Bull Mar Sci. 101(3):1161–1175. 2025
https://doi.org/10.5343/bms.2023.0165

Bulletin of Marine Science
research paper

Spatial and temporal patterns of mangrove forest canopy gaps at the southern distribution limit

Michael Kyei Agyekum [1,2,3] *
Martin Zimmer [1,2,4]
Fiona MacKay [5,6]
Steven Weerts [7,8]
Véronique Helfer [1]

[1] Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany

[2] Faculty 2 Biology/Chemistry, University of Bremen, Bremen, Germany

[3] Current affiliation: Helmholtz Centre for Environmental Research (UFZ), Brückstraße 3A, 39114 Magdeburg, Germany

[4] IUCN SSC Mangrove Specialist Group

[5] Oceanographic Research Institute (ORI), SAAMBR, Durban, South Africa

[6] School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

[7] Council for Scientific and Industrial Research, Durban, South Africa

[8] Department of Zoology, University of Zululand, KwaDlangezwa, South Africa

** Corresponding author email: < michaelk@uni-bremen.de>*

Cartagena Colombia
July | 24-28 | 2023

Proceedings of the 6th Mangrove Macrobenthos and Management meeting

Guest Editors:
Juan Felipe Blanco-Libreros,
Maria Fernanda Adame,
Gustavo A Castellanos-Galindo,
Samantha K Chapman,
Karen Diele,
José Ernesto Mancera Pineda,
Kerrylee Rogers

Handling Editor:
José Ernesto Mancera Pineda

Date Submitted: 30 November, 2023.
Date Accepted: 20 December, 2024.
Available Online: 23 December, 2024.

ABSTRACT.—Mangrove forest canopy gaps occur in 35 countries across the global distribution of mangrove forests in some 110 countries. Yet, their spatial and temporal patterns and drivers of their formation and closure remain poorly understood. Here, we investigated whether gaps are distributed randomly, clustered, or dispersed over space and time in two showcase areas in South Africa, uMhlathuze, near Richards Bay, and Beachwood, near Durban, to prime better understanding of the underlying processes. We mapped canopy gaps using free satellite imagery within Google Earth Pro and fixed wing-acquired aerial images and analyzed spatiotemporal patterns using the Ripley's *K* function and the Emerging Hot Spot Analysis. Kaplan–Meier analyses estimated the time it takes for gaps to close. Canopy gaps in uMhlathuze occurred spatiotemporally clustered, whereas Beachwood canopy gaps primarily exhibited random spatial patterns. The spatial distribution of canopy gaps was linked to great canopy height at both uMhlathuze and Beachwood, supporting the hypothesis of lightning strikes as causal agents of gap formation. Canopy gaps at uMhlathuze remained open for at least 23 yr, and no gap at Beachwood had closed over the 18-yr study time span, rendering our study region near the southern distribution limit of mangroves a contrast to mangrove forests in many other regions of the world. Without active human intervention, the rising frequency of thunderstorms—and consequently, lightning strikes—is expected to increase canopy gap formation in mangrove forests. This will significantly reduce the ability of mangrove and estuarine systems in South Africa to support climate change mitigation and adaptation, weakening the resilience of coastal socioecological systems.

The occurrence of circular or elliptical mangrove forest canopy gaps has been documented in 35 countries worldwide (Agyekum 2024). Those gaps create microhabitats with increased availability of nutrients (upon decomposition of accumulated plant detritus from dead trees) and light penetration through the canopy (Amir 2012, Amir and Duke 2019), and thereby potentially act as cores for mangrove regeneration and rejuvenation (Sherman et al. 2000, Duke 2001). Various drivers of large- and small-scale canopy gap formation have been proposed, including lightning strikes (Clarke and Kerrigan 2000, Sherman et al. 2000), insect and/or pathogen attacks (Feller and McKee 1999, Feller 2002), either directly or as an indirect consequence of lightning strikes upon weakened immune response in struck trees (Gora et al. 2020), hurricanes (Sherman et al. 2001, Zhang et al. 2008), drought (Andrew et al. 2017, Duke et al. 2017), and small-scale forestry (Pinzón et al. 2003).

The existing data on canopy gaps in mangrove forests remains limited, and studies on the fine-scale distribution patterns in both space and time are scarce. Some studies described the patterns as spatially and temporally random (Amir and Duke 2019) or clustered (Sherman et al. 2000). Sherman et al. (2000) examined the spatial patterns of gaps in a 47 km^2 mangrove area in the Dominican Republic using Ripley *K* functions. They initially hypothesized that the canopy gaps would not differ from complete spatial randomness, but their findings showed that the gaps were clustered. They also investigated temporal patterns based on the annual canopy gap formation rate and canopy turnover times. Their temporal analysis revealed that gap formation was not randomly distributed over time. By contrast, Amir and Duke (2019) examined the spatial patterns of canopy gaps through visual interpretation and assessed temporal patterns using a gap closure index in four separate small mangrove stands in Australia. They concluded that canopy gaps were spatially and temporally random.

Vogt et al. (2013) demonstrated that all three spatial patterns (i.e., random, clustered, and dispersed) can occur within the same mangrove stand. They examined the spatial patterns of canopy gaps in a 4721-ha core zone in the Can Gio Biosphere Reserve in Vietnam, where only research, monitoring, and educational activities are allowed. They used the Clark–Evans aggregation index R to analyze these patterns. Zhang et al. (2008) investigated the spatial patterns of canopy gaps in a small mangrove patch at Shark River in the Everglades National Park, USA. Zhang hypothesized that canopy gaps would be spatially random and evaluated their patterns using the Ripley *K* function. The study confirmed that the gaps were randomly distributed.

In this study, we analyzed the spatial and temporal patterns of canopy gap formation and closure in two case study areas in South Africa. Based thereon, we investigated whether the "core for regeneration" hypothesis (Amir and Duke 2019, and references therein) also applies to South Africa.

Materials and Methods

Study Area.—The study was conducted in two mangrove areas on the subtropical east coast of South Africa (Fig. 1). Both areas are declared conservation areas, and the mangrove forests are well protected. The Beachwood forest (Fig. 1C) is situated on the uMgeni Estuary and covers approximately 0.74 km^2. The stand at uMhlathuze, some 150 km to the north, is much larger, covering about 11.5 km^2 (Fig. 1D). Both areas host three mangrove species, *Bruguiera gymnorhiza, Rhizophora mucronata*

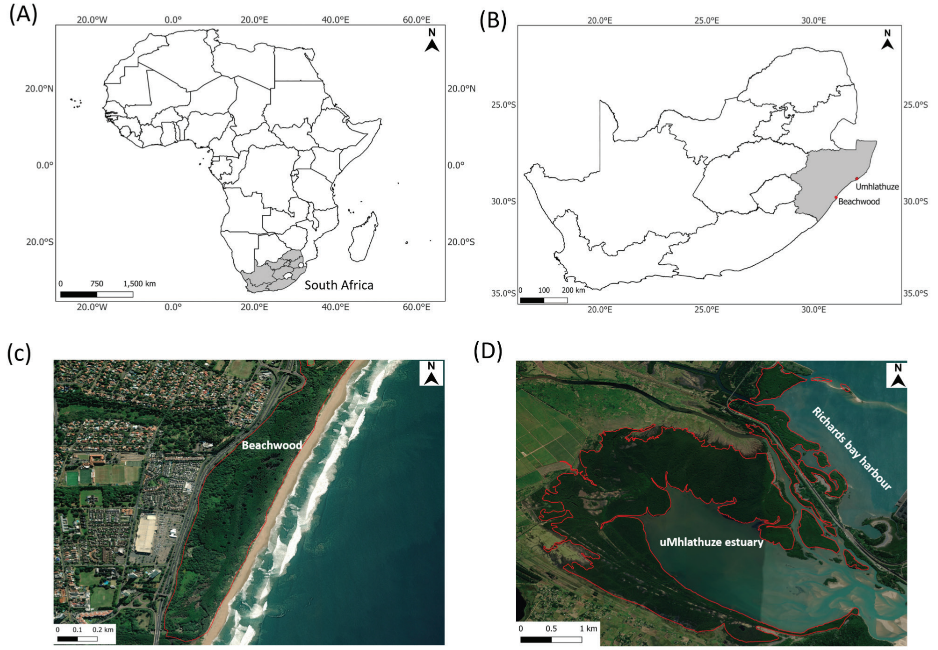

Figure 1. Location of the study sites in: (A) South Africa and (B) KwaZulu-Natal province. (C) Beachwood mangrove forest covering ca 0.74 km^2, and (D) the uMhlathuze site, consisting of the uMhlathuze estuary and Richards Bay harbor mangrove stands, covering about 11.5 km^2. The maps were prepared using QGIS v3.22.11 Białowieża (QGIS Development Team 2021), and the image sources include ESRI, Digital Globe, GeoEye, i-cubed, Maxar, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, and GIS User Community.IGP, GIS User Community. Study areas are demarcated in red.

and *Avicennia marina*, with the latter being highly dominant. In both areas, the mangrove extent has increased considerably in recent years (Rajkaran and Adams 2011, Ezemvelo KZN Wildlife 2013).

The region experiences a mean annual rainfall of 1176 to 1200 mm yr^{-1}, with average temperatures ranging from 11 to 29 °C. (Rajkaran and Adams 2011). The tidal system is semidiurnal with a mean neap tidal range of 0.52 m and a spring tidal amplitude of 1.8 m. The mangrove stands at Beachwood and uMhlathuze are similar in terms of protection status, species composition, and latitude. Therefore, we expected similar spatial and temporal patterns associated with potential natural drivers of canopy gap formation in the region.

Gap Detection and Digitalization.—We employed a combination of very high-resolution historical satellite images (e.g., CNES/AIRBUS, Maxar, and NASA) accessed through Google Earth Pro v7.3.3 (Google Earth 2018) for the time frame of 2004 to 2020 and 2001 to 2018 at uMhlathuze and Beachwood, respectively, and historical aerial photographs for uMhlathuze (orthorectified imagery from 1997, 2006, 2013, and 2018 from South Africa's National Geospatial Information Organization; NGI 2013), to investigate patterns of formation and closure of canopy gaps in the mangrove forests (Supplementary Appendix S1). Both mangrove stands at Beachwood and uMhlathuze were delineated within Google Earth Pro, using on-screen digitizing polygon tools, and saved into separate shapefiles. At both stands, canopy gaps were delineated the same way. The shapefiles were then projected onto the world cylindrical equal area projection in ArcMap 10.5 (ESRI 2016) and further edited, adding the gaps detected from the inspection of the georeferenced aerial photographs delineated using the polygon geometry tools in ArcMap 10.5. We computed the percentage of mangrove area occupied by canopy gaps by dividing the total gap area by the total area of the mangrove stand.

The geographical coordinates and size of gaps were extracted using the calculate geometry tool within ArcMap 10.5. Gaps were labeled with the status "open", "recovering", or "closed" to document the gap dynamics over time (Supplementary Appendix S1, Supplementary Fig. S6). The "open" stage is characterized by visible bare sediments partially covered by decomposing trunks, branches, and twigs. In the early "recovering" stage, new seedlings emerge, creating mixed areas with patches of bare ground and low vegetation within the canopy gaps (Supplementary Fig. S6). In later recovering stages, young trees cover the entire canopy gap, with their height smaller than those of the surrounding intact canopy. In the "closed" stage, the trees had grown to a height comparable to the intact canopy, making the canopy gaps nearly indistinguishable from the surrounding canopy (Supplementary Fig. S6).

We computed the daily net canopy gap formation rate by dividing the number of newly formed canopy gaps visible in one satellite image by the number of days between that image and the preceding satellite image.

Spatial and Temporal Patterns.—For both sites, we computed the Ripley's *K* function (Dixon 2001), using 999 permutations (default value to compute the confidence interval for a random pattern), to evaluate whether canopy gaps exhibit a statistically significant clustered or dispersed spatial pattern, across distances ranging from 0 to 100 m, using 10-m increments (20- or 30-m increments provided poorer results; data not shown); analyses were performed within ArcMap 10.5 using the *L(d)* transformation (Dixon 2001). The graphs were obtained using the ggplot2 package in R (Wickham 2016), based on the Ripley's *K* output table within ArcMap 10.5.

Further spatiotemporal analyses were conducted only for uMhlathuze, as the number of gaps detected in Beachwood was below the limit of the minimal sample size for those analyses (60 for the space-time-pattern mining tool; ArcMap 10.5).

The spatiotemporal patterns of canopy gaps in uMhlathuze were evaluated using the Emerging Hot Spot Analysis (EHSA; Harris et al. 2017, ESRI 2021a), a space-time-pattern mining tool available in ArcMap 10.5. This technique combines the Getis–Ord G_i^* statistic (Ord and Getis 1995, ESRI 2016) to identify the spatial locations of canopy gap formation hot spots with the time-series Mann–Kendall test (Mann 1945, Kendall and Gibbons 1990) and to detect temporal trends (Harris et al. 2017). The Getis–Ord G_i^* statistic measures the clustering intensity of high or low values in a bin in comparison to its neighboring bins in the space-time netCDF (network Common Data Form) data cube (ESRI 2021a). Within this space-time data cube, the sums of values (or point counts) within bins, defined across two spatial dimensions and one temporal dimension, is computed and compared to the sum of all bins in its neighborhood, and *z*-scores and *P*-values are generated for each bin. Subsequently, the Mann–Kendall test was used to determine statistically significant temporal trends across the time series (one for each bin) of *z*-scores resulting from the Getis–Ord G_i^*. Temporal trends are detected by comparing each time step to the following one; if the *z*-score in the following time step is larger, a value of +1 will be generated (increasing trend); if it is smaller, a value of −1 (decreasing trend) will be generated (Harris et al. 2017, Bass 2017, Reddy et al. 2019, ESRI 2021a). The result of the EHSA is a two-dimensional grid that classifies cells according to following temporal clustering patterns: "new", "consecutive", "intensifying", "persistent", "diminishing", "sporadic", "oscillating", or "historical" hot spots (*see* Supplementary Table S1 for full description; Harris et al. 2017). We transformed the data collected (i.e., date and location of canopy gaps) into a space-time netCDF data cube by aggregating the gap locations into space-time bins with a spatial resolution (bin size) of 50 m (Bass 2017, ESRI 2021a; using a bin size of 100 m did not strongly impact the final results; *see* Supplementary Fig. S4). The resulting value for each bin corresponds to the number of canopy gaps observed within that bin in a given year (ESRI 2021a). We computed the Getis–Ord G_i^* statistic (Ord and Getis 1995) to identify the location and degree of spatial clustering of high (hot spots) or low (cold spots) values (i.e., the number of canopy gaps) within neighborhood distances of 150 m, 200 m, 350 m, and 400 m with an assumed time interval of 1 yr for canopy gap formation. The selection of the different neighboring distances served to evaluate whether the neighborhood size would obscure or reveal small hot or cold spots (Reddy et. al. 2019).

Potential Drivers of Canopy Gaps Formation.—In order to better document and understand the spatiotemporal patterns and decipher potential drivers, we collected additional information for both study sites (upon data availability).

First, we investigated the relationship between canopy gap formation and canopy height, using the NASA Shuttle Radar Topography Mission (SRTM) version 3 global 1 arc-second dataset (NASA JPL 2014). We clipped the NASA SRTM data using the delineated mangrove maps of Beachwood and uMhlathuze, ensuring the same map projection (World Cylindrical Equal Area) and environmental settings were applied, and extracted the canopy height values for the entire mangrove stand grid including the areas surrounding the delineated polygons of canopy gaps using the "Extract Multiple Values to Points" tool in ArcMap 10.8.2 (ESRI 2021b). Second, temperature and precipitation data were obtained from the South African Weather Service at uMhlathuze (1995–2020) and Beachwood (1995–2018).

Statistical Analysis.—The normality of the average daily temperature (minimum and maximum), average daily rainfall, daily net gap formation rate, and canopy height data was evaluated using the Shapiro–Wilk test and Q-Q plot in R programming software (R Core Team 2020). To compare canopy heights in the whole forest with those near canopy gaps that were not normally distributed, a Wilcoxon signed rank test was performed. Spearman's rank correlation tests were performed to evaluate the relationship between the average daily temperature (minimum and maximum), average daily rainfall, and the daily net gap formation rate because the data were not normally distributed.

Canopy Gaps as "Cores for Regeneration".—To evaluate whether the "core for regeneration" hypothesis would be supported by our data, we applied the Kaplan–Meier (Stalpers and Kaplan 2018) approach to the dataset from uMhlathuze (not applicable to Beachwood due to absence of gap closure), a nonparametric time-to-event analysis initially designed to estimate survival probability, to estimate

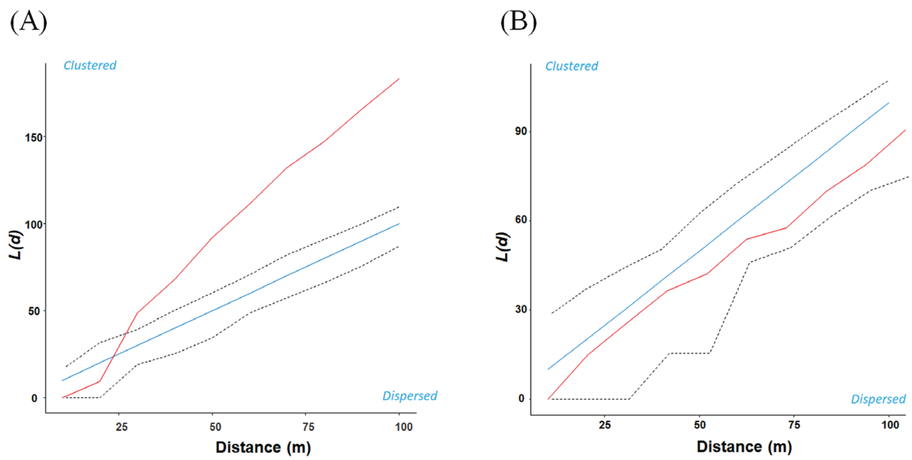

Figure 2. Ripley's *K* function showing the spatial pattern of canopy gaps at various distances in (A) uMhlathuze and (B) Beachwood. The expected (assuming a random pattern) and observed *K* function curves are represented by the blue and red lines, respectively. The black dashed lines represent the 99% confidence interval after 999 iterations. The observed *K* function curve above the expected *K* function curve for uMhlathuze indicates a clustered distribution of canopy gaps, at distances above 25 m. The observed *K* function curve within the 99% confidence interval below the expected *K* function curve for Beachwood indicates a random dispersed distribution of canopy gaps. The two graphs were obtained using ggplot2 (Wickham 2016).

the probability of gaps to stay open (i.e., "survive") over time. This analysis was performed using the R packages survival v3.5-7 (Therneau 2023) and survminer v0.4.9 (Alboukadel et al. 2021). The annual canopy gap closure rate was computed by dividing the number of closed canopy gaps visible in one satellite image by the time in years between that image and the preceding satellite image. The result is further divided by the number of open canopy gaps in the preceding image and expressed as a percentage. The annual canopy gap formation rate was computed by dividing the number of newly formed canopy gaps visible in one satellite image by the time in years between that image and the preceding satellite image.

Results

Spatial and Temporal Patterns.—According to the Ripley's *K* function, canopy gaps in uMhlathuze showed a clustered distribution at distances above 25 m. Below 25 m, the pattern was random (Fig. 2A). While a visual inspection of canopy gaps at Beachwood hinted at a clustered distribution (Fig. 2B), the canopy gap distribution did not differ significantly from a random distribution (Fig. 2B), suggesting a potential lack of statistical power due to small sample size.

The Emerging Hot Spot Analysis revealed significant sporadic hot spots (i.e., locations alternate between being "hot" and "not hot"; Fig. 3). We also observed small isolated clusters of new or consecutive hot spots (i.e., locations that are statistically significant hotspots for the most recent time, or locations with a single uninterrupted run of statistically significant hotspot bins, comprised of less than 90% statistically hot bins, respectively) at the 150 m neighborhood distance (Fig. 3A). By contrast, the neighborhood distances of 200 and 350 m exclusively displayed the sporadic

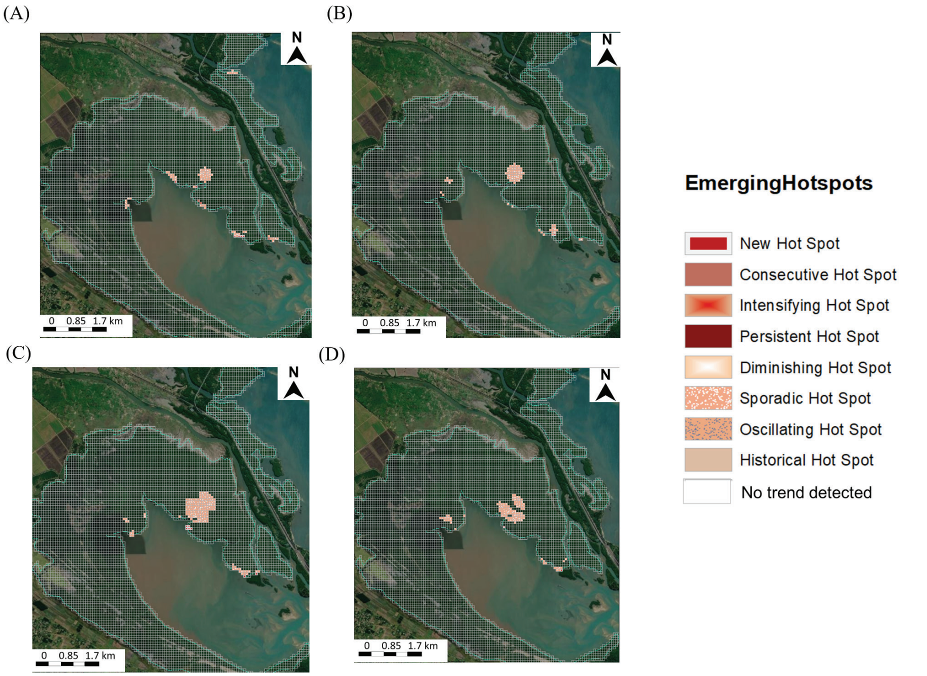

Figure 3. Results of the Emerging Hot Spot Analysis (EHSA; Harris et al. 2017), conducted within ArcGIS (ArcGIS 2016) for uMhlathuze. We used a 50 m bin size and distinct neighborhood distances of (A) 150 m, (B) 200 m, (C) 350 m, and (D) 400 m with a time interval of one year. Each bin (here visualized as a cell) was categorized as significant (with $P < 0.05$ and z-score > 2.65) "New", "Consecutive", "Intensifying", "Persistent", "Diminishing", "Sporadic", "Oscillating", or "Historical" hot spots. Empty bins represent areas where no significant trend was detected ($P > 0.05$ and z-score = 0). The EHSA revealed the following (A) sporadic, small, isolated clusters of new or consecutive hot spots, (B) sporadic and small isolated clusters of new hot spots, (C) sporadic and small isolated clusters of new hot spots, and (D) sporadic hot spots. The background satellite image was obtained from the ESRI South Africa World Imagery basemap.

and small isolated clusters of new hot spots (Fig. 3B and C). Also, the neighborhood distance of 400 m displayed only sporadic hot spots (Fig. 3D).

Potential Drivers of Canopy Gaps Formation.—We observed a total of 291 gaps in uMhlathuze and 20 gaps in Beachwood over the time span from 1997 to 2020 and 2001 to 2018, respectively. Canopy gaps in uMhlathuze and Beachwood covered 1.1% (Supplementary Fig. S2) and 0.4% (Supplementary Fig. S3) of the total mangrove area in the respective sites. The daily net canopy gap formation rate ranged from 0.04 to 0.5 gaps d^{-1} at uMhlathuze, and from 0.001 to 0.06 gaps d^{-1} at Beachwood (Supplementary Fig. S7).

The Spearman's rank correlation showed no apparent relationship between the net daily canopy gap formation rate and average daily temperature (minimum or maximum) or average daily rainfall for uMhlathuze ($r = 0$, $P > 0.05$; Supplementary Figs. S7A and C, S8A and D) or Beachwood ($r = 0$, $P > 0.05$; Supplementary Figs. S7B and D, S8B and D).

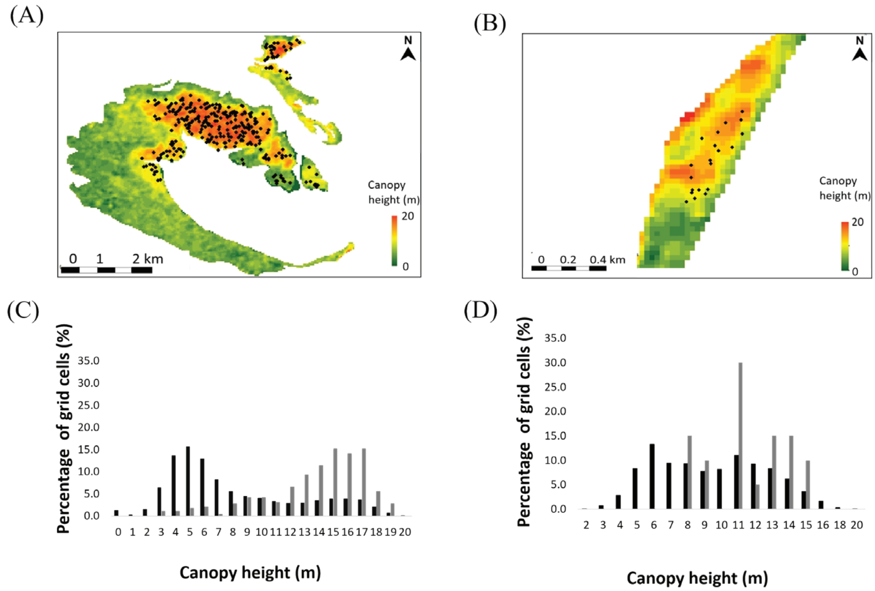

Figure 4. Canopy heights in (A) uMhlathuze and (B) Beachwood mangrove stands depicting the percentage of grid cells with inferred canopy heights at (C) uMhlathuze and (D) Beachwood. Black bars represent the elevations corresponding to canopy height of all trees, grey bars represent the canopy height where gaps formed. Canopy gaps locations are indicated by diamonds in (A) and (B). The maps were prepared using ArcMap 10.5 (ESRI 2016), and the bar graph using Excel.

Canopy height ranged from 12 to 18 m at uMhlathuze (Fig. 4C) and 11 to 15 m at Beachwood (Fig. 4D). The Wilcoxon signed rank test showed that the height of the mangrove canopy surrounding gaps was significantly higher than that of the overall mangrove stands at both uMhlathuze (V = 0, P < 0.001) and Beachwood (V = 0, P < 0.001; Fig. 4A and B, respectively).

Canopy Gaps as "Cores for Regeneration".—The average annual canopy gap formation rate at uMhlathuze ranged from 4 to 10.7 gaps yr^{-1}; the annual average closure rate ranged from 0.4% to 4.6% (Supplementary Table S2). The average annual formation rate ranged from 0.5 to 2 gaps yr^{-1} at Beachwood (Supplementary Table S2); no closure rate could be calculated as all canopy gaps remained open.

Out of the 291 canopy gaps observed in uMhlathuze, about 66% (n = 193) remained open beyond 8000 d (i.e., at least 23 yr; Fig. 5 and Supplementary Fig. S2), 19% were classified as recovering, and 15% closed within 2 to 23 yr after the first observation. Accordingly, the probability of canopy gaps at uMhlathuze closing over 23 yr was only about 30%. None of the 20 canopy gaps in Beachwood had closed, nor were they classified as recovering, over the time span covered by our study (i.e., gaps remained open for at least 18 yr; Supplementary Appendix S1, Supplementary Fig. S3). Hence, we consider the probability of gap closure over 18 yr to approach zero.

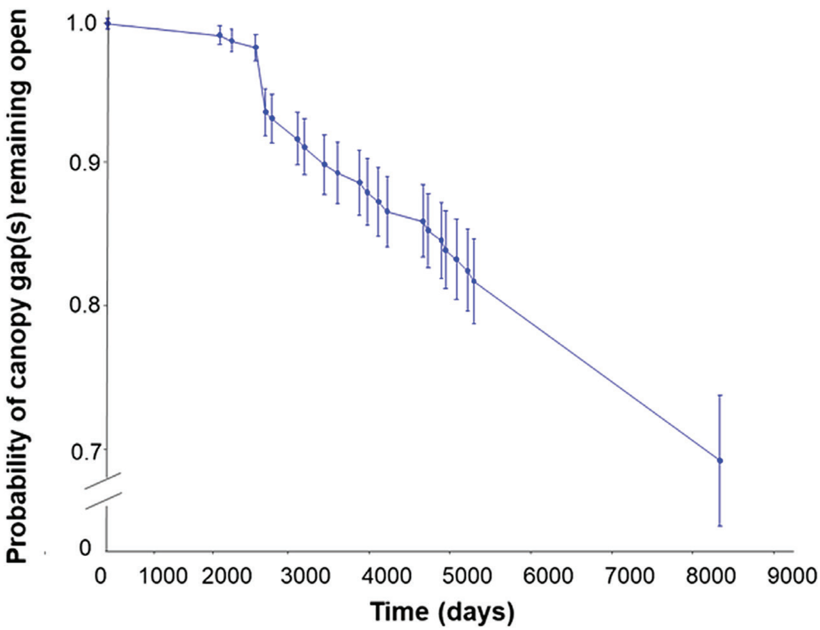

Figure 5. Kaplan–Meier (Stalpers and Kaplan 2018) curve indicating the probability of canopy gap(s) to remain open over the study duration; the dots indicate the median values, and the bars show the standard errors. The estimates were obtained using the survival package v3.5-7 in R (Therneau 2023), and the graph was plotted using ggplot2 (Wickham 2016).

Discussion

Our analysis of mangrove forest canopy gap distribution over space and time in two case study areas of Kwazulu-Natal, South Africa, revealed spatiotemporal clustering of gap formation in one of the largest mangrove areas of South Africa, uMhlathuze. By contrast, gap formation in a very small mangrove stand, the Beachwood forest, exhibited a random spatial pattern. The absence of a relationship between temperature or precipitation and canopy gap formation suggests that there were no extreme climatic conditions that induced the gap formation.

Our findings suggest that high mangrove canopies are more prone to canopy gap formation, suggesting either possible lighting strikes or an effect of tree age (using tree height as a proxy for age) on gap formation. The latter would hint towards canopy gaps supporting the rejuvenation of old-grown mangrove forests. However, the observed canopy gap closure rates in our study areas were very low despite the long-term characteristics of our study. We will discuss the relevance of these spatiotemporal patterns for our understanding of mangrove forest canopy gaps formation and for the "core of regeneration" hypothesis in turn.

Spatial and Temporal Patterns of Mangrove Canopy Gaps in the Two Study Sites.—Our spatial analyses showed a significantly clustered pattern for the canopy gaps in the large mangrove stand of uMhlathuze, while the spatial pattern in the relatively small mangrove stand of Beachwood was not significantly different from a random distribution. The latter may be explained by a mangrove area too small, or a gap density too low, to display spatial patterns other than random. A visual inspection of canopy gaps at Beachwood suggested a clustered distribution that coincides with areas containing tall trees, a pattern also observed in uMhlathuze. This observation suggests that a small sample size poses challenges for analyzing gap dynamics in mangrove forests with limited spatial extent. The varying mangrove extents could influence the formation of clustered and random patterns at uMhlathuze and Beachwood, respectively. This finding aligns with descriptions in the literature. The spatial distribution of gaps in the Can Gio mangrove Biosphere reserve demonstrates the possibility of all three patterns (i.e., random, clustered, and dispersed) occurring within a large-scale mangrove stand (Vogt et al. 2013). Sherman et al. (2000) also found that canopy gaps were clustered in a large mangrove stand in the Dominican Republic. In contrast, Zhang et al. (2008) found that canopy gaps in a relatively small mangrove patch in the Everglades National Park were randomly distributed spatially. Similarly, Amir and Duke (2019) observed that canopy gaps were randomly distributed in four relatively small separate mangrove stands in Australia.

The Emerging Hot Spot Analysis revealed a temporally sporadic hotspot pattern (i.e., locations alternate between being "hot" and "not hot") in uMhlathuze from 1997 to 2020, which we interpret as a temporally clustered pattern. In contrast, small, isolated clusters of new and consecutive hotspots (i.e., locations that are statistically significant hotspots for the most recent time, or locations with a single uninterrupted run of statistically significant hotspot bins, comprised of less than 90% statistically hot bins, respectively) were observed at different neighboring distances. While the amount of data available did not allow for the evaluation of the spatiotemporal patterns via the Emerging Hot Spot Analysis in Beachwood, the number of newly formed gaps per day does not seem to exhibit a temporal pattern distinct from that in uMhlathuze.

Potential Drivers of Canopy Gaps in the Two Study Sites.—Small-scale subsistence forestry has been cited as a driver of mangrove canopy gap formation, albeit typically resulting in larger gaps than those formed by natural causes (Pinzón et al. 2003). We can exclude this driver in either area studied herein, at which mangroves enjoy a high degree of protection and alternative sources of timber are more readily available for subsistence forestry. Further, in situ observations of some of those gaps (three in both study sites) in 2018 showed that most of the dead trees were still standing (*see* Supplementary Fig. S1). Large-scale clear-felling, in turn, would not result in circular or elliptical canopy gaps of the size that we studied herein.

Hurricanes and drought are also considered major disturbances that can cause large-scale dieback of trees in mangrove forests, resulting in the formation of large canopy gaps (Sherman et al. 2001, Duke et al. 2017). However, the resulting large canopy gaps differ significantly from the small circular canopy gaps observed in our study areas. Further, the major drought event in southern Africa began in 2016, whereas we observed the frequent formation of canopy gaps from 1995 onward, i.e., way before this severe drought. Small-scale storms that uproot tall trees that reach out above the surrounding forest canopy, by contrast, would result in fallen dead trees. However, the mangrove forest canopy gaps studied herein are characterized by essentially only standing-dead trees or stems of many small trees lying on the ground. Hence, the above agents can be excluded as drivers of gap formation in the present study in South Africa.

Several observations of lightning strikes reported by experienced forest managers at Beachwood (B Pather, Ezemvelo KZN Wildlife, pers comm) and the presence of several dead trees, either standing or on the forest floor, at Beachwood and uMhlathuze (Supplementary Fig. S1) may suggest a potential connection between lightning strikes and the formation of canopy gaps. This is also supported by the great canopy height in those areas where canopy gap formation was observed. Along this line, our results demonstrate that the majority of canopy gaps at uMhlathuze and Beachwood were established in mangrove stands with high canopies. This is in line with the assumption that taller trees would be more prone to gap formation if lightning strikes or strong winds were the driver (Outcalt 2008, Gora et al. 2020). Windfall, however, would result in large, uprooted trees lying on the ground, whereas most of the gaps we analyzed mostly hosted standing-dead trees. This pattern seems to coincide with lightning strikes as the primary cause of gap formation, either directly or indirectly through lightning-induced weakened defense, that would facilitate subsequent insect and/or pathogen attacks.

The observation of canopy gaps in other locations, such as Vietnam's Can Gio Biosphere mangrove reserve (Vogt et al. 2013), verifies a concentration of canopy gaps in areas of great canopy heights (Supplementary Fig. S5). A recent lightning risk model (Gora et al. 2020) expands on this by predicting that taller trees with exposed large crowns are more susceptible to being struck by lightning and subsequently spreading the electric current to neighboring trees, leading to dead standing trees and circular canopy gaps (Outcalt 2008, Gora et al. 2021, for pine trees in South California; Yanoviak et al. 2020, for a tropical forest in Panama).

If the great canopy height in gap-dense mangrove areas were due to topography rather than tree tallness, environmental conditions in those spots would differ from the neighboring forest and might be a driver of physiological stress for the trees, e.g., upon extensive drought, that, in turn, could lead to circles of standing-dead trees (but see above, excluding drought as a major driver). However, even in this case, the greater canopy height would potentially result in higher lightning strike rates.

Reassessment of the "Core for Regeneration" Hypothesis.—The majority of the gaps observed at both uMhlathuze and Beachwood had not closed (or are not predicted to do so) over the time span of some 20 yr covered by our study. This finding is in stark contrast with previous observations (Amir 2012, Amir and Duke 2019) and the derived hypothesis that canopy gaps act as cores for mangrove regeneration and rejuvenation (Amir and Duke 2019), at least for our study region.

Previous studies have shown that the rate of gap closure varies across regions (Paijmans and Rollet 1976, Sherman et al. 2000, Amir and Duke 2019). In Papua New Guinean mangrove forests, canopy gaps detected in 1957 were no longer visible in aerial photographs from 1972, suggesting a maximum closure time of around 15 yr (Paijmans and Rollet 1976). A gap longevity of eight to 16 yr and 15 to 19 yr, respectively, were observed in mangrove forests in the Dominican Republic (Sherman et al. 2000) and in Malaysia (Amir 2012). By contrast, Amir and Duke (2019) estimated a maximum closure time of about 30 yr in the Australian Moreton Bay mangrove stands. Our findings demonstrate a very slow, if any, regeneration and gap closure in uMhlathuze and no gap closure since their initial formation in

Beachwood. Data on growth rates suggests that *Avicennia marina* and *Bruguiera gymnorhiza* reach maximum tallness after 12 yr and 8 yr, respectively, in South Africa and Kenya (Bosire et al. 2006, Rajkaran and Adams 2012). Accordingly, we would expect to observe gap closure after 12 yr and 8 yr, respectively, provided that seedlings are reaching and establishing inside the canopy gaps shortly after gap formation, or even faster, as seedlings and saplings would benefit from higher nutrient supply and from not being shaded during early life stages.

Field observations in uMhlathuze revealed only a few saplings in those canopy gaps we studied (Supplementary Fig. S1). By contrast, proliferation of seedling recruitment and growth of young treelings was observed nearby these gaps, suggesting that it is not a lack of seedlings from nearby sites or a seedbank that keeps the gaps from closing. In Beachwood, in turn, some of the gaps (inside *A. germinans* stands) visited onsite in 2018 hosted a dense cover of freshly established seedlings of *Bruguiera gymnorhiza*. We could not detect these in satellite images, nor did they develop into treelings or even mature trees within the remainder of our study, ending in 2018 (Beachwood) and 2020 (uMhlathuze). Obviously, environmental conditions inside the canopy gaps did not allow for sufficient recolonization (uMhlathuze) or establishment (Beachwood) over at least two decades. Further in situ studies are needed to determine the cause of slowly or not closing gaps, focusing on environmental characteristics (tidal conditions and sediment physicochemical conditions) and potential biotic factors like herbivory pressure, pathogens, or competition. In any way, the process of canopy gap closure in South African mangrove forests seems to be too slow for considering mangrove forest canopy gaps "cores of regeneration" in this region near the southern distribution limit of mangroves.

Conclusions

Our findings have far-reaching implications for the management of mangrove forests in South Africa. The spatial and temporal dynamics of canopy gap formation and closure observed at uMhlathuze and Beachwood support the hypothesis that lightning strikes, directly or indirectly, drive canopy gap formation. Our results challenge existing evidence that suggests canopy gaps promote rapid mangrove regeneration. *Avicennia marina*, known for its fast recovery upon disturbance in this region, exhibits a high capacity for vegetative regeneration rather than relying solely on propagule production, seedling establishment, and growth. Many gaps at uMhlathuze remained open for at least 23 yr, and none at Beachwood had closed since their formation at least 18 yr before the endpoint of our study. These results highlight the need for human intervention to reforest canopy gaps in areas where natural regeneration appears slow or nonexistent. Increasing rates of mangrove forest canopy gap formation upon increasing frequencies of thunderstorms, and thus, lighting strikes, will have severe impacts on the capacity of mangrove forests and estuarine systems in South Africa to contribute to climate change mitigation and adaptation towards resilient coastal socioecological systems. Without active human intervention the provision of ecosystem services by mangrove forests might be hampered.

Acknowledgments

This study was triggered during field observations in South Africa that were made possible by funding of the collaborative ZMT project DiSeMiNation by the Leibniz Association. MKA is grateful for having received a doctoral studies scholarship from the German Academic Exchange Service (DAAD) and funding for open access from the University of Bremen. The South African Weather Service and South African Surveyor General provided the weather data and the aerial photographs, respectively, that were used in this analysis. We thank three anonymous reviewers for their valuable comments to improve a previous version of the manuscript.

Literature Cited

Agyekum MK. 2024. Canopy gap dynamics in mangrove forests: exploring global patterns and drivers. Doctoral Dissertation. Bremen, Germany: University of Bremen. https://doi.org/10.26092/elib/2748

Alboukadel K, Marcin K, Przemyslaw B. 2021. survminer: drawing survival curves using ggplot2. R package version 0.4.9. Available from: https://CRAN.R-project.org/package=survminer

Amir AA. 2012. Canopy gaps and the natural regeneration of Matang mangroves. For Ecol Manage. 269:60–67. https://doi.org/10.1016/j.foreco.2011.12.040

Amir AA, Duke NC. 2019. Distinct characteristics of canopy gaps in the subtropical mangroves of Moreton Bay, Australia. Estuar Coast Shelf Sci. 222:66–80. https://doi.org/10.1016/j.ecss.2019.04.007

Andrew ME, Ruthrof KX, Matusick G, Hardy GESJ. 2017. Spatial configuration of drought disturbance and forest gap creation across environmental gradients. PLOS ONE. 11(6):1–18. https://doi.org/10.1371/journal.pone.0157154

Bass CA. 2017. Emerging hotspot analysis of Florida manatee (*Trichechus manatus latirostris*) mortality (1974–2012). Master's Thesis. Davie, Florida: Nova Southeastern University. Available from: https://nsuworks.nova.edu/occ_stuetd/456

Bosire JO, Dahdouh-Guebas F, Kairo JG, Wartel S, Kazungu J, Koedam N. 2006. Success rates of recruited tree species and their contribution to the structural development of reforested mangrove stands. Mar Ecol Prog Ser. 325:85–91. https://doi.org/10.3354/meps325085

Clarke PJ, Kerrigan R. 2000. Do forest gaps influence the population structure and species composition of mangrove stands in northern Australia? Biotropica. 32(4):642–652. https://doi.org/10.1111/j.1744-7429.2000.tb00511.x

Dixon PM. 2001. Ripley's K function. *In:* El-Shaarawi AH, Piegorsch WW, editors. Encyclopedia of environmetrics. Chichester (UK): John Wiley & Sons Ltd. p. 1796–1803.

Duke NC. 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. Wetlands Ecol Manage. 9(3):267–279. https://doi.org/10.1023/A:1011121109886

Duke NC, Kovacs JM, Griffiths AD, Preece L, Hill DJE, van Oosterzee P, Mackenzie J, Morning HS, Burrows D. 2017. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. Marine and Freshwater Research. 68(10):1816–1829. https://doi.org/10.1071/MF16322

ESRI. 2016. ArcGIS Desktop: Release 10.5 [Software]. Redlands, CA: Environmental Systems Research Institute.

ESRI. 2021a. How emerging hotspot analysis works. Accessed 4 August, 2021. Available from: https://pro.arcgis.com/en/pro-app/latest/tool-reference/space-time-pattern-mining/learnmoreemerging.htm

ESRI 2021b. ArcGIS Desktop: Release 10.8.2 [Software]. Redlands, CA: Environmental Systems Research Institute.

Ezemvelo KZN Wildlife. 2013. Beachwood Mangroves Nature Reserve: management plan. Version 1.0 (June 2013). Pietermaritzburg, South Africa: Ezemvelo KZN Wildlife.

Available from: https://www.coastkzn.co.za/wp-content/uploads/2019/02/4.eThekwini_Beachwood_mangroves_protected_areas_ezemvelo.pdf

Feller IC. 2002. The role of herbivory by wood boring insects in mangrove ecosystems in Belize. Oikos. 97:167–176. https://doi.org/10.1034/j.1600-0706.2002.970202.x

Feller IC, McKee KL. 1999. Small gap creation in Belizean mangrove forests by a wood-boring insect. Biotropica. 31(4):607–617. https://doi.org/10.1111/j.1744-7429.1999.tb00408.x

Google Earth. 2018. Google Earth Pro Version 7.3.3. [Software]. Available from: https://www.google.com/earth/versions/#earth-pro

Gora EM, Bitzer PM, Burchfield JC, Gutierrez C, Yanoviak SP. 2021. The contributions of lightning to biomass turnover, gap formation and plant mortality in a tropical forest. Ecology. 102(12):e03541. https://doi.org/10.1002/ecy.3541

Gora EM, Muller-Landau HC, Burchfield JC, Bitzer PM, Hubbell SP, Yanoviak SP. 2020. A mechanistic and empirically supported lightning risk model for forest trees. J Ecol. 108(5):1956–1966. https://doi.org/10.1111/1365-2745.13404

Harris NL, Goldman E, Gabris C, Nordling J, Minnemeyer S, Ansari S, Lippmann M, Bennett L, Raad M, Hansen M, et al. 2017. Using spatial statistics to identify emerging hot spots of forest loss. Environ Res Lett. 12(2):024012. https://doi.org/10.1088/1748-9326/aa5a2f

Mann HB. 1945. Nonparametric tests against trend. Econometrica. 13(3):245–259. https://doi.org/10.2307/1907187

NASA JPL. 2014. NASA Shuttle Radar Topography Mission Swath Image Data [Data set]. NASA EOSDIS Land Processes DAAC. Accessed 27 May, 2022. Available from: https://doi.org/https://doi.org/10.5067/MEaSUREs/SRTM/SRTMIMGR.003

NGI (National Geospatial Information). 2013. National Geospatial Information. South Africa: Department of Rural Development and Land Reform. Available from: www.ngi.gov.za

Ord K, Getis A. 1995. Local spatial autocorrelation statistics: distributional issues and application. Georgr. Anal. 27(4):286–306. https://doi.org/10.1111/j.1538-4632.1995.tb00912.x

Outcalt KW. 2008. Lightning, fire and longleaf pine: using natural disturbance to guide management. For Ecol Manage. 255(8–9):3351–3359. https://doi.org/10.1016/j.foreco.2008.02.016

Paijmans K, Rollet B. 1976. The mangroves of galley reach, Papua New Guinea. For Ecol Manage. 1:119–140. https://doi.org/10.1016/0378-1127(76)90016-5

Pinzón ZS, Ewel KC, Putz FE. 2003. Gap formation and forest regeneration in a Micronesian mangrove forest. J Trop Ecol. 19(2):143–153. https://doi.org/10.1017/S026646740300316X

R Core Team. 2020. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

Rajkaran A, Adams J. 2011. Mangrove forests of northern KwaZulu-Natal: sediment conditions and population structure of the largest mangrove forests in South Africa. Western Indian Ocean Journal of Marine Science. 10(1):25–38.

Rajkaran A, Adams J. 2012. The effects of environmental variables on mortality and growth of mangroves at Mngazana Estuary, Eastern Cape, South Africa. Wetlands Ecol Manage. 20(4):297–312. https://doi.org/10.1007/s11273-012-9254-6

Reddy CS, Bird NG, Sreelakshmi S, Manikandan TM, Asra M, Krishna PH, Jha CS, Rao PVN, Diwakar PG. 2019. Identification and characterization of spatio-temporal hotspots of forest fires in South Asia. Environ Monit Assess. 191:791. https://doi.org/10.1007/s10661-019-7695-6

Sherman RE, Fahey TJ, Battles JJ. 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. British Ecological Society. 88(1):165–178. Available from: http://www.jstor.org/stable/2648493

Sherman RE, Fahey TJ, Martinez P. 2001. Hurricane impacts on a mangrove forest in the Dominican Republic: damage patterns and early recovery. Biotropica. 33(3):393–408. https://doi.org/10.1111/j.1744-7429.2001.tb00194.x

Stalpers LJA, Kaplan EL. 2018. Edward L. Kaplan and the Kaplan–Meier survival curve. BSHM Bulletin. 33(2):109–135. https://doi.org/10.1080/17498430.2018.1450055

Therneau T. 2023. A Package for Survival Analysis in R. R package version 3.5-7. Available from: https://CRAN.R-project.org/package=survival

Vogt J, Kautz M, Fontalvo Herazo ML, Triet T, Walther D, Saint-Paul U, Diele K, Berger U. 2013. Do canopy disturbances drive forest plantations into more natural conditions? A case study from Can Gio Biosphere Reserve, Viet Nam. Global Planet Change. 110:249–258. https://doi.org/10.1016/j.gloplacha.2011.09.002

Wickham H. 2016. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag. Available from: https://ggplot2.tidyverse.org/

Yanoviak SP, Gora EM, Bitzer PM, Burchfield JC, Muller-Landau HC, Detto M, Paton S, Hubbell SP. 2020. Lightning is a major cause of large tree mortality in a lowland neotropical forest. New Phytol. 225(5):1936–1944. https://doi.org/10.1111/nph.16260

Zhang K, Simard M, Ross M, Rivera-Monroy VH, Houle P, Ruiz P, Twilley RR, Whelan KRT. 2008. Airborne laser scanning quantification of disturbances from hurricanes and lightning strikes to mangrove forests in Everglades National Park, USA. Sensors (Basel). 8(4):2262–2292. https://doi.org/10.3390/s8042262