance (r). If the observed density is less than expected ($g(r) < 1$), the points are considered dispersed at distance (r). A univariate $g(r)$ was used for points of a single type (tree species, tree diameter, and reconstructed canopy disturbance periods), and a bivariate $g(r)$ was used for analyses with two point types (in our case, to test for significant attraction or repulsion between canopy *P. palustris* saplings and *P. palustris* trees, and between *P. palustris* saplings and Q. trees). The bivariate pair correlation function tests the intensity of one point pattern at radii centered on another point type. For the bivariate pair correlation function, values of $g(r) > 1$ indicate attraction and values of $g(r) < 1$ indicate repulsion.

To test for significant ($p < 0.05$) clustering or dispersion at 1-m intervals from 1 to 25 m, observed spatial patterns of tree attributes were compared with simulated estimates of heterogeneous Poisson null models. The heterogeneous Poisson null model was chosen over a null model of uniform intensity (i.e., complete spatial randomness) because heterogeneous environmental factors (e.g., draws and spurs) could have influenced spatial patterns. Null models were simulated 199 times with Epanechnikov kernel estimators with a bandwidth of 50 m. Of the 199 generated null models, the 5 highest and 5 lowest values were removed, resulting in a 95% confidence envelope of simulated spatial patterns with which to compare our observed spatial patterns. To account for edge effects, we used an isotropic transformation, which is commonly used for Ripley's K point pattern analysis in rectangular windows (Baddeley et al., 2015). A goodness-of-fit test for the null model was also performed.

For univariate analyses, if the observed $g(r)$ was above the envelope at distance (r), then there was significant ($p < 0.05$) clustering (note that a $g(r)$ value > 1 at distance (r) does not necessarily indicate significant clustering). If the observed $g(r)$ was below the envelope at distance (r), then there was significant dispersion (note that a $g(r)$ value < 1 at distance (r) does not necessarily indicate significant dispersion). Values of $g(r)$ contained within the envelope were not significantly clustered or dispersed, and were considered random (regardless of the $g(r)$ value at r). For bivariate analyses, $g(r)$ values above or below the envelope indicated significant attraction or repulsion, respectively, between variables. All point pattern analyses were performed in the grid-based software Programita (Wiegand & Moloney, 2004, 2014). For those seeking additional information on these methods, reference basic texts such as Diggle (2013).

Global spatial pattern analysis summarized the prevailing spatial trend over the entire reference stand, and local spatial analysis characterized the variation of spatial distribution within the study area. To examine the local variation of the prevailing spatial distribution of trees, we used the ICO method to quantify individual trees and characterize the size and number of clumps and openings within the stand (Plotkin et al., 2002; Churchill et al., 2013). Openings were delineated using Euclidian distance from canopy (intermediate,

co-dominant or dominant) trees. Clump compactness was calculated using the Polsby–Popper test. Polsby–Popper values are calculated as $(4\pi(\text{area}))/\text{perimeter}^2$, and range from 0 to 1, with 1 indicating maximum compactness of a perfect circle, 0.86 a hexagon, and 0.79 a square (Polsby & Popper, 1991). The traditional ICO method uses fixed-radius intervals to quantify the occurrence of individuals and tree clumps at multiple crown radii, with a threshold radius that is the distance at which crowns from canopy trees interlock. The ICO method can be modified to use variable-radius intervals based on crown radius of individual trees (Lydersen et al., 2013). We quantified ICO for the reference stand using fixed-radius and variable-radius approaches (Figures 1 and 2). We estimated the crown radius of individual trees using DBH and species-specific equations from Bechtold (2003).

3 | RESULTS

3.1 | General stand information

Tree (live stems ≥ 5 cm DBH) density on the 1-ha permanent site was 394. Basal area on the site was 20.78 m²/ha. The site was dominated by *P. palustris*, which represented over 88% of trees and over 93% of basal area on the site (Table 1). *Quercus* tree density was 22 stems/ha. Species richness for the tree-layer was 11, although 6 of these species had 2 or fewer occurrences. *Pinus palustris* sapling density was 57 stems/ha. The quadratic mean diameter of trees on the site was 25.9 cm DBH and the largest tree recorded on the site was a *P. palustris* with a DBH of 53.6 cm. The mean (\pm SD) estimated canopy radius was 2.61 \pm 0.93 m. The oldest tree was a *P. palustris* that established in 1730. Major pulses of *P. palustris* establishment occurred from 1925 to 1945 and from 1961 to 1981.

From the 189 overstory (co-dominant and dominant) *Pinus* individuals analyzed for disturbance history using the 10-year running mean method, 163 (86%) exhibited at least one release event. A total of 282 release events were detected from the 163 individuals, and 84 (52%) of these trees experienced multiple releases. The mean (\pm SD) release duration was 4.21 \pm 0.07 years.

3.2 | Global spatial patterns and relationships

Trees were generally significantly clustered by taxonomic group. Hardwood species and *P. palustris* were both significantly clustered from the 1–10-m distances. *Pinus taeda* exhibited significant clustering up to the 9-m distance. *Pinus palustris* saplings were significantly clustered up to the 14-m distance. Trees within each of the 5–10, 10–15, and 15–20-cm DBH size class bins were significantly clustered from 1 to 20 m. Beyond the 15–20-cm DBH size class, clustering and dispersion by 5-cm DBH size class was uncommon. Reconstructed canopy disturbance events from 1927 to 1950 were clustered at the 8- and 15-m distances (Figure 3). Canopy disturbance events were significantly clustered up to 3 m

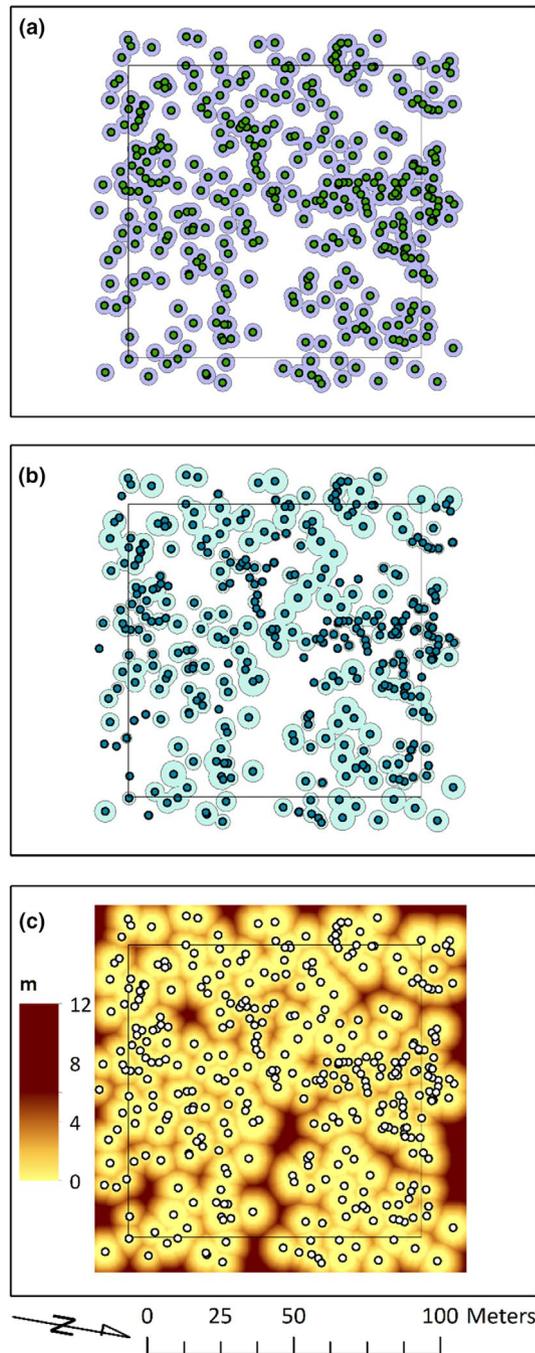


FIGURE 1 Individuals, clumps and openings within a *Pinus palustris* woodland. The traditional, fixed-radius method (a) uses a stand-wide average canopy tree radius. The modified method (b) uses a variable radius based on individual tree diameter. Distance from nearest canopy (c) is shown with darker tones representing longer distances (m)

from 1952 to 1962. From 1967 to 1977, canopy disturbance events were significantly clustered at 2 and 7 m (Figure 3). Spatial randomness was documented for canopy disturbance events from 1981 to 1993 and from 1994 to 2005. *Pinus palustris* saplings exhibited no spatial relationship with canopy *P. palustris* trees at any distance (Figure 4a). *Pinus palustris* saplings were significantly

clustered with *Quercus* trees from 3 to 9 m and repulsed from 17 to 25 m (Figure 4b).

3.3 | Local spatial pattern

The estimated average crown radius for canopy trees was 3 m. With this radius, an intertree distance (t) of 6 m was used to quantify percent distribution of individuals and clumps (Figure 2). Individual stems comprised 10% of total trees at the 6-m threshold. Remaining clump sizes comprised less than 10% individually, except for the ≥ 10 clump size. The ≥ 10 clump size contained 50% of the trees within the site. The variable-radius modification of ICO yielded similar results to the traditional fixed-radius method. Although the percentage of trees within the ≥ 10 clump size was similar between the fixed- and variable-radius methods (50% vs 43%), the fixed 6-m intertree distance had a single clump of more than 50 trees. The variable-radius method did not have a clump size nearly as large.

Using the variable-radius ICO, median clump size was 88.4 m², mean clump size was 124.9 m² and median Polsby-Popper value was 0.57. We found that ca. 50% (4,708 m²) of the reference site was in an opening (not directly underneath the canopy of an intermediate, co-dominant, or dominant tree), and ca. 10% of the site (1,172 m²) consisted of open areas at least two crown radii away from canopy trees. Under the more conservative opening criteria, median opening size was 3.7 m², mean opening size was 39.1 m² and median Polsby-Popper value was 0.52.

4 | DISCUSSION

4.1 | Global spatial patterns and relationships

Spatial clustering by taxa was evident across the study site. Within the reference *P. palustris* woodland, patches of hardwood species and *P. taeda* occurred within the broader matrix of *P. palustris* dominance. Likewise, trees in small size classes were spatially clustered. *Pinus palustris* is known to establish regeneration patches, sometimes referred to as regeneration domes, in canopy openings (Brockway & Outcalt, 1998; Kirkman & Jack, 2017). We suspected this pattern was because smaller trees had less time to differentiate through intraspecific competition within regeneration patches. Conversely, no significant spatial clustering or dispersion was observed for larger tree size classes. Canopy *P. palustris* trees in complex stage stands often exhibit such spatial heterogeneity (Platt et al., 1988; Kush & Meldahl, 2000). With the exception of two disturbance periods (1981–1993 and 1994–2005), canopy disturbances were clustered in space at various distances. Release events clustered at short distances (i.e., <3 m) could be the result of radial growth of two adjacent trees that responded to the same localized canopy disturbance (i.e., canopy gap). The release events during disturbance periods in

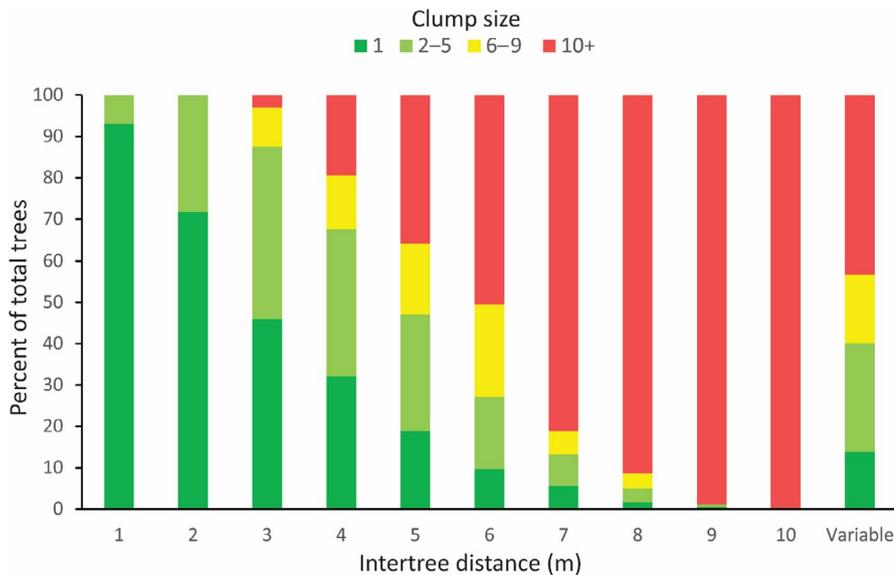


FIGURE 2 Percent distribution of trees within clump sizes at specified intertree distances (m). Intertree distance is the distance from stem to stem and was analyzed at distances of 1–10 m. The variable column represents a modeled intertree distance based on modeled individual tree crown radius. Clump size was evaluated in groups of single trees, two to five trees, six to nine trees, and ten or more trees. For this study, 6 m was the modeled intertree distance based on crown diameter

TABLE 1 Density (stems/ha), relative density, dominance (m^2/ha), relative dominance, frequency, and relative importance (average of relative density, relative dominance, and frequency) for all live stems ≥ 5 cm DBH in a *Pinus palustris* woodland in the Alabama Fall Line Hills

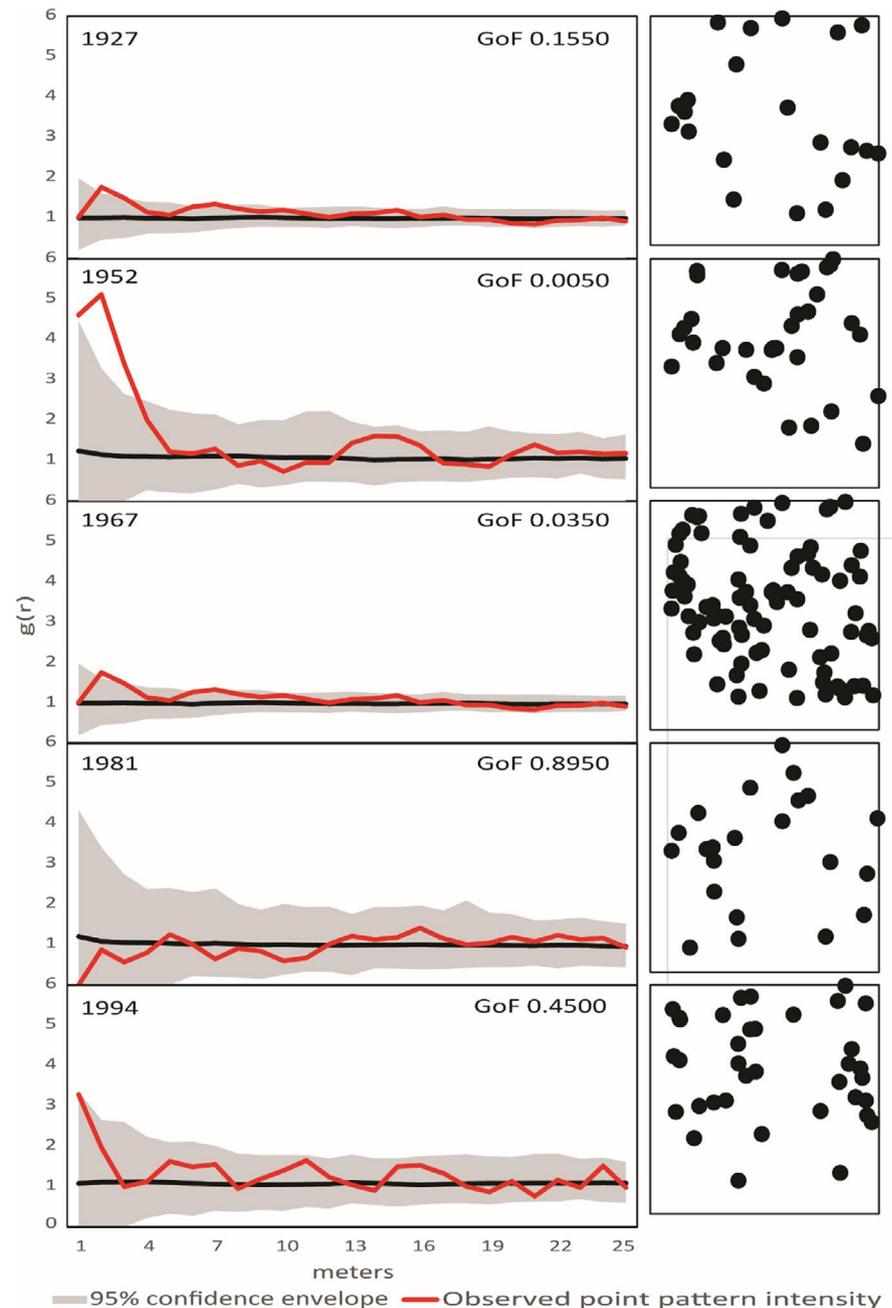
| Species | Density (stems/ha) | Relative Density (%) | Dominance (m^2/ha) | Relative Dominance (%) | Frequency | Relative Importance |
|------------------------------------|-----------------------|-------------------------|---------------------------|---------------------------|-----------|------------------------|
| <i>Pinus palustris</i> | 350 | 88.83 | 19.53 | 93.99 | 95 | 92.61 |
| <i>Quercus marilandica</i> | 14 | 3.55 | 0.30 | 1.43 | 10 | 4.99 |
| <i>Pinus taeda</i> | 9 | 2.28 | 0.45 | 2.17 | 7 | 3.82 |
| <i>Nyssa sylvatica</i> | 6 | 1.52 | 0.20 | 0.96 | 4 | 2.16 |
| <i>Quercus laevis</i> | 7 | 1.78 | 0.07 | 0.35 | 4 | 2.04 |
| <i>Diospyros virginiana</i> | 2 | 0.51 | 0.12 | 0.56 | 2 | 1.02 |
| <i>Liquidambar styraciflua</i> | 2 | 0.51 | 0.01 | 0.03 | 2 | 0.85 |
| <i>Pinus echinata</i> | 1 | 0.25 | 0.06 | 0.30 | 1 | 0.52 |
| <i>Quercus velutina</i> | 1 | 0.25 | 0.04 | 0.18 | 1 | 0.48 |
| <i>Pinus virginiana</i> | 1 | 0.25 | 0.00 | 0.01 | 1 | 0.42 |
| <i>Oxydendrum arboreum</i> | 1 | 0.25 | 0.00 | 0.01 | 1 | 0.42 |
| Total | 394 | 100 | 20.78 | 100 | - | 0 |

which the stand was entered were generally randomly distributed, which could indicate that the stand was perhaps uniformly treated.

Pinus palustris saplings were randomly distributed around canopy *P. palustris*. Lack of a spatial relationship could be caused by homogenous treatments that obscured relationships otherwise evident through shading, root competition, or interactions between *Pinus* needle deposition from canopy trees and resultant fire intensity. Brockway and Outcalt (1998) noted seedling exclusion zones caused by root competition extending 12–16 m from canopy *P. palustris* stems. Light is not as limited in woodland conditions relative to closed-canopy forests. Brockway and Outcalt (1998) found that shade from overstory *P. palustris* stems did not alter the subcanopy light environment of canopy gaps and that increased *Pinus* litter loading coincided with the crown of canopy trees.

Pinus palustris saplings were clustered around *Quercus* trees at distances between 3 and 9 m, but repulsed beginning at the 17-m distance. Recent research has highlighted the importance of fire-facilitating *Quercus* stems in *P. palustris* ecosystems (Hiers et al., 2014; Loudermilk et al., 2016; Johnson et al., 2021). Loudermilk et al. (2016) found that *Q. laevis* densities of 43–1,400 stems/ha facilitated survival of *P. palustris* seedlings on xeric sites by reducing moisture stress. Concurrent with our results, Johnson et al. (2021) found that *P. palustris* saplings were more likely to occur near *Q. laevis* than near *P. palustris* stems. The density of *Quercus* trees on our study site was only 22 stems/ha, however, a significant spatial relationship existed. To facilitate *P. palustris* regeneration, we suggest that managers should retain some fire-facilitating *Quercus* stems in *Pinus* woodlands. Retention of *Quercus* trees in *P. palustris* woodlands will increase

FIGURE 3 Univariate pair correlation function $g(r)$ for detected release events. Shaded areas represent a 95% confidence envelope (199 permutations excluding the five highest and lowest values) in which values exhibit a heterogeneous Poisson distribution. The red line represents observed values. Values above the shaded area indicate significant ($p < 0.05$) clustering (i.e., recorded release events were closer together than expected), and values below the shaded area represent significant dispersion. Goodness-of-fit (GoF) for each $g(r)$ is shown in the corner of each graph. Stem maps showing stems with recorded releases are to the right of the respective $g(r)$



native biodiversity where additional life history and functional traits will occur in the ecosystem. Retention of *Quercus* stems will also promote structural complexity because this genus represents different growth forms compared with the dominant *Pinus* species. Collectively, the retention of *Quercus* trees should enhance adaptation potential of *P. palustris* woodlands (Loudermilk et al., 2016).

4.2 | Local spatial patterns

Shorter intertree distances inherently result in a greater number of individual trees and fewer clumps. However, we found an intertree distance of just 3 m resulted in most stems occurring in clumps rather than as individuals. Churchill et al. (2013) noted that the majority

of stems in a frequent-fire *Pinus* and mixed-conifer forest occurred as individuals until the 6-m intertree distance, at which point most stems occurred as clumps. By contrast, Lydersen et al. (2013) found that the majority of stems in a frequent-fire, mixed-conifer forest were clumped at intertree distances of just 2 m. The Polsby-Popper value of clumps under the variable-radius ICO method was 0.57, indicating some measure of irregularity. Openings in our conservative criteria exhibited greater irregularity than clumps, with a Polsby-Popper value of 0.52.

Using the estimated canopy radius of 3 m (i.e., an intertree distance of 6 m), half of the trees in the reference stand were in large (i.e., ≥ 10 trees) clumps. It is important to visualize clumps in terms of canopy proximity, rather than stem proximity to recognize the actual abundance of tree clumps within a stand. In our reference *P. palustris*

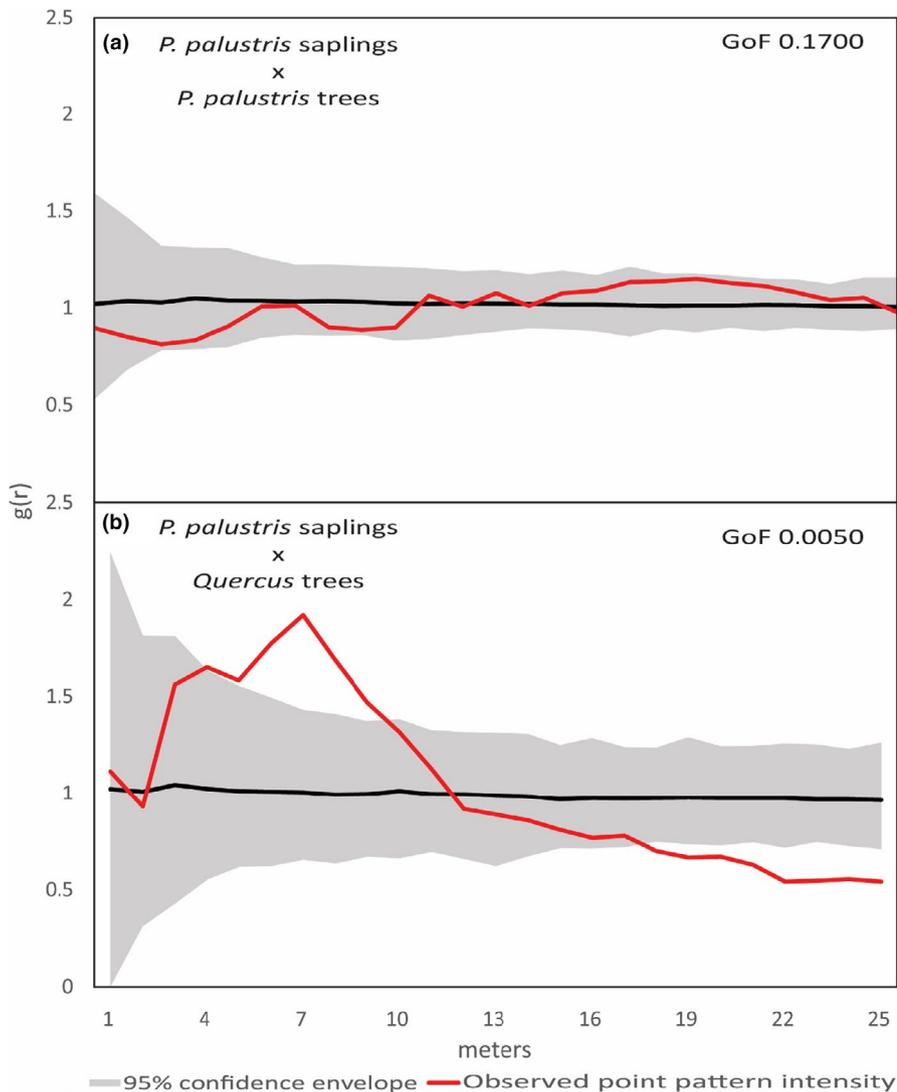


FIGURE 4 Bivariate pair correlation function $g(r)$ for *Pinus palustris* saplings in relation to canopy *P. palustris* (a) and *Quercus* trees (b). Shaded areas represent a 95% confidence envelope (199 permutations excluding the five highest and lowest values) in which values exhibit a heterogeneous Poisson distribution. The red line represents observed values. Values above the shaded area indicate significant ($p < 0.05$) clustering (i.e., *P. palustris* saplings were clustered significantly around *Quercus* stems), and values below the shaded area represent significant dispersion. Goodness-of-fit (GoF) is shown in the corner of each graph

woodland, the variable-radius ICO method yielded similar results to the fixed-radius method which uses a static distance based on mean crown diameter. Differences between the use of the variable- and fixed-radius ICO approaches are clearly influenced by the range of crown diameters within the study stand (Lydersen et al., 2013). Differences in clump identification may not be meaningfully different by either approach in stands that exhibit little crown-diameter variability. Discrepancies between the variable- and fixed-radius ICO methods may become more pronounced in stands with a greater range of crown diameters. Although the variable-radius ICO approach may be more ecologically meaningful, differences may be negligible, as we found. Importantly, timber-marking guidelines based on the fixed-radius ICO approach would be easier to implement because it allows timber markers to focus on a single intertree distance regardless of tree size.

5 | MANAGEMENT IMPLICATIONS

To increase forest ecosystem resilience and promote adaptation potential, especially in relatively monospecific stands, managers may

wish to increase structural complexity. Analyzing spatial patterns of structure in reference stands allows us to elicit spatial relationships and optimize efforts to increase stand structural complexity. Quantified spatial patterns in stands that exhibit desired structural characteristics can be used by managers to develop silvicultural prescriptions to replicate the documented spatial relationships. For example, based on the spatial patterns on our reference site, a structural target may be to have ca. 10% of trees in a stand exist as individuals separated from other canopy trees by at least 6 m so that crowns do not touch those of neighboring trees. Furthermore, ca. 15% of the trees may occur in small clumps of two to five stems, ca. 25% of trees may occur in medium clumps of six to nine stems, and ca. 50% of trees may occur in large clumps of more than ten stems based on the spatial structure of the *P. palustris* woodland studied here. The size and density of smaller openings (i.e., single-tree or two-tree gaps) could be variable based on target tree density in pre-defined clusters. Additionally, we found that tree clumps and openings exhibited a wide range of shapes. Polsby-Popper tests indicated clumps and openings often exhibited irregular forms. Replicating irregularity in these features may further enhance spatial

heterogeneity by adding variability at the clump and opening level, thereby reinforcing spatial heterogeneity at multiple scales (Palik et al., 2021). Guidelines such as these could be incorporated into a variable density thinning treatment to achieve spatial structure goals. We note that our results are from a single 1-ha study site and that quantitative spatial data are required from additional *P. palustris* woodlands to more fully understand general spatial trends before widespread implementation into silvicultural systems. We hope the data presented here will be a catalyst for others to quantify spatial patterns of stand structure in *P. palustris* woodlands, and other forest types, so that we ultimately can develop silvicultural guidelines that will promote resilience in these ecosystems.

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AUTHOR CONTRIBUTIONS

All authors participated in the research conception, data collection, and manuscript production. David L. Phillips and J. Davis Goode performed the statistical analyses.

DATA AVAILABILITY STATEMENT

The data used and analyzed in this study are archived on an internal server of The University of Alabama and are available from the corresponding author upon reasonable request.

ORCID

David L. Phillips  <https://orcid.org/0000-0002-0763-2022>

J. Davis Goode  <https://orcid.org/0000-0003-3659-3736>

Justin L. Hart  <https://orcid.org/0000-0001-6580-0189>

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