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Gap-Scale Disturbance Patterns and Processes in a Montane *Pinus palustris* Woodland

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Abstract: Gap-scale disturbances drive successional and structural development patterns in most forest ecosystems. Although fire-maintained *Pinus palustris* woodlands are less light limited than closed canopy forests, gap-scale disturbance processes may still influence successional and developmental pathways. We quantified biophysical characteristics of 50 canopy gaps in a montane *Pinus palustris* woodland to analyze gap-scale disturbance patterns and processes. We found most gaps (64%) were caused by the death of a single tree. Snag-formed gaps were most common (38%) followed by snapped stems (32%). We hypothesized that insect-induced mortality, perhaps in combination with drought periods, resulted in the high frequency of snag- and snapped stem-formed gaps. We did not find significant differences in gap size or shape based on gap formation or closure mechanisms. Most gaps (74%) were projected to close by lateral crown expansion of gap perimeter trees. We hypothesized most gaps projected to close via subcanopy recruitment would be captured by a *P. palustris* stem. The majority of gaps were small and gap frequency declined with increased gap size. We found gaps were significantly clustered through the woodland at distances of 8–36 m from gap edge to gap edge but were randomly distributed beyond 36 m.

Keywords: canopy gap; LiDAR; longleaf pine; regeneration; succession; stand structure

1. Introduction

All forests are subject to disturbance events which influence stand development patterns and successional pathways. The frequency, magnitude, and spatial extent of these disturbances range from infrequent, catastrophic, stand-wide events to frequent, gap-scale occurrences [1,2]. Localized canopy disturbance events that result from the mortality of small groups of trees, single canopy trees, or even just large branches from canopy dominant stems are the most common natural canopy disturbances in closed canopy forests [3,4]. These gap-scale disturbances initiate structural changes associated with older stands by increasing large woody debris inputs, releasing understory trees from overstory competition resulting in complex vertical stratification of tree crowns, promoting multi-aged structures, and allowing for branch extension and larger tree crowns, among other processes [1,5,6]. Gap-scale disturbance events may also influence species composition patterns via gap-phase succession [7–10]. At the stand-level, gap-scale disturbances may result in a patchwork mosaic of microsites that support different tree species, tree ages, tree sizes, or stem densities [3,4,11]. By altering fine-scale biophysical conditions, gap-scale canopy disturbances modify heterogeneity and biodiversity in forested ecosystems [12,13].

Fire-maintained *Pinus palustris* stands throughout the southeastern USA generally exist in savanna or woodland structures. In contrast to closed canopy stands, savanna and woodland ecosystems are not as light limited [14,15]. Nonetheless, research has established that canopy gap disturbances are important in the regulation of ecosystem processes, structural development, and succession in *P. palustris* savannas and woodlands [14,16,17]. Canopy gap-induced increased insolation in the understory has been shown to improve growth,

establishment, and recruitment of *P. palustris* seedlings and saplings [18–20]. Small-sized *P. palustris* stems are often spatially clustered within canopy gaps [21,22] and ultimately, gap-scale disturbance processes may result in complex stand structures and multiple age classes in these ecosystems [16,23,24].

Frequent, low-intensity surface fires help maintain *P. palustris* dominance and woodland or savanna structures [25,26]. Fires also enhance ground flora cover and diversity [27–30]. *Pinus palustris* needles are an important fuel source as the relatively monospecific canopy results in a continuous fuel bed of fine fuels with a high resin content [31]. Overstory tree density has been linked to the abundance and spatial distribution of *Pinus* needle litter [32]; thus, fuel loading and fuel bed continuity may be influenced by canopy gap disturbances that modify local overstory tree density patterns [33,34]. These modifications may influence fine-scale fire behavior and subsequently fire effects.

Prior studies have examined gap-scale disturbance processes in *P. palustris* ecosystems of the USA Coastal Plain (e.g., [14,16,22,23]). However, no studies have quantified canopy gap patterns and processes in montane *P. palustris* woodlands. *Pinus palustris* ecosystems on the Coastal Plain and montane stands of the Appalachian Highlands are distinct and differ in stand structure and species composition [35–37]. *Pinus palustris* stands on the relatively flat to gently rolling Coastal Plain typically exist as savannas with relatively low tree density and basal area values. In contrast, montane *P. palustris* stands of the topographically complex Appalachian Highlands more frequently occur as woodlands with higher tree density and greater basal area [19,38,39]. As a result, Coastal Plain *P. palustris* savannas are less light limited than woodlands and thus canopy disturbance processes may be comparatively more important in these woodland ecosystems. The overarching goal of our research was to quantify gap-scale disturbance patterns and processes in a montane *P. palustris* woodland. Our specific objectives were to: (1) examine canopy gap formation mechanisms and quantify gap characteristics, (2) document gap closure mechanisms and canopy recruit patterns, (3) examine the impacts of canopy gaps on species composition and stand structure, and (4) quantify the frequency, size, and spatial distribution of canopy gaps through a montane *P. palustris* woodland.

2. Materials and Methods

2.1. Study Site

This study was conducted in the Reed Brake Research Natural Area on the Oakmulgee Ranger District of Talladega National Forest, Alabama, USA. A management priority on the district is the restoration and maintenance of *Pinus palustris* woodland ecosystems [40]. In 1975, the Reed Brake Research Natural Area was established on the Oakmulgee Ranger District because it represented typical forest conditions of the Fall Line Hills [41]. The natural area is 242 ha and contains fire-maintained *P. palustris* woodlands that were established in the 1930s prior to federal land acquisition. Elevation ranges from 90–155 m above mean sea level and the topography is complex and characterized by steep slopes and narrow ridges. The Fall Line Hills are a transition zone between the Appalachian Highland physiographic provinces and the Coastal Plain [42]. The region supports species characteristic of both Coastal Plain and Appalachian Highland forest communities [43–45]. The study site occurs within what Harper [46] classified as the central *Pinus palustris* region. In this region, *P. palustris*-dominated woodlands occur on fire-maintained ridgetops, upper slopes, and south-to-west facing middle slope positions. On more mesic sites, *Quercus* and other hardwood species co-occur with *Pinus taeda* [2,35,43].

The climate of the study area is classified as humid mesothermal, with long, hot summers and short, mild winters [47]. The average yearly precipitation is 1376 mm, with the highest mean precipitation in February (138 mm) and the lowest mean precipitation in October (86 mm). The average yearly temperature is 17.1 °C, and the mean temperature for January and July is 6.5 °C and 26.9 °C, respectively (30-year normal, [48]). The soil parent materials consist of undifferentiated marine sediments of the Cretaceous age Tuscaloosa Group. Soils of the study site are mainly the Maubila–Smithdale complex [49]. The Maubila

soil series is moderately well drained with a ca. 5 cm deep flaggy loam A horizon and clay Bt and C horizons. The Smithdale series is well drained with Ap and E horizons of sandy loam to 33 cm deep and a Bt1 horizon of sandy clay loam and a Bt2 horizon of sandy loam [49].

2.2. Field Methods

To quantify non-gap forest composition and structure, we sampled twenty 0.05-ha circular reference plots in June 2021. Reference plots were installed and inventoried in the same Forest Service-delineated compartment in the Reed Brake Research Natural Area to ensure similar biophysical site conditions, disturbance, and management history. Reference plots were interspersed with canopy gap plots and care was taken to be sure no part of the reference plot was within or bordering a canopy gap. Here, *P. palustris* is dominant on upper slopes, and on south to west facing mid-slopes, while lower slopes are more often dominated by hardwood species [36,44]. Therefore, canopy gaps and reference plots were only sampled on upper slopes and at south to west facing mid-slope positions. On each reference plot, all trees (live woody stems > 10 cm diameter at breast height (dbh, 1.37 m above the root collar)) were identified by species and dbh and crown class were recorded. Crown class categories (dominant, co-dominant, intermediate, overtopped) were determined by examining the direction and amount of light intercepted by the tree crown [1]. Saplings (live woody stems $\geq$ 1 m height, $\leq$10 cm dbh) were tallied by species. Seedlings (live woody stems < 1 m in height) were tallied by species in a 10 m^2 nested subplot located in the center of the 0.05 ha reference plot. Percent ground cover was estimated for rocks, gravel, bare ground, coarse woody debris (CWD, deadwood with a diameter $\geq$ 10 cm), fine woody debris (FWD, dead wood with a diameter < 10 cm), *Pinus* litter, hardwood litter, grass, and forb cover to the nearest 1% [50,51]. Litter depth was recorded to the nearest 0.01 cm at nine locations in the plot, one at plot center, and one at 6.31 m from plot center and 12.62 m from plot center in each cardinal direction. For each plot, the slope gradient, slope aspect, microscale curvature (linear, concave, convex), and topographic position (ridge, shoulder, backslope) were recorded.

Canopy gaps (*n* = 50) were located while walking transects through *P. palustris* dominated stands. Transects were subjectively established on ridgetops and upper-slope positions and to avoid old skid trails. To be sampled, canopy gaps had to meet two criteria (1) a discernable void in the canopy caused by the removal of a canopy tree and (2) the presence of a gapmaker (i.e., the dead tree or trees that caused the canopy gap to form). Each canopy gap along the transects that met these criteria was sampled. Canopy gap voids that did not contain visible gapmakers were not sampled since we could not ascertain if they were created by the death of canopy trees or were open portions of the woodland canopy unassociated with tree mortality (i.e., microsites long devoid of tree cover). Likewise, if a canopy gap had more than one gapmaker of the same species but in different decay classes, the canopy void was not sampled. Gapmakers of the same species with different decay classes may have resulted from different canopy disturbance events, which would confound the effects of each discrete disturbance [52].

For each canopy opening, we sampled the observed and expanded gap areas. The observed gap was defined as the area directly under the canopy void (i.e., unrestricted from above), and the expanded gap was defined as the entire area extending to the bases of the canopy gap perimeter trees [6,53]. Canopy gap length was measured as the greatest distance (i.e., longest axis) of the observed and expanded gaps. The width was the longest distance of the observed and expanded gaps perpendicular to the length. Observed and expanded gap length and width were measured using a hypsometer and transponder. The coordinates for each canopy gap center (i.e., the intersection of gap length and width axes) were recorded using a Trimble Juno T/5 GPS unit. The microscale curvature, topographic position, slope aspect, and slope gradient were also measured for each canopy gap with a clinometer and sighting compass. The number of gap perimeter trees was recorded to determine how many canopy trees had the potential to close the canopy gap through

lateral branch growth. The border of each canopy gap plot was defined by the perimeter trees, which were denoted by observing the canopy and determining which tree crowns constituted the boundaries of the gap. The dbh of all trees (woody stems > 10 cm dbh) within the canopy gap were recorded, including perimeter trees. Based on location, each tree was as classified as within the perimeter, expanded, or observed gap. The crown class and species were also recorded for each tree consistent with the methods used on the reference plots. The formation mechanism of each canopy gap was recorded as a snag (standing dead tree with mostly intact crown), snap (broken bole), or uproot (uplifted root network). In the case of canopy gaps with multiple gapmakers, all formation mechanisms were recorded. The dbh (for snags), or the diameter 1.37 m from the root collar (for downed logs), species, and decay class of each gapmaker were recorded. The decay class was assigned based on Ulyshen et al. [54], which was developed specifically for *P. palustris*. This system includes seven decay classes for downed CWD and five for standing dead wood. The decay classes were used to facilitate the determination of canopy gap formation age. To calculate the average height of the canopy surrounding the canopy gap, the height of four perimeter canopy trees, one in approximately each cardinal direction, was measured using a hypsometer and transponder.

In each canopy gap, saplings were tallied by species and recorded as being either within the expanded or observed gap. Seedlings were tallied by species in a nested 10 m^2 circular plot placed at canopy gap center. Percent ground cover was estimated following the same methods as reference plots. Litter depth measurements were taken in nine locations through the canopy gaps to the nearest 0.01 cm. One measurement was taken at plot center and four measurements were taken equidistant along the length and width from the center. To document changes in forest composition and structure, we recorded the projected closure mechanism for each gap as either lateral capture or understory capture [55–58]. If we projected the canopy void would close by branch elongation of perimeter trees, then the gap was classed as lateral capture. If we projected the canopy void would close partly by the recruitment of a sub-canopy stem, then the gap was classed as understory capture. When this was observed, we documented the species of the probable gap successor. Probable gap successors are individuals deemed likely to fill the canopy void and can often be identified in the field [56,59–62]. Documenting replacement tree species is important to aid our understanding of future stand composition and our mechanistic understanding of gap-phase succession and development patterns [55].

To help determine canopy gap age, an increment borer was used to remove a core sample from three gap perimeter trees, or trees growing within the canopy gap, that were deemed likely to have experienced an increase in radial growth coincident with canopy gap formation. Trees were cored 50 cm above the ground. Once the core sample was collected, it was placed in a paper straw and returned to the laboratory to air dry.

2.3. Analytical Methods

Once dried, all tree cores were mounted with cells vertically aligned and sanded with progressively finer abrasives to reveal the cellular structure of the wood [63]. Annual rings on each sample were dated to the calendar year of formation with the aid of a stereozoom macroscope. For samples that did not contain pith but showed substantial ring curvature, pith estimators were used [64]. The raw-ring widths of the most recent 30 years (1990 to 2021) were then measured to the nearest 0.001 mm using a Velmex measuring stage (Velmex, Incorporated, Bloomfield, NY, USA 2009) interfaced with Measure J2X software (VoorTech Consulting, Holderness, NH, USA 2008). The program COFECHA (Version 6.06, (Richard L. Holmes, Tuscon, AZ, USA) was used to test tree-ring 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 if needed. We adapted the running median method to identify periods of increased radial growth [56,65,66]. Radial growth of each year was compared to the median growth of the preceding 10 years. If growth was $\geq$25% of the

preceding 10-year median, then we recorded that year as having exhibited a release event. If at least two of the three samples for a canopy gap showed a release in the same year (±1 year), that year was considered to be the canopy gap formation year. Line graphs of ring widths were made for each canopy gap to visually assess growth trends and elucidate anomalous growth increases. Gap formation year estimates were also compared against gapmaker decay classes for corroboration.

To quantify gap shape patterns, length to width ratios (L:W) were calculated for expanded gaps. We calculated diameter to height ratios (D:H) with expanded gap width as the diameter and the mean height of the four perimeter canopy trees. Gap characteristics (e.g., gap area, L:W ratio) were compared by gap formation mechanism and gap closure mechanism. The relationship between gap characteristics and response variables (e.g expanded gap area and sapling density) were quantified. All statistical tests (ANOVAs with Scheffe post hoc tests, *t*-tests, Pearson correlations) were conducted with SPSS Statistics (IBM Corp., released 2013, Armonk, NY, USA).

To understand differences between canopy gap plots and reference (non-gap) plots, the density (number of stems), relative density, dominance (basal area, measured in m^2 per hectare), relative dominance, and relative importance (mean relative density and relative dominance) were calculated for all tree species. For the saplings and seedlings in canopy gaps and reference plots, density and relative density were calculated. We calculated Shannon diversity (*H'*) of trees and saplings in canopy gaps and reference plots.

2.4. LiDAR Analysis

To detect canopy gaps at the forest scale, we calculated a canopy height model derived from LiDAR data. LiDAR data are collected using laser pulses and their reflected return signals to generate a point cloud [67]. The discrete point cloud dataset can be used to create digital terrain models (DTM) and digital surface models (DSM). A 1 m spatial resolution canopy height model (CHM) was created by subtracting the DTM from the DSM with the raster calculator function in ArcGIS Pro. Low elevation areas were excluded (<100 m). The LiDAR data were collected in 2019 in support of the National Ecological Observatory Network (NEON) using an Optech Gemini LiDAR system mounted to a fixed-wing aircraft [68]. The NEON LiDAR Point Cloud is downloaded in American Society for Photogrammetry and Remote Sensing LASer format (LAZ), georeferenced to a UTM map projection and ITRF00 datum horizontally and NAVD88 vertically [69]. These data were downloaded from the publicly available NEON database [69]. The DSM and DTM were mosaicked individually and were downloaded in 1 km^2 tiles. NEON collects LiDAR during the growing season, allowing for detection of canopy gaps [69]. The majority (84%) of the canopy gap plots occurred within a single 1 km^2 tile which was selected for canopy gap detection. To ensure there were no edge effects from anthropogenic features, a 10 m buffer was established around abandoned logging roads within the study area. No canopy gap plots were inventoried within these buffer zones. The modified CHM with lower elevations and road buffer removed were analyzed with the "ForestGapR" package in R version 4.2.0 [70]. We used the package to detect canopy openings based on user-defined parameters. We selected a 5 m height threshold [71] and an area range of 25–300 m^2. The parameters used were based on calculated observed gap area in situ.

To determine the size, frequency, and spatial distribution of canopy gaps, we created a gap size-frequency distribution and quantified the spatial patterns of gaps with a modified point pattern analysis approach. Specifically, Wiegand et al. [72] adapted point pattern analysis for objects with finite size and real shape (e.g., detected canopy gaps). For gaps detected from the above LiDAR analyses, we used the grid-based software *Programita* [73] to analyze the spatial pattern of gaps with the non-cumulative O-ring statistic, an adaptation of the well-known Ripley's *K* statistic. The O-ring statistic is the conditional intensity of points (or in this case objects) a *r* distance from an arbitrary point [73]. To prepare the data, a binary categorical raster of 1 × 1 m resolution with pixels categorized as gap vs. non-gap was created. For a given pixel classified as a gap, if one of the eight neighboring pixels

was also classified as a gap, the software grouped the pixels into one unique gap. These grouped pixels (i.e., gaps) were spatially randomized via re-orientation and re-positioning with 99 simulations under the assumption of complete spatial randomness (CSR) to create a confidence envelope by which to compare the observed spatial pattern of detected gaps. If the observed $O(r)$ was above or below the confidence envelope, the pattern was considered significantly clustered or dispersed, respectively.

3. Results

3.1. Canopy Gap and Gapmaker Characteristics

Snag-formed gaps were most common and represented 38% of all documented canopy gaps. Snapped stems accounted for 32% of canopy gaps and a combination of snags and snaps formed 24% of documented gaps. Only one canopy gap was formed by tree uprooting alone and just two of the 50 canopy gaps were formed by a combination of snapped and uprooted stems. No significant difference occurred between the expanded area of gaps formed by single standing gapmakers (snags), single downed gapmakers (snaps and uproots), or multiple gapmakers ($p = 0.893$; Figure 1). We recorded a total of 96 gapmakers, 95 of which were *P. palustris* stems. The lone remaining gapmaker was a *Quercus falcata* snag. Mean expanded gap area was 187 m^2 $\pm$ 116 (SD) m^2 with maximum and minimum expanded gap areas of 479 m^2 and 48 m^2, respectively. The mean observed gap area was 75 m^2 $\pm$ 62 m^2 with a maximum gap area of 255 m^2 a minimum area of just 3 m^2.
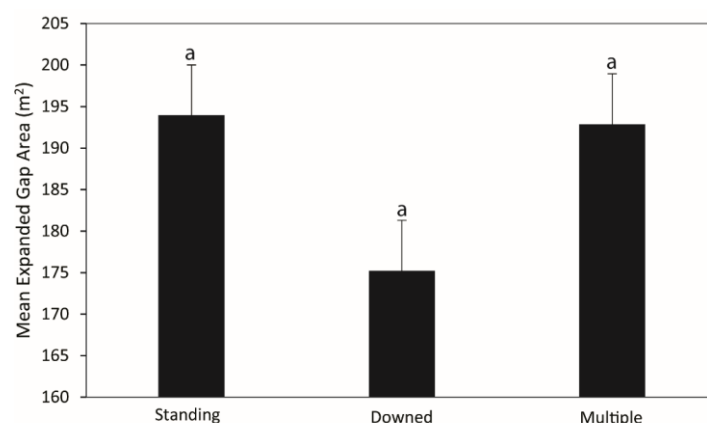
Figure 1. Mean expanded gap area for canopy gaps formed by single standing trees (snags), single downed (snapped and uprooted) trees, and multi-tree gaps in a montane *Pinus palustris* woodland. Different letters indicate a significant ($p < 0.05$) difference between categories.

The majority (64%) of canopy gaps were caused by the death of a single tree. Of the 50 canopy gaps sampled, 20% were formed by the death of two trees and 16% by the death of three or more trees. The highest number of gapmaker trees for a canopy gap was nine, and this was documented twice in our study. The mean basal area lost in canopy gaps formed by single gapmakers was 0.12 m^2/ha $\pm$ 0.04, with a minimum of 0.07 m^2/ha, and a maximum of 0.24 m^2/ha. For multiple (2–9 trees) gapmaker canopy gaps, the mean basal area lost was 0.34 m^2/ha $\pm$ 0.25, with a minimum of 0.09 m^2/ha, and a maximum of 0.87 m^2/ha. The dbh of gapmakers in single tree canopy gaps was significantly greater than the average dbh of multi-tree canopy gaps ($p = 0.007$). Gapmakers did not have a significantly greater mean dbh than other trees within the canopy gap plots ($p = 0.667$). No significant difference was found between the expanded gap area of single tree canopy gaps and multiple tree canopy gaps ($p = 0.943$). No relationships were found between expanded gap area and the number of trees in a gap ($r = -0.003$, $p = 0.981$), expanded gap area and the number of saplings in a gap ($r = -0.093$, $p = 0.522$), or expanded gap area and the total number of stems (trees and saplings combined) in a gap ($r = -0.092$, $p = 0.527$; Figure 2).
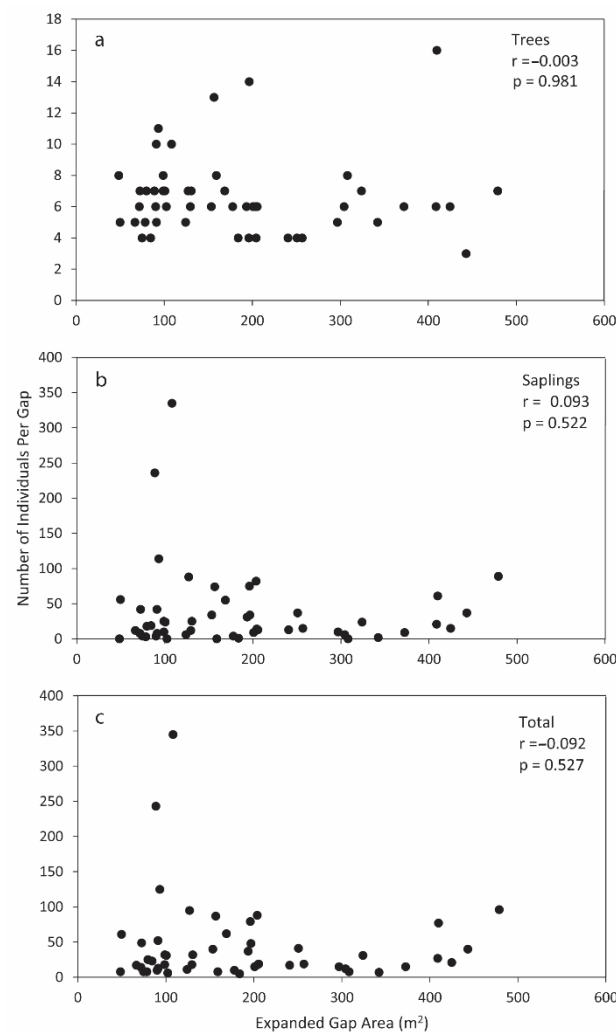
Figure 2. Pearson correlation between expanded gap area and the number of stems for (**a**) trees (live stems ≥ 10 cm dbh), (**b**) saplings (live woody stems ≥ 1 m height, <10 cm dbh), and (**c**) total stems (trees and saplings) in a montane *Pinus palustris* woodland. Note that the *y*-axis varies.

Out of the 50 canopy gaps sampled, 41 were confidently dated to a formation year. The most common canopy gap formation year was 2005, with 22% of sampled canopy gaps forming that year. The next most common canopy gap formation years were 2016 and 2011, each with 10% of sampled canopy gaps forming in those years.

The mean L:W for expanded canopy gaps was 1.59:1, with a minimum of 1.00:1, and a maximum of 3.43:1. Canopy gaps were determined to be primarily elliptical in shape based on L:W ratios. For observed canopy gaps, the mean L:W ratio was 2.08:1, with a minimum of 1.00:1 and a maximum of 15.72:1. Mean expanded gap L:W ratios did not significantly differ between canopy gap formation mechanisms ($p = 0.433$). The mean D:H for expanded canopy gaps was 2.3:1, with a minimum of 1.07:1, and a maximum of 5.8:1. The mean D:H for observed canopy gaps was 5.01:1, with a minimum of 1.67:1, and a maximum of 50:1.

Litter depths in reference plots were found to be significantly greater than litter depths in canopy gap plots ($p < 0.001$). The average litter depth in reference plots was 1.54 cm ± 0.68, with a minimum of 0.10 cm and a maximum of 4.10 cm. Mean litter depth in canopy gap plots was 0.99 cm ± 0.76, with a minimum of 0.00 cm, a maximum of 6.00 cm. *Pinus* litter had the highest mean estimated cover in both canopy gap plots and reference plots (mean estimated cover of 63% in canopy gaps and 80% in reference plots). Following *Pinus* litter, forbs had an estimated cover of 19% in canopy gap plots and 13% in reference

plots, followed by grass with 8% and 2% estimated cover in canopy gap and reference plots, respectively.

3.2. Forest Composition

Pinus palustris was the dominant tree species across canopy gap plots comprising 96% of basal area (Table 1). The next most dominant species, *Q. falcata* and *Q. marilandica*, did not represent more than 1% of basal area. *Pinus palustris* was also the dominant tree species in reference plots with a basal area of 98%. For the reference plots, *P. taeda* was the second most dominant with just under 1% of the basal area, and the third most dominant tree species was *Quercus stellata* also with under 1% of the basal area contribution. Of the nine species in the canopy gap plots, two were not found in reference plots, *Nyssa sylvatica*, and *Quercus alba*. Likewise, two species, *Quercus laevis* and *Pinus virginiana*, were unique to reference plots. Hardwood species comprised only 3% of the basal area of canopy gap plots and only 1% of reference plot basal area. In contrast, *Pinus* species comprised 97% of basal area in canopy gap plots and 99% of basal area of reference plots. *Quercus* species comprised 2% of basal area in canopy gap plots and under 1% of basal area in reference plots.

Table 1. Density, relative density, dominance, relative dominance, and relative importance (average of relative density and relative dominance) for trees (stems $\geq$ 10 cm dbh) for canopy gap and reference (non-gap) plots in a montane *Pinus palustris* woodland.

Species	Canopy Gaps					Reference Plots				
	Density/ha	Rel. den.	Dom. (m²/ha)	Rel. dom.	Rel. imp.	Density/ha	Rel. den.	Dom. (m²/ha)	Rel. dom.	Rel. imp.
Pinus palustris Mill.	32.80	93.03	3.65	96.03	94.53	387.00	94.62	31.90	98.17	96.39
Quercus falcata Michx.	0.43	1.21	0.05	1.41	1.31	1.00	0.24	0.01	0.03	0.14
Quercus marilandica Münchh.	0.53	1.52	0.03	0.73	1.12	3.00	0.73	0.09	0.29	0.51
Pinus taeda L.	0.43	1.21	0.03	0.74	0.98	5.00	1.22	0.21	0.63	0.93
Quercus stellata Wangenh.	0.43	1.21	0.02	0.42	0.81	4.00	0.98	0.12	0.37	0.67
Carya tomentosa (Lam.) Nutt.	0.21	0.61	0.00	0.11	0.36	1.00	0.24	0.02	0.08	0.16
Nyssa sylvatica Marshall.	0.21	0.61	0.00	0.05	0.33	-	-	-	-	-
Oxydendrum arboreum (L.) DC.	0.11	0.30	0.01	0.27	0.29	2.00	0.49	0.02	0.06	0.27
Quercus alba L.	0.11	0.30	0.01	0.24	0.27	-	-	-	-	-
Quercus laevis Walter	-	-	-	-	-	4.00	0.98	0.03	0.08	0.53
Pinus Virginiana Mill.	-	-	-	-	-	2.00	0.49	0.10	0.30	0.40
Total	35.25	100	3.80	100	100	409	100	32.50	100	100

Canopy gap plots contained 32 species in the sapling size class, and reference plots contained 16 species in this size class. The sapling species with the highest relative density in the canopy gap plots was *Vaccinium arboreum*, which represented 60% of all saplings in gaps. *Liquidambar styraciflua* was the sapling species with the second highest relative density followed by *Oxydendrum arboretum* (Table 2). Sapling relative density for reference plots was similar, with *V. arboreum* having the highest relative density (58% of all sapling-sized stems). The sapling species with the second highest relative density was *O. arboreum* followed by *Nyssa sylvatica*. *Pinus palustris* represented just 1% of all canopy gap saplings and 4% of all reference plot saplings.

Seedling density was similar for canopy gap and reference plots (Table 3). Seedling species richness for canopy gap plots was 20 and for reference plots was 17. For both canopy gap and reference plots, *V. arboreum* was the most common seedling species, with 3183 stems/ha in canopy gap plots and 2550 stems/ha in reference plots. The second most common seedling species for gap and refence plots was *Pinus palustris*, with 1098 stems/ha in canopy gap plots and 1095 stems/ha in reference plots.

Table 2. Density and relative density for saplings (stems ≥ 1 m tall, <10 cm dbh) in canopy gap and reference (non-gap) plots in a montane *Pinus palustris* woodland.

Species	Canopy Gaps		Reference Plots	
	Density/ha	Rel. den.	Density/ha	Rel. den.
Vaccinium arboreum Marshall	119	59.81	823	58
Liquidambar styraciflua L.	18	8.84	62	4.37
Oxydendrum arboreum (L.) DC.	16	8.3	305	21.49
Symplocos tinctoria (L.) L'Hér.	16	7.92	33	2.33
Rhus copallinum L.	14	6.9	18	1.27
Diospyros virginiana L.	5	2.69	-	-
Acer rubrum L.	2	1.24	40	2.82
Pinus palustris Mill.	2	1.02	50	3.52
Quercus marilandica Münchh.	1	0.7	-	-
Ditrysinia fruticosa (W. Bartram) Govaerts & Frodin	1	0.54	-	-
Nyssa sylvatica Marshall.	1	0.48	67	4.72
Vaccinium stamineum L.	1	0.27	3	0.21
Cornus florida L.	1	0.22	1	0.07
Quercus falcata Michx.	1	0.22	1	0.07
Carya tomentosa (Lam.) Nutt.	0	0.16	-	-
Quercus laevis Walter	0	0.16	8	0.56
Quercus alba L.	0	0.11	-	-
Quercus nigra L.	0	0.11	-	-
Quercus margaretta (Ashe) Small	0	0.11	-	-
Amelanchier arborea (Michx. f.) Fernald	0	0.05	-	-
Callicarpa americana L.	0	0.05	2	0.14
Magnolia virginiana L.	0	0.05	-	-
Quercus coccinea Münchh.	0	0.05	-	-
Pinus taeda L.	-	-	4	0.28
Quercus hemisphaerica W. Bartram ex Willd.	-	-	1	0.07
Quercus stellata Wangenh.	-	-	1	0.07
Total	198	100	1419	100

Table 3. Density and relative density for seedlings (woody stems < 1 m tall) in canopy gap and reference (non-gap) plots in a montane *Pinus palustris* woodland.

Species	Canopy Gaps		Reference Plots	
	Density/ha	Rel. den.	Density/ha	Rel. den.
Vaccinium arboreum Marshall	3183	61.84	2550	49.8
Pinus palustris Mill.	1098	21.33	1095	21.39
Pinus taeda L.	409	7.94	335	6.54
Symplocos tinctoria (L.) L'Hér.	104	2.03	30	0.59
Rhus copallinum L.	74	1.45	10	0.2
Diospyros virginiana L.	55	1.07	-	-
Liquidambar styraciflua L.	49	0.95	-	-
Quercus falcata Michx.	34	0.66	15	0.29
Nyssa sylvatica Marshall.	21	0.41	10	0.2
Vaccinium stamineum L.	19	0.37	10	0.2
Quercus coccinea Münchh.	17	0.33	5	0.1
Quercus stellata Wangenh.	17	0.33	-	-
Carya glabra (Mill.) Sweet	13	0.25	-	-
Oxydendrum arboreum (L.) DC.	13	0.25	20	0.39
Quercus nigra L.	13	0.25	-	-
Acer rubrum L.	11	0.21	5	0.1
Quercus alba L.	9	0.17	-	-
Quercus marilandica Münchh.	4	0.08	25	0.49
Carya tomentosa (Lam.) Nutt.	2	0.04	5	0.1
Quercus laevis Walter	2	0.04	20	0.39
Gaylussacia dumosa (Andrews) Torr. & A. Gray	-	-	965	18.85
Asimina triloba (L.) Dunal	-	-	10	0.2
Ilex opaca Aiton	-	-	10	0.2
Total	5147	100	5120	100

Shannon diversity of the tree layer for canopy gap plots 0.39 and for reference plots was 0.31. No significant relationship existed between expanded gap area and tree-layer Shannon diversity ($r = -0.273$, $p = 0.055$; Figure 3). Sapling-layer Shannon diversity was

1.50 in canopy gap plots and 1.38 in reference plots. No significant relationship occurred between expanded gap area and sapling-layer Shannon diversity ($r = 0.146$, $p = 0.311$). Likewise, we found no significant relationship between expanded gap area and Shannon diversity of the tree and sapling layers combined ($r = 0.064$, $p = 0.657$). Shannon diversity of the seedling layer in canopy gap plots was 1.26 and was 1.37 in reference plots.
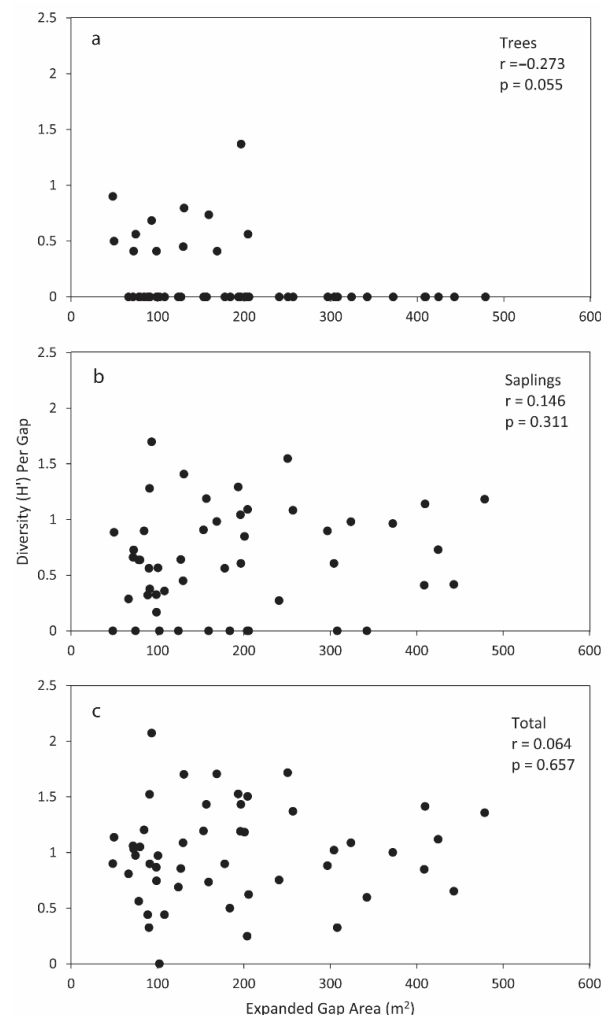
Figure 3. Pearson correlation between expanded gap area and Shannon diversity for (**a**) trees (live stems $\geq$ 10 cm dbh), (**b**) saplings (live woody stems $\geq$ 1 m height, <10 cm dbh), and (**c**) total stems (trees and saplings) in a montane *Pinus palustris* woodland.

3.3. Gap Closure Mechanisms

We projected that 74% of the sampled canopy gaps would close through lateral crown expansion and 26% would close through understory capture. Out of the 13 canopy gaps predicted to close through understory capture, eight were projected to be captured by *Pinus palustris*. We also projected that one canopy gap would be captured by a *Liquidambar styraciflua*, one by a *Pinus taeda*, and one by a *Quercus stellata*. For two canopy gaps projected to close by understory capture, we could not with confidence identify the species of the ascension tree as these gaps had many sub-canopy stems of similar height. Expanded gap area did not significantly differ by canopy gap closure mechanism ($p = 0.300$; Figure 4). Likewise, we found no significant difference between mean basal area lost by projected gap closure mechanism ($p = 0.882$). Similarly, a mean expanded gap L:W and D:H ratios did not significantly differ by a canopy gap closure mechanism ($p = 0.800$ and $p = 0.106$, respectively).
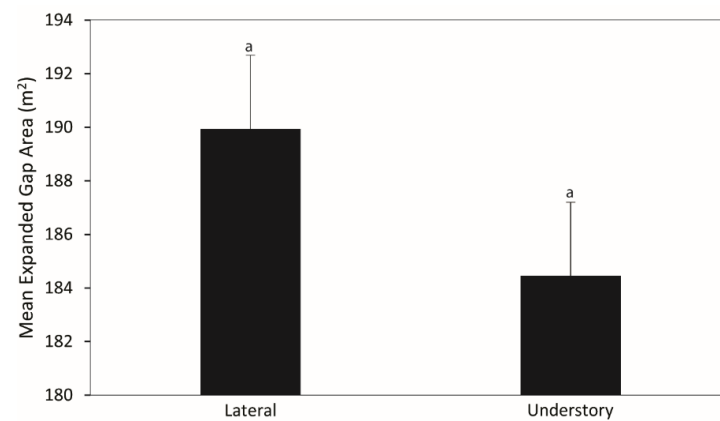
Figure 4. Mean expanded gap area for canopy gaps projected to close via lateral branch elongation and via understory recruitment in a montane *Pinus palustris* woodland. Different letters indicate a significant ($p < 0.05$) difference between categories.

### 3.4. Gap Fraction and Spatial Distribution

From the canopy height model, we detected a total of 742 observed canopy gaps (11 canopy gaps/ha; Figure 5). The average observed canopy gap area was 76 m^2 ± 60, with a minimum area of 25 m^2, and a maximum area of 298 m^2 (Figure 6). The canopy gap size-frequency distribution exhibited a reverse J-shape, with a high frequency of small-area canopy gaps and relatively few large-area canopy gaps (Figure 6). We detected 2.12 gaps/ha in the 50–75 m^2 size bin, 1.17 canopy gaps/ha in the 75–100 m^2 area bin, and 0.71 canopy gaps/ha in the 100–125 m^2 area bin. Detected canopy gaps exhibited significant spatial dispersion at short distances and significant spatial clustering at greater distances (Figure 7). Specifically, canopy gaps were less likely to be observed at distances of 1–8 m from an adjacent gap (significant dispersion). Canopy gaps were more likely to be observed at distances of 12–36 m from an adjacent gap (significant clustering). At distances > 36 m, detected canopy gaps exhibited random spatial distribution.
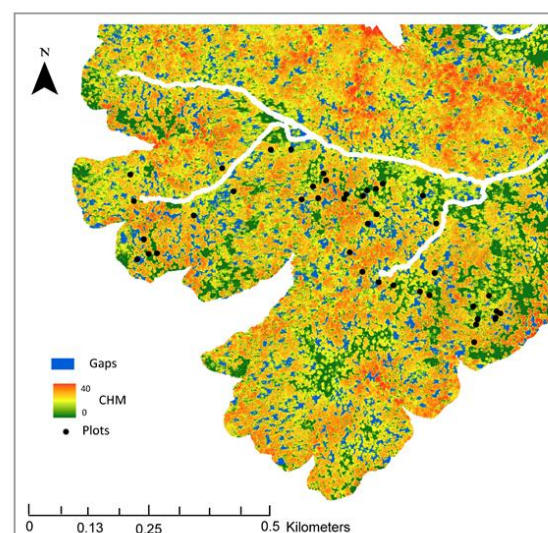
Figure 5. Map of a *Pinus palutris* dominated stand situated in Reed Brake Research Natural Area, Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. The canopy height model displayed was derived from LiDAR data, with detected canopy gaps in blue. Black dots represent canopy gap sampling plots. Note that our maximum gap size threshold was 300 m^2. The white area within the canopy height model is the 10 m buffer around abandoned skid trails.
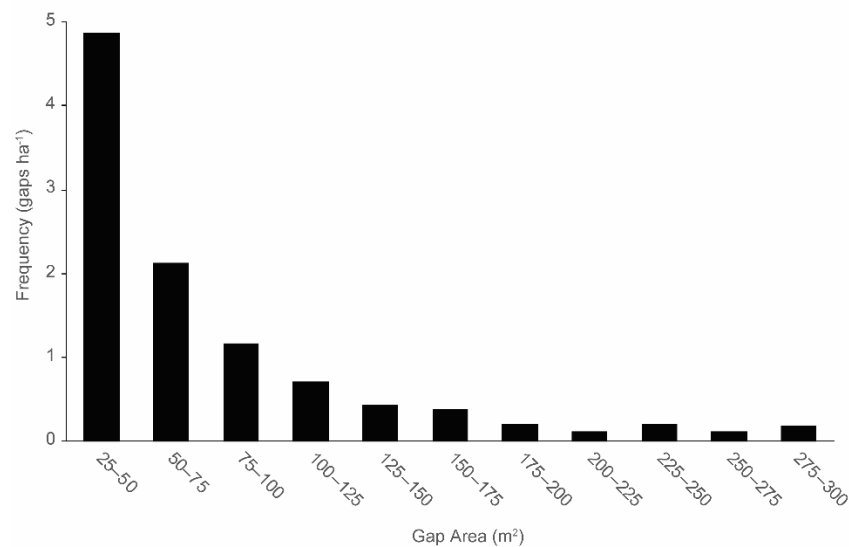
Figure 6. Gap size-frequency distribution of canopy gaps identified from a LiDAR-derived canopy height model. Canopy gap size bins are 25 m^2 size classes. Note our maximum gap size threshold was 300 m^2.
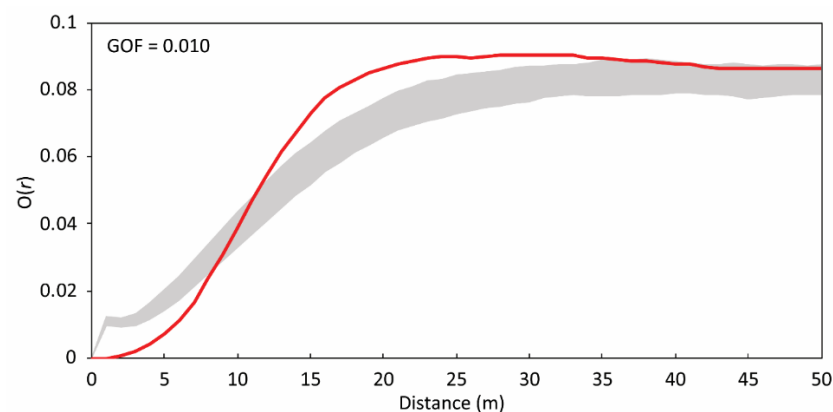
Figure 7. Univariate O-ring function *O(r)* of canopy gaps in a montane *Pinus palutris* woodland. Point-pattern analysis was adapted for objects with finite size and real shape (i.e., canopy gaps). Shaded areas represent a 95% confidence envelope simulated 99 times under the assumption of complete spatial randomness (CSR). The red line is observed values. Values above the gray shaded area indicate significant ($p < 0.05$) clustering (i.e., gaps were closer in space than expected when compared to gap locations simulated under the assumption of CSR), and values below the shaded area represent significant dispersion of gaps. Goodness-of-fit (GOF) is reported in the top left.

4. Discussion

4.1. Canopy Gap and Gapmaker Characteristics

The majority of canopy gaps in this *P. palustris* woodland were formed by single standing dead trees. In contrast, single-tree gaps caused by uprooted or snapped stems were least common. Compared to the co-occurring *Pinus taeda*, *P. palustris* is more susceptible to stem snapping and uprooting when exposed to strong winds [74,75]. *Pinus palustris* snags have been well studied, and they may result from mortality by lightning, insects, or fire and may be important for wildlife habitat and fire ignition [21,31,54,76–78]. In our non-gap reference plots, we found snag density was 5/ha and all but one snag, a *Q. falcata*, was a *P. palustris* stem. Landers and Boyer [76] found a snag density of 7/ha and Varner et al. [19] reported snag density of 9–11/ha for complex stage *P. palustris* stands. When canopy gap areas are included, snag density for this montane, *P. palustris* woodland approximated the

snag density reported in other *P. palustris* stands, including those stands in late stages of stand development.

We posit that many of the snag-formed canopy gaps we documented were caused by *Dendroctonus frontalis* Zimm. activity. In fact, out of 50 plots, 20 showed beetle activity on gapmakers, and 13 of those 20 canopy gaps were formed fully or partially by snags. We found canopy gaps created by gapmakers with evidence of beetle activity formed in 2004, 2005, 2010, 2011, 2012, 2014, 2016, 2018, and 2019. We suspect that insect-induced mortality is an important gap formation mechanism in *P. palustris* woodlands. Attached trees that succumb would become snags that may eventually snap during strong wind events. In contrast, we suspect that strong winds, especially those associated with intense precipitation, may result in relatively more uprooting of living stems [45].

Unexpectedly, multi-tree canopy gaps had marginally smaller mean observed and expanded gap areas than single tree canopy gaps. Although the differences were not significant, the finding was surprising. We suggest this might be related to the size of the trees removed during gap formation. Gapmakers in single tree canopy gaps were significantly larger than gapmakers in multi-tree canopy gaps. Tree diameter is related to crown volume and thus some of the single tree-formed gaps were caused by mortality of relatively large trees that represented accordingly large canopy areas. In contrast, gapmakers in some multi-tree gaps were relatively small and therefore constituted a smaller portion of the forest canopy. Runkle [79] found gapmakers to be larger than surrounding trees; however, other gap-scale disturbance studies have not found this pattern [56,57].

Canopy gap ages ranged from over 20 years to 1 year in our study. Out of 50 canopy gaps sampled, seven gaps had unknown ages, as there was no agreement on the formation year between multiple samples taken for those events. Based on the age distribution we documented, we suspect that canopy gaps in this woodland ecosystem may remain open for ca. 20–25 years, but we note that some gaps would close in shorter periods. The average age of canopy gaps was 10 years (gaps formed in 2011), and the most common age was 16 years (gaps formed in 2005). If canopy gaps are being formed at the approximate rate that canopy gaps are closing, then gap fraction is considered to be in dynamic equilibrium [80]. In such instances, we would expect a high number of young gaps and the number of canopy openings should decrease with increased gap age [6]. The canopy gap age distribution we observed in this *Pinus* woodland indicated that gap fraction was not in equilibrium. This is not unusual or unexpected as superimposed over the natural background mortality rate are exogenous disturbance events that may cause the gap age distribution to become irregular [57].

Canopy openings without gapmakers were found while walking transects through the woodland but were not sampled because they did not meet our established canopy gap criteria. This could be an indication of gap-scale disturbance where the gapmaker(s) had decomposed completely, but more likely indicated intermediate-severity disturbance events where canopy openings would have been larger than that of canopy gaps [2]. Intermediate-severity disturbances would impact larger areas than canopy gaps and would therefore take longer periods to close the canopy voids so that the gap remained after the gapmakers had decomposed. We suspect that some of the canopy openings we observed without visible gapmakers were the result of these broader-scale disturbance events.

As suspected, reference plots (i.e., closed canopy locations) had significantly more litter than canopy gaps plots. Overstory density in *P. palustris* stands has been shown to be a strong predictor of *Pinus* needle litter [32]. We suspect that open canopy conditions caused by the loss of one or more *Pinus* canopy trees reduced *Pinus* litter cover and increased herb cover within canopy gaps [14]. The spatial variability in *Pinus* litter and herb cover may influence fire behavior such that reference plots, with higher fuel loads, would have different fire effects than canopy gap microenvironments [31,81].

L:W ratios can be used to quantify canopy gap shapes and may provide information on micro-scale variations that occur within individual gap types [56]. We found no significant difference between L:W and a gap formation mechanism. Snag-formed gaps have been

shown to be more circular in shape than those caused by uprooted stems which may be more elliptical [56]; however, not all studies have documented relationships between L:W and gap formation mechanism [57]. Canopy closure mechanisms could also be influenced by L:W, as gap L:W may influence insolation in the sub-canopy [82,83]. The shape of the gaps may also influence gap closure as narrow gaps would be more likely to fill by lateral branch extension; however, we noted no relationships between gap closure mechanism and L:W. Similarly, we found no significant relationship between D:H and canopy closure mechanism.

4.2. Forest Composition

Shannon diversity was significantly greater in canopy gap plots than in reference plots for both seedling and sapling sized stems. Higher species diversity within canopy gap plots was not surprising and was likely a function of the increased resources associated with those microenvironments [14,16,22,53]. Hardwood saplings were more abundant than *P. palustris* or other *Pinus* species saplings in both canopy gap and reference plots. Pecot et al. [20] found that hardwood advance reproduction in *P. palustris* canopy gaps had the advantage of established root systems that allowed for faster vertical growth rates. However, with recurring surface fires, hardwood individuals should disproportionately be maintained in the seedling and sapling size categories as stems should continually be top killed [26,84]. Shoot mortality can vary depending, in part, on species and stem size (which can impact bark thickness and bud height) and fire behavior (which can influence the temperatures to which stems are exposed). Shannon diversity of trees, saplings, and total trees and saplings were not significantly correlated with expanded canopy gap area. This indicated that larger canopy gaps do not have higher Shannon diversity values than smaller canopy gaps, but regardless, canopy gap environments do support greater woody plant diversity than non-gap microenvironments.

4.3. Gap Closure Mechanisms

The majority of canopy gaps were projected to close through lateral crown extension. *Pinus palustris* was the species most likely to capture canopy gaps through lateral extension, or from subcanopy height growth. Few canopy gaps were predicted to be captured by a species other than *P. palustris*, despite relatively high species richness in the regeneration layer. The other species projected to capture canopy gaps from below were *Liquidambar styraciflua*, *Quercus stellata*, and *P. taeda*. Notably, the gaps projected to be captured by a *Quercus* or a *P. taeda* contained canopy gap perimeter trees of the same species. The canopy of the woodland was almost purely *P. palustris*, so these microsites that contained canopy trees of other species may have had some underlying conditions that favored those species over *P. palustris*. Nonetheless, most all canopy gaps were projected to be closed via *P. palustris*. Thus, under the current disturbance regime, we suggest that *P. palustris* will remain the dominant species throughout the fire-maintained woodland. Recurring low intensity fires disproportionately kill shoots of fire-sensitive species thereby reducing competition for *P. palustris* recruitment via gap-scale processes [21,30,85].

We suspected that smaller canopy gaps would be more likely to close through lateral crown extension and larger canopy gaps would be more likely to close through understory capture [57,86]. However, the canopy gap closure mechanism was not impacted by expanded gap area or basal area lost via gap formation. In fact, both the largest and smallest canopy gaps were predicted to close through understory capture. This indicated that factors other than expanded canopy gap area and basal area removed by gap formation influence the gap closure mechanism. Lertzman [87] found that gap closure mechanisms were reliant on the presence of advance reproduction in the canopy gap environment and noted that species most abundant in the understory were most likely to fill the canopy void.

4.4. Gap Fraction and Spatial Distribution

Our use of LiDAR to calculate gap fraction removed potential bias that may result from sampling only canopy gaps found along established transects in the field [52]. Observed canopy gap areas for the sampled gaps and the LiDAR detected gaps were similar (mean area of the observed canopy gaps in the field was 75 m^2 and mean area of LiDAR-detected gaps was 76 m^2). In general, the canopy gaps documented in this montane *P. palustris* woodland were smaller than typical sizes observed in *P. palustris* stands on the Coastal Plain [22]. Our analysis did reveal some canopy openings larger than 300 m^2 (the threshold set in our analysis). These large openings indicated the presence of intermediate-severity disturbance events through the *P. palustris* woodland [2]. The gap-size frequency distribution exhibited a reverse-J or negative exponential shape. Although we set a maximum gap area threshold of 300 m^2, we speculated that the frequency of large openings would be less than that of small gaps, as has been reported in many canopy gap-based studies in a variety of forest types and among a variety of disturbance agents (e.g., [88–90]).

The forest-scale spatial distribution of detected canopy gaps exhibited a significantly dispersed pattern (i.e., distance between gaps greater than expected under CSR) at short distances and a significantly clustered pattern (i.e., distance between gaps less than expected under CSR) at distances up to 36 m. The significant dispersion at distances <8 m was likely attributed to *P. palutris* individuals that occurred between single-tree gaps. We expect the crown diameter of canopy *P. palutris* to approximate the distances at which significant dispersion of canopy gaps occurred [91]. At distances of 8–36 m, canopy gaps were clustered in space. The significant clustering of canopy gaps at intermediate distances could be attributed to *Dendroctonus frontalis* activity, localized drought stress, patchy high severity fire, or other exogenous canopy disturbance in which trees in small neighborhoods experienced the same discreet disturbance. Our findings correspond to spatial patterns reported in other canopy gap studies that found both clustered and dispersed patterns of canopy gaps depending on distance. Canopy gaps that result from insects, pests, pathogens or endogenous disturbance have been found to be evenly dispersed or randomly distributed [92–94], which we documented at distances >36 m. Clustered patterns have been associated with exogenous disturbance such as wind, or other gap-enlarging agents, but these patterns manifested at greater distances than what we documented in this study [94,95]. We suspect we may have found significant clustering of canopy gaps at greater distances if large openings (those > 300 m^2) were included in our spatial analyses.

5. Conclusions

Although gap-scale disturbances are the most common disturbance events in forest ecosystems, few studies have analyzed gap-scale disturbance patterns and processes in *Pinus palustris* woodlands. Most canopy gaps (64%) we documented were caused by the death of a single tree, but multi-tree gaps were not uncommon. Snag-formed gaps were most frequent (38%) followed by snapped stem-formed gaps (32%). We speculated that many canopy gaps were caused by insects. Furthermore, we suspected that gap formation may be higher during periods of water stress, but additional research is required. Contrary to our expectations, we did not find significant differences in gap size or shape patterns based on gap formation or closure mechanisms. Most gaps (74%) were projected to close by lateral crown expansion of gap perimeter trees. Through this process, canopy trees, which were almost exclusively *P. palustris*, would increase crown area. We hypothesized that most gaps projected to close via subcanopy recruitment would be captured by a *P. palustris* stem, but we did note a canopy gap projected to close by a *P. taeda*, one projected to close by a *Q. stellata*, and one projected to close by a *L. styraciflua* individual. *Pinus* litter was the most common ground cover in both canopy gap and non-gap environments, but litter depth was significantly greater in non-gap plots. The majority of gaps were small and gap frequency declined with increased gap size. We found gaps were significantly clustered at distances of 8–36 m from gap edge to gap edge, but were randomly distributed beyond 36 m. With frequent prescribed fire, we hypothesized that gap-scale disturbance processes

would maintain *P. palustris* dominance in this woodland and that, through these processes, stand structure would transition to a lower density of larger canopy trees at wider spacings. As stand structure changes over time, gap-scale disturbance patterns and processes may change accordingly.

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