

**Influence of Canopy Gaps on Mangrove vegetation and
Crab communities in the Andaman Islands**

by

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in

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Under the supervision of

Dr. Nehru Prabakaran

Scientist – D



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JUNE 2025



DECLARATION

I hereby declare that the work conducted under the thesis entitled "**Influence of Canopy Gap on Mangrove vegetation and Crab communities in the Andaman Islands**", is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Nehru Prabakaran, Scientist-D** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding, and the particulars given in it are true to the best of my knowledge.

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Perarivalan Sengannan has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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Influence of Canopy Gaps on Mangrove vegetation and Crab communities in the Andaman Islands

1. SUMMARY:

Small-scale, infrequent disturbances enhance habitat heterogeneity in the landscape and promote diversity. Canopy disturbances caused by lightning strikes in mature mangrove stands modify environmental factors such as canopy cover and light intensity. Response of mangrove vegetation and crab communities to such canopy gap formation remains the least investigated aspect among ecologists. The canopy gaps were stratified based on the recent and recovering status of vegetation recruitment along with gap age, and an intact forest plot was sampled as a control treatment. The result shows that canopy opening has a significant effect on water temperature, and it has a profound influence on structuring vegetation and the crab communities in mangroves. Seedling and sapling density was 2-fold higher in canopy gaps than intact forest, and higher sapling survival was witnessed in canopy gaps. 28 species of crabs were recorded collectively from all treatments. Crabs of the family *Ocypodidae* were found in large proportion in canopy gaps, as the organic matter from microalgae and bacteria is their primary food base. Overall, canopy gaps in contiguous mangrove habitats are a hot spot for crab diversity and serve as a regeneration niche for seedlings and saplings by creating structural heterogeneity in the landscape. It suggests that small-scale natural disturbances, such as canopy gaps, promote habitat complexity and crab diversity.

2. INTRODUCTION:

2.1 Background

The drivers of species diversity and distribution patterns are the most discussed topics in the ecological domain. The increasing trend of species richness from the poles to the equator is well known among ecologists and biogeographers (Brown, 2004). Many theories and hypotheses have attempted to explain this phenomenon, yet there is little consensus about the higher species richness in the tropical region. Among the most prominent theories, the Intermediate Disturbance Hypothesis (IDH) suggests that moderate, less frequent disturbance plays a pivotal role in sustaining high diversity (Connell, 1979). These modest levels of disturbance in a saturated environment increase habitat heterogeneity (Pickett and White, 2005), thereby maintaining dynamic balance in the ecosystem and creating opportunities for generalist species to periodically coexist with habitat specialists, which results in higher diversity (Pullin, 2002).

Habitat heterogeneity, in general, is the major driver of high species richness in tropical landscapes (Pickett and White, 1985; Connell, 1979). However, physiological and environmental stressors in a habitat limit species richness by allowing only species with unique adaptations to thrive (Smith, 2001). For example, Salinity and tidal flooding are the critical factors that determine the species richness and zonation in the mangrove ecosystem. Species with special adaptations like salt tolerance, viviparous seed germination, pneumatophores and aerial stilt roots occupy the specific available microhabitat within the mangrove ecosystem (Reddy, 2008).

2.2 Mangroves - an unique ecological system

The word mangrove is originally African and was learnt by the Portuguese in the early fifteenth century and spread throughout the world (Vannucci, 1989). Mangroves are salt-tolerant

vegetation that grows along the intertidal zones of tropical and subtropical regions (Tomlinson, 1986). They have the common traits for growing in a muddy, saline environment with remarkable adaptations of salt tolerance (Reddy,2008). These habitat plays an important role in maintaining coastal biodiversity and provide a wide range of ecosystem services (Mumby et al., 2004; Nagelkerken et al., 2008; Walters et al., 2008). It often appears in predictable, homogenous bands parallel to the coastline, river, and creek, with shared ability to flourish under a specific environmental condition, which are characterised by a distinct pattern of zonation and succession (MacNae,1969).

Mangroves are often exposed to natural disturbances like cyclones, lightning strikes, coastal erosion, and sea level changes, owing to their presence in the intertidal regions (Thampanya et.al, 2006; Whelan, 2005; Peereman et.al, 2022). In general, natural disturbance is a discrete event in time and a common phenomenon that influences the spatial and temporal pattern of the landscape (Seidl et al., 2011). The disturbance can be in the form of fire (Ratz,1995), high winds (Jeltsch,1994) or insect attacks (Coley and Barone, 1996). However, mangrove ecosystems experience different types of natural disturbance, ranging from single tree falls and lightning strikes on a very local scale to medium- and large-scale disturbances such as hurricanes (Smith et.al,2009). These disturbances play a critical role in increasing habitat heterogeneity and species compositions in mangroves (Vogt et.al, 2014; Azad et.al, 2021).

2.3 Canopy Gaps in Mangroves

The canopy gaps are a noticeable feature of mangrove forests all around the world and frequently reported in the literature (Putz and Chan, 1986; Smith, 1992; Feller and McKee, 1999; Clarke and Kerrigan, 2000; Duke, 2001; Whelan, 2005; Amir, 2019; Figure 1). They are referred to as canopy gaps, light gaps or lightning gaps by various researchers. Canopy gaps are areas where, at some point, concerned natural disturbance had caused the death of several mature trees (Clarke and Kerrigan, 2000). They are created across all developmental stages of the mangrove

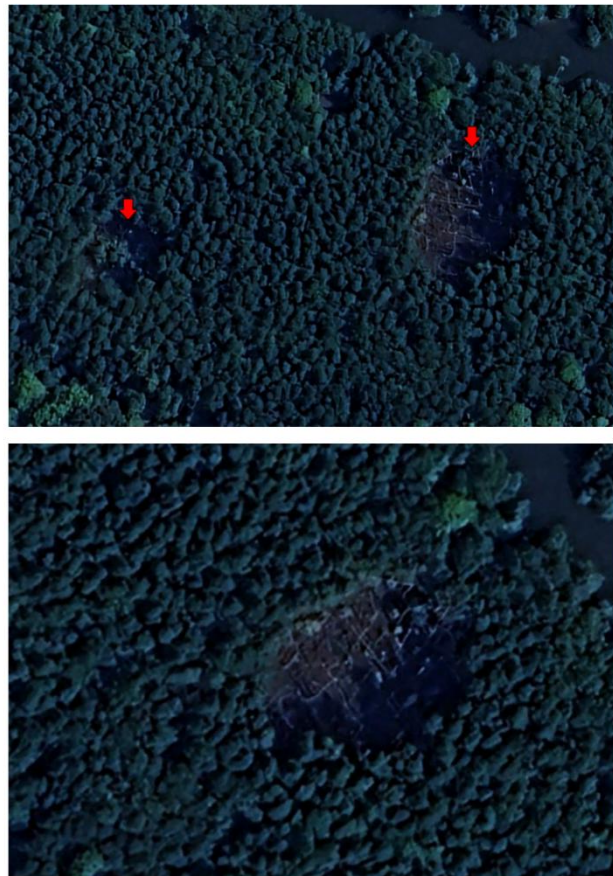


Figure 1: Aerial view of Mangrove Canopy gaps (Image©2025Airbus).

forests by various biological and environmental factors, including the aged mortality of old trees, driftwood scouring, flotsam smothering, sediment deposition, sediment erosion, lightning strikes, hail storms, cyclones pest, and logging (Smith 1992, Duke 2001; Pinzón et al. 2003). The exact cause of the canopy gap is unknown (Amir, 2012), where as lightning strikes are thought to be the most likely reason for small- to medium-sized canopy gap formation in mangroves, with other possible reasons: strong winds, logging, pest attack, mortality of old trees, and changes in sediment (Amir and Duke, 2009; Smith, 1992; Duke, 2001; Pinzón et al., 2003; Putz & Chan, 1986). Although the causes differ, they are all considered small-scale disturbances that are driven by various biotic and environmental factors that have an enormous impact on the mangrove ecosystem.

2.4 Role of Canopy Gaps

Lightning strikes are common in the tropical and subtropical regions, where they leave behind a patch of dead snags with clearance size ranging from 10 to 1900 m² (Craighead,1971; Johns, 1986; Smith 1992; Smith et al. 1994; Sherman et al. 2000; Zhang 2008; Amir and Duke 2019). These gaps are usually



Figure 2: A cluster of dead trees within a contiguous mangrove patch.

circular or elliptical-shaped with no living trees in the clearance (Whelan and Smith 2004; Figure 2). The approaching lightning strike travels laterally into the stem and destroys the membrane structure by permitting salt uptake, which results in tree mortality (Johns,1986). After the tree's death, the canopy gap undergoes a series of structural changes to the forest floor (Amir and Duke 2019). Duke (2001) characterised canopy gap recovery in six phases (Figure 3, Duke,2001). In the proposed schematic diagram, the processes and some physical attributes at the time are used to characterise each phase. The six phases start with a forest with no gap and cycle through gap creation phases and recovery phases.

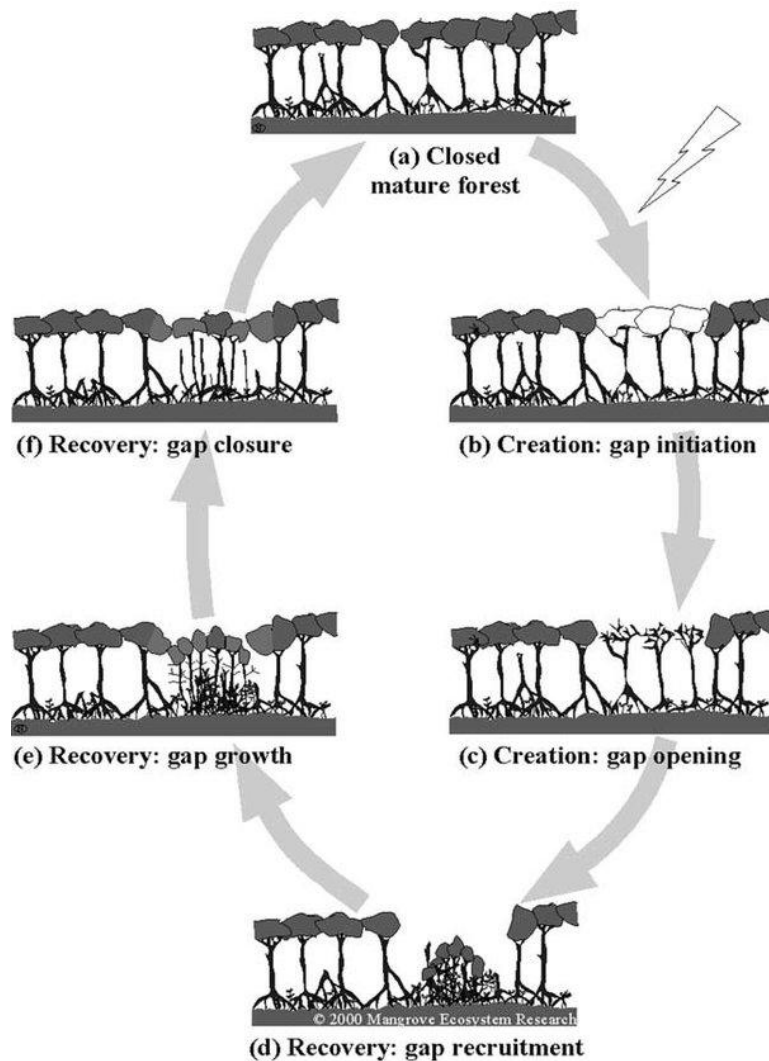


Figure 3: A schematic diagram showing the phases of recovery observed in common mangrove canopy gaps: (1) mature forest, (2) gap initiation, (3) gap opening, (4) gap recruitment, (5) gap growth and (6) gap closure (Duke,2001).

The regeneration starts with seedling establishment in the newly available area in the canopy gap; subsequently, the patch grows and refills to its original state. These complex processes increase structural diversity in the mangrove forests (Duke, 2001; Amir, 2012). Canopy gaps can alter several physical factors and biological processes; these processes are vital in mangrove regeneration, which includes increased Photosynthetic Active Radiation (PAR), humidity, evapotranspiration, light levels, and soil properties - salinity, temperatures, and

nutrients (Smith 1987; Smith 1992; Amir and Duke 2019). Given the adverse effect caused by canopy gaps, it plays a crucial role in mangrove forest dynamics, regeneration, community composition, population size, sediment, water temperature, and other ecological processes (Craighead 1971; Smith 1992; Smith 1994; Sherman et al. 2000; Duke 2001; Whelan 2005; Zhang 2008; Amir and Duke 2019). The increased light availability provides an opportunity for the regeneration of seedlings, and the gap undergoes a series of successions; eventually reaching the senescence stage (Duke, 2012). Leaf litter and fallen branch accumulation contribute to trapping seedlings on the forest floor (Whelan, 2005). Thereby, canopy gaps are the primary sites for tree regeneration (Sousa and Mitchell, 1999).

2.4.1 Vegetation Response to Canopy Gaps

By and large, canopy gaps favour higher recruitment of *Rhizophora* than any other seedlings and saplings (Whelan, 2005). Field experiments in Australia showed inter-specific variation in tree growth, where *Rhizophora stylosa* had the highest growth rate, followed by *Bruguiera gymnorhiza*, *Avicennia marina* and *Ceriops tagal*. In general, *Rhizophora spp.* grow twice as high as *Ceriops spp.* and three times higher under the canopy (Smith 1987). All four species, *Rhizophora stylosa*, *Bruguiera gymnorhiza*, *Avicennia marina* and *Ceriops tagal*, shows significantly higher growth in canopy gaps than under the canopy (Smith,1987). The canopy gaps created by various means for natural recovery, where the dormant seedlings growing under the canopies get the chance to grow and refill the canopy gap (Amir,2012). Hence, canopy gaps provide a means for the natural recovery and promote the youthfulness of the forest by replacing the old trees with a new forest stand (Smith 1992; Smith et al. 1994; Duke 2001; Amir and Duke 2019).

2.6 Research Gap

Earlier studies have primarily focused on the response of mangrove vegetation to canopy gaps (Duke, 2001; Vougt, 2013; Azad, 2012; Amir, 2019; Clarke, 2004). However, the potential impact of canopy gap on benthic invertebrates in the mangrove ecosystem is poorly understood (Whelan, 2005; Diele et al., 2013; Nobbs et al., 2015; Barbaner et al., 2022). Diverse macrofauna inhabits mangrove forests, with crabs and gastropods being dominant and widespread (Fondo and Martens 1998; Cannicci et al. 2008). Crabs play a significant role in the nutrient cycle by consuming a substantial part of primary production (Macintosh et al., 1999). They are known for their leaf litter turnover in mangrove ecosystem systems (Lee, 2008). They increase soil

aeration through digging burrows and eventually increase mangrove productivity (Macintosh et al. 1999; Smith et al., 1991). Brachyuran crabs (Figure 4) of the family *Sesarmidae* are opportunistic scavengers, while many have an essentially herbivorous diet, particularly crabs of the subfamily *Sesarminae* (Skov et al., 2002). whereas crabs of the family *Ocypodidae* are the main consumers of the organic component, derived from macroalgae and bacteria (Cannicci et al. 2008). Crabs belonging to the genera *Astruca*, *Tabuca* and *Gelasimus* are known to



Figure 4: (a) *Gelasimus tetragonon*, a detritivorous crab species, which is found in canopy gaps in large numbers. (b) *Perisesarma emople*, an opportunistic species that dominates all the successional stages in mangroves.

ingest bacteria and microalgae (France, 1998; Bouillon et al.,2002) and are capable of removing high amount of chlorophyll-A and bacteria in the sediment (Kristensen and Alongi,2006). In general, the brachyuran crab community play a significant role in the functioning of the mangrove ecosystem (Macintosh et al., 1999).

India, with a vast stretch of coastline, approximately 11,098.81 km including islands, is home to 46 mangrove species; about 56 % of the world's mangrove species (Ragavan et.al, 2019; MoPSW, 2025). Mangrove research in India has predominantly focused on the distribution and status of mangrove diversity. Previous studies in India predominantly explored the structural responses of mangrove vegetation to sea-level changes, geomorphology, and large-scale disturbances like tsunamis (Singh, 2014; Nehru & Balasubramanian, 2018), whereas the response of benthic communities to such disturbances remains one of the least investigated aspects (Hadiyanto et al 2020, Fulmali et al., 2025 and Kumar & Wesley, 2012).

Mangrove habitat harbours a diverse range of benthic fauna. In particular, crabs play a crucial role in nutrient cycling and ecosystem dynamics. Indian mangroves host 184 species of brachyuran crabs, representing 99 genera and 29 families (Sathish,2023). Various environmental parameters, such as light intensity, temperature, pH, and organic content, influence the diversity and richness of these crabs.

Canopy gaps play a crucial role in the ecosystem by creating unique microhabitat with altered light availability, moisture, and nutrient conditions, which influence vegetation recovery and crab community composition. Therefore, understanding canopy gap dynamics over time is necessary to elucidate mangrove successional processes throughout vegetation recovery. Moreover, there is an absence of studies addressing mangrove habitat responses to lightning-induced disturbances or other small-scale canopy disruptions in India, let alone the Andaman and Nicobar Islands. Also, the influence of canopy gap formation within contiguous mangrove

patches on maintaining species richness of crab communities remains largely unexplored. By and large, the Andaman and Nicobar Islands, with their unique biodiversity, remain underrepresented in mangrove fauna studies, let alone mangrove crabs.

2.7 Study Objectives

The present study aims to understand the influence of canopy gaps in structuring mangrove vegetation and the crab community compositions. The specific objectives of the study include:

1. To understand the role of canopy gaps in shaping the vegetation composition.
2. To understand the response of mangrove crab communities to various stages of vegetation succession in the canopy gaps.
3. To understand the effect of canopy gap formation on physico-chemical parameters (Example: Water temperature, pH, Salinity & Humidity) of mangrove habitat.

2.7.1 Research questions

- a) What is the vegetation composition in the canopy gaps?
- b) Is there any difference in crab community composition among intact forest and canopy gap recovery stages?
- c) What is the effect of canopy gap in the gap microenvironment?

2.7.2 Hypothesis & Predictions

- a) High species richness among the vegetation of recent canopy gaps. Species richness will decline with the increase in the canopy gap age.

Prediction: The dispersing propagules of various mangrove species will have an opportunity to regenerate in the recent canopy gaps. However, with age, the species with efficient adaptation to the microhabitat prevailing in the gaps will outcompete other species, thus reducing the species richness.

b) Canopy gap allows habitat generalist crabs to persist without being eliminated by habitat specialists (Connell,1978).

Prediction: Recent canopy gaps will have more generalist species, and more habitat specialists will be observed in intact forests. At the intermediate stage of succession, recovering canopy gaps will exhibit a higher species richness as the combination of both habitat generalists and habitat specialists.

On the whole, we hypothesised that the change in micro-environment will have an impact on (i) mangrove vegetation recovery and (ii) crab community composition will change over time of mangrove recovery. We also anticipated that the canopy gaps provide a refugia for the *Ocypodidae* family, and *Sesarma* tend to inhabit closed canopies, as they are highly dependent on mangrove leaf litter (Skov et al. 2002). Higher crab diversity will be found in recovering canopy gaps with the combination of *Ocypodidae* and *Sesarmidae* family crabs, as both light and moderate vegetation cover are available in recovering canopy gaps.

3) METHODS

3.1 Study Area

The Andaman and Nicobar Islands (ANI) in the Bay of Bengal are an extended mountain range between the Burmese peninsula and Sumatra (Figure 5). The islands span approximately 8,249 km², with 86.93% of their landmass is designated as forestland (ISFR, 2023). The ANI contributes the longest coastline of 3,083.5 km to the 11,098.81 km Indian coast (MoPSW, 2025). The indented coastline with undulating terrain leads to the formation of innumerable creeks, bays, and estuaries, which support rich

mangrove growth at a high degree of diversity (Ragavan et al. 2019). The most recent estimate from the Forest Survey of India shows that 608.29 km² of land is covered by mangroves, in which the Andaman Islands contributing a significant portion, with 38 mangrove species. (FSI, 2025).



Figure 5: Study area map with study sites in North Andaman, Middle Andaman and South Andaman Island group.

3.2 Sampling design and data collection

The current study examines six major mangrove patches from three main Island groups of the Andaman Islands: North Andaman, Middle Andaman, and South Andaman (Table 1). Google Earth Pro (version 7.3.6.10201) was used to identify and characterise the canopy gap, based on size and year of appearance. Canopy gaps of radius ≥ 10 m were selected to overcome the edge effect from the surrounding intact canopy forest. Subsequently, a unique ID was given for the selected canopy gaps; their exact coordinates were collected, and location points were saved in the All-in-one Offline Maps android application (version 3.15d) for field navigation to the selected canopy gaps. Motorboats and traditional canoes were used to reach the closest proximity of the treatments.

Table 1: The summary table shows the location, treatment type and number of plots per Island group.

S.No	Island Group	Location	Coordinates	Treatment type			Total plots in each site
				Recent	Recovering	Intact	
1.	North Andaman	Aerial bay	13.09181 S 92.09181 E	2	2	4	8
		Kalighat	13.09657 S 92.94423 E	3	3	6	12
		Mayabundar	12.87220 N 92.85506 E	3	3	6	12
2.	Middle Andaman	Bakultala	11.81367 N 92.70714 E	6	6	12	24
3.	South Andaman	Wright myo creek	11.81279 N 92.68997 E	3	6	9	18
		Wimberligunj	11.79275 N 92.70954 E	3	0	3	6
Total plots in each treatment				20	20	40	Grand total = 80

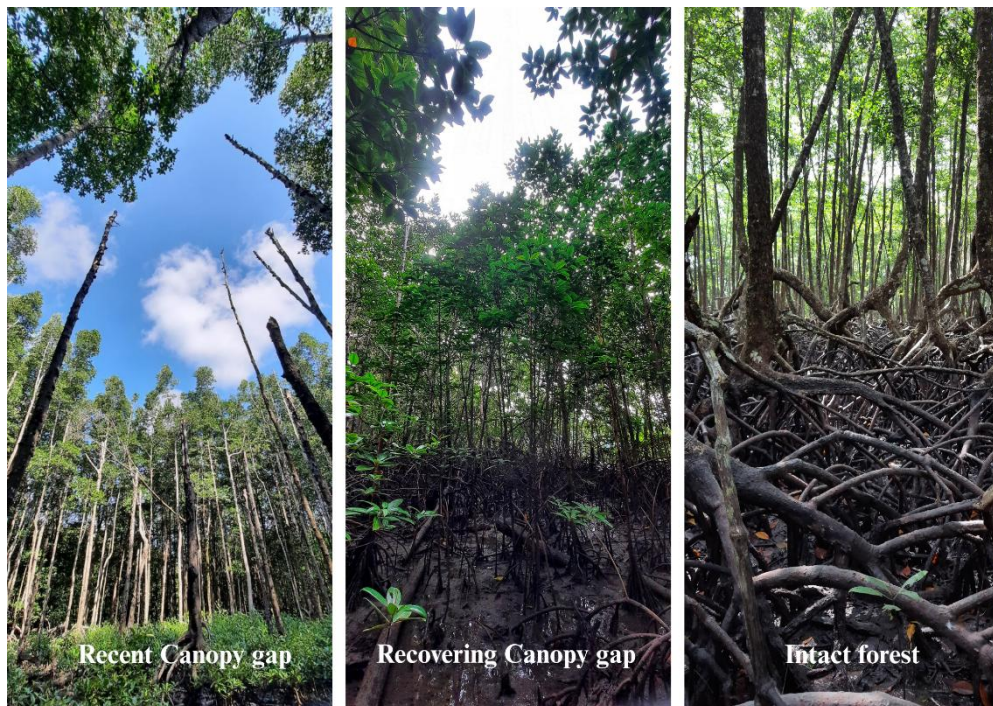


Figure 6: Photographic representation of each treatment: Recent canopy gaps with only seedlings and saplings, Recovering canopy gaps with seedlings, saplings and trees ≥ 10 cm GBH and control plot in closed canopy forest.

3.2.1 Measuring Canopy Gap Environment

A total of 80 plots were sampled spanning across the Andaman Islands, in which treatments were stratified as recently formed canopy gaps (1 to 6 years old), recovering canopy gaps (7 to 16 years old), and Intact forest (Figure: 6). Further, the recent canopy gaps were characterised by the presence of seedlings (upto 1.37 m height) and saplings (> 1.37 m height and upto 10 cm Girth at Breast Height (GBH)) to ensure that the gap had formed recently. The sampling effort for the recent canopy gap category was 8 in the North Andaman, 6 in the Middle Andaman, and 6 in the South Andaman ($n = 20$). The sampling effort was higher for North Andaman, owing to the presence of various large mangrove patches (Mayabundar, Kalighat, and Aerial Bay). The recovering gaps were characterised by the presence of seedlings, and saplings and trees (≥ 10 cm GBH). 8 recovering canopy gaps were sampled in North Andaman, 6 in Middle

Andaman, and 6 in South Andaman. Randomly selected 10 dead trees were measured for GBH at the canopy gaps with the presence of dead snags. Both height and GBH were measured for 10 randomly chosen trees at the gap edge. All the canopy gaps were sampled along with a control plot in an intact canopy forest with a canopy cover of more than 90 %. The distance from the canopy gap to the control plot was maintained at a minimum of 50 m in all locations, with the parallel distance as same as the distance between the canopy gap and the nearby creek. After approaching the canopy gap, the north-to-south and east-to-west diameters were measured (Figure 7) using a meter tape to locate the gap centre at the point of interception between two transects. The gap are was calculate by using the elliptical area formula as per the methodology adopted by Brokaw (1982):

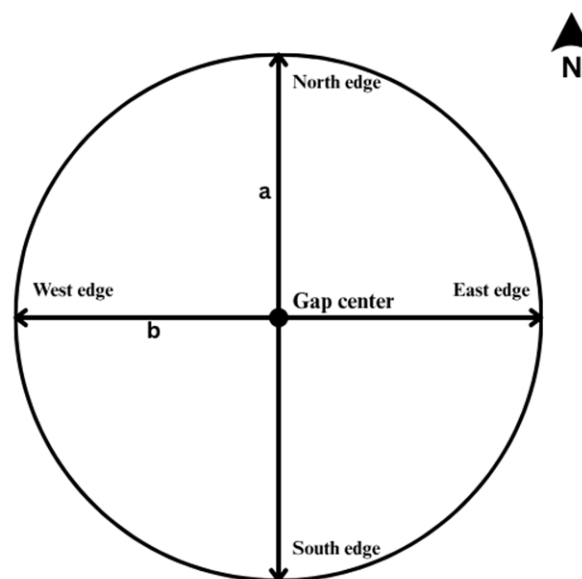


Figure 7: Schematic diagram for measuring gap diameter in the North to South direction and the East to West direction.

$$\text{Gap area} = \pi (a/2) \times (b/2)$$

a = Diameter from North to South, and b = Diameter from East to West.

The environmental variables, such as pH, salinity, water temperature, and canopy cover, were recorded at each treatment. A hydroponic waterproof pH tester (Hanna-model HI98118) was used to measure pH and water temperature in stagnant water at the centre of each treatment. A hand refractometer (ERMA hand refractometer) was used to measure the salinity of the water. The canopy cover was measured from the centre of the plot using a spherical densiometer.

3.2.2 Vegetation Sampling

A circular plot with a seven-meter radius was laid at the center of each treatment for sampling trees. GBH and height were measured for all the trees in the plot. A free-man's tape was used to measure the tree GBH. The Nikon Forestry Pro II laser rangefinder was used to measure the tree height. A nested sub-plot of two-meter radius was planted at the gap center for sampling seedlings and saplings (Figure 8). All the plants were identified and counted. Unidentified plant species were photographed and collected for preparing the herbarium to aid in the identification. The specimens were identified at the Regional Centre of the Botanical Survey of India, Andaman and Nicobar Islands.

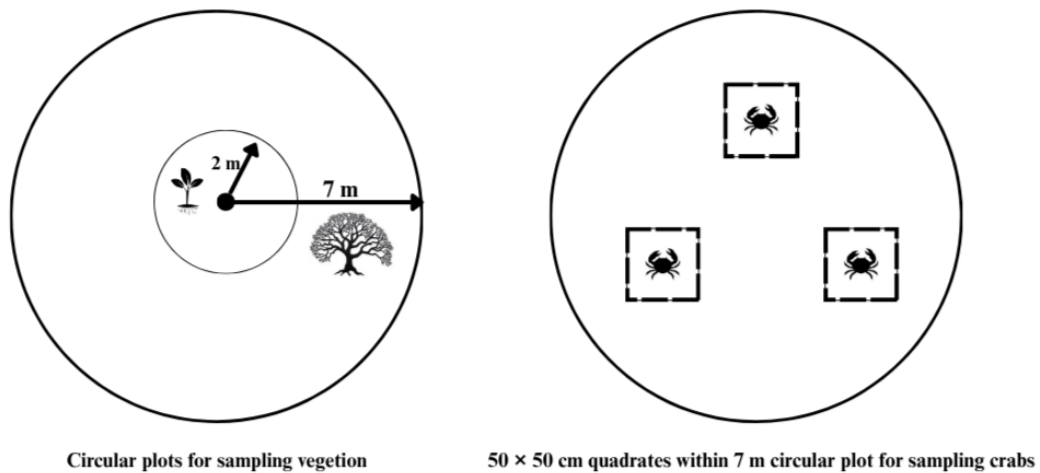


Figure 8: Schematic diagram for vegetation sampling and crab sampling within circular plots.

3.2.3 Crab sampling

Crab sampling was carried out with three 0.25 m² randomly placed quadrats (50 cm x 50 cm) within the 7m radius plots laid for vegetation sampling (Nobbs, 1999). Visual count was conducted according to Skov and Hartnoll (2001). Crabs were counted within the quadrat, after the observer had remained motionless for 15 minutes from a distance of 2 m from the quadrat, which is sufficient time for resumption of full activity for mangrove crabs (Nobbs, 1999). Burrow count and organic matter (incl. leaf, wood debris) per quadrat were enumerated after the visual count. The diameter of each woody debris within the quadrat was measured using a steel ruler. All the crabs within the plot were handled for identification. Unidentified specimens were collected and preserved with 70% ethanol and later identified up to species level using the taxonomic guides (Cannicci et.al, 1997; Shih et al., 2016). All the specimens were photographed with a DSLR Camera (model: Nikon D800E) with a macro lens (model:

NIKKOR 90 mm). The photographs were verified by expert crab taxonomists, and confirmed the species identification.

.3 Data Analysis

3.3.1 Canopy Gap Environment Variable

Data accumulation and segregation were performed using Microsoft Excel 2021 and R (R Core Team, 2020; Wickham, 2011). Canopy gap size was calculated with standard deviation for each treatment of the three island groups. Together, the range of age distribution was also calculated (Table 2). Pearson's correlation matrix was performed between all the variables; ecologically important variables, which correlated by less than 60%, were retained for further statistical analysis. Linear mixed effect model (LMM) ($(y_n) \sim \text{canopy_open}$) was computed to understand the relation among micro-environment variables to the canopy openness.

3.3.2 Vegetation Analysis

Relative dominance, relative frequency, and relative abundance were calculated for all tree species present in the surveyed plots. Subsequently, relative frequency and relative abundance were computed for seedlings and saplings. Important Value Index (IVI%) was calculated by using the following formula (Curtis and McIntosh, 1951):

$$\text{IVI\%} = \text{Relative frequency} + \text{Relative abundance} + \text{Relative dominance (for trees)}$$

$$\text{IVI\%} = \text{Relative frequency} + \text{Relative abundance (for seedlings and saplings)}$$

Shannon diversity Index (H) and Shannon evenness Index (E) were calculated for each treatment, and the average diversity index was calculated using the vegan package in R (ver. 4.4.4). EstimateS (v.9.1.0) was used to estimate vegetation species richness by using the Chao 1 richness estimate. The rarefied-species accumulation plots were visualised using R (R Core Team, 2020; Wickham, 2011) with the package ggplot2. Dissimilarity in tree species

composition between treatments was analysed using the Multi-Response Permutation Procedure (MRPP) with the species abundance data. In MRPP, the A value ranges between 0 to 1, and it is the proxy for dissimilarity between communities. Lower A value signifies a higher variation between the treatments. Seedling density was calculated for each nested 2m radius plot. Shapiro-Wilk test was performed to determine the distribution of data; If the data is normally distributed, ANOVA was performed to compare the mean seedling and sapling count between treatments and Tukey's test was used to compare among treatments. On the other hand, if the data is not normally distributed, Kruskal-Wallis test (Non-parametric test) was performed to compare among the treatments, and Pair-wise Wilcoxon test was used for pairwise comparison between treatments.

3.3.3 Crab community analysis

Shannon diversity index (H) and Shannon evenness (E) were calculated for each treatment using the vegan package in R (ver. 4.4.4). EstimateS (v.9.1.0) was used to estimate crab species richness by using the Chao 1 richness estimate. The rarefied-species accumulation plots were visualised using R (R Core Team, 2020; Wickham, 2011) with the package ggplot2. Rank abundance curves were plotted with species abundance data for each treatment. Non-metric Multi-Dimensional Scaling (Vegan::metaMDS) with Bray-Curtis similarity was performed to visualise the compositional differences between the three treatments (ie, Recent gap, Recovering gap, and Intact forest plots). The Multi-Response Permutation Procedure (MRPP) was used to assess the similarity of the communities across the treatments. Principal Component Analysis (PCA) was performed to summarise and visualise the best-explaining predictor variables. Variables with the most significant change throughout the data were used for GLMM to check family-specific responses to the predictor variable (canopy open, pH, salinity, water temperature). Crab density and burrow density were calculated for each treatment. Shapiro-Wilk test was performed to determine the distribution of data. ANOVA and

Tukey's test were used for normal distribution. As the data was not normally distributed, Kurskal-Wallis test was performed to compare Shannon diversity Index(H), Shannon evenness Index(E), Chao 1 estimator, crab abundance and burrow count between the treatments. Pair-wise Wilcoxon test was performed to compare the treatments.

4) RESULT:

4.1 Canopy Gap Characteristics

A total of 40 canopy gaps with sizes ranging from 270 m² to 2463 m² (mean = 941.37±581 m² SD) were assessed in the study. Majority of the canopy gaps were within 300 – 600 m² in size (38%), while 78% of the gaps were within 300 – 1200 m² in size (Figure 9). The width of canopy gaps ranged between 19.8 and 68.4 m (mean = 34 ± 11 m) and the perimeter ranged from 782 to 5710 m (mean = 2249 ±1316). Overall, the mean canopy gap size was highest in the North Andaman Islands, followed by the Middle Andaman Islands and least in the South Andaman Islands (Table 2). The mean GBH of dead trees within the canopy gap was 68 ± 23 cm, and the average GBH and height of trees at the canopy gap edge were 69 ± 24 cm (GBH) and 16 ± 4 m (Height), respectively.

Table 2: Summary of canopy gap age, size and canopy cover of three island groups.

Island Group	Treatment type	Number of plots	Minimum gap age (Years)	Maximum gap age (Years)	Average gap size (m ²)	Average canopy cover %
North Andaman	Recent gap	8	2	6	1522.4	22
	Recovering gap	8	9	16	1107	53
	Intact forest	16	-	-	-	93
Middle Andaman	Recent gap	6	3	6	1027	21
	Recovering gap	6	6	13	823	74
	Intact forest	12	-	-	-	93
South Andaman	Recent gap	6	2	5	511	15
	Recovering gap	6	8	13	409	82
	Intact forest	12	-	-	-	98

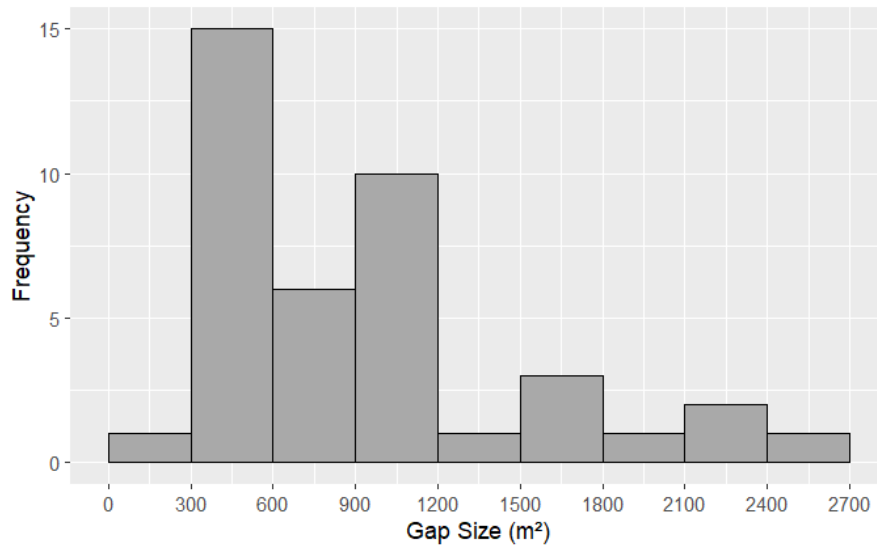


Figure 9: Frequency distribution of canopy gap size measured from the Andaman Islands. (n=40)

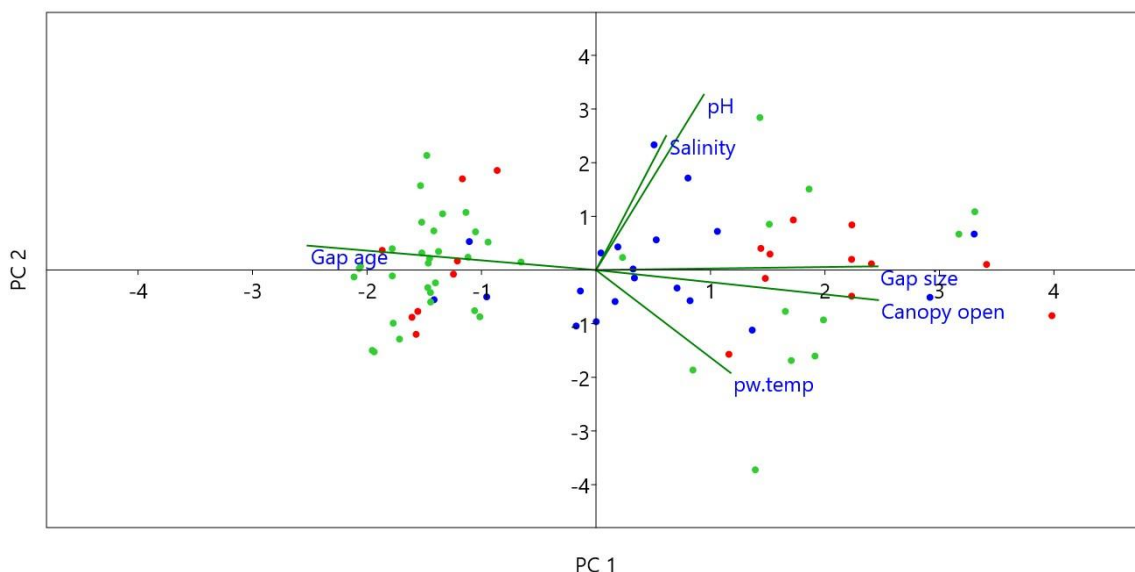


Figure 10: The relation between the canopy opening and other environmental variables. The red, blue and green points represent data points of Recent gaps (red), Recovering gaps (blue) and Intact forest (green), respectively.

Table 3: PC1 and PC2 eigenvalues in PCA.

Variables	PC 1	PC 2
Gap age	-0.54844	0.098929
Gap size	0.53531	0.015033
Canopy open	0.53622	-0.12177
pH	0.20488	0.71103
Salinity	0.13322	0.54388
Water temperature	0.25576	-0.41689

Principal Component Analysis (PCA) of the environment variable explains 41.3 % with PC1 and 19% with PC2. The ordination plot elucidates the positive correlation between canopy openness, water temperature, pH, salinity, and gap size with PC1. Canopy openness and water temperature were highly correlated. The gap age was negatively correlated with PC1 and positively correlated with PC2. Gap age and Gap size were in an independent opposite direction on the x axis, which explains that the increase in gap age, gap size will reduce as the vegetation

recovers in the canopy gap. Canopy opening shows a significant increase in water temperature($p < 0.05$). Whereas pH and salinity positively correlated with canopy openness.

Table 4: Model results for the response of the environment variable to canopy openness.

Model rank (LMM)	Estimate	SE	t value	P value	AICc
water.temp ~ canopy_open + (1 island_group)	0.013835	0.004456	3.105	0.002	297.45
ph ~ canopy_open + (1 island_group)	0.0009301	0.0005759	1.615	0.11	-24.14
salinity ~ canopy_open + (1 island_group)	0.005146	0.008488	0.606	0.546	414.82

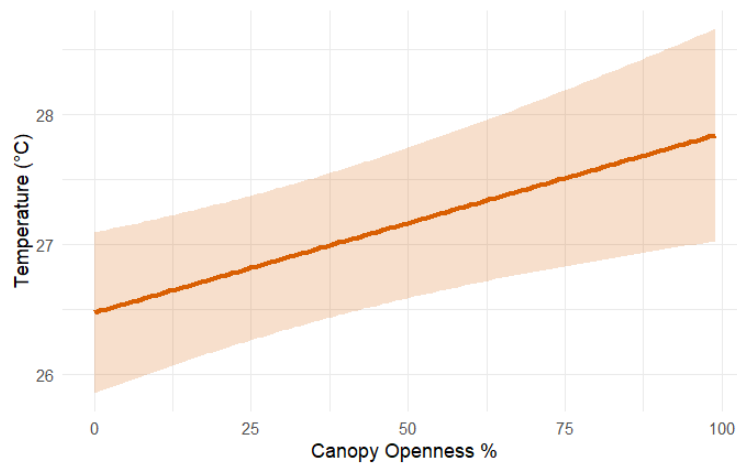


Figure 11: Response curve of water temperature with respect to canopy opening.

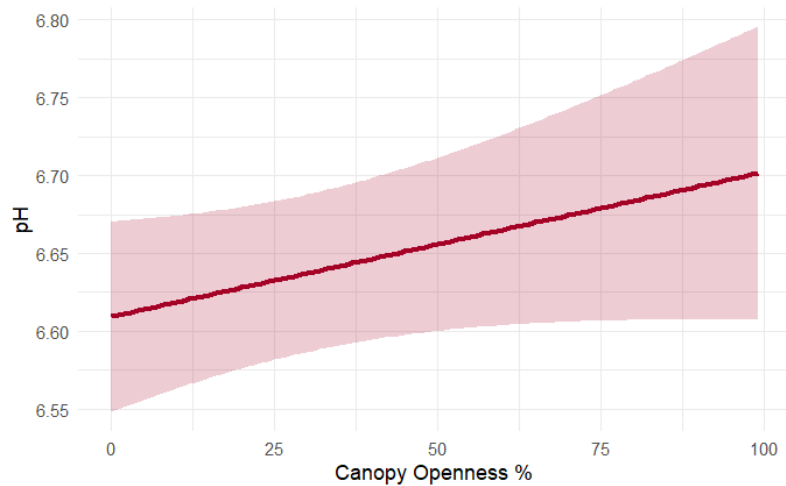


Figure 12: Response curve of pH with respect to canopy opening.

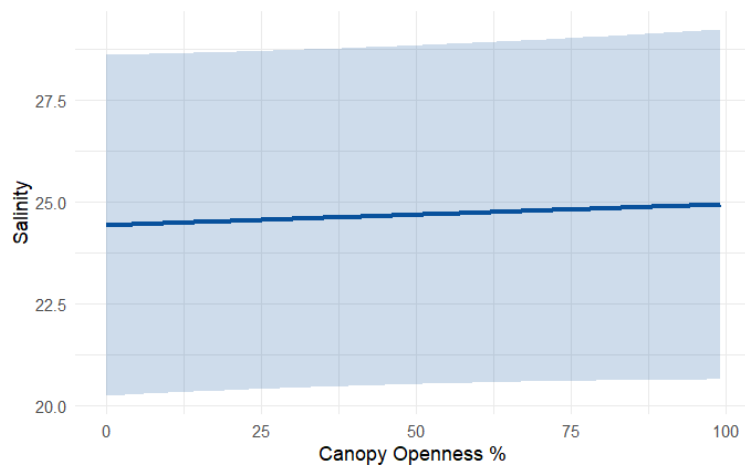


Figure 13: Response curve of Salinity with respect to canopy opening.

4.2 Vegetation composition

4.2.1 Species diversity and composition

A total of 11 species belonging to 8 families were recorded from the surveyed plots. 10 species were found in the recent canopy gap, 8 species in recovering canopy gaps, and 9 species in intact forest. Out of the 11 species observed, we found *Bruguiera gymnorhiza*, *Rhizophora apiculata*, *Rhizophora mucronata*, and *Phoenix paludosa* in all three treatments.

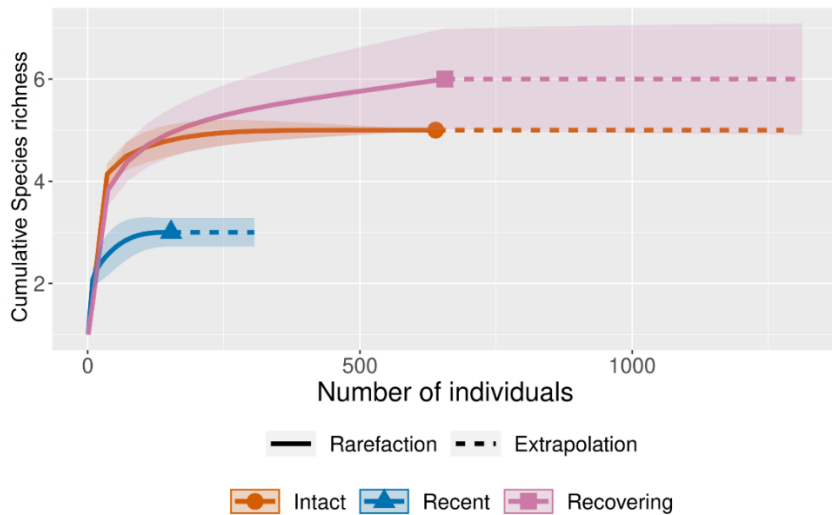


Figure 14: Rarefied Individual-based species accumulation curve for trees in each treatment type.

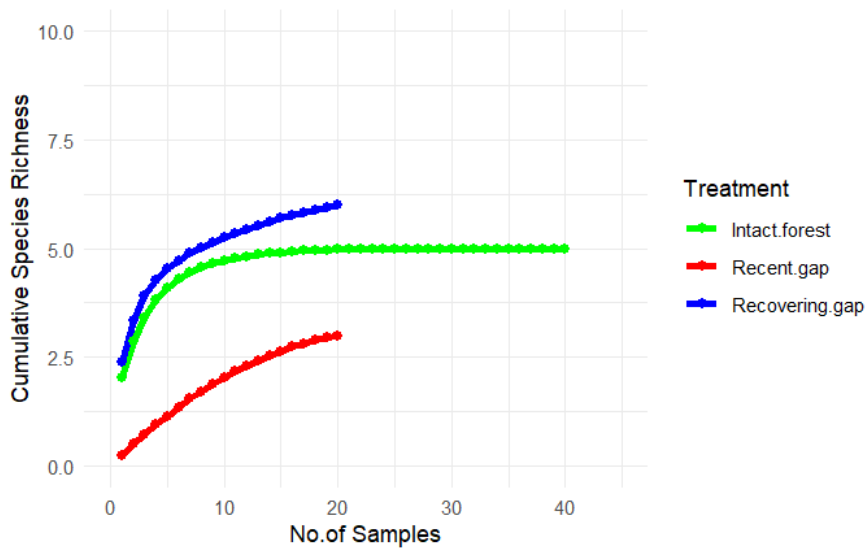


Figure 15: Rarefied Sample-based species accumulation curves for trees in each treatment type.

The individual-based and sample-based species accumulation curve for trees shows that the recovering plots have higher species richness in terms of trees ≥ 10 cm GBH, given the no trees in recent canopy gaps. All three curves have reached an asymptote, indicating sampling adequacy.

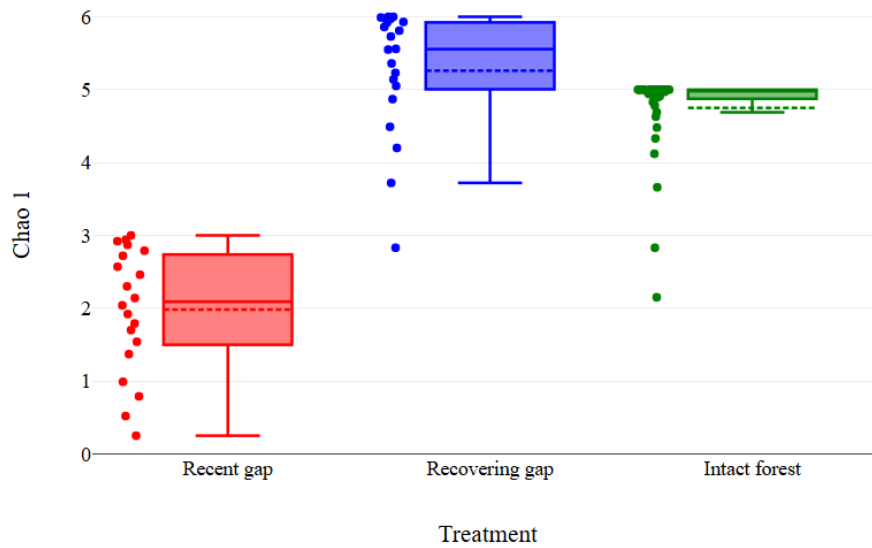


Figure 16: The estimated (Chao 1) richness of mangrove trees in each treatment type.

The Chao 1 species richness estimator for trees showed higher species richness in recovering canopy gaps ($p < 0.05$), which is obvious that canopy gaps allow new species from nearby patches to colonise, and the intact forest patch is dominated by a few species in the monospecies condition in the study area. However, there were no trees in the recent canopy plot, which is visualised as the lowest richness estimate. Diversity was almost the same in recovering and intact forest (Shannon diversity, H' ; Recent gap = 0.43 and Recovering gap = 0.45) and lowest in recent canopy gaps. Higher evenness was observed in intact forests (Shannon Evenness, $E = 0.74$) and lowest in recent canopy gaps.

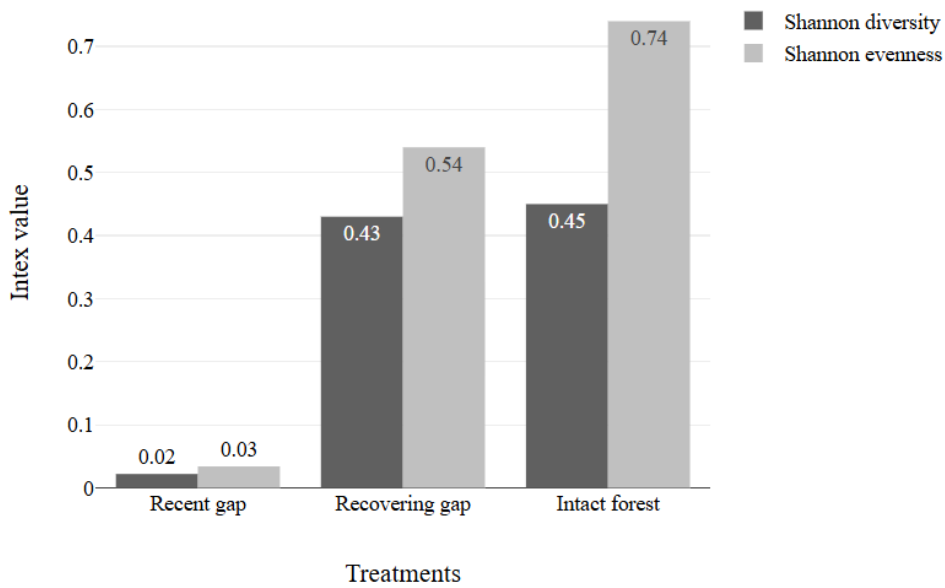


Figure 17: Comparison of Shannon diversity Index (H) and Shannon Evenness Index (E) of trees in each treatment type.

Rarefied species accumulation curves (Individual-based and Sample-based) were plotted separately for seedling and sapling treatments. All the curves reached an asymptote. Both individual based and sample-based curves visualise higher species richness in recent canopy gaps.

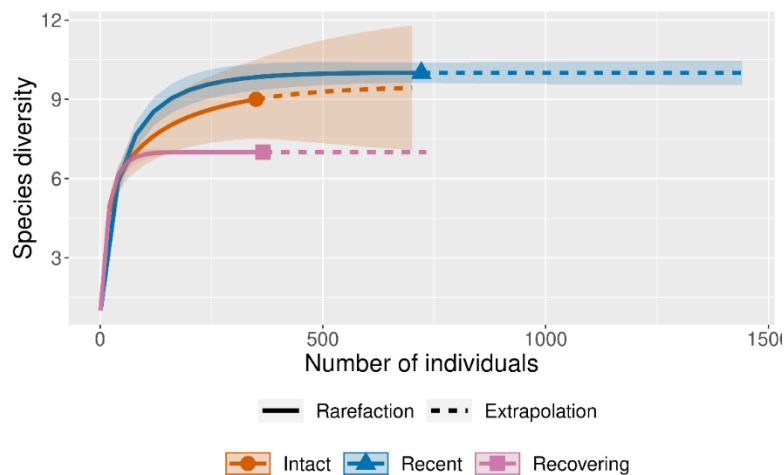


Figure 18: Rarefied Individual-based species accumulation curves for seedlings and saplings.

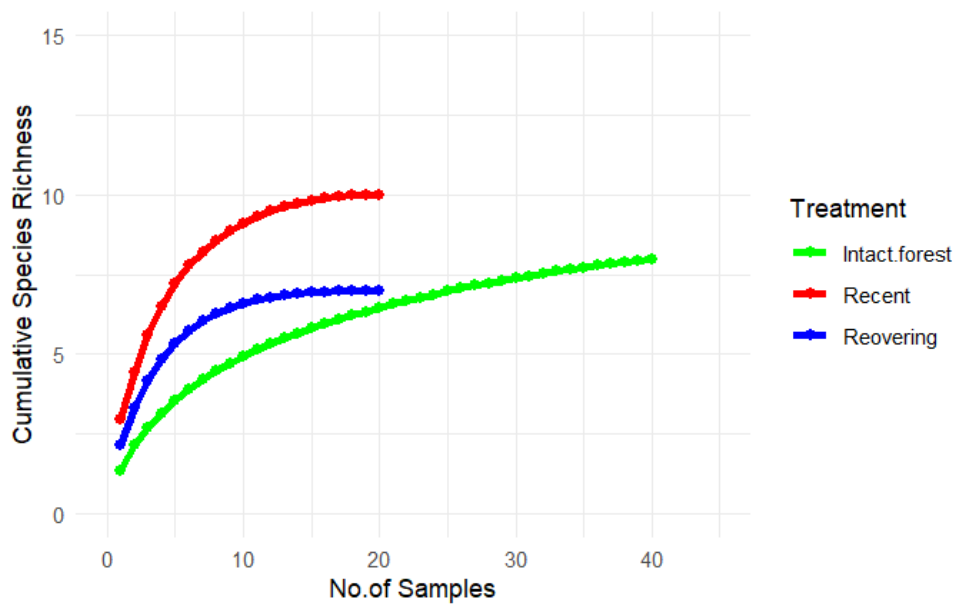


Figure 19: Rarefied Sample-based species accumulation curves for seedlings and saplings in each treatment type.

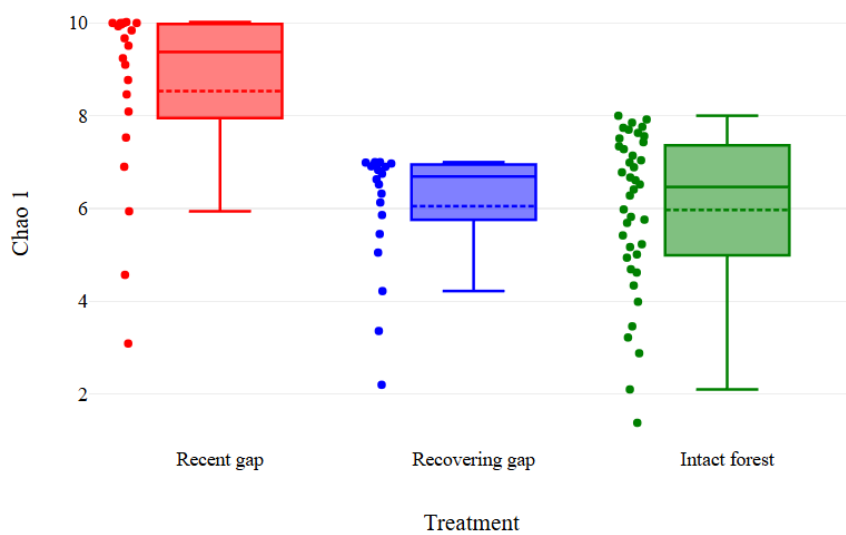


Figure 20: The estimated (Chao 1) richness among treatments for seedlings and saplings.

The Chao 1 richness estimator for seedlings and saplings plots estimates higher species richness in recent canopy gaps ($p < 0.05$), which proves our hypothesis prediction of higher species richness in recent canopy gaps, as it allows more number of species from other patches to colonise in the earlier stage.

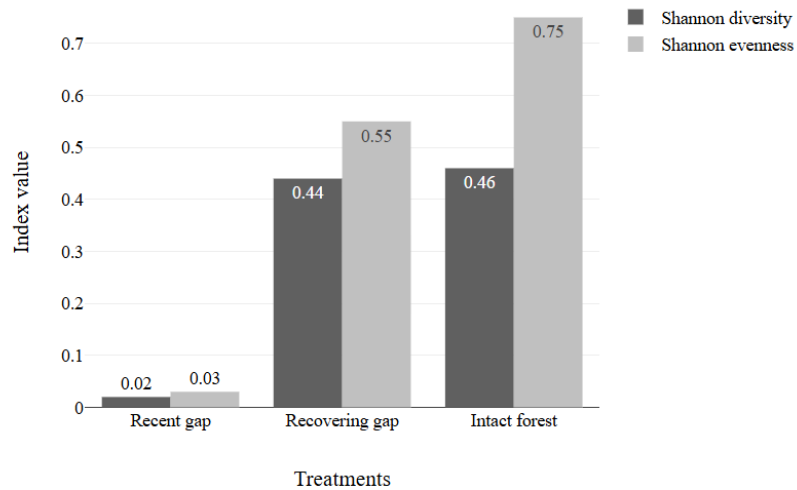


Figure 21: Shannon diversity Index (H) and Shannon Evenness Index (E) of seedlings and saplings in 2m plots.

Diversity was almost the same in recovering and intact forests and lowest in recent canopy gaps, as the recently formed canopy gaps are super dominant with fast colonising *Rhizophora apiculata* seedlings, which is very common in the study area. Evenness was highest in intact forest ($E = 0.75$), followed by recovering canopy gaps and lowest in recent canopy gaps.

Table 5: Summary of Multi-Regression Permutation Procedure (MRPP) among three treatment types for tree species.

Dissimilarity index: bray		
Permutation: free		
Number of permutations: 999	A value	P value
Overall comparison	0.038	0.004
Recent gap vs Recovering gap	0.026	0.917
Recovering vs Intact forest	0.044	0.001
Recent gap vs Intact	0.010	0.155

There was an overall dissimilarity in the community composition across all treatment types ($p < 0.05$). It shows no significant difference between recent and recovering canopy gaps. On the other hand, there is high dissimilarity in community composition between recent and intact forests, and also between recovering and intact.

Table 6: Summary of Multi-Regression Permutation Procedure (MRPP) among three treatments for seedlings among treatment types.

Dissimilarity index: bray		
Permutation: free		
Number of permutations: 999	A value	P value
Overall comparison	0.035	0.011
Recent gap vs Recovering gap	0.013	0.183
Recovering vs Intact forest	0.001	0.452
Recent gap vs Intact	0.051	0.002

There was an overall significant dissimilarity ($p < 0.05$) in the community composition across all treatment types. It shows that all the treatments are significantly different in seedling composition. The higher A value between the recent and intact forest shows higher dissimilarity between the treatments.

Table 7: Summary of Multi-Regression Permutation Procedure (MRPP) among three treatments for saplings among treatment types

Dissimilarity index: bray		
Permutation: free		
Number of permutations: 999	A value	P value
Overall comparison	0.044	0.019
Recent gap vs Recovering gap	0.002	0.341
Recovering vs Intact forest	0.073	0.001
Recent gap vs Intact	0.039	0.024

There is overall marginal significance in sapling species composition, with higher dissimilarity between recovering and intact forest. The results show no significant difference in sapling species composition between recent and recovering canopy gaps.

4.2.2 Species Dominance

A total of 2902 individual plants in the canopy gaps and intact forest plots were included in the study. *Rhizophora apiculata* was the dominant species in all the treatments with 2149 individuals (relative abundance (RA) = 74%), followed by *Rhizophora mucronata* with 237 individuals (RA = 8 %). Along with *Bruguiera gymnorrhiza* and *Ceriops tagal*, these four species constitute 92% of the individuals in the three sampled treatments.

A list of all tree species dominance in terms of important value index (IVI%) is given in Table 9. *Rhizophora apiculata* had the highest IVI% in all three treatments, followed by *Rhizophora mucronata* in the recent and recovering gaps. In intact plots, *Bruguiera gymnorrhiza* has the second highest IVI% (IVI% = 20.66), where *Rhizophora mucronata* is the third dominant species (IVI% = 19.91).

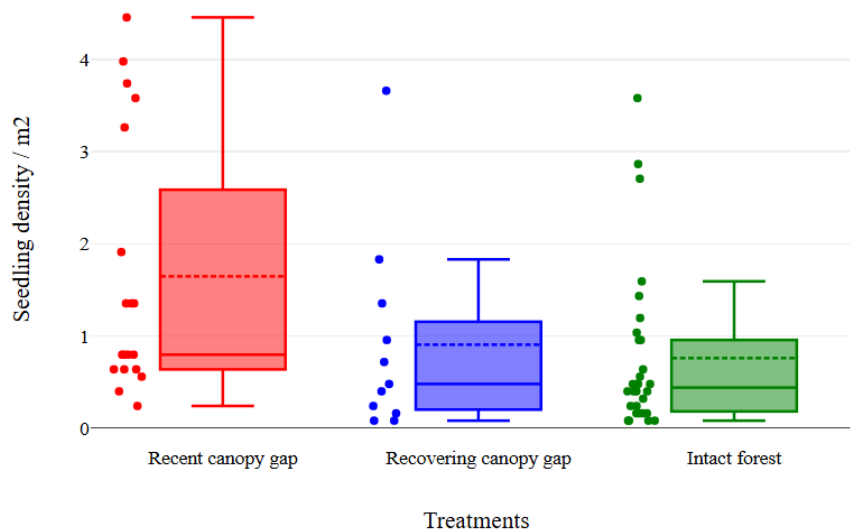


Figure 22: Comparison of seedling density among treatment types.

Both seedling and sapling densities differed significantly between treatments ($p < 0.05$). The recent canopy gaps show the highest seedling density, with more than 2-fold increase compared to intact forests and an 83% increase than recovering canopy gaps (Figure 22). Seedling density was significantly different between the recent and recovering and the recent and intact. No significance between recovering and intact.

The sapling density follows a similar trend as seedling density, with recent gaps displaying the highest density, with over 3 times the density observed in intact forests(Figure 23). Recovering gaps still show significant sapling establishment (2-fold increase than intact forests) but lower than recent gaps. *Rhizophora apiculata* dominated the seedlings and saplings in all the treatments. It covers 73% of the total sample with 1046 individuals of seedlings and saplings, where the total sample size is 1437, with the highest IVI% (Recent canopy gap = 89.66, Recovering canopy gap = 75.56, and Intact forest = 68.14).

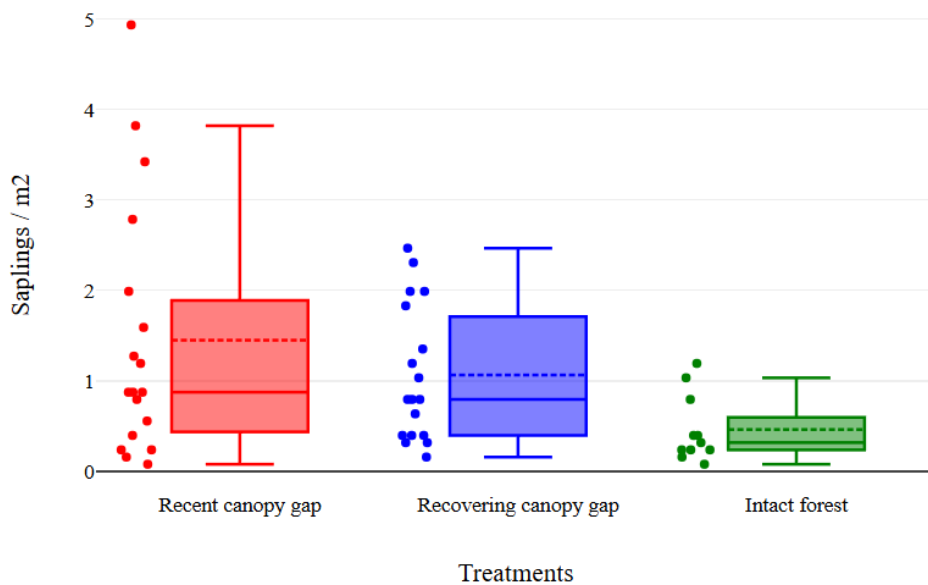


Figure 23: Comparison of Sapling density among treatment types.

Sapling density was significantly different between recent and intact, and also between recovering and intact, but no significant difference between recent and recovering canopy gaps.

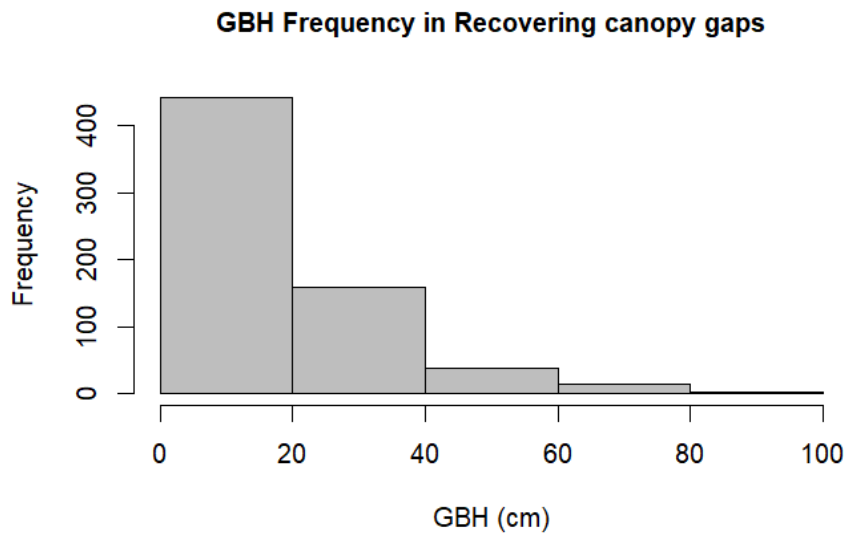


Figure 24: Frequency distribution of GBH in Recovering canopy gaps.

(Figure 23) shows a higher proportion of trees falling under the Girth at Breast Height (GHB), ranging from 10 to 20 cm in recovering canopy gaps. Totally 442 individuals in recovering canopy gaps are within this GBH range. It implies a higher survival of saplings into young trees.

From the calculated IVI% for the seedlings and saplings, *Rhizophora apiculata* emerged as the most dominant in all three treatments, followed by *Rhizophora mucronata* and *Xylocarpus granatum* in recent canopy gaps. In recovering canopy gaps, *Acrosticum aureum* and *Xylocarpus granatum* had the second and third highest values. Seedlings and saplings of *Ceriops tagal* were in the second and *Xylocarpus granatum* in the third highest in the intact forest plots.

4.3 Crab Community Composition

4.3.1 Sampling efficiency and overview:

A total of 28 crab species of 12 genera from three superfamilies (*Ocypodoidea*, *Grapsoidae* & *Portunoidea*) were recorded. All the species except two belonged to the superfamily *Ocypodoidea* (n = 10) and *Grapsoidae* (n = 16). A total of 78.35% of the crab species belong to *Grapsoidae*, and 21.49% belong to the *Ocypodoidea* superfamily respectively. From all the treatments, family *Sesarma* represented 55.55% in the recent canopy gap, 63.63% in the recovering canopy gap, and 91.99% in the intact forest. The family *Ocypodidae* contributes only 21.49% of the total catch. In recent = 38.77%, recovering = 29.9%, and in intact forest = 0.18%, respectively.

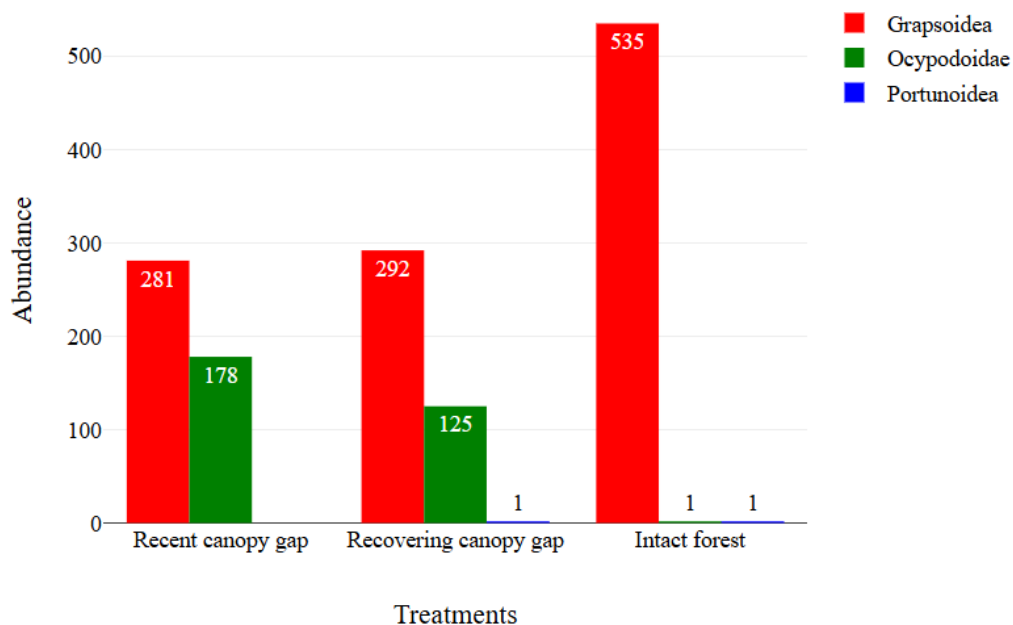


Figure 25: Superfamily-wise total abundance of crabs among treatment types.

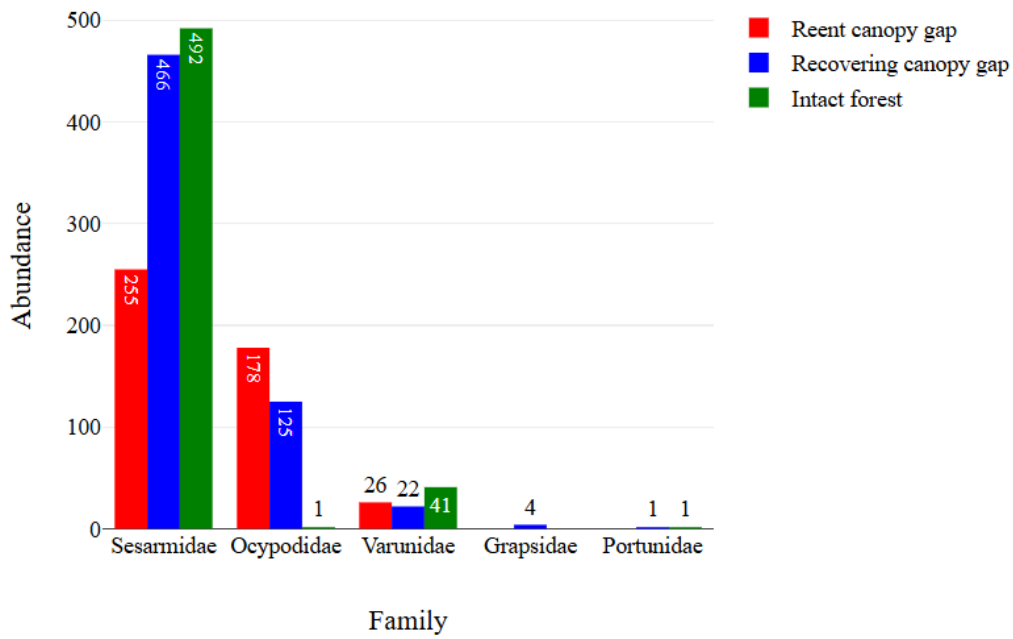


Figure 26: Family-wise total abundance between treatment types.

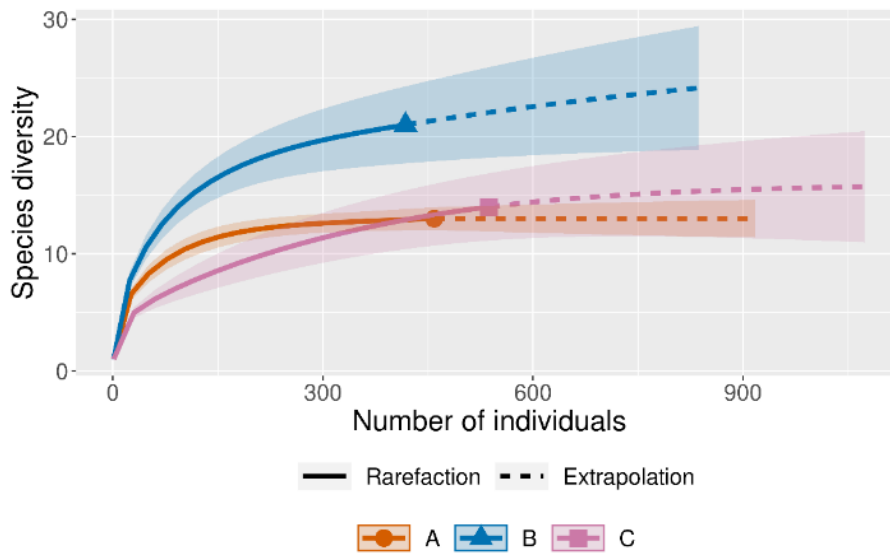


Figure 27: Rarefied individual-based species accumulation curves for crabs in each treatment type.

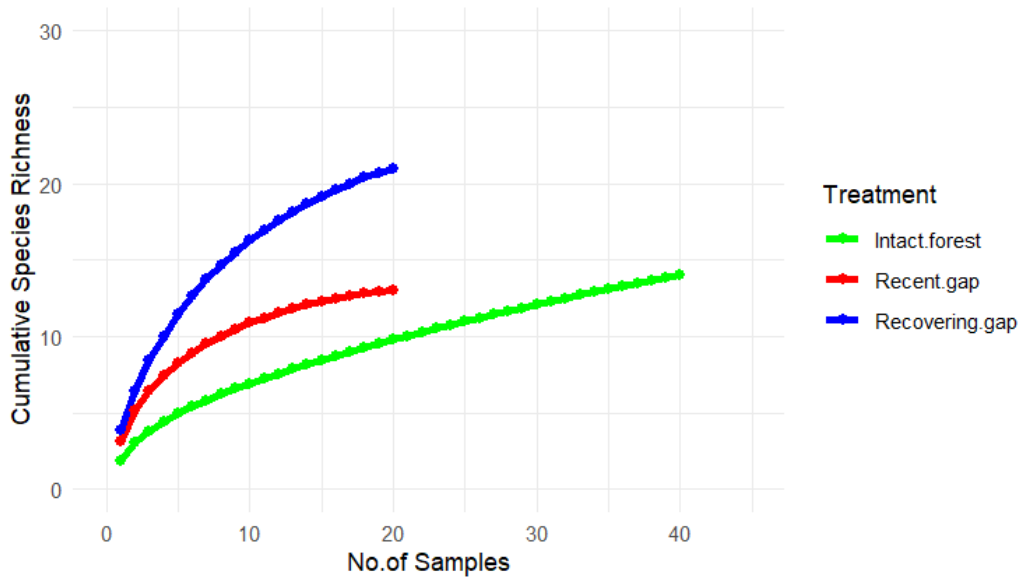


Figure 28: Rarefied Individual-based species accumulation curves for crabs in each treatment type.

Recent canopy gaps and intact forest were relatively well-sampled compared to recovering canopy gaps in both individual-based and sample-based rarefied accumulation curves. The curve for recovering canopy gaps was comparatively sampled less in both the individual-based and sample-based curves.

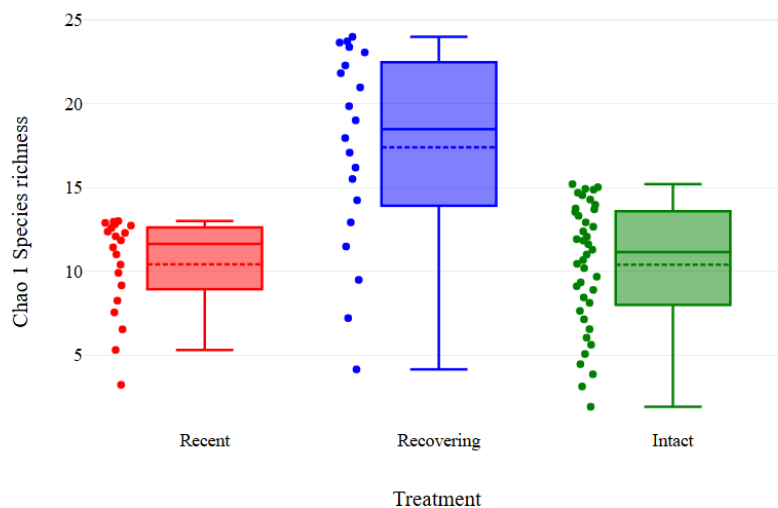


Figure 29: The estimated (Chao 1) richness of crabs among treatment types.

A non-parametric richness estimator (Chao 1) was used to calculate the species richness estimation. Chao 1 value significantly differed between treatments ($p < 0.05$). The estimate shows higher species richness in recovering the canopy gap and no significant difference between recent canopy gaps and intact forest.

Shannon diversity was higher in the recovering canopy gap ($H' = 0.93$) and lowest in the intact forest ($H = 0.38$), and Shannon evenness was almost the same in all treatments ($A = 0.72$, $B = 0.73$, and $C = 0.74$).

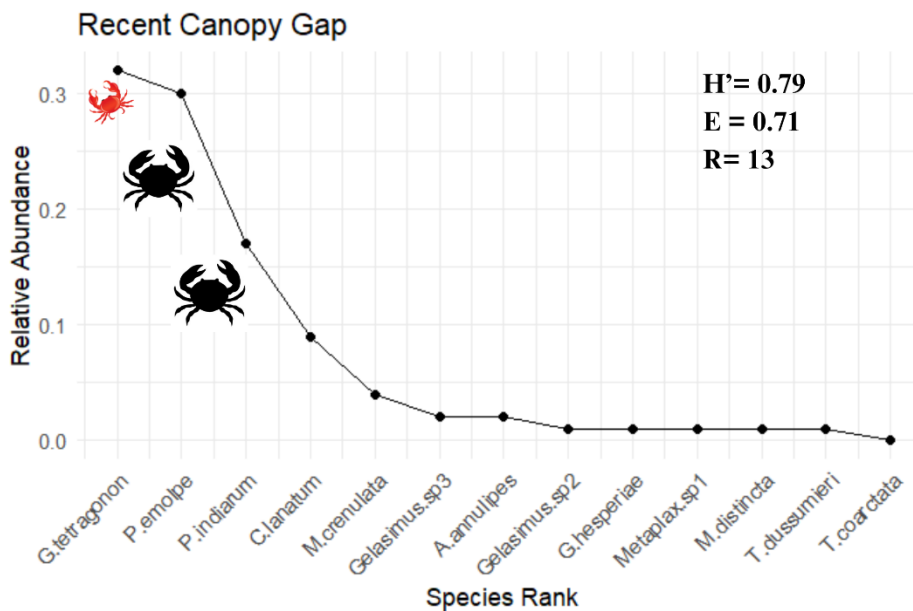


Figure 30: Rank abundance curve for Recent canopy gaps with Shannon Diversity(H'), Shannon Evenness (E) and Absolute richness(R).

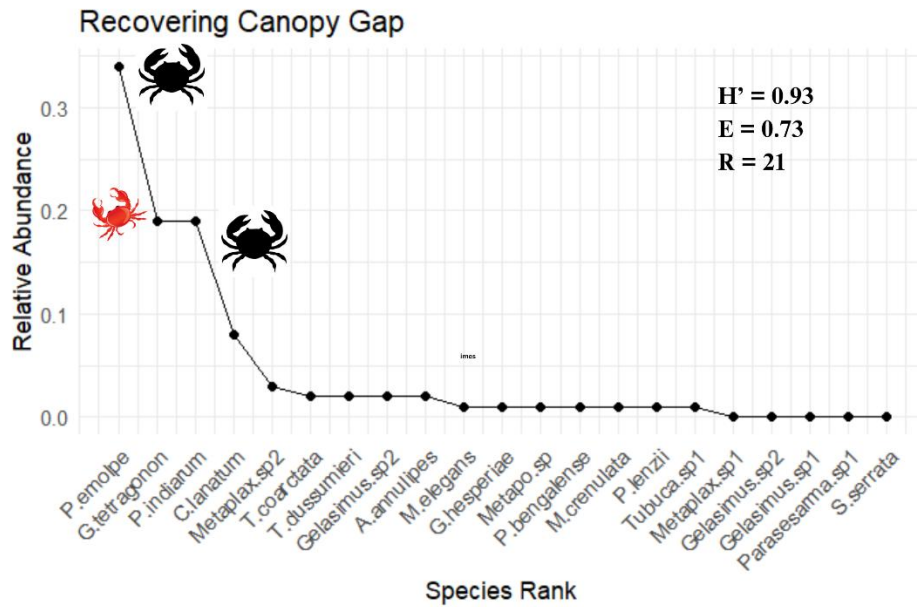


Figure 31: Rank abundance curve for recovering canopy gaps with Shannon Diversity(H'), Shannon Evenness (E) and Absolute richness(R).

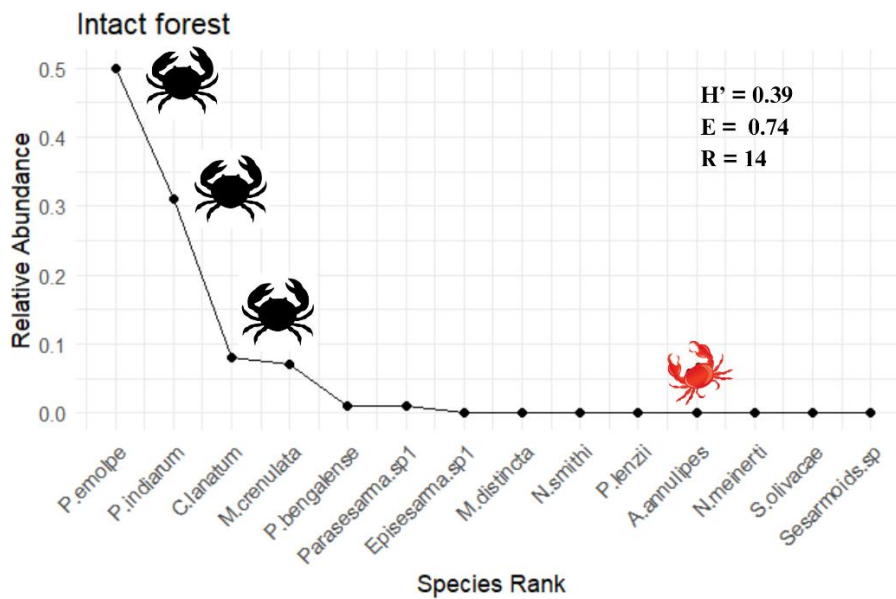


Figure 32: Rank abundance curve for Intact forests with Shannon Diversity(H'), Shannon Evenness (E) and Absolute richness(R).

In recent canopy gaps, *Gelasimus tetragonon* was in the first rank with the highest abundance, followed by *Perisesarma emolpe* and *Perisesarma indiarum* in the second and third ranks, respectively. On the other hand, when succession progresses in recovering canopy gaps, there was a steep decline in *Gelasimus tetragonon* abundance, which resulted in its rank shift to second place, and first place was replaced by *Perisesarma emolpe*. *Perisesarma indium* remains in the third rank with a noticeable increase in abundance. The sampling effort for the Intact plot was twice that of the canopy gap plots (A = 20, B = 20, and C = 40). *Perisesarma emolpe* ranked first, followed by *Perisesarma indiarum* in second place and *Clistocoeloma lanata* in third. *Perisesarma emolpe* and *Perisesarma indiarum* formed a large portion and dominated the community (*P.emolpe* = 49.9 % and *P.indiarum* = 30.54 %). *Gelacimus tetragonon* was not present in intact forest plots. The crab species with the highest total abundance was *Perisesarma emolpe* (n = 548, 38.75% in total), followed by *Perisesarma indiarum* (n = 319, 22.56%), *Gelasimus tetragonon* (n = 226, 15.98%), *Clistocoeloma lanata* (n = 122, 8.62%), and *Metaplax cranulata* (n = 60, 4.24%). All three treatments contained *Perisesarma emolpe*, *Perisesarma indiarum*, *Clistocoeloma lanata*, and *Astruca annulipes*. Eleven of the total recorded species are exclusive to canopy gaps.

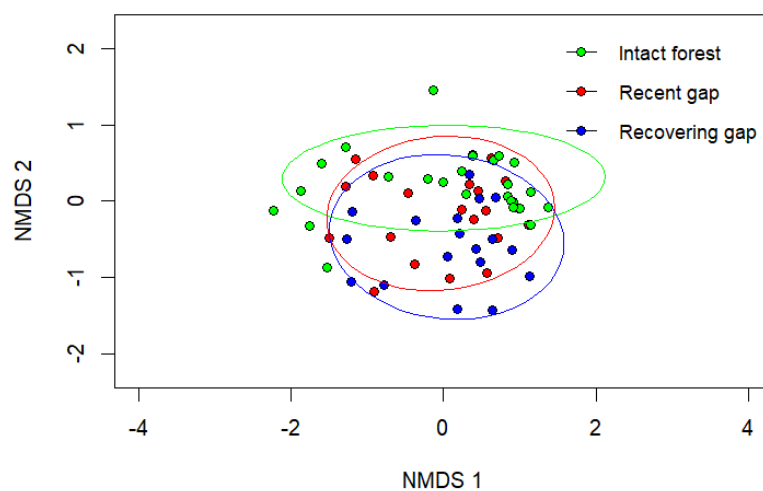


Figure 33: Compositional similarity of crabs among three treatments using non-metric multidimensional scaling (nMDS).

(Figure 33) shows the nMDS ordination of crab abundance data. The plot shows no clear clustering, but there is an overlap between the recent and recovering canopy gaps. The narrow ellipse of intact forest implies that more specialised species inhabit old-growth intact forest.

Table 8: Summary of Multi-Regression Permutation Procedure (MRPP) between three treatments for crab communities

Dissimilarity index: bray		
Permutation: free		
Number of permutations: 999	A value	P value
Overall comparison	0.017	0.04
Recent gap vs Recovering gap	0.005	0.657
Recovering vs Intact forest	0.015	0.041
Recent gap vs Intact	0.019	0.037

The MRPP result shows that there was an overall dissimilarity in the community composition across all treatment types. No significance between recent and recovering canopy gaps, as there is only a slight transition. On the other hand, there is high dissimilarity in crab community composition between recent and intact forests.

4.3.2 Correlation of environment parameters with crabs:

Crabs of the families *Ocypodidae* and *Varunidae* show a significant association ($P < 0.05$) with canopy openness (Figures 34 & 36). Additional models were built to check the response of each family to water temperature. It shows significance with *Ocypodidae* and *Varunidae*. *Sesarmidae* shows a negative response to water temperature. An additive model with water temperature and canopy opening on *Ocypodidae* was the best-fit model with the lowest AICc.

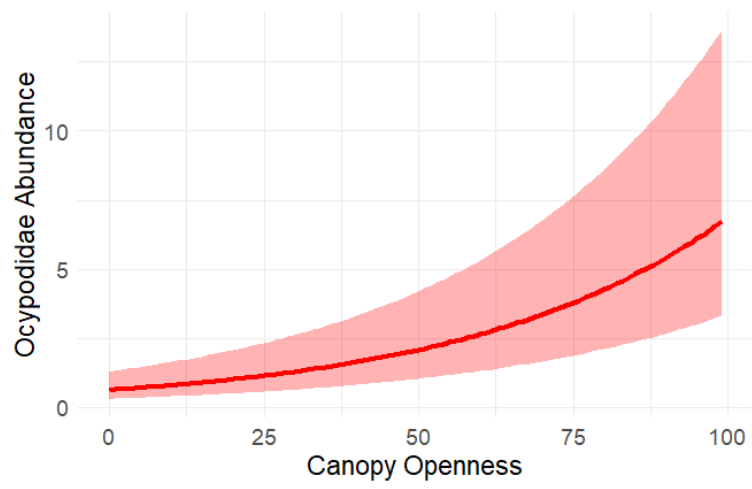


Figure 34: Response curve of *Ocypodidae* family crabs to canopy openness.

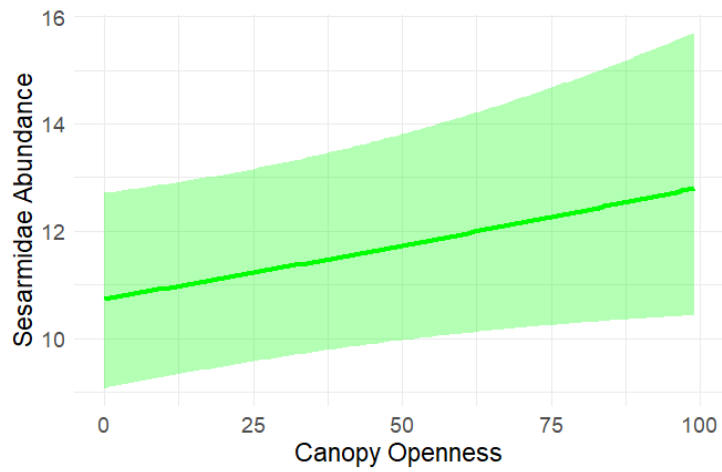


Figure 35: Response curve of *Sesarma* crabs to canopy openness.

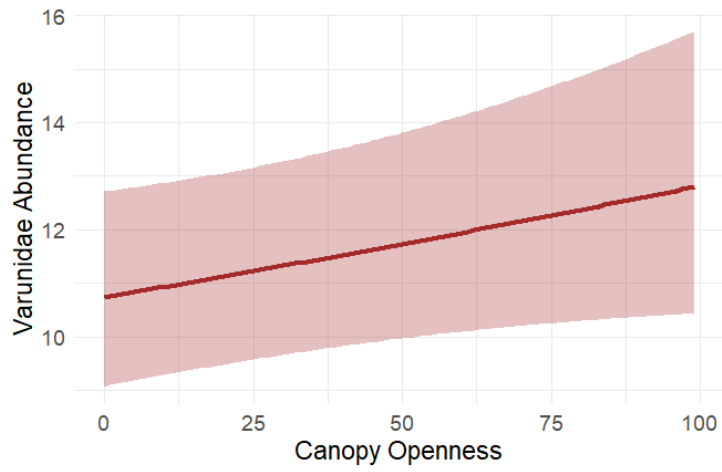


Figure 36: Response curve of *Varunidae* family crabs to canopy opening.

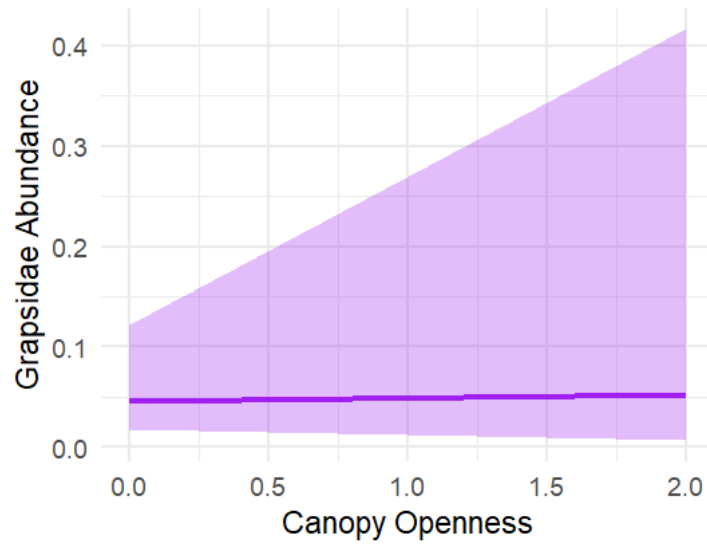


Figure 37: Response curve of *Grapsidae* family crabs to canopy openness.

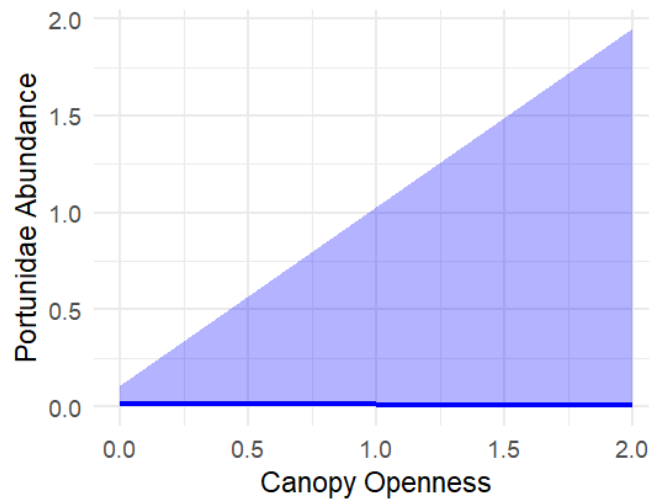


Figure 38: Response curve of *Portunidae* family crabs to canopy opening.

5. DISCUSSION

5.1 Canopy Gap Characteristics

Our results suggested that the mangrove canopy gaps surveyed in the Andaman Islands are comparatively larger than the canopy gaps previously reported (Craighead 1971; Johns 1986; Smith 1992; Smith et al. 1994; Sherman et al. 2000; Zhang 2008; Amir 2012; Amir and Duke 2019). The surveyed canopy gaps were prioritized to be larger for planting a 7m radius plot, which could influence the larger gap areas in the study. Out of the sampled 20 recent canopy gaps, standing dead trees were witnessed in 11 sites, and dead boles on the forest floor were obvious in all recent canopy gaps. These structural components of debris play a crucial role in the food web and nutrient cycle of terrestrial ecosystems (Harmon et al., 1986; Robertson and Daniel, 1989), and this relevance may extend to the mangrove ecosystem. For example, microbes and shrimp worms decomposing the downed wood is an important nutrient for the crabs (Diele et al., 2013), and hence it provides the required microhabitat and nutrients for sustaining different species of crabs. The dominance of *Sesarmids* in all the treatments suggests that they have a flexible-opportunistic diet, as their dominant food resource is primarily woody

debris rather than microphytobenthos, which is the main food source of many *Ocypodidae* crabs (Kon et al., 2007). This explains the dominance of *Sesarmids* in the mangrove ecosystem to exploit various resources.

The higher availability of certain resources in a specific location influences the exclusive occurrence of certain species in such a habitat for a long time (MacKenzie et al., 2011). For example, the presence of standing dead poles and the wood debris in large amount on the forest floors of recent canopy gaps guarantees the prolonged availability of organic matter in canopy gaps for the species exclusively forage on debris. Species such as *Metaplex elegans* and *Clistocoeloma lanatum*, which predominantly feed on woody debris (Diele et al., 2013). Earlier studies have also found a similar pattern that *Metaplex* spp. being exclusive to canopy gaps (Diele et al., 2013). Therefore, the microenvironment created by canopy gaps stimulates a concentrated resource in large quantity, which ensures the presence of certain species in the canopy gaps for the longer duration.

Response to physical stressors, such as disturbance, differs species to species (Pedley, S. M., & Dolman, P. M. (2014). Although our field observation ensures a circular pattern of tree mortality in canopy gaps in, which most of the dead trees belong to *Rhizophora* spp that never recovered after disturbance. We have observed a few disturbed and burnt snags of *Xylocarpus granatum* that were alive with re-sprouting of leaves and a few developed branches. This shows the difference in interspecific responses to lightning strike disturbances. Species such as *Xylocarpus granatum* and *Heriterra littoralis* are having recovery ability to lightning disturbances, whereas other species, *Rhizophora* spp., *Bruguiera*, and *Avicennia*, were 100% mortal in canopy gaps.

Canopy gaps alter several physical factors and biological processes; these processes are vital in mangrove regeneration, which includes increased photosynthetically active radiation, a

decrease in leaf area index, humidity, evapotranspiration, light levels, and soil properties—salinity, temperatures, and nutrients (Smith 1987; Smith 1992; Amir and Duke 2019). We have found that canopy openness had a significant effect on water temperature (Amir and Duke, 2019). This change could subsequently alter physiological and biological factors on the forest floor; for example, increased light penetration in larger gaps likely elevates ground temperatures, affecting hydrological conditions and soil moisture retention. This effect could also influence soil microbial activity, which subsequently promotes detritivorous species to inhabit the canopy gap.

5.2 Vegetation composition

We have found that richness was higher in recent canopy gaps in terms of seedlings and saplings, and the richness shifts to recovering canopy gaps in terms of tree species in a 7m plots. It is obvious to have higher species richness in recovering canopy gaps than in intact forest plots, as there were no trees in recent canopy gaps. The higher species richness in recovering canopy gaps might be the result of surviving seedlings and saplings in recent canopy gaps in early succession.

Rhizophora apiculata dominated all the treatments. Seedlings of *Rhizophora apiculata* are super dominant in the recent canopy gaps, and there was a drastic decline in seedling and sapling recruitment in recovering canopy gaps. A significant decline in seedling density in recovering gaps coincided with a surge in sapling and young tree dominance, especially individuals between 10 to 20 cm Girth at Breast Height (GBH). *Bruguiera gymnorrhiza* emerged as the second most dominant species in intact forests (based on IVI% value), compared to third place in canopy gaps, indicating successional shifts in dominance over time (BF, 1992). Recovering gaps were characterized by cohorts of even-height young trees, suggesting synchronous recruitment from earlier regeneration events.

The observed pattern of *Rhizophora apiculata* dominance in recent gaps suggests the strong initial colonizing ability of the species and potentially reduced interspecific competition as the mono-species dominant situation within the patch. Our hypothesis prediction about higher species richness in recent gaps was significantly proved in terms of seedling and sapling plots. However, field evidence shows that higher richness in recovering canopy gaps with respect to trees in 7m plots. This variation may be explained by the remnant survivors from the recent canopy gaps or the delayed colonization of non-local species from other landward mangrove zones, which arrive and establish over time (MacArthur and Wilson, 2001). These species possibly gain a foothold in recovering gaps before being eventually outcompeted by native, well-adapted species, as evidenced by the reduced diversity in intact forests.

The dominance shift from *Rhizophora mucronata* to *Bruguiera gymnorrhiza* in intact forests may reflect the increasing influence of wood volume in more mature stages of forest development. The strong recruitment of young trees in recovering gaps (with 73% of individuals in the 10–20 cm GBH range) indicates successful progression from saplings to canopy-establishing individuals, which in turn suppresses further recruitment by limiting light and space.

The clear separation of canopy gap stages and the measurement of both diversity and structural parameters (seedlings, saplings, tree GBH, and height) enable process-based insights into mangrove succession across temporal gradients. Inability to track long-term recovery trajectories due to the lack of past GIS data and the assumption that intact forest represents an endpoint of gap recovery may oversimplify successional outcomes, as intact forests may vary widely in age and disturbance history.

Further studies should aim to establish long-term monitoring plots to capture full successional trajectories post-gap formation. Investigating the role of propagule dispersal and seed bank

services by the young trees of canopy gaps must be an interesting study to do in the long term. Understanding vegetation recovery in mangroves following a disturbance is crucial for restoration ecology and forestry management. The finding shows that small-scale natural disturbance may enhance diversity at the intermediate recovery stage and contribute to landscape heterogeneity. Promoting canopy gaps for active restoration by collecting propagules from young trees of these locations might be more viable for growth. Seedling suppression by closed canopies highlights the importance of maintaining light availability in restoration plots. We have witnessed greater recovery of saplings into trees ≥ 10 cm (GBH) in recent canopy gaps of North Andaman. This might be the result of a recent seismic event in the last decade, which caused vertical ground movement and a change in the geomorphology of the area.

5.3 Crab Community Composition

The canopy opening has a profound effect on the ecological and environmental parameters and thus consequently influences the micro- and macrobiota at the substratum (Diele et al., 2013; Barbanara et al., 2022). Our results suggested a clear influence of canopy openness in shaping the mangrove crab community composition. Crabs of the family *Ocypodidae* were found in higher proportion in recently formed canopy gaps, likely due to their reliance on organic matter derived from benthic microalgae and bacteria (Cannicci et al. 2008). As the canopy cover is moderate in recovering canopy gaps, the abundance of *Ocypodidae* sharply declines. It indicates reduced light availability on the forest floor and consequently lower productivity of their major food sources. Higher diversity was observed in recovering canopy gaps, suggesting that the moderate light availability and heterogeneous food resources, including both microalgae and leaf litter from regenerating trees and woody debris from dead trees, support diverse functional groups to coexist. Unsurprisingly, species that depend on complex root structure for burrow construction and those feeding primarily on leaf litter, such as *Sesarmids*, were found mostly in intact forests with dense canopy cover. Interestingly, burrow density and

total crab abundance did not significantly differ across treatments, implying that no ecological niches remained occupied. However, the crab biomass might be lower in canopy gaps due to the smaller body size that is typical of *Ocypodidae*, whereas intact forests the Sesarmids would have high crab biomass as they are relatively larger in body size.

Mangrove crab communities are influenced by a combination of biotic and abiotic factors, including canopy structure, salinity, temperature, and substrate characteristics (Fondo & Martens, 1998). Although environmental variables such as salinity and pH were relatively homogenous across treatments in our study, the variation in canopy cover emerged as the key driver of community turnover (Joshi et al., 2006; Chen et al., 2019; Wu et al., 2020). Our results align with studies from Mozambique, which reported that mangrove faunal presence was more strongly linked to canopy structure than to other features like root and trunk morphology (Fondo & Martens, 1998). Similarly, Ruwa (1988) noted greater crab diversity in moderate canopy conditions, which is consistent with our observation that recovering canopy gaps supported the highest diversity. This pattern is likely to be a result of light penetration for algal growth and leaf litter input for omnivorous opportunistic feeders of *Sesarmidae* and *Varunidae* family crabs, allowing the co-occurrence of all three family groups together in recovering canopy gaps.

Species like *Perisesarma emolpe* and *Perisesarma indiarum* were found in both canopy gaps and intact forests, indicating high functional plasticity across trophic levels (Giraldes et al., 2019). In contrast, the dietary flexibility of leaf-litter-feeding Sesarmids is well-documented and likely contributes to their persistence in varying habitats (Poon et al., 2010). However, the extent to which dietary shifts influenced the observed community turnover could not be directly assessed in this study.

The major strength of this work is in the characterization of canopy gaps into recent and recovering stages and the integration of crab correlation with vegetation recovery to assess crab community response. The use of three distinct treatment types (Recent gaps, Recovering gaps, and Intact forests) provides a gradient of recovery rarely documented in mangrove ecosystems. However, limitations include the use of intact forests as a representative of recovered habitat.

In the absence of spatially explicit GIS data on canopy gaps before two decades, intact forests were used to represent the recovered category, which may not exactly reflect the ecological conditions of truly recovered canopy gaps, making this substitution a source of uncertainty in interpreting long-term recovery dynamics. Additionally, the study lacked direct crab biomass estimates, dietary analysis, and sediment components and was limited to a single replicate across all the canopy gaps, which may not capture seasonal variation in the crab community. Therefore, future studies should incorporate seasonal sampling to assess how temporal variations influence crab community dynamics. The use of gut content analysis would be particularly valuable for understanding the role of dietary shifts in community assembly. Additionally, quantifying crab biomass can also assist in evaluating how functional contributions to ecosystem processes, such as sediment mixing and nutrient cycling vary across gap stages.

Our findings emphasize the importance of canopy structure as a critical regulator of mangrove faunal composition and function. In a rapidly changing world, where forest degradation and fragmentation are escalating (Primavera et al., 2019; Richardson et al., 2020), understanding the functional responses of key faunal groups like crabs becomes essential. These organisms play pivotal roles in bioturbation, nutrient cycling, and litter breakdown, thereby sustaining mangrove ecosystem services (Macintosh et al., 1999). Moreover, effective mangrove management must recognize that even small-scale canopy disturbances can significantly alter

community structures and potentially influence ecosystem functioning (Lee, 2008; Goldenberg et al., 2018).

6. CONCLUSION

Canopy gaps in the *Rhizophora apiculata*-dominated mangrove forest of the Andaman Islands were characterized by the presence of standing dead trees and downed wood on the forest floor. These gaps were relatively larger compared to canopy gaps previously reported in mangrove forests. The seedling and sapling richness was high in the recent canopy gaps, and tree diversity was highest in recovering canopy gaps. The change in canopy cover was assumed to be favourable for higher light availability to the forest floor and facilitating the recruitment and survival of seedlings and saplings in the canopy gaps. The formation of canopy gaps following the death of mangrove trees initiated structural changes to the forest floor. This was manifested by the significant difference in seedling and sapling densities among the treatment types. The difference in seedling density between gap phases demonstrates that each seedling competes, but only a few manage to mature as young trees and eventually fill the canopy gap. This successional pattern provides a crucial ecological framework for understanding mangrove forest dynamics following small-scale disturbance.

The canopy openness strongly influenced the mangrove crab community in the Andaman Islands. The canopy opening results in a significant increase in water temperature, which could influence the resource availability for certain crab species. The recovering canopy gaps with moderate shade and light support the highest species diversity, likely because it provides more resources, such as woody debris, leaf litter, and adequate light for microbial growth on the forest floor. Many *Ocypodidae* family crabs were found in large numbers in the new canopy gaps, and species like *Metaplex elegans* and *Clistocouloma lanatum* thrived there because they had abundant food in canopy gaps, as debris is their main food source. *Sesarma* crabs, more

prevalent in mangrove forests, benefited from the later stages of canopy gap succession. This exhibits a clear correlation between vegetation succession and crab community composition in the mangrove forests. Overall, canopy gaps within contiguous mangrove patches serve as a regeneration niche for mangrove vegetation and a hot spot for crab diversity in the landscape.

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8. APPENDICES

Appendix I

Table 9: Summary of Seedling density per m² in each plot and Important Value Index (IVI) of plant species in each treatment.

S.No	Treatment	Seedling Density/m ²	Species	Relative frequency	Relative Abundance	IVI
1.	Recent Canopy gap	2.86	<i>A.arium</i>	30	4.57	0.17
			<i>A.ilicifolius</i>	10	1.1	0.05
			<i>B.gymnorrhiza</i>	15	1.8	0.08
			<i>C.tagal</i>	25	3.05	0.14
			<i>E.agallocha</i>	10	0.83	0.05
			<i>Insia bijuga</i>	10	0.41	0.05
			<i>P.paludosa</i>	20	1.38	0.1
			<i>R.apiculata</i>	100	79.33	0.89
			<i>R.mucronata</i>	40	5.27	0.22
			<i>X.granatum</i>	35	2.21	0.18
2.	Recovering canopy gap	1.45	<i>A.arium</i>	25	10.92	0.17
			<i>B.gymnorrhiza</i>	10	2.45	0.06
			<i>C.tagal</i>	25	6.83	0.15
			<i>P.paludosa</i>	15	4.91	0.09
			<i>R.apiculata</i>	85	66.12	0.75
			<i>R.mucronata</i>	25	5.73	0.15
			<i>X.granatum</i>	30	3	0.16
3.	Intact forest	0.69	<i>A.arium</i>	5	4.85	0.04

			<i>A.ilicifolius</i>	2.5	1.42	0.01
			<i>B.gymnorrhiza</i>	2.5	0.52	0.01
			<i>C.tagal</i>	20	12.28	0.16
			<i>P.paludosa</i>	5	1.14	0.03
			<i>R.apiculata</i>	70	66.28	0.68
			<i>R.mucronata</i>	10	6.85	0.08
			<i>X.granatum</i>	20	6.28	0.13

Appendix II

Table 10: Summary of taxonomic information with crab abundance in each treatment

Super family	Family	ID	Species	Abundance		
				Recent	Recovering	Intact
<i>Ocypodoidae</i>	<i>Ocypodidae</i>	1	<i>Austruca annulipes</i> (H. Milne Edwards, 1837)	7	7	1
		4	<i>Gelasimus tetragonon</i> (Herbst, 1790)	4	2	0
		5	<i>Gelasimus hesperiae</i> (Crane, 1975)	6	4	0
		6	<i>Gelasimus sp. 1</i> (Latreille, 1817)	0	1	0
		7	<i>Gelasimus sp. 2</i> (Latreille, 1817)	6	9	0
		8	<i>Gelasimus sp. 3</i> (Latreille, 1817)	0	1	0
		25	<i>Tubuca dussumieri</i> (H. Milne Edwards, 1852)	4	10	0
		26	<i>Tubuca coarctata</i> (H. Milne Edwards, 1852)	1	10	0
		27	<i>Tubuca sp. 1</i> (Bott, 1973)	0	3	0
		28	<i>Tubuca sp. 2</i> (Bott, 1973)	8	0	0
<i>Grapsoidae</i>	<i>Grapsidae</i>	14	<i>Metapograpsus sp. 1</i> (H. Milne Edwards, 1853)	0	4	0
	<i>Sesarmidae</i>	15	<i>Neosarmatium meinerti</i> (De Man, 1887)	0	0	1
		16	<i>Neosarmatium smithi</i> (H. Milne Edwards, 1853)	0	0	2
		17	<i>Parasesarma sp. 1</i> (De Man, 1895)	0	1	3
		18	<i>Perisesarma bengalense</i> (Davie, 2003)	0	4	7
		19	<i>Perisesarma emolpe</i> (De Man, 1895)	76	79	164
		20	<i>Perisesarma indiarum</i> (Tweedie, 1940)	136	144	268
		21	<i>Perisesarma lenzii</i> (De Man, 1895)	0	3	2
		24	<i>Sesarmoides sp. 1</i> (Serène & Soh, 1970)	0	0	1
		2	<i>Clistocoeloma lanatum</i> (Alcock, 1900)	43	35	44
		3	<i>Episesarma sp 1</i> (De Man, 1895)	0	0	2
	<i>Varunidae</i>	9	<i>Metaplax crenulate</i> (Gerstaecker, 1856)	4	2	0
		10	<i>Metaplax distincta</i> (H. Milne Edwards, 1852)	4	0	2
		11	<i>Metaplax elegans</i> (De Man, 1888)	0	5	0
		12	<i>Metaplax sp. 1</i> (H. Milne Edwards, 1852)	0	12	0
		13	<i>Metaplax sp. 2</i> (H. Milne Edwards, 1852)	18	3	39
<i>Portunoidea</i>	<i>Portunidae</i>	22	<i>Scylla olivacea</i> (Herbst, 1796)	0	0	1
		23	<i>Scylla serrata</i> (Forskål, 1775)	0	1	0

Appendix III

Table 11: Summary of Canopy gap (n=40) site details with coordinates, year of appearance, actual gap size and gap size using measuring tool (Circle) in Google Earth Pro in the Andaman Islands.

Gap ID	Island Group	Location	Coordinates	Treatment type	Year of appearance	Gap size measured in the field (m ²)	Gap size measured with Google Earth Pro (m ²)
SAT01	South Andaman	Wimberlygunj	11.79275 N 92.70954 E	Recent Gap	2022	316	311
SAT02	South Andaman	Wright Myo Creek	11.55554N 92.65336E	Recent Gap	2019	430	408
SAT03	South Andaman	Wimberlygunj	11.61556 N 92.70726 E	Recent Gap	2022	879	763
SAT04	South Andaman	Wimberlygunj	11.71542 N 92.68641 E	Recent Gap	2020	598	576
SAT05	South Andaman	Wright Myo Creek	11.8144 N 92.69068 E	Recent Gap	2021	412	314
SAT06	South Andaman	Wright Myo Creek	11.61547 N 92.70722 E	Recent Gap	2022	433	474
SBT07	South Andaman	Wright Myo Creek	11.81279 N 92.68997 E	Recovering Gap	2014	270	212
SBT08	South Andaman	Wright Myo Creek	11.61592 N 92.70714 E	Recovering Gap	2015	401	226
SBT09	South Andaman	Wright Myo Creek	11.81459 N 92.69373 E	Recovering Gap	2015	413	211
SBT10	South Andaman	Wright Myo Creek	11.81408 N 92.69484 E	Recovering Gap	2016	330	276
SBT11	South Andaman	Wright Myo Creek	11.81394 N 92.69561 E	Recovering Gap	2011	466	245
SBT12	South Andaman	Wright Myo Creek	11.81367 N 92.69595 E	Recovering Gap	2011	573	409
MAT13	Middle Andaman	Bakultala	11.61592 N 92.70714 E	Recent Gap	2020	1006	1158
MAT14	Middle Andaman	Bakultala	12.48048 N 92.83761 E	Recent Gap	2018	905	877
MAT15	Middle Andaman	Bakultala	12.47916 N 92.83394 E	Recent Gap	2018	1124	936
MAT16	Middle Andaman	Bakultala	12.47904 N 92.83475 E	Recent Gap	2018	1284	881
MAT17	Middle Andaman	Bakultala	12.47833 N 92.8348 E	Recent Gap	2018	1169	812
MAT18	Middle Andaman	Bakultala	12.47788 N 92.8398 E	Recent Gap	2021	672	604
MBT19	Middle Andaman	Bakultala	12.47806 N 92.83934 E	Recovering Gap	2011	673	547
MBT20	Middle Andaman	Bakultala	12.47798 N 92.83937 E	Recovering Gap	2018	586	557
MBT21	Middle Andaman	Bakultala	12.47562 N 92.83008 E	Recovering Gap	2015	993	547
MBT22	Middle Andaman	Bakultala	12.47321 N 92.83188 E	Recovering Gap	2015	1175	1355
MBT23	Middle Andaman	Bakultala	12.47175 N 92.84015 E	Recovering Gap	2011	935	940
MBT24	Middle Andaman	Bakultala	12.47988 N 92.83361 E	Recovering Gap	2015	575	1462
NAT25	North Andaman	Mayabunder	12.87112 N 92.85456 E	Recent Gap	2022	816	786
NAT26	North Andaman	Mayabunder	12.87209 N 92.85509 E	Recent Gap	2022	1074	1414
NAT27	North Andaman	Mayabunder	12.87226 N 92.85663 E	Recent Gap	2020	1705	1173

NBT28	North Andaman	Mayabunder	12.47143 N 92.84042 E	Recovering Gap	2015	802	988
NBT29	North Andaman	Mayabunder	12.87622 N 92.85672 E	Recovering Gap	2015	353	1169
NBT30	North Andaman	Mayabunder	12.87617 N 92.85600 E	Recovering Gap	2009	834	856
NAT31	North Andaman	Kalighat	13.097573 S 92.94423 E	Recent Gap	2022	2256	2218
NAT32	North Andaman	Kalighat	13.09657 S 92.94379 E	Recent Gap	2019	1096	1113
NAT33	North Andaman	Kalighat	13.09538 S 92.9435 E	Recent Gap	2022	1068	707
NBT34	North Andaman	Kalighat	13.09205 S 92.94281 E	Recovering Gap	2011	1519	1275
NBT35	North Andaman	Kalighat	13.09222 S 92.94433 E	Recovering Gap	2011	515	443
NBT36	North Andaman	Kalighat	13.09181 S 92.09181 E	Recovering Gap	2011	494	512
NAT37	North Andaman	Aerial Bay	13.09236 S 92.94599 E	Recent Gap	2022	2463	2304
NBT38	North Andaman	Aerial Bay	13.29689 S 93.02557 E	Recent Gap	2020	1697	2136
NBT39	North Andaman	Aerial Bay	13.29631 S 93.02561 E	Recovering Gap	2014	2342	1241
NBT40	North Andaman	Aerial Bay	13.29689 S 93.02557 E	Recovering Gap	2008	1997	1782

Appendix IV

Table 12: Reported canopy gaps in literature with cause and gap size (Amir and Duke, 2019)

Disturbance	Causes	Impact	Location	Mean Gap Size	Reference
Natural	Lightning strike	Small to large gaps	Everglades, Florida, USA	332m ² Everglades,	Whelan and Smith (2004)
			Everglades, Florida, USA	289 m ²	Whelan (2005)
			Moreton Bay, Queensland, Australia	134m ²	Amir and Duke (2019)
			Pulau Kecil, Matang, Malaysia	1783m ²	Amir (2012)
			Kosrae, Micronesia	700m ²	Allen et al.(2001)
			Los Haitises, Dominican Republic	724m ²	Sherman et al. (2000)
			Punta Galeta, Panama	602m ²	Sousa et al. (2003)
			Everglades, Florida, USA	59m ²	Zhang et.al (2008)
			Galley Reach, Papua New Guinea	1900m ²	Johns (1986)
			Galley Reach, Papua New Guinea	300-700 m ²	Paijmas and Rollet (1977)
	Insect	Small gaps	Central Belize	12 m ²	Feller and McKee (1999)
			Mantang, Malaysia	-	Putz and Chan (1986)
	Hurricane	Major dieback	Everglades, Florida, USA	-	Smith et al. (1994)
		Major dieback	Isla del Venado, Nicaragua	-	Roth (1992)
		Patches of gaps	Los Haitises, Dominican Republic	~700m ²	Sherman et al. (2001)
	Hail	Major dieback	Port Curtis, Queensland	169.9 ha	Houston (1999)
	Tree-fall/Branch fall	Small gaps	Ranong, Thailand	144 m ²	Imai et al. (2006)
	Tree-fall/Branch fall	Small gaps	Kosrae, Micronesia	64m ²	Piczon et al.(1984)
	Severe drought	Major dieback	Gulf of Carpentaria, Australia	7400 ha	Duke et al. (2017)
	Crown shyness	Channel-like gaps between canopy crowns	Parque Nacional de Santa Rosa, Guanacaste, Costa Rica	0-9.5 m width	Putz et al.(1984)
Anthropogenic	Small-scale	patches	Kosrae, Micronesia	-	Allen et al. (2001)
	cutting	Small gaps	Kosrae, Micronesia	158 m ²	Ewel et al. (1998)

		Patches	Kosrae, Micronesia	-	Huff et al. (2006)
		Small to large patches	Metinaro, Timor leste	-	Alongi and de Carvalho (2008)
		Small gaps	Bais bay, The Philippines	3m ²	Walters (2005)
		Large gap	Somone, Sengal	1.4 km ²	Sakho et al.(2011)
	Logging	Small to large gaps	Kosrae, Micronesia	114 m ²	Pinzon et al. (2003)
		Large gaps	Matang, Malaysia	41.4 ha	Muda and Mustafa (2003)
	Oil spill	Major dieback	Bahia Las Minas, Panama	307 ha	Duke et al.(1997)
	Experiment	Small gaps	North Queensland, Australia	50 m ² & 225 m ²	Clarke (2004)

Appendix V
Laboratory crab macro photography





Neosarmatium smithi



Perisesarma indiarum



Perisesarma emolpe



Gelasimus hesperiae



Metaplax crenulate



Episesarma sp

Appendix V I

Field Images









