Canopy gap dynamics in mangrove forests: exploring global patterns and drivers

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To my parents David Kwaku Dokyi and Gladys Opokua Boateng

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Summary

Mangrove forests are located at the interface between land and sea in tropical and subtropical latitudes. They provide several valuable ecosystem services, including carbon sequestration, habitat for diverse fauna, coastal protection, and serving as a source of fuel and timber for coastal communities. However, the unique location of mangrove forests in a highly dynamic environment, makes them susceptible to disturbances which leads to the formation of canopy gaps.

Mangrove canopy gaps may counteract senescence, contributing to maintaining the mangrove forest in a rejuvenated and regenerated state. The rejuvenation and regeneration of canopy gaps have implications for the integrity of the numerous valuable ecosystem services that mangrove forests offer. Despite the socio-ecological implications of canopy gaps, knowledge regarding their global and local extent, drivers, occurrences, densities, and closure rates remains limited.

This thesis addresses the knowledge limitation by conducting a comprehensive investigation of the distribution patterns and dynamics of canopy gaps in mangrove forests on both global and local scales. The investigation employs a multifaceted approach, encompassing extensive literature reviews, remote sensing techniques, and predictive models, to explain the patterns of canopy gaps formation, closure dynamics and reveal their underlying drivers while validating their regeneration capacity.

Canopy gaps are found in 133 mangrove patches distributed across 35 countries spanning America, Africa, Asia, and Oceania. Significant variations in canopy gap sizes, canopy gap densities, and percentage of canopy gaps coverage in mangrove patches across different regions were observed. The occurrence of canopy gaps on a global scale is mainly driven by lightning strikes, and precipitation of the coldest quarter, while their density is driven by lightning strikes, the precipitation of

the wettest and driest months, and the maximum temperature of the warmest month. Overall, these climatic factors have the potential to act synergistically thus contributing to canopy gap occurrences and density within a given mangrove forest patch.

On a local scale, the thesis showed clustered spatiotemporal patterns in South Africa's largest mangrove forest at uMhlathuze (80% of the total mangrove coverage in the country) near Richards Bay. Beachwood canopy gaps primarily exhibited random patterns with some spatial clustering, along with random temporal patterns. The patterns at both sites support the hypothesis that lightning strikes, insects or pathogen attacks or competition potentially contribute to canopy gap formation. Spatial distribution of canopy gaps was linked to high canopy at both uMhlathuze and Beachwood, supporting the lightning strikes hypothesis. Canopy gaps at uMhlathuze remained open for at least 23 years. In contrast, no canopy gap at Beachwood had closed over the time span of 18 years that the study covers. These findings highlight the need for active (re-)establishment of canopy gaps, as the very slow natural regeneration might result in loss of valuable ecosystem services provided by mangroves, such as carbon sequestration and long-term storage of carbon.

Furthermore, the canopy gap closure dynamics and factors influencing their closure across 10 countries and two biogeographical realms—the Atlantic East Pacific and Indo West Pacific were investigated. At higher latitudes above the equator a pattern of relatively shorter canopy gap closure durations and increased annual percentage of canopy gap closure was observed. Approximately 70-100% of the canopy gaps had undergone closure in eight countries. Conversely, during the timeframe encompassed by the study, over 70% of the canopy gaps in Australia exhibited a persistent lack of closure for at least 18 years. Canopy gap closure duration was found to be significantly influenced by the mean temperature of the wettest quarter of the year. Similarly, the annual percentage of canopy gaps closing was significantly influenced by mean temperature of the wettest quarter, mean temperature of the driest quarter, pH, and salinity. This highlights the potential impact of climatic environmental parameters on canopy gap closure dynamics.

The thesis emphasizes the significance of prioritizing the (re-)establishment of mangrove forest areas with non-closing gaps. This is crucial for ensuring the integrity of long-term carbon storage, coastal protection, habitats for diverse fauna, and a sustainable timber supply that supports local livelihoods under climate change.

Overall, this thesis contributes to providing baseline data on mangrove areas with canopy gaps and their potential drivers, both globally and on regional and local scales. It highlights the factors influencing canopy gap closures and mangrove areas facing a lack of regeneration, emphasizing the urgent need for human assistance in (re-)establishing those canopy gaps.

Zusammenfassung

Mangrovenwälder befinden sich an der Schnittstelle zwischen Land und Meer in tropischen und subtropischen Breitengraden. Sie bieten mehrere wertvolle Ökosystemdienstleistungen, darunter Kohlenstoffspeicherung, Lebensraum für vielfältige Fauna, Küstenschutz sowie Brennstoff- und Holzquelle für Küstengemeinden. Die einzigartige Lage der Mangrovenwälder in einer hochdynamischen Umgebung macht sie jedoch anfällig für Störungen, die zur Bildung von Kronenlücken führen.

Kronenlücken können dem Alterungsprozess entgegenwirken und dazu beitragen, den Mangrovenwald in einem verjüngten und regenerierten Zustand zu erhalten. Die Verjüngung und Regeneration von Kronenlücken haben Auswirkungen auf die Integrität der zahlreichen wertvollen Ökosystemdienstleistungen, die Mangrovenwälder bieten. Trotz der sozioökologischen Auswirkungen von Kronenlücken ist das Wissen über ihre globale und lokale Ausdehnung, Ursachen, Vorkommen, Dichten und Schließungsraten begrenzt.

Diese Arbeit befasst sich mit der Wissensbegrenzung, indem sie eine umfassende Untersuchung der Verteilungsmuster und Dynamiken von Kronenlücken in Mangrovenwäldern auf globaler und lokaler Ebene durchführt. Die Untersuchung verwendet einen vielschichtigen Ansatz, der umfangreiche Literaturrecherchen, Fernerkundungstechniken und prädiktive Modelle umfasst, um die Muster der Bildung von Kronenlücken, die Dynamik ihrer Schließung und die zugrunde liegenden Treiber zu erklären und gleichzeitig ihre Regenerationskapazität zu validieren.

Kronenlücken wurden in 133 Mangroven-Patches in 35 Ländern in Amerika, Afrika, Asien und Ozeanien gefunden. Es wurden signifikante Variationen in der Größe der Kronenlücken, der Dichte der Kronenlücken und dem prozentualen Anteil der Kronenlückenabdeckung in Mangroven-Patches in verschiedenen Regionen beobachtet. Das Vorkommen von Kronenlücken auf globaler Ebene wird hauptsächlich durch Blitzschläge und Niederschläge des kältesten Quartals beeinflusst, während ihre Dichte durch Blitzschläge, die Niederschläge der nassesten und trockensten Monate sowie die Höchsttemperatur des wärmsten Monats beeinflusst wird. Insgesamt haben diese klimatischen Faktoren das Potenzial, synergistisch zu wirken und somit zu Vorkommen und Dichte von Kronenlücken in einem gegebenen Mangrovenwald-Patch beizutragen.

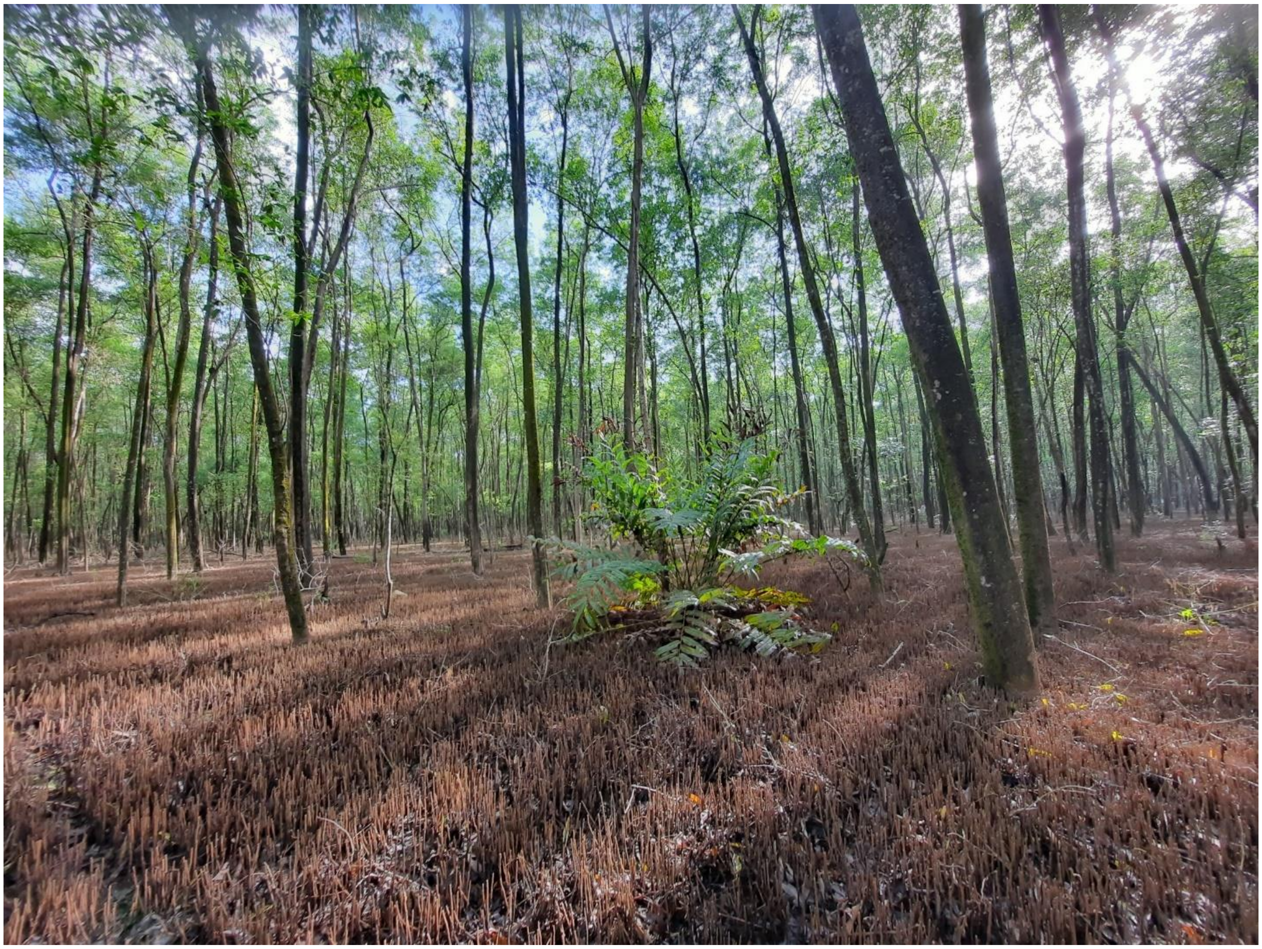
Auf lokaler Ebene zeigte die Arbeit geklammerte räumlich-zeitliche Muster im größten Mangrovenwald Südafrikas in uMhlathuze (80% der gesamten Mangrovenabdeckung im Land) nahe Richards Bay. Die Kronenlücken in Beachwood zeigten hauptsächlich zufällige Muster mit einigen räumlichen Clusterbildungen sowie zufälligen zeitlichen Mustern. Die Muster an beiden Standorten unterstützen die Hypothese, dass Blitzschläge, Insekten- oder Pathogenangriffe oder Wettbewerb möglicherweise zur Bildung von Kronenlücken beitragen. Die räumliche Verteilung von Kronenlücken war mit einer hohen Kronenhöhe sowohl in uMhlathuze als auch in Beachwood verbunden, was die Hypothese der Blitzschläge unterstützt. Kronenlücken in uMhlathuze blieben mindestens 23 Jahre lang offen. Im Gegensatz dazu hatte keine Kronenlücke in Beachwood während des 18-jährigen Studienzeitraums geschlossen. Diese Ergebnisse unterstreichen die Notwendigkeit der aktiven (Wieder-)herstellung von Kronenlücken, da die sehr langsame natürliche Regeneration zu einem Verlust der wertvollen Ökosystemdienstleistungen führen kann, die von Mangroven bereitgestellt werden, wie Kohlenstoffspeicherung und langfristige Kohlenstoffspeicherung.

Darüber hinaus wurden die Dynamiken der Schließung von Kronenlücken und die Faktoren, die ihre Schließung in 10 Ländern und zwei biogeografischen Reichen - dem atlantisch-ostpazifischen und indo-westpazifischen Raum - beeinflussen, untersucht. In höheren Breitengraden über dem Äquator wurde ein Muster relativ kürzer Dauer der Kronenlückenschließung und eine erhöhte jährliche prozentuale Schließung von Kronenlücken beobachtet. Etwa 70-100% der Kronenlücken hatten in acht Ländern eine Schließung durchlaufen. Im Gegensatz dazu zeigten während des im Rahmen der Studie betrachteten Zeitraums über 70% der Kronenlücken in Australien eine anhaltende Nichtschließung über mindestens 18 Jahre. Die Dauer der Kronenlückenschließung wurde signifikant durch die Durchschnittstemperatur des feuchtesten Quartals des Jahres beeinflusst. Ebenso wurde der jährliche Prozentsatz des Schließens von Kronenlücken signifikant von der Durchschnittstemperatur des feuchtesten Quartals, der Durchschnittstemperatur des trockensten Quartals, dem pH-Wert und der Salinität beeinflusst. Dies unterstreicht das potenzielle Auswirkungen von klimatischen Umweltparametern auf die Dynamik der Kronenlückenschließung.

Die Arbeit betont die Bedeutung der Priorisierung der (Wieder-)herstellung von Mangrovenwaldgebieten mit nicht schließenden Kronenlücken. Dies ist entscheidend, um die Integrität der langfristigen Kohlendioxidspeicherung, den Küstenschutz, den Lebensraum für vielfältige Fauna und eine nachhaltige Holzversorgung zur Unterstützung der lokalen Lebensgrundlagen unter dem Einfluss des Klimawandels sicherzustellen. Insgesamt trägt diese Arbeit dazu bei, Baseline-Daten zu Mangrovengebieten mit Kronenlücken und ihren potenziellen Treibern sowohl auf globaler als auch auf regionaler und lokaler Ebene bereitzustellen. Sie hebt die Faktoren hervor, die die Schließung von Kronenlücken beeinflussen, und Mangrovengebiete, die mit einem Mangel an Regeneration konfrontiert sind, und betont die dringende Notwendigkeit menschlicher Unterstützung bei der (Wieder-)herstellung dieser Kronenlücken.

LIST OF ABBREVIATIONS

AEP	Atlantic East Pacific
AIC	Akaike information criterion
EHSA	Emerging Hot Spot Analysis
EP	Ensemble Prediction
ESM	Ensemble of Small Models
GAM	Generalized Additive Models
GBM	Generalized Boosted Models
GLM	Generalized Linear Models
IWP	Indo West Pacific
OHSA	Optimized Hot Spot Analysis
ODMAP	Overview, Data, Model, Assessment and Prediction
RF	Random Forest
VIF	Variance Inflation Factor



Chapter 1 General introduction

1.1 Canopy gap formation and regeneration in mangrove forests

Mangrove forests are woody plants situated at the interface between land and sea in tropical and sub-tropical latitudes, where they thrive in conditions of fluctuating salinity, extreme tides, strong winds, high temperatures, and muddy anoxic sediments (Kathiresan and Bingham, 2001). These forests offer valuable ecosystem services, including carbon sequestration, providing habitat for diverse fauna, coastal protection, and a source of fuel and timber for coastal communities (Zimmer, 2018). However, the unique location of mangrove forests in a highly dynamic environment, makes them susceptible to disturbances (Lassalle et al., 2022). These disturbances lead to the formation of canopy gaps, thereby posing potential socio-ecological implications for the valuable ecosystem services they provide to humans and the entire mangrove ecosystem (Rasquinha and Mishra, 2021; Lassalle et al., 2022).

Canopy gaps are documented in various forest systems like boreal (McCarthy, 2001; de Römer et al., 2007), temperate (Brokaw, 1982; Runkle, 1992) and tropical forests (Gora et al., 2020) around the world. A clear definition of what constitutes a canopy gap in terrestrial studies remains missing (Schliemann and Bockheim, 2011). For instance, Runkle (1992) defined canopy gaps as openings in the forest that extend over more than 2/3 of the stand height. Brokaw (1982) proposed a more restrictive definition, characterizing a canopy gap as “a hole in the forest extending through all levels down to an average height of 2 m above ground”. By these definitions, the death of single tree potentially constitutes a canopy gap in terrestrial systems (Drößler and Von Lüpke, 2005) influencing the variations of gap shapes and sizes reported by previous studies (Schliemann and Bockheim, 2011). By contrast, the definition of canopy gaps in mangrove forests have rather been restricted to their size or diameter and shape. The canopy gaps are formed as a result of the deaths of multiple trees, whether they are standing dead or fallen in the mangrove forests (Amir and Duke, 2019). Previous studies have defined canopy gap in mangrove forest as circular or elliptical with diameters ranging from ≥2 to 82.7 m (i.e. ≥3 to 5112 m^2 gap size) (Pinzón et al. 2003; Amir 2012; Lassalle et al., 2022). For the purpose of this thesis, canopy gaps were defined with diameters ranging from ≥ 6 to 86 m (28 to 5805 m^2 gap size) as most of them were found in the specified range across the mangrove areas in America, Africa, Asia, and Oceania. These circular canopy gaps are clearly distinct from much larger canopy gaps with diameters ranging from ≥ 167 to 289 m (22,000 to 66,000 m^2 in gap size) created via wood extraction for commercial purposes such as charcoal production, poles, and timber as illustrated in Figure 1.1(Otero et al., 2020). Large canopy gaps created by commercial logging activities have the potential to adversely affect the overall regeneration capacity of the mangrove forest (Rasquinha and Mishra, 2021). Therefore, large canopy gaps are not considered in this study.

Lightning strikes, hurricanes or windthrows, insects and or pathogens, extremely high or low temperature and high or low precipitation events, competition, senescence, and small-scale forestry activities have been proposed as driver(s) of canopy gap formation in mangrove forests (Amir, 2012; Amir and Duke, 2019; Sherman et al., 2000; Sousa et al., 2003; Vogt et al., 2011; Whelan, 2005; Zhang, 2008; Agyekum et al. in prep; Figure 1.2).

Nonetheless, the mechanisms driving the formation of canopy gaps have been poorly investigated and documented in tropical forests (Gora et al., 2020). Previous studies have often relied on qualitative observation (Clarke and Kerrigan, 2000; Sherman et al., 2000), anecdotal evidence (Amir, 2012), and conceptual or predictive models (Amir, 2010) to explain the potential causal agents for these canopy gaps. For example, evidence of lightning strikes killing multiple trees, whether standing dead or fallen, has been primarily based on personal observations (Clarke and Kerrigan, 2000; Sherman et al., 2000), with limited or no quantitative measurements of the cloud-to-ground lightning flash rates and tree census of damaged or killed trees (Yanoviak et al., 2017). Insects and pathogen attacks on weakened trees, probably triggered by damages from lightning strikes or extremely high temperatures, or extremely low precipitation, thus leading to their eventual mortality, have been based on anecdotal evidence and personal observations (Feller and McKee, 1999; Sousa et al., 2003). Hurricanes or windthrows (Sherman et al., 2001), extremely high precipitation (van der Meer and Bongers, 1996), extremely low precipitation (McDowell et al., 2018), extremely low temperatures (Duke,2001), and extremely high temperatures (Duke et al., 2017) drive the density of multiple tree deaths on a large scale due to carbon starvation, hydraulic failure, and mechanical damage (Anderegg et al., 2015) which, in turn, leads to the formation of canopy gaps. Competition for scarce or depleted resources within the forest can lead to die-offs, and often, the mechanism is explained by predictive models (Pillet et al., 2018). The deaths of large old trees due to senescence lead to the formation of canopy gaps, and often, the mechanism is based on anecdotes and qualitative observations (Franklin et al., 1987; Duke, 2001). Therefore, further investigations are required to validate the proposed mechanisms responsible for driving the formation of canopy gaps.

The process of canopy gap formation and recovery in mangrove forest follows a distinct sequence of five successive stages (Figure 1.3), as described by Duke (2001).

In the initiation stage, disturbances cause defoliation of trees, leading to identifiable "grey spots" in the green canopy (Figure 1.3a);

The following opening stage is characterized by visible bare sediments partially covered by decomposing trunks, branches, and twigs (Figure 1.3b);

In the recruitment stage, new seedlings emerge from the "seedling bank," creating mixed areas with patches of bare ground and low vegetation within the canopy gaps (Figure 1.3c);

In the growth stage, young trees cover the entire canopy gap, with their height and crown size lower than those of the surrounding intact canopy (Figure 1.3d); and

In the closure stage, the trees grow to heights comparable to the intact canopy, making canopy gaps nearly indistinguishable from the upper canopy view in the closure phase (Figure 1.3e).

Canopy gap formation drastically changes the environmental conditions on and in the sediment, as well as in the formerly vegetated space, with respect to light, nutrients, temperature and moisture (Vepakomma et al., 2011). Dead trees with high biomass and (absolute) productivity are replaced by recolonizing young trees with high growth rates (and thus high relative productivity) in usually higher densities (Amir, 2012; Goessens et al., 2014). While some ecosystem services may rely on the presence of large, structurally voluminous individual trees and complex roots systems for coastal protection and habitat or nursery grounds for various fauna, others, like timber production and carbon sequestration, may depend on the high growth rates of younger trees (Figure 1.4). Clarke and Allaway (1993) found that seedling growth and densities were higher in canopy gaps due to increased availability of light and nutrients in Southern Australia. Sherman et al. (2000) showed that successful recruitment of propagules to the sapling stage within canopy gaps found in the Dominican Republic mangrove patch appeared to be facilitated by the high light conditions of canopy gaps, as both survivorship and growth rates were enhanced as compared to the surrounding understory. Also, Amir and Duke, (2012) demonstrated that gaps created in the Matang forest, Malaysia, led to an increase in light levels, which, in turn, influenced a rise in soil pore water temperature. This increase in light and temperature was also expected to benefit regeneration through the recruitment of propagules and the growth of seedlings (Figure 1.4).

Along the same line, it can be argued that canopy gaps caused by small-scale forestry activities, may have the same regeneration effect as natural canopy gaps (Allen et al., 2001; Pinzón et al., 2003; Imai et al., 2006). Ewel et al. (1998) showed that regeneration of the forest was facilitated upon the formation of canopy gap due to small-scale extraction of mangrove wood in the Federated States of Micronesia. Recently, Rasquinha and Mishra (2021) showed that small-scale harvesting of mangrove wood for fuel in India created canopy gaps, resulting in higher densities of mangrove seedlings compared to the intact forest. The recruitment of these seedlings is enhanced by the availability of light, nutrients, and temperature, thus highlighting the overall regeneration potential of canopy gaps formed through small-scale forestry within the mangrove forest (Allen et al., 2001). Hence, clear-felling of spatially limited mangrove forest areas might not necessarily always and only have negative effects, but holds similar potential for keeping the mangrove stand in a regenerated state, similar to naturally formed canopy gaps (Figure 1.4).

Circular or elliptical canopy gaps in mangrove forests have been studied across America, Africa, Asia and Oceania, but detailed information on the topic is still scarce, and resides in a small body of literature (Amir and Duke, 2019). Given the importance of canopy gaps as core areas for mangrove regeneration, the lack of knowledge on their global distribution and drivers of their formation presents a major challenge for understanding of ecosystem processes and services on a mangrove forest landscape scale (Sherman et al., 2000; Amir & Duke, 2019). Data on the spatiotemporal patterns of canopy gaps remain inconclusive, making it difficult to decipher the drivers of the gaps on a local scale (Vogt et al., 2011). Furthermore, understanding the dynamics of canopy gap closure is crucial not only for mangrove forest regeneration but also the socio-ecological context in terms of carbon sequestration, long-term storage of carbon, habitat for diverse fauna, timber as source of livelihoods and broader perspective of coastal protection for the nearby communities. Nevertheless, global data on canopy gap closure dynamics is still lacking, impeding understanding of the impact of canopy gaps on valuable ecosystem services.

This thesis provides comprehensive information on the drivers of canopy gap occurrence and density, offering plausible explanations for the mechanisms behind these causal agents. Additionally, spatiotemporal patterns were examined on a local scale in South Africa to explain the underlying factors in the mangrove forest and examine the assumption of canopy gaps serving as core for mangrove regeneration. To address the canopy gap closure dynamics, two biogeographical regions across 10 countries were examined to provide comprehensive information on the patterns and underlying factors for the closure of canopy gaps.

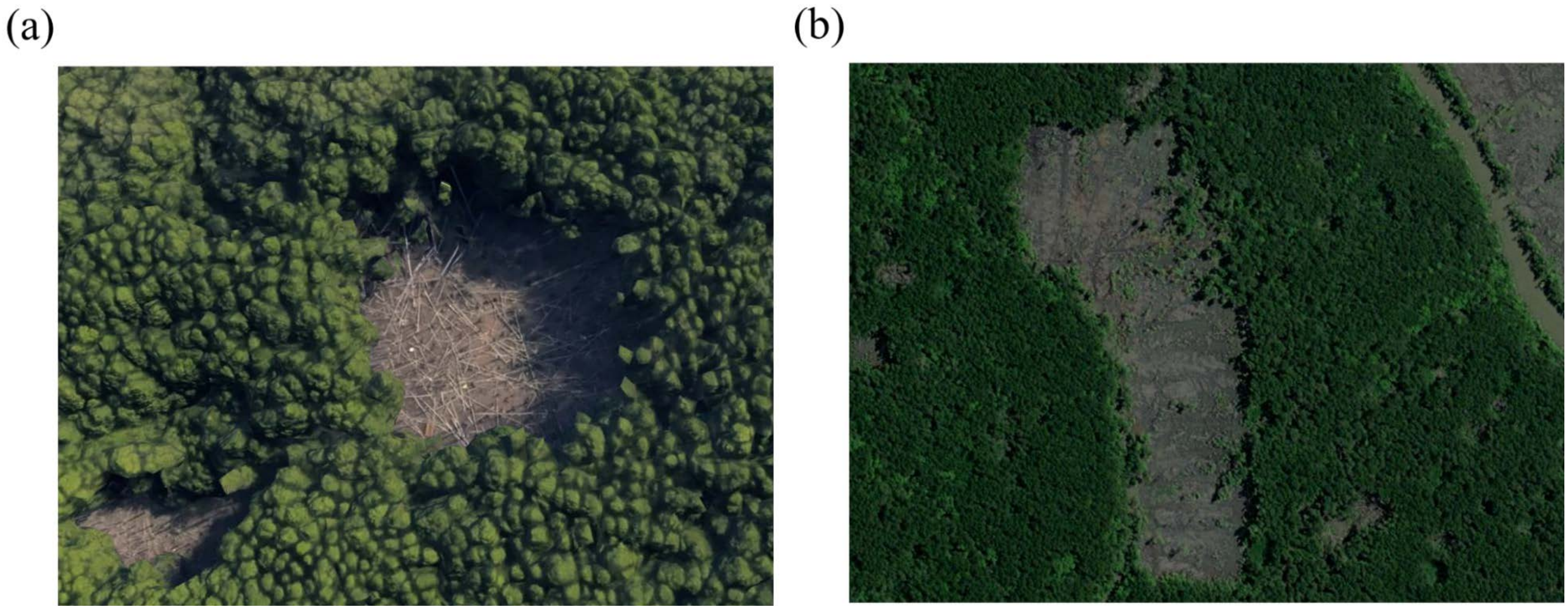


Figure 1.1 Illustration of the different types of canopy gaps in mangrove forest, showing: (a) Circular small canopy gap caused by natural disturbances, and (b) Large canopy gap created due to wood extraction for commercial purposes. The image sources were obtained from Maxar and CNES/Airbus.

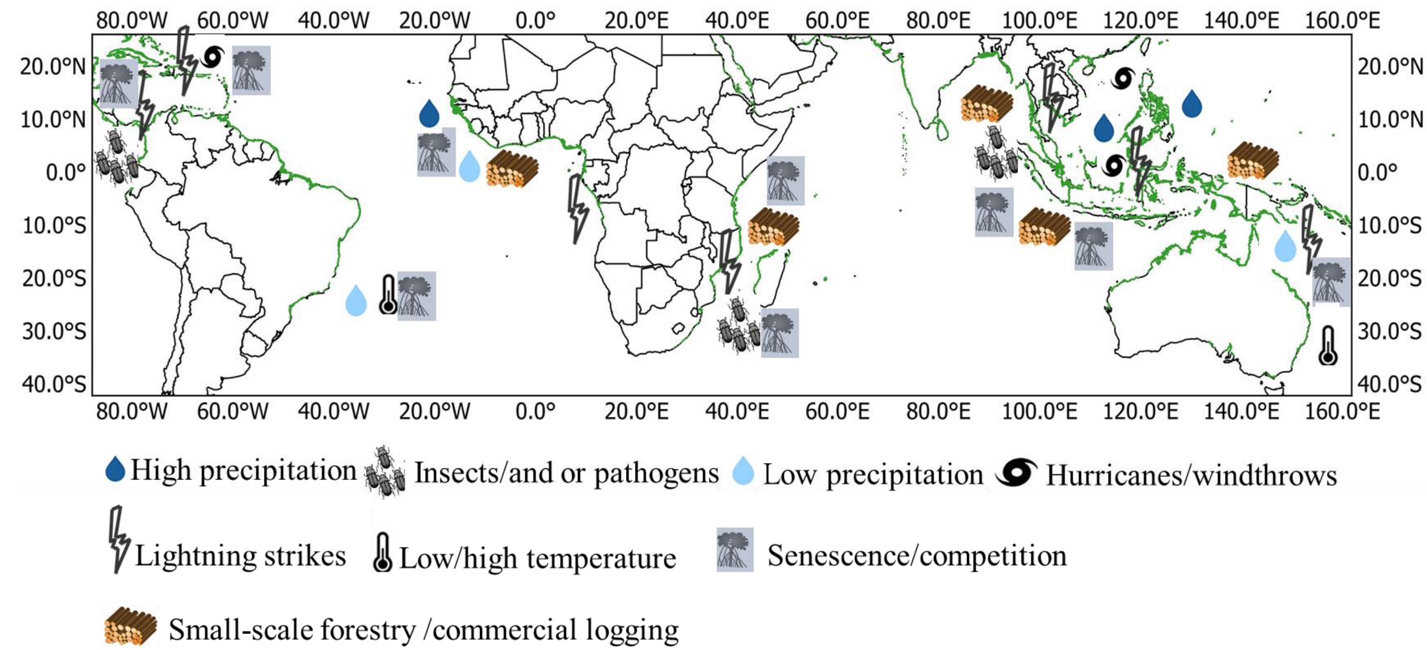


Figure 1.2. Proposed drivers of canopy gap formation in mangrove forests globally based on existing datasets and literature reviews. High precipitation van der Meer and Bongers (1996). Insects and or pathogen attacks based on Putz and Chan (1986), Feller and McKee 1999 and Sousa et al.(2003). Low precipitation based on McDowell et al. (2018) and Duke et al. (2017). Hurricanes or windthrows based on Sherman et al. (2001), Imai et al. (2006), Zhang et al. (2008). Lightning strikes based on Osborne and Smith (1990), Sousa and Mitchell, (1999), Clarke and Kerrigan (2000) , Sherman et al. (2000), Vogt et al. (2011), Whelan, (2005), Zhang (2008), Amir (2012), Amir and Duke (2019) and Agyekum et al. (in prep). Low or high temperature based on Duke (2001) and Duke et al. (2017). Senescence based on (Franklin et al. (1987) and Duke (2001), and competition based on Pillet et al. (2018). Small-scale forestry or commercial logging based on Ewel et al. (1998), Allen et al. (2001), Pinzón et al. (2003), and Rasquinha and Mishra (2021). The green outline delineates the mangrove extent, downloaded from the Global Mangrove Watch datasets version 3 (Bunting et al., 2022).

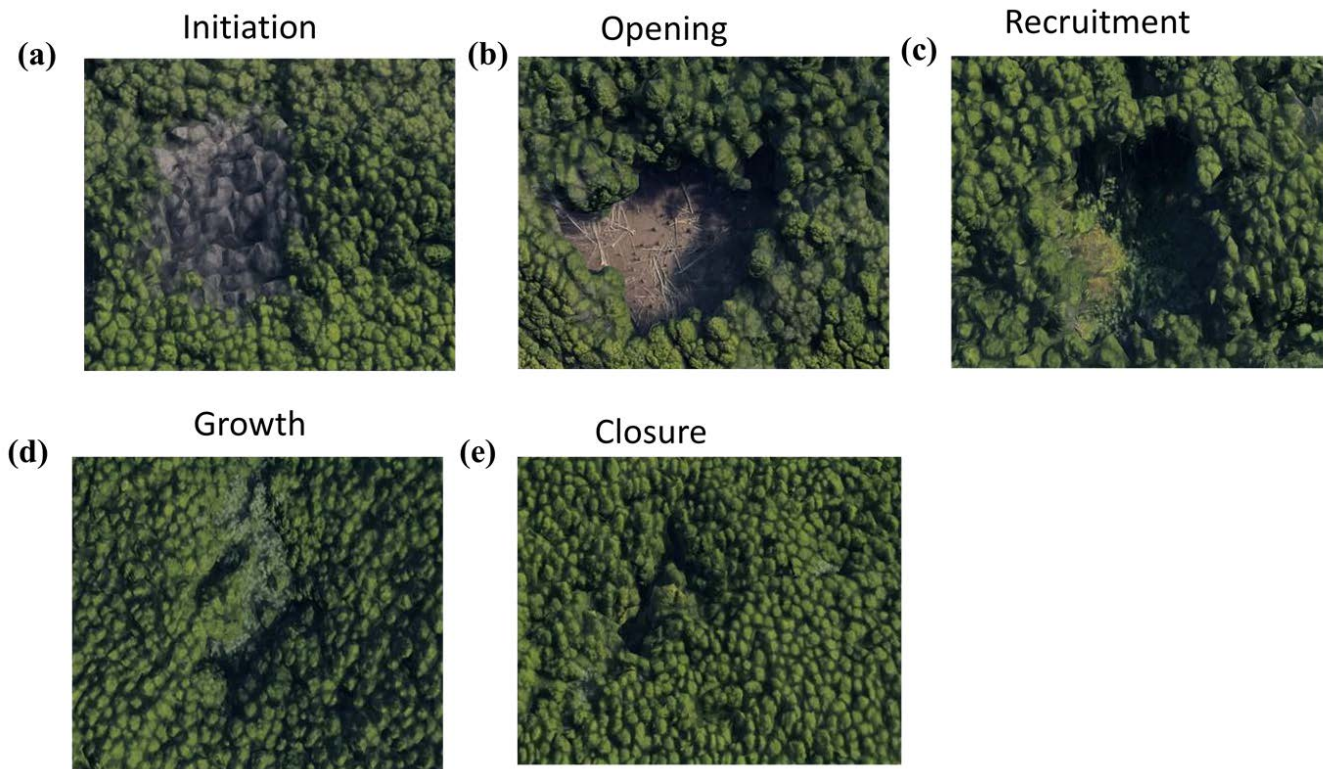


Figure 1.3. Sequential phases of regeneration that occur when canopy gaps form in a mangrove forest: (a) In the initiation stage, disturbances cause defoliation of leaves, leading to identifiable "grey spots" in the green canopy (b) The following opening stage is characterized by visible bare sediments partially covered by decomposing trunks, branches, and twigs (c) In the recruitment stage, new seedlings emerge from the "seedling bank," creating mixed areas with patches of bare ground and low vegetation within the canopy gaps (d) In the growth stage, young trees cover the entire canopy gap, with their height and crown size lower than those of the surrounding intact canopy (e) In the closure stage, the trees grow to heights comparable to the intact canopy, making canopy gaps nearly indistinguishable from the upper canopy view in the closure phase. The schematic representation of the gap phases was adapted from Duke (2001). The image sources were obtained from Maxar and CNES/Airbus.

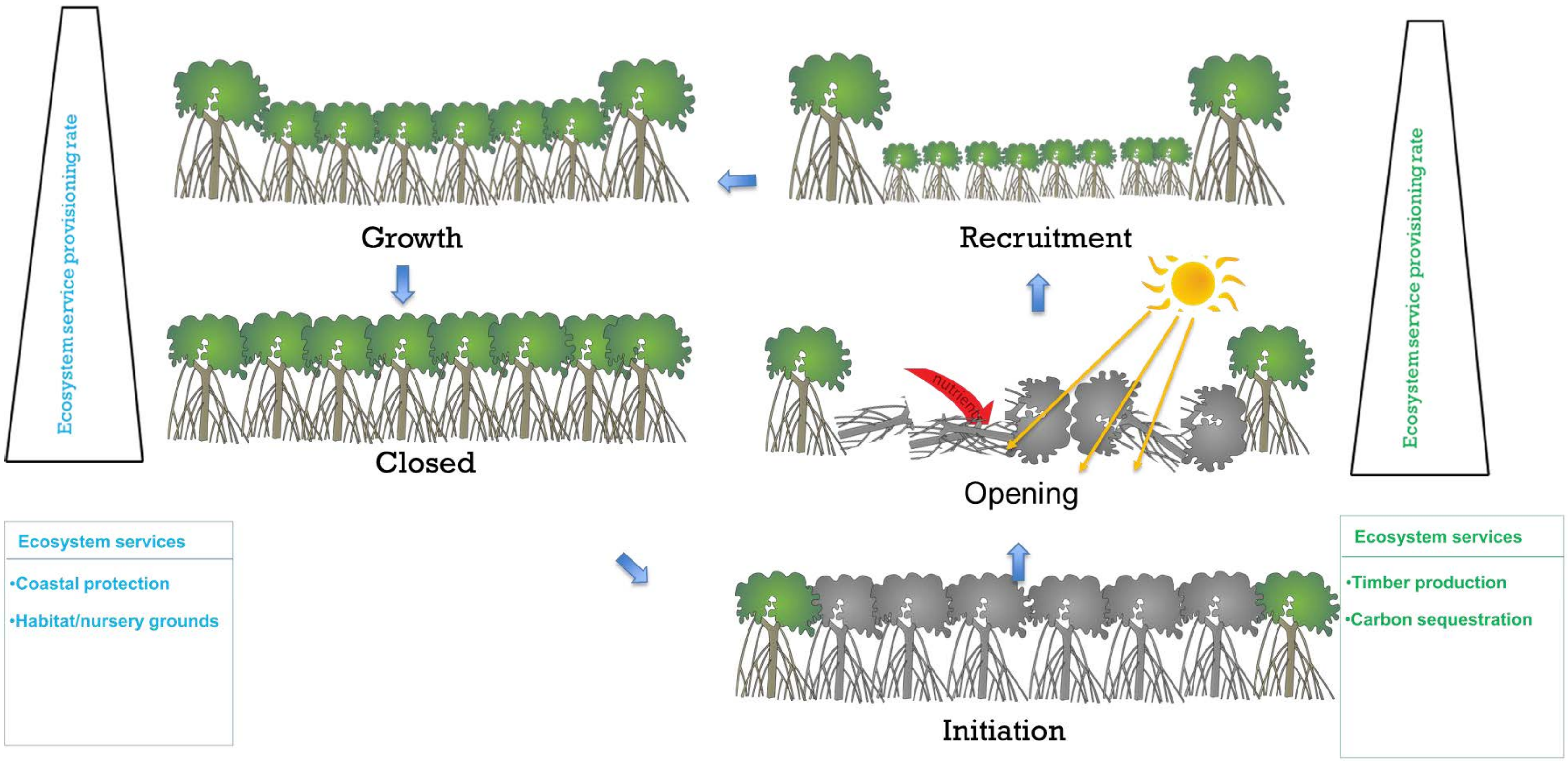


Figure 1.4. Conceptualization of the regeneration effect of naturally formed canopy gaps on mangrove ecosystem service provisioning rate. The green box shows the positive effect of gaps on the ecosystem service provisioning rate on timber production and carbon sequestration. The blue box shows the positive effect of gaps on the ecosystem service provisioning rate on coastal protection and habitat or nursery grounds for fauna. The blue arrows show the cycle of regeneration.

1.2 Thesis Scope

Presently, there is lack of globally synthesized data regarding the geographical range of canopy gaps and their correlation with potential drivers within mangrove forests. This limitation hinders the understanding of canopy gap dynamics concerning ecosystem processes and services. This thesis seeks to establish a foundation for the current state of canopy gaps in mangrove forests worldwide and their potential drivers. Also, at the local scale, there is limited data on the spatiotemporal patterns of canopy gaps, making it difficult to link these patterns to potential drivers of mangrove forest dynamics. For a detailed examination, South Africa's largest mangrove forest at uMhlathuze (constituting 80% of the total mangrove coverage in the country) near Richards Bay and a smaller mangrove stand in Beachwood near Durban are chosen as case studies. These case studies aim to explore spatiotemporal patterns, with the objective of explaining the underlying potential drivers and testing the hypothesis of canopy gaps as the core of mangrove regeneration. Moreover, there is a lack of information on the dynamics of canopy gap closure, which hampers a thorough understanding of the role of canopy gaps on carbon sequestration and long-term carbon storage. The thesis tackles these limitations by examining the dynamics of canopy gap closure and the factors contributing to their closure in 10 countries with a high concentration of canopy gaps across two biogeographical regions and along latitudinal gradients. The overarching goal of this thesis is to provide baseline information on the distribution patterns of naturally formed canopy gaps at both local and global scales, elucidate the reasons for their formation and closure, and validate the global canopy gap regeneration capacity within mangrove forests.

To achieve these objectives, three main research questions (see section below) are addressed in three separate chapters.

1.3 Research Questions

1. Which factors determine the global distribution and density of canopy gaps?
2. Which spatiotemporal patterns characterize canopy gaps and what are the factors influencing them on a local scale?
3. Which factors influence the closure rates and duration of canopy gaps across different latitudes?

1.4 Chapter Overview

Chapter 2 Mangrove canopy gaps: a global synthesis on their distribution and potential drivers

In this chapter, the objective is to identify the distribution of canopy gaps worldwide and understand the factors that drive their formation and density. To achieve this, a combination of remote sensing techniques, comprehensive literature reviews, and predictive models are utilized. By doing so, a comprehensive data on canopy gap dynamics on a global scale is provided.

Chapter 3 Spatial and temporal pattern of canopy gaps in mangrove forest: What do we learn from South Africa?

This chapter shifts the focus to a more localized context, specifically in South Africa's largest mangrove stand at uMhlathuze (comprising 80% of the total mangrove coverage in the country) near Richards Bay and a smaller mangrove stand in Beachwood near Durban. The main objectives are to (i) determine the spatial and temporal patterns of mangrove canopy gaps in the two study sites, (ii) assess the potential causal agents, and (iii) test the core regeneration hypothesis. Overall, this chapter provides a synthesis of the spatial and temporal factors driving canopy gaps and their connection to the regeneration of the mangrove forest stands, with potential implications for mangrove forest (re-)establishment efforts.

Chapter 4 Canopy gaps closure dynamics in mangrove forests: A global perspective on the factors influencing closure.

This investigation is based on the insights gained in Chapter 3, which highlighted a lack of canopy gap regeneration over the time span of the study in South Africa. To shed light on this phenomenon, several metrics are developed to explore canopy gap closure durations and rates across 10 countries, focusing on two distinct biogeographical regions. The main objectives are to (i) to determine the temporal dynamics of canopy gap closure and (ii) to identify the environmental factors that influence canopy gap closure.

Chapter 5: General discussion

This chapter provides a synthesized discussion of the preceding chapters, delving into the socio-ecological implications of canopy gaps. It also proposes practical applications for the protection, conservation, and (re-)establishment of mangroves. Furthermore, the chapter offers an outlook that includes potential avenues for future research, limitations, strengths and conclusion.

1.5 Author's contribution

The author's contribution varied across chapters, according to the study's conceptualization and design, participation in data acquisition, analysis and interpretation of data, the development of figures and tables, and drafting of manuscripts (Table 1.1).

Table 1.1. The Contributions of the doctoral candidate in percentages to the various chapters contained in this thesis.

Chapters	Concept and design	Data acquisition	Figures and tables	Data analysis and interpretation	Drafting of manuscript	State of publication
2	70	90	90	90	70	In preparation
3	70	90	90	90	80	Submitted
4	70	90	90	90	100	In preparation

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Chapter 2 Mangrove canopy gaps: a global synthesis on their distribution and potential drivers

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2.1 Abstract

Circular or elliptical canopy gaps observed in forests worldwide have also been described and studied in mangrove forests. While canopy gaps are considered crucial for mangrove forest rejuvenation and regeneration, the underlying processes and drivers of canopy gap formation remain unclear, posing a challenge to understanding the large-scale effects of gap formation on mangrove forest dynamics. In this study, we conducted an extensive literature review to collect data on the locations where mangrove canopy gaps have been reported, their size, density, and potential causes of formation. We compared the review results with a spatial survey of mangrove canopy gaps using remote sensing techniques to determine their global distribution and local abundance. We used ensembles of small models to identify the drivers of canopy gap occurrences in mangrove forests and employed generalized linear models to assess the factors affecting gap density. Based on the bibliographic review, canopy gaps were documented in 13 countries. Our spatial survey identified 133 different mangrove patches, each covering more than 5 km², distributed across 35 countries in America, Africa, Asia, and Oceania. The average canopy gap size ranged from 340.4 m² (Oceania) to 607.5 m² (America), and canopy gap density ranged from 2.6 (Asia) to 0.4 (Africa & Oceania) gaps per km^2. The average canopy gap size followed a power law distribution with an alpha (α) value of 4.6. The percentage coverage by canopy gaps per mangrove patch varied from 0.01% (Africa & Oceania) to 0.12% (Asia).

Precipitation of the coldest quarter and lightning flash rate density were the most important drivers for canopy gap occurrences. Similarly, canopy gap density was primarily influenced by the maximum temperature of the warmest month, lightning flash rate density, precipitation during the wettest month, and precipitation during the driest month. Our study highlights the contribution of multiple climatic factors in driving canopy gap occurrence and density in mangrove forests. These findings underscore the need for further scientific investigation to better understand the relationships among these likely causal factors in mangrove forests.

Keywords: ensemble of small models (ESMs), lightning strikes, remote sensing, generalized linear model (GLM), hurricanes, insects, pathogens, bioclim variables

2.2 Introduction

Canopy gap dynamics (McCarthy, 2001; Fajardo and De Graaf, 2004; de Römer et al., 2007; Muscolo et al., 2014) have been extensively studied for several decades in boreal (de Römer et al., 2007; McCarthy, 2001), temperate (Brokaw, 1982; Runkle, 1982; Gutiérrez et al., 2021) and tropical (Attiwill, 1994) forests. Canopy gaps have considerable impact on forest properties and processes, such as biodiversity, succession, nutrient cycling and organic matter turnover (Muscolo et al., 2014). For instance, light penetration towards the forest floor changes considerably when a canopy gap opens, influencing the establishment of seedlings or saplings and, thus, the structure and composition of the forest (Lu et al., 2018). In terrestrial forests, the creation of a natural gap is often associated with the fall of a single tree or multiple trees (Brokaw, 1982; Runkle, 1982) due to snowfall, senescence, windthrows, hurricanes, lightning strikes, drought, insect, and or pathogen attack (McCarthy, 2001; Schliemann & Bockheim, 2011; Yanoviak et al., 2017, 2020). In mangrove forests, canopy gaps are often referred to as a group of standing dead trees (Pinzón et al., 2003; Duke, 2001; Amir and Duke, 2019). As mangrove canopy gaps are usually recolonized by seedlings from the forest (Clarke & Kerrigan, 2000; Sherman et al., 2000; Duke, 2001), they are considered local hot spots of natural regeneration and forest rejuvenation (Roth, 1992; Feller 2002; Whelan, 2005; Amir, 2012). Thus, it has been proposed that the formation and subsequent closure of canopy gaps prevent mangrove forests from reaching a senescent stage (Duke, 2001; Amir and Duke, 2019).

Although mangrove forest canopy gaps have been reported in several locations (Amir and Duke, 2019), knowledge about their global distribution and the potential drivers of their formation is limited. This lack of knowledge hampers the understanding of large-scale effects of these gaps on mangrove forest properties and their associated ecosystem processes and services. This is important considering the socio-ecological role of mangrove ecosystems. In this study, we performed a comprehensive literature review and collected information on mangrove canopy gaps location, characteristics, and the potential causes of formation. In addition, a geospatial survey was conducted based on satellite imagery visual inspection. Based on the geospatial data collected, the occurrence (presence/absence) and density of canopy gaps in mangrove forests were modelled at the global scale using bioclimatic variables

(Fick & Hijmans, 2017; http://www.worldclim.org/), geographical coordinates and lightning flash rate density data (Albrecht et al., 2016a; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc) as explanatory variables. The objectives of this study were to determine (i) the global distribution of canopy gaps based on current literature and on geospatial survey, and to (ii) determine the potential driver(s) of canopy gap occurrence (presence/absence) and canopy gap density.

2.3 Materials and methods

2.3.1 Bibliographic review

We reviewed the pertinent literature following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Page et al., 2020) guidelines, to assess current knowledge and data on global geographic distribution of canopy gaps in mangrove forests and the potential drivers of their formation. The Web of Science and Scopus databases were accessed on 10th October 2020, using their default settings. The search terms were categorized into three groups of similar terms related to: (1) canopy gaps in general, (2) drivers of canopy gaps, (3) recovery of canopy gaps. The titles, keywords and abstracts of all publications (non-English publications were excluded) were searched using the following syntax for all three respective groups: (1) (mangrove* OR "tidal forest" OR "estuarine wetland") AND ("light gap*" OR "forest gap*" OR "canopy opening" OR "canopy gap*" OR "gap opening") (2) (hurricane* OR lightning * OR "insect attack" OR pathogen* OR windthrow* OR "die-back") AND (mangrove* OR "tidal forest" OR "estuarine wetland") (3) (regeneration* OR rejuvenation*) AND (mangrove* OR "tidal forest" OR "estuarine wetland"). Results of the three separate searches were exported and then combined in an excel file separately. The resulting dataset, encompassed 1,543 articles (617 from Web of Science and 926 from Scopus; Figure S2.1).

148 publications were screened for full text reading (34 from Web of Science, 114 from Scopus) after discarding a total of 1,395 duplicates and publications not related to mangrove forests (583 from Web of science and 812 from Scopus). 52 publications that mentioned both the location and the driver of the canopy gaps were retained as eligible (i.e. 22 from Web of Science, 30 from Scopus). Results from the two databases were combined using excel and the duplicates removed. Ultimately, 30 publications were retained and the following information were extracted: (i) author

name and publication years, (ii) location of the mangrove patch containing the gaps (country, latitude and longitude), (iii) canopy gap size, (iv) proposed driver of canopy gap, (v) methods used for canopy gap detection and (vi) canopy gap size (vii) canopy gap density.

2.3.2 Global geospatial survey

We visually inspected mangrove patches with high concentrations of canopy gaps in a preliminary investigation guided by previous studies (Duke, 2001; Amir and Duke, 2019) and our own assessment of potential locations. We discovered that mangrove patches with high concentrations of canopy gaps were present in areas larger than 5 km^2 across America, Africa, Asia, and Oceania. Therefore, we hypothesized that this spatial distribution would follow a global pattern of canopy gaps in mangrove patches larger than 5 km^2.

From the USGS global distribution of mangrove forests map version 1.4 (Giri et al. 2011; https://data.unepwcmc.org/pdfs/4/WCMC_010_Global_Distribution_of_Mangrove-foests_USGS.pdf?1617121566), mangrove patches >5 km^2 in area were selected (*n = 3,954*) and overlaid on the layer "World Imagery" provided as Basemap (Table S2.1) in ArcGIS 10.8.2 for visual detection of canopy gaps to document their global distribution with spatial resolution of 1x1 km^2. Maps were displayed using a cylindrical equal-area projection to ensure preservation of relative areas. In this study, canopy gaps were defined as circular or elliptical openings with a diameter ranging from ≥ 6 to 86 m. This definition was established through the preliminary investigations conducted across America, Africa, Asia and Ocean. The observed canopy gap sizes consistently fell within the specified diameter range. Canopy gaps were manually digitized using the "Create Features" from the editor toolbox in ArcGIS 10.8.2. Then the following information was extracted for (a) each mangrove patch: spatial location (latitude and longitude) of the centroid, mangrove patch size (area), and the number of canopy gaps; and (b) each canopy gap: spatial location (latitude and longitude) of the centroid, canopy gap size (area). We subsequently determined the canopy gap density for each mangrove patch as the number of gaps per km² of the mangrove patch. The percentage coverage of canopy gaps per mangrove patch was determined as the ratio of the total area of the canopy gaps to the total area of the mangrove patch.

Also, the average canopy gap size frequency distribution was modelled using a continuous power-law function following the methodology of Reis et al. (2022) where the probability for average canopy gap size (m^2) x is given by

Equation 1 $$p(x) = \alpha \left(\frac{\alpha - 1}{x_{min}}\right)\left(\frac{x}{x_{min}}\right)^{-\alpha}$$

where x_{min} is the truncation point, and scaling parameter α quantifies the disturbance level.

As a rule of thumb, α values > 2 are found in forests dominated by small canopy gaps and with less intense disturbance events, whereas α values < 2 indicate a higher proportion of large canopy gaps with high intense disturbance (Asner et al., 2013). To test whether the canopy gap frequency distribution follows a power law distribution we fitted the bootstrap_p function with 5000 iterations to handle the uncertainty of the x_{min} and the scaling parameter (α). The R code was adopted from the poweRlaw package (Gillespie, 2015).

Additionally, the statistical significance of the relationship among average canopy gap size, mangrove patch size and canopy gap density was evaluated using Pearson's method of correlation and visualized the data by fitting loess curves. Kruskal-Wallis test was performed to examine the variations among regions regarding average canopy gap size, canopy gap density, and the percentage coverage of canopy gaps per mangrove patch, (Kruskal and Wallis, 1952). Subsequently, post-hoc multiple comparisons were conducted using Dunn's test, incorporating the Bonferroni correction to address potential Type I error (Dinno, 2017). Level of significance was set at $p < 0.05$. All tests were conducted using R version 4.0 (R Core Team, 2020).

2.3.3 Drivers of canopy gap occurrence and density

Spatial data on potential environmental predictors were prepared in ArcGIS 10.8.2, using the same spatial resolution (1x1 km^2) and projection (world cylindrical equal area) as the canopy gaps map. Nineteen bioclimatic (bioclim) variables were downloaded from the WorldClim database (Fick & Hijmans, 2017; http://www.worldclim.org/).

In addition, the world distribution of lightning flash rate density was obtained from the NASA Earthdata database (Albrecht et al. 2016a; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc).

The latitude and the cosine-transformed longitude (to account for the spherical shape of the Earth; Soininen et al., 2016) of each mangrove patch were also considered as potential predictors of canopy gap occurrence and density. Pairwise correlations were computed among all variables to avoid including highly correlated predictors ($r \geq 0.70$; Dormann et al., 2013; Guisan et al., 2017), as multicollinearity is known to increase uncertainty in model parameters and reduce statistical power (Guisan and Zimmermann, 2000). Excluding highly correlated variables ($r \geq 0.70$) produced a final set of 11 potential predictor variables (Table 2.1).

Due to the limited amount of presence data ($n = 133$) compared to absence data ($n = 3,821$), canopy gap occurrence (presence/absence data) was modelled using the "ensemble of small models" approach (ESM; Lomba et al., 2010; Breiner et al., 2015) developed to model rare species and to account for related statistical challenges (e.g., model overfitting and inaccurate predictions). The main concept for the ESM approach is to build small bivariate models (i.e., models that contain two predictors) and then combine them into an ensemble (Figure 2.1). The ESM strategy was implemented in R following the steps outlined in the 'ecospat' package version 3.1 (Broennimann et al., 2020; Breiner et al., 2018; Di Cola et al., 2017). The occurrence dataset was partitioned using a 10-fold split for cross-validation, with 50% training data to calibrate the model and 50% testing data for model evaluation. The ESM was fitted with four different modeling techniques: generalized linear models (GLM), generalized boosted models (GBM), generalized additive models (GAM) and random forest (RF), chosen for their frequent usage (GLM, RF and GAM; Guisan & Zimmermann, 2000; Guisan et al., 2017) and their robust performance for species distribution modelling (GBM; Guisan & Zimmermann, 2000; Guisan et al., 2017). The default parameter settings were applied for each modeling technique. All possible combinations of the eleven predictors (Table 2.1), resulted in 55 bivariate models for each modelling technique (i.e., GLM, GBM, GAM, and RF). For each modelling technique ESM's were built using Somers' D score ($D = 2 \times (AUC - 0{\cdot}5)$) weighted average of the 55 bivariate models to ensure reliable model predictions (Collart et al., 2021). Bivariate models with a Somers' D score lower than 0 were considered worse than a random model and were excluded when building the ESM (Breiner et al., 2015, 2018; Di Cola et al., 2017). A final ensemble prediction (ESM_{EP}) was built by averaging across the four ESMs using the Somers' D weights (Breiner et al., 2018; Broennimann et al., 2020). The model performance for the four ESMs and the final ensemble prediction (ESM_{EP}) were evaluated using the area under the curve (AUC) and the Boyce index (Allouche et al., 2006; Petit Pierre et al., 2012; Shabani et al., 2016).

Each predictor's contribution to the four separate ESMs (ESM_{GLM}, ESM_{GBM}, ESM_{GAM}, and ESM_{RF}) and the ESM_{EP} were calculated as the ratio between the sums of weights (based on Somers' D weights) of bivariate models, where a given predictor was used and the sum of weights (based on Somer's D weights) of all bivariate models (Broennimann et al., 2020).

To identify factors influencing canopy gap density (number of gaps per km^2), a generalized linear model (GLM) was used. The response variable, number of gaps per km^2, was log-transformed to account for the right skewed data (Figure S2.3) (Guisan and Zimmermann, 2000; Guisan et al., 2017). A first degree polynomial was initially applied and then a second degree polynomial transformation to account for the nonlinear relationship between the response variable and the predictor. A stepwise selection method, using the Akaike information criterion (AIC), was applied in both forward and backward directions to select the optimal model (Guisan & Zimmermann, 2000; Guisan et al., 2017). The adjusted R squared of the optimal model was determined using the 'rsq' R package version 2.5 (Dabao, 2022). The percentage of deviance of the predictors explaining canopy gap density was determined using analysis of deviance table (Guisan et al., 2017).

The R code used to model both canopy gap occurrence and density is available under: https://github.com/michaelkyei66/Mangrove-canopy-gaps-and-their-potential-drivers-A-synthetic-review-from-a-global-perspective.git. To ensure transparency and reproducibility, the modelling approach and analyses were documented (see protocols in Appendix S2.1) following the "Overview, Data, Model, Assessment and Prediction" (ODMAP) approach, using ODMAP version 1.0 (Zurell et al., 2020; https://odmap.wsl.ch/) (Appendix S2.1).

Table 2.1. Variables used as predictors to determine possible drivers of canopy gap occurrence and density. Bioclim variables were downloaded from the worldclim database (Fick & Hijmans, 2017; http://www.worldclim.org/), and the Lightning map layer from the Earthdata database (Albrecht et al., 2016a; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc). The Latitude and cosine-transformed longitude were extracted for each mangrove patch ≥5 km^2 from the Global Distribution of Mangroves USGS (2011) map version 1.4 (Giri et al., 2011; https://data.unepwcmc.org/pdfs/4/WCMC_010_Global_Distribution_of_Mangroves_USGS.pdf?1617121566)

Variables	Description
Bio 1	Annual Mean Temperature (°C)
Bio 5	Maximum Temperature of warmest month (°C)
Bio 6	Minimum Temperature of Coldest month (°C)
Bio 9	Mean Temperature of Driest Quarter (°C)
Bio 13	Precipitation of Wettest Month (mm)
Bio 14	Precipitation of Driest Month (mm)
Bio 18	Precipitation of Warmest Quarter (mm)
Bio 19	Precipitation of Coldest Quarter (mm)
Cos (Lon)	Cosine-transformed Longitude (°E-W)
Lat	Latitude (°N-S)
Lightning	Lightning flash rate density (flash $km^{-2}y^{-1}$)

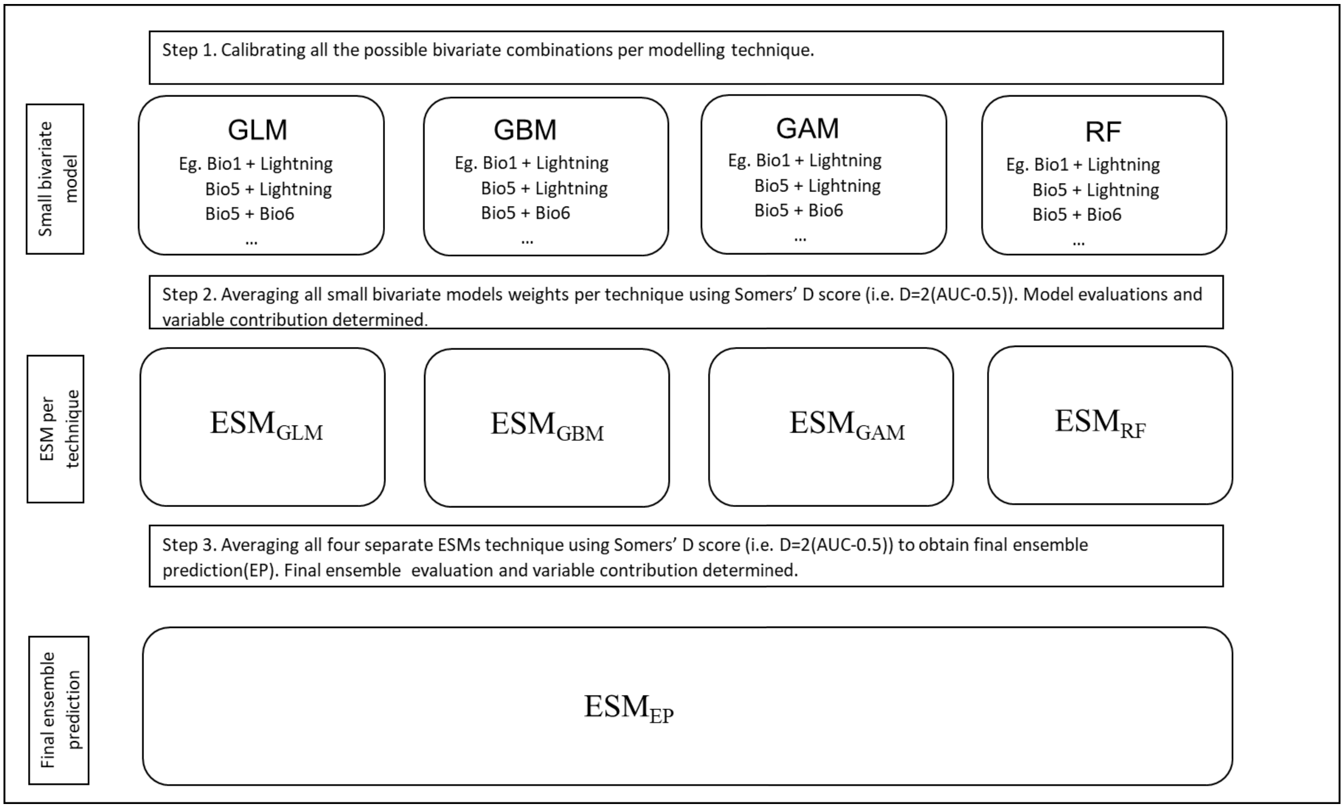

Figure 2.1 Schematic diagram of the ESM (Ensemble of Small Models) following Breiner et al. (2018) steps: (1) All possible bivariate combinations of the 11 predictors resulted in 55 small bivariate models per technique; (2) Weighted average of Somers's D scores per technique. (3) Final ensemble prediction (EP) obtained by averaging across all four separate ESMs using Somers' D weights

2.4 Results

2.4.1 Bibliographic review

Our literature search retrieved 30 studies on mangrove canopy gaps, published between 1986 and 2019 (Table 2.2). Canopy gaps were documented in 13 countries and varied greatly in size (3 to 1783 m², Table 2.2). In the literature reviewed, canopy gap formation was assumed to be driven either by lightning strikes alone (*n=11*) or pathogens (*n=1*), wood harvesting (*n=7*), hurricanes (*n=6*), insect infestation (*n=3*), drought (*n=1*), or experimental manipulation (*n=1*). In most instances, the identification of the causative agent of canopy gap formation was supported by empirical evidence (Table 2.2), but in some cases, the causative agent was determined based on qualitative or anecdotal observations (e.g. some studies referring to lightning strikes, lightning strikes in combination with hurricanes; see Table 2.2). Sherman et al. (2000) assumed that canopy gaps with an average size of 724 m² in a Dominican Republic mangrove forest were caused by lightning strikes without any empirical evidence to support this assumption. Similarly, Clarke and Kerrigan (2000) made a qualitative observation that Australian canopy gaps, with gap size ranging from 253 m² to 756 m², were probably driven by lightning strikes or pathogen. Amir and Duke (2019) presumed that lightning strikes created circular or elliptical canopy gaps ranging from 27 m² to 474 m² in Australian mangrove forests. Amir (2012) suggested that lightning strikes were the drivers of canopy gaps in the Matang forest (Malaysia) based on anecdotes from experienced foresters. Claims of lightning-driven canopy gaps in Can Gio mangrove forest (Vietnam) were based on personal observations (Kautz et al., 2011; Vogt et al., 2011). The variations of canopy gaps sizes (Table 2.2) reported at the Can Gio mangrove forest by Kautz et al. (2011) and Vogt et al., (2011) highlight the scale of the presumed lightning strikes within the mangrove forest. Several studies concluded that the mosaic of canopy gaps in mangrove forest of the Everglades park, with sizes ranging from 59 m² to 289 m², were caused by lightning strikes (Whelan and Smith 2004, Whelan 2005; Zhang 2008), based on lightning strikes data collected by Huffines (1999) for over a decade in Florida, USA.

Additionally, there have been reports of some unique locations of suspected lightning strikes that had coincided with hurricanes in the same sites which further resulted in the formation of canopy gaps (Smith et al., 1994; Baldwin et al. 2001; Zhang et al., 2008). For instance, the mangrove forests in the Everglades park had been reported as a hot spot for hurricanes and lightning strikes (Smith et al., 1994, Zhang 2008, Zhang et al., 2008). These hurricanes uprooted several individual trees or broke their stems and branches to create canopy gaps with a density of about 4,000 gaps per km² (Zhang et al., 2008). Also, in the Dominican Republic, Sherman et al. (2000), based on personal observations, had earlier reported that the formation of canopy gaps pre-hurricane was caused by lightning strikes. At the same site, Sherman et al. (2001) observed that strong windthrows from Hurricane Georges caused the mortality of individual trees further generating canopy gaps. Imai et al. (2006) suggested that strong winds were the main “gap makers” in the Thailand’s mangrove forests.

Notwithstanding the limited studies (Table 2.2) on the role of insect infestation in the creation of canopy gaps, Putz and Chan (1986) demonstrated that sap-eating termites caused damage to several trees in the Malaysian Matang Forest, leading to their eventual death and leaving behind small canopy gaps in the forest. Feller and McKee (1999) showed that girdling, pruning and hollowing wood-borers created small canopy gaps ranging in size from 12 m² to 144 m² in a Belizean mangrove forest. Sousa et al. (2003) reported high mortality of Rhizophora seedlings induced by stem-boring beetles to have caused canopy gaps in Panama after a presumed lightning strike event had killed several individuals or groups of standing trees at the same site previously (Sousa and Mitchell 1999).

Small-scale felling of mangrove trees can result in the formation of canopy gaps that resemble naturally formed canopy gaps. For example, studies conducted in the Federated States of Micronesia observed that small-scale felling of mangrove forests resulted in the formation of canopy gaps with sizes varying between 10 to 1000 m^2 fostering natural regeneration by allowing seedlings to regrow in the canopy gaps (Ewel et al., 1998; Allen et al., 2001; Pinzón et al., 2003). However, the wide variations in canopy gap sizes observed on the small island of Micronesia (Allen et al., 2001; Pinzón et al., 2003) highlight the potential threat to the mangrove forests. This threat arises from increased wood harvesting due to a growing coastal community (Allen et al., 2001). Blanchard and Prado (1995) demonstrated that small-scale mangrove-felling in Ecuador created numerous small canopy gaps in the mangrove forest. Walters (2005) observed that two-thirds of the canopy gaps in mangrove forests of the Philippines were due to small-scale wood harvesting and Alongi and Carvalho (2008) reported that 30-50% of the mangrove forests have been lost in Timor Leste due to small-scale felling of the mangrove trees resulting in small canopy gaps.

Table 2.2. Result of the literature search conducted using Scopus and Web of Science databases (accessed on 10th October 2020). For each publication, we indicate the author names, the publication year, the location (country, latitude and longitude) where the gaps were identified, the proposed drivers of gap formation, the method used for gaps detection, the mean or range canopy gap size (m²) and the mean or range canopy gap density per kilometer square.

Author name	Year	Country	Latitude	Longitude	Driver	Method of gap detection	Canopy gap size (mean or range in m²)	Canopy gap density (mean or range in km-²)
Osborne and Smith	1990	Australia	18°15'S	146°12'E	Lightning strikes*	Ground-truthing	x	x
Clarke and Kerrigan	2000	Australia	x	x	Lightning strikes or pathogens*	Ground-truthing	253-756	x
Clarke	2004	Australia	19°17'S	147°03'E	Experimental manipulation**	Ground-truthing	50- 225	x
Amir and Duke	2019	Australia	27° 22′ 20.44″S	153° 8′ 51.48″E	Lightning strikes*	Ground-truthing	27-474	x
Duke et al.	2017	Australia	14°45'	135°23'	Drought**	Remote sensing & Ground-truthing	x	x
Feller and McKee	1999	Belize	x	x	Insect infestation (wood-boring insect)**	Ground-truthing	12-144	x
Sherman et al.	2000	Dominican Republic	19 °10'N	60°40'W	Lightning strikes*	Ground-truthing	724	x
Sherman et al.	2001	Dominican Republic	19"10'N	69"40'W	Hurricane*	Ground-truthing	700	x
Blanchard and Prado	1995	Ecuador	1°20'N	78°54'W	Wood harvesting**	Ground-truthing	x	x
Ewel et al.	1998	Federated States of Micronesia	5°19'N	163°00'E	Wood harvesting **	Ground-truthing	158	x
Allen et al.	2001	Federated States of Micronesia	5°19'N	163°00'E	Wood harvesting **	Ground-truthing	10-1000	x
Pinzón et al.	2003	Federated States of Micronesia	5°19'N	163°00'E	Wood harvesting**	Ground-truthing	114	x
Putz and Chan	1986	Malaysia	4°48'N	100°35'E	Insect infestation (termites)**	Ground-truthing	x	x
Amir	2012	Malaysia	4°26'047.15"–5°0'45.99"N	100°25'27.05"-100°39'27.61"E	Lightning strikes*	Remote sensing & Ground-truthing	1783	x

Wan et al.	2018	Malaysia	06º22′53.3″N	99º53′34.5″E	Wood harvesting**	Ground-truthing	x	x
Roth	1992	Nicaragua	11°55'N	83°45'	Hurricane*	Ground-truthing	x	x
Sousa and Mitchell	1999	Panama	9°24'18"N	79°51'48.5"W	Lightning strikes*	Ground-truthing	201-1075	x
Sousa et al.	2003	Panama	9°24'18"N	79°51'48.5"W	Insect infestation (stem boring-beetle)**	Ground-truthing	329	x
Walters	2005	Philippine	9°N	123°E	Wood harvesting**	Ground-truthing	3	x
Imai et al.	2006	Thailand	9°50' N	98°35' E	Hurricane*	Ground-truthing	51-144	x
Alongi and de Carvalho	2008	Timor Leste	8°30.5'S,	125°47.1'E	Wood harvesting**	Ground-truthing	x	x
Smith, et al.	1994	USA	x	x	Hurricane**	Ground-truthing	x	x
Baldwin et al.	2001	USA	25° 37'N	80°18'W	Hurricane**	Ground-truthing	x	x
Whelan and Smith	2004	USA	x	x	Lightning strikes**	Ground-truthing	134	x
Whelan	2005	USA	x	x	Lightning strikes*	Ground-truthing	289	x
Zhang et al.	2008	USA	x	x	Hurricane**	Remote sensing	740-830	4,000
Zhang	2008	USA	x	x	Lightning strikes**	Remote sensing	59	400-500
Vogt et al.	2011	Viet Nam	10°22′–10°40′ N	106°46′–107°00′E	Lightning strikes*	Remote sensing & Ground-truthing	250	x
Kautz et al.	2011	Viet Nam	699000 N 704000 N	1165000 W 1168000 W	Lightning strikes*	Remote sensing & Ground-truthing	40-617 49-964	x x

Note: * represents anecdotal or qualitative observations as proof of driver of gap formation; ** represents empirical evidence as proof of driver of gap formation. x stands for non-available information.

2.4.2 Global spatial distribution of mangrove canopy gaps

Our global geographical survey detected canopy gaps in 133 mangrove patches distributed across 35 countries (Table S2.2 and Figure 2.2) with a higher proportion of mangrove patches containing canopy gaps in Asia (70.2%, Figure 2.3) than America (23.3%, Figure 2.3), Africa (5.3%, Figure 2.3), and Oceania (1.1%, Figure 2.3). Similarly, the canopy gap density per kilometer square was significantly different in Asia (median 2.6 gaps km^{-2}, Figure 2.4 and Table S2.3) and America (median 1.4 gaps km^{-2}, Figure 2.4 and Table S2.3) than other regions (median 0.4 gaps km^{-2} for Africa and Oceania). Also, the average canopy gap sizes in Asia (median 435.9 m^2, Figure 2.4 and Table S2.4) and America (median 607.5 m^2, Figure 2.5 and Table S2.4) were significantly different from Africa (median 259.7 m^2, Figure 2.5 and Table S2.4).

The percentage of area covered by canopy gaps per mangrove patch in Asia (median coverage 0.12%, Table S2.4) and America (median coverage of 0.10%, Figure S2.2 and Table S4) significantly differed from Africa (median coverage 0.01%) and Oceania (median coverage 0.01%, Figure S2.2 and Table S2.5).

There were no significant relationships between canopy gap density, average canopy gap size, and mangrove patch size (Figure 2.6 a-b. Despite the lack of a significant relationship, there is an interesting trend of canopy gap density increasing and decreasing simultaneously with changes in average canopy gap size (Figure 2.6c). The majority of the gaps were smaller than 1,000 m^2 (Figure S2.3). The average canopy gap size followed a power law distribution with alpha value of 4.6 and goodness of fit of 0.09 (Figure S2.4).

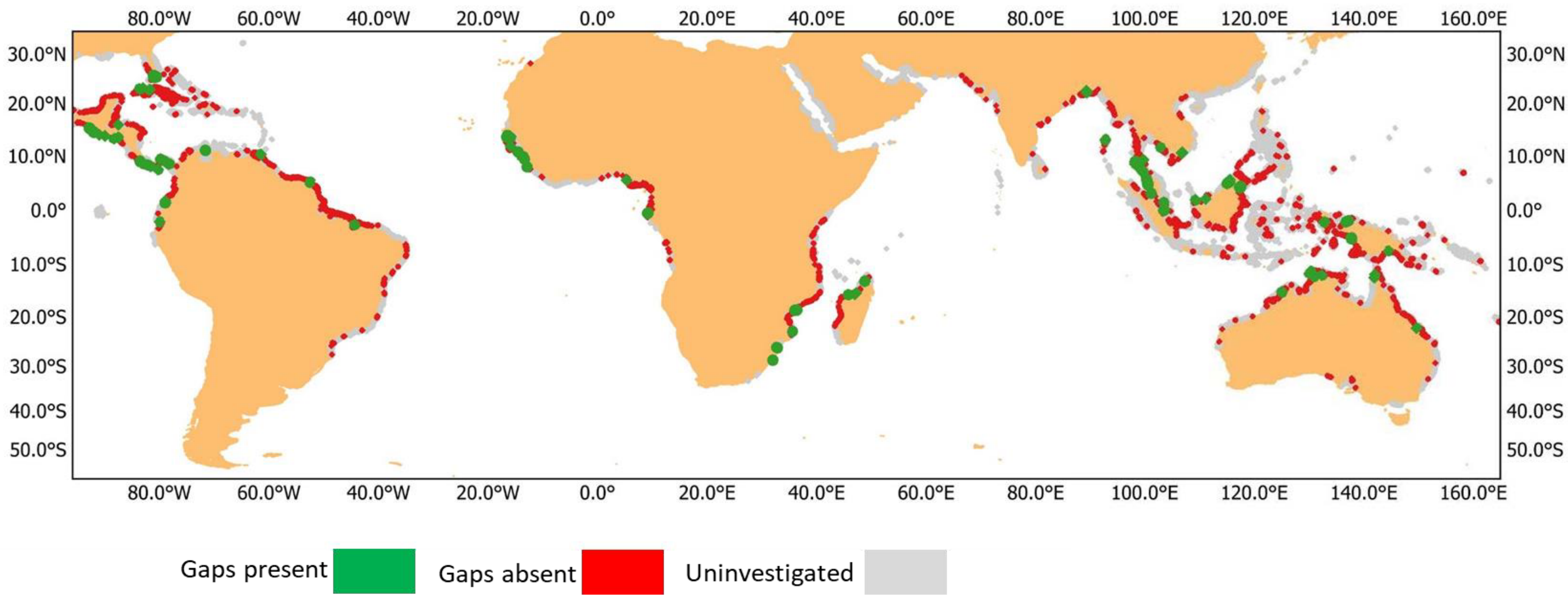

Figure 2.2. Global distribution of canopy gaps in mangrove forests. Green and red spots represent mangrove patches with and without canopy gaps respectively; grey spots represent mangrove patches that were not investigated.

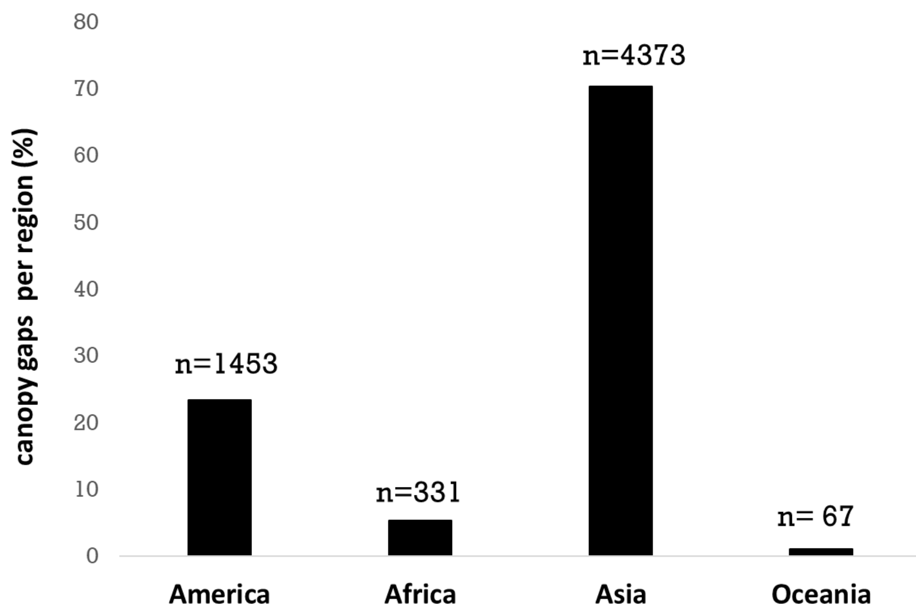

Figure 2.3. Global distribution of mangrove canopy gaps by region. ‘n’ represents the number of canopy gaps per region. The number of mangrove patches (>5 km²) investigated for the presence or absence of canopy gaps per region is as follows: America (1,068), Africa (833), Asia (1,553), and Oceania (500).

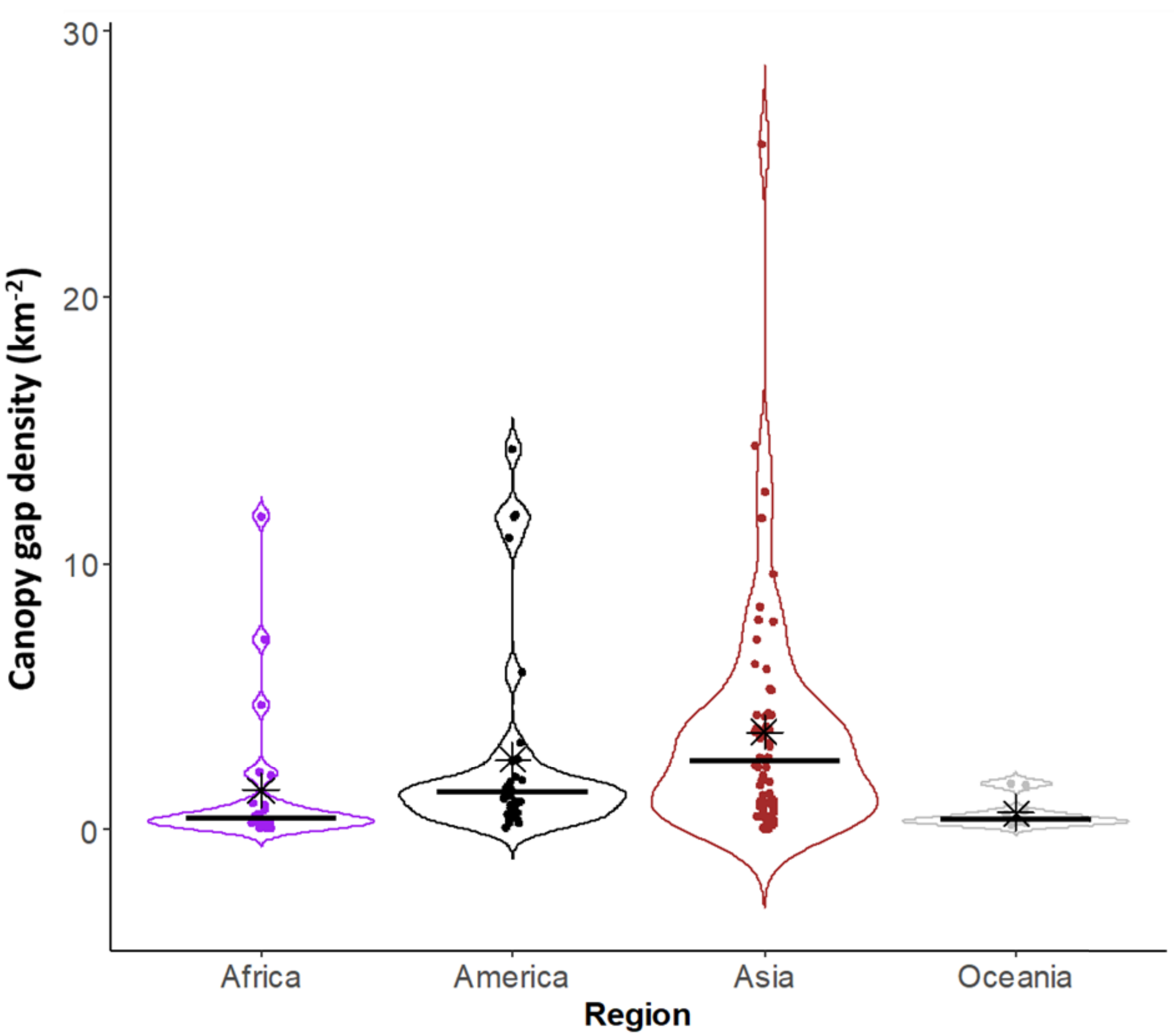

Figure 2.4. Canopy gap density (number of canopy gaps per km^{-2}) per geographical region. Black line represents the median whiles the asterisk shows the mean. The black, purple, brown and grey dots represent the data from America, Africa, Asia and Oceania respectively. Graph was obtained using R package ggplot2 (Wickham 2016).

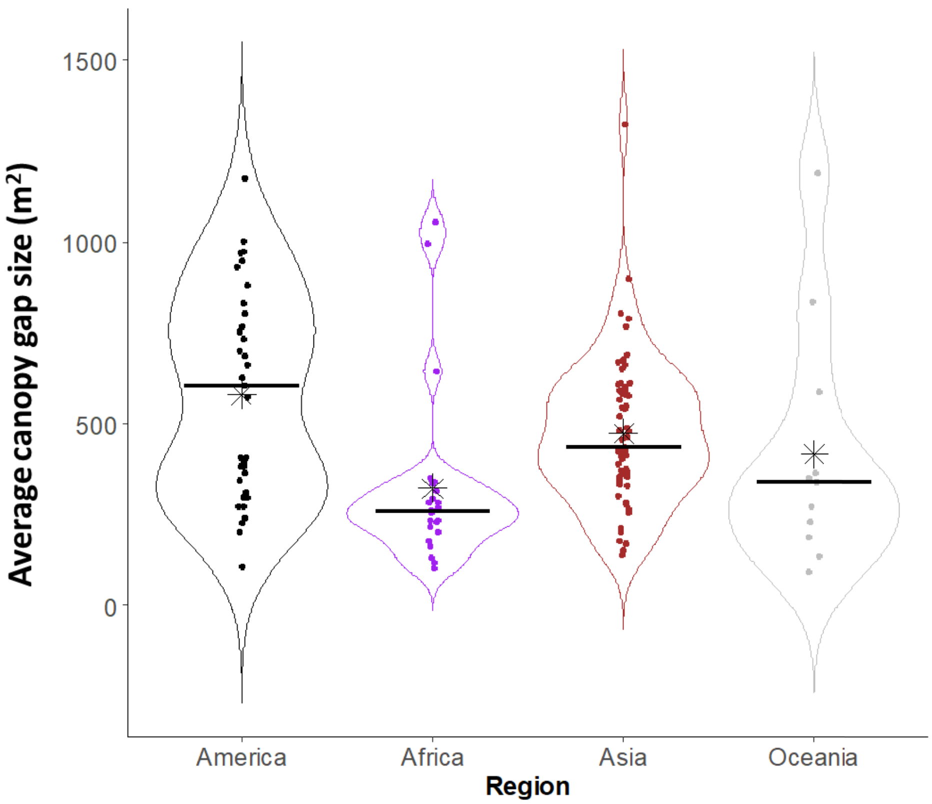

Figure 2.5. Average canopy gap size (m²) in each mangrove patch by geographical region. Black line represents the median whiles the asterisk shows the mean. The black, purple, brown and grey dots represent the data from America, Africa, Asia and Oceania respectively. Graph was obtained using R package ggplot2 (Wickham 2016).

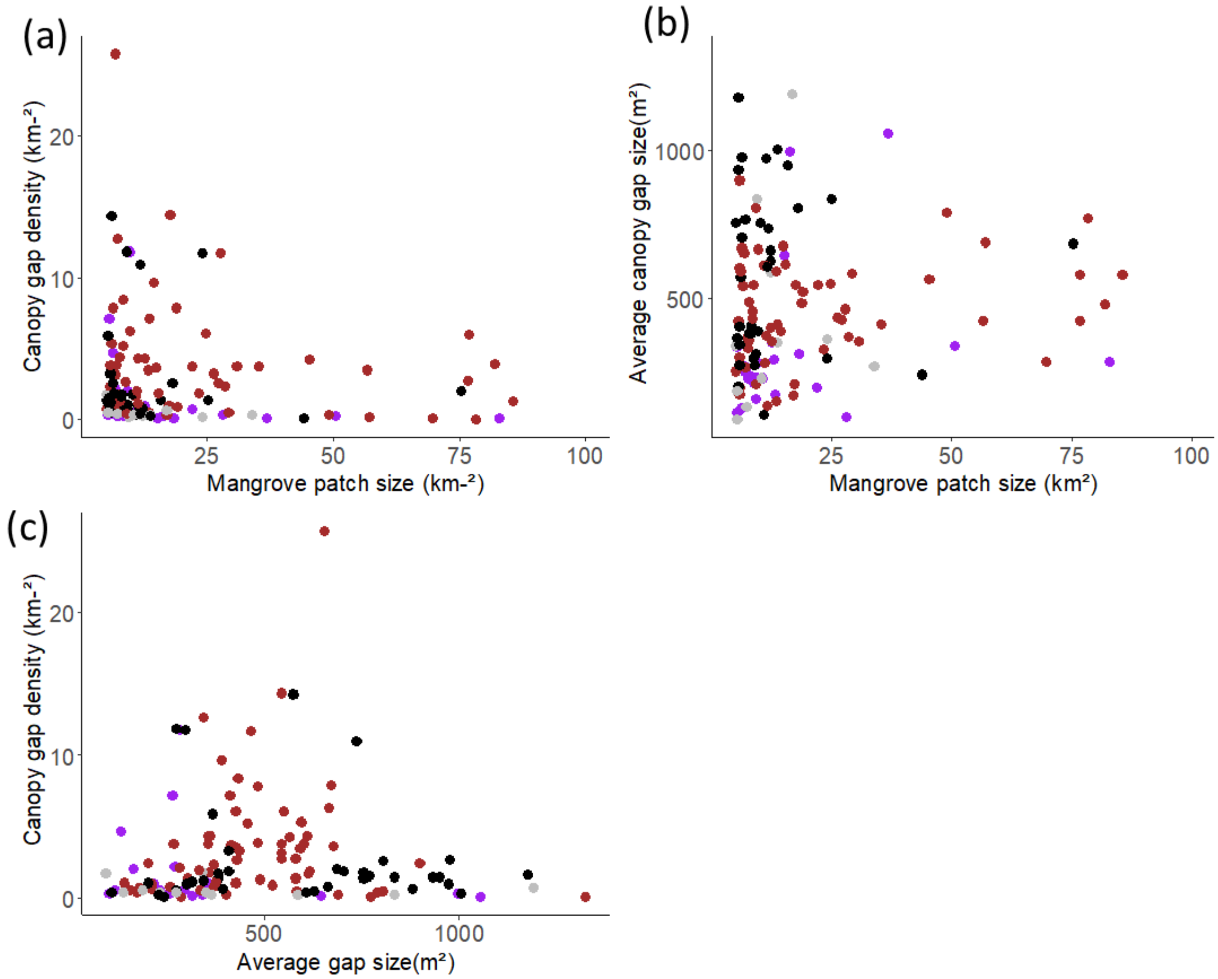

Figure 2.6. Relationship between (a) canopy gap density and mangrove patch size, (b) average canopy gap size and mangrove patch size, and (c) canopy gap density and average gap size. The black, purple, brown and grey dots represent the data from America, Africa, Asia and Oceania respectively. Graph was obtained using R package ggplot2 (Wickham 2016).

2.4.3 Main drivers of canopy gap occurrence and canopy gap density

The model performance for the final ensemble prediction (ESM_{EP}) of canopy gap occurrences, based on the four single modeling techniques (Figure S2.5), yielded a median AUC of 0.71 and a Boyce index of 0.87.

The main factors contributing to the predictions of canopy gap occurrences were lightning flash rate density, latitude, and precipitation of the coldest quarter (Figure 2.7). Concerning the model for canopy gap density, the adjusted R-squared value explained approximately 34% of the variance. The main predictors significantly related to the canopy gap density were maximum temperature of the warmest month, lightning flash rate density, precipitation during the driest month, and precipitation during the wettest month (Table 2.3).

Canopy gap density exhibited notably higher values in the Asian region during maximum summer temperatures ranging from 30 to 35°C and in the winter months between 21 and 24°C (Figure 2.8). Furthermore, canopy gap density displayed an inclination to increase in Asia with higher precipitation during the wettest month (300-500 mm) and the driest month (100-200 mm), in comparison to the regions of America, Africa, and Oceania (Figure 2.8). Furthermore, canopy gap density displayed an inclination to increase in Asia with higher precipitation during the wettest month (300-500 mm) and the driest month (100-200 mm), in comparison to the regions of America, Africa, and Oceania (Figure 2.8). A pattern of increasing lightning flash rate density ($km^{-2}yr^{-1}$) was observed particularly in Asia as compared to the other regions (Figure 2.8).

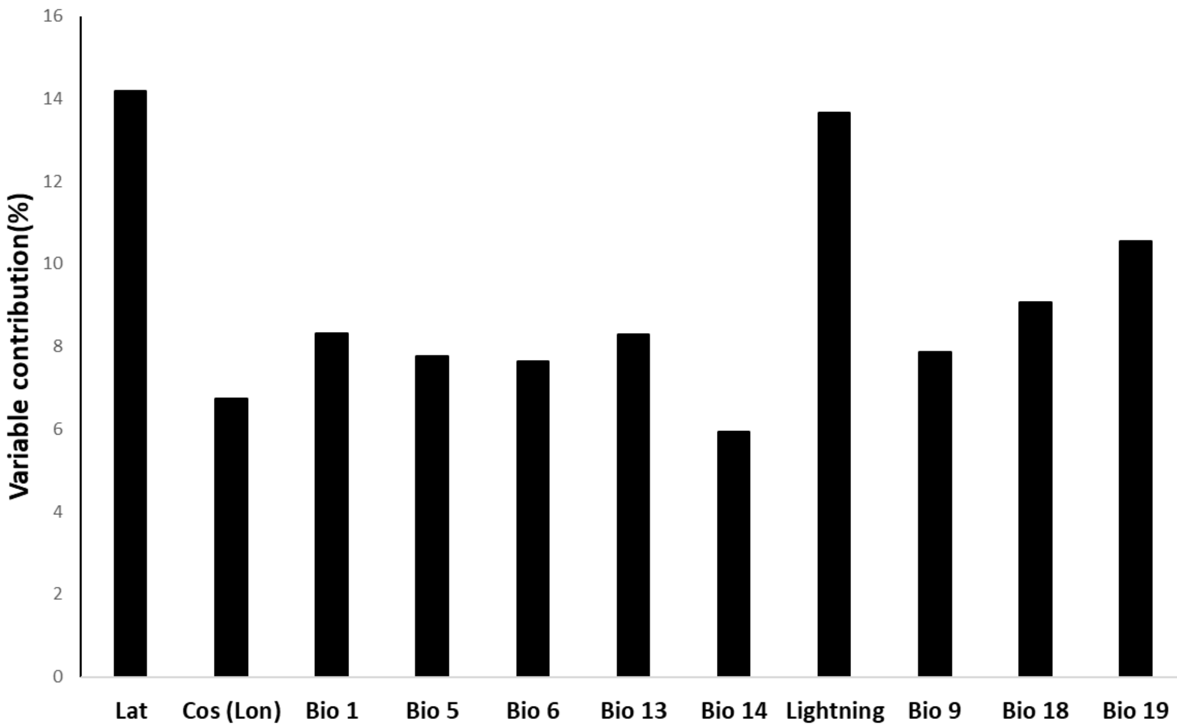

Figure 2.7. Contributions of each predictor to the final ensemble prediction (ESM_{EP}) in determining the drivers of the canopy gap occurrences. The predictors used in the model were: latitude (Lat), cosine transformed longitude (Cos(Lon)), annual mean temperature (Bio 1), maximum temperature of warmest month (Bio 5), minimum temperature of coldest month (Bio 6), precipitation of wettest month (Bio 13), precipitation of driest month (Bio 14), lightning flash rate density (Lightning), mean temperature of driest quarter (Bio 9), precipitation of warmest quarter (Bio 18), precipitation of coldest quarter (Bio 19).

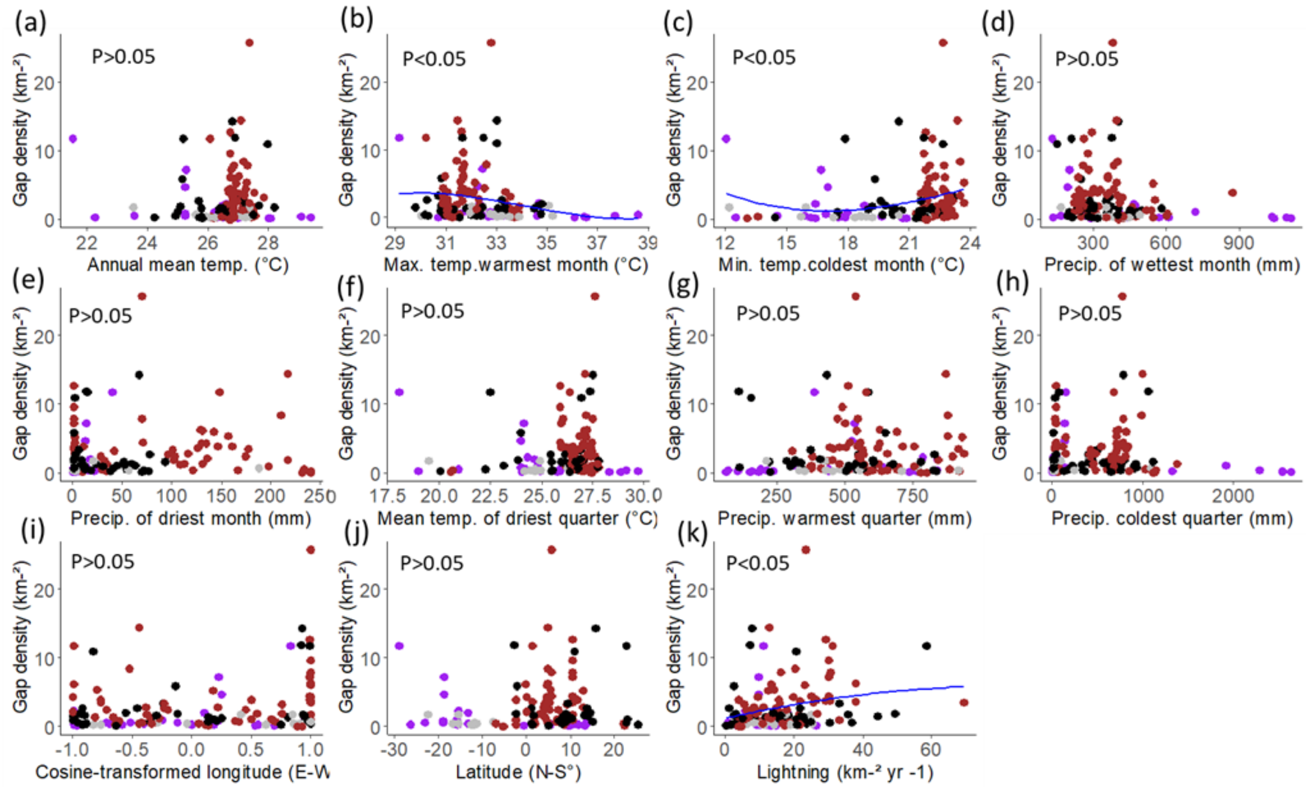

Figure 2.8. Relationships of canopy gap density with the various predictors used in the modelling approach: a) Annual mean temperature, b) Maximum temperature of warmest month, c) Minimum temperature of coldest month, d) Precipitation of wettest month, e) Precipitation of driest month, f) Mean temperature of driest quarter, g) Precipitation of warmest quarter, h) Precipitation of coldest quarter, i) Cosine transformed longitude j) Latitude, k) Lightning flash rate density. The black, purple, brown and grey dots represents the data from America, Africa, Asia and Oceania respectively. The blue line is a polynomial regression showing significant relationship at $P<0.05$. Graph was obtained using R package ggplot2 (Wickham 2016).

Table 2.3. Analysis of deviance table showing the percentage of deviance of the predictors explaining canopy gap density (bold font indicates significant values). The maximum temperature of the warmest month, followed by the lightning flash rate density, the precipitation of the wettest month and the precipitation of the driest month are the main drivers of gap density. The “poly” 2 indicates quadratic polynomial term.

	Df	Deviance	Resid. Df	Resid.Dev	P>Chi
NULL			132	236.47	
poly(Annual Mean Temperature)2	2	0.07	130	236.40	0.970
poly(Max. Temperature of Warmest Month)2	2	50.77	128	185.63	**4.03E-10**
poly(Mean Temperature of Driest Quarter)2	2	4.48	126	181.15	0.146
poly(Precipitation of Wettest Month)2	2	9.47	124	171.68	**0.018**
poly(Precipitation of Driest Month)2	2	9.54	122	162.14	**0.017**
poly(Precipitation of Warmest Quarter)2	2	4.34	120	157.80	0.160
poly(Lightning)2	2	14.95	118	142.85	**0.002**
poly(Cosine-transformed Longitude) 2	2	6.72	116	136.13	0.057

2.5 Discussion

Circular or elliptical canopy gaps in mangrove forests have been studied for more than three decades, but detailed information on the topic is still scarce, and resides in a small body of literature. Given the importance of canopy gaps as core areas for mangrove rejuvenation and regeneration, the lack of knowledge on their global distribution and drivers of their formation presents a major challenge for understanding of ecosystem processes and services on a mangrove forest landscape scale (Smith et al., 1994; Sherman et al., 2000; Amir & Duke, 2019). The study highlights the occurrence and density of circular or elliptical canopy gaps in America, Africa, Asia, and Oceania. Among the 11 variables tested, lightning flash rate density, precipitation of the coldest quarter were the most important drivers of canopy gap occurrence. Canopy gap density in mangrove forests is at least partially determined by maximum temperature of warmest month, lightning flash rate density, and precipitation of wettest and driest months. Average canopy gap size, canopy gap density, and percentage coverage of canopy gaps per mangrove patch varied across the different geographical regions.

Lightning flash rate density (i.e. assumed to eventually hit a tree to result in strikes that cause tree mortality), latitude, and precipitation of coldest quarter together explained about 40% of the occurrence of mangrove canopy gaps, suggesting that lightning strikes were not necessarily responsible for the majority of canopy gap formation at the global scale, nor might they be the major driver of canopy gap formation as has been reported by previous studies (Table 2.2). Frequent lightning strikes occur mostly in the tropics and subtropics (Albrecht et al., 2016b), coinciding with the global distribution of mangrove forests. But the evidence of most studies on canopy gaps in mangrove forests being caused by lightning strikes has often been based on anecdotal or at best qualitative observation (Table 2). The mechanism of how lightning strikes would kill mangrove trees remain uncertain (Clarke and Kerrigan, 2000; Sherman et al., 2000). For example, Amir (2010) proposed that when a tree is struck by lightning strikes, electric discharges travel down the trunk of the tree and disperses into the surrounding sediment through its root system. The presence of root grafts, which connect neighboring trees, is likely to enhance the conductivity within the root system (Duke, 2001). As a result, the effects of the lightning strikes are distributed over a larger area, impacting not only the central tree directly struck but also the neighboring trees. Recent findings from a lightning risk model for terrestrial trees also demonstrate that lightning strikes could potentially hit taller trees with large crowns directly and subsequently damage neighboring large trees through flashover, which is the transfer of electric discharges from one tree to another across an air gap (Gora et al., 2020). There are only a few quantitative terrestrial studies that have tested this lightning risk model. For instance, a recent study on a neotropical forest showed that lightning accounted for about 40% of the mortality of large trees in the short term and probably 9% over a longer term (Yanoviak et al. 2019). Studies on pine forests showed that lightning damage was common on larger trees (Palik & Pederson, 1996; Outcalt, 2008). Nonetheless, other attempts to corroborate this lightning tree risk model have been inconclusive (Mäkelä et al. 2009), and lightning physicists would likely argue that small differences in crown height are insignificant relative to the large scale of a single lightning stroke (Bazelyan and Raizer 2000).

The effect of lightning strikes on canopy gap formation may be indirect (Yanoviak et al., 2020). Terrestrial studies indicate that tree defenses are compromised by injuries from lightning strikes, leading to a reduction in secondary metabolites (e.g., resins). This impact may weaken trees' defense mechanisms (Anderson, 1964; Parlato et al., 2020), likely making them more susceptible to insects and or pathogens attack. This increased vulnerability may ultimately result in tree mortality and, consequently, the formation of canopy gaps. Sousa et al. (2003) provided evidence of a beetle attack on mangrove forests following presumed lightning events in Panama. Recent findings by Parlato et al. (2020) further corroborate the facilitation of beetle attacks after lightning strikes. This potential combination of lightning strikes and beetle attack damage trees, may result in the formation of small canopy gaps (Feller & McKee, 1999). Extensive mortality of mangrove forests due to pathogenic fungi (Pegg et al., 1980) after presumed lightning strikes in Australia (Clarke & Kerrigan, 2000) also resulted in the formation of several gaps.

Considering the limited evidence from previous studies on mangrove forests (Table 2.2), it is unclear whether precipitation of the coldest quarter plays a role as a driver for canopy gap occurrences. Nevertheless, the pattern of canopy gap occurrences may be more pronounced in mangrove forests in colder regions, as trees may be damaged or die while standing during cold winters (McCarthy, 2001; Song et al., 2020). Precipitation in the coldest quarter is often associated with hailstorms in subtropical regions where mangrove forests may be located (Houston, 1999; Lima et al., 2023). Hailstorms may occur when there is meteorological instability and elevated humidity, leading to strong winds that suspend hail in the atmosphere until it reaches a sufficient threshold to fall (Foote, 1984; Wallace & Hobbs, 2006). During such events, physical damage to the mangrove forest includes the stripping of leaves from plants, holes punched through leaves, bruising to bark, divots removed from bark, and eventual tree mortality (Lima et al., 2023). Additionally, the strong winds accompanying hail may cause mechanical damage by uprooting trees or breaking tree trunks and branches. For instance, Houston (1999) demonstrated the severe damage of hailstorms to mangrove forests in Australia. Recently, Lima et al. (2023) showed that more than 90% of the tree trunks were damaged by a hailstorm in the Southeastern Brazilian forest, leading to the formation of canopy gaps. Indeed, precipitation of coldest quarter may not be the only important driver in explaining canopy gap occurrences as they may be accompanied by lightning strikes during such events (Seity et al., 2001; Lafon, 2004; Kolmašová et al., 2022) in driving the canopy gap occurrences in some mangrove regions.

Whereas lightning flash rate density, and precipitation of coldest quarter are demonstrated by the model as the most important drivers of circular canopy gap formation in mangrove forest, evidence from other vegetated coastal ecosystems (i.e. salt marshes and seagrass meadows) indicates that ecological processes such as nutrient depletion, and facilitative competitive interactions among the plants could drive the formation of fairy circles (i.e. circular gaps) (Getzin et al., 2016, 2021; Ruiz-Reynés et al., 2017; Zhao et al., 2021). For instance, Zhao et al. (2021) showed by combining mathematical models and experimental evidence that nutrient depletion plays a key role as an ecological process explaining the formation of circular gaps in the salt marshes. The field experiments showed clearly that nitrogen fertilization mitigated nutrient depletion stress and shifted the plant growth from negative to positive in gap centers. Ruiz-Reynés et al. (2017) developed a parsimonious model to demonstrate that fairy circles (i.e. circular gaps) emerged as a result of local demographic imbalances along facilitative and competitive interactions in seagrass meadows. Competition for scarce or depleted resources within terrestrial forests can lead to die-offs, and often, the mechanism is explained by predictive models (Pillet et al., 2018). Although nutrient depletion and facilitative competitive interactions among plants were not included as predictors of canopy gap formation in the study, the mechanism remains unclear in terms of mangrove forests. Therefore, further investigations are required at different regional and local scales to validate the mechanism within mangrove forests.

According to the model of canopy gap density, the maximum temperature of the warmest month, lightning flash rate density, precipitation of wettest month and precipitation of driest month were by far the strongest predictors of canopy gap density. High temperatures (i.e. maximum temperature of the warmest month in the model) (Asbridge et al., 2015) and low rainfall (precipitation of driest month in the model) may cause similar physiological stress (i.e. carbon starvation and hydraulic failure) in trees (Andrews et al, .2016; Duke et al., 2017; McDowell et al., 2018). Hydraulic failure may occur due to partial or complete loss of xylem function from embolism that inhibits water transport through the vasculature, likely leading to tissue desiccation (Adams et al., 2017; McDowell et al., 2011). Carbon starvation may occur due to potentially reduced carbohydrate supply from available stores and photosynthesis owing to stomatal closure, thus, further reducing the carbohydrate supply which is required to drive phloem transport, maintain turgor and refill embolized xylem (McDowell et al., 2011; Andrews et al., 2016; Aleixo et al., 2019). This may result in tree die-off with the possibility of creating canopy gaps if this coincides with prolonged months of extremely low rainfall or higher temperatures (Aleixo et al., 2019). The corresponding hypothesis that the outbreak of insects (Shaw et al., 2005; Fettig et al., 2007) or pathogens could be related to climatic factors has been tested repeatedly (McDowell et al., 2008). Similarly, during seasons of extremely low rainfall or high temperatures, the cascading effects of carbon starvation and hydraulic failure (McDowell et al., 2008) may make mangrove trees susceptible to sporadic attack of insects (Fettig et al., 2007) and pathogens (Houston, 1987), due to weakened tree defence capacity

(Phillips et al., 2010; McDowell et al., 2018) possibly leading to the mortality of trees and thus generating canopy gaps (Aleixo et al., 2019).

Also, precipitation of the wettest months (i.e. high rainfall) partially influences canopy gaps density. For example, Van de Meer and Bongers (1996) reported that the rate of tree-fall correlated with the pattern of rainfall in generating canopy gaps in tropical rainforests. However, floods due to extremely high rainfall could drive canopy gaps density (van der Meer & Bongers, 1996) in mangrove forests by uprooting already weakened trees that may have been infected by pathogens (Uhl et al., 1988; Rizzo et al. 2000). Floods may remove sediments, break branches, trunks and uproot trees thus potentially could result in formation of canopy gaps (Uhl et al., 1988; Van de Meer and Bongers, 1996).

Moreover, the variation in estimates of canopy gap density may be related to methodological approaches used in detecting canopy gaps (Zhang, 2008). For instance, field surveys may underestimate the number of the gaps per km^2 due to logistical constraints and difficulties in surveying in dense mangrove forests to detect and measure each gap (Zhang et al., 2008). The type and frequency of the driver(s) of gap formation also mediates canopy gap density (Muscolo et al., 2014). For example, Zhang et al. (2008) suggested that the density of canopy gaps in mangrove forests in Florida (USA), presumably initially caused by lightning strikes, increased significantly upon subsequent hurricane disturbance.

In the same manner, the variation in canopy gap sizes across different regions (Figure 5) may result from a combination of factors, which could include site-specific characteristics and the frequency of the underlying driver(s), aspects which were not modelled in this study. The role of site-specific stand characteristics in influencing individual canopy gap sizes has been demonstrated in previous studies (Clarke and Kerrigan, 2000; Sherman et al., 2000; Amir and Duke, 2019). For instance, Amir (2012) postulated that canopy gap size variation depends on site-specific characteristics such as tree species, size, root architecture, sediment structure, and the frequency of lightning strikes. Furthermore, the analysis of the average canopy gap sizes reveal that they follow a power-law distribution with an alpha (α) value of 4.6. This finding indicates that majority of the average canopy gaps sizes are small, suggesting natural factors as potential drivers. A recent study by Reis et al. (2022) used a power-law model to characterize canopy gap size distribution and explored how the alpha (α) value varied in response to disturbances from both human activities and natural processes in the Amazon forest. Their findings indicated that smaller canopy gaps, with an alpha (α) value > 2, were primarily associated with natural environmental phenomena. In contrast, they also observed that larger canopy gaps, with an alpha (α) value < 2, could be attributed to natural agents like lightning strikes, strong winds, and drought, although the majority of large canopy gaps were human-induced. Nonetheless, it is crucial to conduct further ins-situ investigations on local scales to ascertain the specific factors driving canopy gap sizes.

The combined study, reviewing both the pertinent literature and available remote sensing information, suffers from some methodological limitations. The model did not include some of the potential natural drivers of mangrove canopy gap formation, such as hurricanes, insects, pathogens, nutrient depletion, and competitive interactions among the plants. Nonetheless, the results are particularly robust for two reasons. First, the models in this study are based on documented drivers of canopy gaps (Clarke and Kerrigan, 2000; Sherman et al., 2000; Yanoviak et al., 2017; Amir and Duke, 2019). Second, the predicted drivers for both canopy gap occurrence and canopy gap density are supported by empirical patterns and complement anecdotal descriptions of canopy gap formation in mangrove forests in America and Asia (Sousa et al., 2003; Whelan, 2005; Amir and Duke, 2019).

Future studies should ensure extensive in situ validation of remotely sensed data to account for canopy gaps that were possibly not detected due to limited availability of data or cloud coverage in some regions. Additionally, model simulations should be conducted to assess the impacts of possible increasing lightning strikes, droughts, and flooding on canopy gap formation. However, it is important to note that these results were only correlated with potential drivers of canopy gap occurrences and density. Therefore, cautious interpretation should be assigned as the potential drivers do not indicate causal factors. Further global re-assessment of potential drivers of canopy gaps on local and regional scales should be considered in future studies.

Conclusions

1. Circular or elliptical canopy gaps in mangrove forests are found in America, Africa, Asia, and Oceania.
2. The study revealed that the potential drivers of canopy gap occurrences may include lightning flash rate density, and precipitation of the coldest quarter. Additionally, the canopy gap density may be influenced by the maximum temperature of the warmest month, lightning flash rate density, and precipitation of the wettest and driest months.
3. A higher proportion of mangrove patches containing gaps were found in Asia. Furthermore, significant regional variations of canopy gap density, average canopy gap sizes, and the percentage of canopy gap coverage were observed. The results also indicate that the average canopy gap sizes followed a power-law distribution, suggesting that the majority of the smaller gaps may be influenced by natural factors.
4. The study highlights that drivers of canopy gaps in mangrove forests may be linked to multiple climatic factors in driving the occurrence and density on a global scale. Further studies are needed

on regional and local scales to investigate the relationships between the causes of canopy gap occurrence and density in mangrove forests to fully understand the dynamics of these factors and their impact on mangrove forest structure.

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2.8 Supplementary material

Table S2.1. This dataset contains the information related to the geographic regions and countries containing canopy gaps, along with unique identifiers for images, date acquisition, resolution and sources.

Region	Country	Image ID	Date	Resolution	Source
America	Brazil	Vivid_standard_Sao_Luis_BR21Q4	02/08/2021	0.5	Maxar
America	Colombia	Vivid_standard_CO04_22Q2	13/07/2020	0.31	Maxar
America	Costa Rica	Vivid_standard_PA01_22Q1	15/06/2021	0.31	Maxar
America	Cuba	Vivid_standard_CU01_22Q1	22/05/2021	0.31	Maxar
America	Ecuador	Vivid_standard_EC01_22Q2	28/10/2021	0.5	Maxar
America	El Salvador	Vivid_standard_HN01_22Q2	11/11/2019	0.5	Maxar
America	French Guiana	Vivid_standard_SR01_22Q2	10/06/2020	0.31	Maxar
America	Guatamela	Vivid_standard_HN01_22Q2	07/11/2021	0.5	Maxar
America	Honduras	Vivid_standard_HN01_22Q2	27/04/2020	0.5	Maxar
America	Mexico	Vivid_standard_MX08_22Q2	16/12/2019	0.5	Maxar
America	Panama	Vivid_standard_PA01_22Q1	04/01/2019	0.46	Maxar
America	Tinidad & Tobego	Vivid_standard_GP01_22Q1	02/01/2020	0.46	Maxar
America	USA	Monroe_County-FL-USA-24-CMP-20211220	29/01/2021	0.24	Maxar
America	Venezuela	Vivid_standard_VE01_22Q2	13/03/2021	0.5	Maxar
Africa	Gabon	Vivid_standard_GA01_22Q2	13/05/2019	0.5	Maxar
Africa	Gambia	Vivid_standard_GM01_22Q1	14/01/2020	0.31	Maxar
Africa	Guinea	Vivid_standard_GN01_22Q1	06/02/2020	0.5	Maxar
Africa	Guinea Bissau	Vivid_standard_SN01_22Q2	16/05/2020	0.46	Maxar
Africa	Madagascar	Vivid_standard_MG01_22Q2	26/08/2021	0.5	Maxar
Africa	Mozambique	Vivid_standard_MZ03_22Q4	04/12/2019	0.5	Maxar
Africa	Nigeria	Vivid_standard_NG03_22Q1	23/11/2021	0.5	Maxar
Africa	Senegal	Vivid_standard_SN01_22Q2	30/04/2022	0.5	Maxar
Africa	Sierra Leone	Vivid_standard_SL01_22Q1	24/12/2021	0.5	Maxar

Region	Country	Image ID	Date	Resolution	Source
Africa	South Africa	Vivid_standard_SA01_22Q2	11/08/2019	0.46	Maxar
Asia	Bangladesh	Vivid_standard_BD01_22Q2	22/04/2019	0.5	Maxar
Asia	Brunei	Vivid_standard_MY02_22Q1	18/06/2019	0.31	Maxar
Asia	Cambodia	Vivid_standard_KH01_22Q2	25/01/2022	0.31	Maxar
Asia	India	Vivid_standard_IN12_22Q2	22/11/2021	0.5	Maxar
Asia	Indonesia	Vivid_standard_ID06_22Q1	19/03/2017	0.5	Maxar
Asia	Malaysia	Vivid_standard_MY06_22Q2	10/02/2018	0.31	Maxar
Asia	Thailand	Vivid_standard_TH02_22Q1	18/04/2013	0.46	Maxar
Oceania	Australia	Vivid_standard_PG02_22Q1	25/04/2021	0.46	Maxar
Oceania	Fiji	Vivid_standard_FI02_22Q2	14/01/2020	0.5	Maxar
Oceania	Papau New Guinea	Vivid_standard_PG02_22Q1	25/04/2021	0.46	Maxar
Oceania	Viet Nam	Vivid_standard_VN02_22Q2	05/03/2019	0.31	Maxar

Table S2.2 Table showing the summary statistics of canopy gaps per mangrove patch by geographical locations.

Region	Country	Average canopy gap size (m^2)	Canopy gap density (km^{-2})	Canopy gap coverage (%)	Mangrove patch size (km^2)	Longitude (°E-W)	Latitude (°N-S)
Oceania	Australia	94.11	1.70	0.0160	5.30	149.65	-22.34
Oceania	Australia	272.81	0.35	0.0096	33.93	125.12	-15.30
Oceania	Australia	340.35	1.77	0.0601	5.09	125.10	-15.36
Oceania	Australia	137.16	0.41	0.0056	7.29	130.34	-11.34
Oceania	Australia	188.09	0.55	0.0104	5.44	130.08	-11.78
Oceania	Australia	351.31	0.36	0.0127	13.86	132.37	-12.11
Oceania	Australia	365.42	0.21	0.0076	24.01	131.05	-12.34
Oceania	Australia	834.91	0.21	0.0176	9.50	142.08	-11.97
Oceania	Australia	586.92	0.24	0.0143	12.31	141.96	-12.57

Table S2.2 continued

Region	Country	Average canopy gap size (m²)	Canopy gap density (km^{-2})	Canopy gap coverage (%)	Mangrove patch size (km^{-2})	Longitude (°E-W)	Latitude (°N-S)
Asia	Bangladesh	285.10	0.07	0.0020	69.68	89.40	22.40
Asia	Bangladesh	172.66	0.35	0.0061	17.07	89.48	22.07
America	Brazil	273.91	11.84	0.3244	9.04	-44.39	-2.76
Asia	Brunei	545.62	14.40	0.7858	17.64	115.13	4.89
Asia	Brunei	583.43	0.51	0.0298	29.38	115.10	4.82
Asia	Cambodia	265.93	3.81	0.1014	7.08	102.98	11.55
America	Colombia	1175.13	1.57	0.1851	5.72	-78.98	1.66
America	Costa Rica	392.76	0.63	0.0246	9.60	-83.61	9.01
America	Costa Rica	314.10	1.09	0.0343	9.17	-83.60	8.93
America	Costa Rica	754.41	1.37	0.1032	5.12	-83.12	8.53
America	Costa Rica	382.23	1.65	0.0629	7.89	-83.56	8.91
America	Cuba	203.70	1.05	0.0214	5.70	-83.07	22.99
America	Cuba	274.55	0.51	0.0141	5.84	-83.69	22.78
America	Cuba	296.91	11.75	0.3490	24.16	-81.81	22.67
America	Ecuador	1003.97	0.29	0.0290	13.83	-78.95	1.29
America	Ecuador	976.10	2.65	0.2587	6.41	-78.95	1.26
America	Ecuador	367.01	5.90	0.2167	5.42	-79.98	-2.21
America	Ecuador	702.80	1.86	0.1306	6.46	-79.99	-2.27
America	Ecuador	607.53	0.43	0.0260	11.70	-79.01	1.24
America	El Salvador	804.76	2.60	0.2091	18.09	-90.01	13.71
America	El Salvador	767.83	1.54	0.1185	7.13	-88.31	13.19
Oceania	Fiji	231.40	0.38	0.0088	10.49	178.60	-16.81
America	French Gui-ana	242.31	0.09	0.0022	44.01	-52.53	5.07
Africa	Gabon	285.79	0.07	0.0021	82.87	9.17	-0.61
Africa	Gambia	233.41	0.27	0.0063	7.45	-16.65	13.45
Africa	Gambia	315.35	0.11	0.0034	18.37	-15.97	13.41

Table S2.2 continued

Region	Country	Average canopy gap size (m^2)	Canopy gap density (km^{-2})	Canopy gap coverage (%)	Mangrove patch size (km^{-2})	Longitude (°E-W)	Latitude (°N-S)
America	Guatemala	948.91	1.44	0.1366	15.98	-91.04	13.93
America	Guatemala	686.76	2.01	0.1379	75.21	-92.08	14.46
Africa	Guinea	339.77	0.26	0.0087	50.59	-14.14	10.09
Africa	Guinea	1055.55	0.08	0.0086	36.84	-13.58	9.80
Africa	Guinea	645.62	0.13	0.0085	15.24	-13.37	9.36
Africa	Guinea	233.42	0.42	0.0098	9.54	-14.55	10.71
Africa	Guinea Bissau	254.53	0.28	0.0071	7.12	-15.95	11.80
America	Honduras	753.15	1.78	0.1339	10.12	-87.60	13.44
America	Honduras	573.79	14.30	0.8207	6.15	-87.58	15.82
Asia	India	544.69	2.73	0.1489	8.78	92.89	13.01
Asia	India	456.31	5.23	0.2386	8.41	92.85	12.93
Asia	Indonesia	601.99	3.80	0.2288	5.79	132.99	-2.26
Asia	Indonesia	690.12	0.19	0.0133	57.04	136.77	-2.25
Asia	Indonesia	521.87	0.89	0.0464	19.13	132.78	-2.26
Asia	Indonesia	488.27	1.29	0.0632	7.73	109.34	1.83
Asia	Indonesia	789.94	0.39	0.0306	49.02	138.84	-6.87
Asia	Indonesia	614.92	1.89	0.1159	15.38	132.99	-2.26
Asia	Indonesia	770.44	0.05	0.0039	78.39	137.83	-5.34
Asia	Indonesia	354.67	4.33	0.1535	12.71	103.63	-0.03
Asia	Indonesia	281.21	2.08	0.0586	11.04	103.66	-0.03
Asia	Indonesia	549.64	6.08	0.3341	24.84	103.55	-0.10
Asia	Indonesia	579.48	2.75	0.1592	76.79	117.41	4.06
Asia	Indonesia	581.16	1.33	0.0774	85.65	117.45	4.16
Asia	Indonesia	1324.37	0.05	0.0062	148.66	137.75	-5.21
Africa	Madagascar	177.58	0.45	0.0080	13.24	48.82	-13.21
Africa	Madagascar	163.88	2.04	0.0335	9.29	48.80	-13.32

Table S2.2 continued

Region	Country	Average canopy gap size (m²)	Canopy gap density (km^{-2})	Canopy gap coverage (%)	Mangrove patch size (km^{-2})	Longitude (°E-W)	Latitude (°N-S)
Africa	Madagascar	270.29	2.20	0.0595	6.82	47.24	-15.49
Africa	Madagascar	995.56	0.31	0.0305	16.34	46.98	-15.72
Africa	Madagascar	216.28	0.92	0.0198	8.72	45.80	-15.80
Asia	Malaysia	465.95	11.73	0.5467	27.79	103.51	1.38
Asia	Malaysia	804.34	0.44	0.0352	9.14	111.18	1.99
Asia	Malaysia	375.52	1.15	0.0432	11.29	117.72	4.38
Asia	Malaysia	652.40	25.74	1.6795	6.84	100.44	5.66
Asia	Malaysia	671.32	7.90	0.5304	6.33	100.44	5.63
Asia	Malaysia	593.54	5.35	0.3174	6.17	115.60	5.53
Asia	Malaysia	899.49	2.41	0.2167	5.81	115.47	5.28
Asia	Malaysia	676.85	3.63	0.2454	14.89	103.51	1.38
Asia	Malaysia	664.07	6.25	0.4153	9.75	100.56	4.88
Asia	Malaysia	566.18	4.24	0.2402	45.26	100.62	4.60
Asia	Malaysia	330.76	1.89	0.0625	23.29	101.25	3.03
Asia	Malaysia	433.39	8.41	0.3646	8.44	115.22	4.94
Asia	Malaysia	610.24	4.34	0.2649	11.29	100.38	5.64
Asia	Malaysia	590.91	3.49	0.2062	13.47	115.54	5.21
Asia	Malaysia	430.97	2.64	0.1137	27.30	117.58	4.19
Asia	Malaysia	435.90	3.28	0.1429	26.24	117.57	4.23
Asia	Malaysia	369.88	2.33	0.0863	28.71	117.60	4.26
Asia	Malaysia	481.69	3.91	0.1881	81.94	100.66	4.73
Asia	Malaysia	426.93	6.03	0.2573	76.81	100.62	4.72
America	Mexico	881.71	0.60	0.0532	188.92	-92.81	15.16
Africa	Mozambique	295.02	0.54	0.0159	12.97	36.00	-18.82
Africa	Mozambique	102.50	0.32	0.0033	28.09	32.80	-26.27

Table S2.2 Continued

Region	Country	Average canopy gap size (m²)	Canopy gap density (km^{-2})	Canopy gap coverage (%)	Mangrove patch size (km^{-2})	Longitude (°E-W)	Latitude (°N-S)
Africa	Mozambique	264.78	7.15	0.1894	5.59	36.36	-18.73
Africa	Mozambique	131.22	4.69	0.0615	6.40	36.38	-18.76
Africa	Mozambique	202.35	0.77	0.0156	22.04	36.35	-18.78
Africa	Nigeria	235.57	0.24	0.0057	8.25	5.30	5.44
America	Panama	407.90	3.29	0.1340	5.78	-79.87	9.39
America	Panama	408.54	1.83	0.0748	8.19	-78.89	8.90
America	Panama	931.53	1.43	0.1331	5.60	-78.72	8.77
America	Panama	972.30	0.97	0.0939	11.39	-78.59	8.69
America	Panama	834.25	1.43	0.1194	25.14	-78.55	8.67
America	Panama	626.63	0.48	0.0304	12.38	-78.25	8.46
America	Panama	383.68	1.34	0.0516	8.19	-82.32	8.30
America	Panama	299.30	0.92	0.0277	8.66	-81.98	8.22
America	Panama	109.16	0.37	0.0040	10.85	-81.70	8.06
America	Panama	661.61	0.81	0.0539	12.28	-80.32	7.42
Oceania	Papua New Guinea	1189.20	0.71	0.0840	16.99	144.58	-7.59
Africa	Senegal	337.42	0.37	0.0125	5.41	-16.51	13.61
Africa	Senegal	231.97	0.56	0.0130	10.72	-16.47	13.83
Africa	Sierra Leon	351.47	1.03	0.0362	12.62	-12.89	7.92
Africa	South Africa	282.91	11.79	0.3336	9.75	32.01	-28.83
Asia	Thailand	543.38	3.14	0.1709	6.68	99.82	9.24
Asia	Thailand	154.69	0.52	0.0080	13.57	98.30	8.95
Asia	Thailand	371.49	0.80	0.0297	7.49	98.30	8.88
Asia	Thailand	404.43	0.24	0.0099	12.28	98.26	8.51
Asia	Thailand	302.26	1.35	0.0409	5.92	98.24	8.47
Asia	Thailand	612.50	1.66	0.1018	10.84	98.57	8.42

Table S2.2 continued

Region	Country	Average canopy gap size (m^2)	Canopy gap density (km^{-2})	Canopy gap coverage (%)	Mangrove patch size (km^{-2})	Longitude (°E-W)	Latitude (°N-S)
Asia	Thailand	334.75	0.53	0.0178	7.51	98.64	8.39
Asia	Thailand	257.33	0.78	0.0202	5.10	99.33	7.55
Asia	Thailand	178.87	0.69	0.0123	5.80	99.36	7.38
Asia	Thailand	426.68	1.06	0.0451	5.68	99.48	7.33
Asia	Thailand	202.46	2.37	0.0480	5.90	99.42	7.26
Asia	Thailand	139.63	1.02	0.0143	11.73	99.69	7.15
Asia	Thailand	212.55	0.64	0.0137	9.31	99.74	6.87
America	Trinidad and Tobago	343.83	1.21	0.0415	5.80	-61.51	10.23
America	USA	229.15	0.26	0.0060	826.07	-80.96	25.30
America	Venezuela	735.18	10.96	0.8058	11.77	-71.66	10.99
Asia	Viet Nam	212.40	0.97	0.0207	17.44	106.92	10.63
Asia	Viet Nam	361.88	4.37	0.1580	7.56	106.95	10.60
Asia	Viet Nam	354.86	3.77	0.1336	30.80	106.89	10.61
Asia	Viet Nam	342.89	12.70	0.4355	7.17	106.96	10.58
Asia	Viet Nam	392.08	9.65	0.3784	14.51	106.91	10.56
Asia	Viet Nam	412.41	7.16	0.2954	13.68	106.94	10.56
Asia	Viet Nam	416.12	3.71	0.1544	35.31	106.87	10.55
Asia	Viet Nam	425.83	3.51	0.1495	56.68	106.82	10.53
Asia	Viet Nam	482.25	7.83	0.3777	18.90	106.91	10.51
Asia	Viet Nam	359.88	1.79	0.0644	7.82	106.78	10.49
Asia	Viet Nam	544.86	3.76	0.2048	22.08	106.83	10.48

Table S2.3. Post-hoc multiple comparisons of canopy gap density (i.e. number canopy gaps per km^{-2} of a mangrove patch) in each region. Bold font is the significant pairs.

Region	Africa	America	Asia
America	**0.04**		
Asia	**0.0001**	0.34	
Oceania	1.00	**0.03**	**0.0006**

Table S2.4. Post-hoc multiple comparisons of average canopy gap size (m^2) per mangrove patch by geographical region. Bold font is the significant pairs.

Region	Africa	America	Asia
America	**0.000**		
Asia	**0.0007**	0.58	
Oceania	0.89	0.07	0.38

Table S2.5. Post-hoc multiple comparisons of percentage of coverage of canopy per mangrove patch by geographical region. Bold font is the significant pairs.

Regions	Africa	America	Asia
America	**0.0005**		
Asia	**0.0000**	1.0000	
Oceania	1.0000	**0.0089**	**0.0008**

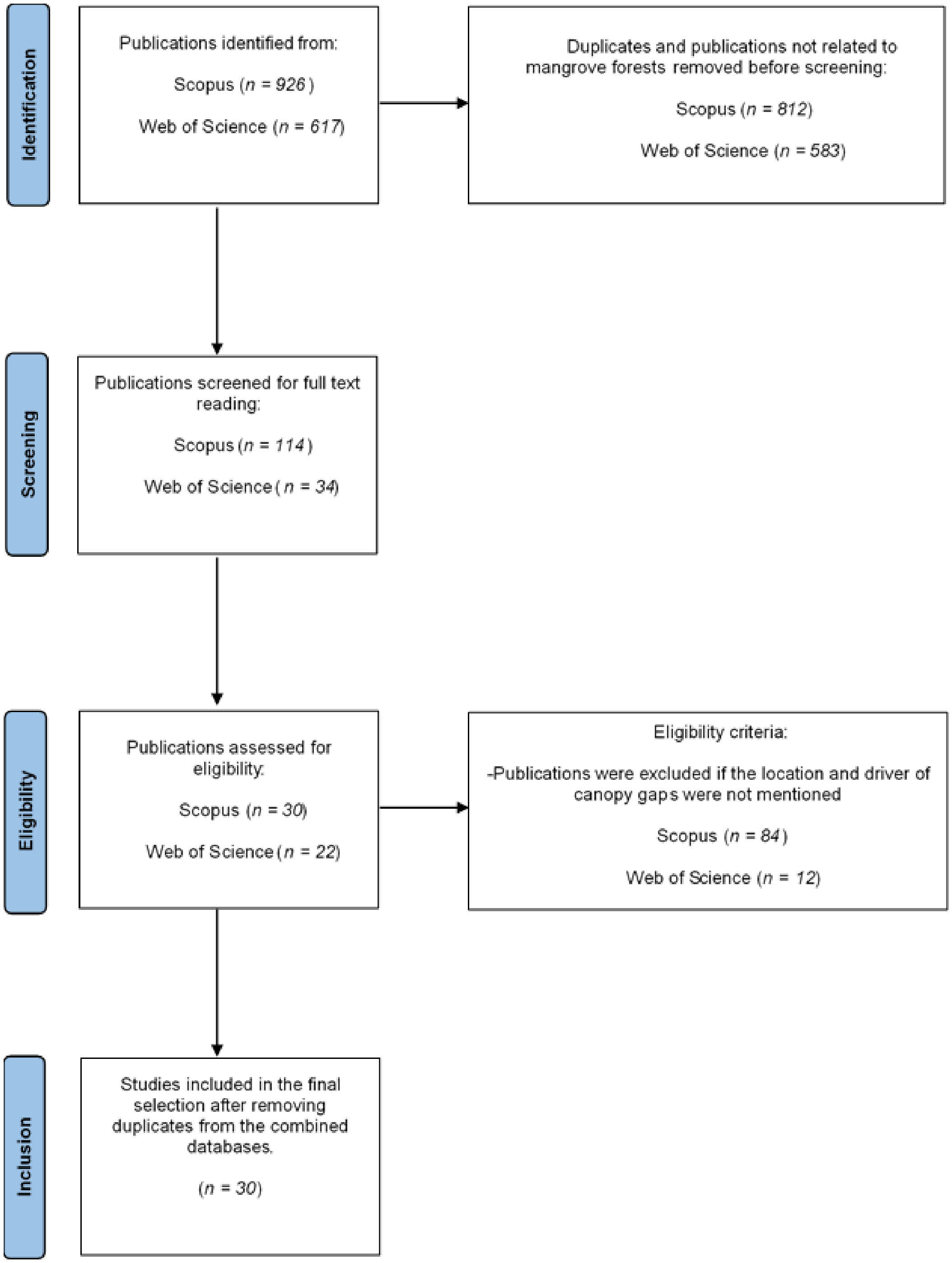

Figure S2.1. Flowchart of the literature review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Page et al., 2020). Duplicates and publication not related to mangrove forests were removed from Scopus and Web of Science databases at the identification stage. Publications were screened for full text reading. The final selection (eligibility step) retained those publications that mentioned at least the location and drivers of the canopy gaps and excluded those that did not meet the criteria. Finally, the results from Scopus and Web of Science databases were combined and duplicates removed, leading to a final set of publications that were considered for further data extraction.

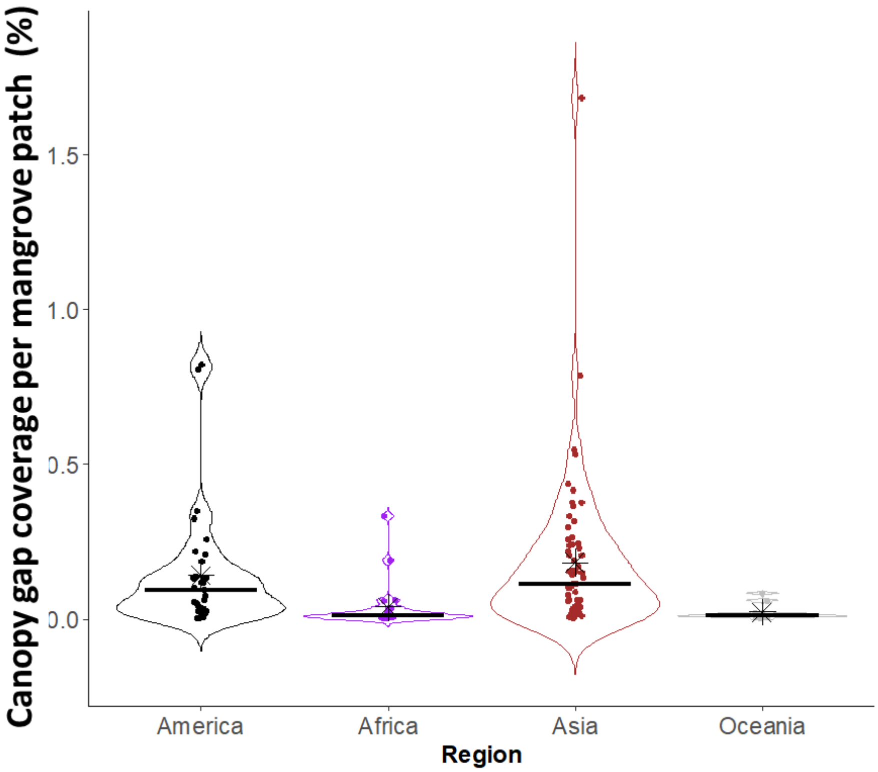

Figure S2.2. Percentage of area covered by canopy gaps per mangrove patch by geographical region. Black line represents the median whiles the asterisk shows the mean. The black, purple, brown and grey dots represent the data from America, Africa, Asia and Oceania respectively. Graph was obtained using R package ggplot2 (Wickham 2016).

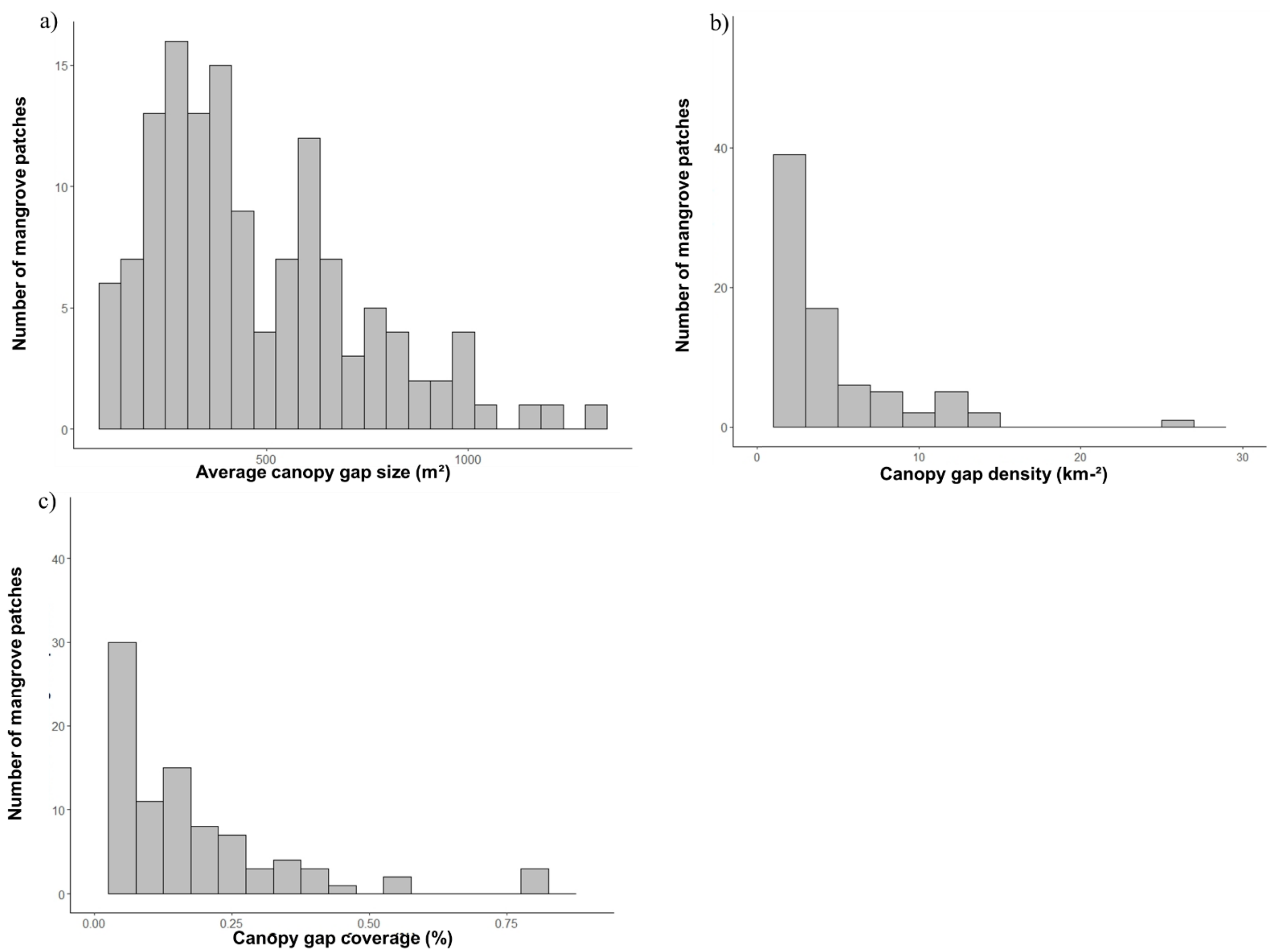

Figure S2.3. Histogram showing the distribution of: (a) Average canopy gap size (b) Canopy gap density (c) Percentage of area covered by canopy gaps per mangrove patch. Graph was obtained using R package ggplot2 (Wickham 2016).

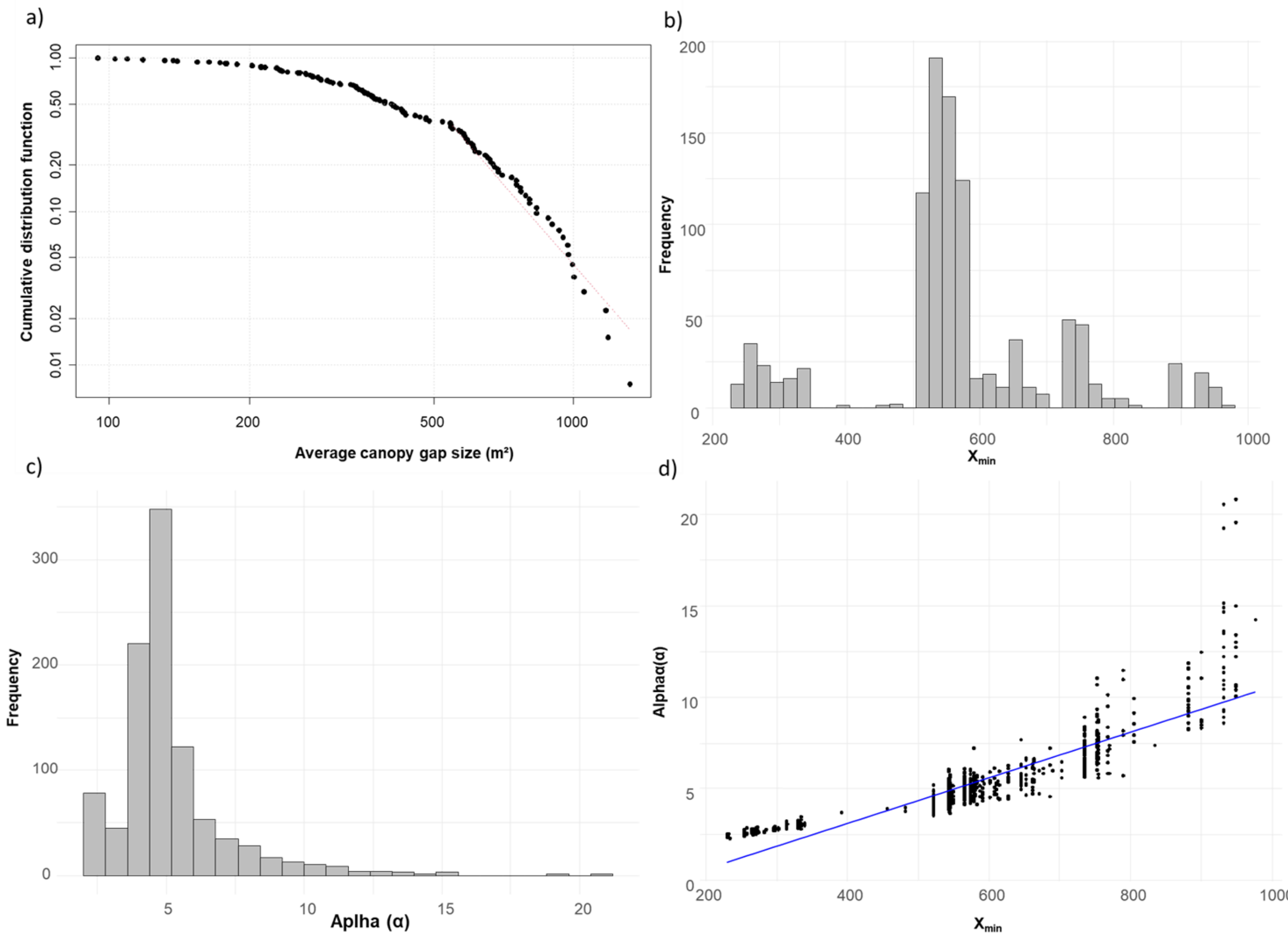

Figure S2.4. Power law distribution of average canopy gap size showing (a) Cumulative distribution function(b) Histogram showing the uncertainty of X_{min} parameter (median = 544.7 m^2, standard deviation =147.6m^2) based on boostrap with 5000 iterations (c) Histogram of the scaling parameter (α) (median =4.6, standard deviation =2.1) based on bootstrap with 5000 iterations (d) Bivariate relationship between the Xmin parameter and scaling parameter (α) showing strong correlation (r^2=0.85, p<2.2 e-16).Redline line show the power law distribution and blue line show the regression line. Graphs were obtained using R packages of powerRlaw (Gillespie, 2015) and ggplot2 (Wickham, 2016)

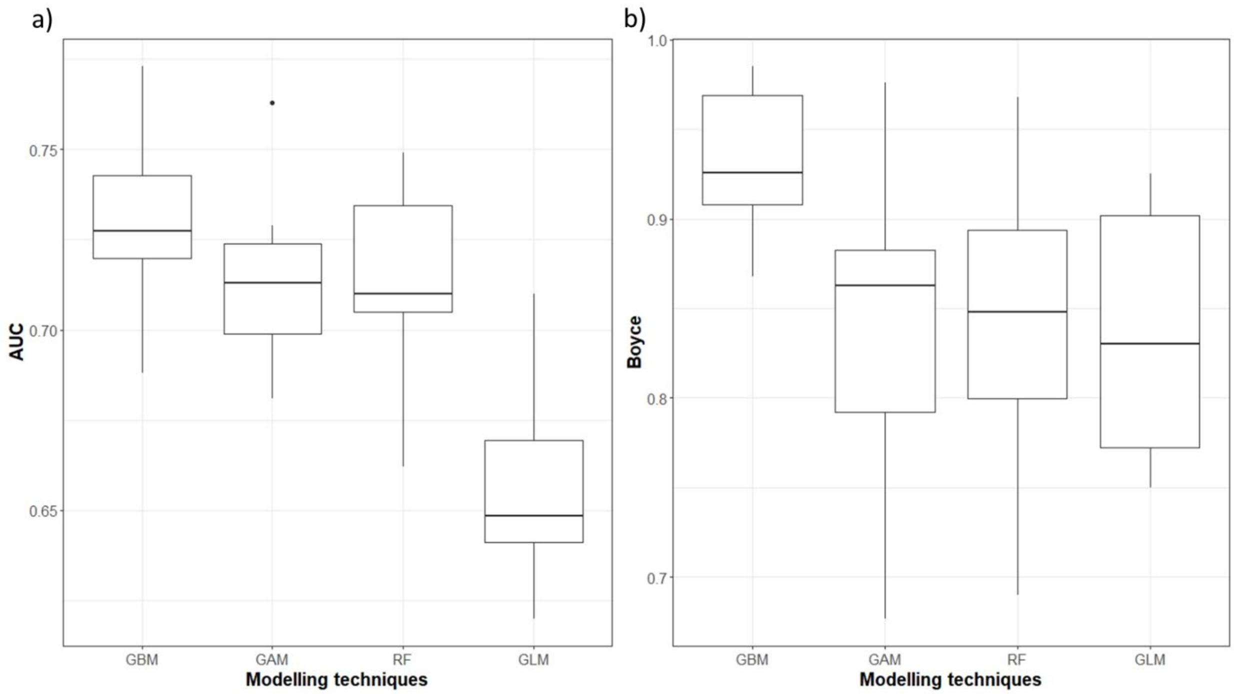

Figure S2.5. Boxplot of the model performances based on A) AUC and B) Boyce indices. The ensemble of small models strategy was applied to the four modelling techniques (GAM, GBM, GLM and RF) which were averaged to build an ensemble prediction (EP). The black middle line in the boxplot represents the median values. Graph was obtained using R package ggplot2 (Wickham 2016).

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Gillespie, C. S. (2015). Fitting heavy tailed distributions: The poweRlaw package. *Journal of Statistical Software*. https://doi.org/10.18637/jss.v064.i02

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Appendix S2.1. Protocol on reporting distribution model using ODMAP version 1 (Zurell et al., 2020; https://odmap.wsl.ch/).

Detailed protocol for modelling canopy gap occurrence

ODMAP element	Content
OVERVIEW	
Authorship	• **Title**: **Mangrove canopy gaps: a global synthesis on their distribution and potential drivers** • **Authors**: Michael Kyei Agyekum; Martin Zimmer; Steven Weerts; Fiona MacKay; Véronique Helfer •**Contact** : michaelk@uni-bremen.de •**DOI**: NA
Model objective	Inference and explanation
Focal Taxon	Mangrove canopy gaps
Location	Global
Spatial extent	•**Processed spatial extent: -**180°E, 180°W, -38.8°S, 32.4°N •**Processed spatial resolution:** 1km •**Type of extent boundary** : rectangular •**Projected co-ordinate system**: World cylindrical equal area
Biodiversity data	•**Observation type**: Visual detection •**Response data type**: presence/absence
Types of Predictors	**Bioclimatic variables** : Annual mean Temperature (°C), Maximum Temperature of Warmest Month (°C), Minimum Temperature of Coldest Month (°C), Mean Temperature of Driest Quarter (°C), Precipitation of Wettest Month (mm), Precipitation of Driest Month (mm), Precipitation of Warmest Quarter (mm), Precipitation of Coldest Quarter (mm)), Fick & Hijmans, 2017; http://www.worldclim.org/) **Lighting** : Lightning flash rate density (flash $km^{-2}y^{-1}$) (Albrecht et al., 2016; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc) **Geolocation** : Cosine-transformed longitude (°E-W), Latitude (°N-S)
Conceptual model/Hypotheses	Climatic variables, geographic locations of mangroves patches (i.e. cosine transformed longitude & latitude) drive the formation of canopy gaps in mangrove forest.

Assumptions	Potential climatic variables responsible for canopy gap occurrences were included in the model
Modelling techniques	Generalized linear models (GLM); generalized boosted models (GBM); generalized additive models (GAM); and random forest (RF)
Model complexity	Due to the limited amount of data, canopy gap occurrences (presence/absence data) were modeled using the ensemble of small models approach (ESM; Lomba et al., 2010; Breiner et al., 2015), developed to model rare species and account for related statistical challenges (i.e. model over-fitting and inaccurate predictions).
Model averaging	The ensemble model of the possible bivariate combinations of the eleven predictors (**Table 2.1**) were used.
Model workflow	All possible combinations of the eleven predictors (Table 2.1), resulted in 55 bivariate models for each modelling technique (i.e., GLM, GBM, GAM, and RF). For each modelling technique ESM's were built using Somers' D score ($D = 2 \times (AUC - 0{\cdot}5)$) weighted average of the 55 bi-variate models to ensure reliable model predictions (Collart et al., 2021). Bivariate models with a Somers' D score lower than 0 were considered worse than a random model and were excluded when building the ESM (Breiner et al., 2015, 2018; Di Cola et al., 2017). A final ensemble pre-diction (ESMEP) was built by averaging across the four ESMs using the Somers' D weights (Breiner et al., 2018; Broennimann et al., 2020).
Software	R package Ecospat 3.1 (Broennimann et al.,2020)
Code availability	https://github.com/michaelkyei66/Mangrove-canopy-gaps-and-their-potential-drivers-A-synthetic-review-from-a-global-perspective.git
Data availability	Data can be made available upon request
DATA	

Biodiversity data	•**Taxon**: Mangrove forests •**Raw Spatial extent**: -180, 180, -38.8, 32.4 •**Raw resolution**: 30m •**Raw Reference system**: WGS 84 •Temporal extent: 1997-2000 •**Data source**: The global distribution of mangrove forest datasets were derived from the USGS observed planet earth satellite images (Giri et al. 2011; https://data.unep-wcmc.org/pdfs/4/WCMC_010_Global_Distribution_of_Mangroves_USGS.pdf?1617121566) •**Sample size**: A total of 3954 mangrove patches greater than or equal to 5km² were selected and processed to 1x1km resolution and projected on the world cylindrical equal area projection system. •**Sampling design**: Canopy gaps were visualized by the world imagery map and delineated using geometry tools (i.e. available in ArcGIS 10.8.2) •**Absences**: Mangrove patches greater or equal to 5km² without canopy gaps
Data partitioning	50% training data and 50% test data.

Predictor variables	**Bioclimatic variables** : Annual mean Temperature (°C), Maximum Temperature of Warmest Month (°C), Minimum Temperature of Coldest Month (°C), Mean Temperature of Driest Quarter (°C), Precipitation of Wettest Month (mm), Precipitation of Driest Month (mm), Precipitation of Warmest Quarter (mm), Precipitation of Coldest Quarter (mm)), Fick & Hijmans, 2017; http://www.worldclim.org/) **Lighting** : Lightning flash rate density (flash km-^{2}y-^{1}) (Albrecht et al., 2016; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc) **Geolocation** : Cosine-transformed longitude (°E-W), Latitude (°N-S)•**Data sources:** (1) The bioclimatic variables were based on a 30 second grid with resolution of 1km (Fick & Hijmans, 2017; http://www.worldclim.org/). (2) The Lightning flash rate density was obtained from the earth data(Albrecht et al.2016; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc) (3) Latitude and Cosine-transformed longitude of the mangrove patches were obtained from the USGS global distribution of mangroves map(Giri et al. 2011; https://data.unep-wcmc.org/pdfs/4/WCMC_010_Global_Distribution_of_Mangroves_USGS.pdf?1617121566) •**Spatial resolution of raw data**: The raw spatial resolution of the bioclim data was 1km whiles the lightning flash data was 0.1° . •**Spatial extent /co-ordinate reference system of raw data**: (1) The bioclim variables: -180E, 180W, -90S, 90N /WGS84 (2) Lightning flash rate: -180E, 180W, -38S, 38N/ Unknown •**Temporal extent**: (1) The bioclim variables: 1970-2000 (2) Lightning flash rate: 1998-2013 •**Data Processing**: The map of mangroves distribution (Giri et al., 2011) was used as a mask to clip the bioclim variable (bio1-annual mean temperature) in the same spatial resolution(1x1km) and map projection(World cylindrical equal area). Subsequently, all the other bioclim variables and lightning flash rate density data were set to the same extent, cell size, and snap raster using the same environment settings of the first clipped bioclim variable. The mean values for each predictor were extracted using the zonal statistics tables (ArcGIS 10.8.2). The longitude variable was cosine transformed to account for the spherical nature of the earth.
MODEL	
Variable pre-selection	Variables were pre-selected based on the assumptions and evidences of previous studies (**Table 2.2**).

Multicollinearity	The Spearman's rank correlations were conducted between all pairs of variables. Variables that were highly correlated with others (|ρ| < 0.70) were excluded to reduce the risk of overfitting during model calibration. The final set of predictors were 11 (Table 2.1)
Model settings	Generalized linear models (GLM), Generalized boosted models (GBM), Generalized additive models, and Random forest (RF) were all fitted as default settings.
Model selection	•**Small bivariate model selection**: small bivariate models were selected by a weighted Somer's D score. Somer's D score was set to zero (i.e. AUC<0.5) allowing worse performing models to be excluded and selecting models of high variability (Figure 2.1). •**Model ensemble/averaging**: All possible bivariate combinations of predictors were built separately per modeling technique (i.e.$ESM_{GLM,}$ $ESM_{GBM,}$ $ESM_{GAM,}$ and $ESM_{RF,}$). The final ensemble prediction (EP) were then built by averaging of the four modelling techniques (Figure 2.1).
ASSESSMENT	
Performance statistics	The model performance was evaluated using the area under the receiver operating characteristic curve (AUC), and the Boyce index (Breiner et al., 2015)
Plausibility check	Plausibility is checked with response curves showing relationship between environmental predictors and gap occurrences.

Detailed protocol for t modelling canopy gap density.

ODMAP element	Content
OVERVIEW	
Authorship	• **Title**: **Mangrove canopy gaps: a global synthesis on their distribution and potential drivers** • **Authors**: Michael Kyei Agyekum; Martin Zimmer; Steven Weerts; Fiona MacKay; Véronique Helfer •**Contact** : michaelk@uni-bremen.de •**DOI**: NA
Model objective	Inference and explanation
Focal Taxon	Mangrove canopy gaps
Location	Global
Spatial extent	•**Processed spatial extent: -**180°E, 180°W, -38.8°S, 32.4°N •**Processed spatial resolution:** 1km •**Type of extent boundary** : rectangular •**Projected co-ordinate system**: cylindrical equal-area
Biodiversity data	•**Observation type**: Visual detection •**Response data type**: Continuous data
Types of Predictors	**Bioclimatic variables** : Annual mean Temperature (°C), Maximum Temperature of Warmest Month (°C), Minimum Temperature of Coldest Month (°C), Mean Temperature of Driest Quarter (°C), Precipitation of Wettest Month (mm), Precipitation of Driest Month (mm), Precipitation of Warmest Quarter (mm), Precipitation of Coldest Quarter (mm)), Fick & Hijmans, 2017; http://www.worldclim.org/) **Lighting** : Lightning flash rate density (flash $km^{-2}y^{-1}$) (Albrecht et al., 2016; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc) **Geolocation** : Cosine-transformed longitude (°E-W), Latitude (°N-S)
Conceptual model/Hypotheses	Climatic variables, geographic locations of mangroves patches (i.e. cosine-transformed longitude & latitude) were hypothesized to drive the canopy gap density.
Assumptions	Potential climatic variables responsible for canopy gap occurrences were included in the model
Modelling technique	Generalized linear models (GLM)

Model complexity	Due to the possible linear and non-linear relationships with predictors, the generalized linear model was adopted to handle the complexity of the relationships as well to provide reliable model predictions.
Model workflow	The response variable, number of gaps per km^2, was log-transformed to account for the right skewed data (Figure S2.3) (Guisan and Zimmermann, 2000; Guisan et al., 2017). A first degree polynomial was initially applied and then a second degree polynomial transformation to account for the nonlinear relationship between the response variable and the predictor. A stepwise selection method, using the Akaike information criterion (AIC), was applied in both forward and backward directions to select the optimal model (Guisan & Zimmermann, 2000; Guisan et al., 2017). The adjusted R squared of the optimal model was determined using the 'rsq' R package version 2.5 (Dabao, 2022). The rankings of the predictors influencing canopy gap density were extracted using an analysis of the deviance table (Guisan et al., 2017).
Software	R (R Core Team,2020)
Code availability	https://github.com/michaelkyei66/Mangrove-canopy-gaps-and-their-potential-drivers-A-synthetic-review-from-a-global-perspective.git
Data availability	Data can be made available upon request
DATA	
Biodiversity data	•**Taxon**: Mangrove forests •**Raw Spatial extent**: -180, 180, -38.8, 32.4 •**Raw resolution**: 30m •**Raw Reference system**: WGS 84 •Temporal extent: 1997-2000 •**Data source**: The global distribution of mangrove forest datasets were derived from the USGS observed planet earth satellite images (Giri et al. 2011; https://data.unep-wcmc.org/pdfs/4/WCMC_010_Global_Distribution_of_Mangroves_USGS.pdf?1617121566) •**Sample size**: A total of 3954 mangrove patches greater than or equal to $5km^2$ were selected and processed to 1x1km resolution and projected on the world cylindrical equal area projection system. •**Sampling design**: Canopy gaps were visualized by the world imagery map and delineated using geometry tools (i.e. available in ArcGIS 10.8.2) •**Absences**: Mangrove patches greater or equal to $5km^2$ without canopy gaps

<table>
<tr><td>Predictor variables</td><td>•Predictor variables :

Bioclimatic variables : Annual mean Temperature (°C), Maximum Temperature of Warmest Month (°C), Minimum Temperature of Coldest Month (°C), Mean Temperature of Driest Quarter (°C), Precipitation of Wettest Month (mm), Precipitation of Driest Month (mm), Precipitation of Warmest Quarter (mm), Precipitation of Coldest Quarter (mm)), Fick & Hijmans, 2017; http://www.worldclim.org/)
Lighting : Lightning flash rate density (flash km-^{2}y-^{1}) (Albrecht et al., 2016; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc)
Geolocation : Cosine-transformed longitude (°E-W), Latitude (°N-S)
•Data sources:
(1) The bioclimatic variables were based on a 30 second grid with resolution of 1km (Fick & Hijmans, 2017; http://www.worldclim.org/).
(2) The Lightning flash rate density was obtained from the earth data(Albrecht et al.2016; https://ghrc.nsstc.nasa.gov/hydro/details/lisvhrfc)
(3)Geolocation of latitude and cosine-transformed longitude of the mangrove patches were obtained from the USGS global distribution of mangroves map(Giri et al. 2011; https://data.unep-wcmc.org/pdfs/4/WCMC_010_Global_Distribution_of_Mangroves_USGS.pdf?1617121566)
•Spatial resolution of raw data:
The raw spatial resolution of the bioclim data was 1km whiles the lightning flash data was 0.1° .
•Spatial extent /co-ordinate reference system of raw data:
(1) The bioclim variables: -180E, 180W, -90S, 90N /WGS84
(2) Lightning flash rate: -180E, 180W, -38S, 38N/ Unknown
•Temporal extent:
(1) The bioclim variables: 1970-2000
(2) Lightning flash rate: 1998-2013
•Data Processing: The map of mangroves distribution (Giri et al., 2011) was used as a mask to clip the bioclim variable (bio1-annual mean temperature) in the same spatial resolution(1x1km^2) and map projection(World cylindrical equal area). Subsequently, all the other bioclim variables and lightning flash rate density data were set to the same extent, cell size, and snap raster using the same environment settings of the first clipped bioclim variable. The mean values for each predictor were extracted using the zonal statistics tables (ArcGIS 10.8.2). The longitude variable was cosine transformed to account for the spherical nature of the earth.</td></tr>
<tr><td colspan="2">MODEL</td></tr>
<tr><td>Variable pre-selection</td><td>Variables were pre-selected based on the assumptions and evidences of previous studies (Table 2.2).</td></tr>
</table>

Multicollinearity	The Spearman's rank correlations were conducted between all pairs of variables. Variables that were highly correlated with others (|ρ| < 0.70) were excluded to reduce the risk of overfitting during model calibration. The final set of predictors were 11 (**Table 2.1**)
Model settings	Generalized linear models (GLM) default settings was used.
Model selection	A stepwise selection method, using the Akaike information criterion (AIC), was applied in both forward and backward directions to select the optimal model (Guisan & Zimmermann, 2000; Guisan et al., 2017).
ASSESSMENT	
Performance statistics	The model performance was evaluated using the adjusted R-squared
Plausibility check	Plausibility is checked with diagnostic plots

References

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Chapter 3 Spatial and temporal pattern of mangrove forest canopy gaps: What do we learn from South Africa?

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[5] School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa
[6] Council for Scientific and Industrial Research, Durban, South Africa
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Submitted to the Bulletin of Marine Science: Michael Kyei Agyekum, Martin Zimmer, Fiona MacKay, Steven Weerts, and Véronique Helfer

Disclaimer: According to the guidelines and revision of the journal to which the manuscript was submitted, the content and structure of Chapter 3 may have changed in the process of publication of the present thesis.

3.1 Abstract

Mangrove canopy gaps occur in over 35 countries across the global distribution of mangrove forests, yet their spatial and temporal patterns remain poorly understood. Here, we investigated whether gaps are randomly distributed, clustered, or dispersed over space and time in two showcase areas in the South African Province KwaZulu-Natal. We mapped canopy gaps, using free satellite imagery within Google Earth Pro and aerial images, and analyzed spatial patterns using Getis Ord-Gi* statistic, Global Moran's I, and Ripley's *K* function. The estimated time it takes for gaps to close was determined using Kaplan-Meier analysis. Spatiotemporal patterns were analyzed using Getis Ord-Gi* statistic and Mann-Kendall test. Our results showed clustered spatiotemporal patterns at uMhlathuze. Beachwood canopy gaps primarily exhibited random patterns with some spa-

tial clustering, along with random temporal patterns. The patterns at both sites support the hypothesis that lightning strikes, insects or pathogen attacks or competition could potentially contribute to canopy gap formation. Spatial distribution of canopy gaps was linked to great canopy height at both uMhlathuze and Beachwood, supporting the lightning strikes hypothesis. Canopy gaps at uMhlathuze remained open for at least 23 years but none at Beachwood had closed over the time span of 18 years that our study covers. Those findings highlight the need for actively reforesting canopy gaps, as the very slow natural regeneration might result in loss of carbon sequestration and long-term storage by mangrove forests. Overall, drivers of gap formation and potential consequences for mangrove forest dynamics differ regionally and warrant future in-depth studies.

3.2 Introduction

The occurrence of circular or elliptic canopy gaps in mangrove ecosystems has been documented in over 35 countries at the global scale (Agyekum et al. in prep.) Various potential drivers of canopy gaps have been proposed:

- Lightning strikes (Clarke and Kerrigan 2000, Sherman et al. 2000),
- Insect and/or pathogen attacks (Feller and McKee 1999, 2002, Sousa et al. 2003),
- Extreme temperatures (Asbridge et al. 2015, McDowell et al. 2011, 2018),
- Too high (Van der Meer and Bongers 1996) or too low precipitations (Anderegg et al. 2015, McDowell et al. 2018, Zhu et al. 2019),
- Senescence (Duke, 2001, Silver et al. 2014)
- Small-scale forestry activities (Blanchard et al. 1995, Pinzón et al. 2003) and
- Competition (Ruiz-Reynés et al. 2017, Zhao et al. 2021).
- Hurricanes or windthrows (Sherman et al. 2001, Zhang et al. 2008)

Looking at the consequences, it has been reported in some instances, that those gaps create micro-habitats 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 act as cores for mangrove regeneration and rejuvenation (Sherman et al. 2000, Duke 2001). Nonetheless, data on the fine-scale distribution patterns in both space and time are scarce (Sherman et al. 2000, Amir and Duke 2019). The findings of previous studies on spatial patterns of canopy gaps have been inconclusive (Sherman et al. 2000, Vogt et al. 2011, Amir and Duke 2019). Some studies described them as random (Amir and Duke 2019) or clustered (Sherman et al. 2000), while others showed the possibility of all three patterns (i.e. random, clustered or dispersed) occurring within a mangrove forest stand (Vogt et al. 2011). Therefore, the spatial and temporal pattern of canopy gap remains difficult to predict, and their causes and consequences (such as the "core for regeneration" hypothesis) difficult to verify. Here, we propose a conceptual model describing what spatial and temporal pattern would be expected depending on the causal agent, and investigated whether the "core for regeneration" hypothesis derived from data collected in Australia (Clarke, 2004, Amir and Duke 2019), Costa Rica (Putz et al. 1984), Belize (Feller and McKee 1999), Dominican Republic (Sherman et al. 2000), Malaysia (Putz and Chan 1986, Amir 2012), Micronesia (Allen et al. 2001, Pinzón et al. 2003), Nicaragua (Roth, 1992), Panama (Sousa and Mitchell 1999, Sousa et al. 2003), Papua New Guinea (Paijmans and Rollet 1977); Philippines (Walters 2005), Senegal (Muda and Mustafa 2003), Thailand (Imai et al. 2006), Timor Leste (Alongi and de Carvalho 2008), and USA (Whelan 2005, Zhang et al. 2008) also verifies in South Africa.

Our conceptual model for the potential causal agents (Figure 3.1) makes the following predictions: (i) Lightning strikes: Some studies (Zhang 2008, Amir and Duke 2019), assuming lightning strikes to be the drivers of gap formation, found random distributions of canopy gaps. Vogt et al. (2011)

showed an inconclusive pattern of random, dispersed and clustered distributions of canopy gaps in the Can Gio mangrove forest in Viet Nam with lightning strikes as the presumed causative agent. Some studies also show that large trees are more likely to be struck by lightning, driving a clustered distribution of canopy gaps (Outcalt et al.2008, Gora et al. 2020). We predict that canopy gaps would exhibit a mostly random spatial and temporal pattern. In this scenario, gap formation would correlate with tree tallness.

(ii) Insects and/or pathogen attacks: Girdling, boring or pruning by insects render mangrove trees susceptible to opportunistic pathogen infestation (Feller and McKee 1999, 2002, Sousa et al. 2003). Further, plant-pathogenic fungal symbionts of wood-boring insects can increase the negative effects of the insect attack on trees (Linnakoski and Forbes 2019). Depending on the scale of the insect and/or pathogen attacks, they could drive canopy gaps in a clustered manner. We predict a clustered spatial pattern and an either clustered or random temporal pattern, if gap formation was driven by insect and/or pathogen attacks.

(iii) Extreme temperatures: Extreme temperatures cause physiological stress (i.e. carbon starvation and hydraulic failure) to tropical trees, resulting in the formation of canopy gaps being clustered or random spatially (Franklain and Shugart 1987, Bentz et al. 2010, Anderegg et al. 2015, Boyd et al. 2013, Linnakoski and Forbes 2019). Considering the scale of the extreme temperatures and the resilience of the mangrove forest species composition, canopy gaps would occur either with a random or clustered spatiotemporal pattern, if their formation was driven by extreme temperatures.

(iv) Too high or too low precipitation: high precipitation events can lead to flooding, which can result in the uprooting of trees (Van der Meer and Bongers 1996), while low precipitation events can lead to conditions of carbon starvation and hydraulic stress in trees, resulting in their mortality (McDowell et al. 2018, Zhu et al. 2019). The magnitude and scale of high or low precipitation could influence spatiotemporal patterns of random or clustered canopy gap formation. If canopy gap formation is influenced by excessively high or low precipitation levels, we predict that the spatial and temporal patterns would be either random or clustered.

(v) Senescence: The mortality of large old voluminous trees drives the formation of canopy gaps (Duke 2001, Silver et al. 2014) that could be either random or clustered depending on the spatial distribution of old trees which, in turn, will depend on forest history and small-scale variation in environmental conditions. Therefore, we predict the spatial distribution of canopy gaps be either clustered or random, and their temporal distribution to display a random pattern if driven by senescence.

(vi) Small-scale forestry activities: Small-scale forestry depends on the magnitude of wood extraction, potentially resulting in clustered or dispersed, potentially random, patterns. Therefore, we predict clustered, dispersed, or potentially random, spatial and temporal patterns, if gap formation was driven by small-scale forestry.

(vii) Competition: Competition: Competition for scarce or depleted resources, such as water, nutrients, or light, can lead to the formation of circular gaps, known as fairy circles (Fernandez-Oto et al. 2014, Ruiz-Reynés et al. 2017, Zhao et al. 2021). Spatially explicit modeling by Liao et al. (2015) demonstrated that interspecific competition among plants resulted in clustered gaps. Similarly, Pillet et al. (2017) found that self-thinning (competition) in tropical rainforest stands generated clustered gaps at a very local scale. We predict spatially clustered, randomly or dispersed, and temporally random canopy gap formation, if driven by competition for resources among the trees.

Based on the above-model and on spatial and temporal information about canopy gaps detected in South African mangrove stands at uMhlathuze and in Beachwood, we (i) determined the spatial and temporal patterns of mangrove canopy gap in the two study sites, (ii) assessed the potential causal agents and (iii) tested the “core for regeneration” hypothesis.

Temporal pattern \ Spatial pattern	random	clustered	dispersed
random	lightning strikes [A,B] insects and/or pathogens [C,D,E] extreme temperatures [F,G,H] high or low precipitation [I, J, K, L] senescence [M,N] small-scale forestry [O,P] competition [Q,R,S]	lightning strikes [A,B] insects and/or pathogens [C,D,E] extreme temperatures [F,G,H] high or low precipitation [I, J, K, L] small-scale forestry [O,P] competition [Q,R,S]	small-scale forestry [O,P,] competition [Q,R,S]
clustered	lightning strikes [A,B] extreme temperatures [F,G,H] high or low precipitation [I, J, K, L] small-scale forestry [O,P]	lightning strikes [A,B] insects and/or pathogens [C,D,E] small-scale forestry [O,P]	small-scale forestry [O,P]
dispersed	lightning strikes [A,B] small-scale forestry [O,P]	lightning strikes [A,B] small-scale forestry [O,P]	small-scale forestry [O,P]

Figure 1. Conceptual model of the spatial and temporal patterns of gap formation in mangrove forests. The causes and their respective references are as follows: (1) lightning strikes (Clarke and Kerrigan [A] 2000, Sherman et al. 2000[B]), (2) insect and/or pathogen attacks (Feller and McKee 1999[C], 2002[D], Sousa et al. 2003[E]), (3) extreme temperatures (Asbridge et al. 2015[F], McDowell et al. 2011[G], 2018[H]), (4) too high or low precipitation (Van der Meer and Bongers, 1996[I], Anderegg et al. 2015[J], McDowell et al. 2018[K], Zhu et al. 2019[L]), (5) senescence (Duke, 2001[M], Silver eta l. 2014[N]) (6) small-scale forestry activities (Blanchard et al. 1995[O], Pinzón et al., 2003[P]) or (7) Competition (Fernandez-Oto et al. 2014[Q], Ruiz-Reynés et al. 2017[R], Zhao et al. 2021[S])

3.3 Materials and methods

3.3.1 Study area

We selected two study sites in the South African Province KwaZulu-Natal along the east coast of South Africa (Figure 3.2). The Beachwood mangrove nature reserve (KwaZulu-Natal), near Durban, has an extent of about 0.75 km^2 (Figure 3.2C). The mangrove stands are dominated by *Bruguiera gymnorhiza* and *Avicennia marina. Rhizophora mucronata*, introduced from Durban Bay, is also present but in lower densities (Ezemvelo KZN Wildlife, 2013).

The Richards Bay embayment (KwaZulu-Natal) consists of the Richards Bay harbour and the uMhlathuze estuary with mangrove extent of about 11.5 km^2 (Figure 3.2D), rendering this forest the largest mangrove stand of the country (80% of the total South African mangrove area). The region experiences a mean annual rainfall of 1,176 mm yr^{-1}, with temperatures ranging from 10.3 to 32.4° C (Rajkaran and Adams, 2011). The tidal system is semi-diurnal with a mean neap tidal range of 0.52 m and a spring tidal amplitude of 1.8 m (Rajkaran and Adams, 2011). Three mangrove species (*Avicennia marina, Bruguiera gymnorhiza and Rhizophora mucronata*) are present at both the Richards Bay harbour area and the uMhlathuze estuary, but the current dominance of *Avicennia marina* has established after the harbour construction in 1960 (Rajkaran & Adams, 2011). For the purposes of this study, both Richards Bay harbour mangroves and the uMhlathuze estuary were combined and analyzed as a single site referred to as uMhlathuze.

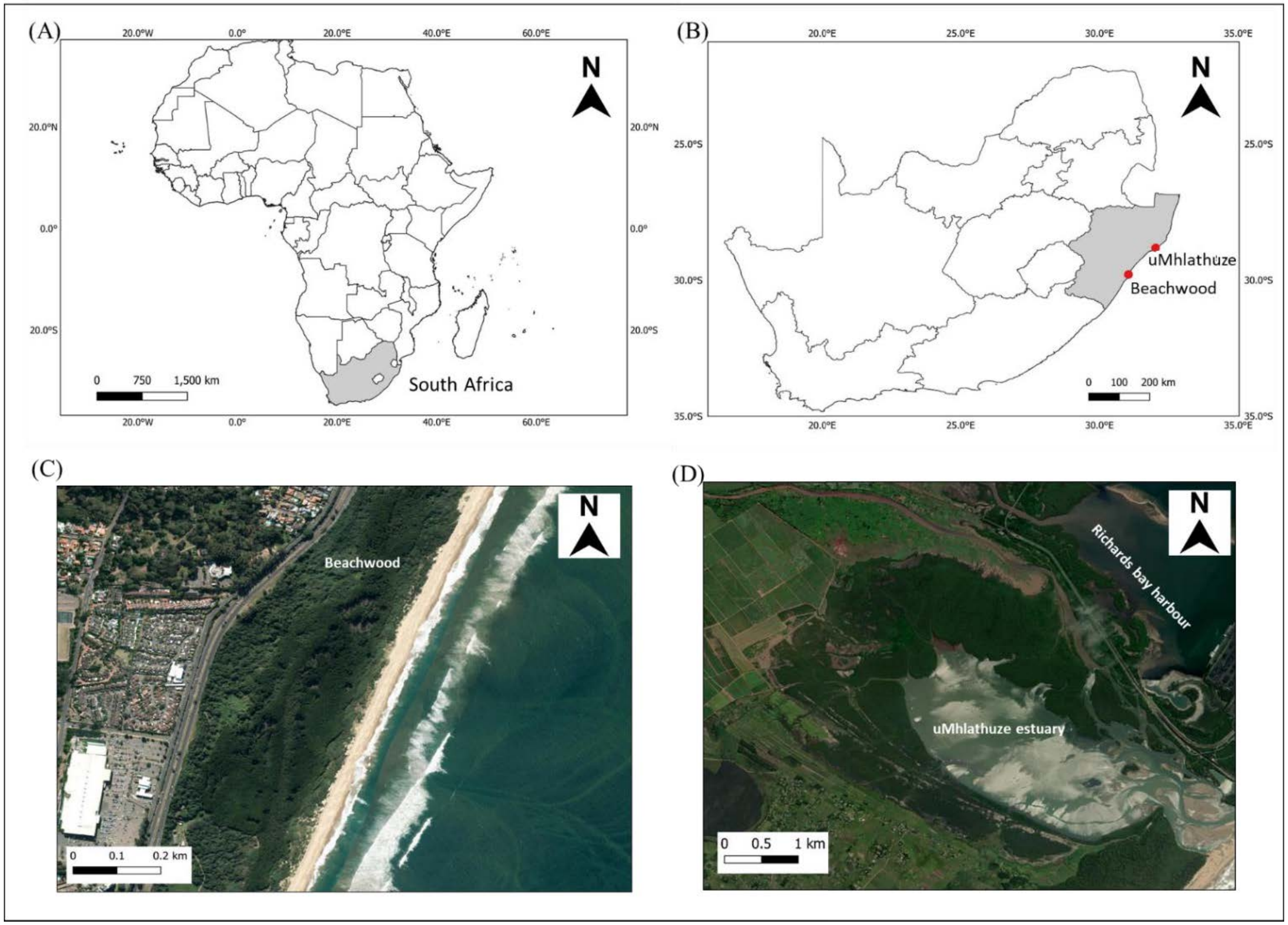

Figure 3.2. The study sites in : (A) South Africa (B) KwaZulu-Natal province, showing (C) Beachwood mangrove stands, and (D) the uMhlathuze site, consisting of the uMhlathuze estuary and Richards Bay harbor mangrove stands. The maps were prepared using QGIS version 3.22.11 Białowieża (QGIS Development 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

3.3.2 Spatial and Temporal Analysis

We employed a combination of very high-resolution satellite images (e.g. "CNES/AIRBUS", "Maxar" and "NASA" satellite imageries), and aerial photographs (CSIR Aerial Photograph) to investigate patterns of formation and closure of canopy gaps in mangrove forests at uMhlathuze and Beachwood (see Appendix S3.1). The satellite imageries were accessed through Google Earth Pro Version 7.3.3 (Google Earth 2018), and canopy gaps were delineated using on-screen digitizing polygon tools and saved into a single shapefile for further processing. Historical aerial photographs were obtained from CSIR (Council for Scientific and Industrial Research, Durban, South Africa, see Appendix S3.1) to complement unavailable datasets and sun-shaded images in Google Earth Pro. The polygon map containing the gaps delineated in Google Earth Pro was projected onto the cylindrical-equal area projection in ArcMap 10.5 (ArcGIS 2016). Gaps detected from the inspection of the georeferenced aerial photographs were delineated using the polygon geometry tools in ArcMap 10.5 (ArcGIS 2016) and saved in the shapefile containing the canopy gaps derived from satellite imagery inspection. Gaps in the aerial photographs were also delineated and labeled with the status of 'open,' 'recovering,' or 'closed' to identify each gap and document its development over time using the polygon geometry tool in ArcMap 10.5 (Appendix S3.1). The gap geographical coordinates and gap size were extracted using the ‘calculate’ geometry tool within ArcMap 10.5 (ArcGIS 2016; see Appendix S3.1).

At each study site, we delineated the total mangrove area based on the latest satellite image available (Appendix S3.1), using the ‘calculate’ geometry tool in ArcMap 10.5 (ArcGIS 2016); this allowed deriving the percentage of the forest area detected in a gap phase.

As the two study sites differed in terms of the number of detected gaps (20 gaps observed in Beachwood compared to 291 in uMhlathuze), the spatiotemporal statistical tools used for Beachwood were more restricted due to the limitations of the Optimized Hot Spot Analysis and Space-Time Pattern Mining tool to process fewer than 30 feature points and 60 feature points, respectively, within ArcMap 10.5 (ArcGIS 2016).

For both sites, we computed the Ripley's *K* function (Dixon 2001) using 999 permutations (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 meters, using 10-meters increments (20- or 30-meters increments provided poorer results; data not shown); analyses were performed within ArcMap 10.5 (ArcGIS 2016) using the *L(d)* transformation (Dixon 2001). The graph was obtained using the ggplot2 package in R (Wickham 2016), based on the Ripley's *K* output table within ArcMap 10.5 (ArcGIS 2016).

To further investigate spatial patterns of all canopy gaps at uMhlathuze having occurred between 1997 and 2020, we conducted within Arcmap 10.5 a Global Moran's I analysis (Ord and Getis 1995) that assesses the overall spatial autocorrelation among features in a given area, thereby evaluating whether the spatial pattern is random, clustered or dispersed.

Subsequently, we applied the Optimized Hot Spot Analysis tool with a bin size of 50 meters in ArcMap 10.5 (ArcGIS 2016) to identify significant hot spots (clusters of high values, >3) and cold spots (clusters of low values, < 3) using Getis-Ord Gi* statistic (Harris et al. 2017). The Getis-Ord Gi* statistic returns for each gap location in the dataset a z-score (standard deviation) and an associated *p*-value for each bin (group of cells; here, we used a bin size of 50 meters, as the 100 meters bin size did not yield improved results) (Harris et al., 2017). The larger the positive z-score, the more intense the clustering of high values (hot spot) is (e.g. values greater than 1, 2 and 3 correspond to confidence levels of 90%, 95% and 99% respectively); the smaller the negative z-scores, the more intense the clustering of low values (cold spot) is (with -1, -2 and -3 corresponding to confidence levels of 90%, 95% and 99% respectively; see e.g. Harris et al. 2017, ArcGIS 2016). The spatio-temporal patterns of canopy gaps in uMhlathuze observed between 1997 and 2020 were further evaluated using the Emerging Hot Spot Analysis (EHSA; Harris et al. 2017), a Space Time Pattern Mining tool available in ArcMap 10.5 (ArcGIS 10.5). This technique combines the Getis-Ord Gi* statistic (Ord and Getis 1995, ArcGIS, 2016) to identify the spatial locations of hot spot canopy gaps with the time-series Mann-Kendall test (Mann 1945, Kendall and Gibbons1990), to detect the temporal trends at each location (Harris et al. 2017). The Getis-Ord Gi* 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 (ArcGIS, 2016). 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 is used to determine statistically significant temporal trends across the time series (one for each bin) of z-scores resulting from the Getis-Ord Gi*. 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 (ArcGIS 2016, Harris et al. 2017, Bass 2017, Reddy et al. 2019). The result of the EHSA is a two-dimensional grid that classifies cells according to various temporal clustering patterns (see Table S1): "New", "Consecutive"," "Intensifying", "Persistent", "Diminishing", "Sporadic", "Oscillating", or "Historical" hot spots (Harris et al. 2017).

Here, we transformed the data collected for uMhlathuze (i.e. date of satellite image 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 meters (ArcGIS 2016, Bass 2017); using a bin size of 100 meters did not strongly impact the final results (see Figures S3); the resulting value for each bin correspond to the number of canopy gaps observed within that bin in a given year (ArcGIS 2016). We computed the Getis-Ord Gi* 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 meters, 200 meters, 350 meters, and 400 meters with a time interval of one year selected based on the datasets (Appendix S3.1). The selection of the different neighboring distances was to evaluate whether the neighborhood size would obscure or reveal small hot or cold spots (Reddy et. al. 2019).

For both study sites, canopy height was obtained from the NASA Shuttle Radar Topography Mission version 3 global 1 arc-second dataset (NASA JPL 2014), in order to corroborate (or not) lightning strikes as potential causative agent. In addition, temperature and data was obtained from the South African Weather Service at uMhlathuze (1995-2020) and Beachwood (1995-2018) to evaluate their correlation to the net rate of canopy gap formation per day. The net canopy gap formation rate was computed based on the number of newly formed canopy gaps on a satellite image divided by the number of days between two consecutive satellite images.

To evaluate whether the “core for regeneration” hypothesis would be supported by data from our study sites, we utilized a non-parametric time-to-event analysis, specifically the Kaplan-Meier curve (Stalpers and Kaplan 2018), to estimate the probability of gaps to close over time. This analysis was performed using the R packages survival version 3.5-7 (Therneau 2023) and survminer version 0.4.9 (Alboukadel et al. 2021).

3.4 Results

Canopy gaps in uMhlathuze and Beachwood covered 1.1% (Figure S3.1) and 0.4% (Figure S3.2) of the total mangrove area in the respective sites (0.74 km² and 11.5 km² respectively; see Appendix S3.1). According to the Ripley's *K* function, canopy gaps in uMhlathuze showed a clustered distribution at distances above 25 meters; below 25 meters, the pattern was random (Figure 3.3A). At Beachwood, the canopy gap distribution did not differ significantly from a random distribution (Figure 3.3B). Visual inspection showed clustered canopy gaps at some areas within the mangrove stand at Beachwood (Figure 6B).

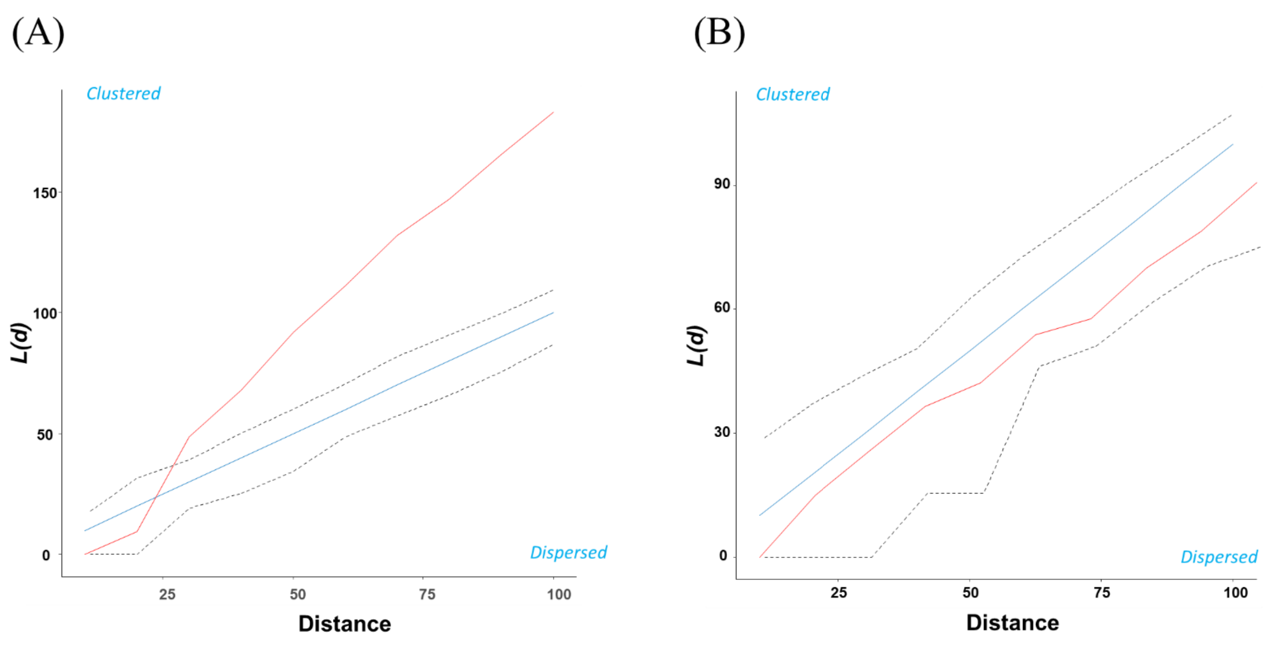

Figure 3.3. Ripley K function showing the spatial pattern of canopy gaps at various distances in (A) uMhlathuze (B) Beachwood. The expected K is represented by the blue line; the observed K is indicated by the red line. The black dashed line represents the 99% confidence interval after 999 iterations. The observed K function curve above the expected K function curve for uMhlathuze indicates a clustered distribution of canopy gaps. The observed K function curve below the expected K function curve for Beachwood indicates a random distribution of canopy gaps. The graph was obtained using ggplot2 (Wickham 2016).

The clustered pattern in uMhlathuze was confirmed by the Global Moran's I analysis, detecting significant spatial autocorrelation (Global Moran's I index of 0.43) with a z-score (reflecting the standard deviation) of 19.89, indicating a less than 1% likelihood of observing a clustered pattern by random chance (see Figure 3.4A). The Optimized Hot Spot Analysis showed significant hot spots and cold spots in uMhlathuze mangrove forest stands. Significant hotspots were observed in the northeast, with cold spots found in the western and southeastern sections of the uMhlathuze mangrove stands (Figure 3.4B).

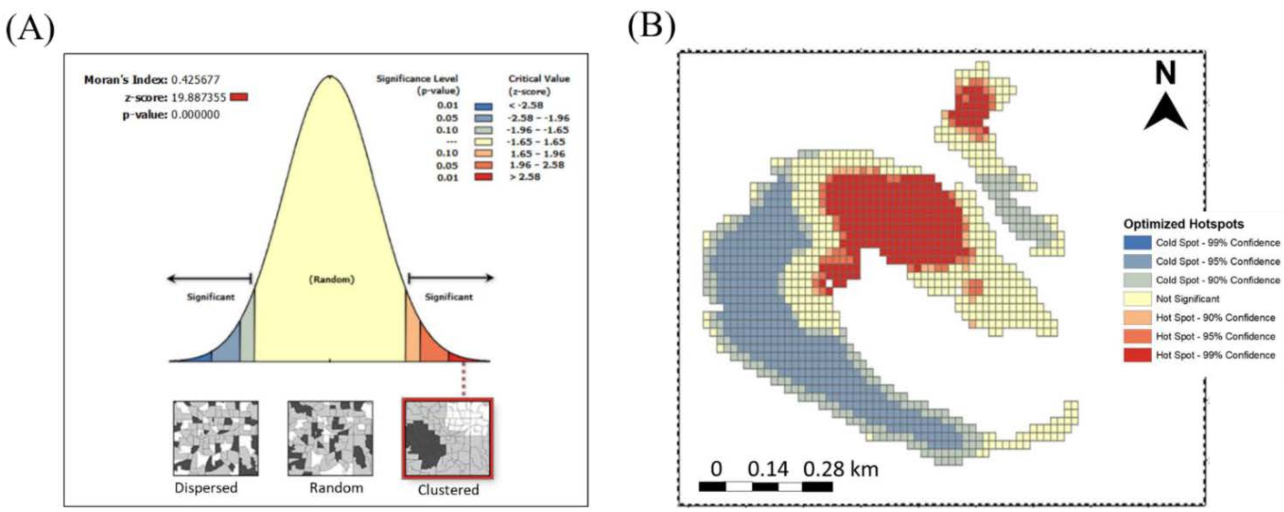

Figure 3.4. Spatial analysis of gaps at uMhlathuze showing (A) patterns of hot and cold spots (B) spatial autocorrelation of distribution patterns. For statistically significant hotspots, a larger z-score within the range of confidence level bins (Gi_bins) > 1 (90% confidence level), > 2 (95% confidence level), or > 3 (99% confidence level) indicates a more intense clustering of high values (hotspot), while clustering for features with 0 for the Gi_bin field is not statistically significant. Conversely, for statistically significant coldspots, a smaller z-score within the range of G_bin > -1 (90% confidence level), > -2 (95% confidence level), or > -3 (99% confidence level) signifies a more intense clustering of low values (cold spot). Additionally, when examining spatial autocorrelation patterns, a z-score above +1.96 falls within the range of statistically significant clustering, while a z-score below -1.96 falls within the range of statistically significant dispersed. Values that falls within -1.65 to +1.65 is not significant. The graph was obtained using ArcMap 10.5 (ArcGIS, 2016).

The Emerging Hot Spot Analysis conducted at uMhlathuze revealed significant sporadic spatio-temporal patterns (Figure 3.5). In addition to the dominant sporadic hot spots, we also observed small isolated clusters of new and consecutive hot spots at the 150 m neighborhood distance (Figure 3.5A). Concerning the small isolated clusters, neighborhood distances of 200, 350, and 400 m exclusively displayed new hot spots (Figures 3.5B, 3.5C, 3.5D).

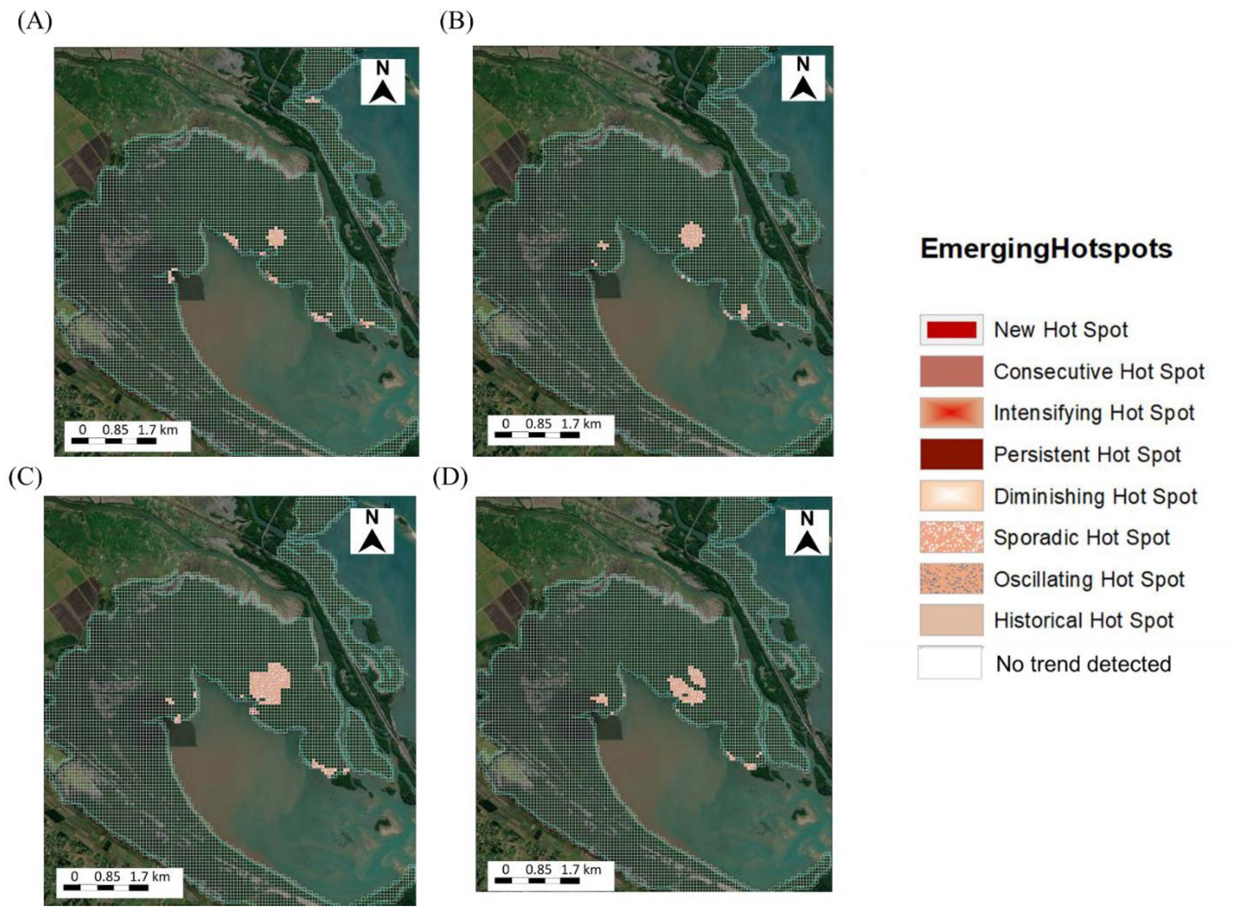

Figure 3.5. Results of the Emerging Hot Spot Analysis (EHSA; Harris et al., 2017), conducted within ArcGIS (ArcGIS 2016) for uMhlathuze. We used a 50 m bin size and distinct neighborhood distances of (A) 150 m (B) 200m (C) 350m (D) 400m with time interval of a year. Each bin (here visualized as cells) 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 were no significant trend were detected ($p > 0.05$ and z-score = 0). The satellite image used as background was obtained from ESRI South Africa (2021).

A clear relationship between canopy height and canopy gap distribution could be observed for both sites (see Figure 3.6A and 3.6B for uMhlathuze and Beachwood respectively); a higher percentage of grid cells with great canopy height was observed in areas where gaps formed, compared to the whole area (see Figure 3.6C and 3.6D for uMhlathuze and Beachwood respectively).

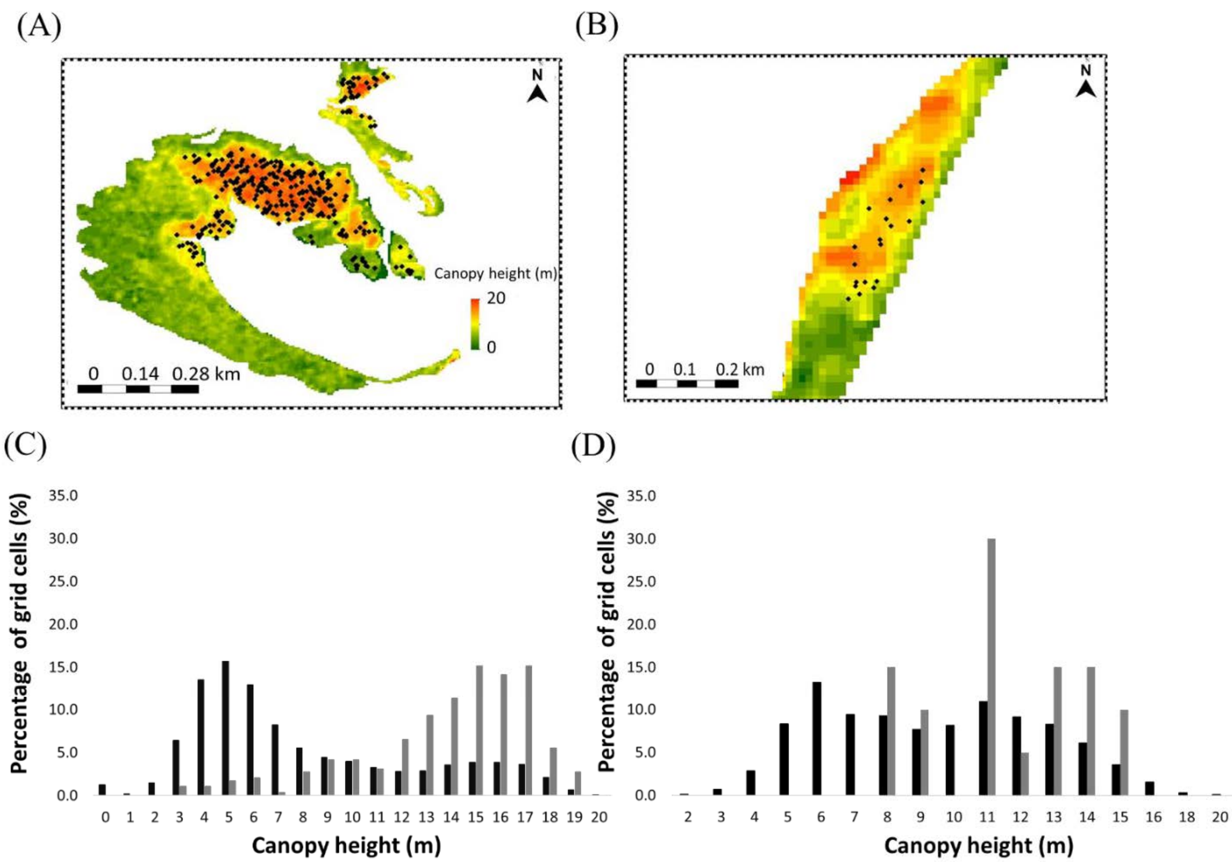

Figure 3.6. Canopy heights of gaps locations at (A) uMhlathuze (B) Beachwood mangroves, and bar graphs depicting the percentage of grid cells with inferred canopy heights at (C) uMhlathuze (B) Beachwood. Black bars represent the elevations corresponding to canopy height of all trees, grey bars represent the canopy height where gaps formed. The canopy gaps locations are indicated by squares. Graphs were obtained using Arcmap 10.5 (ArcGIS, 2016) and Microsoft (2013).

We could not detect a clear relationship between the number of gaps per day and average daily temperature (minimum or maximum) or average daily rainfall for uMhlathuze (Figure 3.7A and 3.7C respectively) or Beachwood (Figure 3.7B and 3.7D respectively).

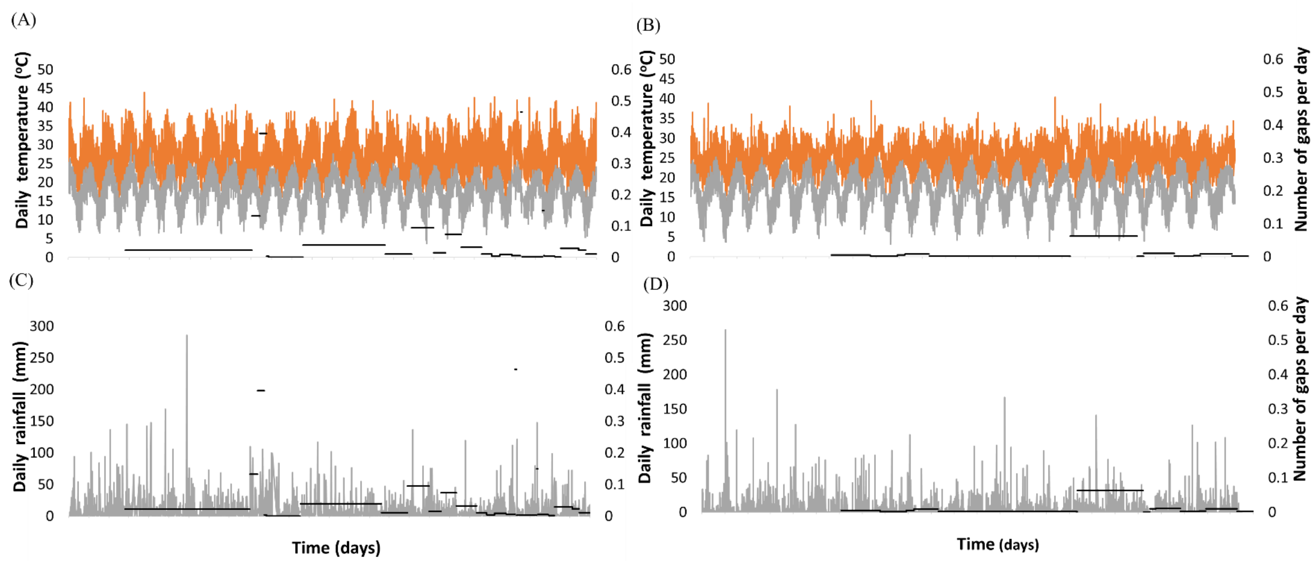

Figure 3.7. Number of canopy gaps per day, computed as the number of newly formed canopy gaps on a satellite image divided by the number of days between the next satellite image in relation with i) daily minimum (orange line) and maximum (grey line) temperatures (source: South African Weather Service) for uMhlathuze between 1995 and 2020 (A) and Beachwood between 1995 and 2018 (B), and ii) daily rainfall (grey line) at uMhlathuze between 1995 and 2020 (C) and Beachwood between 1995 and 2018 (D). Graphs were prepared using Microsoft Excel (Microsoft, 2013).

About 75% of the canopy gaps in uMhlathuze remained open beyond 8,000 days (i.e., at least 23 years; Figure 3.8A and Figure S3.1), while none of the canopy gaps in Beachwood had closed over the time span covered by our study (i.e., gaps remained open for at least18 years; Figure 3.8B; and Figure S3.2).

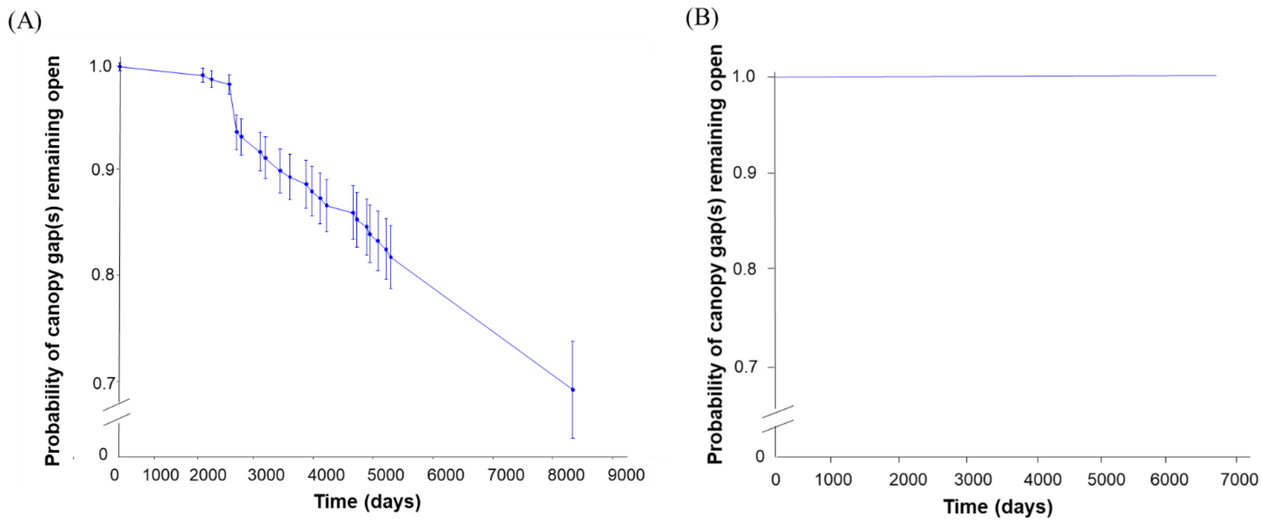

Figure 3.8. Kaplan Meier curves showing the estimated time for gap closure in (A) uMhlathuze (B) Beachwood. The lines indicate the probabilities of canopy gap(s) remaining open; the indicate dot indicate the median and the bars show the standard errors. The estimates were performed using the survival package R version 3.5-7 (Therneau 2023) and the graphs plotted using ggplot2 (Wickham 2016).

3.5 Discussion

3.4.1 Spatial and temporal patterns of mangrove canopy gaps in the two study sites

Our spatial analyses showed a significant clustered pattern for the canopy gaps in uMhlathuze, while the spatial pattern in Beachwood was not significantly different from a random distribution. Nonetheless, a visual inspection of the gap distribution in relation to the canopy height shows that gaps in Beachwood are concentrated in the regions with tall trees, as observed in uMhlathuze, and are therefore clustered in some areas in the mangrove forest.

The Emerging Hot Spot Analysis revealed a temporally sporadic hot spot pattern that we interpret as a clustered pattern. By contrast, isolated new and consecutive hot spots were observed at different neigbouring distances, requiring further investigation.

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 (see Figure 5) does not seem to exhibit a temporal pattern distinct from that in uMhlathuze. We, therefore, will discuss the temporal dynamics of canopy gaps in light of the results obtained for uMhlathuze.

3.4.2 Potential causal agents of gap formation based on conceptual predictions

The spatially clustered pattern observed in uMhlathuze, and the sporadic temporal hot spot do not help supporting or rejecting any of our hypotheses. According to our conceptual scheme, this would require incorporating additional parameters beyond spatiotemporal patterns of gap formation or closure.

In Beachwood, the spatial distribution did not significantly differ from a random pattern, and the distribution of number of new gaps per day would suggest a random temporal pattern, both coinciding with the predictions we made for various potential causal agents. The lack of relationship between minimum and maximum average daily temperatures and average daily rainfall and the temporal distribution of canopy gap formation allows to reject weather conditions as potential causal agent. By contrast, the strong relation observed between the spatial canopy gap distribution and the canopy height in both uMhlathuze and Beachwood suggest lightning strikes as a highly probable causal agent of canopy gap formation at the local scale. The sporadic temporal distribution of canopy gap observed in uMhlathuze also aligns with this interpretation. Indeed, lightning is characterized by its sporadic and unpredictable occurrence during storm events (Yanoviak et al. 2017, Gora et al.2021). It tends to deliver multiple strokes in microseconds, but some continuing current strokes persist for hundreds of seconds at various locations and frequencies, potentially initiating forest fires and causing damage to the largest trees within a given forest patch (Yanoviak et al. 2017, Gora et al. 2021). Various studies have already mentioned lightning strikes as a possible causative agent, when observing clustered canopy gaps in mangrove forests from the Dominican Republic (Sherman et al. 2000) or in tropical terrestrial forests (Yanoviak et al. 2020, Gora et al. 2020).

Our results demonstrated that the majority of canopy gaps at uMhlathuze and Beachwood were established in mangrove stands with high canopies, which is in line with the assumption that taller trees would be more prone to gap formation, if lighting strikes were the driver (Outcalt, 2008, Gora et al. 2020). 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 (Gora et al. 2021, Outcalt 2008, for pine trees in South Califormia, and Yanoviak et al. 2020, for a tropical forest in Panama).

Nonetheless, the close proximity of canopy gaps to each other (Figures 3 and 4), i.e., their spatially clustered appearance, could indicate a locally small-scale resource depletion, potentially due to high plant density, high biomass (tall trees) or differences in microhabitat characteristics, rendering competition and resource depletion potential causal agents. Indeed, canopy height is a digital surface model derived from remote sensing, that could either indicate a difference in tree tallness or differences in the topography. Should the canopy height be due to a change in topography rather than tree tallness, then indeed, environmental conditions in those areas would differ from the neighboring forest and might be the driver of physiological stress for the trees. However, even in this case, the greater canopy height would potentially result in higher lightning strike rates. Further data, like onsite measurements or LIDAR data would help clarifying the potential drivers of changes in canopy height and thereby the potential causal agent of canopy gaps.

A clustered spatial pattern could also suggest the influence of insect and/or pathogen attacks, the relationship observed with canopy height tends to suggest the likelihood of this potential causal agent. For instance, Osorio et al. (2016, 2017) have documented the impact of insect and pathogen attacks on South African mangroves, with *Avicennia marina* predominantly affected by branch and stem cankers, wood-boring insects or leaf galls, resulting in die-back in uMhlathuze. They proposed that the insect and pathogen attack may have been triggered by a previous lightning strike event, which could explain the infestation of weakened trees by insects or pathogens, ultimately leading to the major die-back of the mangrove trees and the clustered canopy gaps observed in this study. In Beachwood, Demetriades (2009) and Osorio et al. (2016) documented that *Bruguiera gymnorhiza* was more strongly affected by lightning strikes than *A. marina*, suggesting that also susceptibility to insect or pathogen attack may vary among different mangrove species. Accordingly, the distribution of canopy gaps would potentially follow the distribution of a given species in a mixed forest. The species composition of mangroves in these stands highlights the tolerance of these species to withstand physiological stress caused by injuries, physical damages from lightning strikes, as well as attacks from insects and pathogens. Further investigations should be conducted to validate this observation.

Finally, we cannot exclude that the distinct causal agents discussed here above may also act in parallel or even synergistically. Lightning strikes, storms, droughts, and elevated temperatures, can indeed cause physical damage and weaken tree defenses (Allen et al. 2010), making them susceptible to opportunistic attacks by insects or pathogens (Feller and McKee 1999, 2002, Sousa et al. 2003, Boyd et al. 2013, Linnakoski and Forbes, 2019). Sousa et al. (2003) suggested that a presumed lightning event in Panama triggered opportunistic beetle infestation that killed mangrove saplings in canopy gaps. Similarly, Parlato et al. (2020) found that the abundance of beetle holes on the trunks of tropical trees increased with increasing crown-die back of lightning-damaged trees. Deciphering the causal agent(s) of canopy gaps in mangrove forests at the local scale, based on their spatial and temporal distributions, remains difficult and requires further investigation, including field studies, taking advantage of region- and species-specific additional information, such as data related to the topography, the tidal conditions or in-situ measurements of physico-chemical conditions in the sediments and health status of trees.

3.5.3 Reassessment of the "canopy gaps as core for mangrove regeneration" hypothesis

The majority of the gaps observed at both uMthlathuze and Beachwood had not closed (or are not predicted to do so) over the time spans covered by our study. This finding is in stark contrast with the observations of Amir (2012) and 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 1977, 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 years (Paijmans and Rollet 1977). A gap longevity of eight to 16 years and 15 to 19 years, 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 years in the Australian Moreton Bay mangroves. Our findings demonstrate a very slow, if any, regeneration and gap closure in uMhlathuze (Figure 3.8A, Figure S3.1) and no gap closure since their initial formation in Beachwood (Figure 3.8B, Figure S3.2). Data on growth rates suggests that *Avicennia marina* and *Bruguiera gymnorhiza* reach maximum tallness after 12 years and 8 years, respectively, in South Africa and Kenya (Bosire et al. 2006, Rajkaran and Adams 2012). Accordingly, we would expect to observe gap closure after 12 years and 8 years, respectively, provided that seedlings are reaching and establishing inside the canopy gaps shortly after gap formation – or even faster as seedlings, sapling and seedlings would benefit from not being shaded during early life stages. The reasons for the lack of gap closure and lack of signs of regeneration at our two study sites are not clear and require further in situ investigation, looking at seedling availability, environmental characteristics (tidal conditions and sediment physico-chemical conditions) or biotic factors (herbivory pressure, pathogens, and competition).

3.6 Conclusion

Our results have far-reaching implications for the management of mangrove forests in South Africa. Our results show clustered spatiotemporal patterns at uMhlathuze. Beachwood canopy gaps primarily exhibited random patterns with some spatial clustering, along with random temporal patterns. The spatial and temporal dynamics of canopy gap formation and closure observed at uMhlathuze and Beachwood support the hypothesis that lightning strikes, insect or pathogen attacks and/or competition could potentially drive canopy gap formation. We found evidence for taller trees being more susceptible to acting as the core of canopy gap formation. Contrary to evidence indicating that canopy gaps facilitate mangrove regeneration in relatively short time, our results show that many of the gaps remained open for at least 23 years at uMhlathuze, and none of the gaps at Beachwood had closed since their initial formation at least 18 years before. These results highlight the urgent need for human intervention to reforest canopy gaps in areas where natural regeneration appears slow. Overall, drivers of gap formation and potential consequences for mangrove forest dynamics differ regionally and warrant future in-depth studies.

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3.9 Supplementary material

Appendix S3.1

This dataset contain information on the status of canopy gaps sizes at uMhlathuze and Beachwood sites, along with unique their identifiers, date of satellite image acquisition, and sources.

Gap ID	Site	Status	Longitude	Latitude	Gap size [m²]	Date	Source
UW1	uMhlathuze	Closed	32.01	-28.81	506.9	2004-01-12	Maxar
UW2	uMhlathuze	Closed	32.00	-28.81	270.34	2004-06-04	Maxar
UW3	uMhlathuze	Closed	32.00	-28.81	235.03	2004-06-04	Maxar
UW4	uMhlathuze	Closed	32.01	-28.81	769.35	2004-06-04	Maxar
UW5	uMhlathuze	Closed	32.01	-28.81	500.44	2004-06-04	Maxar
UW6	uMhlathuze	Closed	32.01	-28.81	201.41	2004-06-04	Maxar
UW7	uMhlathuze	Closed	32.02	-28.81	593.6	2004-06-04	Maxar
UW8	uMhlathuze	Closed	32.02	-28.81	236.1	2004-06-04	Maxar
UW9	uMhlathuze	Closed	32.02	-28.81	442.14	2004-10-03	Maxar
UW10	uMhlathuze	Closed	32.02	-28.82	188.57	2004-06-04	Maxar
UW11	uMhlathuze	Closed	32.02	-28.82	200.54	2004-06-04	Maxar
UW12	uMhlathuze	Closed	32.02	-28.82	293.53	2004-06-04	Maxar
UW13	uMhlathuze	Closed	32.02	-28.82	236.21	2004-06-04	Maxar
UW14	uMhlathuze	Closed	32.02	-28.82	336.22	2004-06-04	Maxar
UW15	uMhlathuze	Closed	32.01	-28.82	426.09	2004-06-04	Maxar
UW16	uMhlathuze	Closed	32.01	-28.82	614.37	2004-06-04	Maxar
UW17	uMhlathuze	Closed	32.01	-28.82	229.16	2004-01-12	Maxar
UW18	uMhlathuze	Closed	32.01	-28.82	212	2004-06-04	Maxar
UW19	uMhlathuze	Closed	32.01	-28.82	210.52	2004-06-04	Maxar
UW20	uMhlathuze	Closed	32.01	-28.81	215.67	2004-06-04	Maxar
UW21	uMhlathuze	Recov-ering	32.01	-28.82	506.9	2010-08-05	Maxar

UW22	uMhlathuze	Recov-ering	32.01	-28.82	870	2011-11-21	Maxar
UW23	uMhlathuze	Open	32.01	-28.82	235.03	2014-05-03	Maxar
UW24	uMhlathuze	Open	32.01	-28.82	569.93	2018-12-06	Maxar
UW25	uMhlathuze	Open	32.00	-28.82	500.55	2017-04-05	Maxar
UW26	uMhlathuze	Open	32.01	-28.82	201.41	2018-12-06	Maxar
UW27	uMhlathuze	Open	32.01	-28.82	1593.6	2010-08-05	Maxar
UW28	uMhlathuze	Open	32.01	-28.82	2236.1	2013-07-27	CSIR Aerial Photograph
UW29	uMhlathuze	Recov-ering	32.00	-28.82	442.14	2004-01-12	Maxar
UW30	uMhlathuze	Recov-ering	32.00	-28.82	2088.57	2010-08-05	Maxar
UW31	uMhlathuze	Open	32.01	-28.82	200.54	2018-05-06	CSIR Aerial Photograph
UW32	uMhlathuze	Open	32.01	-28.82	293.53	2010-08-05	Maxar
UW33	uMhlathuze	Open	32.01	-28.83	236.21	2013-07-27	CSIR Aerial Photograph
UW34	uMhlathuze	Open	32.00	-28.83	1036.22	2019-06-05	Maxar
UW35	uMhlathuze	Open	32.00	-28.82	826.09	2010-08-05	Maxar
UW36	uMhlathuze	Open	32.00	-28.82	614.37	2010-08-05	Maxar
UW37	uMhlathuze	Open	32.00	-28.82	229.16	2004-06-04	Maxar
UW38	uMhlathuze	Open	32.00	-28.83	1912	2016-03-27	Maxar
UW39	uMhlathuze	Open	32.00	-28.83	1210.52	2006-07-21	CSIR Aerial Photograph
UW40	uMhlathuze	Open	32.00	-28.83	2215.67	2006-07-21	CSIR Aerial Photograph
UW41	uMhlathuze	Open	32.00	-28.83	240.06	2010-08-05	Maxar
UW42	uMhlathuze	Open	32.00	-28.83	883.62	2004-01-12	Maxar
UW43	uMhlathuze	Open	32.00	-28.83	1072.2	2004-01-12	Maxar
UW44	uMhlathuze	Open	32.00	-28.83	220.76	2013-07-27	CSIR Aerial Photograph
UW45	uMhlathuze	Open	32.00	-28.83	411.02	2004-06-04	Maxar
UW46	uMhlathuze	Open	32.00	-28.83	176.93	2004-01-12	Maxar
UW47	uMhlathuze	Open	32.00	-28.83	261.99	2004-01-12	Maxar
UW48	uMhlathuze	Open	32.00	-28.83	136.55	2004-01-12	Maxar
UW49	uMhlathuze	Open	32.01	-28.82	176.14	2015-11-06	Maxar

UW50	uMhlathuze	Open	32.01	-28.82	162.05	2011-11-21	Maxar
UW51	uMhlathuze	Open	32.01	-28.82	366.99	2010-08-05	Maxar
UW52	uMhlathuze	Open	32.01	-28.82	263.78	2004-06-04	Maxar
UW53	uMhlathuze	Open	32.01	-28.82	130.43	2004-06-04	Maxar
UW54	uMhlathuze	Open	32.01	-28.82	326.19	2004-06-04	Maxar
UW55	uMhlathuze	Open	32.01	-28.82	614.49	2004-06-04	Maxar
UW56	uMhlathuze	Open	32.01	-28.82	395.21	2004-01-12	Maxar
UW57	uMhlathuze	Open	32.01	-28.82	245.24	2004-01-12	Maxar
UW58	uMhlathuze	Open	32.01	-28.82	158.24	2010-08-05	Maxar
UW59	uMhlathuze	Open	32.01	-28.82	341.85	2006-07-21	CSIR Aerial Photograph
UW60	uMhlathuze	Open	32.02	-28.82	326.84	2006-07-21	CSIR Aerial Photograph
UW61	uMhlathuze	Open	32.02	-28.82	183.67	2004-06-04	Maxar
UW62	uMhlathuze	Open	32.02	-28.82	317.46	2004-06-04	Maxar
UW63	uMhlathuze	Open	32.02	-28.81	250.87	2004-06-04	Maxar
UW64	uMhlathuze	Open	32.02	-28.82	277.4	2010-08-05	Maxar
UW65	uMhlathuze	Open	32.02	-28.81	165.03	2011-11-21	Maxar
UW66	uMhlathuze	Open	32.02	-28.81	800.3	2017-04-05	Maxar
UW67	uMhlathuze	Open	32.02	-28.81	945.2	2018-12-06	CNES/AIRBUS
UW68	uMhlathuze	Open	32.02	-28.82	796.08	2013-07-27	CSIR Aerial Photograph
UW69	uMhlathuze	Open	32.02	-28.82	196.25	2011-11-21	Maxar
UW70	uMhlathuze	Open	32.02	-28.82	383.64	2018-05-06	CSIR Aerial Photograph
UW71	uMhlathuze	Open	32.02	-28.82	178.36	2011-11-21	Maxar
UW72	uMhlathuze	Open	32.02	-28.82	237.36	2017-04-05	Maxar
UW73	uMhlathuze	Open	32.02	-28.82	762.21	2011-11-21	Maxar
UW74	uMhlathuze	Open	32.02	-28.82	327.54	2017-04-05	Maxar
UW75	uMhlathuze	Open	32.02	-28.82	330.29	2017-04-05	Maxar
UW76	uMhlathuze	Open	32.02	-28.82	799.32	2017-04-05	Maxar
UW77	uMhlathuze	Open	32.02	-28.82	286.18	2018-05-06	CSIR Aerial Photograph
UW78	uMhlathuze	Open	32.02	-28.82	2058.52	2011-11-21	Maxar
UW79	uMhlathuze	Open	32.02	-28.82	409.85	2014-05-03	Maxar
UW80	uMhlathuze	Open	32.02	-28.82	346.88	2011-11-21	Maxar

UW81	uMhlathuze	Open	32.02	-28.82	493.09	2014-05-03	Maxar
UW82	uMhlathuze	Open	32.02	-28.82	317.94	2011-11-21	Maxar
UW83	uMhlathuze	Open	32.02	-28.82	1098.72	2011-11-21	Maxar
UW84	uMhlathuze	Open	32.02	-28.82	320.3	2017-04-05	Maxar
UW85	uMhlathuze	Open	32.02	-28.82	117.38	2004-06-04	Maxar
UW86	uMhlathuze	Open	32.02	-28.82	119.88	2004-06-04	Maxar
UW87	uMhlathuze	Open	32.02	-28.82	151.13	2011-11-21	Maxar
UW88	uMhlathuze	Open	32.02	-28.82	438.48	2004-06-04	Maxar
UW89	uMhlathuze	Open	32.02	-28.82	229.91	2011-11-21	Maxar
UW90	uMhlathuze	Open	32.02	-28.82	272.32	2010-08-05	Maxar
UW91	uMhlathuze	Open	32.02	-28.82	959.29	2014-05-03	Maxar
UW92	uMhlathuze	Open	32.02	-28.82	1769.53	2011-11-21	Maxar
UW93	uMhlathuze	Open	32.02	-28.82	394.73	2011-11-21	Maxar
UW94	uMhlathuze	Open	32.02	-28.82	251.19	2006-07-21	CSIR Aerial Photograph
UW95	uMhlathuze	Open	32.02	-28.82	362.46	2004-06-04	Maxar
UW96	uMhlathuze	Open	32.02	-28.82	378.97	2020-06-22	Maxar
UW97	uMhlathuze	Open	32.02	-28.82	106.96	2020-06-22	Maxar
UW98	uMhlathuze	Open	32.02	-28.82	178.77	2020-02-12	Maxar
UW99	uMhlathuze	Open	32.02	-28.82	244.29	2020-02-12	Maxar
UW100	uMhlathuze	Open	32.02	-28.82	159.61	2016-10-27	Maxar
UW101	uMhlathuze	Open	32.01	-28.82	123.5	2017-05-03	Maxar
UW102	uMhlathuze	Open	32.01	-28.82	538.87	2015-05-05	Maxar
UW103	uMhlathuze	Open	32.01	-28.82	231.56	2012-12-22	Maxar
UW104	uMhlathuze	Open	32.01	-28.82	1021.6	2013-07-27	CSIR Aerial Photograph
UW105	uMhlathuze	Open	32.01	-28.82	263.71	2013-07-27	CSIR Aerial Photograph
UW106	uMhlathuze	Open	32.01	-28.82	523.05	2006-07-21	CSIR Aerial Photograph
UW107	uMhlathuze	Open	32.02	-28.82	174.1	2004-06-04	Maxar
UW108	uMhlathuze	Open	32.01	-28.82	185.47	2015-05-05	Maxar
UW109	uMhlathuze	Open	32.01	-28.82	224.1	2013-07-27	CSIR Aerial Photograph
UW110	uMhlathuze	Open	32.01	-28.82	229.7	2010-08-05	Maxar
UW111	uMhlathuze	Open	32.01	-28.82	518.79	2020-06-22	Maxar

UW112	uMhlathuze	Open	32.01	-28.82	201.7	2004-11-12	Maxar
UW113	uMhlathuze	Open	32.01	-28.82	2256.41	2014-05-03	Maxar
UW114	uMhlathuze	Open	32.01	-28.82	1001.73	2013-07-27	CSIR Aerial Photograph
UW115	uMhlathuze	Open	32.01	-28.82	132.19	2011-11-21	Maxar
UW116	uMhlathuze	Open	32.01	-28.82	173.68	2004-01-12	Maxar
UW117	uMhlathuze	Open	32.01	-28.82	240.77	2011-11-21	Maxar
UW118	uMhlathuze	Open	32.01	-28.82	641.62	2011-11-21	Maxar
UW119	uMhlathuze	Open	32.01	-28.82	499.74	2010-08-05	Maxar
UW120	uMhlathuze	Open	32.01	-28.82	932.38	2011-11-21	Maxar
UW121	uMhlathuze	Open	32.01	-28.82	254.33	2014-05-03	Maxar
UW122	uMhlathuze	Open	32.01	-28.82	244.68	2013-07-27	CSIR Aerial Photograph
UW123	uMhlathuze	Open	32.01	-28.82	1231.52	2004-01-12	Maxar
UW124	uMhlathuze	Open	32.01	-28.82	149.05	2010-08-05	Maxar
UW125	uMhlathuze	Open	32.01	-28.81	108.16	2004-06-04	Maxar
UW126	uMhlathuze	Open	32.01	-28.81	795.3	2004-01-12	Maxar
UW127	uMhlathuze	Open	32.01	-28.81	168.72	2004-01-12	Maxar
UW128	uMhlathuze	Open	32.01	-28.81	338.47	2004-01-12	Maxar
UW129	uMhlathuze	Open	32.01	-28.81	149.46	2004-01-12	Maxar
UW130	uMhlathuze	Open	32.01	-28.81	144.98	2006-07-21	CSIR Aerial Photograph
UW131	uMhlathuze	Open	32.01	-28.81	298.34	2013-07-27	CSIR Aerial Photograph
UW132	uMhlathuze	Open	32.01	-28.81	194.71	2004-01-12	Maxar
UW133	uMhlathuze	Open	32.01	-28.81	419.08	2004-01-12	Maxar
UW134	uMhlathuze	Open	32.01	-28.81	182.93	2004-01-12	Maxar
UW135	uMhlathuze	Open	32.01	-28.81	214.44	2010-08-05	Maxar
UW136	uMhlathuze	Open	32.01	-28.81	374.47	2017-04-05	Maxar
UW137	uMhlathuze	Open	32.01	-28.81	341.98	2011-11-21	Maxar
UW138	uMhlathuze	Open	32.01	-28.81	313.19	2004-06-04	Maxar
UW139	uMhlathuze	Open	32.01	-28.81	698.39	2006-07-21	CSIR Aerial Photograph
UW140	uMhlathuze	Open	32.02	-28.81	1084.19	2004-06-04	Maxar
UW141	uMhlathuze	Open	32.01	-28.81	1771.09	2020-06-22	Maxar
UW142	uMhlathuze	Open	32.01	-28.81	241.67	2004-06-04	Maxar

UW143	uMhlathuze	Open	32.01	-28.81	134.46	2010-08-05	Maxar
UW144	uMhlathuze	Open	32.01	-28.81	1088.22	2004-06-04	Maxar
UW145	uMhlathuze	Open	32.01	-28.81	1162.7	2006-07-21	CSIR Aerial Photograph
UW146	uMhlathuze	Open	32.02	-28.81	863.94	2017-04-05	Maxar
UW147	uMhlathuze	Open	32.02	-28.81	986.13	2017-04-05	Maxar
UW148	uMhlathuze	Open	32.02	-28.81	102.42	2011-11-21	Maxar
UW149	uMhlathuze	Open	32.02	-28.83	599.46	2011-11-21	Maxar
UW150	uMhlathuze	Open	32.02	-28.83	793.7	2019-06-05	Maxar
UW151	uMhlathuze	Open	32.02	-28.82	202.31	2018-05-06	CSIR Aerial Photograph
UW152	uMhlathuze	Open	32.02	-28.82	198.67	2011-11-21	Maxar
UW153	uMhlathuze	Open	32.02	-28.82	124.48	2011-11-21	Maxar
UW154	uMhlathuze	Open	32.02	-28.82	1688.58	2011-11-21	Maxar
UW155	uMhlathuze	Open	32.02	-28.82	147.02	2011-11-21	Maxar
UW156	uMhlathuze	Open	32.03	-28.82	2239.05	2019-03-29	Maxar
UW157	uMhlathuze	Open	32.03	-28.82	295.27	2011-11-21	Maxar
UW158	uMhlathuze	Open	32.03	-28.82	1087	2011-11-21	Maxar
UW159	uMhlathuze	Open	32.03	-28.82	697.26	2013-07-27	CSIR Aerial Photograph
UW160	uMhlathuze	Open	32.03	-28.82	1449.35	2014-05-03	Maxar
UW161	uMhlathuze	Open	32.03	-28.82	1873.29	2017-04-05	Maxar
UW162	uMhlathuze	Open	32.02	-28.83	233.98	2014-05-03	Maxar
UW163	uMhlathuze	Open	32.03	-28.83	686.21	2011-11-21	Maxar
UW164	uMhlathuze	Open	32.03	-28.83	560.96	2013-07-27	CSIR Aerial Photograph
UW165	uMhlathuze	Open	32.03	-28.83	555.5	2013-07-27	CSIR Aerial Photograph
UW166	uMhlathuze	Open	32.03	-28.83	1895.27	2011-11-21	Maxar
UW167	uMhlathuze	Open	32.03	-28.83	371.23	2011-11-21	Maxar
UW168	uMhlathuze	Open	32.03	-28.83	842.84	2011-11-21	Maxar
UW169	uMhlathuze	Open	32.03	-28.83	2060.79	2012-12-22	Maxar
UW170	uMhlathuze	Open	32.03	-28.83	485.43	2012-12-22	Maxar
UW171	uMhlathuze	Open	32.03	-28.83	802.36	2020-02-12	Maxar
UW172	uMhlathuze	Open	32.03	-28.83	1563.75	2020-06-22	Maxar
UW173	uMhlathuze	Open	32.03	-28.83	162.92	2011-11-21	Maxar

UW174	uMhlathuze	Open	32.03	-28.83	195.35	2004-06-04	Maxar
UW175	uMhlathuze	Open	32.03	-28.83	145.83	2011-11-21	Maxar
UW176	uMhlathuze	Open	32.03	-28.83	343.62	2016-03-27	Maxar
UW177	uMhlathuze	Open	32.03	-28.83	1579.76	2018-12-12	CNES/AIRBUS
UW178	uMhlathuze	Open	32.03	-28.83	686.09	2012-12-22	Maxar
UW179	uMhlathuze	Open	32.03	-28.83	1262.51	2014-05-03	Maxar
UW180	uMhlathuze	Open	32.04	-28.83	1517.89	2015-11-06	Maxar
UW181	uMhlathuze	Open	32.03	-28.83	713.35	2013-07-27	CSIR Aerial Photograph
UW182	uMhlathuze	Open	32.03	-28.83	310.64	2013-07-27	CSIR Aerial Photograph
UW183	uMhlathuze	Open	32.03	-28.80	255.79	2004-06-04	NASA
UW184	uMhlathuze	Open	32.03	-28.80	2125.84	2004-06-04	NASA
UW185	uMhlathuze	Open	32.03	-28.80	786.79	2004-06-04	Maxar
UW186	uMhlathuze	Open	32.03	-28.80	1065.07	2012-12-22	Maxar
UW187	uMhlathuze	Open	32.03	-28.80	818.29	2011-11-21	Maxar
UW188	uMhlathuze	Open	32.03	-28.80	676.15	2011-11-21	Maxar
UW189	uMhlathuze	Open	32.03	-28.80	201.38	2011-11-21	Maxar
UW190	uMhlathuze	Open	32.03	-28.80	1074.34	2017-04-05	Maxar
UW191	uMhlathuze	Open	32.03	-28.80	213.22	2011-11-21	Maxar
UW192	uMhlathuze	Open	32.02	-28.80	143.54	2011-11-21	Maxar
UW193	uMhlathuze	Open	32.02	-28.80	1510.1	2012-12-22	Maxar
UW194	uMhlathuze	Open	32.02	-28.80	1615.2	2006-07-21	CSIR Aerial Photograph
UW195	uMhlathuze	Open	32.03	-28.80	108.29	2004-06-04	Maxar
UW196	uMhlathuze	Open	32.02	-28.80	1983.27	2011-11-21	Maxar
UW197	uMhlathuze	Open	32.02	-28.80	2083.27	2011-11-21	Maxar
UW198	uMhlathuze	Recov-ering	32.02	-28.80	394.25	2004-06-04	Maxar
UW199	uMhlathuze	Open	32.03	-28.80	1676.55	2017-04-05	Maxar
UW200	uMhlathuze	Open	32.02	-28.80	785.23	2006-07-21	CSIR Aerial Photograph
UW201	uMhlathuze	Open	32.03	-28.80	823.24	2004-06-04	Maxar
UW202	uMhlathuze	Open	32.03	-28.80	1021.49	2006-07-21	CSIR Aerial Photograph
UW203	uMhlathuze	Open	32.03	-28.80	1271.12	2011-11-21	Maxar

UW204	uMhlathuze	Open	32.02	-28.80	222.09	2004-06-04	Maxar
UW205	uMhlathuze	Open	32.02	-28.80	1843.93	2004-06-04	Maxar
UW206	uMhlathuze	Open	32.02	-28.80	182.24	2011-11-21	Maxar
UW207	uMhlathuze	Open	32.02	-28.80	906.54	2004-06-04	Maxar
UW208	uMhlathuze	Open	32.02	-28.80	704.49	2016-10-27	Maxar
UW209	uMhlathuze	Open	32.02	-28.80	238.61	2013-07-27	CSIR Aerial Photograph
UW210	uMhlathuze	Open	32.02	-28.80	200.94	2004-06-04	Maxar
UW211	uMhlathuze	Open	32.02	-28.80	1978.13	2011-11-21	Maxar
UW212	uMhlathuze	Open	32.02	-28.80	845.26	2011-11-21	Maxar
UW213	uMhlathuze	Open	32.02	-28.80	165.41	2019-03-29	Maxar
UW214	uMhlathuze	Open	32.03	-28.81	778.45	2004-06-04	Maxar
UW215	uMhlathuze	Open	32.03	-28.81	603.88	2016-10-27	Maxar
UW216	uMhlathuze	Open	32.03	-28.81	677.43	2006-07-21	CSIR Aerial Photograph
UW217	uMhlathuze	Open	32.03	-28.81	1914.3	2011-11-21	Maxar
UW218	uMhlathuze	Closed	32.02	-28.82	240.06	2006-07-21	CSIR Aerial Photograph
UW219	uMhlathuze	Closed	32.02	-28.82	183.62	2006-07-21	CSIR Aerial Photograph
UW220	uMhlathuze	Closed	32.01	-28.82	172.2	2004-06-04	Maxar
UW221	uMhlathuze	Closed	32.01	-28.82	220.76	2004-06-04	Maxar
UW222	uMhlathuze	Closed	32.01	-28.82	411.02	2006-07-21	CSIR Aerial Photograph
UW223	uMhlathuze	Closed	32.01	-28.82	1176.93	2006-07-21	CSIR Aerial Photograph
UW224	uMhlathuze	Closed	32.01	-28.82	261.99	2004-06-04	Maxar
UW225	uMhlathuze	Closed	32.00	-28.82	136.55	2006-07-21	CSIR Aerial Photograph
UW226	uMhlathuze	Closed	32.00	-28.82	176.14	2006-07-21	CSIR Aerial Photograph
UW227	uMhlathuze	Open	32.02	-28.82	162.05	2006-07-21	CSIR Aerial Photograph
UW228	uMhlathuze	Closed	32.02	-28.82	366.99	2006-07-21	CSIR Aerial Photograph
UW229	uMhlathuze	Closed	32.02	-28.81	263.78	2004-06-04	Maxar
UW230	uMhlathuze	Closed	32.02	-28.81	130.43	2006-07-21	CSIR Aerial Photograph
UW231	uMhlathuze	Closed	32.02	-28.81	326.19	2004-06-04	Maxar
UW232	uMhlathuze	Closed	32.02	-28.81	614.49	2004-06-04	Maxar
UW233	uMhlathuze	Closed	32.01	-28.81	395.21	1997-10-20	CSIR Aerial photograph
UW234	uMhlathuze	Closed	32.01	-28.81	245.24	1997-10-20	CSIR Aerial photograph

UW235	uMhlathuze	Closed	32.01	-28.81	158.24	1997-10-20	CSIR Aerial photograph
UW236	uMhlathuze	Closed	32.01	-28.81	341.85	1997-10-20	CSIR Aerial photograph
UW237	uMhlathuze	Closed	32.01	-28.81	326.84	1997-10-20	CSIR Aerial photograph
UW238	uMhlathuze	Closed	32.01	-28.81	183.67	1997-10-20	CSIR Aerial photograph
UW239	uMhlathuze	Closed	32.01	-28.81	317.46	1997-10-20	CSIR Aerial photograph
UW240	uMhlathuze	Closed	32.01	-28.81	250.87	1997-10-20	CSIR Aerial photograph
UW241	uMhlathuze	Closed	32.01	-28.81	277.4	1997-10-20	CSIR Aerial photograph
UW242	uMhlathuze	Closed	32.00	-28.81	165.03	1997-10-20	CSIR Aerial photograph
UW243	uMhlathuze	Closed	32.00	-28.81	100.3	1997-10-20	CSIR Aerial photograph
UW244	uMhlathuze	Closed	32.00	-28.81	145.2	1997-10-20	CSIR Aerial photograph
UW245	uMhlathuze	Closed	32.00	-28.81	96.08	1997-10-20	CSIR Aerial photograph
UW246	uMhlathuze	Closed	32.01	-28.81	196.25	1997-10-20	CSIR Aerial photograph
UW247	uMhlathuze	Closed	32.01	-28.81	383.64	1997-10-20	CSIR Aerial photograph
UW248	uMhlathuze	Closed	32.00	-28.81	178.36	1997-10-20	CSIR Aerial photograph
UW249	uMhlathuze	Closed	32.00	-28.82	237.36	1997-10-20	CSIR Aerial photograph
UW250	uMhlathuze	Closed	32.00	-28.81	762.21	1997-10-20	CSIR Aerial photograph
UW251	uMhlathuze	Closed	32.00	-28.82	327.54	1997-10-20	CSIR Aerial photograph
UW252	uMhlathuze	Closed	32.00	-28.82	330.29	1997-10-20	CSIR Aerial photograph
UW253	uMhlathuze	Closed	32.01	-28.82	499.32	1997-10-20	CSIR Aerial photograph
UW254	uMhlathuze	Closed	32.01	-28.82	286.18	1997-10-20	CSIR Aerial photograph
UW255	uMhlathuze	Closed	32.01	-28.82	238.52	1997-10-20	CSIR Aerial photograph
UW256	uMhlathuze	Closed	32.01	-28.81	409.85	1997-10-20	CSIR Aerial photograph
UW257	uMhlathuze	Closed	32.01	-28.81	346.88	1997-10-20	CSIR Aerial photograph
UW258	uMhlathuze	Closed	32.01	-28.81	493.09	1997-10-20	CSIR Aerial photograph
UW259	uMhlathuze	Closed	32.01	-28.81	317.94	1997-10-20	CSIR Aerial photograph
UW260	uMhlathuze	Closed	32.01	-28.81	98.72	1997-10-20	CSIR Aerial photograph
UW261	uMhlathuze	Closed	32.01	-28.82	320.3	1997-10-20	CSIR Aerial photograph
UW262	uMhlathuze	Closed	32.01	-28.82	117.38	1997-10-20	CSIR Aerial photograph
UW263	uMhlathuze	Closed	32.01	-28.82	119.88	1997-10-20	CSIR Aerial photograph
UW264	uMhlathuze	Closed	32.01	-28.81	151.13	1997-10-20	CSIR Aerial photograph
UW265	uMhlathuze	Closed	32.01	-28.81	438.48	1997-10-20	CSIR Aerial photograph

UW266	uMhlathuze	Closed	32.01	-28.82	229.91	1997-10-20	CSIR Aerial photograph
UW267	uMhlathuze	Closed	32.01	-28.82	272.32	1997-10-20	CSIR Aerial photograph
UW268	uMhlathuze	Closed	32.01	-28.82	159.29	1997-10-20	CSIR Aerial photograph
UW269	uMhlathuze	Closed	32.02	-28.82	89.53	1997-10-20	CSIR Aerial photograph
UW270	uMhlathuze	Closed	32.02	-28.81	394.73	1997-10-20	CSIR Aerial photograph
UW271	uMhlathuze	Closed	32.02	-28.82	251.19	1997-10-20	CSIR Aerial photograph
UW272	uMhlathuze	Closed	32.02	-28.82	362.46	1997-10-20	CSIR Aerial photograph
UW273	uMhlathuze	Closed	32.02	-28.82	378.97	1997-10-20	CSIR Aerial photograph
UW274	uMhlathuze	Closed	32.02	-28.82	106.96	1997-10-20	CSIR Aerial photograph
UW275	uMhlathuze	Closed	32.02	-28.82	178.77	1997-10-20	CSIR Aerial photograph
UW276	uMhlathuze	Closed	32.02	-28.82	244.29	1997-10-20	CSIR Aerial photograph
UW277	uMhlathuze	Closed	32.01	-28.82	159.61	1997-10-20	CSIR Aerial photograph
UW278	uMhlathuze	Closed	32.01	-28.82	123.5	1997-10-20	CSIR Aerial photograph
UW279	uMhlathuze	Closed	32.01	-28.82	538.87	1997-10-20	CSIR Aerial photograph
UW280	uMhlathuze	Closed	32.01	-28.82	231.56	1997-10-20	CSIR Aerial photograph
UW281	uMhlathuze	Closed	32.01	-28.82	241.6	1997-10-20	CSIR Aerial photograph
UW282	uMhlathuze	Closed	32.01	-28.82	263.71	1997-10-20	CSIR Aerial photograph
UW283	uMhlathuze	Closed	32.02	-28.82	523.05	1997-10-20	CSIR Aerial photograph
UW284	uMhlathuze	Closed	32.02	-28.82	174.1	1997-10-20	CSIR Aerial photograph
UW285	uMhlathuze	Closed	32.02	-28.82	185.47	1997-10-20	CSIR Aerial photograph
UW286	uMhlathuze	Closed	32.02	-28.82	224.1	1997-10-20	CSIR Aerial photograph
UW287	uMhlathuze	Closed	32.02	-28.82	229.7	1997-10-20	CSIR Aerial photograph
UW288	uMhlathuze	Closed	32.02	-28.82	518.79	1997-10-20	CSIR Aerial photograph
UW289	uMhlathuze	Closed	32.02	-28.82	201.7	1997-10-20	CSIR Aerial photograph
UW290	uMhlathuze	Closed	32.02	-28.82	256.41	1997-10-20	CSIR Aerial photograph
UW291	uMhlathuze	Closed	32.03	-28.82	456.23	1997-10-20	CSIR Aerial photograph
BW1	Beachwood	Open	31.04	-29.80	105.3	2002-10-10	Maxar
BW2	Beachwood	Open	31.04	-29.80	118.2	2016-12-07	Maxar
BW3	Beachwood	Open	31.04	-29.80	133.2	2018-04-18	Maxar
BW4	Beachwood	Open	31.04	-29.80	121.8	2011-04-20	Maxar
BW5	Beachwood	Open	31.04	-29.80	91.2	2011-05-06	Maxar

BW6	Beachwood	Open	31.04	-29.80	140.7	2001-02-02	Maxar
BW7	Beachwood	Open	31.04	-29.80	85.3	2001-02-02	Maxar
BW8	Beachwood	Open	31.04	-29.80	101.9	2016-08-23	Maxar
BW9	Beachwood	Open	31.04	-29.80	170.9	2005-04-19	Maxar
BW10	Beachwood	Open	31.04	-29.80	319.7	2003-12-01	Maxar
BW11	Beachwood	Open	31.04	-29.80	119.1	2014-10-06	Maxar
BW12	Beachwood	Open	31.04	-29.80	180.3	2001-02-02	Maxar
BW13	Beachwood	Open	31.04	-29.80	217.1	2003-12-01	Maxar
BW14	Beachwood	Open	31.04	-29.80	104.2	2004-03-29	Maxar
BW15	Beachwood	Open	31.04	-29.80	101.9	2014-07-01	Maxar
BW16	Beachwood	Open	31.04	-29.80	154.1	2014-03-23	Maxar
BW17	Beachwood	Open	31.04	-29.80	317	2006-04-27	Maxar
BW18	Beachwood	Open	31.04	-29.80	197.1	2015-10-28	Maxar
BW19	Beachwood	Open	31.04	-29.80	163.6	2011-04-20	Maxar
BW20	Beachwood	Open	31.04	-29.80	308.5	2011-04-20	Maxar

Table showing the summary of the canopy gap area, mangrove area and the percentage of the forest in gap phase

Site	Total gap area (m^2)	Total mangrove area (km^2)	Total mangrove area (m^2)	Percentage of forest in gap phase (%)
uMhlathuze	130925.3	11.46	11467615.52	1.1
Beachwood	3251.1	0.74	736786.7	0.4

Appendix S3.2

Table S1. Emerging hotspot analysis classification patterns and definitions (Harris et al. 2017)

Hotspot pattern	Definition
New	A location that is statistically significant hotspot for the most recent time
Consecutive	A location with a single uninterrupted run of statistically significant hotspot bins, comprised of less than 90% statistically hot bins
Intensifying	A location that has been statistically significant for 90% of the time step intervals, and be-coming hotter over time.
Persistent	A location with 90% of the time intervals as hotspots with no trend of decrease or increase.
Diminishing	A location of which 90% of the time intervals are hot and becoming less hot overtime.
Sporadic	A location that is statically significant on again and off again hot.
Oscillating	A location that has some time intervals as hotspot and some intervals as cold spots. Less than 90% of the time intervals have been statistically significant hotspots and none have been sta-tistically significant cold spots.
Historical	A location with at least 90% of the time interval as hotspots but the recent time interval is not hot.

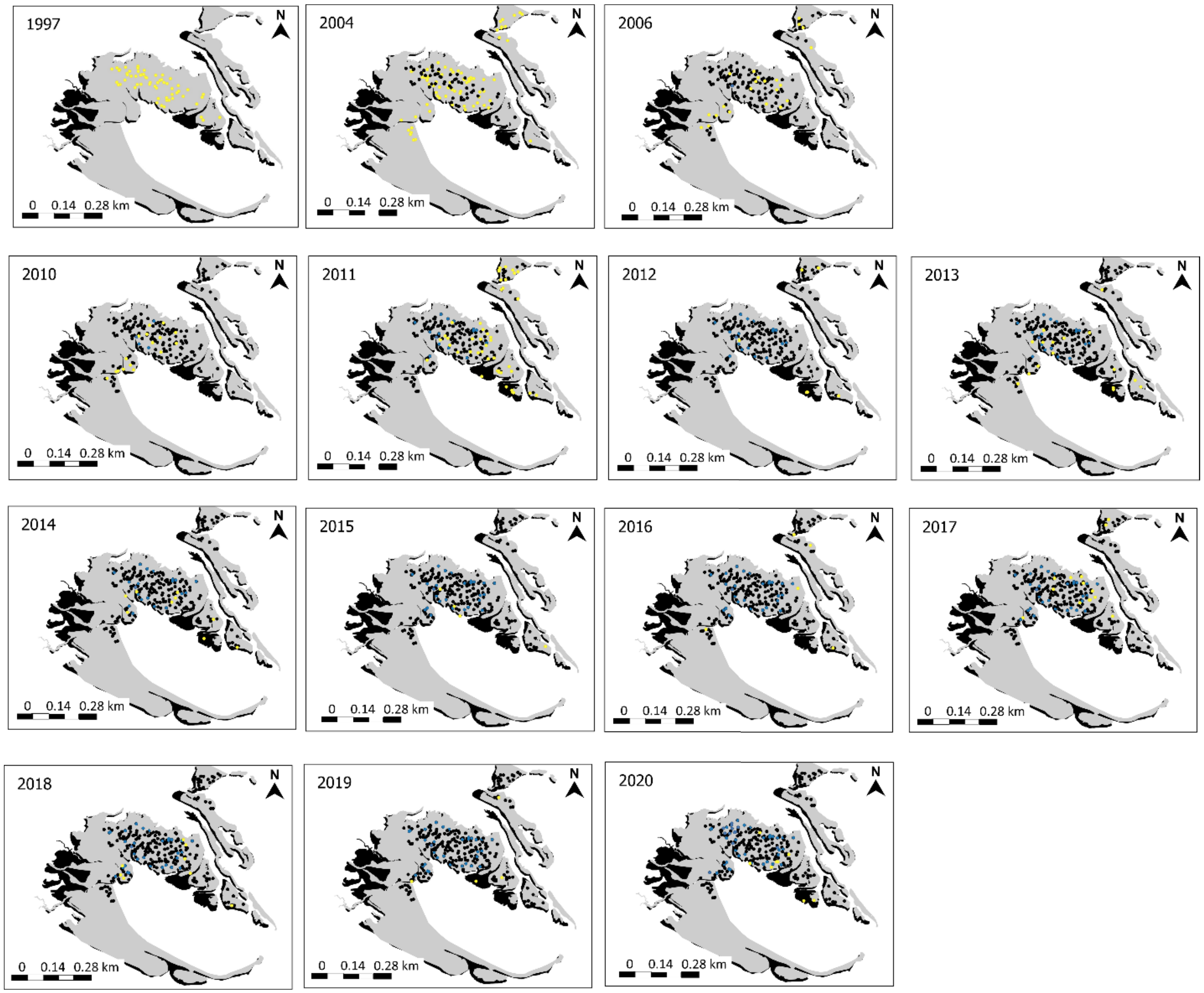

Figure S3.1. Distribution of canopy gaps in mangrove stands of uMhlathuze between 1997 and 2020. Yellow dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and blue dots represent closed gaps. Outline of mangrove patch in grey represents the year 1997, and the outline in black represent the mangrove patch in 2020.

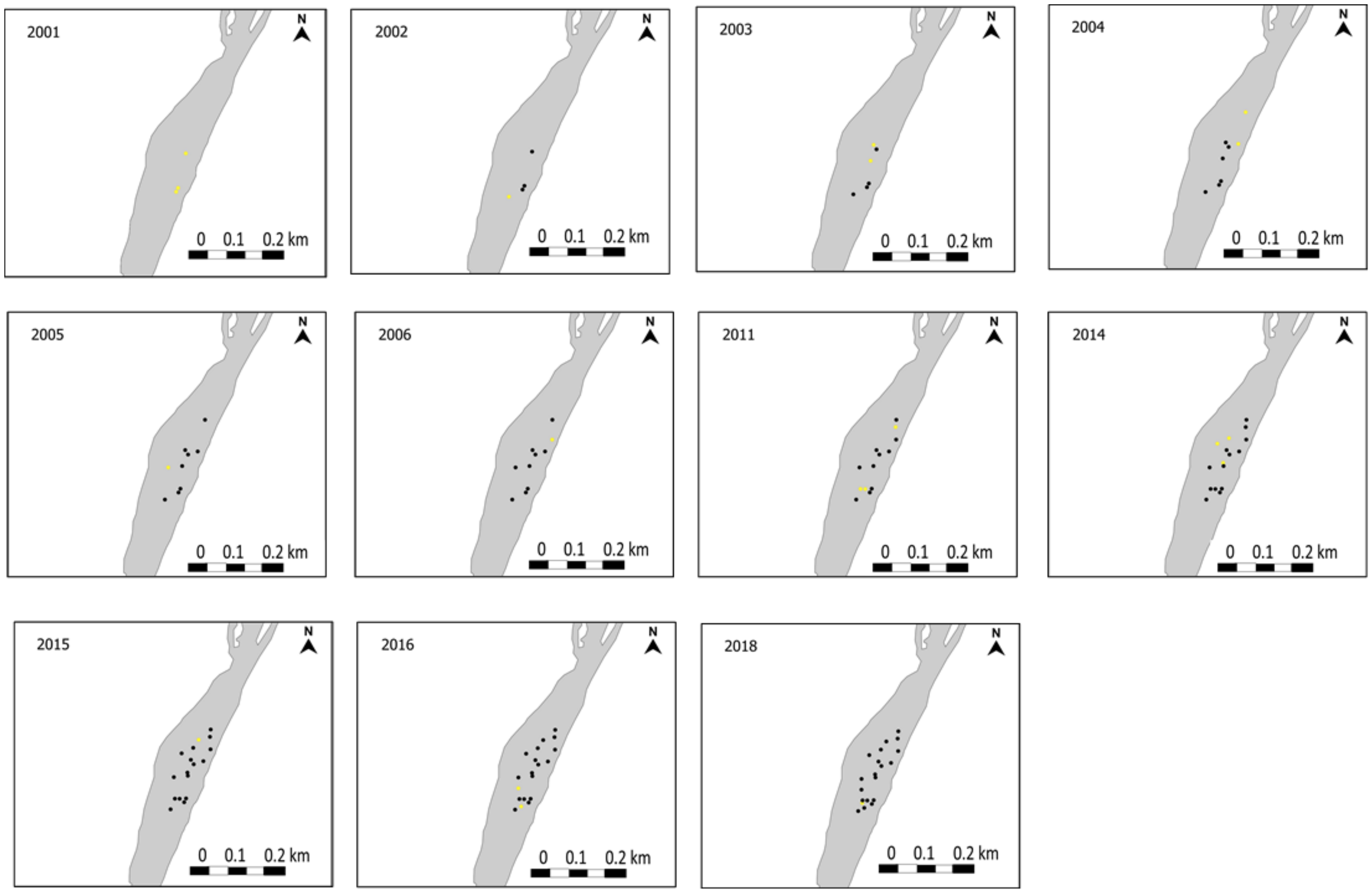

Figure S3.2. Distribution of canopy gaps in the mangrove stand of Beachwood between 2001 and 2018. Yellow dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous year.

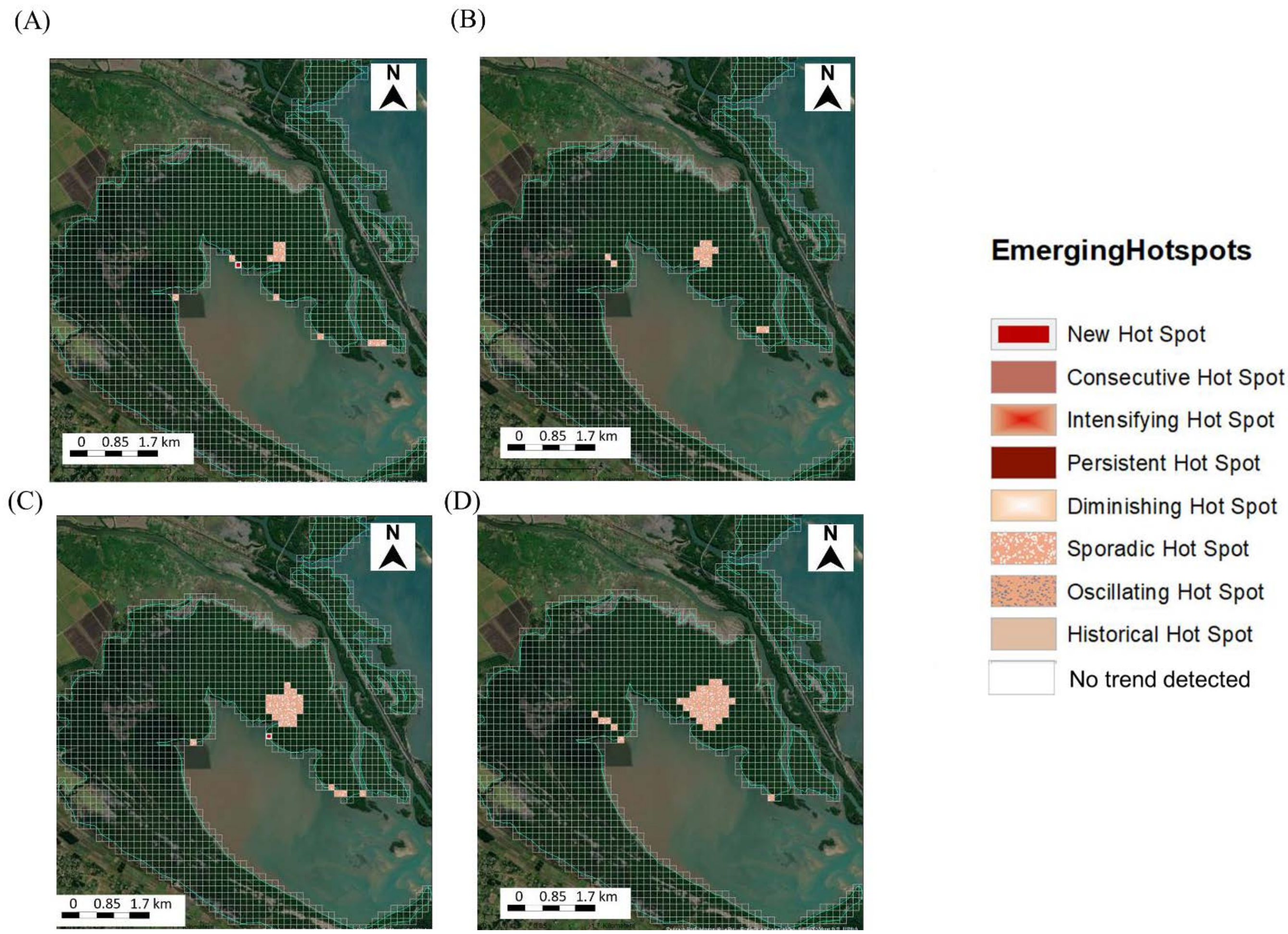

Figure S3.3. Results of the Emerging Hot Spot Analysis (EHSA; Harris et al., 2017), conducted within ArcGIS (ArcGIS,2016) for uMhlathuze. We used a 100 m bin size and distinct neighborhood distances of (A) 150 m (B) 200m (C) 350m (D) 400m with time interval of a year. Each bin (here visualized as cells) 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 were no significant trend were detected ($p > 0.05$ and z-score = 0). The satellite image used as background was obtained from ESRI South Africa (2021).

Chapter 4 Canopy gaps closure dynamics in mangrove forests: A global perspective on factors influencing closure

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4.1 Abstract

Canopy gap closure is fundamental to mangrove regeneration, impacting carbon sequestration and long-term storage. However, the lack of synthesized data on the temporal dynamics of canopy gap closure and its driving factors across different latitudinal positions impedes the understanding of their influence on mangrove forest dynamics. To address this limitation, a study was conducted across 10 countries in two biogeographical regions (Atlantic East Pacific and Indo West Pacific). Freely accessible high-resolution satellite images from Google Earth Pro were used to document the temporal development of canopy gaps across the study sites. Analytical metrics were developed to assess the canopy gap closure dynamics. The potential drivers of canopy gap closure rate and duration were also modelled using generalized linear model. The findings reveal significant variation in canopy gap closure durations across the 10 countries in Atlantic East Pacific and Indo West Pacific. A pattern of relatively shorter canopy gap closure durations and increased annual percentage of canopy gap closure at higher latitudes above the equator was observed. The canopy gap age upon closure varied across the ten countries. Approximately 70-100% of the canopy gaps had undergone closure in eight countries. Conversely, during the timeframe encompassed by the study, over 70% of the canopy gaps in Australia exhibited a persistent lack of closure. The species composition of the mangrove stand may influence the canopy gap regeneration. Canopy gap closure duration was found to be significantly influenced by mean temperature during the wettest

quarter. Similarly, the median annual canopy gap closure rate was significantly influenced by mean temperature during the wettest quarter, mean temperature during the driest quarter, pH, and salinity. The study highlights the influence of rising temperatures on closure of canopy gaps at higher latitudes consistent with the poleward expansion of mangrove forests in the context climate change. The study partly contributes to understanding the factors involved in canopy gap closure and emphasizes the necessity for human intervention to replant in mangrove forests where regeneration of canopy gaps is lacking.

Keywords: gap annual closure rate, gap dynamics, gap duration, climate change, non-closure

4.2 Introduction

Mangrove forests are woody plants situated in the intertidal zone between land and sea, primarily found in tropical and subtropical regions where they typically thrive under harsh conditions (Kathiresan and Bingham, 2001). They offer numerous valuable ecosystem services, including coastal protection, carbon sequestration, and habitats for various fauna, while also providing fuel and timber to coastal communities (Zimmer and Helfer, 2022). The dynamic coastal environment in which mangrove forests flourish makes them susceptible to various disturbances, including lightning strikes, insect and pathogen attacks, competition, extreme temperatures, senescence, extreme precipitation, and forestry practices (Amir and Duke, 2019; Agyekum et al., unpubl. data.). These disturbances create canopy gaps that are integral components of the forest dynamics (Muscolo et al., 2014) as they “drive a regeneration cycle” by increasing availability of light, nutrients, and temperature. This promotes the rapid growth of young seedlings, replacing dead trees and ultimately maintaining the mangrove forest in a regenerated state (Amir and Duke, 2019). However, within this cycle, the canopy gap closure phase plays a crucial role in contributing to the forest structure, carbon sequestration and long term storage of carbon (Duke, 2001; Lassalle et al., 2022). Despite this significance, only a few studies have examined canopy gap closure durations (Paijmans & Rollet 1977; Sherman et al., 2000). For instance, Paijmans & Rollet (1977) demonstrated that the canopy gap closure duration ranges from 15 to 18 years. Similarly, Sherman et al., (2000) found that gaps closed around the age of 8 to 15 years in the Dominican Republic. More recently, Agyekum et al. (unpubl. data) demonstrated that canopy gaps were not closing in South Africa over a span of 18 to 23 years.

Canopy gap closure is a complex process influenced by a multitude of interacting factors, encompassing microclimatic conditions within the gap and various biotic factors (Whelan, 2005). Temperature plays a significant role in seedling germination and subsequent growth in canopy gaps (Amir and Duke, 2019). High temperatures can promote faster seedling growth, but extreme temperatures, whether too hot or too cold, can be detrimental to the seedling establishment in canopy gaps (Duke et al., 1998). For example, Fetcher et al. (1985) demonstrated that optimum temperature and humidity facilitated a return to pre-gap levels within two years after tree-fall gap formation in lowland tropical forests in Costa Rica. Clarke and Allaway (1993) showed that, besides temperature, light availability and nutrient levels were crucial for the recruitment of *Avicennia marina* seedlings into the sapling stage.

Additionally, salinity and pH (Wakushima et al., 1994; Biber, 2006; Nguyen et al., 2015) play significant roles in establishing seedlings that contribute to closing the canopy gap (Amir and Duke, 2019). Mangrove seedlings exhibit distinct tolerance ranges for pH and salinity, which can significantly affect their successful establishment as they develop (Kodikara et al., 2018). For instance, *Avicennia marina* demonstrates high tolerance to a wide range of salinity levels, thriving in conditions of both high salinity and high pH (Burchett et al., 1984).

In contrast, Wakushima, et al.1994 showed that the seedlings of *Rhizophora spp*, *Kandelia candel*, and *Bruguiera gymnorrhiza* thrive in lower salinity and neutral conditions. Therefore, the establishment of seedlings just be-fore or immediately after gap formation, which eventually grow into mature trees, may initially be constrained by the prevailing pH and salinity conditions.

Nonetheless, the closure of canopy gaps may also be mediated by other factors including the species composition, herbivory, tides, and seedlings dispersal (Osborne & Smith, 1990; Duke et al., 1998; Bosire et al., 2005; Amir, 2012) which are often not accounted in the hypothesis of canopy gaps as core of mangrove regeneration (Amir, 2012). Despite these insights, synthesized data on the closure dynamics and factors driving canopy gap closure globally are lacking, impeding understanding of the canopy gaps on valuable ecosystem services, including carbon sequestration and long term storage of carbon. In this study, canopy gaps were investigated across 10 countries spanning two biogeographical regions—the Atlantic East Pacific and Indo West Pacific—with the objectives: (1) to determine the temporal dynamics of canopy gap closure and (2) to identify the environmental factors that influence canopy gap closure.

4.3 Methods

4.2.1 Study sites

For this study, mangrove sites that exhibited abundance of canopy gaps, guided by the findings of Agyekum et al. (unpubl. data) were selected (Figure 1). These diverse study sites spanned across different latitudinal positions and offered a range of diverse mangrove forest stands for the analysis.

Moreton Bay, Australia: This region hosts a diverse array of shrubs and trees, ranging from 2 to 30 meters in height, representing six distinct species. *Avicennia marina* are the dominant species (Amir & Duke, 2009; Kamal et al., 2014).

São Luis coast, northeast Brazil: This coastal mangrove area comprises several stands near the Mearim River, with tree heights ranging from under 2.5 meters to 24 meters. Dominant species here include *Avicennia germinans* and *Rhizophora racemosa*, and *Rhizophora mangle* (De Menezes et al., 2008).

Canal de Bertioga, Southeast Brazil: This is a mixed forest of *Laguncularia racemosa*, *Rhizophora mangle and Avicennia schaueriana*, with a slight dominance of *Rhizophora mangle* (Soares & Schaeffer-Novelli, 2005).

Sundarbans, Bangladesh: These mangrove forest stands are jointly shared with India and are characterized by the dominance of species like *Heritiera fomes, Excoecaria agallocha, Ceriops decandra,* and *Xylocarpus mekongensis* (Sarker et al., 2016).

Barra de Santiago, El Salvador: This Ramsar site comprises stands of four mangrove species, with an average tree height ranging from 7 to 18 meters. The main species observed in this site include *Rhizophora mangle, Rhizophora racemosa, Avicennia germinans,* and *Laguncularia racemosa* (Lara & Esquivel, 1993).

Matang, Malaysia: The Matang mangrove forest remains one of the largest managed mangrove forests in the world. The mangrove stands are dominated by *Rhizophora apiculata* which are harvested in a 30year rotational cycle for charcoal production (Amir, 2012).

Punta Galeta, Panama: This forest is a mixed stand comprising *Rhizophora mangle, Avicennia germinans, and Laguncularia rac*emosa (Sousa et al., 2003).

Hasan Maubesi bay, Timor Leste: The mangrove stand here consists of *Rhizophora spp, Bruguiera gymnorrhiza, Ceriops tagal, and Sonneratia spp* (UNDP-MAF, 2018).

Florida, USA: The Everglades National Park mangrove stands has *Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa* as the main species within the park (Xiong et al., 2022).

Richards's bay, South Africa: The uMhlathuze estuary is the largest mangrove forest stand within South Africa comprising about 80% of the total mangrove coverage. The estuary is dominated by *Avicennia marina*. The inclusion of this site is informed by the study of Agyekum et al. (unpubl. data) to allow comparison with the analysis of this current study.

Can Gio Biosphere, Viet Nam: This is a Biosphere reserve site which comprises several stands dominated by the *Rhizophora apiculata* species (Vogt et al., 2013) .

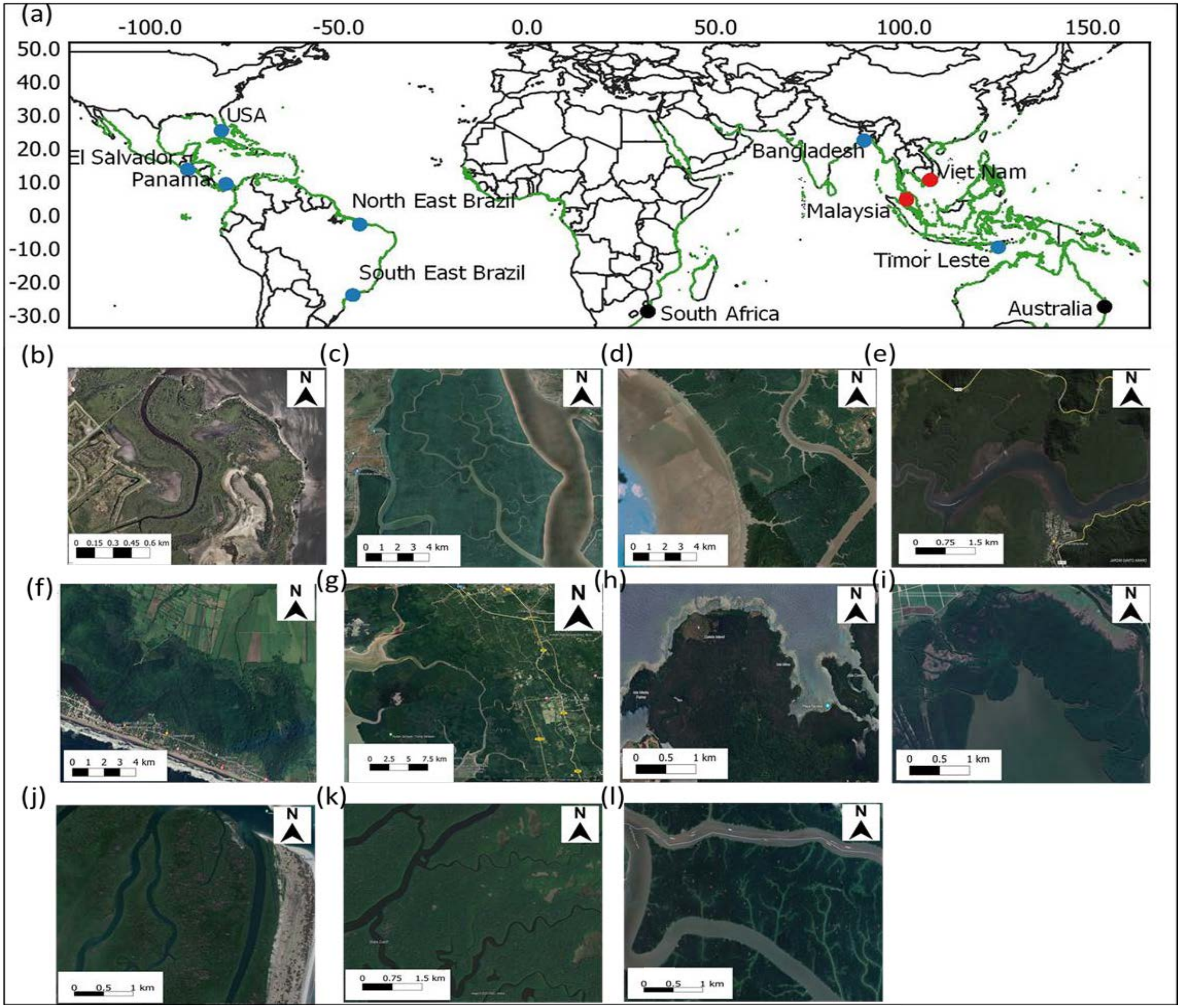
(a)
-100.0
-50.0
0.0
50.0
100.0
150.0
50.0
40.0
30.0
20.0
10.0
0.0
-10.0
-20.0
-30.0
USA
El Salvador
Panama
North East Brazil
South East Brazil
South Africa
Bangladesh
Viet Nam
Malaysia
Timor Leste
Australia
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
N
0 0.15 0.3 0.45 0.6 km
0 1 2 3 4 km
0 0.75 1.5 km
0 2.5 5 7.5 km
0 0.5 1 km

Figure 4.1. a) Geographical distribution of the mangrove stand sites in b) Australia c) Bangladesh d) North East Brazil e) South East Brazil f) El Salvador g) Malaysia h) Panama i) South Africa j) Timor Leste k) United States America l) Viet Nam. The blue dot represents mixed stands, the red dot indicates *Rhizophora spp* dominant stands, and the black dot represents *Avicennia marina* dominant stands. The green outline delineates the mangrove extent, downloaded from the Global Mangrove Watch datasets version 3 (Bunting et al., 2022). The se-lection of study sites was guided by the datasets of Agyekum et al. (unpubl. data).

4.2.2 Data Collection

At each mangrove site, a series of satellite images were examined to assess the development of canopy gaps, following the methodology outlined in Agyekum et al. (unpublished data). The satellite images were accessed through Google Earth Pro Version 7.3.3 (Google Earth, 2018), and canopy gaps were delineated using on-screen digitizing polygon tools and saved into a shapefile for further processing. Gap statuses in each image were categorized as "open," "recovering," or "closed," and their corresponding dates on the satellite images were recorded. The centroids of the canopy gaps were extracted using the "Calculate geometry" tool in ArcGIS 10.8.2 (ArcGIS, 2023) using the world cylindrical equal area projection system. Analytical metrics were developed and detailed in Table S4.1 as follows: (i) Annual canopy gap closure rate (%) (ii) Annual canopy gap closure (N) (iii) Average annual canopy gap formation rate (N) (iv) Canopy gap closure duration (days) (v) Median annual canopy gap closure rate (%).

4.2.3 Environmental factors preparation

Spatial data on potential environmental factors were prepared in ArcGIS 10.8.2 (ArcGIS, 2023), utilizing the same spatial resolution (1x1 km^2) and projection (World Cylindrical Equal Area). Nineteen bioclimatic (bioclim) variables were downloaded from the WorldClim database (Fick & Hijmans, 2017; http://www.worldclim.org/). Salinity and pH data were obtained from Bio-oracle version 2.0 (Tyberghein et al., 2012; Assis et al., 2017; https://bio-oracle.org/downloads-to-email.php). To ensure that the model's predictors were not highly correlated ($r \geq 0.70$), we computed pairwise correlations among all variables. Multicollinearity, which can arise from highly correlated predictors, is known to increase uncertainty in model parameters and reduce statistical power (Guisan et al., 2017). The selection was further refined using the Variance Inflation Factor (VIF) technique, excluding variables with VIF > 10 from the final model selection (Gómez et al., 2016). This was done as a precautionary step to avoid overfitting of the model. Ultimately, a final set of 4 variables were selected for inclusion in the model (see Table 4.1)

4.2.4 Statistical analysis

To identify the factors that explain canopy gap closure dynamics, a generalized linear model was employed that accommodated both linear and nonlinear data by using gamma log and inverse link functions to account for the right skewed data of the response variable (Figure S4.11). Initially, we applied a linear term, followed by a quadratic term to account for potential nonlinear relationships between the environmental predictors and the response variable. To select the optimal model, a stepwise selection method was utilized, incorporating both forward and backward directions, guided by the AIC (Guisan et al., 2017; Guisan and Zimmermann, 2000). The adjusted R-squared value was calculated using the rsq R package version 2.5 (Dabao, 2022). Visualizations of the graphs were created using ggplot2 (Wickham, 2016) and scatterplot3d (Ligges and Mächler, 2003). For estimating the probability of canopy gap closure, non-parametric time-to-event analysis were employed, specifically the Kaplan-Meier curve method (Stalpers & Kaplan, 2018). This analysis was conducted using R packages survival version 3.5-7 (Lumley et al., 2023) and survminer version 0.4.9 (Kassambara et al., 2022). Level of significance was set at $p < 0.05$.

Table 4.1. Variables used as predictors to determine possible drivers of canopy gap closure. The bioclimatic (bioclim) variables were sourced from the WorldClim database (Fick & Hijmans, 2017; http://www.worldclim.org/). Salinity and pH data were obtained from Bio-oracle version 2.0 (Tyberghein et al., 2012; Assis et al., 2017; https://bio-oracle.org/downloads-to-email.php).

Variables	Description
Bio 8	Mean Temperature of Wettest Quarter (°C)
Bio 9	Mean Temperature of Driest Quarter (°C)
Salinity	Salinity of Seawater (PSS)
pH	pH of Seawater

4.4 Results

The probability of canopy gaps remaining open across the 10 countries were significantly different ($\chi^2 = 1152$, $p < 0.05$; Figure 4.2). The pairwise post-hoc comparisons (Table 4.2) showed significant differences between 49 pairs of countries ($p < 0.05$). In eight countries, 70-100% of the canopy gaps reached closure over the time span of the study (Figure 4.2). By contrast, more than 70% of the canopy gaps (Figure 4.2) did not reach closure in Australia (i.e. at least 18 years; 6731 days) similar to South Africa (i.e. at least 23 years; 8333 days previously reported by Agyekum et al. (unpubl. data).

30% of the canopy gaps showed shorter durations at higher latitudes above the equator (1787 to 3675 days) (Figure 4.3a). Also, the median annual canopy gap closure rate (%) increased at higher latitudes above the equator (3.5 to 18.8%) (Figure 4.3b). Canopy gap age upon closure varied across the 10 countries (Figure S1-10; Table S4.2-4.12) ranging from 2 (Table S4.6 and S4.11) to 23 years (Table S4.9).

Regarding bivariate relationships, a significant negative correlation ($r = -0.63$, $p < 0.05$; Figure 4.4a) was observed between canopy gap closure duration in days and the mean temperature of the wettest quarter. However, there were no significant correlations found between median annual canopy gap closure rate (%) and the mean temperature of the wettest quarter ($r = 0.59$, $p > 0.05$;

Figure 4.4b), mean temperature of the driest quarter ($r = 0.24$, $p > 0.05$; Figure 4.4c), salinity ($r = -0.53$, $p > 0.05$; Figure 4.4d), or pH ($r = 0.21$, $p > 0.05$; Figure 4.4e).

According to the analysis of deviance table detailed in Table 4.3, the mean temperature of the wettest quarter was significantly related ($P < 0.05$) in explaining canopy gap closure duration, with an adjusted R-squared value of 0.91. Salinity, on the other hand, was not found to be significantly related in explaining canopy gap closure in days ($P > 0.05$).

Also, the analysis of deviance table detailed in Table 4.4 showed that the mean temperature of the wettest quarter, mean temperature of the driest quarter, salinity, and pH were all significantly related ($P < 0.05$) in explaining the percent of median annual canopy gap closure rate, with an R-squared value of 0.93.

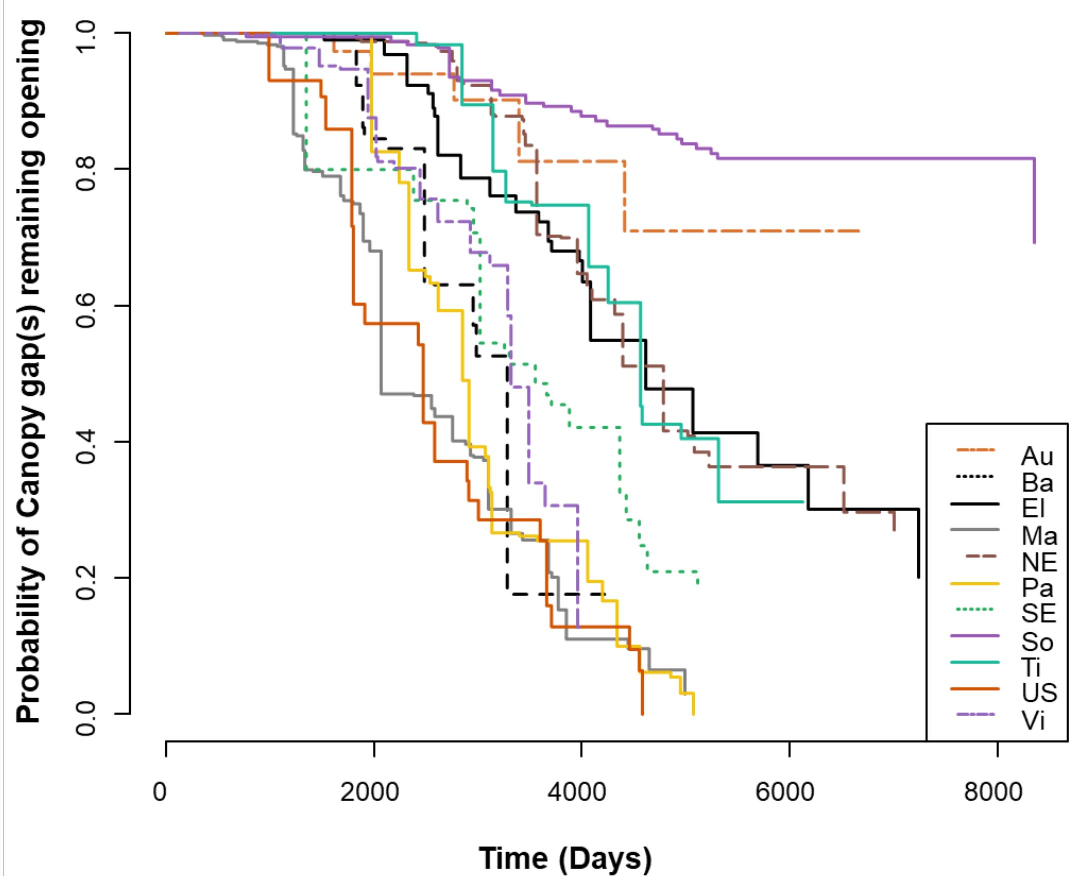

Figure 4.2. Estimated duration of canopy gap closure at: (Au) Australia (Ba) Bangladesh (El) El Salvador (Ma) Malaysia (NE) North East Brazil (Pa) Panama (SE) South East Brazil (So) South Africa (Ti) Timor Leste (US) United States America (Vi) Viet Nam. The data from South Africa was obtained from Agyekum et al. (unpubl. data). The graph was obtained using the plot function in R version 4.0.3 (R Studio Team, 2021).

Table 4.2. Pairwise comparisons of the estimated canopy gap closure duration across the study sites. Figures highlighted in bold are significant values at P<0.05.

Country	Australia	Bangladesh	El Salvador	Malaysia	North East Brazil	Panama	South East Brazil	South Africa	Timor Leste	USA
Bangladesh	**1.5E-5**	-	-	-	-	-	-	-	-	-
El Salvador	0.095	**3.3E-07**	-	-	-	-	-	-	-	-
Malaysia	**2.3E-9**	**0.013**	**< 2e-16**	-	-	-	-	-	-	-
North East Brazil	0.302	**< 2e-16**	0.3638	**< 2e-16**	-	-	-	-	-	-
Panama	**7.7E-9**	**0.23273**	**< 2e-16**	**0.00141**	**< 2e-16**	-	-	-	-	-
South East Brazil	**0.00034**	**0.05348**	**9.2E-5**	**3.3E-9**	**< 2e-16**	**0.0003**	-	-	-	-
South Africa	**0.238**	**< 2e-16**	**4.3E-15**	**< 2e-16**	**4.10E-15**	**< 2e-16**	**< 2e-16**	-	-	-
Timor Leste	**0.15094**	**6.40E-14**	**0.81923**	**< 2e-16**	0.95736	**< 2e-16**	**1.70E-10**	**1.30E-14**	-	-
USA	**3.4E-09**	**0.01523**	**1.1E-14**	**0.29593**	**< 2e-16**	**0.0128**	**5.50E-05**	**< 2e-16**	**< 2e-16**	-
Viet Nam	**1.9E-05**	**0.01961**	**7.8E-13**	**4.5E-11**	**< 2e-16**	0.1895	0.07635	**< 2e-16**	**< 2e-16**	**0.0008**

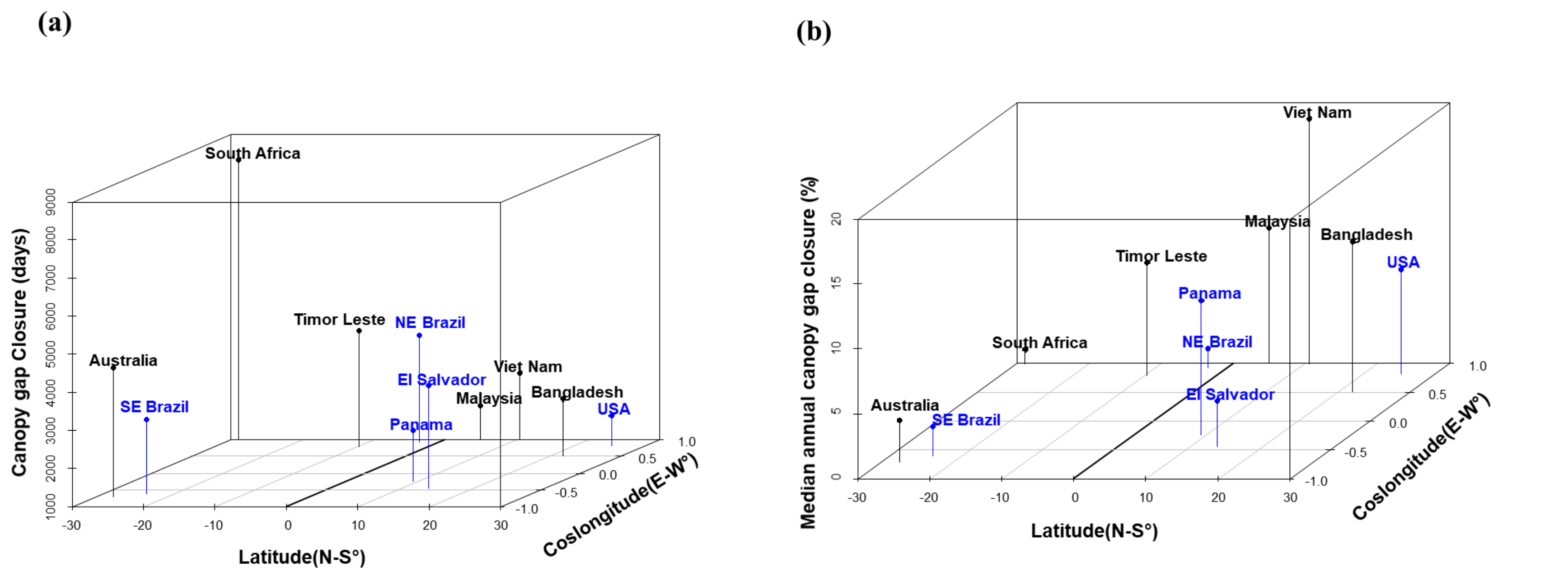

Figure 4.3. A 3D scatter plot showing the relationships of the latitude: (a) Canopy gap closure and longitude (b) Median annual canopy gap closure and longitude. Canopy gap closure denotes the time required for 30% of canopy gaps to reach closure in days. Median annual canopy gap closure signifies the rate at which canopy gaps close per year. Blue dots represent gaps located in the Atlantic East Pacific (AEP), while the black dot represents the Indo West Pacific (IWP). The graph was obtained using the scatterplot3d package in R (Ligges & Mächler, 2003)

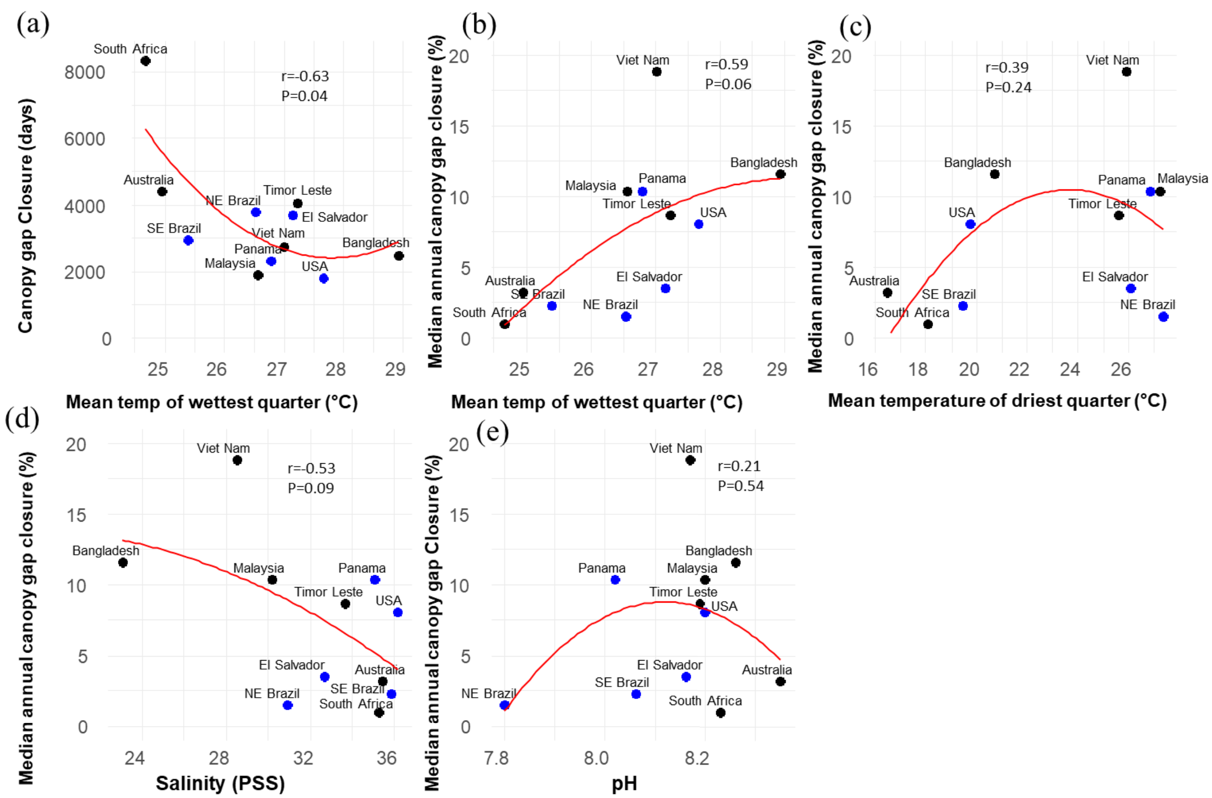

Figure 4.4. Bivariate relationships between: (a) Canopy gap closure and mean temperature of wettest quarter, (b) Median annual canopy gap closure and mean temperature of the wettest quarter (c) Median annual canopy gap closure and mean temperature of the driest quarter (d) Median annual canopy gap closure and salinity (e) Median annual canopy gap closure and pH. Canopy gap closure denotes the time required for 30% of canopy gaps to achieve closure in days. Median annual canopy gap closure signifies the annual rate at which canopy gaps close. Blue dots represent gaps located in the Atlantic East Pacific (AEP), while the black dot represents the Indo West Pacific (IWP). The red line depicts the regression line. The r indicates the correlation of co-efficient based on Pearson correlation estimates and the significance between the variables was indicated at P<0.05. The graphs were obtained using ggplot2 (Wickham, 2016) package in R version 4.0.3 (RStudio Team, 2021).

Table 4.2. Analysis of deviance table showing the percentage of deviance explained by the environmental factor(s) for canopy gap closure (Days). Significance level set at P < 0.05, indicated in bold font. Quadratic terms are denoted by 2. The error distribution was Gamma with log link. The poly 2 indicates the quadratic term.

Predictor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL			10	2.12	
poly(Salinity)2	2	0.26	8	1.86	0.09835
(Mean temperature of the wettest quarter)2	2	1.46	6	0.40	**2.61E-06**

Table 4.3. Analysis of deviance table showing the percentage of deviance explained by the environmental factors explaining the median annual canopy gap closure rate (%). Significance was set at P < 0.05 (indicated in bold font). Quadratic terms are indicated by 2. The error distribution was Gamma with inverse link. The poly 2 indicates the quadratic term.

Predictor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL			10	7.55	
poly(Salinity)2	2	1.59	8	5.96	**6.96E-11**
poly(pH)2	2	2.14	6	3.82	**2.40E-14**
poly(Mean temperature of the wettest quarter)2	2	2.94	4	0.89	**1.80E-19**
poly(Mean temperature of the driest quarter)2	2	0.82	2	0.07	**6.01E-06**

4.5 Discussion

Canopy gap closure plays a crucial role in the regeneration of mangrove forests, and the failure of these gaps to close has significant implications for forest structure and carbon dynamics. An investigation was conducted to assess the duration and rates of canopy gap closure, as well as to identify the factors influencing the closure of these gaps across 10 countries in two biogeographical regions. The data revealed variations in canopy gap closure duration among the ten countries, with instances of gap non-closure observed in Australia. Mean temperature of the wettest quarter significantly could influence canopy gap closure duration. Also, salinity, pH, mean temperature of the wettest quarter, and mean temperature of the driest quarter significantly influence the median annual canopy gap closure rate (%). These results highlight the role of environmental factors in influencing canopy gap closure duration and rates across different latitudinal positions.

4. 4.1 Canopy gap closure temporal patterns

The findings revealed variations in canopy gap closure across the 10 countries (Figure 4.2), in line with previous studies. Canopy gap closure ranged from 15 to 30 years (Paijmans and Rollet, 1977; Sherman et al., 2000; Amir, 2012; Amir and Duke, 2019), with an average of 15 years for most mangrove species to reach closure (Duke, 2001). In this satellite satellite imageries were not consistent in all years to document the canopy gap closure rates, therefore additional in-situ field surveys and satellite data could prove to give a more accurate assessment of the temporal development of the canopy gaps (Schliemann & Bockheim, 2011). Nonetheless, 70-100% of canopy gaps reached closure in eight countries which had diverse mangrove forests. By contrast, we observed that within the *Avicennia marina* dominant stand in Moreton Bay, Australia, over 70% of the canopy gaps remained opened for at least 18 years that the study timeframe covers. This pattern of non-closure and lack of regeneration within mangrove stands dominated by Avicennia marina is consistent with the findings of Agyekum et al. (unpublished data) in South Africa, potentially suggesting a species-specific effect. The factors contributing to the lack of canopy gap closure remain unclear and demand additional on-site investigation. This investigation should explore seedling availability, environmental conditions (such as tidal conditions and sediment physico-chemical conditions), and biotic factors (including herbivory pressure and species composition). The persistent non-closure of these canopy gaps poses a significant threat to the long-term sustainability of the mangroves. Therefore, it is imperative to actively engage human efforts in refilling these gaps to mitigate the potential fragmentation of the mangrove patch.

4.4.2 Factors influencing canopy gaps closure

The duration of canopy gap closure is influenced by the mean temperature during the wettest quarter. Additionally, the median annual canopy gap closure rate (%) may be influenced by both the mean temperatures of the wettest and driest quarters, as detailed in Tables 4.2 and 4.3. Increasing mean temperature has a direct biological impact on the abundance and distribution of mangrove forests (Cavanaugh et al., 2014). This is evident in influencing the seedlings establishment and their subsequent high densities within canopy gaps (Amir, 2012). The findings align with mean temperatures (Figures 4a-c) generally creating favorable conditions for canopy gap regeneration under optimal conditions (Amir & Duke, 2019). Ball, (2002) emphasized that higher temperatures tend to result in increased growth, respiration, photosynthesis, and reproduction rates. Most mangrove species show peak rates of leaf photosynthesis at approximately 30°C, with leaf CO_2 assimilation declining at temperatures ranging from 30 to 35°C (Ball, 2002). Notwithstanding, Amir, (2012) showed that the canopy gap regeneration does not rely only on just increased mean temperature but also on light availability on the forest floor to stimulate the rapid growth of mangrove seedlings. Clarke & Allaway (1993) showed that light, and nutrients besides temperature are also key to the successful establishment of mangrove seedlings within canopy gaps.

However, the observed pattern of increased canopy gap closure rates and shortened time to reach closure at higher latitudes (Figure 4.3) suggests that temperature may be influencing the closure at those higher latitude (Figures 4a-b). For instance, Chapman et al. (2021) conducted an experimental study that revealed an increase in mangrove growth rates in height due to warming conditions. Coldren et al. (2019) also reported on their experimental study that chronic warming doubled plant height and expansion of the mangrove habitat in Florida, USA.

Saintilan et al., (2014) found that mangrove expansion in the USA, South Africa, Peru and New Zealand were consistent with temperature increase at the higher latitudes. Further investigations must be conducted in-situ to gain insight on the potential effect of rising temperatures on canopy gap closure on local and regional scales and their ecological implications for the future of mangroves.

Simultaneously, the results showed that median annual canopy gap closure rate (%) may be influenced by salinity (Table 4.3). The pattern of increasing median annual canopy gap closure rate with a decreasing salinity levels (Figure 4.4d) suggests that relatively lower salinity ranges may be the optimum for the successful establishment and survival of many mangrove seedlings (Kodikara et al., 2018; Krauss & Ball, 2013; Smith & Snedaker, 1995). Mangroves, as facultative halophytes, possess the remarkable ability to thrive under low and high salinities (Smith & Snedaker, 1995). In the initial stages of their life cycle, many mangrove species seedlings typically require lower salinity levels for successful establishment (Biber, 2006). As they mature, they may gradually shift their preference towards moderate salinity ranges (Kodikara et al., 2018; Krauss & Ball, 2013) thus the survival of the seedlings at lower to moderate salinity ranges (Figure 4d) is an important factor to be considered for canopy gap closure duration and rates. However, there is evidence indicating that different mangrove species exhibit varying tolerances and salinity optima (Biber, 2006). For instance, Nguyen et al. (2015) demonstrated that *Avicennia marina* seedlings failed to grow in 0-5% of seawater but maximal growth was observed in 50-75% of seawater. *Rhizophora apiculata,* and *Rhiziophora stlylosa* usually reach optimal growth in less than 40% of seawater (Biber, 2006; Kodikara et al., 2018). Similarly, Kodikara et al. (2018) showed in their experimental study that *Bruguiera gymnorhiza* and *Bruguiera sexangula* seedlings could survive in less than 40% of seawater.

The study also demonstrated that median canopy gap closure rate (%) may be influenced by pH (Table 3). The optimum pH signifies the tolerable range within which young seedlings thrive and grow before reaching maturity (Wakushima, et al., 1994). It promotes the uptake of essential nutrients like nitrogen, phosphorus, and potassium (Joshi & Ghose, 2003; Wakushima et al., 1994). For instance, in their experimental study, Wakushima et al., (1994) demonstrated that the nutrition of mangroves was linked to the pH tolerance range. *Rhizophora spp* showed no visible chlorosis under neutral and high pH conditions, whereas *Kandelia spp* showed pale yellowish leaves. However, caution should be exercised when interpreting the canopy gap closure rates and dura-tion solely based on the factors considered for the model. Further in-situ investigations on the dis-persal of seedlings, tides, herbivory, and suppression of seedlings by opportunistic ferns (Amir, 2012; Saintilan et al., 2014), which were not considered in the model, should be included in future studies.

4.6 References

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4.7 Supplementary material

Appendix S1

Table S4.1. Description of how metrics used in the statistical analysis were determined.

Metrics	Description
Annual Canopy Gap Closure Rate (%)	This metric quantifies the annual closure of canopy gaps by dividing the number of gaps closed between two satellite images by the time span (in years) between those images. The result is further divided by the number of open canopy gaps in the preceding image, and expressed as a percentage.
Annual Canopy Gap Closure Rate (N)	This refers to the number of canopy gaps closed between two satellite images divided by time (years) between the two images.
Average Annual Canopy Gap Formation Rate (N)	The metric refers to number of canopy gaps opened between two satellite images divided by time (years) between the two images.
Canopy Gap Closure Duration (days)	This metric refers to the duration, measured in days, required to achieve a 30% closure of canopy gaps. The calculation is based on the Kaplan-Meier survival analysis curve.
Canopy Gap Age Upon Closure (years)	This involves the duration, measured in years, from the initial appearance of a canopy gap on a satellite image to its last observation on a satellite image.
Median Annual Canopy Gap Closure Rate (%)	This metric refers to the median of all the annual canopy gap closure rates.

Table S4.2. Summary table of canopy gap dynamics at the Australia mangrove patch over time (2003-2022). Canopy gap age upon closure with either the same minimum, median or maximum age is indicated once. “N” refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed gaps	Canopy gap age upon closure (min, med, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2003	1	–	–	–	–	–	–
2006	2	1	0.3	–	–	–	–
2007	4	2	2.0	–	–	–	–
2009	9	5	2.5	–	–	–	–
2011	10	1	0.5	–	–	–	–
2012	14	4	4.0	–	–	–	–
2013	21	7	7.0	–	–	–	–
2014	26	5	5.0	–	–	–	–
2015	29	3	3.0	–	–	–	–
2016	31	3	3.0	1	9	1	3.3
2017	37	7	7.0	1	4	1	3.1
2019	42	6	3.0	1	12	0.5	1.3
2020	42	2	2.0	2	5,6.5,8	2	4.7
2022	42	–	–	–	–	–	–

Table S4.3. Summary table of gap dynamics at the Bangladesh mangrove patch over time (2011-2022). Canopy gap age upon closure with either the same minimum, median or maximum age is indicated once. "N" refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, med, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2011	31	–	–	–	–	–	–
2013	34	3	1.5	–	–	–	–
2014	44	10	10	–	–	–	–
2015	48	4	4	–	–	–	–
2016	57	14	14	5	5	5	10.6
2017	61	4	4	–	–	–	
2019	71	12	6	2	5,8	1	1.7
2020	54	6	6	24	6,7,9	23	34.3
2022	41	–	–	13	5,6,8	6.5	12.5

Table S4.4. Summary table of gap dynamics at the northeast Brazil mangrove patch over time (2002-2021). Gap age upon closure with either the same minimum, median or maximum age is indicated once. “N” refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, med, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2002	22	–	–	–	–	-	
2007	34	12	2.4	–	–	–	–
2008	100	66	66	–	–	–	–
2009	129	29	29	–	–	–	–
2010	333	204	204	–	–	–	–
2011	372	39	39	–	–	–	–
2012	442	70	70	–	–	–	–
2013	487	50	50	5	11	5	1.1
2014	504	19	19	2	12	2	0.4
2015	670	179	179	13	5,7,13	13	2.6
2016	804	136	136	2	14	2	0.3
2017	862	70	70	12	7	12	1.5
2018	955	93	93	–	–	–	–
2020	942	64	32	77	11,14.5,18	38.5	4.0
2021	897	59	59	104	14,19	104	11.0

Table S4.5. Summary table of gap dynamics at the South East Brazil mangrove patch over time (2009-2022). Gap age upon closure with either the same minimum, median or maximum age is indicated once. “N” refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, med, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2009	47	–	–	–	–	–	–
2010	58	11	11	–	–	–	–
2011	71	13	13	–	–	–	–
2012	72	1	1	–	–	–	–
2013	41	4	4	35	4	35	48.6
2014	44	3	3	–		–	–
2015	65	21	21	–		–	–
2016	70	9	9	4	6	4	6.2
2017	112	42	42	–		–	–
2018	123	12	12	1	9	1	0.9
2019	133	11	11	1	10	1	0.8
2020	131	–	–	2	8.5	2	1.5
2021	139	11	11	3	12	3	2.3
2022	132	2	2	9	11	9	6.5

Table S4.6. Summary table of gap dynamics at the Malaysia mangrove patch over time (2005-2019). Gap age upon closure with either the same minimum, median or maximum age is indicated once. "N" refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, median, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2005	142	–	–	–	–	–	–
2006	146	4	4	–	–	–	–
2010	151	5	1.25	–	–	–	–
2011	165	95	95	81	6	81	53.6
2014	195	42	14	12	3,9	4	2.4
2015	227	44	44	12	3,9,3	12	6.2
2016	384	190	190	33	2,11	33	14.5
2018	439	103	51.5	48	2,7,3	24	6.3
2019	368	54	54	125	1,3,14	125	28.5

Table S4.7. Summary table of gap dynamics at the El Salvador mangrove patch over time (2003-2022). Gap age upon closure with either the same minimum, median or maximum age is indicated once. "N" refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, med, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2003	12	–	–	–	–	–	–
2004	21	9	9	–	–	–	–
2006	58	37	18.5	–	–	–	–
2009	63	9	3	4	6	1.3	2.3
2010	65	4	4	2	7	2	3.2
2012	68	3	1.5	2	6,7.5,9	1	1.5
2013	68	7	7	7	7,10	7	10.3
2015	74	6	3	–	–	–	–
2016	80	8	8	2	10	2	2.7
2017	73	3	3	10	7,11	10	12.5
2018	66	7	7	14	6,12,14	14	19.2
2020	68	7	3.5	5	11,16	2.5	3.8
2021	67	–	–	1	5	1	1.5
2022	62	–	–	5	16,19	5	7.5

Table S4.8. Summary table of gap dynamics at the Panama mangrove patch over time (2004-2021). Gap age upon closure with either the same minimum, median or maximum age is indicated once. “N” refers to number.

Year	Canopy gaps present	New canopy gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy Gap age upon closure (min, median, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2004	39	–	–	–	–	–	–
2006	46	7	3.5	–	–	–	–
2008	55	9	4.5	–	–	–	–
2009	75	20	20	–	–	–	–
2011	79	4	2	–	–	–	–
2012	87	15	15	7	8	7	8.9
2013	105	18	18	–	–	–	–
2015	158	91	45.5	38	6,9,11	19	18.1
2016	154	4	4	8	8,12	8	5.1
2017	141	3	3	16	8,13	16	10.4
2018	147	12	12	6	7,12	6	4.3
2019	160	13	13	–	–	–	–
2020	126	20	20	54	5,9	54	33.8
2021	84	–	–	42	6,8	42	33.3

Table S4.9. Summary table of gap dynamics at the South Africa mangrove patch over time (1997-2020). Canopy gap age upon closure with either the same minimum, median or maximum age is indicated once. "N" refers to number.

Year	Canopy gaps present	New gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, median, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
1997	59	–	–	–	–	–	–
2004	133	75	10.7	–	–	–	–
2006	152	22	11	1	2	0.5	0.4
2010	157	16	4	3	6	0.75	0.5
2011	199	45	45	11	7	11	7.0
2012	205	6	6	3	8	3	1.5
2013	219	16	16	–	–	–	–
2014	222	9	9	2	6,7,8	2	0.9
2015	225	4	4	6	9,10,11	6	2.7
2016	228	5	5	1	12	1	0.4
2017	240	14	14	2	11,12,13	2	0.9
2018	247	8	8	2	14	2	0.8
2019	240	4	4	1	13	1	0.4
2020	248	8	8	11	14,23	11	4.6

Table S4.10. Summary table of gap dynamics at the Timor Leste mangrove patch over time (2005-2021). Canopy gap age upon closure with either the same minimum, median or maximum age is indicated once.“N” refers to number.

Year	Canopy gaps present	New gaps	Average annual canopy gap formation rate (N)	Closed canopy gaps	Canopy Gap age upon closure (min, median, max)	Average annual closure rate (N)	Average annual closure rate (%)
2005	40	-	–	–	–	–	–
2006	66	26	26	–	–	–	–
2007	73	7	7	–	–	–	–
2008	94	21	21	–	–	–	–
2009	133	39	39	–	–	–	–
2012	140	7	2.3	–	–	–	–
2013	177	37	37	–	–	–	–
2014	187	10	10	–	–	–	–
2016	182	10	5	15	11	7.5	4
2017	176	10	10	16	8,9	16	8.8
2018	196	20	20	–	–	–	–
2019	192	13	13	17	10,13	17	8.7
2020	198	6	6	–	–	–	–
2021	154	3	3	47	7,9,15	47	23.7

Table S4.11. Summary table of gap dynamics at the USA mangrove patch over time (1995-2021). Canopy gap age upon closure with either the same minimum, median or maximum age is indicated once. "N" refers to number.

Year	Gaps present	New gaps	Average annual formation rate (N)	Closed gaps	Gap age upon closure (min, med, max)	Average annual closure rate (N)	Average annual closure rate (%)
1995	1	–	–	–	–	–	–
1999	2	1	0.25	–	–	–	–
2004	7	6	1.2	1	9	0.2	10
2007	9	3	1	1	8	0.3	4.8
2010	12	4	1.3	1	6	0.3	3.7
2013	23	11	3.7	–	–	–	–
2014	27	5	5	1	10	1	4.3
2017	27	12	4	12	4,10,13	4	14.8
2018	23	–	–	4	5,8	4	14.8
2019	16	6	6	13	2,5,6	13	56.5
2021	14	–	–	2	2,4,8	1	6.3

Table S4.12. Summary table of gap dynamics at the Viet Nam mangrove patch over time (2002-2022). Canopy gap age upon closure with either the same minimum, median or maximum age is indicated once. "N" refers to number.

Year	Canopy gaps present	New gaps	Average annual formation rate (N)	Closed canopy gaps	Canopy gap age upon closure (min, med, max)	Average annual canopy gap closure rate (N)	Average annual canopy gap closure rate (%)
2002	46	–	–	–	–	–	–
2006	99	53	13.25	–	–	–	–
2008	166	67	33.5	–	–	–	–
2010	181	24	12	9	8	4.5	2.7
2012	173	29	14.5	37	10	18.5	10.2
2013	185	12	12	0	–	–	–
2014	201	21	21	5	8	5	2.7
2015	206	5	5	–	–	–	–
2016	212	6	6	–	–	–	–
2017	179	35	35	68	9,11	68	32.1
2018	161	12	12	30	6,10	30	16.8
2019	105	5	5	61	7,11	61	37.9
2020	80	12	12	37	3,6,11	37	35.2
2021	69	4	4	15	6,8	15	18.8
2022	92	36	36	13	3,4	13	18.8

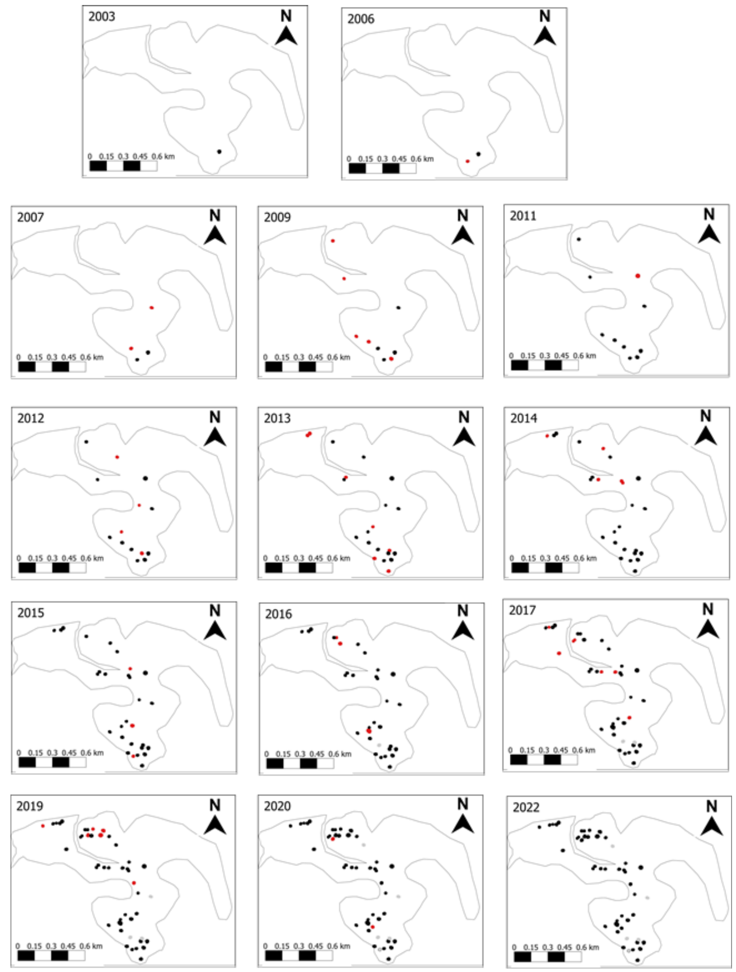

Figure S4.1**.** Temporal development of canopy gaps in the Australia Mangrove Patch (2003-2022): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

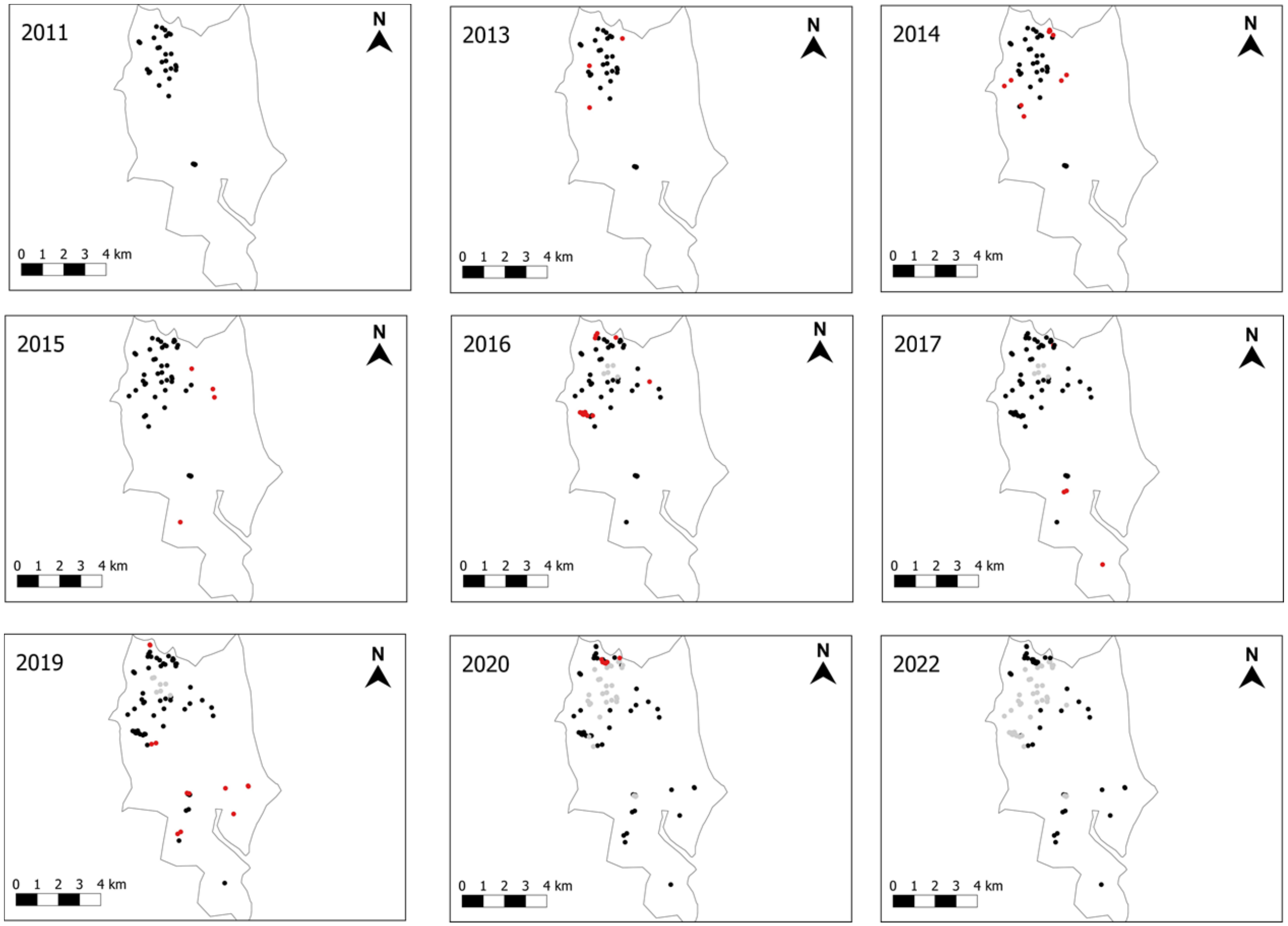

Figure S4.2. Temporal development of canopy gaps in the Bangladesh mangrove patch (2011-2022): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

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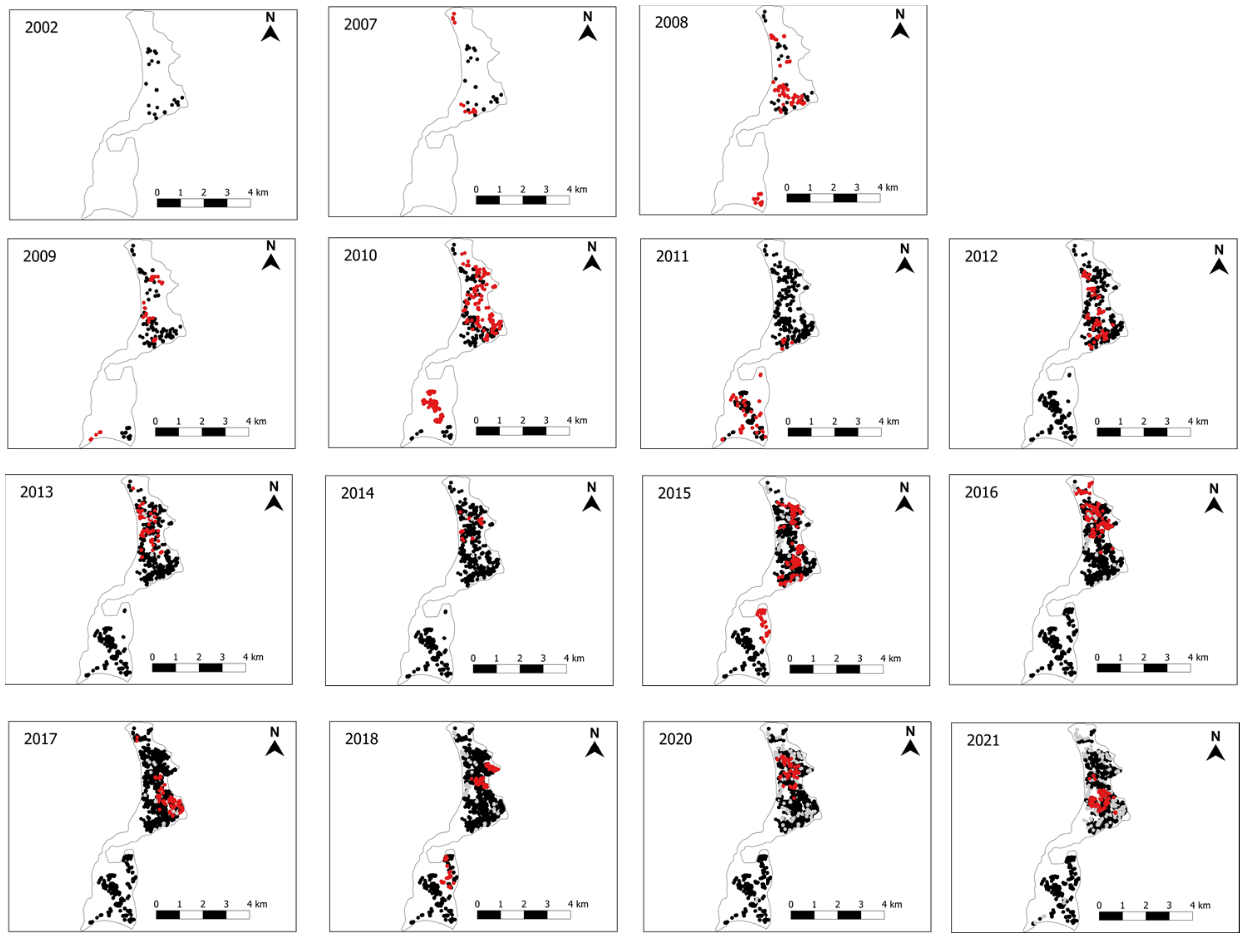

Figure S4.3. Temporal development of canopy gaps in the North East Brazil Mangrove Patch (2011-2022): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

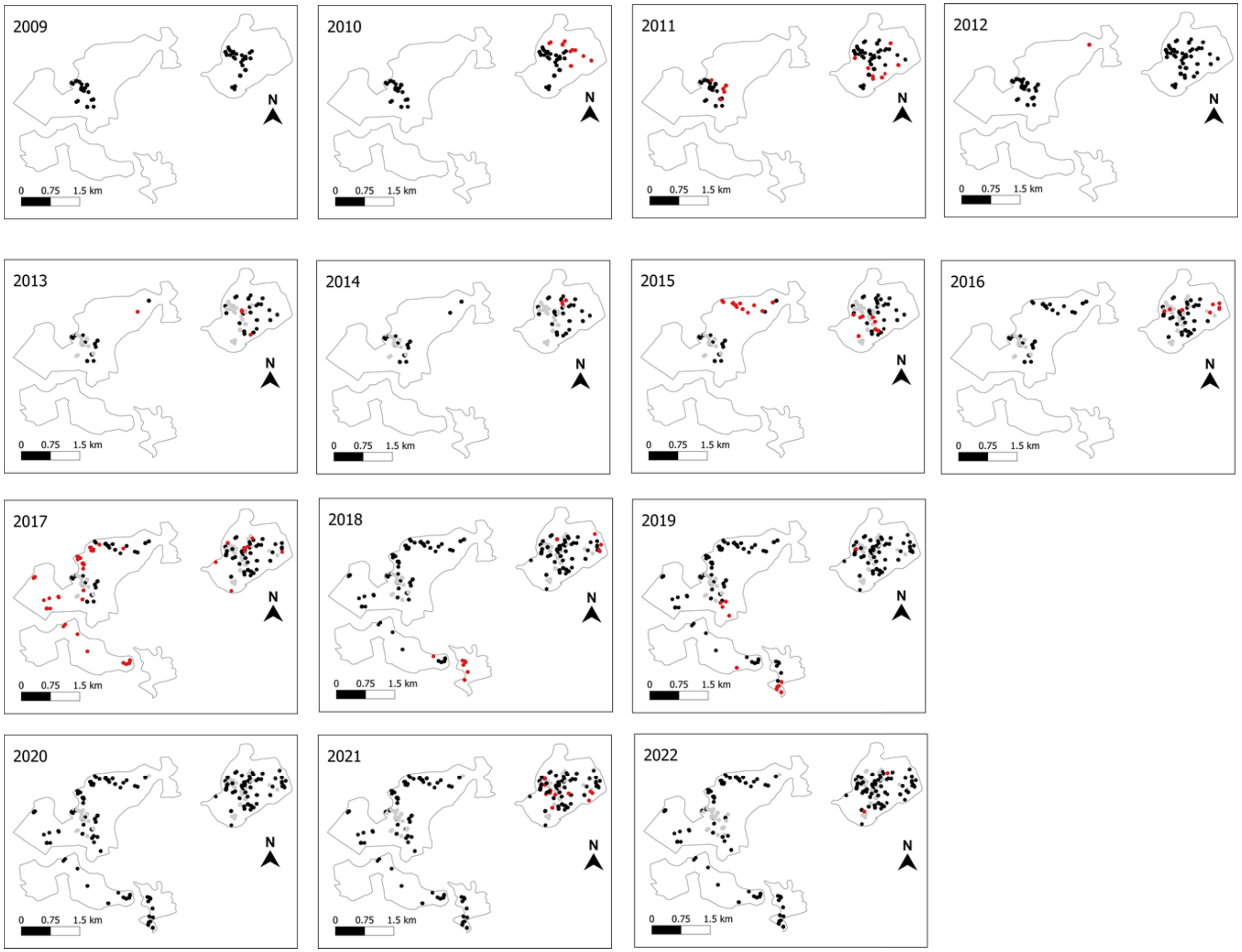

Figure S4.4 Temporal Development of canopy gaps in the South East Brazil mangrove patch (2009-2022): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

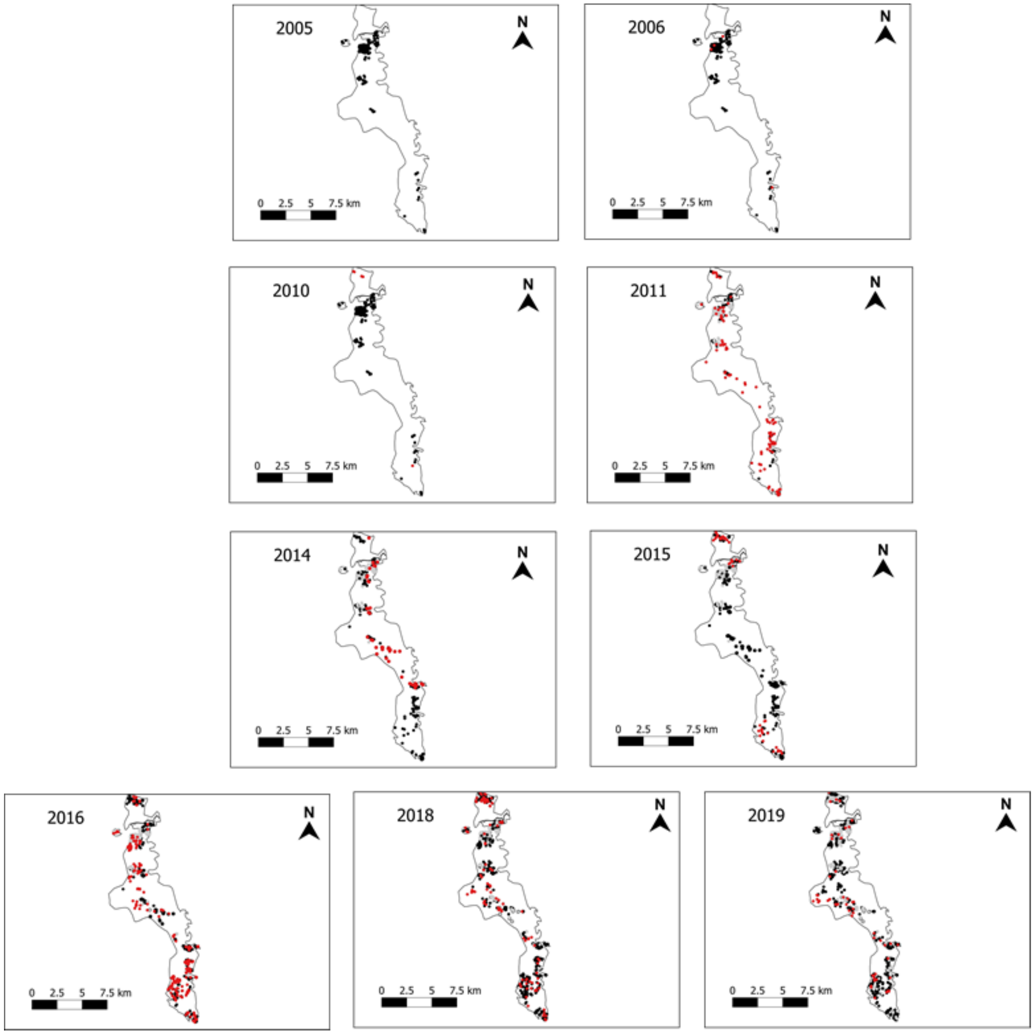

Figure S4.5. Temporal Development of canopy gaps in the Malaysia mangrove patch (2005-2019): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

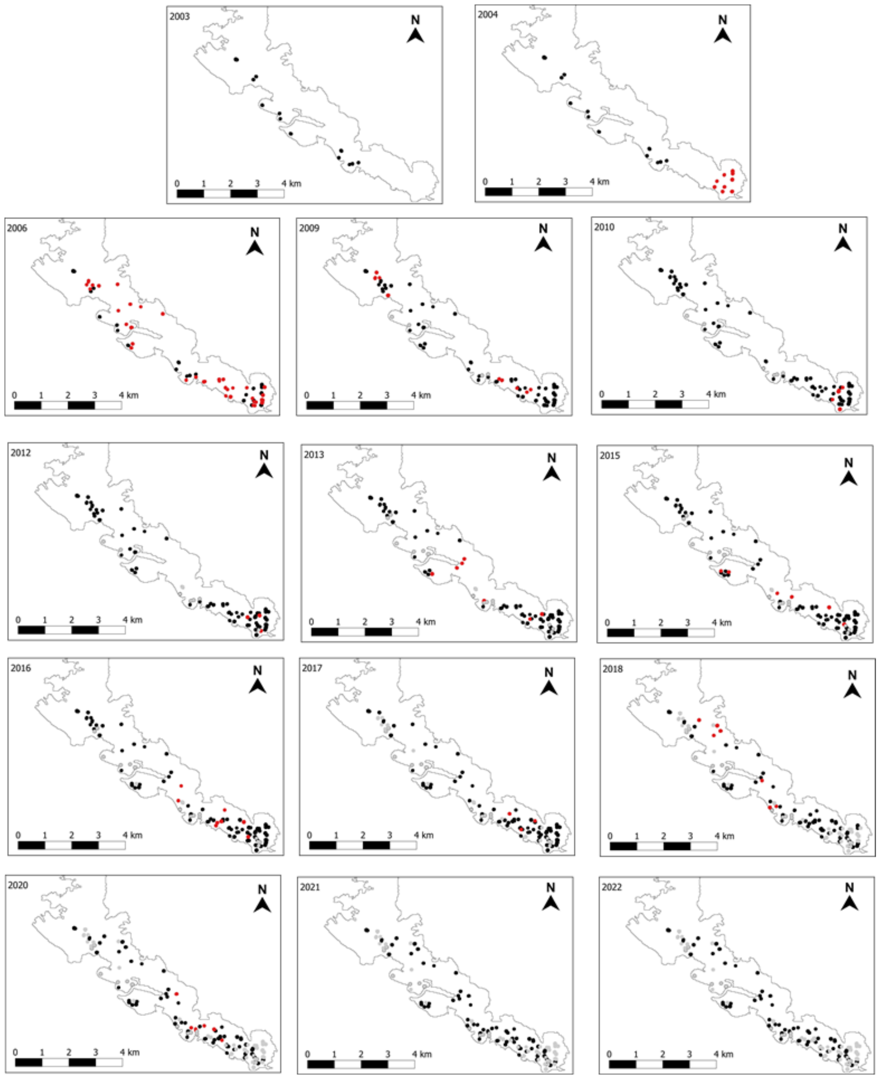

Figure S4.6. Temporal development of canopy gaps in the El Salvador Mangrove Patch (2003-2022): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

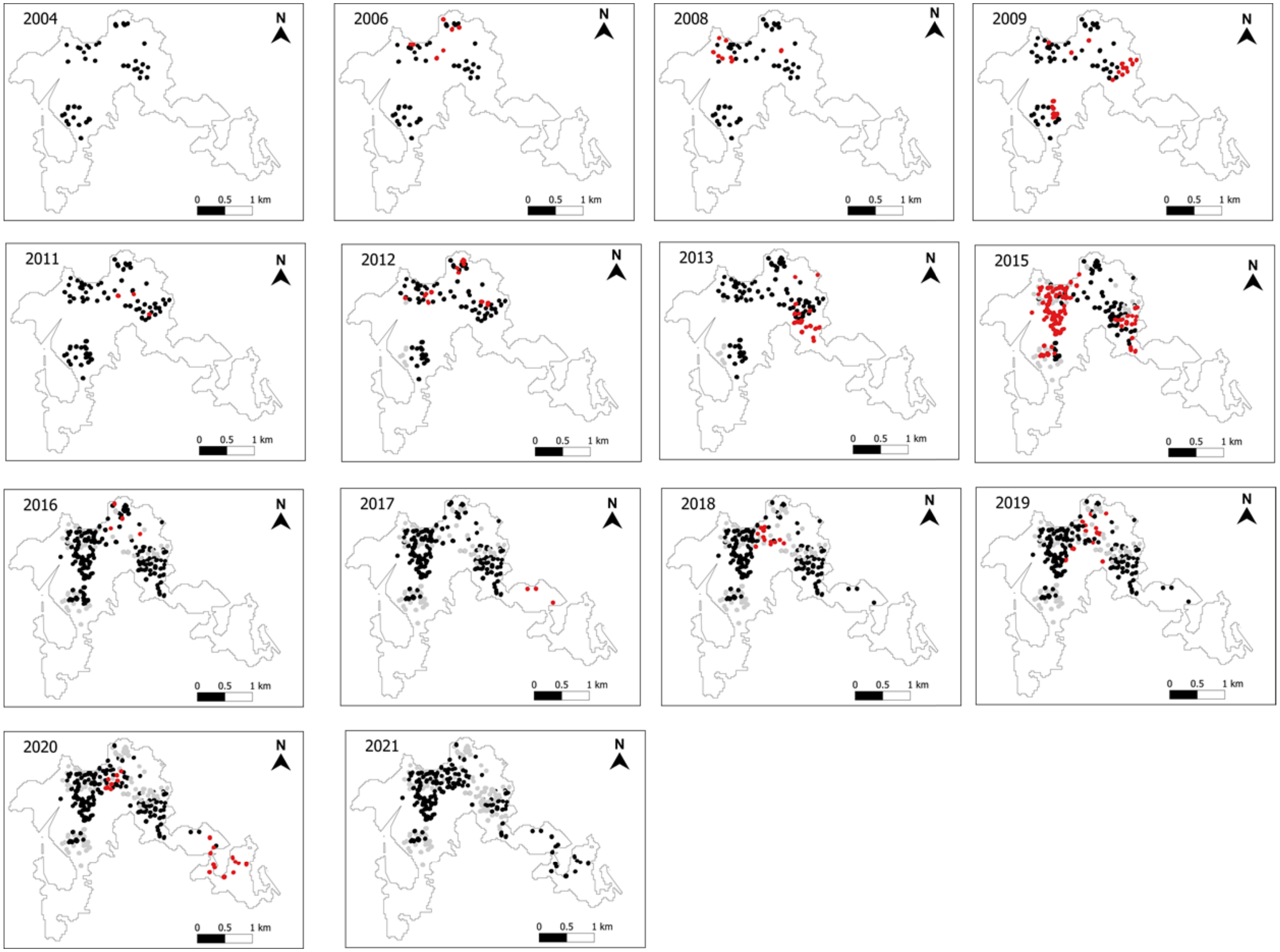

Figure S4.7. Temporal development of canopy gaps in the Panama Mangrove Patch (2004-2021): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

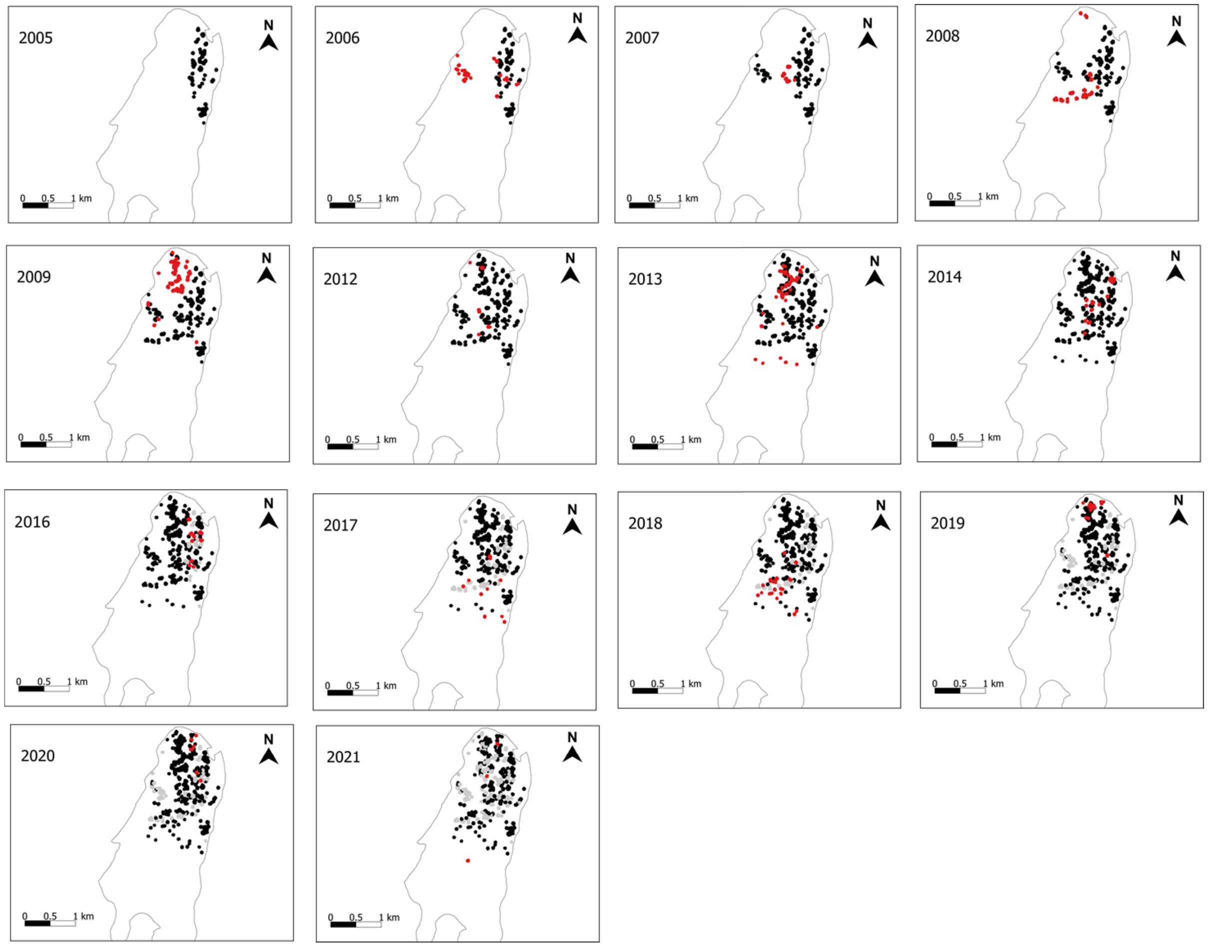

Figure S4.8. Temporal development of canopy gaps in the Timor Leste Mangrove Patch (2005-2021): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

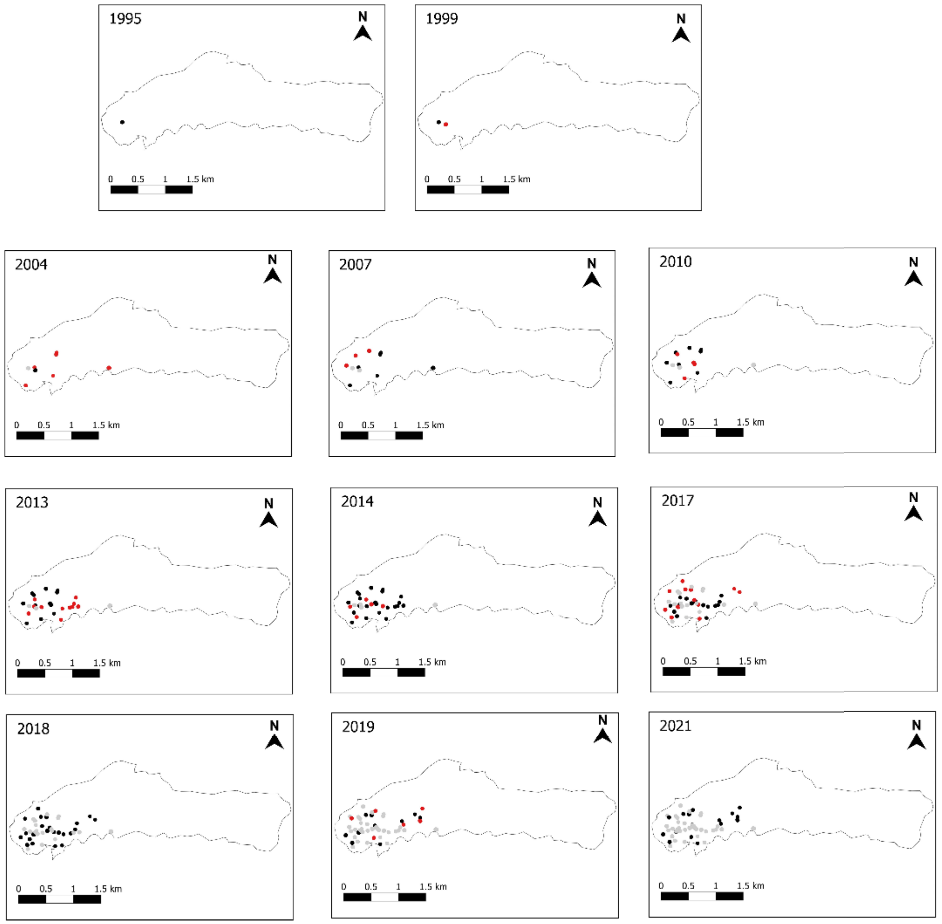

Figure S4.9. Temporal development of canopy gaps in the USA Mangrove Patch (1995-2021): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

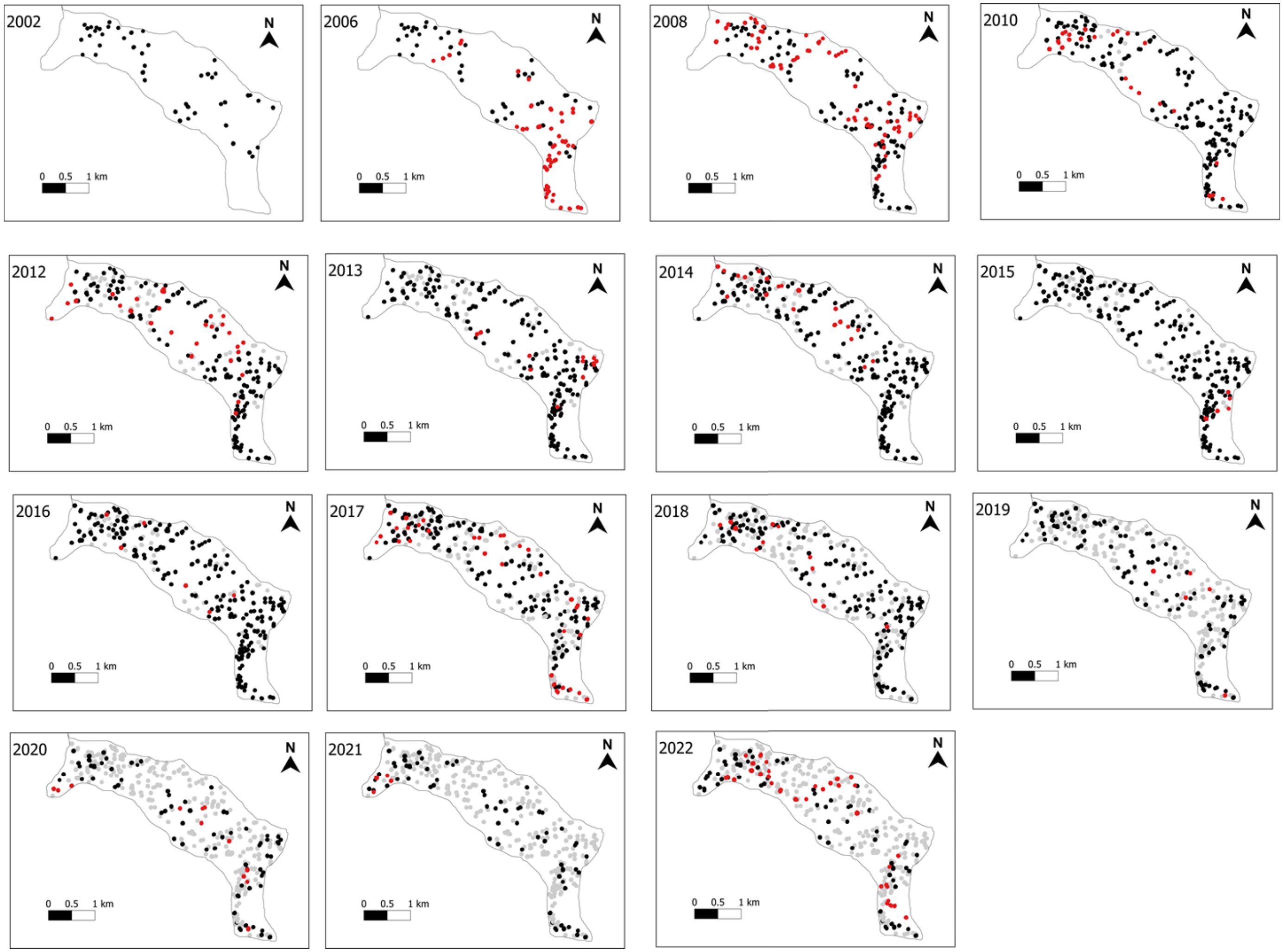

Figure S4.10. Temporal development of canopy gaps in the Viet Nam Mangrove Patch (2002-2022): Visualizing the patterns using google earth satellite images. Red dots represent newly developed gaps in a particular year, black dots represent gaps developed in previous years, and grey dots represent closed gaps.

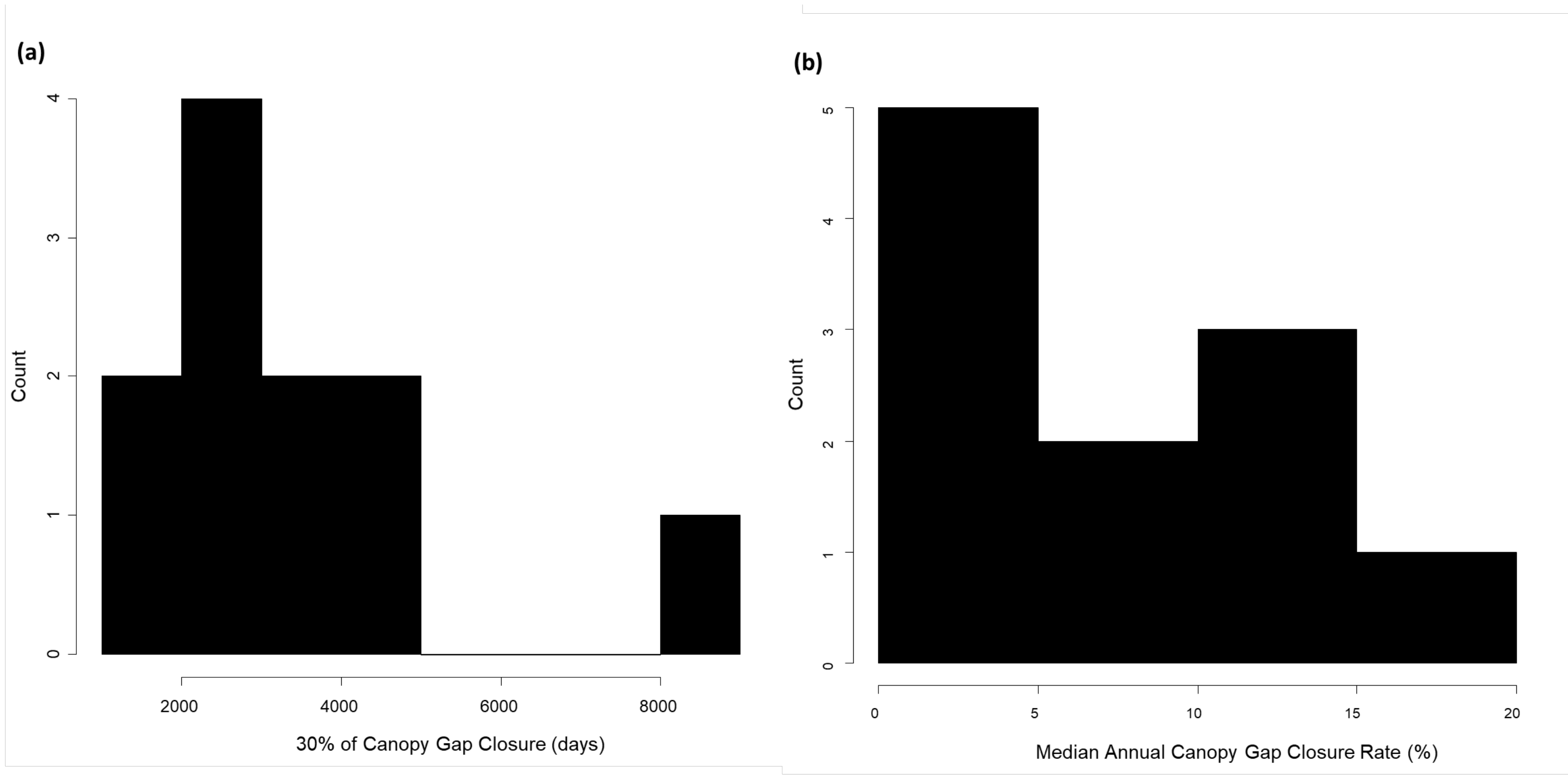

Figure S4.11. Histogram showing the (a) 30% Canopy Gap Closure in days (b) Median Annual Canopy Gap Closure Rate (%

Chapter 5 General discussion

5.1 Overview of the thesis findings

The primary goal of this thesis is to provide baseline data on the distribution patterns and dynamics of naturally formed canopy gaps at both local and global scales, elucidate the reasons for their formation and closure, and validate the global canopy gap regeneration capacity within mangrove forests. The three questions posed in this thesis were addressed in three separate chapters, as discussed below.

5.1.1 Which factors determine the global distribution and density of canopy gaps?

In Chapter 2, we identified the potential drivers influencing the occurrence and density of canopy gaps, as well as the spatial distribution of the canopy gaps. We employed an ensemble of small models and generalized linear models to explain the predictors on a global scale. We found that canopy gaps occurrences may be influenced by lightning strikes, and precipitation of the coldest quarter. The canopy gap density could be influenced by lightning strikes, precipitation of the wettest month, precipitation of the driest month, and the maximum temperature of the warmest month. Furthermore, we found canopy gaps in several countries across America, Africa, Asia, and Oceania. This reveals other unknown geographical range of canopy gap distribution that were not reported in previous studies (Amir, 2012; Amir and Duke, 2019; Sherman et al., 2000; Vogt et al., 2011), suggesting that, although canopy gaps are rare (Chapter 2), they are not restricted to specific geographical regions. Also, the geographical distribution of canopy gaps across the globe suggests multiple drivers of canopy gaps, and not just lightning strikes as have been previously assumed (Chapter 2). While lightings (i.e. the sporadic and unpredictable occurrence of electrical discharges due to thunderstorms) are common in the tropics and subtropics (Albrecht et al., 2016), where mangrove forests are located, the flash rate density (i.e. number of flashes per square kilometer per year) in those locations of mangrove forest varies (Chapter 2). The lightning flash rate density is a key factor to be considered in the occurrence and density of canopy gaps (Amir and Duke, 2019, Chapter 2). The assumption of lightning strikes (i.e. when the electrical discharges hit a tree) being the primary driver of canopy gaps must be interpreted cautiously, taking into account the available quantitative measurements of the cloud-to-ground lightning flash rate within a given mangrove patch area per year (Yanoviak et al., 2019). To validate the qualitative assumptions and anecdotes related to canopy gap occurrences (Chapter 2), I propose that the climatic data of the mangrove area should be taken into account. This can provide a more reliable prediction of the potential canopy gap drivers. Furthermore, an in-situ investigation of the species composition of the dead trees, the proportion of dead trees, and physical damages, including defoliation, broken trunks, broken branches, uprooted trees, and dead standing or fallen trees, should also be taken into account.

5.1.2 Which spatiotemporal patterns characterize canopy gaps and what are the factors influencing them on a local scale?

In Chapter 3, we used an integrated conceptual model, and spatiotemporal models to predict the spatiotemporal patterns of canopy gaps in South Africa's largest mangrove stand at uMhlathuze (80% of the total mangrove coverage in the country) near Richards Bay and a smaller mangrove stand in Beachwood near Durban to explain the drivers behind those canopy gaps and test the hypothesis of canopy gaps as a core of mangrove regeneration. We observed clustered spatiotemporal patterns at uMhlathuze. Beachwood canopy gaps primarily exhibited random patterns with some spatial clustering, along with random temporal patterns. The patterns at both sites support the hypothesis that lightning strikes, insects or pathogen attacks or competition potentially contribute to canopy gap formation. This aligns with the inconclusive evidence regarding the spatio-temporal patterns of canopy gaps in mangrove forests, particularly concerning lightning strikes as a causal agent (Amir, 2012; Amir and Duke, 2019; Sherman et al., 2000; Vogt et al., 2011). The ambiguity in the evidence regarding spatial distribution patterns is attributed to the chosen scale of the study site (Chapter 3). Mapping every canopy gap during field surveys can prove challenging given the scale of the study site and the limitations in physically navigating through dense forest and muddy sediment to account for each gap. These challenges can impact the interpretation of spatial patterns (Zhang et al., 2008). While we utilized satellite images to map the spatial patterns of the canopy gaps (Chapter 3), the selection of uMhlathuze and Beachwood sites showcased two contrasting spatial scales (i.e. large versus small mangrove stand) and the configurations of the dead standing or fallen tall trees within the mangrove stand influence the interpretation of the spatial patterns (Chapter 3). For instance, Vogt et al. (2011) reported inconclusive patterns (i.e., random, clustered, and regular) in the spatial distribution of canopy gaps within the five subplots of small and large mangrove stands analyzed in their study. Some other studies demonstrated spatially random patterns in a small mangrove patch (Amir, 2012; Amir and Duke, 2019) and clustered patterns of canopy gaps in a large mangrove patch (Sherman et al., 2000). Additionally, the scale of the seasonal occurrence of the potential driver has a similar effect on the temporal pattern. The temporal pattern of lightning strikes is associated with thunderstorms in the summer months of South Africa (Evert & Gijben, 2017; Essa et al., 2022), thus interpreted as clustered (Chapter 3). However, there could be random occurrence of thunderstorms resulting in lightning strikes (Evert & Gijben, 2017; Essa et al., 2022) beyond the summer months, thus interpreted as random (Chapter 3). Similar patterns of clustered and random occurrences of lightning strikes and hurricane seasons driving the temporal patterns have been reported in the USA and the Dominican Republic (Smith et al., 1994; Sherman et al., 2000, 2001; Zhang et al., 2008, Whelan 2004). In this thesis, I propose that the assessment of temporal patterns should consider historical climatic data in a given mangrove area. The investigation of canopy gap patterns should extend to larger scales, encompassing space and time, to reach conclusive results on their patterns and corresponding drivers.

In Chapter 3, we found no evidence of the occurrence of canopy gaps correlating with high or low temperature and precipitation in South Africa. As this observation pertains to a specific mangrove area and a limited time frame, drawing definitive conclusions about the role of temperature and rainfall in driving canopy gap occurrence is challenging. Further in-situ investigations should be conducted at different regional and local scales to validate the potential driver of canopy gap attributed to temperature and precipitation events.

5.1.3 Which factors influence the closure rates and duration of canopy gaps across different latitudes?

In Chapter 4, we used analytical metrics, Kaplan-Meier curves and generalized linear models to determine the canopy gap closure temporal dynamics and the factors influencing the closure. We found that the duration it takes for canopy gaps to close is potentially influenced by the mean temperature of the wettest quarter. Additionally, the rate of closure for canopy gaps is possibly influenced by the mean temperature of the wettest quarter, mean temperature of the driest quarter, pH, and salinity. The findings in the study partially explain the reasons for canopy gap closure (Chapter 4). The factors influencing canopy gap closure vary based on the local climatic conditions, geomorphological settings, and sediment resources of the mangrove forest (Osborne & Smith, 1990; Duke et al., 1998; Bosire et al., 2005; Amir, 2012). For instance, some previous studies suggest that the availability of light, the tidal regime, seedling dispersal, herbivory, and nutrients contribute to the closure of canopy gaps (Duke et al., 1998; Bosire et al., 2005). These factors were not included in this study due to a lack of available datasets.

Notwithstanding, the majority of the canopy gaps observed in South Africa (Chapter 3) and Australia (Chapter 4) have not closed over the time spans covered by the study (i.e. 18 to 23 years), despite the expectation that mangrove canopy gaps in general would close within 15 years (Duke, 2001). The findings of Chapters 3 and 4 significantly contradict the observations of Duke (2001) and Amir (2012), as well as the hypothesis derived from their work that canopy gaps serve as cores for mangrove regeneration (Amir & Duke, 2019). Their hypothesis lacks consideration of species effect, the tidal regime, herbivory, seedlings dispersal, and nutrient. Instead, they rely on the assumption that once canopy gaps are formed, the availability of light and temperature increases, facilitating the rapid regrowth of seedlings in those canopy gaps at higher densities. This process, they assume, contributes to the regeneration of the mangrove forest, preventing it from reaching a senescent stage without accounting for the aforementioned variables. However, we observed a lack of regeneration in canopy gaps, particularly in monospecific stands dominated by *Avicennia marina* and *Bruguiera gymnorhiza* (Chapter 3 and 4). In contrast, relatively fast regeneration was observed in stands dominated by *Rhizophora* spp and mixed stands of other mangrove species (Chapter 4). For instance, Whelan (2005) demonstrated the rapid recovery of canopy gaps in the Everglades National Park, USA, dominated by *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. Similarly, Amir (2012) showed the regeneration of canopy gaps in the *Rhizophora apiculata* dominant forest in Malaysia. This observation suggests that the species' effect on canopy gap regeneration should be further investigated in situ at different regional and local scales to validate these findings.

5.2 Ecological implications in the context of climate change

The factors identified as potential drivers of canopy gap occurrence and density imposes physiological stress on the mangrove trees (Chapter 2). This may ultimately lead to the mortality of mangrove trees and the formation of canopy gaps (Chapters 2 and 3). The changing climate, characterized by extremely high temperatures, storm events, and droughts, is likely to exacerbate the physiological stress on the trees, resulting in increased tree mortality (Clinton et al., 1993; McDowell et al., 2018, 2008; Anderegg et al., 2015; Ndlovu & Demlie, 2020, Chapter 2). Consequently, this is expected to increase the occurrence of canopy gaps in mangrove forests (Zhang, 2008). Despite the challenges in predicting long-term impacts, the negative consequences of climate change may jeopardize the structural integrity and equilibrium of mangrove forests.

In Chapter 3, we observed that the small-scale distribution of canopy gaps aligned with the locations of the tallest trees within the mangrove stands in South Africa. This disruption in the mangrove forest structure can impact the long-term storage of sequestered carbon in the trees (Yanoviak et al., 2019; Alongi, 2020; Gora & Esquivel-Muelbert, 2021). The largest trees within mangrove forests not only efficiently sequester atmospheric carbon but also store substantial amounts. Consequently, the death of such large trees can potentially lead to the release of stored carbon (Donato et al., 2011). Moreover, the death of the trees exposes the anoxic sediment to atmospheric oxygen and microbes, allowing for a faster decomposition rate of the organic material within the sediment. This, in turn, leads to the release of greenhouse gases such as carbon dioxide back into the atmosphere, potentially exacerbating global warming (Hamilton & Friess, 2018). As a result, the release of stored carbon due to increased tree mortality under climate change (Yanoviak et al., 2019; Alongi, 2020; Gora & Esquivel-Muelbert, 2021) and the lack of canopy gap regeneration (Chapter 3 and 4) could have profound consequences, disrupting the potential of mangrove forests as a nature-based solution for long-term climate change mitigation and adaptation strategies (Zimmer & Helfer, 2022).

Also, If the lack of regeneration of canopy gaps, as discussed in Chapters 3 and 4, is not proactively addressed in (re-)establishment efforts, especially within the context of climate change, it can worsen the fragmentation of the mangrove forest. The disruption of the forest, coupled with the release of stored carbon, worsens global warming and contributes to sea-level rise (Gilman et al., 2008). Large mangrove trees possess the ability to trap, augment sediment deposition, enhancing elevation and thereby expanding the mangrove's development seaward, reinforcing the mangrove resilience against sea-level rise (Kimeli et al.,2022; Ward eal.,2016). Conversely, the mortality of large trees and lack of canopy gap regeneration of the mangrove forest, as detailed in Chapters 3 and 4, may compromise the potential of mangrove forests to accrete sediment vertically. This can result in landward expansion under sea-level rise and potential reduction of mangrove habitat due to coastal squeeze from anthropogenic activities such as the construction of aquaculture ponds, small and large scale forestry, and coastal urbanization (Ward et al.,2016).

5.3 Socio-ecological implications in the context of climate change

Considering the socio-ecological role of mangrove forests (Walters et al., 2008), the climatic drivers of canopy gaps (Chapter 2) mediated by anthropogenic activities (i.e. construction of aquaculture ponds, small and large scale forestry, and coastal urbanization) in those regions that lack canopy gap regeneration (Chapter 3 and 4) can lead to substantial loss of mangrove habitats. This can lead to the loss of habitat for diverse fauna, serving as a source of food and income for coastal communities. Coastal communities relying on mangrove wood and fisheries for their economic livelihoods, especially in regions where canopy gaps are not regenerating (Chapter 3 and 4) may have to relocate to other mangrove areas if the frequency of climatic drivers (Chapter 2) is increasing (Zhang, 2008) and posing further threats to the regeneration of the mangrove canopy gaps. Moreover, displacement of coastal communities can exacerbate the anthropogenic pressures on the mangrove forests as these communities seek alternative locations, potentially leading to over-exploitation of the mangrove wood, fisheries in new areas (Polidoro et al., 2010). This migration may also result in conflicts over resource use among different communities competing for limited mangrove resources (Gammage et al., 2002). To address this challenge, community stakeholder engagements on the use of mangrove resources and community-based ecological (re-)establishment should be implemented to protect and rehabilitate existing mangrove forests in regions that lack canopy gap regeneration (Chapter 3 and 4) and face existential threats due to the increasing frequency of climatic drivers of canopy gaps (Chapter 2).

In the context of coastal resilience, large mangrove trees, with their complex root systems, serve as natural barriers against storm surges and coastal erosion, significantly contributing to the resilience of coastal communities (Alongi, 2008). Therefore, increased canopy gap occurrence due to climatic drivers (Zhang,2008, Chapter 2), coupled with a lack of canopy gap regeneration (Chapter 3 and 4), can weaken the coastal protection capacity of the mangroves, exposing the shoreline to tidal wave action and storm surges that potentially could destroy coastal communities (Gilman et al., 2008). Preserving and (re-)establishment of mangrove forests is imperative for sustaining the needs of the coastal communities and diverse fauna that depend on them (Zimmer et al., 2022). Therefore, prioritizing (re-)establishment of the forest is crucial, especially in mangrove areas where canopy gaps persist (Chapter 3 and 4), posing a risk of the forest fragmentation. Addressing these issues not only protect diverse ecosystems and the livelihoods they support but also enhances the overall resilience of coastal communities in the face of environmental challenges.

5.4 Practical applications

Chapter 2 presents a global spatial distribution map of mangrove patches with canopy gaps, while Chapter 3 focuses on a local spatiotemporal pattern map in South Africa. These maps can serve as practical guides for forest managers to prioritize mangrove areas at risk of non-closure (Chapter 4) and develop appropriate measures to (re-)establish the mangrove forests. The maps can also aid in selecting suitable locations for future (re-)establishment projects taking into account those sites that are not closing and require human intervention. Additionally, the maps can provide valuable insights for coastal communities, empowering them to make informed decisions to reduce or avoid small-scale or commercial logging activities in areas where canopy regeneration is lacking and gap formation can result in forest fragmentation. This proactive approach can ensure the sustainable management of the forest, while the local communities take proactive steps in (re-)establishing those non-closing canopy gaps (Chapter 3 and 4).

Human intervention is needed to address the areas experiencing lack of regeneration and rejuvenation within the mangrove forest (Chapter 3 and 4). Replanting in those non-closing canopy gaps should not only focus on refilling the gaps but should account for both the needs of coastal communities and the entire mangrove ecosystem to "build with nature" in providing valuable ecosystem services (Zimmer & Helfer, 2022). For instance, it may be important to consider re-engineering the hydrological system within the mangrove forest and not only provide seedlings where establishment may be doubtful (Lewis & Brown, 2014). The hydrological system includes the flooding depth, frequency, and duration which are crucial for the survival of the seedlings (Lewis & Brown, 2014). Previous replanting efforts failed due to either poor hydrological conditions or a limited supply of seedlings carried by the natural tidal inundation regime, which was cut-off (Lewis, 2005). Fertilization of the canopy gaps may be required to facilitate the regeneration of the gaps and thus rejuvenation of the forest (Clarke and Allaway, 1993). The species composition of the mangrove forest should be considered to account for replacing slowly re-growing species with fast-growing productive species which may already exist in the forest stand but possibly not found in those canopy gaps (Rahman et al., 2021; Zimmer et al., 2022). This approach is essential to sustain the economic livelihoods of coastal communities that depend on them for small-scale forestry (Zimmer, 2018). Additionally, (re-)establishment efforts should not be a one-off event; instead, a continuous monitoring program should be implemented to ensure the rejuvenation and regeneration of the mangrove forest.

5.5 Outlook

Hurricanes, insects, pathogens, and competition were briefly discussed in the study, necessitating in-situ investigations to establish their contribution to canopy gaps. The interactive effects of insects or pathogens and climatic factors that pose physiological stress on trees should also be further explored in-situ. Furthermore, the role of canopy gaps in valuable ecosystem services such as carbon sequestration and long-term storage requires additional in-situ investigations. Detritivores play a crucial role in the decomposition of organic matter and overall long-term carbon storage within mangrove forests. Further in-situ investigations should be conducted to understand the influence of canopy gaps on these organisms.

Similarly, the regeneration of canopy gaps should be monitored, particularly in regions where non-closing gaps persist. Factors such as light, temperature, tidal regimes, seedling dispersal, herbivory, species composition, and nutrients should be examined to inform mangrove practitioners on appropriate measures to take when (re-)establishing mangrove forests in those regions.

This thesis encountered certain methodological limitations across various chapters. One significant challenge involved the inconsistent temporal data in satellite images obtained from Google Earth Pro. This inconsistency could potentially lead to an underestimation of the temporal development of canopy gaps at specific sites. The presence of clouds and sun-shaded images might also contribute to the underestimation of the temporal development of canopy gaps.

Moreover, circular or elliptical canopy gaps generated by small-scale forestry and abandoned aquaculture ponds closely resemble those induced by natural processes, as observed in satellite imagery. Therefore, further in-situ investigations are necessary to distinguish canopy gaps created through natural processes from those associated with anthropogenic activities.

Future studies should also consider additional data sources of satellite images to comprehensively monitor the development of canopy gaps within a given mangrove forest. The development of an automated tool, such as deep learning algorithms, for detecting canopy gaps should be explored. This would facilitate real-time monitoring of canopy gaps and inform mangrove practitioners on prioritizing areas that require human intervention.

Notwithstanding the limitations observed in this thesis, its strength lies in the integrated spatio-temporal models, predictive models, and conceptual models used, which allowed overcoming the challenge of missing temporal data at some mangrove sites. This thesis employs a robust analysis that advances knowledge about the global distribution of canopy gaps in mangrove forests and their potential drivers on both global and local scales. Additionally, it explores the factors influencing gap closure, demonstrating spatiotemporal patterns of canopy gaps and areas within mangroves that lack regeneration. The analysis clearly reveals consistent patterns with previous datasets and provides alternative approaches and reasons for canopy gap formation and closure on both global and local scales.

Overall, this thesis contributes to providing baseline data on canopy gap distribution, emphasizing the urgent need for human assistance in (re-)establishment canopy gaps in those regions that lack natural gap regeneration. This is important in the context of safeguarding the integrity of valuable ecosystem processes and services to meet both human needs and ecological processes and properties crucial for the entire mangrove ecosystem.

5.6 References

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