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# *Spatial variability of benthic community composition in the Maldivian Archipelago: Management Effects and Atoll-scale Differentiation*

## Variabilità spaziale della composizione della comunità bentonica nell’Arcipelago Maldiviano: Effetti della Gestione e Differenziazione su scala di Atollo

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# RIASSUNTO

Le scogliere coralline sono sempre più esposte a ricorrenti ondate di calore marine e a pressioni locali persistenti che ne compromettono la stabilità strutturale e la capacità di recupero. L'arcipelago delle Maldive è tra le aree più vulnerabili agli eventi climatici estremi ed è stato più volte interessato, negli ultimi decenni, da episodi di sbiancamento di massa. Comprendere la variabilità spaziale dello stato di salute è quindi fondamentale per valutare i pattern di resilienza in un contesto di cambiamento climatico in accelerazione. Questo studio fornisce una valutazione latitudinale dello stato dei reef nelle regioni settentrionale, centrale e meridionale delle Maldive, integrando analisi delle comunità bentoniche con indici ecologici funzionali. Le immagini subacquee sono state analizzate mediante un approccio automatizzato (*CoralNet*), precedentemente validato attraverso il confronto con un metodo tradizionale (*PhotoQuad*). I risultati evidenziano una marcata variabilità nella struttura delle comunità bentoniche lungo il gradiente latitudinale, tra differenti tipologie di reef (lagunari e oceanici) e lungo il gradiente batimetrico (reef flat, 10 m e 20 m).

Le aree centrali e del sud hanno mostrato una copertura corallina più elevata, soprattutto nei reef lagunari sul flat, al contrario il nord ha mostrato coperture più basse. Gli indici funzionali (Indice di Predominanza Corallo-Alga, Indice Abiotico-Biotico e Indice di Consolidamento del Reef) hanno mostrato che la sostenibilità dei reef dipende dall'equilibrio tra produzione carbonatica ed erosione, evidenziando differenze strutturali anche tra siti con copertura corallina simile. Lo stato di salute dei reef non risulta uniforme tra gli atolli, indicando che la resilienza è un processo spazialmente variabile. Gli effetti degli eventi ricorrenti di sbiancamento sono modulati dalle condizioni ambientali locali e dalle pressioni antropiche. Sebbene siano stati osservati segnali di riorganizzazione post-disturbo, la progressiva riduzione dell'intervallo tra eventi termici solleva preoccupazioni circa la futura capacità di accrescimento carbonatico e la stabilità geomorfologica nel lungo periodo.

Nel complesso, questi risultati evidenziano la necessità di superare valutazioni basate su un unico indicatore di salute del reef, adottando approcci spazialmente espliciti e orientati alla funzionalità ecosistemica.

# ABSTRACT

Coral reefs are increasingly exposed to recurrent marine heatwaves and persistent local pressures that compromise their structural stability and recovery capacity. The Maldives archipelago is among the areas most vulnerable to extreme climatic events and has been repeatedly affected, over the past decades, by episodes of mass bleaching. Understanding the spatial variability in reef health is therefore essential to assess resilience patterns in the context of accelerating climate change. This study provides a latitudinal assessment of reef condition across the northern, central, and southern regions of the Maldives, integrating benthic community analyses with functional ecological indices.

Underwater images were analyzed using an automated approach (*CoralNet*), previously validated through comparison with a traditional method (*PhotoQuad*). The results highlight marked variability in benthic community structure along the latitudinal gradient, among different reef types (lagoonal and oceanic), and across the bathymetric gradient (reef flat, 10 m and 20 m). Central and southern areas showed higher coral cover, particularly in lagoonal reefs on the reef flat, whereas northern sites exhibited lower coral cover. Functional indices (Coral–Algae Predominance Index, Biotic–Abiotic Index, and Reef Consolidation Index) indicated that reef sustainability depends on the balance between carbonate production and erosion, revealing structural differences even among sites with similar coral cover. Reef health was not uniform across atolls, suggesting that resilience is a spatially variable process. The effects of recurrent bleaching events are modulated by local environmental conditions and anthropogenic pressures. Although signs of post-disturbance reorganization were observed, the progressive reduction in the interval between thermal events raises concerns about the future capacity for carbonate accretion and long-term geomorphological stability.

Overall, these findings underscore the need to move beyond assessments based on a single reef health indicator, adopting spatially explicit and ecosystem-function–oriented approaches.

# SUMMARY

# 1 INTRODUCTION

## *1.1 CORAL REEFS AND THEIR IMPORTANCE*

Approximately 560 million years ago, a phylogenetic split occurred within the phylum Cnidaria, specifically in the class Anthozoa. This event separated the lineage that would later give rise to the organisms currently classified in the order Actiniaria (sea anemones) from the clade from which modern Scleractinia and Corallimorpharia subsequently evolved (Wang *et al.*, 2021). During the early Palaeozoic, soft-bodied coral-like taxa and primitive scleractinian precursors with aragonitic skeletons emerged, some already displaying septal structures comparable to those observed in extant corals (Stolarski *et al.*, 2011). The definitive cladogenetic separation between these ancestral groups is estimated to have occurred approximately 308 million years ago, indicating a remarkably ancient divergence within hexacorallian corals. Over time, these stem-group scleractinians progressively evolved and acquired the biomineralization capabilities required for the formation of calcifying corals (Wang *et al.*, 2021), a long evolutionary trajectory that culminated in the Middle Triassic (around 240 million years ago), when reef-building corals became established and initiated the construction of the modern ecosystems (Stolarski *et al.,* 2011). These structures represent not only ancient biological innovation, but also the foundation of one of the most productive marine ecosystems on Earth (Sheppard *et al.*, 2018). Coral reefs are marine limestone frameworks produced by calcium-carbonate-secreting organisms, which support highly diverse and biomass-rich tropical communities in the surrounding waters (Hatcher, 1997). Despite occupying approximately 284,300 km$^2$ (Goodwin, 2006), tropical coral ecosystems host nearly 25% of known marine biodiversity. Reefs occur mainly in three major biogeographic regions: the Indo-Pacific, the Red Sea, and the Western Atlantic (Brown *et al.*, 1998), predominantly within coastal areas between 30° N and 30° S, where environmental conditions favour the growth of reef-building corals (Kleypas *et al.*, 1999). Beyond these latitudes, reduced calcification rates prevent the formation of stable reef frameworks; coral colonies may still occur, but their skeletons are rapidly eroded and do not accumulate significantly over time. Conversely, in low-latitude tropical waters, calcium carbonate deposition exceeds both physical and biological erosion, allowing long-term reef accretion.

Overall, reef formation is strongly controlled by the balance between calcification and erosion across latitudinal gradients (Hoegh-Guldberg, 2011). Calcification is primarily carried out by marine invertebrates of the class Anthozoa, subclass Hexacorallia, order Scleractinia. The fundamental structural unit of corals is the polyp, a cylindrical organism possessing a central mouth surrounded by tentacles whose number is taxonomically relevant at the subclass level. This individual can secrete a calcium carbonate skeleton that provides mechanical support and protection under adverse environmental conditions. Within a colony, neighbouring units are connected by living tissues that allow communication and nutrient transfer. Corals obtain their energetic requirements through both heterotrophic feeding and a symbiotic association with photosynthetic dinoflagellates (zooxanthellae) (Brown *et al.*, 1998; Miththapala, 2008), a relationship that originated at least in the Mesozoic era, concomitant with the emergence of modern coral reefs. These symbionts, primarily dinoflagellates of the family Symbiodiniaceae (LaJeunesse, 2020) inhabit coral tissues and, through photosynthesis, provide organic compounds that sustain essential and energetically costly metabolic processes, facilitating corals to thrive in nutrient-poor tropical waters. However, this mutualism is highly sensitive to environmental change: elevated sea temperatures can impair algal photosynthesis and induce the expulsion of symbionts, a process known as coral bleaching, which frequently leads to reduced calcification, compromised health, or mortality. The future persistence of coral reefs therefore depends on the capacity of coral–algae associations to adapt to warming and increasingly unstable ocean conditions (Muller-Parker *et al.,* 2015; LaJeunesse, 2020)

Bioconstruction in shallow tropical reefs is predominantly driven by hermatypic scleractinian corals, which represent the primary agents responsible for framework formation through the deposition of calcium carbonate ($CaCO_3$) (Montefalcone *et al.*, 2018). Although ahermatypic corals are also present, their limited or absent calcification prevents them from contributing to reef accretion (Brown *et al.,* 1998). Framework-building taxa can be subdivided into primary builders, such as *Acropora* spp., foliose corals, *Tubastraea micranthus*, *Heliopora coerulea* and *Millepora* spp., which significantly contribute to vertical and lateral accretion due to their high calcification rates, and secondary builders, including massive corals, Fungiidae and large bivalves, which supply additional calcareous material reinforcing and consolidating the reef skeleton. Binders, principally coralline algae and encrusting corals, further stabilize the reef by cementing skeletal fragments and filling interstitial voids, thereby enhancing the structural integrity of the carbonate matrix. Finally, bafflers, composed of non-calcifying soft-bodied organisms, indirectly support bioconstruction by trapping sediments within the reef structure, contributing to its physical stabilization despite the absence of active calcification. The components that support reef structure, classified as biotic elements, also enable bioconstructor settlement (Germani *et al.,* 2025). Reef accretion thus results from the combined action of these organisms and persists only when calcium carbonate deposition keeps pace with sea-level rise; reefs can maintain or recover their structure (“keep-up” and “catch-up” reefs), whereas insufficient growth leads to submergence and functional collapse (“give-up” reefs) (Montefalcone *et al.*, 2018). Nevertheless, this equilibrium is counterbalanced by bioerosion, a process carried out by various reef organisms that degrade coral and algal skeletons, thereby modulating accretion rates and potentially weakening the carbonate framework (Glynn & Manzello, 2015).

Coral reefs can be classified into various structural types (Figure 1):

- Fringing reefs: the most common reef formation, growing directly along the shoreline, often bordering rocky uplifted coasts or the edges of exposed limestone islands.
- Patch reefs: smaller, standalone coral structures that appear as scattered fragments rather than continuous formations.
- Barrier reefs: form farther from land in areas where coral growth is able to match the slow subsidence of the seabed.
- Atolls: ring-shaped coral reefs named after the Dhivehi word *atholhu.* They form as volcanic islands sink and coral growth keeps pace with subsidence. The karst processes and major sea-level fluctuations also shaped their form: during low sea levels, exposed carbonates dissolved, and when sea levels rose, corals recolonized the depressions, forming atolls (Cesar, 2002; Stevens & Froman, 2019; Di Fiore *et al.,* 2020). Mature atolls often display curved, bight-like shapes, which are thought to result from large submarine slope collapses commonly affecting volcanic margins (Terry & Goff, 2013).
- Emergent platform reefs (EP): isolated, self-contained structures, forming a broad “platform” that rises from the seafloor and grows upward until it reaches, or even breaks, the ocean surface (Tunnell, 2007).

Coral reef ecosystems are found predominantly in areas where environmental conditions fall within particular thresholds, defined by characteristic ranges of key physical and chemical parameters (Hoegh-Guldberg, 2011):

- Temperature: the general thermal range for coral reefs is ~18–36 °C, with optimal growth at 26–28 °C. Deviations beyond optimal limits can severely impair coral health, leading to bleaching and, in extreme cases, reef collapse.
- Salinity: optimal values are ~3.3–3.6%; departures from this range inhibit coral growth and shift carbonate production to other organisms.
- Nutrient availability: nutrient exchange and waste removal are controlled by the oceanographic regime, regulated primarily by wave-driven water motion. Elevated nutrients obstruct coral growth and favor competitors like algae and sponges, ultimately leading to reef degradation.
- Light levels: decrease with depth and turbidity, reducing coral photosynthesis and calcification. Consequently, many species shift from dome-shaped forms in shallow waters to plate-like morphologies in deeper zones, where growth rates are significantly slower (Hubbard, 2015).
- Aragonite saturation: surface waters are consistently supersaturated (Ω arag > 1), with the highest values (~2.0–4.2) occurring in tropical and subtropical regions, while saturation declines toward high latitudes (Jiang *et al.*, 2015)

Reef ecosystems exhibit the highest known animal diversity on the planet, hosting 32 of the 34 recognized *phyla*, though most species remain undescribed (Sheppard *et al.,* 2018), potentially encompassing an estimated 1–8 million undiscovered *taxa* (van den Hoek & Bayoumi, 2017).

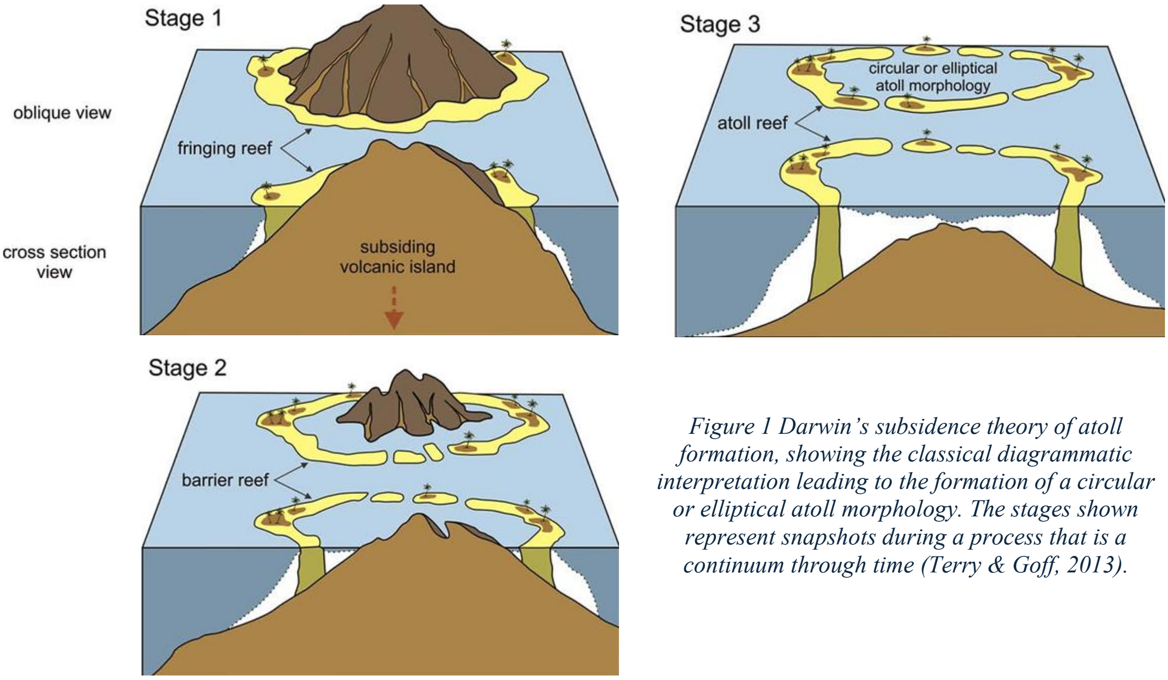

*Figure 1 Darwin's subsidence theory of atoll formation, showing the classical diagrammatic interpretation leading to the formation of a circular or elliptical atoll morphology. The stages shown represent snapshots during a process that is a continuum through time (Terry & Goff, 2013).*

## *1.2 ECOLOGICAL AND ECONOMIC IMPORTANCE OF CORAL REEFS*

Although coral reefs occupy only 0.1–0.5% of the ocean floor (Moberg & Folke, 1999), they play a fundamental role in sustaining marine life (Goodwin, 2006) and provide essential economic, means of living, and food-security benefits to human communities (Cinner, 2014). Their estimated global value exceeds USD 1 trillion (Heron *et al.*, 2017), supporting approximately 500 million people who rely on them for their daily subsistence, with 30 million people depending completely on reef resources (Hoegh-Guldberg, 2011a; van den Hoek & Bayoumi, 2017).

Human provision is organized as a system of services that sustain individual and collective needs. Despite being largely illegal, coral is extensively mined for lime, construction, and agricultural uses, with annual extraction around 20,000 $m^3$. Such activities can also produce mineral oil and gas through long-term physicochemical transformation of reef biomass (Miththapala, 2008; Moberg & Folke, 1999).

Local communities harvest a wide range of seafood, including fish, crustaceans, sea cucumbers, seaweed, clams, and turtles, contributing up to 10% of the global fish catch, and in certain developing regions reaching 25% (Moberg & Folke, 1999; Moberg & Rönnbäck, 2003; Albert *et al.*, 2015). For populations, reef-based fisheries provide an essential source of protein and nutrients, supporting food security and acting as a safety net during economic or climatic crises (Abdulla *et al.,* 2024). Well-managed reefs can yield around 15 tonnes of seafood per $km^2$ annually, with demand projected to double in the next 25 years (Miththapala, 2008). Sustainable alternatives, such as mariculture and aquaculture, including seaweed farming for agar and carrageenan, are increasingly promoted to reduce pressure on wild stocks (Moberg & Folke, 1999; Cinner, 2014). Additionally, reef organisms, including marine turtles, sea stars, sea urchins, fish, and lobsters, are harvested for commercial purposes such as the aquarium trade, souvenirs, and curios. Materials like mother-of-pearl, cuttlebone, and chitin are also collected and used in food, jewelry, and specialty products, including calcium supplements for pet birds and violin varnish to enhance hardness and tonal quality. Coral reefs also offer a wealth of medicinal resources. Hundreds of marine species are investigated for bioactive compounds with anticancer, antimicrobial, anti-inflammatory, anticoagulant, and immune-modulating properties. Hard corals, sponges, molluscs, sea anemones, and cone snails have yielded compounds used in bone grafts, sunscreens, and potential non-addictive venoms, highlighting the reefs' value for human health (Brown *et al.,* 1998; Moberg & Folke, 1999; Miththapala, 2008). Even though coral reefs occupy just a tiny portion of the ocean, they support over a quarter of all known fish species (van den Hoek & Bayoumi, 2017) and are often called the "rainforests of the sea" (Miththapala, 2008). The complex structure of coral reefs sustains biodiversity and genetic diversity, provides habitats for spawning, nursery, breeding, and feeding, and supports 'mobile link' organisms that move to mangroves and seagrass beds, facilitating the transfer of energy and nutrients across habitats and supporting connected marine ecosystems (Moberg & Folke, 1999).

Primary production on reefs is driven by various algae, including symbiotic algae in hard corals, fast-growing turf algae, fleshy red, brown, and green algae, and calcareous species, and is supported by rapid biomass turnover and interactions with animals that enhance light capture and nutrient recycling (McClanahan *et al.,* 2002; Hatcher, 1988). Reefs contribute to global biogeochemical cycles through nitrogen fixation by associated organisms, carbon sequestration, $CaCO_3$ formation, and the provision of ecosystem services, although their capacity to detoxify pollutants declines under chronic contamination (Moberg & Folke, 1999; Cesar, 2002; McClanahan *et al.,* 2002). Coral reefs act as valuable archives of past marine conditions. Coral growth bands, chemical composition, and fluorescent markers reveal historical sea levels, environmental changes, and seasonal patterns, providing a unique source of paleoclimate information for tropical oceans unavailable from other proxies (Brown *et al.,* 1998; Moberg & Folke, 1999; van den Hoek & Bayoumi, 2017).

Finally, coral reefs serve as natural coastal defenses, limiting flooding while maintaining clear waters and clean coastlines. The reef crest, key geomorphological feature, absorbs approximately 86% of incoming wave energy, while the reef flat dissipates the remainder. Coral fragments contribute to beach formation, and by forming a barrier against storm surges, currents, tides, winds, hurricanes, and typhoons, reefs help prevent coastal erosion and protect infrastructure (Moberg & Folke, 1999; Moberg & Rönnbäck, 2003; Miththapala, 2008; Hoegh-Guldberg, 2011a; Ferrario *et al.*, 2014).

In tropical and subtropical countries, reef tourism is vital for the economy, generating significant revenue and supporting hundreds of thousands of jobs (Miththapala, 2008). People worldwide visit these ecosystems for activities such as SCUBA diving, snorkeling, and beach recreation (Brown *et al.,* 1998). These remarkable seascapes inspire art, films, and literature (Moberg & Folke, 1999) and support environmental balance and social cohesion in coastal communities. In some regions, they also play an important role in ceremonies, community feasts, and spiritual or cultural practices (Hoegh-Guldberg, 2011a; Cinner, 2014).

## *1.3 LOCAL AND GLOBAL STRESSORS*

Coral reefs have always been a fundamental ecological and economic resource (Hughes *et al.*, 2003; Obura *et al.*, 2019). Paradoxically, the very processes that support their survival can also create fragility: when natural dynamics or human activities intensify or change, they can degrade the ecosystem, often causing irreversible damage (Hughes *et al.*, 2017; Wedding *et al.*, 2018). Ecological systems can become overwhelmed when multiple stressors act simultaneously, whether harmful, beneficial, or simply demanding. These stressors may interact in synergistic, additive, or antagonistic ways, producing unexpected outcomes (Wheaton & Montazer, 2009; Brown *et al.*, 2013; Ban *et al.*, 2014; Ellis *et al.,* 2019; Good & Bahr, 2021).

Due to their value and vulnerability, coral reefs serve as essential indicators of global environmental change. Current trends, however, show a gradual decline, with only about 6% of reefs likely free from both local and global threats. Approximately 11% are affected solely by global pressures, 22% by local pressures, and 61% face a combination of both. Increasing ocean acidity and rising temperatures are weakening corals' ability to build skeletons, resulting in smaller, less resilient ecosystems (Obura *et al.*, 2019; França *et al.,* 2020; Carriger *et al.,* 2021; Good & Bahr, 2021).

Temperature is the most studied stressor. Seawater warming of 1–2 °C places corals near their upper thermal tolerance threshold, which generally corresponds to the local maximum monthly mean temperature (~31 °C) and amplify the impacts of other stressors (Ban *et al.*, 2014; Schoepf *et al.*, 2015; Good & Bahr, 2021). This warming is partly driven by greenhouse gas emissions from fossil fuel use and deforestation, which trap heat in the atmosphere and raise sea temperatures (Brown *et al.*, 1998). From 1871 to 2007, global land and sea temperatures rose by about 0.7°C, while tropical sea surface temperatures increased by roughly 0.5°C. By 2100 tropical waters are projected to warm 1.3–2.8°C depending on emissions scenarios (Munday *et al.*, 2009). Moreover, tropical ocean temperatures are influenced by El Niño (+0.5°C) and La Niña (−0.5°C), causing opposite effects on marine ecosystems (Miththapala, 2008). Prolonged high temperatures force corals to expel their symbiotic algae, a process known as bleaching. Even a temperature rise of ~1 °C above the summer maximum can trigger bleaching, whose severity depends on local conditions. Beyond natural variability, climate change is intensifying marine heatwaves, which rapidly trigger coral bleaching and often lead to mass mortality and disruption of the coral microbiome. These impacts increase disease prevalence and accelerate reef decline, frequently resulting in reduced coral cover and slow or incomplete recovery (Ateweberhan *et al.*, 2013; Prada *et al.*, 2017; Fordyce *et al.,* 2019; Montefalcone *et al.* 2020; Good & Bahr, 2021).

Similarly, ocean acidification, driven by increasing atmospheric $CO_2$ from fossil fuel use, compromises the capacity of corals to build and maintain calcium carbonate ($CaCO_3$) skeletons. About 25–30% of human-emitted $CO_2$ dissolves into the oceans, where it reacts with water to form carbonic acid, which then dissociates into bicarbonate ions ($HCO_3^-$) and protons ($H^+$). These protons react with carbonate ions ($CO_3^{2-}$), reducing their availability, which normally combine with calcium ions ($Ca^{2+}$) in seawater to form calcium carbonate ($CaCO_3$), the main building material of coral skeletons and other calcifying organisms (Weston, 2000; Good & Bahr, 2021). As a result, calcification slows down, and in extreme cases, existing skeletons may dissolve, compromising growth and reef stability (Ateweberhan *et al.*, 2013). Under elevated $CO_2$ levels, doubling pre-industrial concentrations (~560 ppm), can reduce coral calcification and growth by up to 40%, while carbonate accretion may approach zero when aragonite saturation drops below 3.3, menacing the resilience of reef ecosystems. Currently, concentrations already exceed 380 ppm, higher than at any time in the past 420,000–740,000 years, and are rising much faster than most natural changes (Hoegh-Guldberg *et al.*, 2007). With levels projected to reach 500–600 ppm and ocean warming of 2–4 °C, many coral species may decline or go extinct, while rapid adaptation is unlikely to keep pace (Hoegh-Guldberg *et al.*, 2007; Eakin *et al.,* 2008; Lüthi *et al.*, 2008). This phenomenon has increased ocean acidity by 30%, lowering seawater pH from 8.2 to 8.1, with a projected fall to 7.8 by century's end (Allemand & Osborn, 2019).

Future climate projections are concerning: tropical cyclones are expected to become more intense (2–11% increase) but less frequent globally (6–34%), with the strongest storms bringing up to 20% more rainfall near their centers damaging physically coral reefs (Knutson *et al.* 2010; França *et al.,* 2020). At the same time, microplastics transported by ocean currents continuously expose fish and invertebrates to contaminants, further compromising the health of marine communities (Bowley *et al.*, 2021; Huang *et al.*, 2021). Additionally, melting ice sheets are causing sea levels to rise, projected to reach 2 meters by 2100, which increases the vulnerability of these ecosystems (Good & Bahr, 2021).

Apart from global drivers, coral reef habitats face various local stressors, influenced by geographic setting and the intensity of the surrounding human footprint (Good & Bahr, 2021). Overtourism is a major contributor: developing and operating resorts on small, remote islands can negatively affect by reducing coral cover and increasing sedimentation (Cowburn *et al.*, 2018). Direct impacts include diving and snorkeling activities, while indirect effects arise from poorly planned coastal modification, such as dredging that increases water turbidity and mismanaged pollution or solid waste (Spalding *et al.,* 2017; Pancrazi *et al.*, 2025). Elevated nutrient levels from terrestrial runoff and storm-driven sediment resuspension, together with human-derived waste, can further degrade reefs by triggering crown-of-thorns starfish outbreaks and increasing pathogen prevalence (Ban *et al.*, 2014). Additional human-induced stressors include artificial lighting from resorts, which alters natural light conditions and affects symbiont assemblages in early coral life stages, as well as boat noise, which impairs juvenile fish movement and predator avoidance (Tamir *et al.*, 2020). Furthermore, ballast water from ship can introduce invasive species in the local environment (Miththapala, 2008; McCormick *et al.*, 2018; Tamir *et al.*, 2020) and frequently anchoring causes physical damage to corals, breaking or dislodging them, with waves and currents hindering recovery (McManus *et al.*, 1997).

Reefs also face the pressure of overfishing, which occurs directly at the human hand through destructive practices like blast fishing or cyanide fishing and indirectly through abandoned or lost “ghost” fishing gear. The first uses homemade explosives to stun or kill fish, destroying coral structures and reducing species diversity and three-dimensionality. The second involves squirting sodium cyanide into reef crevices to stun fish for capture, and even low concentrations of cyanide can negatively affect fish growth, metabolism, and reproduction. Lastly, lost or abandoned fishing gear continues to trap and kill marine organisms. Long-lasting gear damages benthic habitats for extended periods, breaking coral structures, impairing recovery, and altering reef fish communities. Because resident fish help maintain coral health by controlling algal growth, ghost fishing indirectly reduces coral resilience and disrupts overall reef functioning. Even though all these practices are dangerous and sometimes illegal, they persist for economic gain, causing coral and fish mortality, bleaching, and damage. This highlights the urgent need for regulation, sustainable fishing, and habitat restoration. (McManus *et al.*, 1997; Mak *et al.,* 2005; Beneli *et al.,* 2020; Hampton-Smith *et al.,* 2021).

## *1.4 MALDIVES ARCHIPELAGO*

### 1.4.1 Maldivian Coral Reef

Built upon a broad submarine plateau, deeper in the north (over 500 m) and shallower in the south (300–400 m), the islands of the Maldives Archipelago developed on a volcanic or non-organic basement. Coral growth on this platform formed banks that eventually reached sea level, creating islands of coral rock or sand. Uplifted reef layers indicate past relative sea-level changes. Typical atoll morphology arose as reefs expanded outward while interior erosion deepened lagoons; in some cases, erosion removed the original island entirely, leaving ring-shaped reefs that evolved into *faros* and fully formed atolls (Gardiner, 1902; Di Fiore *et al.,* 2020; Kunnummal & Anand, 2022).

This chain of atolls rests atop the Maldive Ridge (MR), a north–south bathymetric high about 900 km long, bounded by the Arabian Basin to the west and the Central Indian Basin to the east. The ridge has a volcanic base overlain by roughly 3.3 km of shallow-water carbonate sediments. Formed near the Central Indian Ridge through interaction with the Réunion plume, it has thickened oceanic crust. It represents the central segment of the Chagos–Laccadive Ridge (CLR), an aseismic, gently curved feature extending 3,000 km from 10°S to 15°N, including the Laccadive Ridge in the north and the Chagos Bank in the south (Gardiner, 1902; Di Fiore *et al.,* 2020; Kunnummal & Anand, 2022).

The Maldives (Figure 2) is a coral archipelago located in the Indian Ocean, approximately 700 km southwest of Sri Lanka, spanning roughly 868 km north–south and 130 km east–west, from 7°06'30"N in the north to just beyond the equator at 0°42'30"S in the south. The archipelago comprises 1,192 coral landforms, formed from sand and rubble, covering a total area of only 160 km². These are organized into 25 natural atolls, including 14 large, 7 small, and 4 reef-fringed structures, and have been inhabited since at least 500 B.C. Around 120 islands are dedicated to tourism (85 as resorts and 35 leased for new developments), while the remaining are divided into inhabited and uninhabited areas.

This chain of coral reefs and islands varies in size and number. Smaller atolls typically have more continuous reef margins, shallower lagoons, fewer lagoonal reefs, and lack marginal channels and *faroes*. The Maldives host the eighth-largest coral reef system in the world, covering about 4,513 km² and hosting an estimated 900,000 marine species, including 1,900 fish, 187 coral, and 350 crustacean species.

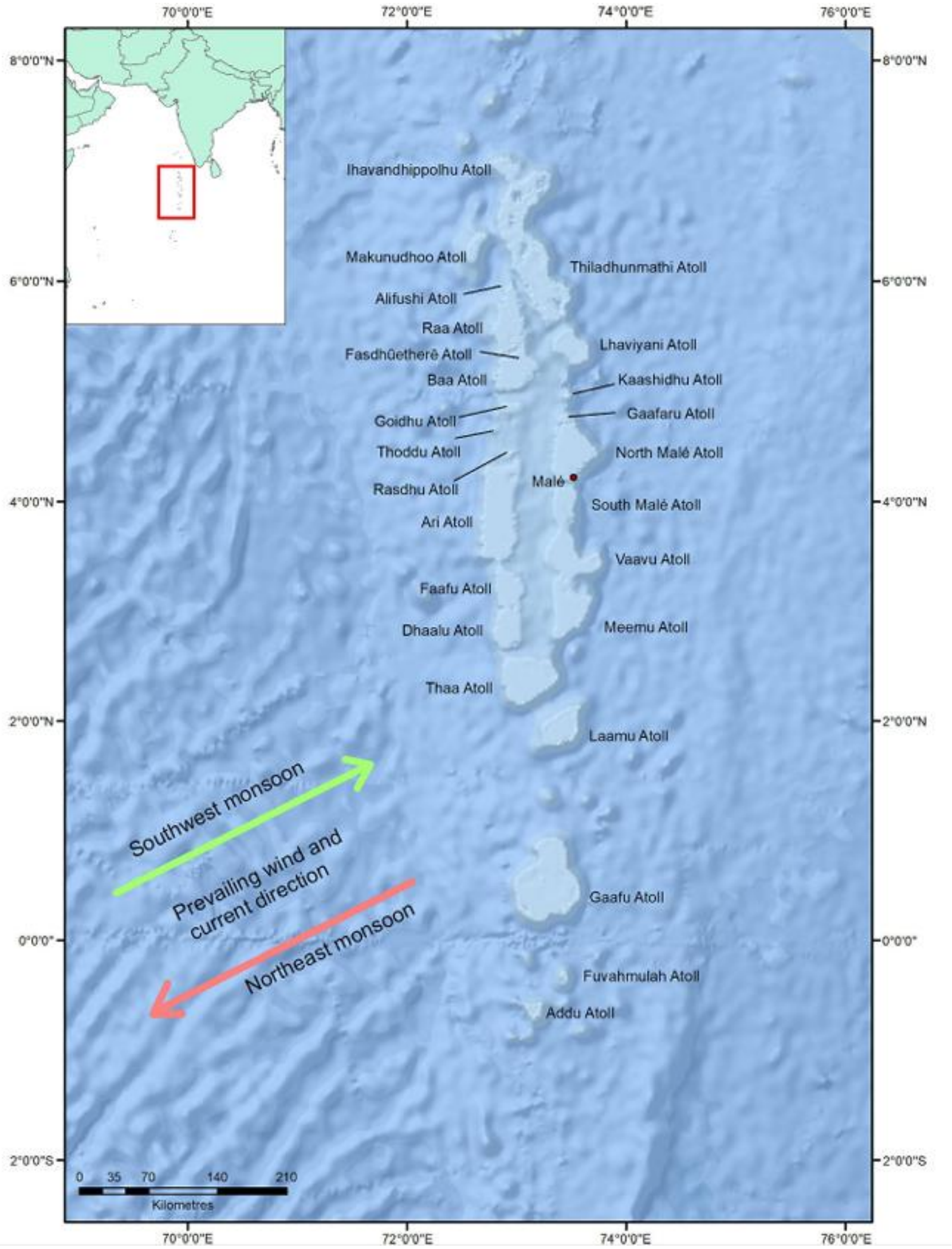

*Figure 2 Map of the Maldives archipelago, with the names of the atolls. The green and red arrows indicate the direction of the prevailing winds during two monsoons (Stevens & Froman, 2019).*

Although the Maldives’ maritime territory covers about 90,000 km², only 300 km² consists of permanent dry land, most of which lies less than 1 m above sea level. A 0.5 m rise in sea level could flood 77% of the islands, while a 1 m rise would inundate nearly all. As the world’s lowest country, the Maldives has an average elevation of just 1.5 m, with a maximum of 2.4 m (Naseer & Hatcher, 2004; Nasser, 2006; Harwood & Bryning, 2009; Jaleel, 2013; Gischler *et al.,* 2014; Stevens & Froman, 2019; Di Fiore *et al.,* 2020; Chaudhuri *et al.,* 2021).

Atolls exhibit a wide range of physical structures. Some are open formations with numerous islands. The development of these islands typically begins with low-lying accumulations of coral rubble, either locally produced or deposited by storms, which trap finer sediments and form unstable sand cays known as *Finolhu*. These cays may shift or even disappear entirely until stabilized by vegetation and cementation processes, such as beachrock formation, eventually resulting in more permanent islands. Open formations also include *faroes*, small, circular reefs with sandy lagoons up to 30 m deep that emerge at low tide and are fringed with living corals. They are most abundant in the north-central atolls and are shaped by wind, storms, and karst processes. *Faroes* are more common in lagoons connected to the open sea, while enclosed eastern lagoons tend to have few or none. Between islands or *faroes*, channels called *kandu*, gaps in the marginal reefs with strong currents, occur, becoming less frequent from north to south and ranging in depth from 10 to 40 m. Other atolls are nearly closed, featuring fewer lagoons and a more compact reef structure.

Darwin's model proposes that coral reefs begin as fringing systems around volcanic islands and progressively transform as the island subsides. As the volcanic foundation slowly sinks, corals keep pace by growing upward, increasing the distance between the shoreline and the reef. Over time, this process converts fringing reefs into barrier reefs with a wide lagoon, and eventually into atolls once the volcanic island is fully submerged.

In the Maldives, the inner body of water enclosed by a reef, the lagoon, is typically 50–60 m deep, reaching up to 90 m in the southern atolls. Many lagoons are largely filled with sandy sediments, about half of which derive from mechanical and biological erosion of the reef, with smaller contributions from sand-dwelling benthic organisms and planktonic foraminifera. Within these lagoons, over 1,100 patch reefs, known as *thila* (submerged reefs with coral-lined walls) or *giri* (smaller, shallower reefs), have been identified. Most are pinnacle-shaped and some are capped by small sand islands that can rise to 40 m above the lagoon floor (Island, 2000; Jaleel, 2013; Gischler *et al.,* 2014; Hubbard, 2015; Di Fiore *et al.,* 2020).

These features host diverse habitats, including beaches, mangroves, and seagrass beds (Brown *et al.*, 1998). Mangroves are highly productive coastal ecosystems, covering about 6% of the islands, mainly in the northern and southern atolls. They grow in brackish water ("*kuhli*") or muddy areas without standing water ("*chasbin*") and provide nursery grounds for reef fish, habitats for birds, and protection against erosion, storms, and tsunamis.

The Maldives hosts 14 mangrove species from 10 genera, with *Bruguiera cylindrica* being the most common, along with a rich community of associated plants, marine fungi, birds, fishes and invertebrates. Seagrass meadows are shallow-water habitats that have expanded in some areas due to nutrient enrichment from tourism, sewage, and dredging. They enhance biodiversity, support fisheries, stabilize sediments, and provide habitats for fish, shrimps, sea cucumbers, seahorses, crabs, and mollusks. Together, they provide key ecological services, supporting food webs, nutrient cycling, and the health of coral reefs. Despite their ecological and economic importance, these ecosystems face increasing threats from land reclamation, tourism, agriculture, resort development and pollution. They lack formal protection but remain visible from satellite imagery, particularly near economically active islands (Dhunya *et al.*, 2017; Stevens & Froman, 2019).

Marginal reefs of Maldivian atolls differ with ocean exposure: outer reefs are subjected to harsh conditions, featuring extensive platforms, low structural complexity, and strong wave action, whereas inner, lagoon-facing reefs are more sheltered, with smaller platforms, greater morphological heterogeneity, and reduced hydrodynamic energy (Lasagna *et al.,* 2010). These reefs can be broadly divided into three zones. Closest to the lagoon is the reef flat, a shallow, highly illuminated area where coral cover and diversity tend to be low, often dominated by just a few species. Environmental factors such as substrate type, elevation, and exposure to waves and currents strongly influence coral distribution, so even slight changes in depth or distance can produce significant shifts in coral communities.

Moving outward, the reef crest is the shallowest and most wave-exposed zone, marked by continuous wave breaking. It supports a relatively small but highly specialized community of organisms adapted to intense hydrodynamic stress and periodic exposure.

Beyond the crest lies the fore reef, the steep outer slope of the atoll, often characterized by spur-and-groove formations. The upper fore reef gets plenty of light and plankton, supporting diverse marine life shaped by water movement. Deeper sections receive less light and exhibit distinct geomorphological features, allowing only species adapted to low-light environments to thrive, including both reef-building and non-reef-building corals, which generally cannot withstand the strong wave action of shallow zones (Done, 1982; Brown *et al.*, 1998; Lasagna *et al.,* 2010; Gischler *et al.,* 2014; Semprucci *et al.,* 2018).

The Maldives, also known as “Flower of the Indies,” experiences a tropical climate with warm temperatures year-round, largely influenced by monsoon winds. The southwest monsoon (*Hulhangu*), from May to November, brings stronger winds (averaging 5.1 m/s), higher humidity, heavier rainfall, rougher seas, particularly in the northern islands, and enhanced upwelling, with wave energy 3–5 times higher than during the northeast monsoon. In contrast, the northeast monsoon (*Iruvai*), from January to March (sometimes extending from October to December), is milder (winds around 4.9 m/s), primarily affects the southern atolls, and brings occasional rain and thunderstorms, while most of the region enjoys clear skies, calm seas, and transparent waters. During this period, wave energy is lower and lacks a clear west-to-east gradient, although refracted ocean swells deliver more energy to western reefs. These variations in wave energy strongly influence island formation: western reefs experience high energy that removes sediments, resulting in few islands; central reefs retain sediments and form circular islands and eastern reefs enjoy lower, more stable energy, allowing a higher concentration of islands. Furthermore, although tropical cyclones rarely strike the Maldives and coral reefs help reduce their impact, they can still cause severe damage, producing winds over 150 km/h, heavy rainfall, and storm surges of 4–5 m (Island, 2000; Kench *et al.,* 2006; Kench & Brander, 2006; Gischler *et al.,* 2014; Stevens & Froman, 2019; Di Fiore *et al.,* 2020; Chaudhuri *et al.,* 2021).

In the beginning, the Maldives were likely used mainly as stopover points rather than sites of long-term settlement. Permanent habitation began at least 2,000 years ago, with early settlers probably arriving from India or Sri Lanka. Their South Asian origins are still evident today in Maldivian traditions and the Dhivehi language, a legacy also supported by genetic studies. Despite scarce natural resources, these early communities adapted effectively, developing distinctive skills such as advanced boatbuilding. The nation was long ruled by kings and sultans from seven major dynasties, governing according to Islamic law. Foreign interruptions included periods of Portuguese and later British control, until independence in 1965. In 1968, the monarchy was formally abolished when parliament voted to establish a republic. The first constitution was adopted in 1932, followed by several revisions, with the current constitution coming into force in 2008, establishing the Maldives as a constitutional republic with separation of powers among the executive, legislature, and judiciary (Pijpe *et al.,* 2013; Hazum, 2023).

For administrative purposes, the Government of the Maldives has reorganized the country into 7 provinces and 19 regions, by merging or dividing atolls. The capital Malé, located in North Malé Atoll, is considered a separate unit, bringing the total number of administrative areas to 20 (Sathiendrakumar & Tisdell, 1989; Stevens & Froman, 2019).

The islands are classified as uninhabited, inhabited, or resort islands, with about 120 used exclusively for tourism (Chaudhuri *et al.,* 2021). Tourism generally follows a “one island, one resort” model, placing pressure on surrounding coral reefs. Recent developments also include small “picnic islands,” valued for their pristine natural environment. Uninhabited islands are state-managed and, under Law No. 20/98, many of the 880 islands are leased, often through the Varuvaa system, for coconut cultivation, timber, or to private individuals and companies. Inhabited islands have more complex land tenure systems, including homestead plots, *goi* land, and *faalabba* land, which influence agricultural practices. Homestead plots are provided free, are inheritable, and owners retain any trees grown there. *Goi* land, often featuring coconut palms, is government-owned and leased to the highest bidder, while *faalabba* land near residential areas allows cultivation with official permission. The absence of hills and rivers limits agricultural development, which is concentrated on a few larger islands and usually leased on a long-term basis, covering only about 10% of the land. The islands feature tropical vegetation, including breadfruit trees, dense shrubs, and flowers. Approximately 2,600 hectares are cultivated with crops such as taro, anabas, coconuts, and various fruits (Nasser, 2006; Karthikheyan, 2010).

Originally a Buddhist country, the Maldives later converted to Sunni Islam, a faith that today strongly shapes its laws and culture (Pijpe *et al.,* 2013). Its language, Dhivehi, is unique and has roots in Sinhalese (Hazum, 2023). The population of about 530,000 (Worldometers) is unevenly distributed: most residents live in the capital city, while the other inhabited islands have low population densities (Chaudhuri *et al.,* 2021). Overpopulation in the capital has led to significant environmental, social, and infrastructural challenges, including pollution, unplanned urban growth, and inadequate waste management (Karthikheyan, 2010).

### 1.4.2 Bleaching events

Throughout their life cycle, corals are exposed to numerous stress factors which they must continuously withstand. Among human-induced pressures and natural disturbances, one stands out for its severity: ENSO, a natural climate event whose frequency and intensity have increased in the last decades due to climate change. The acronym refers to El Niño Southern Oscillation, a climate cycle shifting between neutral, warm (El Niño), and cool (La Niña) phases (Harborne *et al.,* 2017; Claar *et al.,* 2018; Hoegh-Guldberg *et al.,* 2023). El Niño, meaning "the little boy," is named after the Christ child because it typically occurs around Christmas. Under normal conditions, trade winds push warm surface waters westward, raising sea levels by approximately 0.5 m and warming the western Pacific. During El Niño events (ENSO +), weakened trade winds allow warm surface waters and air to shift eastward, generating sea surface temperature anomalies. These changes alter atmospheric circulation, bringing increased rainfall to normally dry regions and droughts to typically wet areas, while elevated temperatures and warm waters extend over broader areas. Following, La Niña, meaning "the little girl", typically occurs, producing opposite effects. La Niña usually lowers sea surface temperatures by about 0.5 °C, generating negative anomalies. During ENSO− years, extreme high temperatures are less likely, while cooler temperatures remain comparable to neutral conditions. ENSO+ asymmetry intensifies episodic warming, causing localized heat stress above 1 °C that varies among ENSO phases (Miththapala, 2008; Claar *et al.,* 2018; De Falco *et al.,* 2020).

From April to June, following strong El Niño events, sea surface temperatures often remain 1–2 °C above average for extended periods, intensifying the severity, duration, and frequency of coral bleaching (De Falco *et al.,* 2020; Montefalcone *et al.,* 2020). These episodic stress events strongly impact coral reefs by reducing coral tissue proteins, and disrupting the coral–algae symbiosis (Glynn & D'croz, 1990; Abrego *et al.,* 2008; Claar *et al.,* 2018). At the cellular level, bleaching occurs when corals expel *Symbiodinium*, exposing skeletons that appear white. Bleaching susceptibility varies among symbioses, with branching corals like *Acropora* and *Pocillopora* generally more affected, reflecting differences in *Symbiodinium* ecology and coral host physiology. This genus of algae is genetically diverse, divided into phylotypes A through F. Ribotypes A, B, and C are widespread, although C is rare at high latitudes. Colonies dominated by B show resistance to heat and light stress, whereas C declines during bleaching. Some corals can replace sensitive ribotypes with more tolerant ones (e.g., D), which may persist for 9–12 months;

however, this is not a universal phonomenon. The selective choice of symbionts also influences host growth, reproduction, and disease resistance (Douglas, 2003; Abrego *et al.,* 2008). Beyond cellular mechanisms, bleaching can be triggered and exacerbated by a range of environmental and biological stressors, including:

- Temperature and light stress: extreme temperatures, intense or insufficient light, air exposure during low tides.
- Water conditions: calm waters, changes in salinity, turbidity, sedimentation.
- Biological stressors: parasitic and infectious diseases.
- Pollution and chemical stressors: heavy metals, pollutants, prolonged darkness

Tissue deterioration may result from heat stress, nutrient deficiencies, or loss of UV-protective compounds (Glynn & D'croz, 1990; Douglas, 2003).

Although reef corals are generally stenothermic, some species can tolerate temperature extremes. Survival depends on stress intensity and duration, prior thermal history, and acclimation (Coles *et al.,* 1976; Douglas, 2003). Two main hypotheses address coral survival strategies. The Adaptive Bleaching Hypothesis (ABH) proposes that bleaching, though risky, may benefit corals by allowing the replacement of less tolerant symbionts with more resilient strains. This process relies on flexible host–symbiont partnerships and the ability of bleached corals to acquire new symbionts, potentially restoring the original associations once stress subsides. However, rapid warming may exceed corals' adaptive capacity, and overall diversity and community structure are expected to decline despite partial acclimation (Kinzie III *et al.,* 2001; Douglas, 2003; Fautin & Buddemeier 2004; Montefalcone *et al.,* 2020). The Deep Refuge Hypothesis (DRH) suggests that mesophotic reefs (30–165 m) are partly sheltered from surface stress, providing larvae to aid shallow reef recovery, though their refuge potential is limited by vertical connectivity and vulnerability to algal blooms and disease. (Douglas, 2003; Bongaerts *et al.,* 2010; Montefalcone *et al.,* 2020).

Corals employ several protective mechanisms to reduce the risk of bleaching. One important strategy involves the production of fluorescent proteins, which absorb high-energy light and re-emit or scatter it at longer wavelengths. This process reduces photodamage to the photosynthetic system of their symbionts and enhances resistance to bleaching (Salih *et al.,* 2000). Another key mechanism is Non-Photochemical Quenching (NPQ), a process common in photosynthetic organisms, including symbiotic algae, that dissipates excess light energy as heat. By preventing overexcitation of the photosystems, NPQ limits oxidative damage under high-light stress conditions (Hill *et al.,* 2005). Thermal and light stress also promote the production of reactive oxygen species (ROS), which represent a major trigger of coral bleaching. Both corals and their symbionts counteract ROS through antioxidant defenses, such as superoxide dismutase and catalase, while heat shock proteins (HSPs) play a critical role in protecting cellular proteins and maintaining homeostasis under stress. Enhanced antioxidant activity and stronger HSP responses have been consistently associated with higher bleaching tolerance (Krueger *et al.,* 2015; Madaschi *et al.,* 2024). Accurate assessment of past and future coral bleaching requires tools that reliably quantify thermal stress worldwide, with NOAA's Coral Reef Watch program serving as a primary global resource for detecting and forecasting temperature anomalies on coral reefs. It relies on satellite-derived sea surface temperature (SST) data processed using standardized indicators. To minimize the influence of daytime warming, the system uses nighttime SST and compares these values to the Maximum Monthly Mean (MMM), defined as the long-term average temperature of the warmest month. Deviations above this threshold are identified as thermal anomalies, known as HotSpots. HotSpots equal to or greater than 1 °C indicate the onset of coral thermal stress. To account for both the intensity and duration of heat stress, Coral Reef Watch employs Degree Heating Weeks (DHW), which accumulate HotSpots over a 12-week period. DHW values around 4 are associated with a high risk of bleaching, whereas values equal to or exceeding 8 are often linked to severe or potentially lethal bleaching events. By integrating HotSpots and DHW, the system generates Bleaching Alert Areas (BAA), which classify reef conditions into progressively higher alert levels, ranging from "No Stress" to "Alert Level 2," indicating a very high risk of severe bleaching and coral mortality. Updated daily, these products transform satellite temperature data into operational tools for global reef monitoring, early warning, and management (Liu *et al.,* 2014; NOAA).

Historically, ENSO events have been responsible for severe coral mortality worldwide. The 1982–1983 El Niño caused up to 95–100% coral loss in parts of the eastern Pacific and Indonesia, whereas Central Pacific ('Modoki') events, such as in 2002–2003, show maximum warming near the equator around the dateline (Claar *et al.,* 2018). Over the past four decades, major El Niño events have driven three completed global coral bleaching events, with a fourth currently ongoing since 2024. In 1998, many tropical regions exceeded critical thermal thresholds for several consecutive months Although the eastern Pacific and Caribbean were less affected, the western Pacific and Indian Ocean suffered severe coral mortality, with the Maldives among the hardest-hit areas in the Indo-Pacific. Sea surface temperatures reached extreme values, resulting in estimated coral mortality ranging from 60% to 100% in many locations. Branching corals, such as *Acropora* and *Pocillopora*, experienced near-total mortality, whereas massive corals generally suffered only partial damage. *Millepora* and many zooxanthellate soft corals disappeared entirely.

Consequently, the three-dimensional structure of the reefs was severely degraded, and live coral cover was reduced to a small fraction of its original extent (Goreau *et al.,* 2000; Bianchi *et al.,* 2006). Dead corals were subsequently overgrown by filamentous algae, calcareous algae, macroalgae, and eventually sponges. These shifts caused declines in coral-dependent invertebrates and fish, alongside a relative increase in herbivorous species. (Goreau *et al.,* 2000).

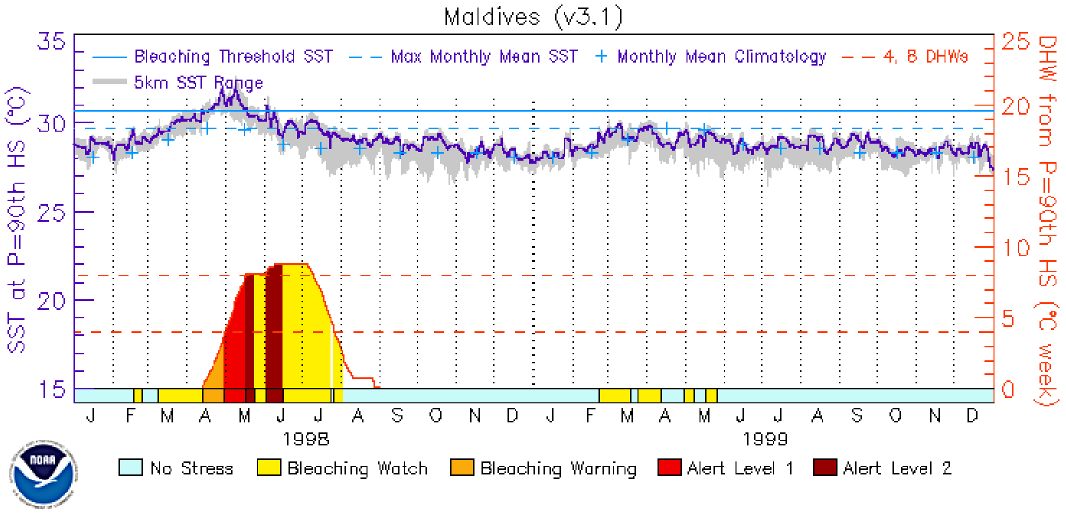

*Figure 3 Time series of sea surface temperature (SST) and thermal stress conditions for the Maldives during 1998–1999. The blue solid line represents the weekly SST at the 90th percentile hotspot (HS), while the dashed blue line indicates the maximum monthly mean SST. The bleaching threshold SST is shown as a horizontal reference line. Shaded grey areas denote the 5 km SST range. Thermal stress accumulation is expressed as Degree Heating Weeks (DHWs), shown on the right y-axis. Color-coded bars indicate coral bleaching risk levels: no stress (light blue), bleaching watch (yellow), bleaching warning (orange), Alert Level 1 (red), and Alert Level 2 (dark red) (NOAA).*

During mid-1998 (Figure 3), SSTs exceeded the bleaching threshold for several consecutive months, resulting in extreme thermal stress and Degree Heating Week (DHW) values above 8 °C-weeks. Northern Maldivian atolls experienced more intense bleaching and greater coral mortality than southern atolls, and recovery of branching coral genera was notably slower in these northern regions (Tkachenko, 2012).

From 1999 to 2002, most branching and tabular corals disappeared, while massive and encrusting forms became dominant. This shift led to a simplified benthic community and an increased dominance of abiotic components. Between 2003 and 2004, reef communities remained unstable and highly vulnerable; however, early signs of recovery began to emerge, marked by the gradual return of hard corals and a pronounced proliferation of corallimorpharians, particularly in lagoonal reefs. From 2005 to 2010, branching *Acropora* species progressively regained their ecological role, while corallimorpharians largely declined. This transition resulted in increasing substrate complexity and signaled a clear phase of ecological recovery (Morri *et al.,* 2015). In 2010, a second coral bleaching event occurred; however, its intensity was markedly lower than that of the 1998 event, leading to limited coral mortality and minimal impacts on overall reef structure (Guest *et al.,* 2012).

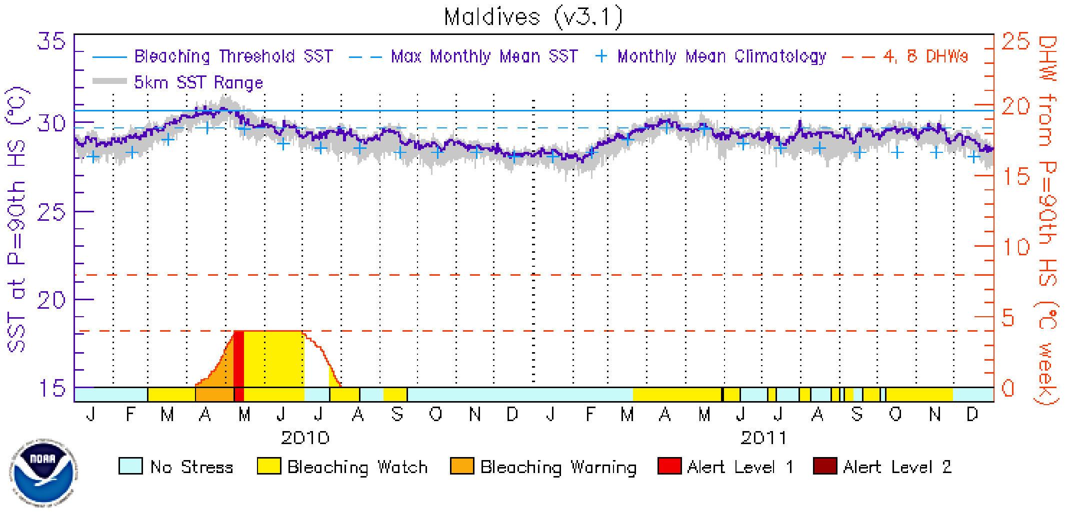

*Figure 4 Time series of sea surface temperature (SST) and thermal stress conditions for the Maldives during 2010–2011. The solid blue line represents weekly SST values at the 90th percentile hotspot (HS), while the dashed blue line indicates the maximum monthly mean SST. The bleaching threshold SST is shown as a horizontal reference line, and the shaded grey area represents the 5 km SST range. Degree Heating Weeks (DHWs), displayed on the right y-axis, quantify the accumulation of thermal stress over time. Colored bars indicate coral bleaching risk categories: no stress (light blue), bleaching watch (yellow), bleaching warning (orange), Alert Level 1 (red), and Alert Level 2 (dark red) (NOAA).*

In 2010 (Figure 4), sea surface temperatures (SSTs) briefly exceeded the bleaching threshold, resulting in moderate thermal stress and Degree Heating Week (DHW) values that remained relatively low compared to those recorded in 1998. Following this event, Maldivian coral reefs continued to recover, although in an irregular manner due to the recurrence of thermal disturbances.

During the post-2010 recovery phase, *Acropora* species became the dominant group in both coral recruitment and reef framework rebuilding. In contrast, some key components of the pre-1998 community, such as *Millepora*, failed to re-establish. Soft corals declined, while foliose corals increased in abundance. Although the reef system demonstrated resilience in terms of total coral cover, it also exhibited substantial plasticity and marked shifts in community composition, indicating a recovery that was partial rather than fully reversible.

Between 2010 and 2014, coral cover continued to increase, exceeding 50% by 2014. Nevertheless, recovery remained slow, requiring approximately 15 years and remaining incomplete for several community components (Morri *et al.,* 2015; Pisapia *et al.,* 2016). The 2015–2016 El Niño event subsequently triggered one of the most intense coral bleaching episodes ever documented in the Maldives. Compared to the 1998 event, increased human pressures had further reduced the reefs' capacity to recover. On the national scale, more than 73% of corals experienced bleaching, with no significant differences between reefs exposed to open-ocean conditions and those in more sheltered environments. As observed in previous events, *Acropora* species were the most vulnerable, whereas massive corals belonging to the genera *Porites* and *Goniopora* exhibited the highest resistance to thermal stress (Ibrahim *et al.,* 2017).

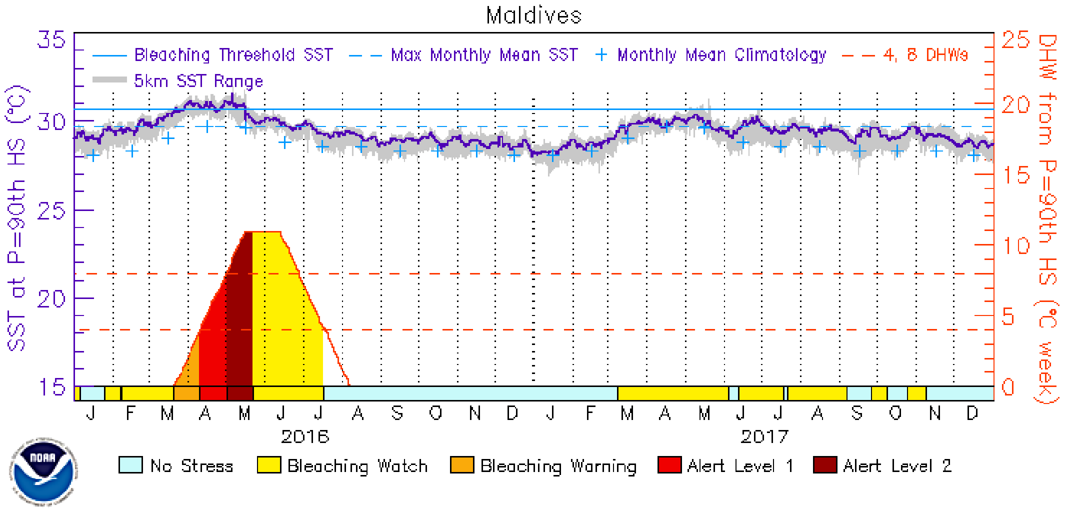

*Figure 5 Time series of sea surface temperature (SST) and thermal stress conditions for the Maldives during 2016–2017. The solid blue line shows weekly SST values at the 90th percentile hotspot (HS), while the dashed blue line represents the maximum monthly mean SST. The bleaching threshold SST is indicated by a horizontal reference line, and the grey shaded envelope depicts the 5 km SST spatial range. Degree Heating Weeks (DHWs), shown on the right y-axis, quantify the cumulative thermal stress experienced by corals over time. Colored bars along the bottom indicate coral bleaching risk categories: no stress (light blue), bleaching watch (yellow), bleaching warning (orange), Alert Level 1 (red), and Alert Level 2 (dark red) (NOOA).*

During 2016 (Figure 5), sea surface temperatures (SSTs) rose well above the bleaching threshold for a prolonged period, resulting in intense and sustained thermal stress. This was reflected in the rapid accumulation of Degree Heating Weeks (DHWs), which reached high values (4–11) and triggered both Alert Level 1 and Alert Level 2 conditions during the boreal spring. The magnitude and persistence of this heat stress indicate the occurrence of a severe marine heatwave in the Maldives, causing substantial coral mortality and long-lasting impacts on reef structure.

Central and southern atolls experienced particularly severe coral mortality, with live coral cover reduced to 6–20% and bleaching affecting approximately 73% of corals between 0 and 13 m depth. In contrast, northern atolls suffered lower, though still considerable, mortality, with post-event live coral cover ranging from 3% to 27% and branching coral losses of about 40%, compared to 70–80% in other regions. This relatively reduced impact in the north has been linked to lower levels of anthropogenic pressure (Dryden *et al.,* 2020; Bessell-Browne *et al.,* 2021). Although the 2016 bleaching event affected reefs nationwide, recovery trajectories varied markedly among locations. Reefs in remote areas generally displayed higher resilience, retaining much of their structural complexity and species diversity. In contrast, reefs near urban centres or intensive tourism development experienced more pronounced declines, with some shifting toward altered ecological states characterized by algal dominance or reduced coral diversity. Some 'hope spots' experienced bleaching in only a quarter or fewer corals, highlighting the strong spatial heterogeneity of impacts and the interplay between local environmental conditions and global climate drivers in shaping reef recovery (Pancrazi *et al.,* 2025). In the years following the disturbance, reef recovery was slow and uneven. Massive corals persisted, while fast-growing taxa re-established more gradually. From around 2020, recovery accelerated as branching and digitate corals expanded, secondary reef builders exceeded pre-impact levels, and overall reef-building capacity increased. By 2023, benthic communities and coral cover approached 2015 levels, though some functional groups remained reduced, indicating incomplete recovery (Germani *et al.,* 2025).

The fourth global coral bleaching event began in the Caribbean during the summer of 2023 and subsequently spread across tropical regions, reaching the Maldives on 15 April 2024. In parts of the Indo-Pacific, Degree Heating Weeks exceeded all previously recorded values, prompting NOAA to introduce new alert categories for the first time and signaling the risk of near-total coral mortality. Notably, the two most recent global bleaching events (2014–2017 and 2023–2024) were not triggered by strong El Niño conditions; instead, they occurred before the development of such events, indicating that ongoing background climate warming was the dominant driving factor (Reimer *et al.,* 2024).
As usual, the most vulnerable species, such as *Acropora*, were heavily impacted, whereas massive corals exhibited higher survival rates (Migliaccio, 2024).

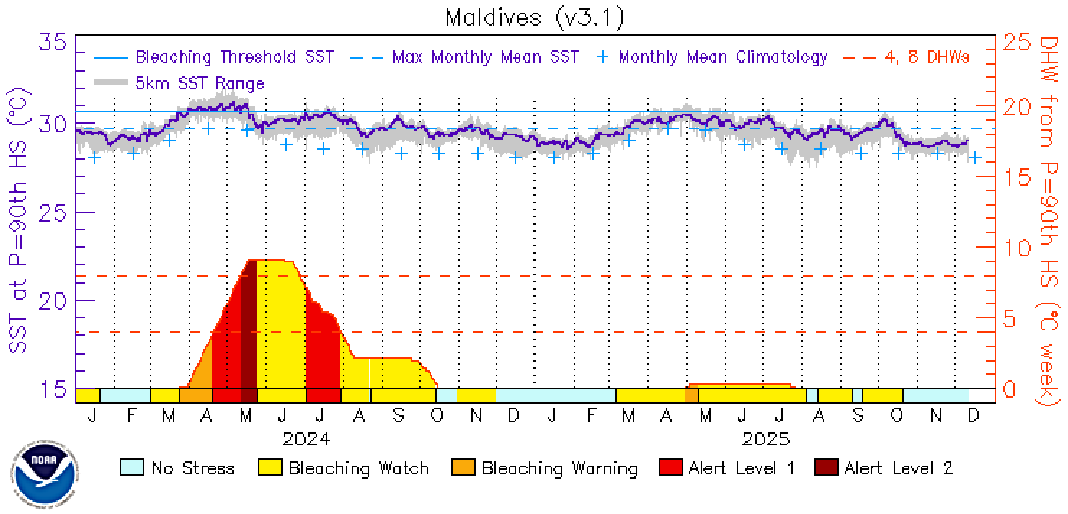

*Figure 6 Time series of sea surface temperature (SST) and thermal stress conditions for the Maldives during 2024–2025. The solid blue line represents weekly SST values at the 90th percentile hotspot (HS), while the dashed blue line shows the maximum monthly mean SST. The horizontal dashed line marks the bleaching threshold SST, above which corals experience thermal stress. The grey shaded area illustrates the 5 km SST spatial range. Degree Heating Weeks (DHWs), shown on the right y-axis in orange/red, quantify the cumulative thermal stress experienced by corals over time. Colored bars along the bottom indicate coral bleaching risk categories: no stress (light blue), bleaching watch (yellow), bleaching warning (orange), Alert Level 1 (red), and Alert Level 2 (dark red) (NOAA).*

During 2024 (Figure 6), sea surface temperatures (SSTs) began to exceed the bleaching threshold in March and peaked between May and July. This resulted in pronounced thermal stress, with Degree Heating Weeks (DHWs) reaching values associated with Alert Level 1 and Alert Level 2 conditions, indicating a high risk of severe coral bleaching.

After August 2024, SSTs declined below the bleaching threshold, and thermal stress progressively diminished. By early 2025, only minor bleaching watch conditions were observed, indicating a temporary relief from extreme thermal stress.

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# 2 AIMS OF THE THESIS

This thesis aims to provide multi-scale assessment of the reefs' status across the Maldivian archipelago, by combining ecological analyses, functional metrics, and management context to improve understanding of reef resilience in a climate-stressed tropical system.

First, two image-based approaches for benthic cover quantification (*PhotoQuad* and *CoralNet*) were compared to evaluate their reliability and suitability for large-scale ecological applications, assessing their consistency across depth gradients and reef typologies.

Second, spatial variation in benthic communities was examined along the Maldives' main geographic gradient (North, Central, South), testing the influence of latitude, depth, and reef habitat, and their interactions across cross-shelf and bathymetric gradients.

Reef condition was then characterized using three complementary ecological indices (CAPI, BAI, and RCI) to evaluate coral–algal balance, biotic–abiotic proportions, and reef framework consolidation.

Finally, the study examined how management regimes and atoll-scale variability jointly influence reef condition, disentangling human pressures from natural environmental gradients and assessing their combined effects on substrate composition and coral cover.

# 3 MATERIALS AND METHODS

## *3.1 STUDY AREA*

The study was conducted across the entire Maldivian archipelago, encompassing the three principal regions: the northern, central, and southern areas of the country.

The northernmost part of the Maldives is formed by the Haa Atoll, which is divided into two administrative atolls: Haa Alifu and Haa Dhaalu.

Extending between 7°06′–6°54′ N and 72°47′–72°59′ E, Haa Alifu covers an area of approximately 330 km² and has maximum dimensions of about 21 km (Tkachenko, 2012). Officially known as *Thiladhunmathi Uthuruburi*, it constitutes the northernmost administrative division of the Maldives and includes the natural atoll of *Ihavandhippolhu*, the northernmost atoll of the Maldivian archipelago, together with the northern section of the larger *Thiladhunmathi* (Tiladummati) Atoll. In total, it comprises 42 islands, 14 of which are permanently inhabited, and currently hosts three tourist resorts. In terms of both population and land area, Northern *Thiladhunmathi* ranks as the third largest atoll in the Maldives. Owing to its location at the northern extremity of the archipelago, it is the Maldivian atoll closest to Sri Lanka and India, highlighting its regional significance within the Indian Ocean (https://www.atollsofmaldives.gov.mv).

The atoll (Figure 7) (Table 1) hosts a population of approximately 14,000–15,000 inhabitants (https://www.citypopulation.de/en/). The islands within the atoll are highly heterogeneous: some remain uninhabited, others are inhabited, and several are designated for resort development. They vary widely in size and function, supporting activities such as agriculture and fishing, while some have been established as marine protected areas (https://www.atollsofmaldives.gov.mv). *Ihavandhippolhu* Atoll is a remote and lightly impacted region, characterized by low population density and limited tourism compared to the central and southern atolls. Consequently, local anthropogenic pressures are reduced, creating favourable conditions for the persistence and recovery of vulnerable species such as *Millepora* (Pancrazi *et al.,* 2024).

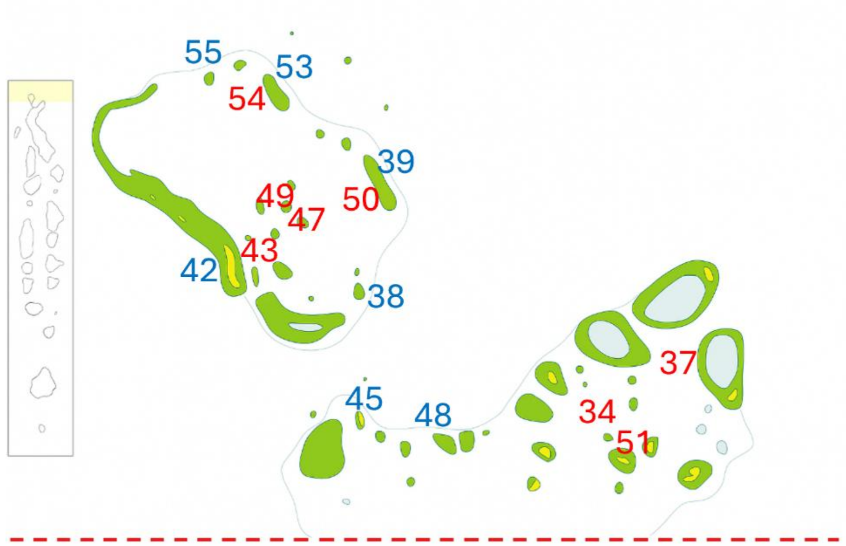


*Figure 7 Map of Haa Alifu Atoll. The dotted red line shows the division of Haa Atoll. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 1 Summary table of surveyed reef sites in the Haa Alifu Atolls, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Haa Alifu | 34 | Inner | Alidhoo Dhahafalhi | 6°51.084' N 73°09.061'E | Resort |
| Haa Alifu | 37 | Inner | Fihladhoo Ethere | 6°54.274' N 73°12.3791' E | Inhabited |
| Haa Alifu | 38 | Outer | Gallandhoo Beyru | 6°56.596' N 72°59.174' E | Uninhabited |
| Haa Alifu | 39 | Outer | Gambas | 7°01.616' N 72°59.722' E | Inhabited |
| Haa Alifu | 42 | Outer | Huvahandhoo Beyru | 6°57'09.46"N 72°53'56.30" E | Inhabited |
| Haa Alifu | 43 | Inner | Huvahandhoo Ethere | 6°57.518' N 72°54.507' E | Inhabited |
| Haa Alifu | 45 | Outer | Maarandhoo Beyru | 6°51.546' N 72°59.084' E | Inhabited |
| Haa Alifu | 47 | Inner | Manafaru | 6°59.674' N 72°56.657' E | Resort |
| Haa Alifu | 48 | Outer | Mathi Faru | 6°51.131' N 73°02.557' E | Resort |
| Haa Alifu | 49 | Inner | Medafushi | 7°00.605' N 72°55.844' E | Uninhabited |
| Haa Alifu | 50 | Inner | Muladhoo Ethere | 7°01.650' N 72°59.005' E | Inhabited |
| Haa Alifu | 51 | Inner | Muraidhoo Kanmathi | 6°49.969' N 73°10.023' E | Inhabited |
| Haa Alifu | 53 | Outer | Uligan Beyru | 7°04.816' N 72°56.136' E | Inhabited |
| Haa Alifu | 54 | Inner | Uligan Ethere | 7°05.309' N 72°54.934' E | Inhabited |
| Haa Alifu | 55 | Outer | Vagaaru | 7°05.980' N 72°52.410' E | Uninhabited |

Haa Dhaalu Atoll, officially *Thiladhunmathi Dhekunuburi*, is an administrative division of 16 inhabited islands forming the southern part of the natural *Thiladhunmathi* Atoll and including Makunudhoo Island with its reef (https://www.atollsofmaldives.gov.mv). Its capital, Kulhudhuffushi is the main urban centre in the northern Maldives (Masters, 2021). The islands of the atoll (Figure 8) (Table 2) are inhabited by approximately 10,540 people (https://www.citypopulation.de/en/). In this atoll, Hanimaadhoo, the largest island with about 3,000 inhabitants, is strategically important, hosting an international airport, an agricultural centre, a meteorological office, and tourist facilities. The island faces climate change impacts, including erosion from storms, heavy rainfall, and flooding, which are perceived differently by residents. There is also growing awareness of the benefits of renewable energy for the community (Zama *et al.,* 2023).

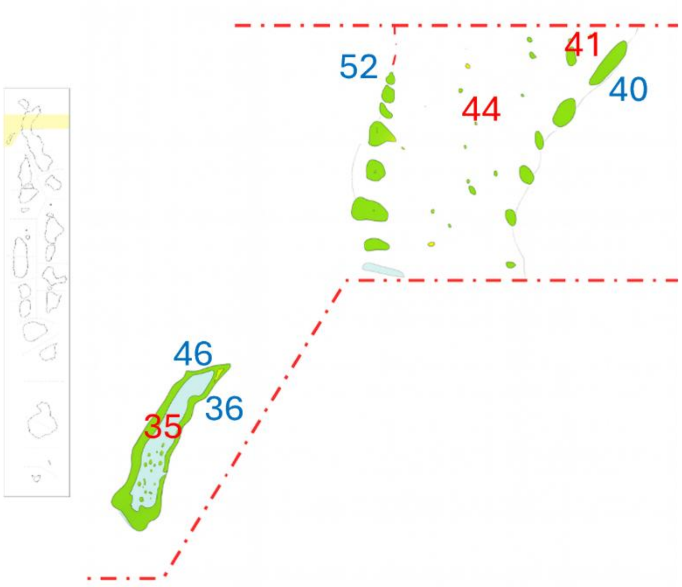


*Figure 8 Map of Haa Dhaalu Atoll. The atoll is delineated by red dashed lines. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 2 Summary table of surveyed reef sites in the Haa Dhaalu Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Haa Dhaalu | 35 | Inner | Fari Gau | 6°20.908' N 72°39.015' E | Uninhabited |
| Haa Dhaalu | 36 | Outer | Fenboahuraa Beyru | 6°23.611' N 72°41.968' E | Uninhabited |
| Haa Dhaalu | 40 | Outer | Hanimaadhoo Beyru | 6°46.520' N 73°11.207' E | Inhabited |
| Haa Dhaalu | 41 | Inner | Hanimaadhoo Bodu Kalhu | 6°46'14.44"N 73°10'16.47"E | Inhabited |
| Haa Dhaalu | 44 | Inner | Keylakunu West | 6°36.047' N 73°00.279' E | Uninhabited |
| Haa Dhaalu | 46 | Outer | Makunudhoo Beyru | 6°25.191'N 72°42.032' E | Inhabited |
| Haa Dhaalu | 52 | Outer | Naavaidhoo Bodu | 6°45.159' N 72°55.698' E | Inhabited |

Central Maldivian atolls such as North and South Malé, Rasdhoo, Ari, and Vaavu host extensive coral reef structures, deep lagoons, and interconnected channels (*kandu*), and collectively represent the ecological and biological characteristics of the broader Maldivian reef province (Dryden & Basheer, 2020). The central atolls considered in this study are: Kaafu Atoll (Figure 9) (Table 3), made up of North and South Malé Atolls, lies in the central part of the Maldives and is the most populated and developed atoll, largely because it hosts the capital city, Malé. Featuring fringing reefs, deep lagoons, and channels that regulate water flow, this atoll faces significant environmental pressures from human activities like land reclamation and coastal modification, requiring careful monitoring and impact assessments (Solutions, 2013; 2017). North Malé Atoll and South Malé Atoll are large, complex atolls forming most of the administrative Malé Atoll.

North Malé Atoll measures ~60 km in length and ~40 km in width (Rasheed *et al.,* 2020), with a surface area of ~1568.18 km² and more than 189 reefs covering 349 km² (Naseer & Hatcher, 2004). The atoll contains numerous *faro*, mainly concentrated in the northern and southern regions. The southern islands, including Malé, Hulhulé, Hulhumalé, and Villimalè, host over 200,000 inhabitants (almost half of the national population). Tourism-driven development has resulted in extensive coastal modification and land reclamation, with nearly half of the existing land area reclaimed (Rasheed *et al.,* 2020). South Malé Atoll is separated from North Malé Atoll by the 5 km-wide Vaadhoo Kandu channel, with depths of nearly 400 m (Luthfee, 1995). Covering about 558.31 km², it contains 112 reefs totaling roughly 175.60 km² (Naseer & Hatcher, 2004). Unlike North Malé, its outer rim is more continuous, with fewer channels, and the atoll has experienced considerable land reclamation in recent years (Rasheed *et al.,* 2020).

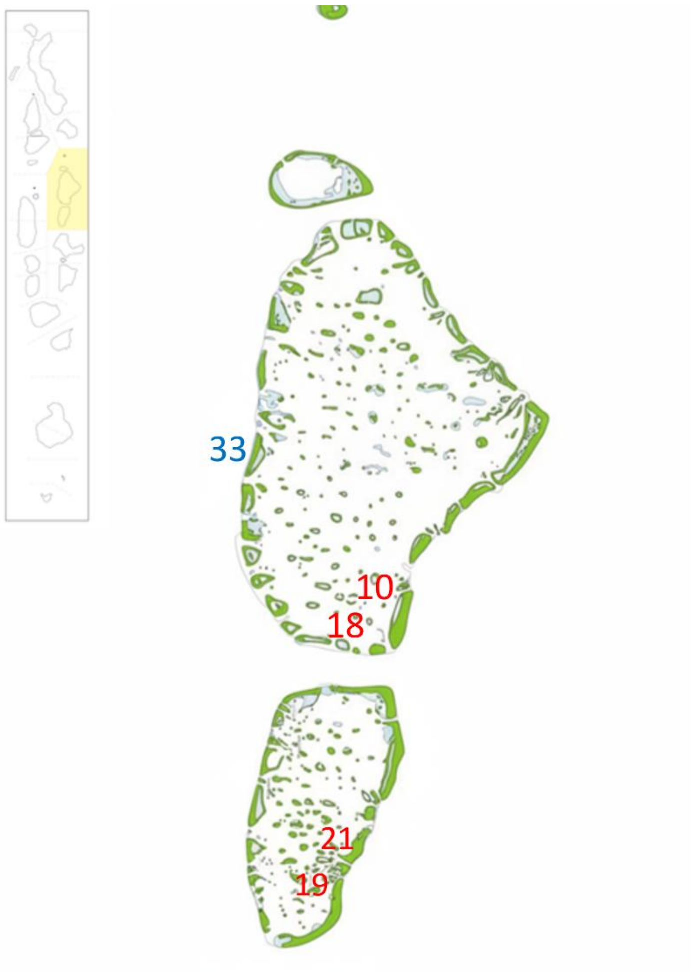


*Figure 9 Map of Kaafu Atoll. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 3 Summary table of surveyed reef sites in the Malè Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| North Malè | 10 | Inner | Kuda Banana Reef | 4°14.032' N 73°31.945' E | Inhabited |
| North Malè | 18 | Inner | Villimalé west | 4°10'31.32"N 73°28'57.31"E | Inhabited |
| North Malè | 33 | Outer | Rasfari Beyru | 4°24.871' N 73°21.117' E | Uninhabited |
| South Malè | 19 | Inner | Villivaru Kuda Giri | 3°54.234' N 73°26.663' E | Uninhabited |
| South Malè | 21 | Inner | Bajiya Giri | 3°55'57.71"N 73°27'54.34"E | Uninhabited |

The adjacent atoll, known as Alifu Atoll (or Ari Atoll) (Figure 10) (Table 4), covers a total area of 2,271.75 km², comprising 489.40 km² of reefs and 8.30 km² of islands (Naseer & Hatcher, 2004). It has the highest number of reefs among the studied atolls, with 268 distinct formations, and features deep lagoons, mature rim reefs, and numerous patch reefs (Naseer, 2006). Ari Atoll is administratively divided into two sectors: North Ari (Alifu Alifu) and South Ari (Alifu Dhaalu) (Ducarme, 2016).

Rasdhoo, a small ring-shaped atoll in the western Maldivian atolls, lies to the northeast of North Ari and measures 9.25 km in diameter, covering an area of 61.84 km² (Naseer & Hatcher, 2004). Its continuous marginal reef hosts five islands (Kuramathi, Rasdhoo, Madivaru, Madivaru Finolhu, and Veligadu, from west to east) and three channels connect the 40 m-deep lagoons, containing around 40 patch reefs, to the open ocean. A sand apron and an elongated ridge shape part of the lagoon, while the fore reef slope is narrow and steep, except on the western side (Gischler, 2006).

On March 1, 1984, Ari Atoll (formerly Alifu Atoll) was split into North and South sections, forming the administrative divisions of Alifu Alifu and Alifu Dhaalu Atolls. Alifu Dhaalu (South Ari Atoll) lies south of the Himendhoo Dhekunukandu–Genburugau Kandu line (https://www.atollsofmaldives.gov.mv).

Northern Ari Atoll is the northern administrative sector of the Ari Atoll. Several islands have been inhabited since ancient times, with archaeological remains from the Maldivian Buddhist period (https://www.atollsofmaldives.gov.mv). The atoll includes community islands, 8 inhabited islands with 24 guesthouses, 13 resort islands, and smaller uninhabited islands. It hosts coral reefs, seagrass beds, mangroves, and tidal flats, which support fisheries, subsistence, and tourism. These ecosystem services expose the atoll to pressures from tourism, coastal modifications, pollution, overfishing, and coral bleaching (Agardy *et al.,* 2017). Tourist islands managed as resorts tend to have stricter oversight, which facilitates the recovery of sensitive corals following bleaching events (Pisapia *et al.,* 2016).

South Ari Atoll comprises islands, flat reefs, and deep channels, hosting ~250 hard coral species, over 1,200 reef fish species, marine turtles, large predators, and diverse invertebrates. This area is heavily exploit for tourism, with 17 resorts, 16 guesthouses, and numerous liveaboards and safari boats. In 2009, the Maldives' largest marine area was established: the South Ari Marine Protected Area (SAMPA), with the aim to protect whale shark aggregation and support sustainable tourism and research (Dryden *et al.,* 2020a)

*Figure 10 Map of Ari Atoll and Rasdhoo Atoll. The red dotted line marks the division between North and South Ari Atoll. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 4 Summary table of surveyed reef sites in the Ari Atoll and Rasdhoo Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Rasdhoo | 28 | Outer | Madivaru Beyru | 4°16.215' N 73°00.405' E | Uninhabited |
| North Ari | 23 | Inner | Defah Thoshi | 4°14.558'N 72°46.404'E | Uninhabited |
| North Ari | 24 | Outer | Dhinnolhu Beyru | 4°8.412' N 72°43.685' E | Uninhabited |
| North Ari | 27 | Outer | Maavaru Falhu Beyru | 3°52.588' N 72°42.295' E | Uninhabited |
| South Ari | 20 | Inner | Badhibinhau | 3°52.572' N 72°49.811' E | Uninhabited |
| South Ari | 26 | Inner | Kalhahandhi Huraa | 3° 48.128'N 72° 42.636' E | Uninhabited |
| South Ari | 31 | Outer | Panettone Beyru | 3°47.948' N 72°42.234' E | Uninhabited |

According to Naseer & Hatcher, Vaavu Atoll (or Felidhe Atholhu) (Figure 11) (Table 5) has a total surface area of 1,090.97 km², of which 251.10 km² are reefs spread across 203 formations, while the land area is just 0.92 km² (Naseer & Hatcher, 2004). The smallest administrative atoll by population in the Maldives, Vaavu includes Felidhu Atoll and the tiny Vattaru Reef. Located about 40 miles from Malé, it can be reached in roughly 90 minutes by speedboat or 5 hours by traditional dhoni. Vattaru Reef has only one small island and measures around 9 km across. The easternmost point of the Maldives lies at Fottheyo Muli (https://www.atollsofmaldives.gov.mv). In Vaavu Atoll, President Ibrahim Mohamed Solih announced a major tourism project involving the reclamation of 400 hectares of Fottheyo Falhu lagoon for the development of resorts and related infrastructure, including an airport. The Atoll Council has raised concerns about the area’s ecological importance, which is protected, and Shujau Ali has publicly criticized the project as a “mega criminal project,” urging its immediate suspension (https://atolltimes.mv).

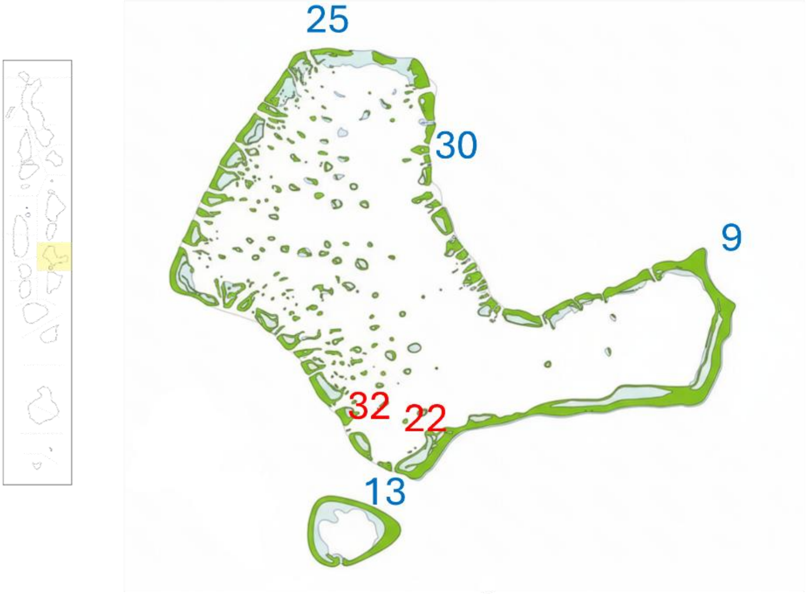


*Figure 11 Map of Vaavu Atoll. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 5 Summary table of surveyed reef sites in the Vaavu Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Vaavu | 9 | Outer | Fotteyo Beyru | 3°30.313’N 73°44.569'E | Uninhabited |
| Vaavu | 13 | Outer | Rakeedhoo Kandu | 3°18.702' N 73°27.931' E | Inhabited |
| Vaavu | 22 | Inner | Bodu Mohora Giri | 3°19.563' N 73°29.175' E | Uninhabited |
| Vaavu | 25 | Outer | Fulidhoo Beyru | 3°41.010' N 73°24.966' E | Inhabited |
| Vaavu | 30 | Outer | Miyaru Kandu | 3°35.868' N 73°30.241' E | Resort |
| Vaavu | 32 | Inner | Rakeedhoo Ethere | 3°19.057' N 73°28.151' E | Inhabited |

In the southern Maldives, lagoons are 80–100 m deep, inner patch reefs are rarer, the atoll rim is more continuous, and more of the perimeter is occupied by islands, likely due to increasing annual rainfall from north to south (Pernetta & Wells, 1993). South of the One and a Half Degree Channel (Aslam & Kench, 2017), the southern Maldives include the atolls of Huvadhoo, Fuvahmulah, and, at the southern limit of the archipelago, Addu Atoll. Located in the southern Maldives (03°20′N, 73°17′E), Huvadhoo Atoll (Gaafu Atoll) (Figure 12) (Table 6) is the largest atoll, with a perimeter of 261.4 km and an area of 3,279 km² with 241 reefs (437.9 km²) and 241 vegetated islands (2,754 ha), ranging in size from 0.01 to 238.1 ha (Naseer & Hatcher, 2004). It extends about 80 km north-south and 60 km east-west, with a highly fragmented rim featuring passes that allow ocean swells and currents into the lagoon, which reaches a maximum depth of 80 m. The atoll has about 200 islands along the periphery, 41 on lagoonal reefs, and 19 inhabited. Island shapes are changing due to reclamation and erosion, with smaller islands shrinking and larger ones growing; western islands are gravel and sand, while lagoonal and eastern islands are mostly sandy (East *et al.,* 2016; Liang *et al.,* 2016; Aslam & Kench, 2017). Huvadhoo Atoll was divided into two administrative districts on February 8, 1962: Gaafu Alifu in the northeast, with Vilingili as its capital, and Gaafu Dhaalu in the southwest, with Thinadhoo as its capital. Gaafu Dhaalu includes 153 islands, 10 inhabited, and lies about 340 km south of Malé (https://www.atollsofmaldives.gov.mv).

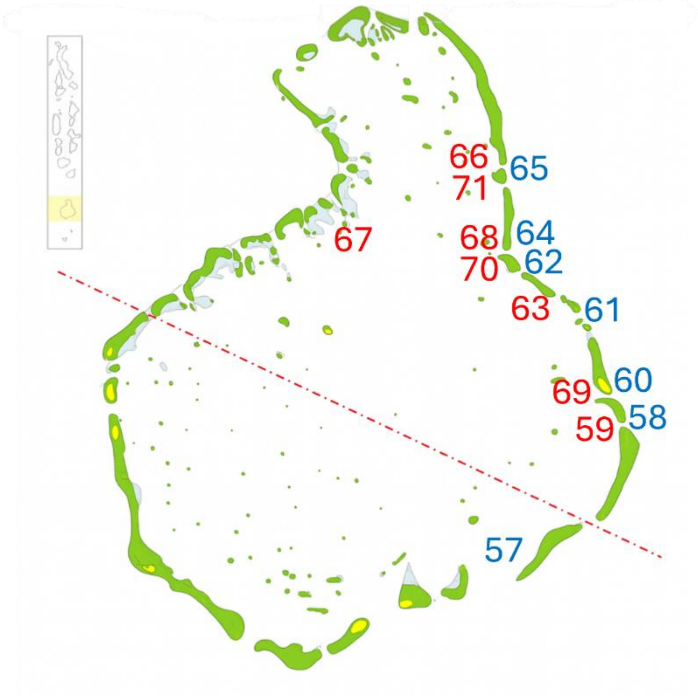


*Figure 12 Map of Huvadhoo Atoll. The dotted red line indicates the boundary between Gaafu Alifu and Gaafu Dhaalu. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 6 Summary table of surveyed reef sites in the Huvadhoo Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Huvadhoo | 57 | Inner | Tiger Wall | 00°18.311'S 73°26.462'E | Inhabited |
| Huvadhoo | 58 | Outer | Haanjhyle Athiri | 00°18.948'S 73°25.747'E | Uninhabited |
| Huvadhoo | 59 | Inner | Maareha Beyru North | 00°27.663'N 73°34.155'E | Uninhabited |
| Huvadhoo | 60 | Outer | Diyadhoo Ethere | 00°28.615'N 73°31.784'E | Uninhabited |
| Huvadhoo | 61 | Outer | Kondey Kandu North | 00°29.732'N 73°33.443'E | Inhabited |
| Huvadhoo | 62 | Outer | Mahahdhoo Beyru | 00°34.996'N 73°31.119'E | Uninhabited |
| Huvadhoo | 63 | Inner | Nilandhoo Beyru | 00°38.108'N 73°27.232'E | Inhabited |
| Huvadhoo | 64 | Outer | Nilandhoo Giri | 00°36.854'N 73°26.542'E | Uninhabited |
| Huvadhoo | 65 | Outer | Kuredhdhoo Beyru | 00°39.450'N 73°26.636'E | Inhabited |
| Huvadhoo | 66 | Inner | Kooddoo Beyru | 00°44.368'N 73°26.355'E | Inhabited |
| Huvadhoo | 67 | Inner | Villingili Housereef | 00°45.050'N 73°25.906'E | Inhabited |
| Huvadhoo | 68 | Inner | Boaddoo | 00°42.545'N 73°19.672'E | Uninhabited |
| Huvadhoo | 69 | Inner | Odegalla Coral Garde | 00°39.501'N 73°24.963'E | Uninhabited |
| Huvadhoo | 70 | Inner | Kondeymatheelaabadhoo | 00°30.195'N 73° 29.916'E | Uninhabited |
| Huvadhoo | 71 | Inner | Kuredhdhoo Finolhu | 00°39.498'N 73°26.096'E | Inhabited |

Fuvahmulah (Gnaviyani Atoll) is the smallest administrative division of the Maldives and corresponds to the natural atoll of Fuvahmulah, located in the Equatorial Channel between Huvadhoo and Addu Atolls (https://www.atollsofmaldives.gov.mv). Fuvahmulah (Figure 13) (Table 7) is a remote oceanic island that alone forms the administrative atoll of Gnaviyani, making it unique within the Maldives. It is among the country's largest islands (approximately 4.5 km × 1.2 km), of volcanic origin, and supports a dense population with well-established infrastructure and a diversified economy. Unlike most Maldivian islands, Fuvahmulah contains inland freshwater lakes and lacks a sheltered reef lagoon, leaving it highly exposed to the open ocean and more susceptible to coastal erosion (Energy, 2016; David & Schlurmann, 2020). Fuvahmulah is recognized as a UNESCO Biosphere Reserve, a designation that highlights its ecological and cultural uniqueness within the Maldivian archipelago. Covering 1,316 hectares, the reserve encompasses highly diverse terrestrial and marine ecosystems, ranging from mangroves and coral reefs to freshwater lakes, which together support a rich fauna, including green turtles, blacktip sharks, and numerous pelagic species (https://www.unesco.org).

*Figure 13 Map of Fuvahmulah Atoll. Blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 7 Summary table of surveyed reef sites in the Fuvahmulah Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Fuvahmulah | 56 | Outer | Tiger Wall | 00°18.311'S 73°26.462'E | Inhabited |
| Fuvahmulah | 72 | Outer | Gan Ethere | 00°41.224'S 73°09.210'E | Inhabited |

Addu Atoll (Seenu Atoll) (Figure 14) (Table 8) is the southernmost atoll of the Maldives, extending into the Southern Hemisphere, with a maximum diameter of 28.4 km. Reef flats and islands cover about 41% of its total area (Taylor, 1978). It has a total area of 157.22 km², comprising 70.32 km² of reef spread across 7 reefs and 15.00 km² of land (Naseer & Hatcher, 2004). Its capital, Addu City (about 35,000 people) (Faroog *et al.,* 2023), is the country's second-largest city by population and includes the inhabited islands of Hulhudhoo, Maradhoo, Feydhoo, and Hithadhoo. Gan Island, part of the atoll, is home to Gan International Airport (https://www.atollsofmaldives.gov.mv). The designation of Addu Atoll as a UNESCO Biosphere Reserve in 2020 established an integrated management model combining conservation, sustainable development, and cultural promotion. The Action and Conservation Plan identifies seven core areas of high ecological value, including wetlands, mangroves, house reefs, and marine megafauna aggregation sites. Addu is a national hotspot for key species, including the manta ray *Mobula alfredi* and coastal sharks. The strategy includes ecological monitoring, regulation of productive activities, energy transition, and fortified local governance coordinated by the Addu City Council (Addu City Council, IUCN, & USAID, 2024).

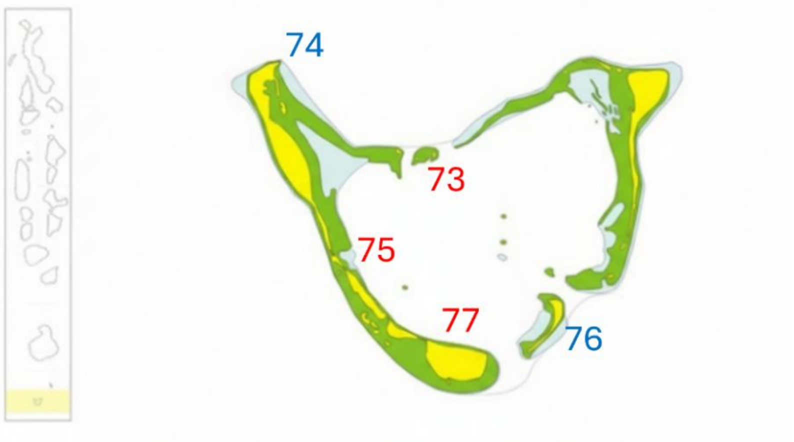


*Figure 14 Map of Addu Atoll. Red numbers indicate inner, lagoonal sites sheltered within the atoll, while blue numbers indicate outer, oceanic sites exposed to open water.*

*Table 8 Summary table of surveyed reef sites in the Addu Atoll, showing reef type, site name, GPS location, and management category (inhabited, uninhabited, or resort).*

| Atoll | N° | Reef typology | Site Name | Coordinates | Management |
|---|---|---|---|---|---|
| Addu | 73 | Inner | Kandihera Ethere | 00°37.135'S 73°08.554'E | Uninhabited |
| Addu | 74 | Outer | Koattey Beyru | 00°34.770'S 73°05.451'E | Inhabited |
| Addu | 75 | Inner | Maradhoo Ethere | 00°39.127'S 73°11.080'E | Inhabited |
| Addu | 76 | Outer | Villingili Beyru | 00°41.280'S 73°11.641'E | Inhabited |
| Addu | 77 | Inner | Gan Ethere | 00°41.224'S 73°09.210'E | Inhabited |

## *3.2 FIELD ACTIVITY*

Field surveys were conducted across reef sites spanning the entire Maldivian archipelago, including atolls from the northern, central, and southern regions. Benthic community data were collected through SCUBA diving using standardized photoquadrat surveys with a 1 m × 1 m PVC (polyvinyl chloride) quadrat frame. At each site, sampling was performed at three depth strata (Flat, 10, and 20 m), with 12 replicate photoquadrats per depth, resulting in 36 images per site and a total of approximately 3,000 images analyzed.

Both inner reef (lagoonal) and outer reef (ocean-facing) habitats were surveyed. Sites were selected to represent distinct management regimes, including resort-managed, inhabited, and uninhabited islands. Data from the northern and central atolls were collected in 2024, while surveys in the southern atolls were conducted at the beginning of 2025. This dataset was used to evaluate spatial variation in coral reef community structure across the Maldives.

Categories representing the primary coral taxa were used to classify the benthic community, as follows (Table 9):

1. Hard Coral:
    - ❖ *Acropora* growth form:
        - *Acropora* branching
            - *Acropora* branching Live (a)
            - *Acropora* branching Bleached (a.1.)
            - *Acropora* branching Dead (a.2.)
        - *Acropora* digitate
            - *Acropora* digitate Live (b)
            - *Acropora* digitate Bleached (b.1.)
            - *Acropora* digitate Dead (b.2.)
        - *Acropora* tabular
            - *Acropora* tabular Live (c)
            - *Acropora* tabular Bleached (c.1.)
            - *Acropora* tabular Dead (c.2.)

    - ❖ *Pocillopora:*
        - *Pocillopora* Live (d)
        - *Pocillopora* Bleached (d.1.)
        - *Pocillopora* Dead (d.2)

- Other branching coral
  - Other branching coral Live (e)
  - Other branching coral Bleached (e.1.)
  - Other branching coral Dead (e.2.)

- Foliose coral
  - Foliose coral Live (f)
  - Foliose coral Bleached (f.1.)
  - Foliose coral Dead (f.2.)

- Massive coral
  - Massive coral Live (g)
  - Massive coral Bleached (g.1.)
  - Massive coral Dead (g.2.)

- Encrusting coral
  - Encrusting coral Live (h)
  - Encrusting coral Bleached (h.1.)
  - Encrusting coral Dead (h.2.)

- Fungiidae
  - Fungiidae Live (i)
  - Fungiidae Bleached (i.1.)
  - Fungiidae Dead (i.2.)

- *Tubastrea* (j)

- Corallimorpharia (k)

2. Minor components:

   - *Heliopora coerulea* (l)

   - *Millepora* (m)

   - Soft coral (n)

   - Sponges (o)

   - Giant clam (p)

   - Corallinae algae (q)

- Macroalgae (r)
- *Halimeda spp.* (s)
- Ascidians (t)
- Zoantharia (u)
- Gorgonians/Black corals/Whip corals (v)
- Cyanobacteria (w)

*3.* Abiotic components:

- Rock (x)
- Coral Rubble (y)
- Sand (z)

*Table 9 Table listing various benthic indicators alongside their corresponding acronyms. The table is organized in two columns, with the first column showing the indicator names and the second column displaying their abbreviations.*

| **Indicators** | **Acronym** |
|---|---|
| *Acropora branching Live* | AB |
| *Acropora branching Bleached* | BAB |
| *Acropora branching Dead* | DAB |
| *Acropora digitate Live* | AD |
| *Acropora digitate Bleached* | BAD |
| *Acropora digitate Dead* | DAD |
| *Acropora tabular Live* | AT |
| *Acropora tabular Bleached* | BAT |
| *Acropora tabular Dead* | DAT |
| *Pocillopora Live* | PO |
| *Pocillopora Bleached* | BPO |
| *Pocillopora Dead* | DPO |
| *Other branching coral Live* | OBC |
| *Other branching coral Bleached* | BOBC |
| *Other branching coral Dead* | DOBC |
| *Foliose coral Live* | FC |
| *Foliose coral Bleached* | BFC |
| *Foliose coral Dead* | DFC |
| *Massive coral Live* | MC |
| *Massive coral Bleached* | BMC |
| *Massive coral Dead* | DMC |
| *Encrusting coral Live* | EC |
| *Encrusting coral Bleached* | BEC |
| *Encrusting coral Dead* | DEC |
| *Fungiidae Live* | FU |
| *Fungiidae Bleached* | BFU |
| *Fungiidae Dead* | DFU |
| *Tubastrea* | TU |
| *Corallimorpharia* | CorMor |
| *Heliopora coerulea* | HEL |
| *Millepora* | MIL |
| *Soft coral* | SC |
| *Sponges* | SP |
| *Giant clam* | GiCl |
| *Corallinae algae* | CoA |
| *Macroalgae* | MAL |
| *Halimeda spp.* | HAL |
| *Ascidians* | ASC |
| *Zoantharia* | ZOA |
| *Gorgonians/Black corals/Whip coral* | GORG |
| *Cyanobacteria* | CYA |
| *Rock* | RC |
| *Coral rubble* | CR |
| *Sand* | SA |

*a) Acropora branching Live*
*(AB)*

*a.1.) Acropora branching Bleached*
*(BAB)*

*a.2.) Acropora branching Dead*
*(DAB)*

*b) Acropora digitate Live*
*(AD)*

*b.1.) Acropora digitate Bleached*
*(BAD)*

*b.2.) Acropora digitate Dead*
*(DAD)*

*c) Acropora tabular Live*
*(AT)*

*c.1.) Acropora tabular Bleached*
*(BAT)*

*c.2.) Acropora tabular Dead*
*(DAT)*

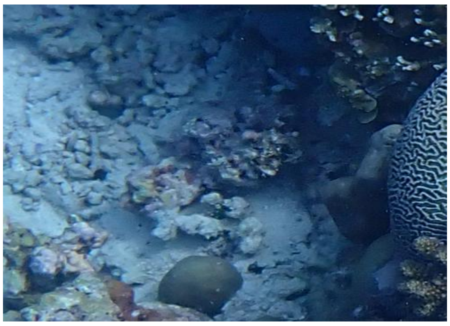
*d) Pocillopora Live*
*(PO)*

*d.1.) Pocillopora Bleached*
*(BPO)*

*d.2.) Pocillopora Dead*
*(DPO)*

*e) Other branching coral Live (OBC)*

*e.1.) Other branching coral Bleached (BOBC)*



*e.2.) Other branching coral Dead (DOBC)*

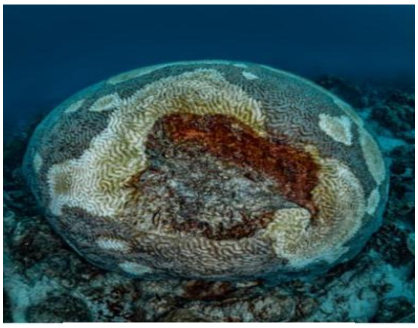
*f) Foliose coral Live (FC)*

*f.1.) Foliose coral Bleached (BFC)*

*f.2.) Foliose coral Dead (DFC)*

*g) Massive coral Live (MC)*

*g.1.) Massive coral Bleached (BMC)*

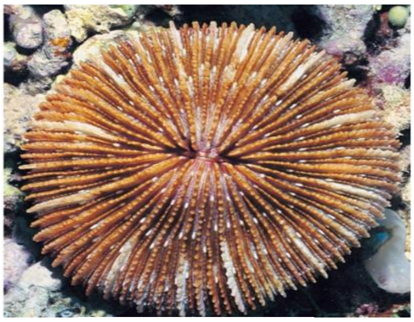


*g.2.) Massive coral Dead (DM0C)*

*h) Encrusting coral Live (EC)*

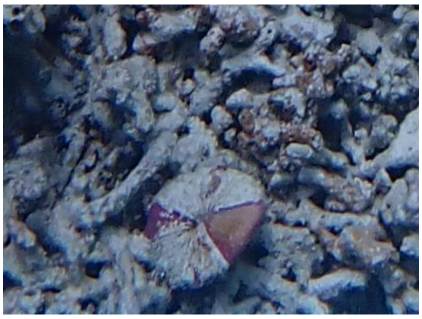
*h.1.) Encrusting coral Bleached (BEC)*

*h.2.) Encrusting coral Dead (DEC)*

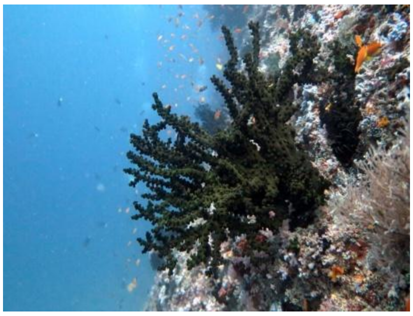


i) *Fungiidae Live*
*(FU)*

*i.1.) Fungiidae Bleached*
*(BFU)*

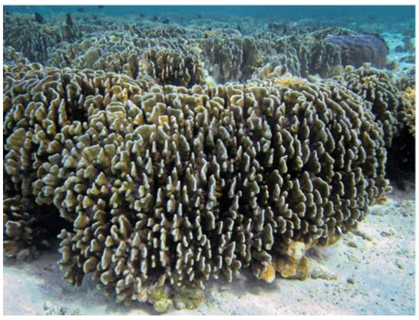


*i.2.) Fungiidae Dead*
*(DFU)*

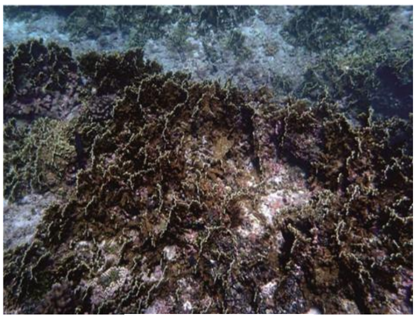


*j) Tubastrea*
*(TU)*

*k) Corallimorpharia*
*(CorMor)*



*l) Heliopora coerulea*
*(HEL)*



*m) Millepora*
*(MIL)*

*n) Soft coral*
*(SC)*

*o) Sponges*
*(SP)*

*p) Giant clam*
*(GiCl)*

*q) Corallinae algae*
*(CoA)*

*r) Macroagae*
*(MAL)*

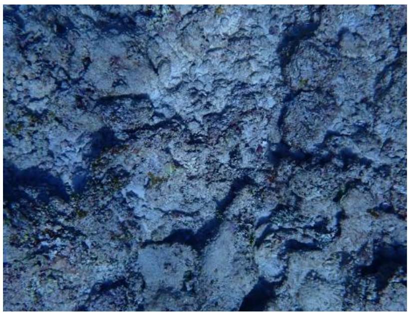

s) *Halimeda spp.*
*(HAL)*


t) *Ascidians*
*(ASC)*


u) *Zoantharia*
*(ZOA)*


v) *Gorgonians/Black corals/Whip coral*
*(GORG)*


w) *Cyanobacteria*
*(CYA)*


x) *Rock*
*(RC)*


y) *Coral rubble*
*(CR)*


z) *Sand*
*(SA)*

Biodiversity assessments and reef monitoring often rely on quantifying sessile benthic organisms using direct observation or underwater imagery. Quadrat sampling provides information on species presence, density, and percent cover (Bianchi *et al.,* 2004). Photoquadrats, images taken orthogonally to the seabed within a fixed square at a consistent distance from the substrate, were used to compile benthic community datasets across atoll sites (Carneiro *et al.,* 2024). Two complementary software tools, *photoQuad* and *CoralNet*, were evaluated for analysis, each offering distinct strengths and widely used in benthic studies. After analyzing the quadrats from the northern atolls, *CoralNet* was chosen as definitive software.

### 3.2.1 *PhotoQuad*

*PhotoQuad* is a specialized image-processing software designed for the rapid, non-destructive analysis of quadrat-based ecological data derived from digital photographs. It integrates a suite of two-dimensional analytical tools within a layer-based framework, allowing multiple analyses to be performed simultaneously on high-resolution images. The software supports common image formats, efficiently handles large files without requiring prior down sampling, and ensures reproducible analyses through streamlined data management and the use of native layer files. The program provides four main two-dimensional analysis methods for benthic photoquadrats: automatic multiscale segmentation (SG), freehand regions (FH), grid cell counts (CL), and random point counts (RP). The SG method performs automated object detection based on color and texture, enabling fast and reproducible measurements when species boundaries are well defined. The CL method estimates benthic cover by overlaying a grid and calculating the proportion of occupied cells, offering rapid but coarse assessments. The RP method assigns species identity to randomly distributed points, producing unbiased estimates, although with higher variability, particularly for small or patchy taxa.

Among these approaches, the freehand region (FH) method is most suitable when species contours are clearly visible and require precise manual delineation. In this technique, the user traces polygons directly on calibrated images, from which *photoQuad* calculates area and percent cover. Species identity is manually assigned using a user-defined library, ensuring taxonomic accuracy. This method was applied in the present study to obtain detailed and reliable estimates of benthic cover (Trygonis & Sini, 2012).

### 3.2.2 *CoralNet*

*CoralNet* is a web-based platform designed for the annotation and analysis of benthic images, particularly photoquadrats used in coral reef monitoring programs. Analysis is based on a point-count approach, where random points generated on each image are assigned to benthic categories to consistently estimate percent cover across sites, regions, and years. The platform integrates machine learning algorithms that, once trained on a sufficient number of manually annotated images, can automatically suggest the most likely category for each point, reducing analyst workload while retaining human oversight of the classification process. This program supports batch image uploads, structured project management through “sources,” and the association of spatial and operational metadata, which are essential for large-scale monitoring programs such as the Pacific RAMP and NOAA’s National Coral Reef Monitoring Program (NCRMP). Annotated data can be exported for subsequent statistical analyses, for example using dedicated R scripts. The platform employs a hierarchical classification system with multiple levels: Tier 1 includes broad functional categories (corals, algae, sediments), while lower levels (Tier 2 and Tier 3c) allow finer classification down to genus or morphological group. NOAA has developed a standardized label set to ensure consistency and comparability across regions and monitoring campaigns. High-quality, well-calibrated images are essential for accurate annotation and classifier performance, and standardized photographic procedures, including calibrated cameras, optimized settings, and grey-card white balance, help achieve this (Lamirand *et al.,* 2022). In 2021, *CoralNet* 1.0 was released, introducing a deep learning engine based on transfer learning with an EfficientNet-B0 backbone, trained on over 16 million image patches from global sources. The system uses a per-source classifier that is continuously updated with new user annotations, progressively improving accuracy even for smaller datasets. Compared to the Beta version, the new architecture achieved an average 18% increase in accuracy while maintaining faster inference times and lower computational costs. The addition of a hierarchical classifier further optimizes performance by adapting model complexity to the size of the available training data (Chen *et al.,* 2021). Validation studies show that *CoralNet* provides benthic cover estimates highly comparable to those of human analysts ($r > 0.97$; mean differences < 2–3%), particularly when habitat-specific training is applied. Despite some challenges in classifying certain categories (e.g., turf algae), the system is considered reliable for large-scale reef monitoring (Williams *et al.,* 2019).

## *3.3 DATA ANALYSIS*

A total of more than 3,000 underwater photographs were analyzed in this study. Images from the northern and central Maldives were collected in early 2024, while photographs from the southern Maldives were acquired in early 2025. All images were processed to generate a benthic dataset used for subsequent statistical analyses.

Two image analysis methodologies, *PhotoQuad* and *CoralNet*, were initially applied to a subset of images to assess their comparability and suitability for large-scale image processing. Differences between methods were evaluated by testing multivariate dispersion using an analysis of variance (ANOVA) and visualized through non-metric multidimensional scaling (NMDS) to explore patterns of similarity among samples and the relative positioning of group centroids. A permutation-based multivariate analysis of variance (PERMANOVA) was subsequently performed to test methodological differences across depth and reef typology. As no significant differences ($p > 0.05$) were detected between methods, *CoralNet* was selected for the analysis of the full image dataset due to its higher efficiency in processing large numbers of images.

Benthic community composition was explored using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities calculated from square-root–transformed percentage cover data, to visualize patterns across geographic areas, reef typologies and depths. Differences in community composition were formally tested using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Homogeneity of multivariate dispersions was assessed using PERMDISP to evaluate whether significant PERMANOVA results were influenced by differences in within-group variability. Similarity percentage (SIMPER) analyses were then used descriptively to identify benthic categories contributing most to differences among major contrasts (considering area and reef typology).

Subsequent analyses focused on live hard coral assemblages, whose cover was calculated by summing healthy and bleached coral categories while excluding dead coral. Coral cover was first visualized using stacked bar plots to illustrate the relative contribution of the coral categories across areas, reef typologies, and depths. Differences among these factors and their interactions were then tested using PERMANOVA, which revealed significant interactive effects. Drivers of variation in total live hard coral cover were formally tested using linear mixed-effects models (LMMs) fitted to quadrat-level data. The models were based on an unbalanced design because the number of sites sampled varied among the three areas (North, Central, and South). Coral cover proportions were arcsine square-root transformed before analysis. Fixed effects included Area, reef Typology, Depth, and their interactions, while Site nested within Atoll was included as a random effect. Significance of fixed effects was assessed using Type III ANOVA with Satterthwaite's approximation, and model-predicted marginal means were back-transformed to percentage cover for graphical representation.

Coral diversity was quantified by using coral categories and analyzed using a Poisson generalized linear mixed-effects model (GLMM) with a log link function, adopting the same fixed and random effects structure. Significance of effects was assessed using Type III Wald $\chi^2$ tests, and predicted marginal means (± SE throughout) were used to visualize spatial and depth-related patterns in richness.

To complement benthic community analyses, three functional indices were calculated for each quadrat: the Coral–Algae Predominance Index (CAPI), the Biotic–Abiotic Index (BAI), and the Reef Consolidation Index (RCI), based on percentage cover of benthic categories derived from photographic analyses.

The Coral–Algal Phase Index (CAPI) quantified the balance between live coral tissue and algal competitors, providing an estimate of coral dominance relative to benthic groups commonly associated with competitive overgrowth and phase shifts. The index was calculated as:

$$\frac{\text{Live coral cover}}{\text{Macroalgae} + \text{Turf} + \text{Cyanobacteria} + \text{Halimeda} + \text{Corallinae algae}}$$

Live coral cover was defined as the sum of all morpho-functional coral groups, including both unbleached and bleached but still living coral tissue. Algal competitors were calculated as the combined cover of macroalgae, calcareous and fleshy algal forms, and cyanobacteria. Substrate nature was inferred by comparing index values to a threshold of 1, with values greater or lower than 1 indicating different substrate conditions. For visual analyses, the index was log-transformed ($\log_{10}(\text{CAPI} + 1)$) to reduce heteroscedasticity and stabilize variance.

The Biotic–Abiotic Index (BAI) calculate the relative contribution of living benthic organisms versus abiotic substrate. The biotic component included all living categories (e.g. corals, algae and sessile invertebrates), whereas the abiotic component comprised consolidated reef rock, dead coral rubble and unconsolidated sand. The formula is:

$$\frac{\text{Corals} + \text{Algae} + \text{Biota}}{\text{Rock} + \text{Coral rubble} + \text{Sand}}$$

Higher values indicate a habitat predominantly structured by biological components rather than by bare substrate.

The Reef Consolidation Index (RCI) was used to quantify reef structural stability. Consolidated cover included reef rock, crustose coralline algae, giant clams, cemented dead coral skeletons, and living hard corals, while unconsolidated cover consisted of mobile rubble and sand. The index was calculated as:

$$\frac{\text{Rock} + \text{Corallinae algae} + \text{Giant clam} + \text{Hard coral}}{\text{Coral rubble} + \text{Sand}}$$

Higher RCI values indicate structurally stable, well-consolidated reef surfaces, whereas lower values reflect substrata dominated by rubble or sand.

Spatial variation in CAPI, BAI, and RCI was explored using boxplots grouped by Area (North, Central, South), reef typology (inner vs outer reefs), and depth (Flat, 10, and 20 m). For each index, mixed-effects models were fitted with Area, Typology, and Depth included as fixed factors along with their full interaction, while the hierarchical structure of the sampling design was accounted for by including Site nested within Atoll as a random effect. Owing to differences in scale and distribution among indices, distinct modelling approaches were applied. CAPI was log-transformed [$\log_{10}(\text{CAPI} + 1)$] and analyzed using Gaussian mixed-effects models. BAI, constrained between 0 and 1, was modelled using beta regression with a logit link. RCI, characterized by positive and right-skewed values, was analyzed with a Gamma generalized linear mixed-effects model using a log link; for graphical purposes only, RCI values were square-root transformed to enhance visual clarity and reduce the influence of extreme values observed on shallow outer reefs.

Model adequacy was assessed through residual diagnostics. Because interaction terms were frequently significant, results were interpreted in a context-dependent manner rather than relying solely on main effects. Inference based on model outputs was used to support patterns evident in the boxplots, and the significance of fixed effects was evaluated using Type III Wald chi-square tests to accommodate the unbalanced design and the inclusion of interaction terms.

Subsequently, analyses were structured to examine patterns related to management. Reefs were categorized according to management regime (Inhabited, Resort, Uninhabited) and grouped geographically into North, Central, and South areas. Percentage cover data were converted to proportions and arcsine square-root transformed before univariate analyses to improve normality and stabilize variances. To investigate patterns in overall benthic community composition, non-metric multidimensional scaling (NMDS) ordinations were performed using Bray–Curtis dissimilarities calculated on square-root transformed percentage cover data. To further examine context-dependent management effects, separate NMDS ordinations were performed for Inner (lagoon) and Outer (ocean) reefs at each depth (Flat, 10, and 20 m). For these stratified analyses, differences among management regimes were again tested using PERMANOVA, and homogeneity of dispersion was evaluated using both PERMDISP and betadisper, with permutation tests applied to assess statistical significance. When two-dimensional stress values exceeded acceptable thresholds, three-dimensional NMDS solutions were computed and visualized using the first two axes. For each quadrat, percentage cover was recorded for all benthic categories, including live coral growth forms, bleached and dead corals, abiotic substrates (sand, rock, coral rubble), macroalgae, and other benthic organisms. To quantify management effects on key benthic components, linear mixed-effects models (LMMs) were fitted for:

1. total live coral cover (sum of all live scleractinian corals; bleached and unbleached forms combined), with additional analyses conducted separately for sensitive and resistant groups;
2. abiotic substrate cover (sand, rock, coral rubble, and dead corals);
3. macroalgal cover (MAL).

Management, Reef Typology (Inner and Outer), Depth, and Area were included as fixed effects, with all two- and three-way interactions among Management, Typology, and Depth tested. Atoll was included as a random intercept to account for the spatial clustering of quadrats within atolls. Model-based predicted marginal means were calculated for each management category within combinations of reef typology and depth, averaged over Area and random atoll effects. Predicted values were back-transformed to percentage cover and presented as mean ± SE. Significance of fixed effects was assessed using Type III ANOVA with Satterthwaite's approximation. When significant higher-order interactions were detected, main effects were interpreted conditionally.

To examine large-scale spatial patterns, benthic community composition was analyzed at the atoll level. A global PERMANOVA was conducted to test for differences in multivariate community composition among atolls, and homogeneity of multivariate dispersion was evaluated using PERMDISP with associated ANOVA. To explore spatial patterns within different reef contexts, analyses were conducted separately for inner (lagoon) and outer (ocean) reefs. NMDS ordinations based on Bray–Curtis dissimilarities were performed to visualize patterns of community composition, with percentage cover data square-root transformed prior to distance calculation. In these stratified analyses, differences among atolls were tested using PERMANOVA, with depth and area included as covariates where appropriate, and homogeneity of dispersion was assessed using PERMDISP. To further quantify atoll-scale differences in reef condition at the univariate level, linear mixed-effects models (LMMs) were fitted to quadrat-level data. Response variables included total live hard coral cover (healthy and bleached corals combined, arcsine square-root transformed) and abiotic substrate cover (sand, rubble, rock, and dead corals). Coral categories were additionally grouped into sensitive and resistant functional groups, and separate models were fitted to evaluate whether atoll-level differences disproportionately affected vulnerable categories.

Fixed effects included Atoll, Reef Typology, Depth, and their interactions. Site was included as a random intercept to account for non-independence of quadrats within sites, while Area was incorporated as a fixed effect to control for broader geographic variation. Significance of fixed effects was assessed using Type III ANOVA with Satterthwaite's approximation, and model-predicted marginal means were extracted to visualize atoll-specific patterns while accounting for other predictors.

# 4 RESULTS

## *4.1 IMAGE ANALYSIS METHODS*

Prior to the quantitative analyses, the two methodological approaches employed for the evaluation of benthic cover, *PhotoQuad* and *CoralNet*, are presented by describing their main operating principles, analytical strategies, and associated advantages and limitations. This section establishes the methodological framework used for dataset analysis and is complemented by example images processed with both methods to illustrate the practical differences between the two approaches. The first method is based on the *PhotoQuad* software, which offers a high degree of user control and can be adapted to different ecological contexts and taxonomic resolutions. Its flexibility in defining benthic categories and sampling areas ensures a transparent and reproducible classification process, while its widespread use in scientific literature facilitates direct comparison with previous studies (Trygonis & Sini, 2012). Nevertheless, the *PhotoQuad* approach presents some constraints. The analysis of individual images is relatively time-intensive, requiring approximately 45–50 minutes per image, thereby limiting its suitability for large image datasets. Furthermore, the manual nature of the classification process may introduce operator-related variability, representing a potential source of bias. Consequently, it is more appropriate for studies involving small to medium numbers of images or species or genus-specific studies (Figure 15; 16; 17).

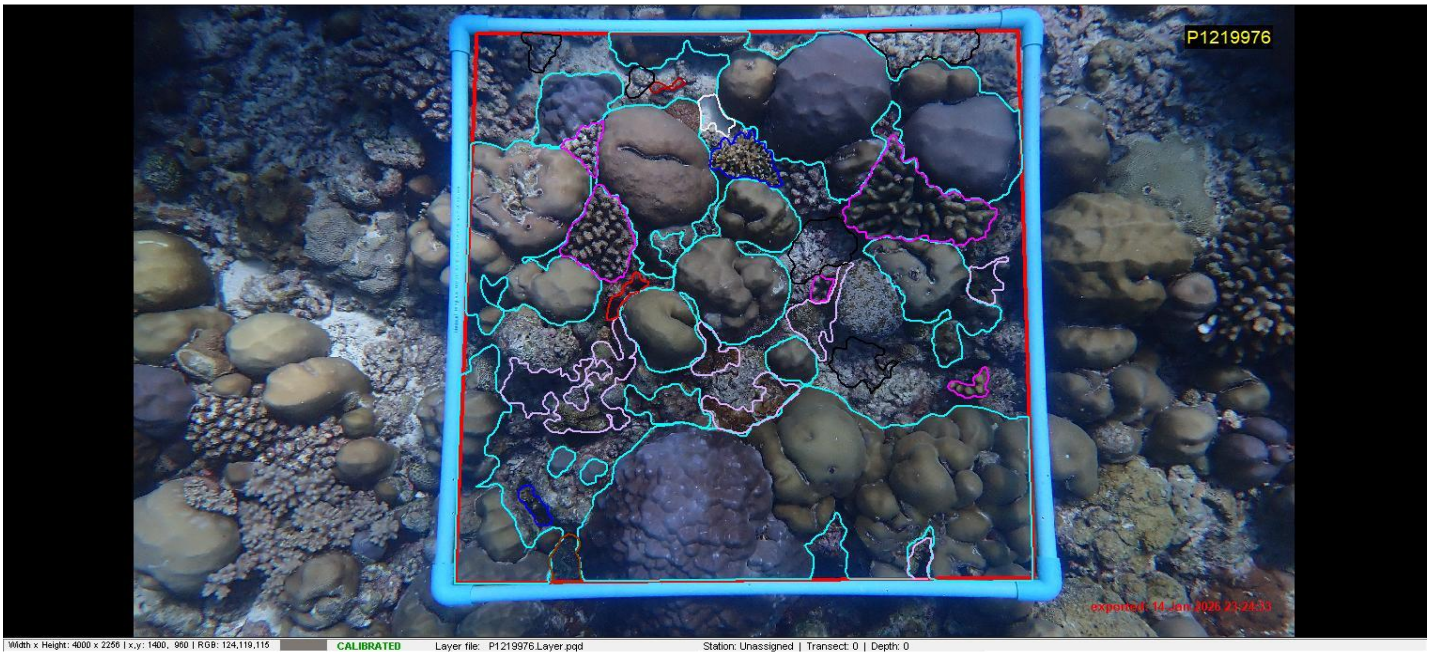


*Figure 15 Example of a coral reef benthic image at Flat depth analyzed using PhotoQuad. The sampling quadrat defines the analysis area, within which different benthic categories were identified and classified. Colored outlines highlight the contours of the main indicators considered, allowing the estimation of the percentage cover of the different components of the benthic community (black= coral rubble (CR); sky blue= massive coral (MC); pink= Pocillopora (PO); light pink= encrusting coral (EC); blue= other branching coral (OBC); brown= giant clam (GiCl), red= corallinae algae (CoA) and uncolored part= rock (RC)).*

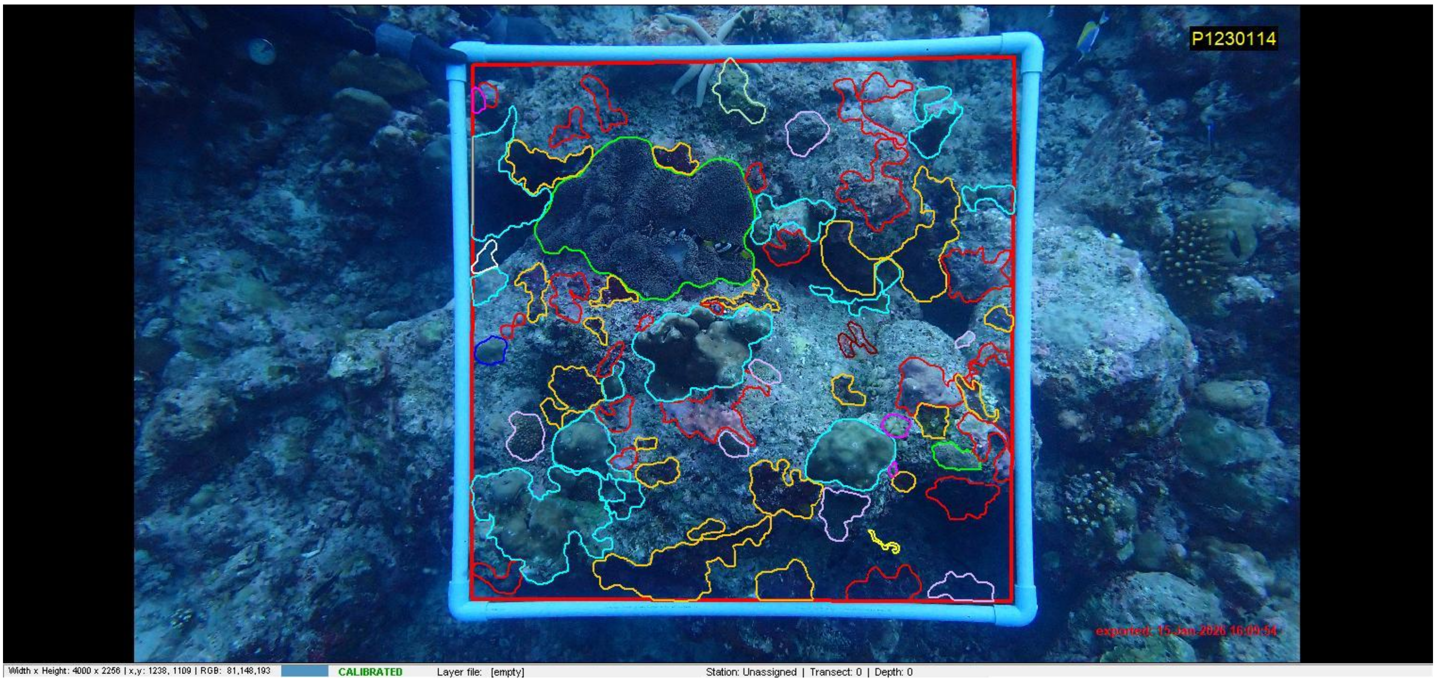


*Figure 16 Example of a coral reef benthic image at 10 m depth analyzed using PhotoQuad. The sampling quadrat defines the analysis area, within which different benthic categories were identified and classified. Colored outlines highlight the contours of the main indicators considered, allowing the estimation of the percentage cover of the different components of the benthic community (sky blue= massive coral (MC); yellow=gorgonian/black coral/whip coral (GORG); orange= sponges (SP), red= corallinae algae (CoA); green= zoantharia (ZOA), light pink= encrusting coral (EC), dark red= cyanobacteria (CYA), white= sand (SA), pink= Pocillopora (PO); blue= other branching coral (OBC); light green= macroalgae (MAL) and uncolored part= rock (RC)).*

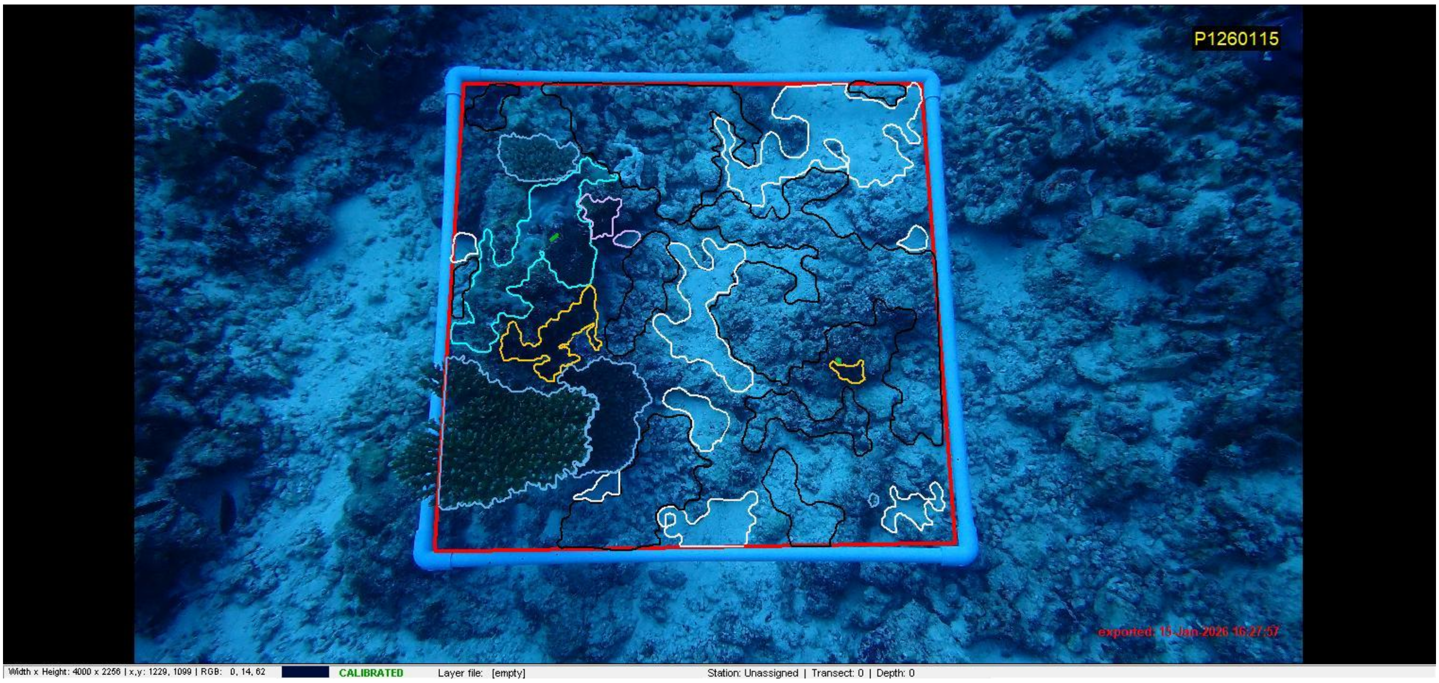


*Figure 17 Example of a coral reef benthic image at 20 m depth analyzed using PhotoQuad. The sampling quadrat defines the analysis area, within which different benthic categories were identified and classified. Colored outlines highlight the contours of the main indicators considered, allowing the estimation of the percentage cover of the different components of the benthic community (pale blue= acropora branching (AB), orange= sponges (SP), white= sand (SA), black= coral rubble (CR), light pink= encrusting coral (EC), dark green= ascidians (ASC) and uncolored part= rock (RC)).*

The second platform tested in this study is based on artificial intelligence and machine learning techniques and was developed for the automatic or semi-automatic annotation of coral reef imagery. The system relies on deep neural networks trained on annotated image datasets to automatically classify sampling random points within underwater photographs (Chen *et al.,* 2021). Each image represented a 1 × 1 m photoquadrat, within which 49 randomly distributed points were automatically generated following the standardized protocol established by the Nanwan Bay research group, led by Tung-Yung Fan and Chih Jui Tan (Beijbom *et al.,* 2015). The implementation of *CoralNet* substantially reduces analysis time (5-10 minutes per image), allowing the efficient processing of large image datasets and ensuring a high level of classification reproducibility once the model has been adequately trained. However, the accuracy of the automated classifications is strongly dependent on the quality, size, and representativeness of the training dataset. In particular, classification performance may decrease for rare benthic categories or morphologically similar taxa, and the approach provides less direct operator control over individual classification decisions compared to manual annotation methods (Figure 18).

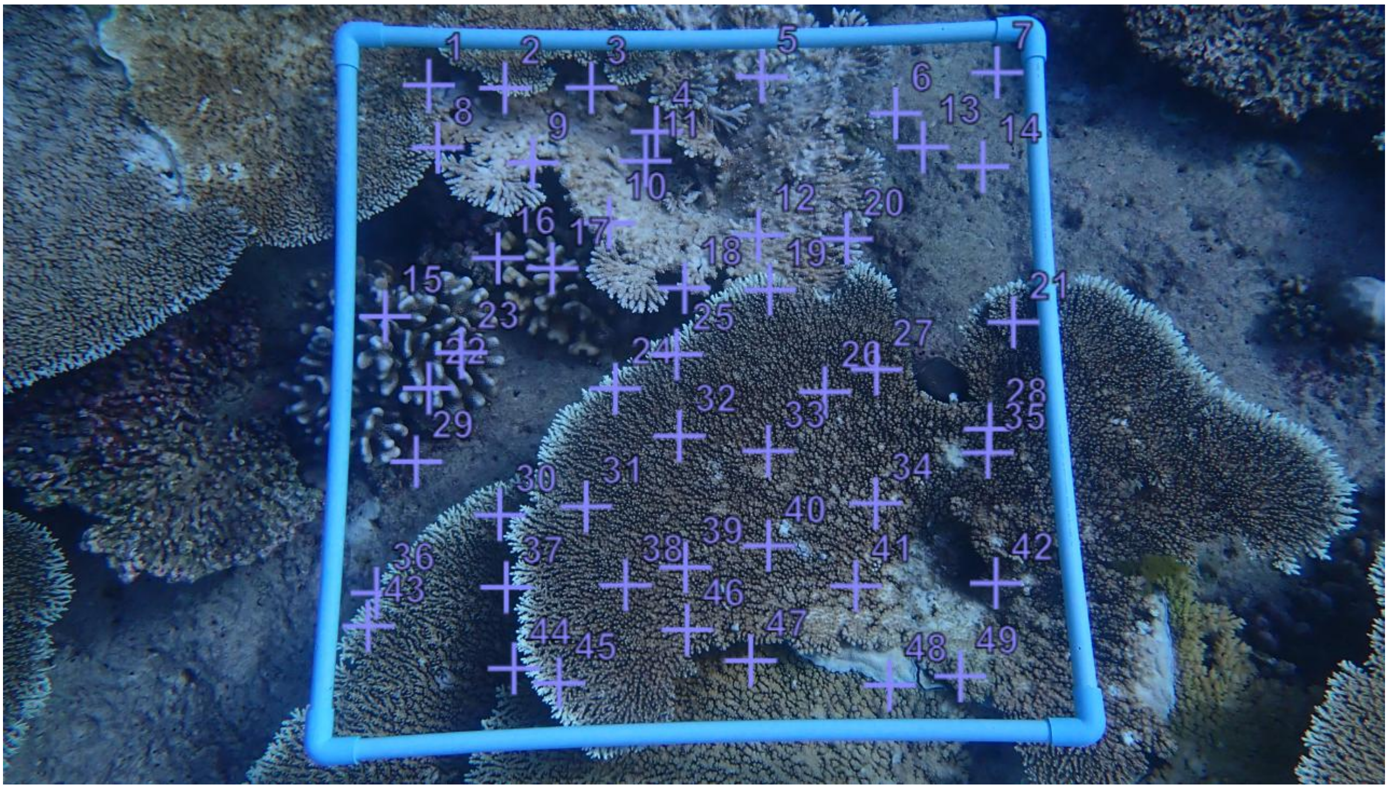


*Figure 18 Example of a coral reef benthic image at Flat depth analyzed using CoralNet. The analysis area is defined by the sampling quadrat, within which benthic categories were automatically identified and classified at randomly distributed sampling points, allowing the estimation of the percentage cover of the different components of the benthic community.*

Patterns of similarity among samples were visualized using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities. The ordination shows a high degree of overlap between samples derived from two methodologies, with no clear separation between methodologies or depth categories (Figure 19).

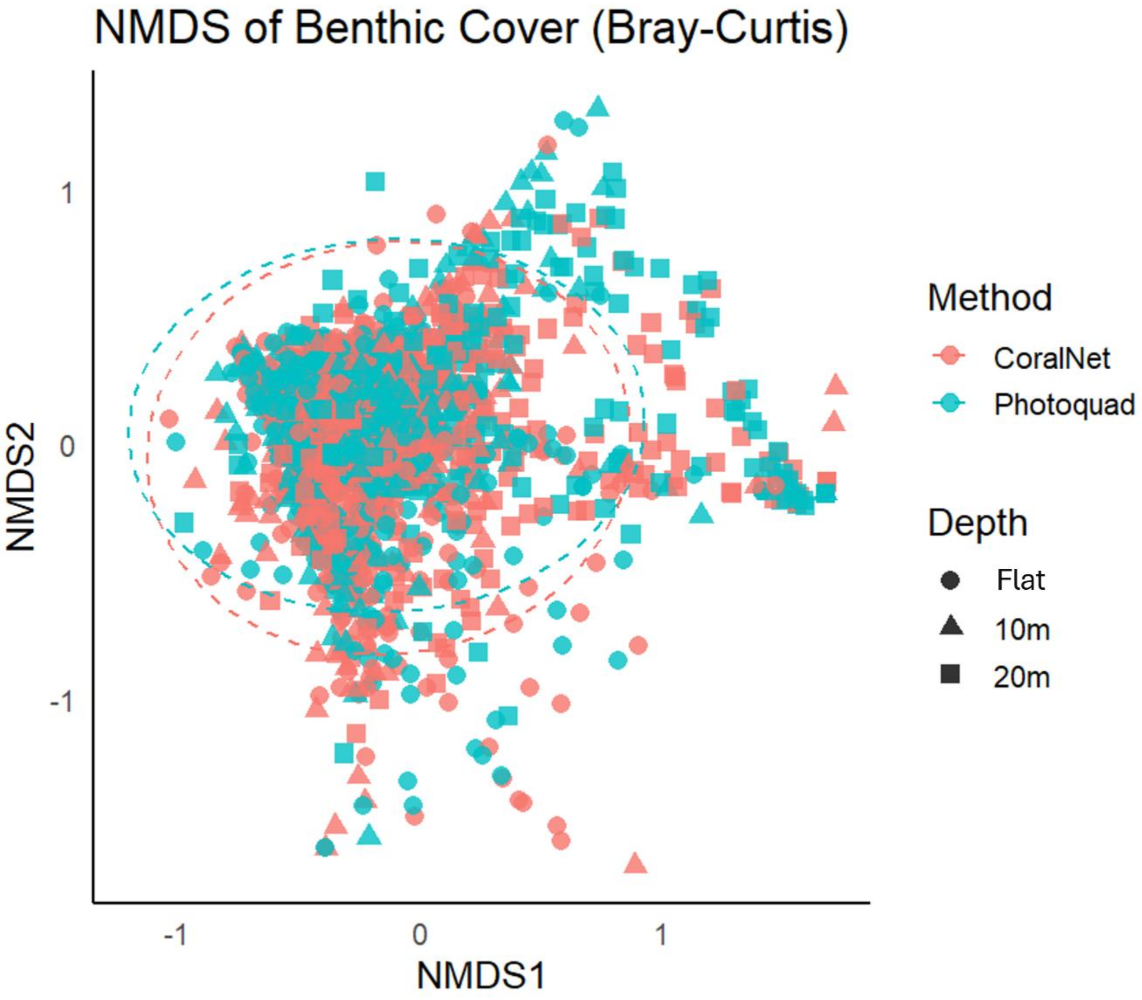


*Figure 19 NMDS ordination of benthic community composition based on Bray–Curtis dissimilarities, showing samples grouped by methodology (CoralNet vs. PhotoQuad) and depth.*

This visual pattern is broadly consistent with the results of the three-way PERMANOVA (including methodology, depth, and reef type), which indicate no significant effect of methodology on benthic community composition ($F = 0.9671$, $R^2 = 0.00103$, $p = 0.201$) (Table 10).

*Table 10 Results of the three-way PERMANOVA testing the effects of methodology, depth, and reef type on benthic community composition based on Bray–Curtis dissimilarities.*

**PERMANOVA**

Permutation N: 999

| **Source** | **Df** | **Sum Of Sqs** | **R²** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Method:Depth:Reef_Type | 2 | 0.271 | 0.00103 | 0.9671 | 0.201 |
| Residual | 1569 | 220.179 | 0.83325 | | |
| Total | 1580 | 264.242 | 1.00000 | | |

Homogeneity of multivariate dispersion between methods was subsequently assessed using PERMDISP, which revealed no significant differences in within-group variability (F = 0.0496, p = 0.8238), supporting the interpretation of the PERMANOVA results (Table 11).

*Table 11 The one-way ANOVA analysis shows that there is no statistically significant difference among the groups (methods) considered (F = 0.0496; p = 0.8238). Most of the total variability is attributable to the residuals, indicating that the grouping factor does not have a significant effect on the variable analyzed.*

**ANOVA**

| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|
| Groups | 1 | 0.002 | 0.00169 | 0.0496 | 0.8238 |
| Residuals | 1579 | 53,809 | 0.03408 | | |

Based on these results, subsequent image analyses were conducted exclusively using *CoralNet*, as both methodologies provided comparable estimates of benthic community composition, while *CoralNet* offered greater efficiency in data processing and analysis time.

## 4.2 *VARIATION IN BENTHIC COMMUNITY COMPOSITION*

Benthic community composition was first explored using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities calculated from square-root–transformed percentage cover data. NMDS ordinations were used as an exploratory tool to visualize patterns in benthic assemblages across areas (North, Central, and South), reef typology (inner and outer reefs), and depth (Flat, 10, and 20 m). The dataset comprised 792 sites from the northern region, 648 from the central region, and 792 from the southern region.

The NMDS ordination of the whole benthic community (stress = 0.161) revealed a high degree of overlap among samples from the northern, central, and southern Maldives (Figure 20).

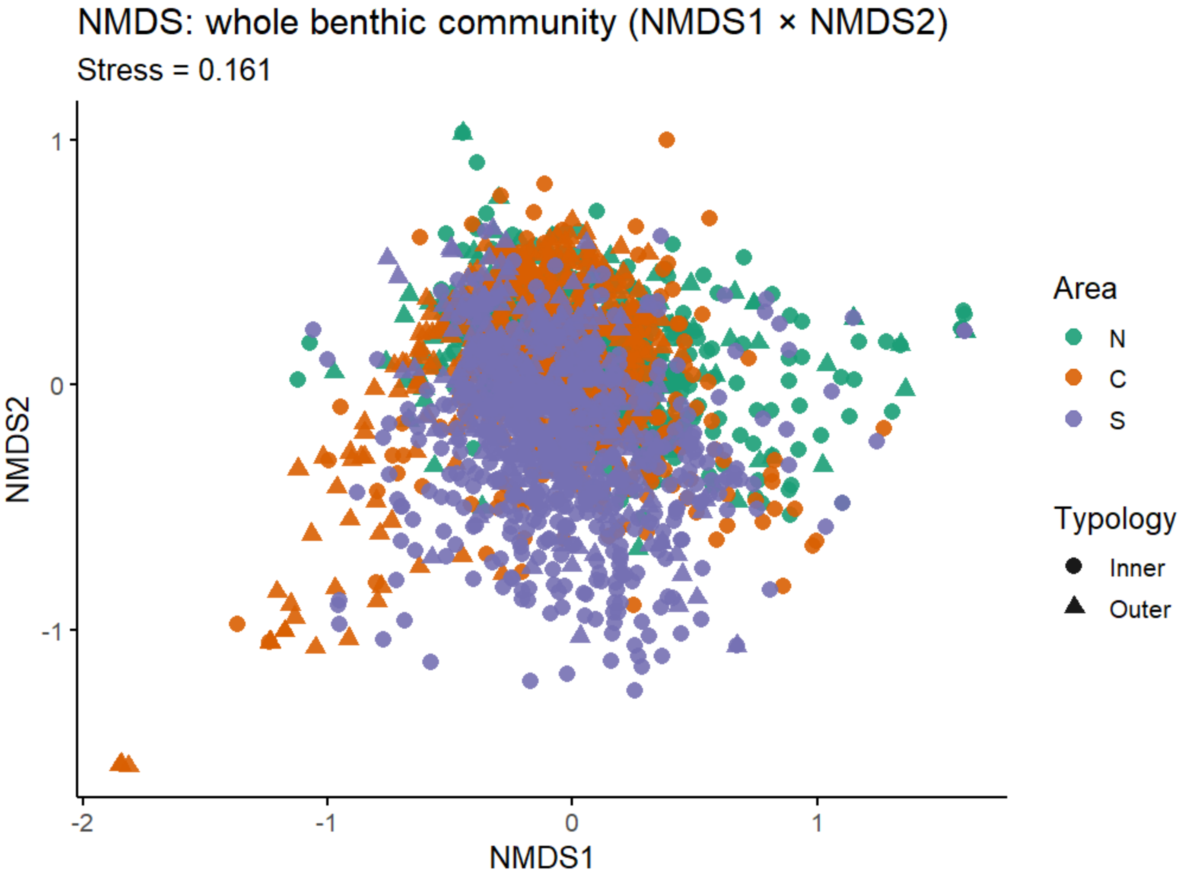


*Figure 20 Non-metric Multidimensional Scaling (NMDS) ordination of benthic community composition based on Bray–Curtis dissimilarities. Each point represents a sample, colored according to geographic area (North, Central and South Maldives) and shaped according to reef typology (inner vs outer reefs). The ordination shows a high degree of overlap among groups, suggesting gradual variation in community composition rather than discrete clustering (stress = 0.161).*

Group centroids were subsequently calculated to characterize the spatial arrangement of the three areas within the NMDS ordination. The ordination revealed a clear spatial gradient, with northern sites positioned at positive values along both NMDS axes, central sites clustered near the origin, and southern sites occupying negative values on both axes. Accordingly, North, Center, and South occupied distinct regions of the NMDS space, with the Central area displaying an intermediate position between the other two (Table 12).

*Table 12 NMDS ordination of benthic community composition based on Bray–Curtis dissimilarities showing group centroids for geographic areas (North, Central and South Maldives). Centroids were calculated as the mean NMDS coordinates of samples within each area and are shown to facilitate visual interpretation of spatial patterns in community composition.*

**CENTROIDS**

| Area | centroid_NMDS1 | centroid_NMDS2 | n |
|---|---|---|---|
| N | 0.140 | 0.145 | 792 |
| C | -0.0451 | -0.0104 | 648 |
| S | -0.103 | -0.137 | 792 |

In addition, a permutation test (PERMANOVA) on Euclidean distances of NMDS centroid scores revealed significant differences among areas ($R^2 = 0.074$, $F = 88.9$, $p = 0.001$), with northern and southern reefs occupying opposite positions along the ordination axes and central reefs exhibiting intermediate centroid values (Table 13).

*Table 13 A permutation-based analysis conducted on Euclidean distances derived from the two-dimensional NMDS ordination scores revealed significant differences among groups ($R^2 = 0.074$, $F = 88.9$, $p = 0.001$). The bold values indicate significance ($p<0.005$).*

**PERMANOVA**

Permutation N: 999

| **Source** | **Df** | **Sum Of Sqs** | **R²** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Model | 2 | 56.74 | 0.0739 | 88.939 | **0.001** |
| Residual | 2229 | 710.99 | 0.9261 | | |
| Total | 2231 | 767.72 | 1.0000 | | |

Subsequently, a PERMANOVA based on Bray–Curtis dissimilarities was performed, revealing significant effects of geographic area, depth and reef typology on benthic community composition ($p < 0.05$). Significant two-way and three-way interactions ($p < 0.005$) were also detected, indicating that spatial patterns in community composition vary in relation to depth and reef type (Table 14).

*Table 14 Results of PERMANOVA based on Bray–Curtis dissimilarities testing the effects of area, depth and reef typology on benthic community composition. The bold values indicate significance (p<0.005).*

| **PERMANOVA** | |
|---|---|
| Permutation N: | 999 |

| **Source** | **Df** | **Sum Of Sqs** | **$R^2$** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Area | 2 | 16.51 | 0.04756 | 67.6610 | **0.001** |
| Depth | 2 | 16.87 | 0.04861 | 69.1429 | **0.001** |
| Typology | 1 | 18.76 | 0.05405 | 153.7892 | **0.001** |
| Area:Depth | 4 | 9.37 | 0.02700 | 19.2022 | **0.001** |
| Area:Typology | 2 | 8.64 | 0.02489 | 35.4057 | **0.001** |
| Depth:Typology | 2 | 3.39 | 0.00978 | 13.9069 | **0.001** |
| Area:Depth:Typology | 4 | 3.44 | 0.00992 | 7.0557 | **0.001** |
| Residual | 2214 | 270.05 | 0.77819 | | |
| Total | 2231 | 347.02 | 1.00000 | | |

Significant differences in multivariate dispersion were detected among Area × Typology × Depth groups (F = 21.15, p = 0.001) (Table 15), indicating unequal within-group variability in benthic community composition. Distances to group centroids varied across depths and reef typologies within each area (Table 16), suggesting that spatial and bathymetric gradients influence not only the position of communities in multivariate space but also their internal heterogeneity.

*Table 15 Results of PERMDISP based on Bray–Curtis dissimilarities, assessing differences in multivariate dispersion among Area × Typology × Depth groups. The bold values indicate significance (p<0.005).*

| **PERMDISP** | |
|---|---|
| Permutation N: | 999 |

| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Groups | 17 | 5.579 | 0.32818 | 21.149 | **0.001** |
| Residuals | 2214 | 34.356 | 0.01552 | | |

*Table 16 Analysis of variance (ANOVA) on distances of samples to group centroids, performed as part of the PERMDISP procedure to test for differences in multivariate dispersion among Area × Typology × Depth groups. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|
| Groups | 17 | 5.579 | 0.32818 | 21.149 | **< 2.2e-16** |
| Residuals | 2214 | 34 | 0.01552 | | |

The observed heterogeneity in multivariate dispersion is visually illustrated in Figure 21, which shows the distribution of distances to group centroids across areas, reef typologies and depths. Boxplots of distances to centroids indicate higher dispersion in inner reefs compared to outer reefs across all depths, with relatively greater variability at shallow and intermediate depths. Given the significant differences in dispersion among groups, PERMANOVA results were interpreted as reflecting both differences in community composition and variation in within-group variability, rather than differences in centroid position alone.

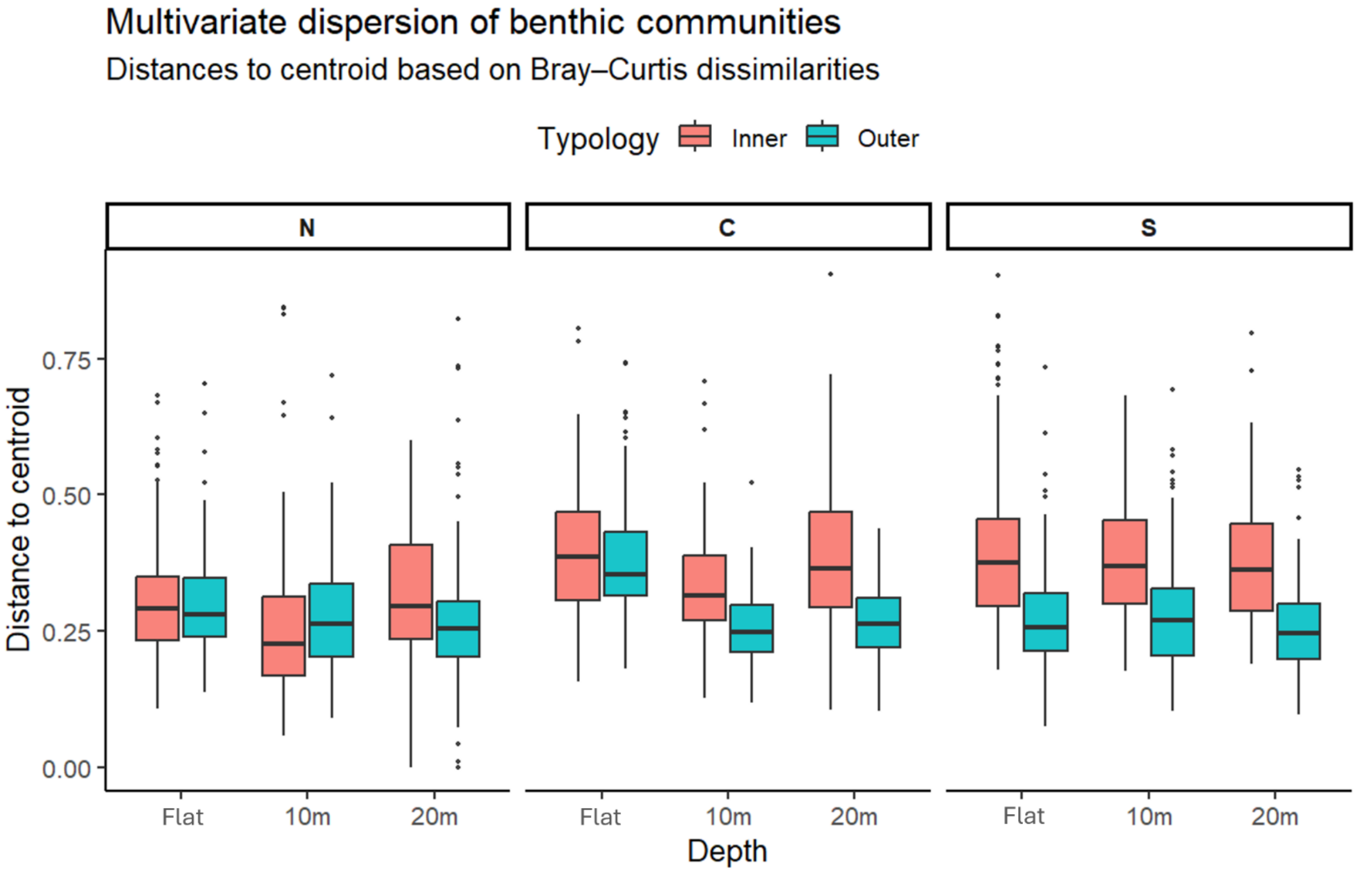


*Figure 21 Boxplots of multivariate dispersion of benthic communities, expressed as distances of samples to group centroids based on Bray–Curtis dissimilarities, shown by geographic area (North, Central and South), reef typology (inner and outer reefs) and depth (Flat, 10 m and 20 m).*

Significant differences in dispersion were detected among geographic areas (F = 32.9, p = 0.001) (Table 17), depths (F = 6.21, p = 0.003) (Table 18) and reef typologies (F = 132.9, p = 0.001) (Table 19), indicating heterogeneous within-group variability. Therefore, PERMANOVA results were interpreted considering both differences in centroid location and dispersion.

*Table 17 Results of PERMDISP testing homogeneity of multivariate dispersions among geographic areas (North, Central and South Maldives) based on Bray–Curtis dissimilarities. The bold values indicate significance (p<0.005).*

**PERMDISP (AREA)**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 1.330 | 0.66475 | 32.917 | **0.001** |
| Residuals | 2229 | 45.013 | 0.02019 | | |

*Table 18 Results of PERMDISP testing homogeneity of multivariate dispersions among depth levels based on Bray–Curtis dissimilarities. The bold values indicate significance (p<0.005).*

**PERMDISP (DEPTH)**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 0.248 | 0.123810 | 6.2125 | **0.003** |
| Residuals | 2229 | 44.422 | 0.019929 | | |

*Table 19 Results of PERMDISP testing homogeneity of multivariate dispersions between reef typologies (inner vs outer reefs) based on Bray–Curtis dissimilarities. The bold values indicate significance (p<0.005).*

**PERMDISP (TYPOLOGY)**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 2.412 | 2.41230 | 132.85 | **0.001** |
| Residuals | 2230 | 40.494 | 0.01816 | | |

PAIRWISE analyses indicated significant differences in benthic community composition among all geographic areas, with variable effect sizes. The biggest differences were observed between northern and southern reefs ($R^2 = 0.101$, F = 177.84), indicating marked spatial differentiation (Table 20). Differences between northern and central reefs were of intermediate magnitude ($R^2 = 0.046$, F = 69.76) (Table 21), whereas central and southern reefs exhibited more similar community composition ($R^2 = 0.013$, F = 19.53) (Table 22).

*Table 20 Pairwise based on Bray–Curtis dissimilarities comparing benthic community composition between northern and southern reef areas. The bold values indicate significance ($p<0.005$).*

**PAIRWISE (N vs S)**

Permutation N: 999

| **Source** | **Df** | **Sum Of Sqs** | **R²** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Model | 1 | 54.78 | 0.10105 | 177.84 | **0.001** |
| Residual | 1582 | 487.32 | 0.89895 | | |
| Total | 1583 | 542.10 | 1.00000 | | |

*Table 21 Pairwise based on Bray–Curtis dissimilarities comparing benthic community composition between northern and central reef areas. The bold values indicate significance ($p<0.005$).*

**PAIRWISE (N vs C)**

Permutation N: 999

| **Source** | **Df** | **Sum Of Sqs** | **R²** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Model | 1 | 20.82 | 0.04627 | 69.757 | **0.001** |
| Residual | 1438 | 429.14 | 0.95373 | | |
| Total | 1439 | 449.96 | 1.00000 | | |

*Table 22 Pairwise based on Bray–Curtis dissimilarities comparing benthic community composition between central and southern reef areas. The bold values indicate significance ($p<0.005$).*

**PAIRWISE (C vs S)**

Permutation N: 999

| **Source** | **Df** | **Sum Of Sqs** | **R²** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Model | 1 | 6.87 | 0.0134 | 19.534 | **0.001** |
| Residual | 1438 | 505.51 | 0.9866 | | |
| Total | 1439 | 512.37 | 1.0000 | | |

SIMPER analysis was applied to determine which benthic categories contributed most to the dissimilarities among areas, with interpretation restricted to variables accounting for approximately 70% of the cumulative average Bray–Curtis dissimilarity (top eight contributors). The analysis indicated that regional variation in benthic assemblages was primarily associated with differences in abiotic substrate composition and coral growth forms (Figure 22). Northern reefs were dominated by higher proportions of sand and consolidated rock, along with a greater presence of massive and encrusting corals. In contrast, southern reefs were characterized by increased coral rubble cover and markedly higher abundances of branching corals, particularly *Acropora* and *Pocillopora*. Reefs in the central region displayed intermediate conditions, with lower amounts of unconsolidated substrate than southern reefs but higher abundances of branching corals compared to northern reefs. The most pronounced dissimilarities were observed between northern and southern reefs, reflecting a transition from relatively stable, rock-based reef structures in the North to more dynamic, rubble-dominated systems with a higher prevalence of branching corals in the South.

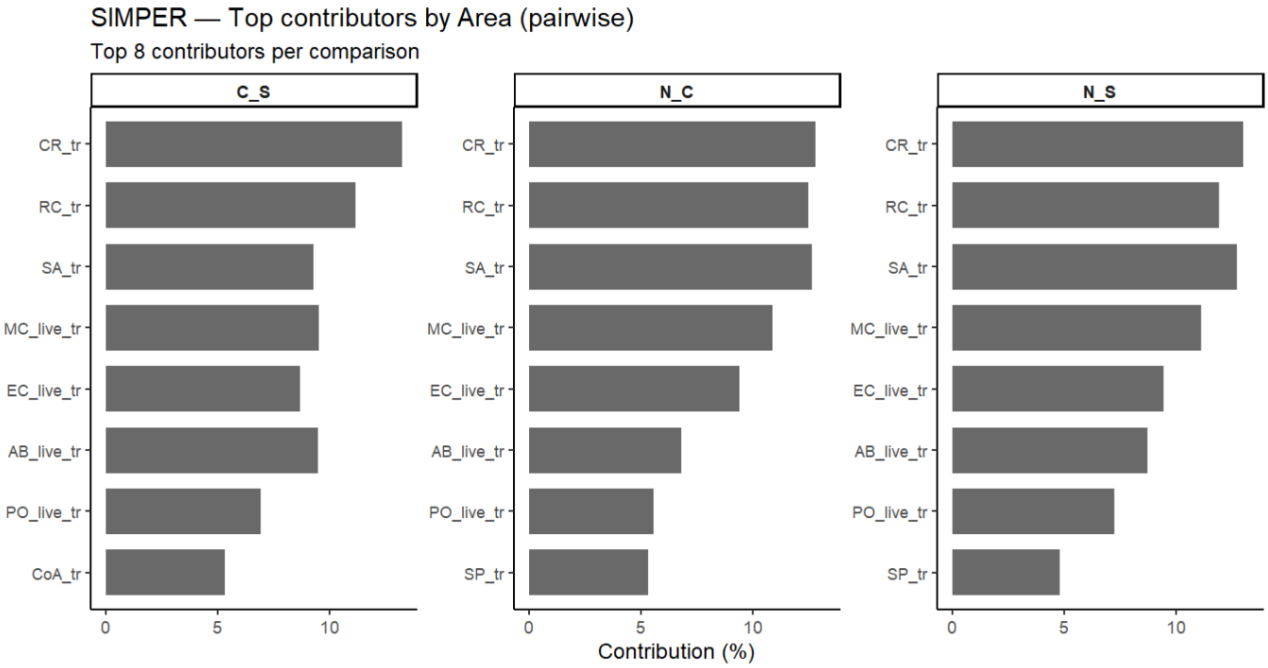


*Figure 22 SIMPER analysis showing the top eight benthic components contributing to pairwise dissimilarities in community composition among geographic areas (Central–South, North–Central and North–South). Bars represent the percentage contribution of each benthic category to the average Bray–Curtis dissimilarity for each comparison. The 8 contributors are CR=Coral Rubble, RC= Rock, SA= Sand, MC_live= Massive Coral Live, EC_live= Encrusting Coral Live, AB_live= Acropora Branching Live, PO_live= Pocillopora Live, CoA= Corallinae Algae*

SIMPER analysis indicated that differences between inner and outer reefs were primarily driven by abiotic categories. The highest contributors to dissimilarity were coral rubble (CR_tr), rock (RC_tr), sand (SA_tr), followed by massive corals (MC_live_tr), encrusting corals (EC_live_tr), branching *Acropora* (AB_live_tr) and *Pocillopora* (PO_live_tr), which together accounted for approximately 70% of the average dissimilarity. Inner reefs were characterised by higher contributions of coral rubble, sand and branching *Acropora*, whereas outer reefs showed greater contributions of rock, massive and encrusting corals, and *Pocillopora* (Figure 23).

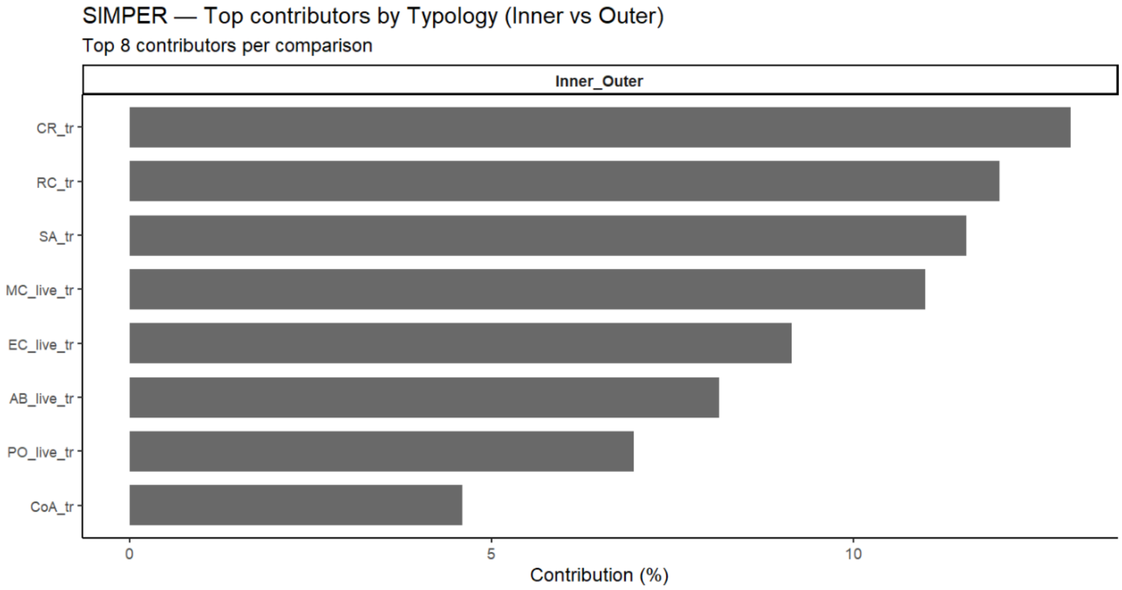


*Figure 23 SIMPER analysis showing the top benthic categories contributing to the Bray–Curtis dissimilarity between inner and outer reef typologies. The 8 contributors are CR=Coral Rubble, RC= Rock, SA= Sand, MC_live= Massive Coral Live, EC_live= Encrusting Coral Live, AB_live= Acropora Branching Live, PO_live= Pocillopora Live, CoA= Corallinae Algae*

SIMPER analysis identified a consistent set of benthic components driving dissimilarities among depths (Flat, 10 m, and 20 m). Across all pairwise depth comparisons, rubble (CR), sand (SA), and rock (RC) were the dominant contributors to compositional differences, each contributing substantially to overall dissimilarity. Live coral components, particularly massive corals (MC_live), encrusting corals (EC_live), and Acropora branching forms (AB_live), also consistently contributed to depth-related differences, although with lower relative importance than abiotic substrates. Comparisons involving shallow reefs (Flat vs 10 m and Flat vs 20 m) showed a stronger contribution of live corals, whereas the comparison between deeper strata (10 m vs 20 m) was more strongly influenced by differences in unconsolidated substrates and rubble, with reduced contribution from the genus *Acropora.*

Overall, SIMPER results indicate that depth-related changes in benthic community composition are primarily driven by shifts in abiotic substrate composition, with secondary contributions from changes in coral indicators (Figure 24).

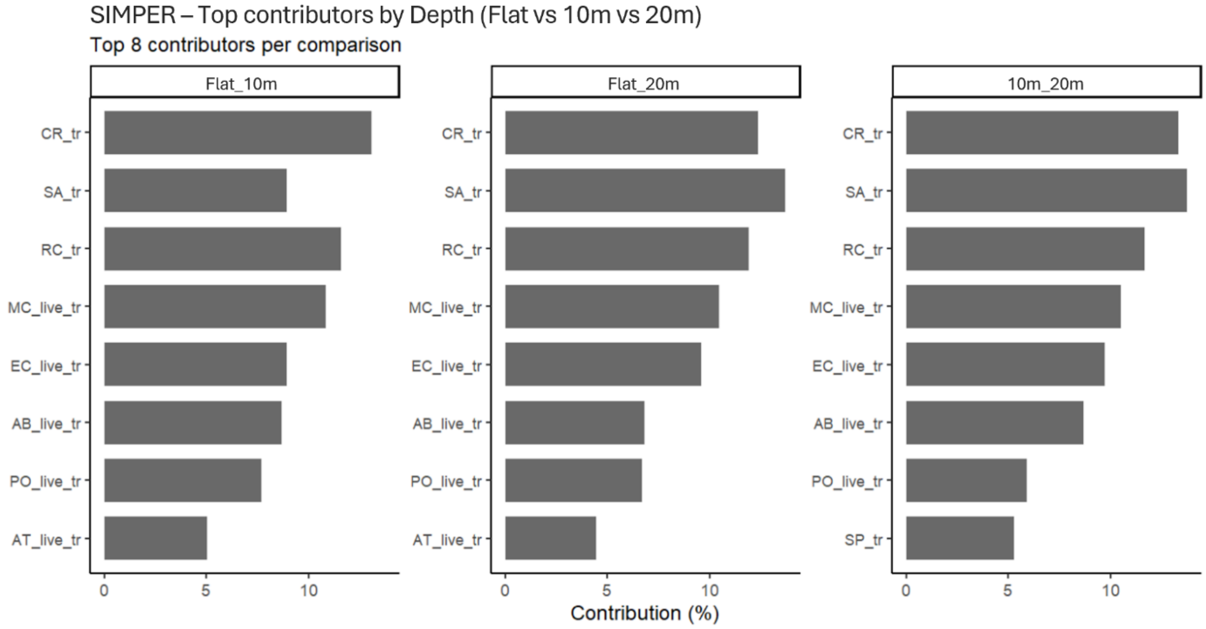


*Figure 24 SIMPER analysis showing the top benthic categories contributing to pairwise Bray–Curtis dissimilarities among depth levels (Flat vs 10 m, Flat vs 20 m, and 10 m vs 20 m). The 8 contributors are CR=Coral Rubble, RC= Rock, SA= Sand, MC_live= Massive Coral Live, EC_live= Encrusting Coral Live, AB_live= Acropora Branching Live, PO_live= Pocillopora Live, CoA= Corallinae Algae*

Figure 25 illustrates variation in benthic community composition across depth and reef typology. Overall, outer reefs showed consistently higher mean hard coral cover than inner reefs at all depths, with a more homogeneous composition among areas. In contrast, inner reefs exhibited greater variability in both hard coral cover and taxonomic composition, showing a higher diversity of indicators. Spatial differences were also evident, with northern reefs generally displaying lower hard coral cover compared to central and southern reefs, particularly at depths of 10 m and 20 m. The way coral assemblages change with depth differs between Inner and Outer reefs, and this depth–typology relationship itself varies across Areas (North, Central, South).

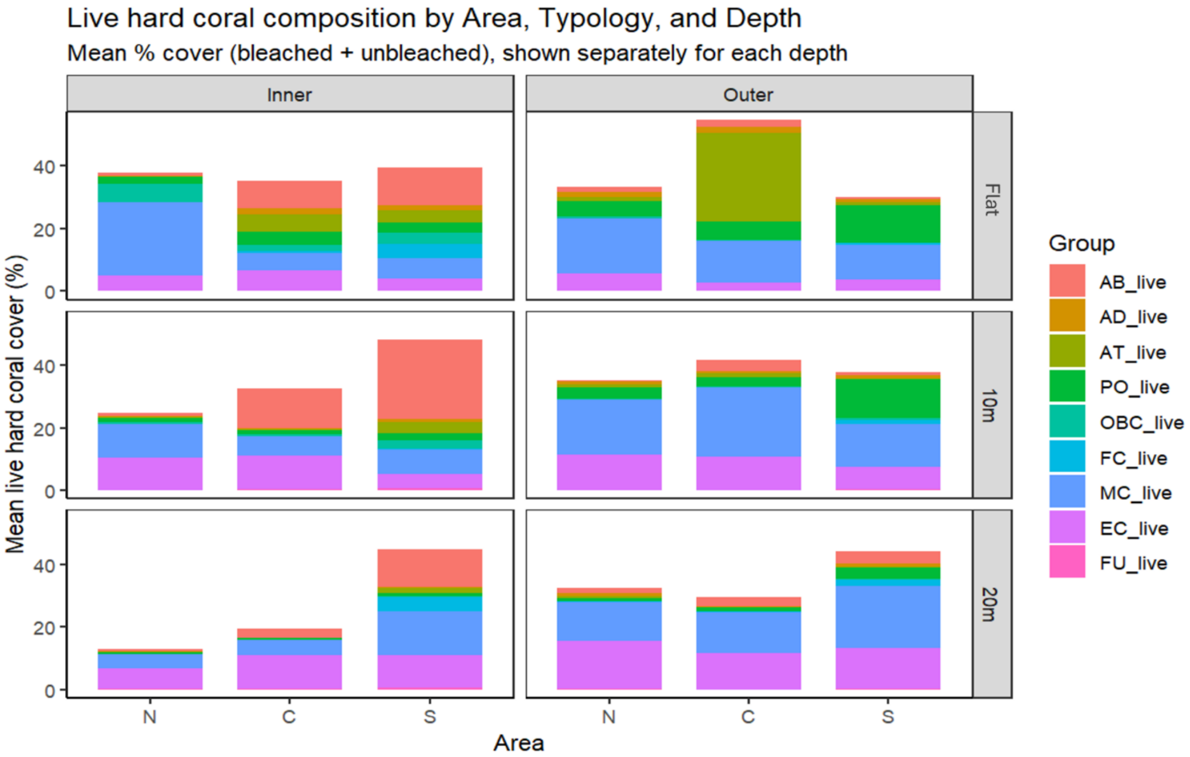


*Figure 25 Mean live hard coral cover and composition across geographic areas (North, Central and South), reef typologies (inner and outer reefs) and depths (Flat, 10 m and 20 m). Bars represent mean percentage cover of hard corals, subdivided by coral growth forms.*

PERMANOVA (Table 23) revealed significant effects of Area, Typology, and Depth on coral assemblage composition, with all two-way and three-way interactions also significant (p = 0.001). PERMDISP (Table 24) indicated significant differences in multivariate dispersion among Area × Typology × Depth groups (F = 29.06, p = 0.001), demonstrating unequal within-group variability.

*Table 23 Results of PERMANOVA based on Bray–Curtis dissimilarities testing the effects of Area, Depth and Reef Typology, and their interactions, on benthic community composition. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| **Source** | **Df** | **SumOfSqs** | **R2** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Area | 2 | 20.54 | 0.05278 | 70.4129 | **0.001** |
| Typology | 1 | 17.73 | 0.04557 | 121.5983 | **0.001** |
| Depth | 2 | 19.16 | 0.04924 | 65.6920 | **0.001** |
| Area:Typology | 2 | 11.48 | 0.02951 | 39.3711 | **0.001** |
| Area:Depth | | 8.39 | 0.02157 | 14.3867 | **0.001** |
| Typology:Depth | 2 | 4.08 | 4 0.01049 | 13.9964 | **0.001** |
| Area:Typology:Depth | 4 | 4.71 | 0.01210 | 8.0703 | **0.001** |
| Residual | 2078 | 303.02 | 0.77875 | | |
| Total | 2095 | 389.10 | 1.00000 | | |

*Table 24 Results of PERMDISP (permutation test for homogeneity of multivariate dispersions) based on Bray–Curtis dissimilarities, assessing differences in multivariate dispersion among Area × Depth × Reef Typology groups. The bold values indicate significance (p<0.005).*

**PERMDISP**

Permutation N: 999

| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| Groups | 17 | 11.259 | 0.66228 | 29.059 | **0.001** |
| Residuals | 2078 | 47.360 | 0.02279 | | |

To test whether mean live hard coral cover differed among depths, geographic areas and reef typologies, a linear mixed-effects model was fitted, including Area, Typology and Depth as fixed effects and Site nested within Atoll as a random effect.

Model-predicted marginal means indicated a consistent decline in live hard coral cover with increasing depth, although the magnitude of this decline differed between reef typologies and among geographic areas. In inner reefs, coral cover decreased markedly with depth in both northern and central regions, whereas outer reefs showed more homogeneous coral cover across the depth range from Flat to 20 m. Southern reefs generally exhibited higher coral cover at shallow depths (Figure 26).

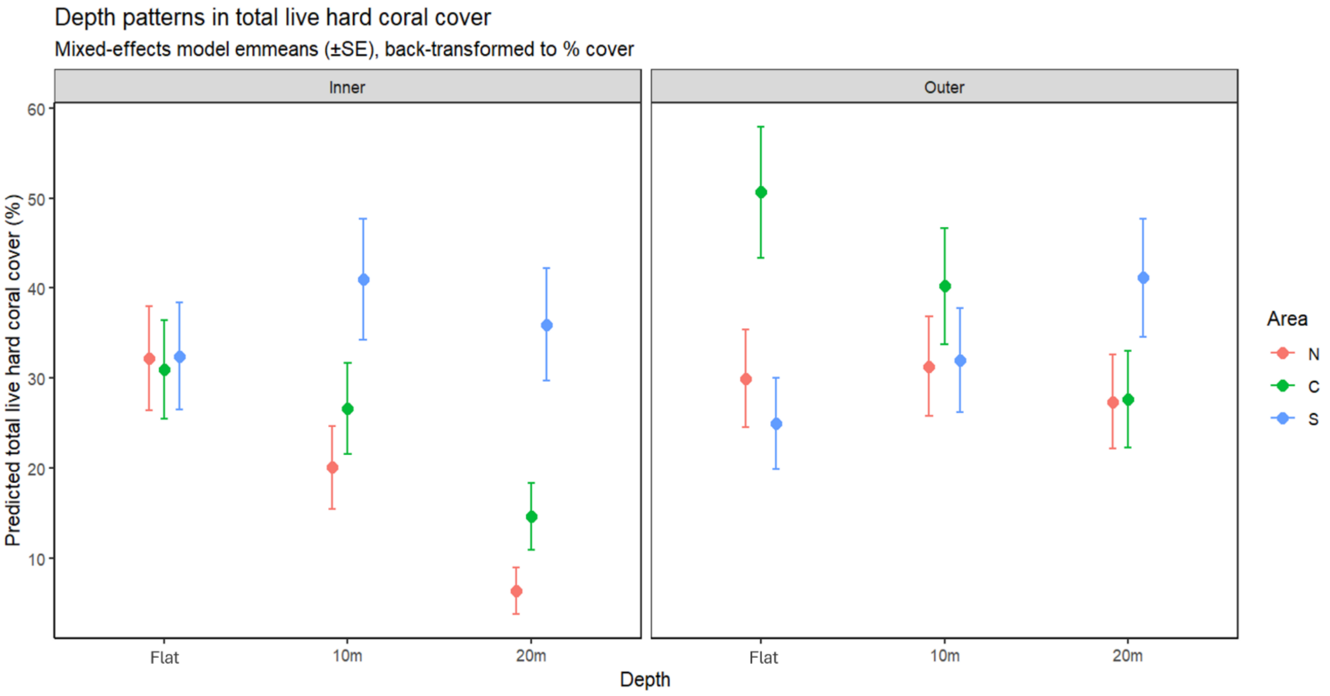


*Figure 26 Model-predicted marginal means (± SE) of live hard coral cover (%) across depths, areas and reef typologies, estimated from a linear mixed-effects model.*

ANOVA applied to the linear mixed-effects model showed no significant main effect of Area when considered alone (p = 0.266), indicating no overall differences among areas when averaged across depths and reef typologies. In contrast, a significant Area × Typology × Depth interaction (LMM, F = 11.13, p < 0.001) revealed that live hard coral cover is strongly structured by depth, with depth-related responses differing between inner and outer reefs and among geographic areas (Table 25).

*Table 25 Results of Type III analysis of variance (ANOVA) for the linear mixed-effects model testing the effects of area, reef typology, depth, and their interactions on total live hard coral cover. F- and p-values were obtained using Satterthwaite's approximation for degrees of freedom. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| Area | 12.59 | 6.294 | 2 | 3.71 | 1.9309 | 0.26633 |
| Typology | 16.23 | 16.235 | 1 | 55.02 | 4.9807 | **0.02972** |
| Depth | 324.79 | 162.397 | 2 | 2158.01 | 49.8228 | **< 0.001** |
| Area:Typology | 17.70 | 8.851 | 2 | 54.60 | 2.7153 | 0.07512 |
| Area:Depth | 572.69 | 143.171 | 4 | 2158.01 | 43.9245 | **< 0.001** |
| Typology:Depth | 170.05 | 85.023 | 2 | 2158.01 | 26.0848 | **<0.001** |
| Area:Typology:Depth | 145.13 | 36.282 | 4 | 2158.01 | 11.1312 | **<0.001** |

Figure 27 shows how hard coral richness varies as a function of depth, reef typology and geographic area. In inner reefs, species richness generally declines with increasing depth, particularly in northern and central areas, whereas southern inner reefs display more uniform richness across depths. In contrast, outer reefs show more stable richness patterns along the depth gradient, with limited spatial variability, except at 20 m where northern reefs tend to exhibit lower richness compared to central and southern reefs.

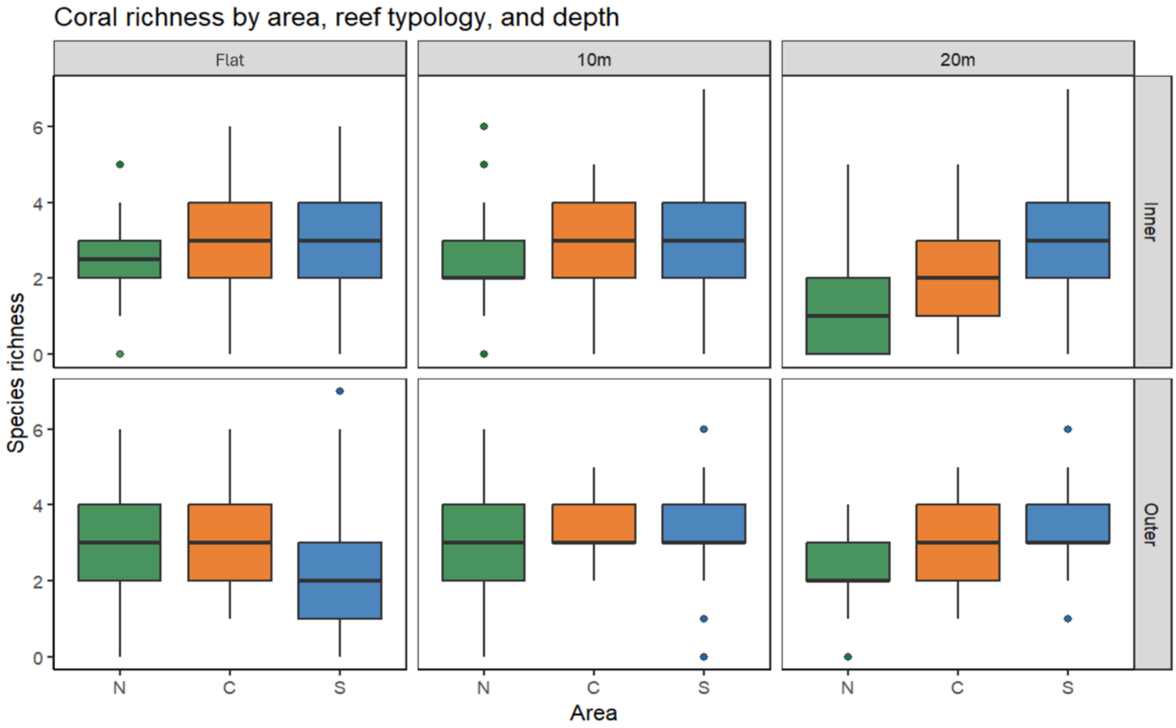


*Figure 27 Hard coral species richness across geographic areas, reef typologies and depths. Boxplots show median values, interquartile ranges and outliers, highlighting depth-related and spatial differences in species richness between reef typologies*

The descriptive patterns observed in the figure were supported by a generalized linear mixed-effects model (GLMM), which tested the effects of depth, area and reef typology on hard coral richness while accounting for the hierarchical structure of the data (site nested within atoll). This modelling approach allowed an integrated assessment of these factors without relying on multiple separate multivariate tests (Figure 28).

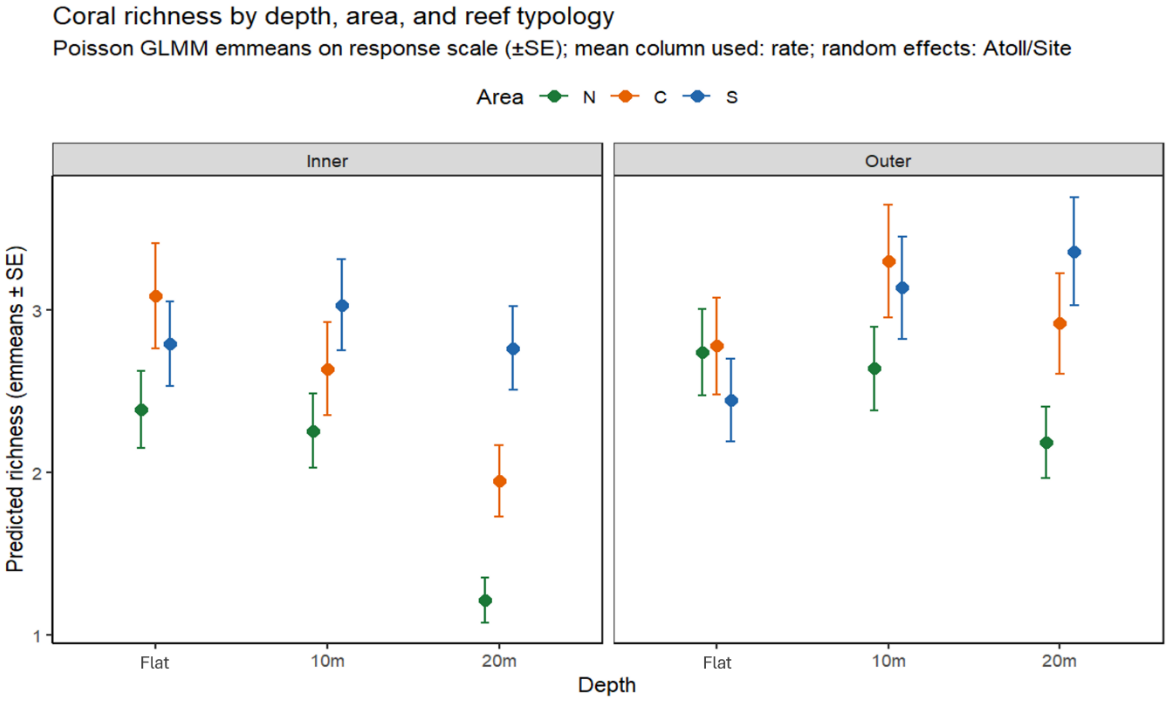


*Figure 28 Model-predicted marginal means (± SE) of hard coral species richness across depths, geographic areas and reef typologies, estimated using a Poisson generalized linear mixed-effects model with Atoll and Site included as random effects.*

Coral richness was strongly structured by depth ($\chi^2 = 56.8$, $p < 0.001$), with depth-related patterns differing among areas (Area × Depth: $\chi^2 = 39.9$, $p < 0.001$) and between inner and outer reefs (Typology × Depth: $\chi^2 = 15.9$, $p < 0.001$). The three-way interaction was not significant ($p > 0.05$), indicating that area- and typology-specific depth effects acted independently (Table 26).

*Table 26 Type III analysis of deviance ($\chi^2$ tests) from a Poisson generalized linear mixed-effects model testing effects of area, reef typology, and depth on coral richness. The bold values indicate significance ($p<0.005$).*

**ANOVA**

| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
|---|---|---|---|
| Area | 3.2517 | 2 | 0.196742 |
| Typology | 0.9974 | 1 | 0.317949 |
| Depth | 56.7746 | 2 | **<0.001** |
| Area:Typology | 2.2734 | 2 | 0.320871 |
| Area:Depth | 39.9067 | 4 | **<0.001** |
| Typology:Depth | 15.9496 | 2 | **0.000344** |
| Area:Typology:Depth | 5.9789 | 4 | 0.200733 |

## *4.3 INDEX-BASED ASSESSMENT OF REEF CONDITION*

Reef condition varied markedly across the Maldivian archipelago, showing consistent spatial patterns across all three ecological indices.

The Coral–Algae Predominance Index (CAPI) showed strong spatial variation across reef typologies and depths, with higher values in shallow zones declining with depth, indicating a shift toward algae dominance. In inner reefs, northern and southern areas exhibited higher values, indicative of coral-dominated assemblages (>1), whereas central lagoon sites were consistently more algae-dominated across all depths (<1). This reduction in coral dominance in central lagoons was most pronounced at 10 and 20 m depth. In contrast, outer reefs showed an opposite pattern: central offshore reefs displayed the highest CAPI values, reflecting strong coral dominance at Flat depth, while southern outer reefs were comparatively algae-dominated, particularly at 0 and 10 m. Northern outer reefs exhibited intermediate conditions. Together, these contrasting lagoon–ocean patterns highlight a marked cross-shelf reorganization of coral–algae dominance along the latitudinal gradient (Figure 29).

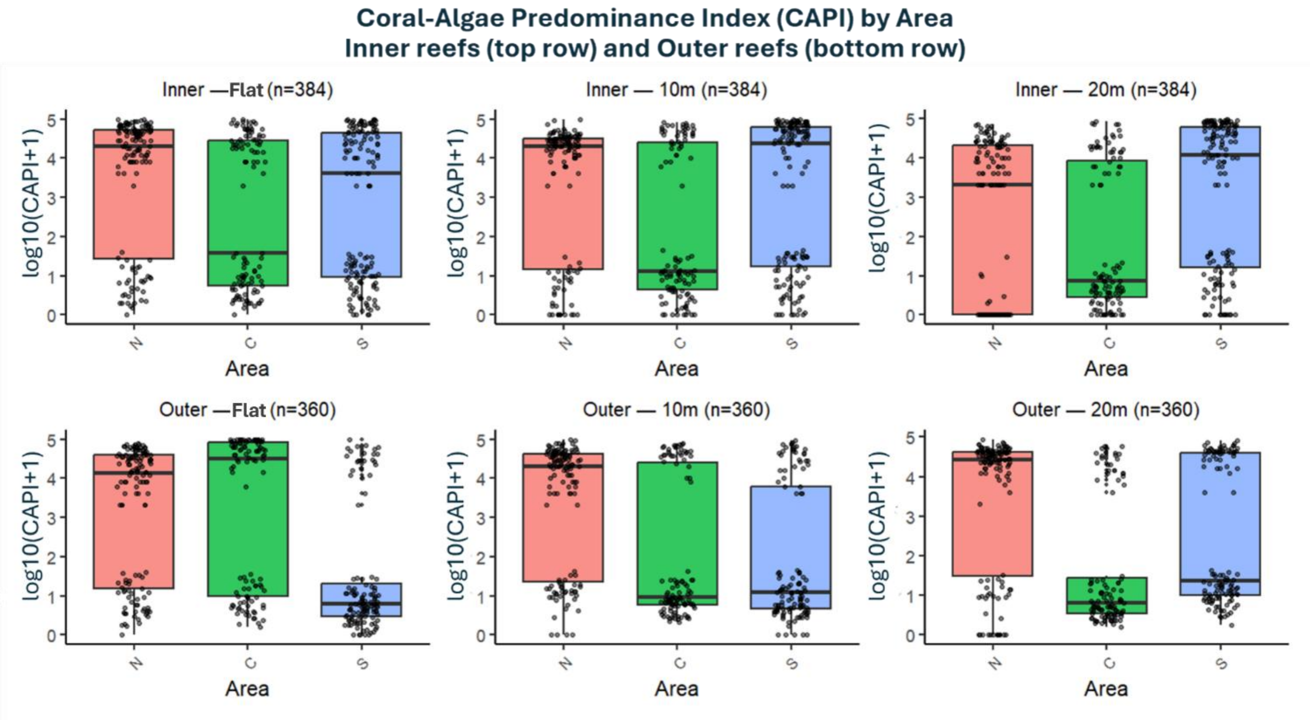


*Figure 29 Boxplots of the Coral–Algae Predominance Index (CAPI; log10(CAPI + 1)) across areas (North, Central, South) for inner (top row) and outer reefs (bottom row) at Flat, 10, and 20 m depth.*

CAPI was significantly influenced by both areas ($p = 0.006$) and depth ($p < 0.001$), with depth emerging as the dominant driver and several significant interaction effects. While reef typology alone showed no significant main effect ($p = 0.274$), the presence of significant typology–depth interactions and a three-way interaction among area, typology, and depth ($p = 0.001$) suggests that depth-related shifts in coral–algae dominance varied between inner and outer reefs and across different areas (Table 27).

*Table 27 Results of the linear mixed-effects model testing the effects of Area, reef Typology, and Depth on the Coral–Algae Predominance Index (CAPI). Reported values are Type III Wald chi-square tests for fixed effects. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
|---|---|---|---|
| Area | 10.1611 | 2 | **0.006217** |
| Typology | 1.1963 | 1 | 0.274072 |
| Depth | 100.6975 | 2 | **<0.001** |
| Area:Typology | 3.8217 | 2 | 0.147957 |
| Area:Depth | 71.6505 | 4 | **<0.001** |
| Typology:Depth | 34.7109 | 2 | **0.000344** |
| Area:Typology:Depth | 17.7127 | 4 | **0.001404** |

The Biotic–Abiotic Index (BAI) revealed clear spatial gradients in the relative dominance of living biota versus abiotic substrates. Observed BAI values were generally higher in shallow zones and on outer reefs, indicating a greater contribution of biotic components relative to abiotic substrates, while depth-related patterns varied among areas and reef typologies. In inner reefs, BAI increased from north to south across all depths, indicating a progressive shift toward biologically dominated substrates in southern lagoons; this gradient was most pronounced at 10 and 20 m, where northern reefs remained strongly abiotic-dominated. In outer reefs, central sites consistently exhibited the highest BAI values across depths, reflecting a greater contribution of living benthic organisms, whereas southern reefs were persistently more abiotic-dominated, with northern reefs showing intermediate conditions (Figure 30).

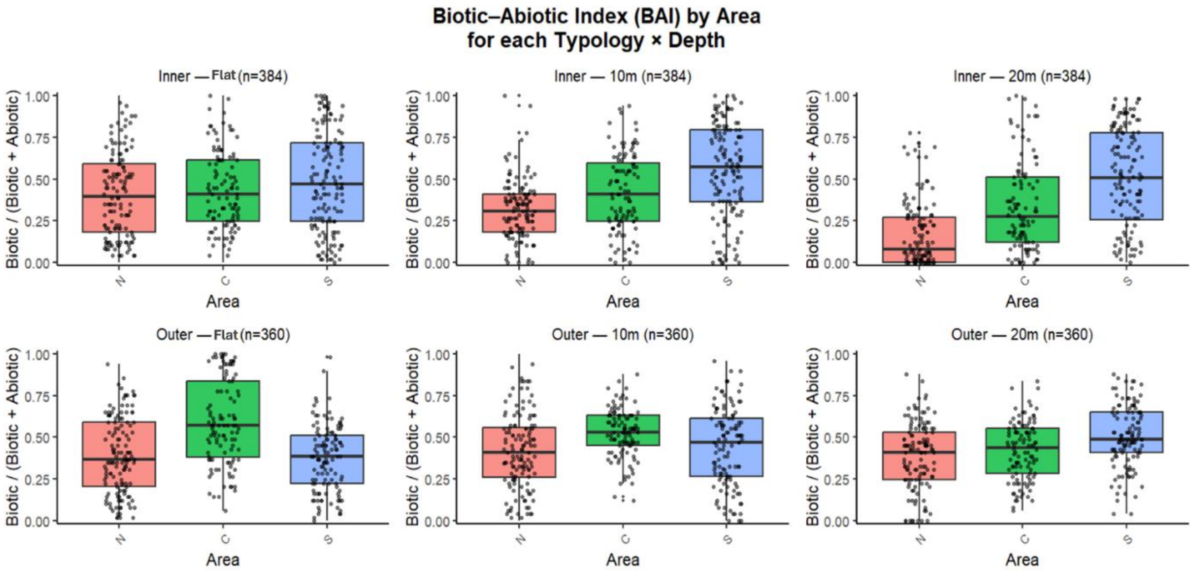


*Figure 30 Boxplots of the Biotic-Abiotic Index (BAI) across areas (North, Central, South) for inner (top row) and outer reefs (bottom row) at Flat, 10, and 20 m depth.*

Area (p = 0.266) and reef typology (p = 0.899) were not significant predictors of BAI, whereas depth showed a significant effect (p < 0.001). However, several two-way and three-way interaction terms (p < 0.001) were significant, indicating that the effect of depth on BAI differed among areas and between inner and outer reef typologies (Table 28).

*Table 28 Results of the beta regression mixed-effects model testing the effects of Area, reef Typology, and Depth on the Biotic–Abiotic Index (BAI). Reported values are Type III Wald chi-square tests for fixed effects. The bold values indicate significance (p<0.005).*

| **ANOVA** | | | |
|---|---|---|---|
| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
| Area | 2.6480 | 2 | **0.26607** |
| Typology | 0.0161 | 1 | **0.89899** |
| Depth | 150.1656 | 2 | **<0.001** |
| Area:Typology | 9.6794 | 2 | **0.00791** |
| Area:Depth | 53.1998 | 4 | **<0.001** |
| Typology:Depth | 51.9728 | 2 | **<0.001** |
| Area:Typology:Depth | 43.4713 | 4 | **<0.001** |

The Reef Consolidation Index (RCI) exhibited clear spatial patterns across areas, reef typologies, and depths. RCI values were highest on shallow outer reefs and declined with increasing depth, a trend that was particularly pronounced on inner reefs, where higher median values were observed in the northern and southern areas compared to the central area, indicating greater consolidation at the latitudinal extremes; however, these differences among areas became less marked at 20 m depth. In contrast, on outer reefs the spatial pattern was reversed, with the central area consistently displaying the highest median RCI values, especially at Flat and 10 m, while lower median values were recorded in the northern and southern areas (Figure 31).

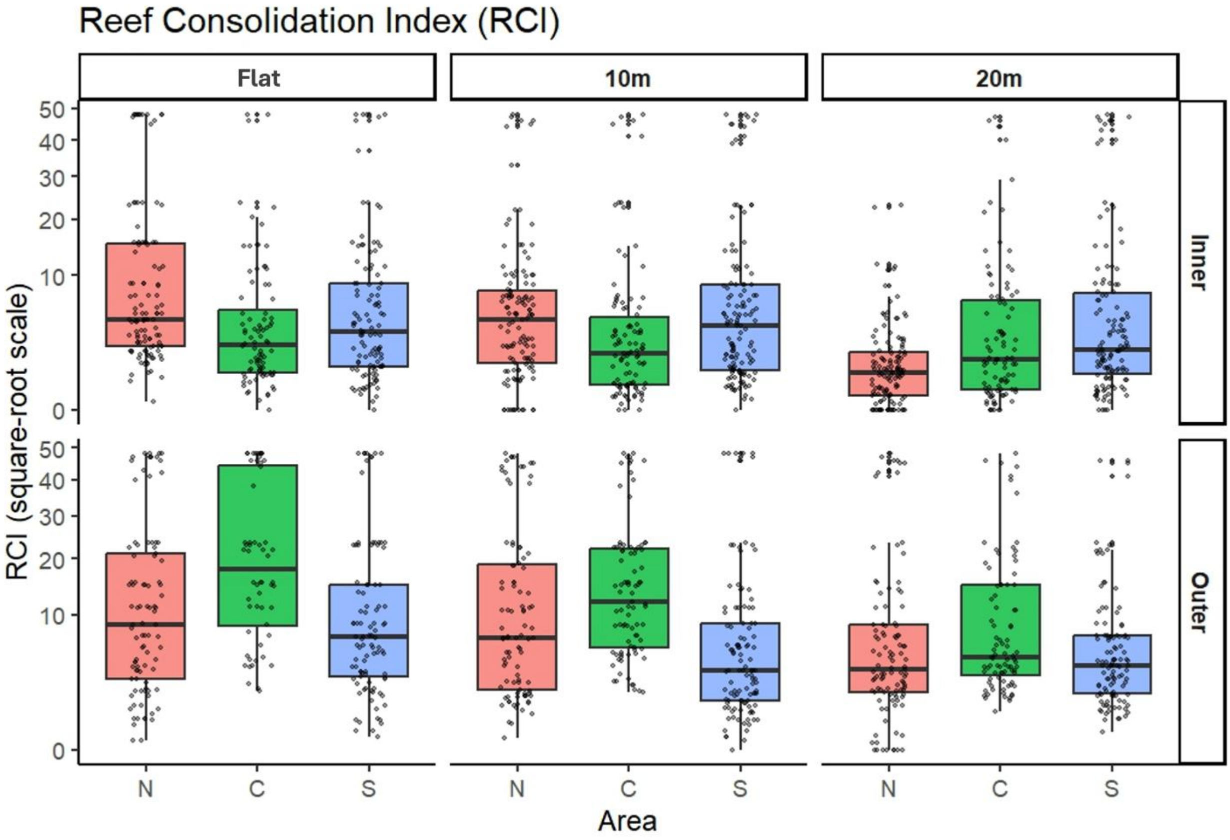


*Figure 31 Boxplots of the Reef Consolidation Index (RCI) across areas (North, Central, South) for inner (top row) and outer reefs (bottom row) at Flat, 10, and 20 m depth.*

RCI was strongly influenced by depth ($p < 0.001$), with a significant three-way interaction among Area, Typology, and Depth ($p < 0.001$). While area ($p = 0.313$) and typology ($p = 0.438$) didn't have a significant main effect, area-specific differences emerged across depth gradients and differed between inner and outer reefs (Table 29).

*Table 29 Results of the Gamma generalized linear mixed-effects model testing the effects of Area, reef Typology, and Depth on the Reef Consolidation Index (RCI). Reported values are Type III Wald chi-square tests for fixed effects. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
|---|---|---|---|
| Area | 2.3227 | 2 | 0.31306 |
| Typology | 0.6024 | 1 | 0.43767 |
| Depth | 152.0902 | 2 | **<0.001** |
| Area:Typology | 7.2633 | 2 | **0.02647** |
| Area:Depth | 82.6178 | 4 | **<0.001** |
| Typology:Depth | 29.6705 | 2 | **<0.001** |
| Area:Typology:Depth | 36.7330 | 4 | **<0.001** |

## 4.4 MANAGEMENT EFFECTS ON REEF CONDITION

Benthic community composition differed significantly across management regimes, depth strata, and reef typologies, with all main effects and interaction terms being significant ($p = 0.001$). Reef typology ($R^2 = 0.056$) and depth ($R^2 = 0.049$) accounted for the largest shares of explained variance, whereas management had a smaller overall effect ($R^2 = 0.017$) that was strongly context-dependent, as reflected by significant two- and three-way interactions (Table 30). Multivariate dispersion differed significantly among groups ($p = 0.001$), indicating differences in within-group heterogeneity of community composition (Table 31).

*Table 30 PERMANOVA results showing the effects of Management, Depth, Typology, and their interactions on data variability. The bold values indicate significance ($p<0.005$).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 6.01 | 0.01733 | 22.8592 | **0.001** |
| Depth | 2 | 16.87 | 0.04859 | 64.1053 | **0.001** |
| Typology | 1 | 19.58 | 0.05641 | 148.8492 | **0.001** |
| Management:Depth | 4 | 3.26 | 0.00938 | 6.1889 | **0.001** |
| Management:Typology | 2 | 4.91 | 0.01413 | 18.6489 | **0.001** |
| Depth:Typology | 2 | 3.80 | 0.01094 | 14.4291 | **0.001** |
| Management:Depth:Typology | 4 | 1.45 | 0.00418 | 2.7569 | **0.001** |
| Residual | 2214 | 291.29 | 0.83904 | | |
| Total | 2231 | 347.16 | 1.00000 | | |

*Table 31 PERMDISP results showing differences in multivariate dispersion among groups. The bold values indicate significance ($p<0.005$).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 17 | 5.015 | 0.29499 | 18.349 | **0.001** |
| Residuals | 2214 | 35.594 | 0.01608 | | |

Sample sizes differ significantly among management categories. Inhabited reefs are more extensively represented in outer reef typologies, whereas uninhabited reefs are more prevalent in inner reefs. By contrast, the number of samples from resort reefs is consistent across reef typologies.

To facilitate interpretation of interaction effects, NMDS ordinations were visualized separately for each reef typology and depth; analyses were conducted in three dimensions to minimize stress, with only the first two axes presented for clarity. The NMDS ordination for inner reefs at Flat depth (stress = 0.17) reveals substantial overlap among management categories (inhabited, resort, and uninhabited reefs). Nevertheless, uninhabited reefs show a slightly broader dispersion toward the right side of the ordination, whereas inhabited reefs are mainly distributed toward the left. Resort reefs occupy an intermediate position and form a more compact cluster. Across depths within inner reefs, inhabited and uninhabited sites remain consistently separated, being located on opposite sides of the ordination along the depth gradient. In contrast, outer reefs show considerable overlap among management categories already at the reef flat, with samples becoming increasingly compact and converging toward the centre of the ordination at 20 m depth (Figure 32).

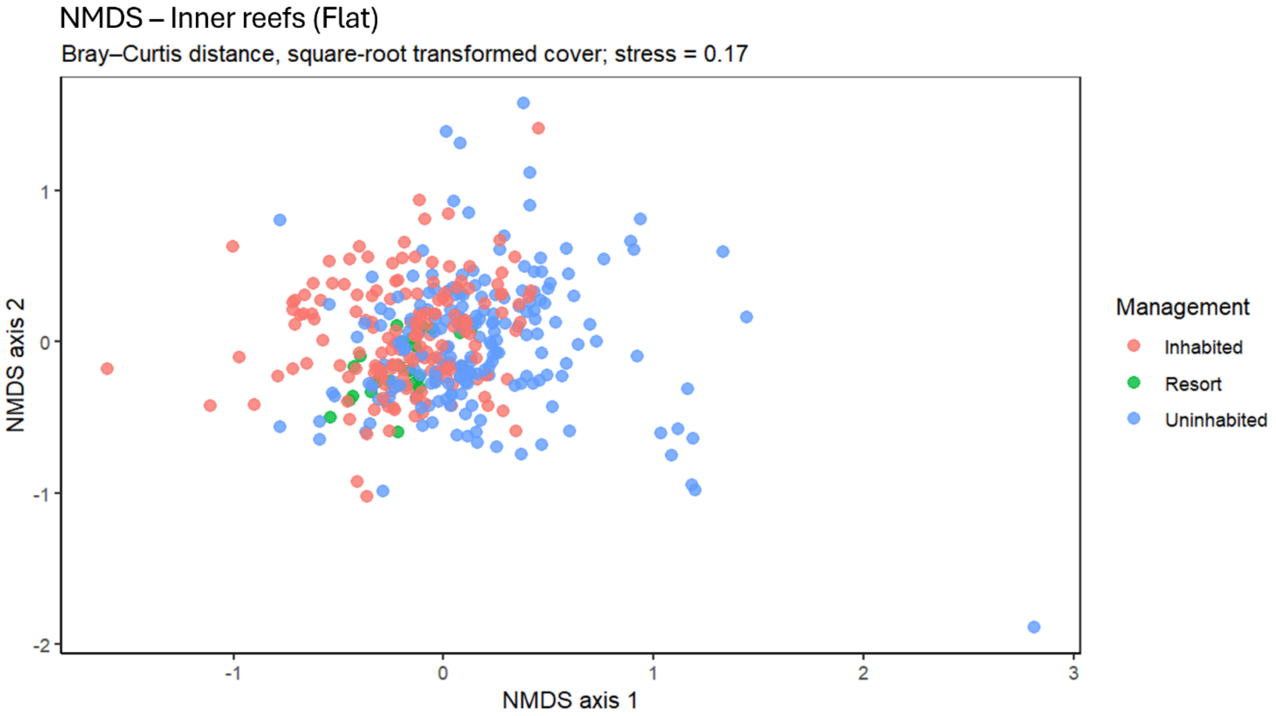


*Figure 32 NMDS ordination of benthic community composition for inner reefs at Flat depth based on Bray–Curtis dissimilarity of square-root transformed cover data (stress = 0.17). Points represent samples colored by management category (inhabited = red, resort = green, uninhabited = blue).*

The PERMANOVA highlights a significant effect of management in relation to the Flat depth and the internal reef type ($p = 0.001$), although the proportion of explained variability is relatively low ($R^2 = 0.057$) (Table 32). The PERMDISP test is significant ($p = 0.001$), indicating differences in within-group dispersion, which contribute to the observed structure and suggest marked intra-group heterogeneity (Table 33).

*Table 32 PERMANOVA results for samples collected at Flat depth on internal reefs, highlighting a significant effect of management on multivariate structure. The $R^2$ value indicates a low proportion of explained variability, suggesting a statistically significant but limited effect size. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 3.735 | 0.05734 | 11.588 | **0.001** |
| Residual | 381 | 61.406 | 0.94266 | | |
| Total | 383 | 65.141 | 1.00000 | | |

*Table 33 PERMDISP test results for samples collected at Flat depth on internal reefs, highlighting significant differences in within-group dispersion among management groups. The bold values indicate significance (p<0.005).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 0.4829 | 0.241455 | 14.04 | **0.001** |
| Residuals | 381 | 6.5521 | 0.017197 | | |

The BETADISPER test highlights differences in within-group variability. Resort sites show the lowest dispersion values (0.2479), suggesting greater homogeneity and a more compact community structure (Table 34). The ANOVA applied to Betadisper distances was significant ($p < 0.001$), confirming that dispersion differs significantly among the analyzed groups (Table 35).

*Table 34 Betadisper analysis of multivariate within-group dispersion for Resort, Inhabited, and Uninhabited sites. Values represent the mean distance to the group median; lower values indicate greater homogeneity in community structure.*

**BETADISPER**

Average distance to median:

| Inhabited | Resort | Uninhabited |
|---|---|---|
| 0.3737 | 0.2479 | 0.3976 |

*Table 35 Results of the ANOVA applied to Betadisper distances, showing significant differences in within-group dispersion among the analyzed site categories ($p < 0.001$). The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 0.4829 | 0.241455 | 14.04 | **<0.001** |
| Residuals | 381 | 6.5521 | 0.017197 | | |

The NMDS ordination (stress = 0.13), based on Bray–Curtis dissimilarities of square-root transformed cover data, reveals differences in the spatial distribution of samples among management categories. Resort sites form a relatively compact cluster, indicating lower within-group variability, whereas Inhabited and Uninhabited sites show a broader spread in ordination space, suggesting greater dispersion (Figure 33).

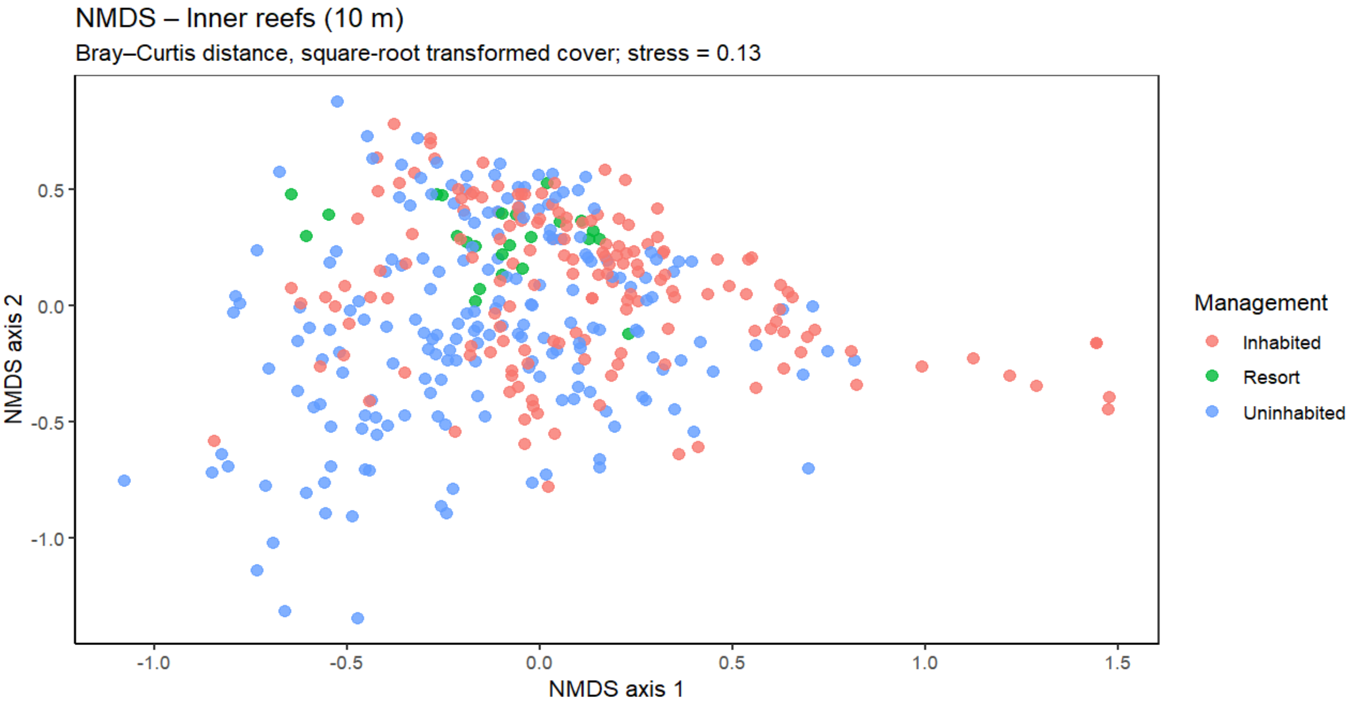


*Figure 33 NMDS ordination of benthic community composition for inner reefs at 10 m depth based on Bray–Curtis dissimilarity of square-root transformed cover data (stress = 0.13). Points represent samples colored by management category (inhabited = red, resort = green, uninhabited = blue).*

Management had a significant effect at 10 m depth in the inner reef according to PERMANOVA (p = 0.001), although it explained only a small proportion of the total variability (R² = 0.064), higher than at Flat depth (Table 36). A significant PERMDISP result (p = 0.001) indicates that variability differs among groups, suggesting that the observed structure is partly driven by pronounced within-group heterogeneity (Table 37).

*Table 36 PERMANOVA results for samples collected at 10 m depth on internal reefs, highlighting a significant effect of management on multivariate structure. The R² value indicates a low proportion of explained variability. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | R² | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 3.785 | 0.06409 | 13.045 | **0.001** |
| Residual | 381 | 55.272 | 0.93591 | | |
| Total | 383 | 59.057 | 1.00000 | | |

*Table 37 PERMDISP test results for samples collected at 10 m depth on internal reefs, highlighting significant differences in within-group dispersion among management groups.*

| **PERMDISP** | | | | | |
|---|---|---|---|---|---|
| Permutation N: | 999 | | | | |
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F** | **Pr(>F)** |
| Groups | 2 | 0.5796 | 0.289800 | 17.244 | **0.001** |
| Residuals | 381 | 6.4028 | 0.016805 | | |

Results from the BETADISPER test indicate differences in within-group dispersion. Resort sites exhibit the lowest mean dispersion value (0.2058), reflecting a more homogeneous and tightly clustered community structure, whereas Inhabited and Uninhabited sites show higher dispersion values, indicative of greater within-group heterogeneity (Table 38). The ANOVA yielded a significant result (p < 0.001), indicating significant differences in dispersion among the analyzed groups (Table 39).

*Table 38 Betadisper analysis of multivariate within-group dispersion for Resort, Inhabited, and Uninhabited sites. Values represent the mean distance to the group median; lower values indicate greater homogeneity in community structure.*

| **BETADISPER** | | |
|---|---|---|
| Average distance to median: | | |
| **Inhabited** | **Resort** | **Uninhabited** |
| 0.3683 | 0.2058 | 0.3640 |

*Table 39 Results of the ANOVA applied to Betadisper distances, showing significant differences in within-group dispersion among the analyzed site categories (p < 0.001). The bold values indicate significance (p<0.005).*

| **ANOVA** | | | | | |
|---|---|---|---|---|---|
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| Groups | 2 | 0.5796 | 0.289800 | 17.244 | **<0.001** |
| Residuals | 381 | 6.4028 | 0.016805 | | |

At 20 m depth, the NMDS ordination (stress = 0.12) shows a high degree of point dispersion and substantial overlap among management categories. Compared to Flat and 10 m, samples are more widely scattered across the ordination space. Resort sites appear more centrally clustered, whereas Inhabited and Uninhabited sites show greater dispersion along the NMDS axes (Figure 34).

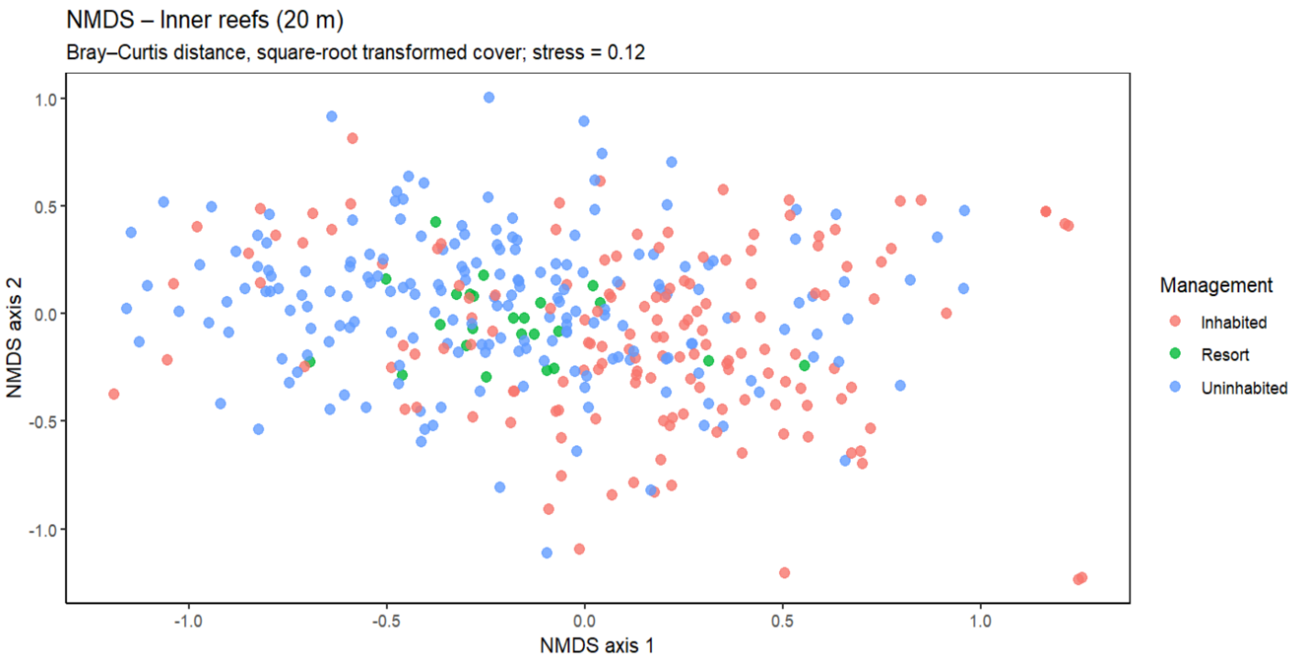


*Figure 34 NMDS ordination of benthic community composition for inner reefs at 20 m depth based on Bray–Curtis dissimilarity of square-root transformed cover data (stress = 0.12). Points represent samples colored by management category (inhabited = red, resort = green, uninhabited = blue).*

Within inner reef sites at 20 m depth, PERMANOVA revealed a significant influence of management ($p = 0.001$). Although the proportion of explained variation remains relatively small ($R^2 = 0.075$), this value is the highest observed among inner reef sites, suggesting that management accounts for a comparatively greater proportion of community variability at this depth (Table 40). Significant PERMDISP outcomes ($p = 0.001$) reveal unequal dispersion among groups, indicating that the observed structure is, at least in part, shaped by pronounced intra-group heterogeneity (Table 41).

*Table 40 PERMANOVA results for samples collected at 20 m depth on internal reefs, highlighting a significant effect of management on multivariate structure. The $R^2$ value indicates a low proportion of explained variability. The bold values indicate significance ($p<0.005$).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 4.868 | 0.07549 | 15.555 | **0.001** |
| Residual | 381 | 59.621 | 0.92451 | | |
| Total | 383 | 64.489 | 1.00000 | | |

*Table 41 PERMDISP test results for samples collected at 20 m depth on internal reefs, highlighting significant differences in within-group dispersion among management groups. The bold values indicate significance (p<0.005).*

| **PERMDISP** | | | | | |
|---|---|---|---|---|---|
| Permutation N: | 999 | | | | |
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F** | **Pr(>F)** |
| Groups | 2 | 0.7362 | 0.36811 | 18.663 | **0.001** |
| Residuals | 381 | 7.5150 | 0.01972 | | |

BETADISPER results show that Resort sites display the lowest mean dispersion value (0.1975) recorded across all depths and within the inner reef, indicating the most homogeneous community structure. In contrast, Inhabited (0.3815) and Uninhabited (0.3749) sites are characterized by higher dispersion values, reflecting greater within-group heterogeneity (Table 42). Consistently, the ANOVA on Betadisper distances was significant (p < 0.001), confirming that dispersion differs significantly among the analyzed groups (Table 43).

*Table 42 Betadisper analysis of multivariate within-group dispersion for Resort, Inhabited, and Uninhabited sites. Values represent the mean distance to the group median; lower values indicate greater homogeneity in community structure.*

| **BETADISPER** | | |
|---|---|---|
| Average distance to median: | | |
| **Inhabited** | **Resort** | **Uninhabited** |
| 0.3815 | 0.1975 | 0.3749 |

*Table 43 Results of the ANOVA applied to Betadisper distances, showing significant differences in within-group dispersion among the analyzed site categories (p < 0.001). The bold values indicate significance (p<0.005).*

| **ANOVA** | | | | | |
|---|---|---|---|---|---|
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| Groups | 2 | 0.7362 | 0.36811 | 18.663 | **<0.001** |
| Residuals | 381 | 7.5150 | 0.01972 | | |

Differences among management categories involve both shifts in benthic community composition and multivariate dispersion, with resort reefs consistently exhibiting lower within-group variability across depths. Rather than weakening, the influence of management remains stable and shows a slight increase with depth.

Management influences benthic community structure on shallow outer reefs, but its effect is markedly weaker than in lagoon reefs. Outer reefs appear more buffered by hydrodynamic processes, with management effects persisting but remaining limited in magnitude and homogenization compared to inner reefs.

The NMDS ordination of shallow outer reefs (Flat), based on Bray–Curtis dissimilarity and square-root–transformed benthic cover data, shows a high degree of overlap among sites under different management regimes. The stress value of 0.16 indicates an adequate two-dimensional representation of the dissimilarity patterns. Uninhabited and inhabited sites exhibit greater dispersion along the first NMDS axis, suggesting higher variability in benthic composition, whereas resort sites are more tightly clustered, indicating more homogeneous benthic communities. Nevertheless, no clear separation among management regimes is evident (Figure 35).

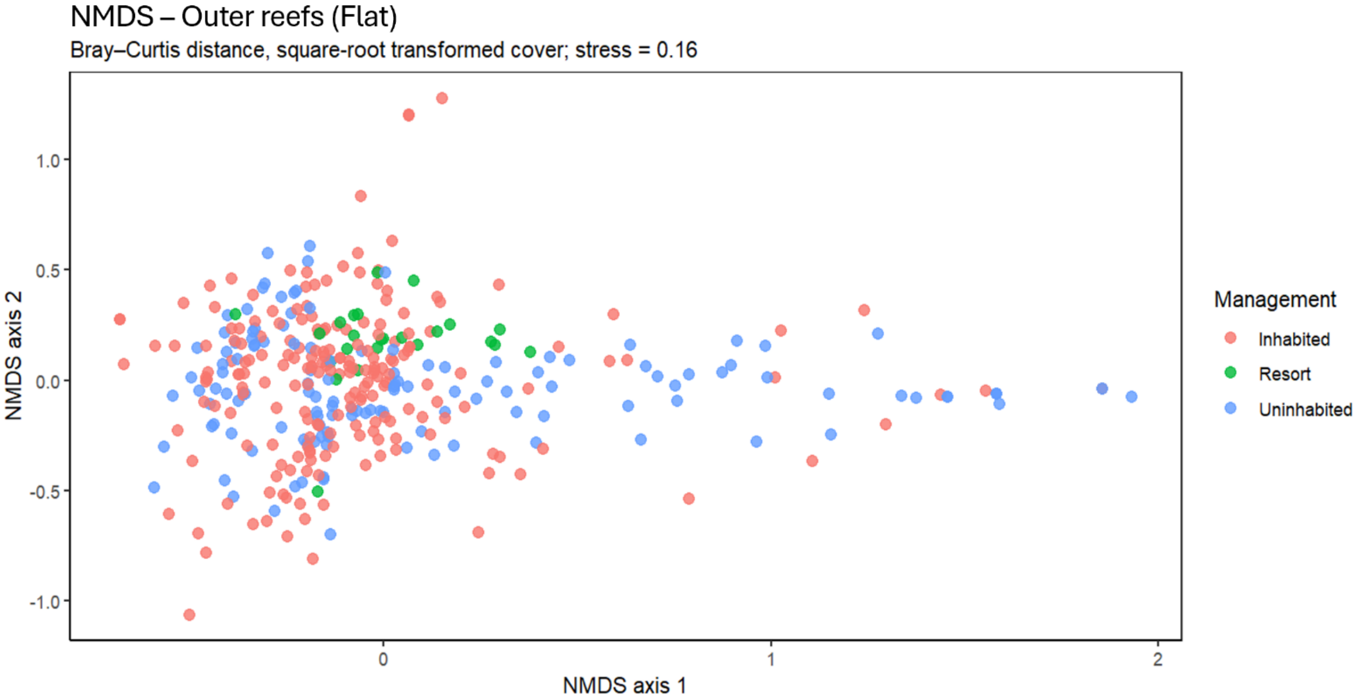


*Figure 35 NMDS ordination of benthic community composition for outer reefs at Flat depth based on Bray–Curtis dissimilarity of square-root transformed cover data (stress = 0.16). Points represent samples colored by management category (inhabited = red, resort = green, uninhabited = blue).*

PERMANOVA results for outer reef sites at Flat depth indicate that management has a statistically significant effect on benthic community composition (p = 0.001). Despite this significance, management explains only a limited proportion of the total variation observed ($R^2 = 0.036$), suggesting a relatively weak influence on overall community patterns (Table 44).

The significant PERMDISP results ($p = 0.001$) further indicate differences in multivariate dispersion among management categories, implying that the detected structure is at least partly attributable to substantial within-group variability rather than to distinct separation among groups (Table 45).

*Table 44 PERMANOVA results for samples collected at Flat depth on outer reefs, highlighting a significant effect of management on multivariate structure. The $R^2$ value indicates a low proportion of explained variability. The bold values indicate significance ($p<0.005$).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 1.801 | 0.03609 | 6.6836 | **0.001** |
| Residual | 357 | 48.100 | 0.96391 | | |
| Total | 359 | 49.901 | 1.00000 | | |

*Table 45 PERMDISP test results for samples collected at Flat depth on outer reefs, highlighting significant differences in within-group dispersion among management groups. The bold values indicate significance ($p<0.005$).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 0.1975 | 0.098759 | 5.263 | **0.004** |
| Residuals | 357 | 6.6990 | 0.018765 | | |

Results from the BETADISPER analysis indicate that resort sites are characterized by the lowest mean dispersion value (0.265), reflecting a more homogeneous benthic community structure compared to the other management categories, which exhibit higher within-group heterogeneity (Table 46). This pattern is supported by the ANOVA on betadisper distances, which was highly significant ($p < 0.001$), confirming that multivariate dispersion differs significantly among the management groups considered (Table 47).

*Table 46 Betadisper analysis of multivariate within-group dispersion for Resort, Inhabited, and Uninhabited sites. Values represent the mean distance to the group median; lower values indicate greater homogeneity in community structure.*

**BETADISPER**

Average distance to median:

| Inhabited | Resort | Uninhabited |
|---|---|---|
| 0.3368 | 0.265 | 0.3615 |

*Table 47 Results of the ANOVA applied to Betadisper distances, showing significant differences in within-group dispersion among the analyzed site categories. The bold values indicate significance (p<0.005).*

| ANOVA | | | | | |
|---|---|---|---|---|---|
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| Groups | 2 | 0.1975 | 0.098759 | 5.263 | **0.006** |
| Residuals | 357 | 6.6990 | 0.018765 | | |

The NMDS ordination (stress = 0.17) shows substantial overlap among management categories, indicating limited differences in benthic community composition on outer reefs at 10 m depth. Inhabited sites exhibit greater variability, while uninhabited sites largely overlap with them; resort sites show only a weak shift along the first axis. Overall, natural environmental variability appears more influential than management regime (Figure 36).

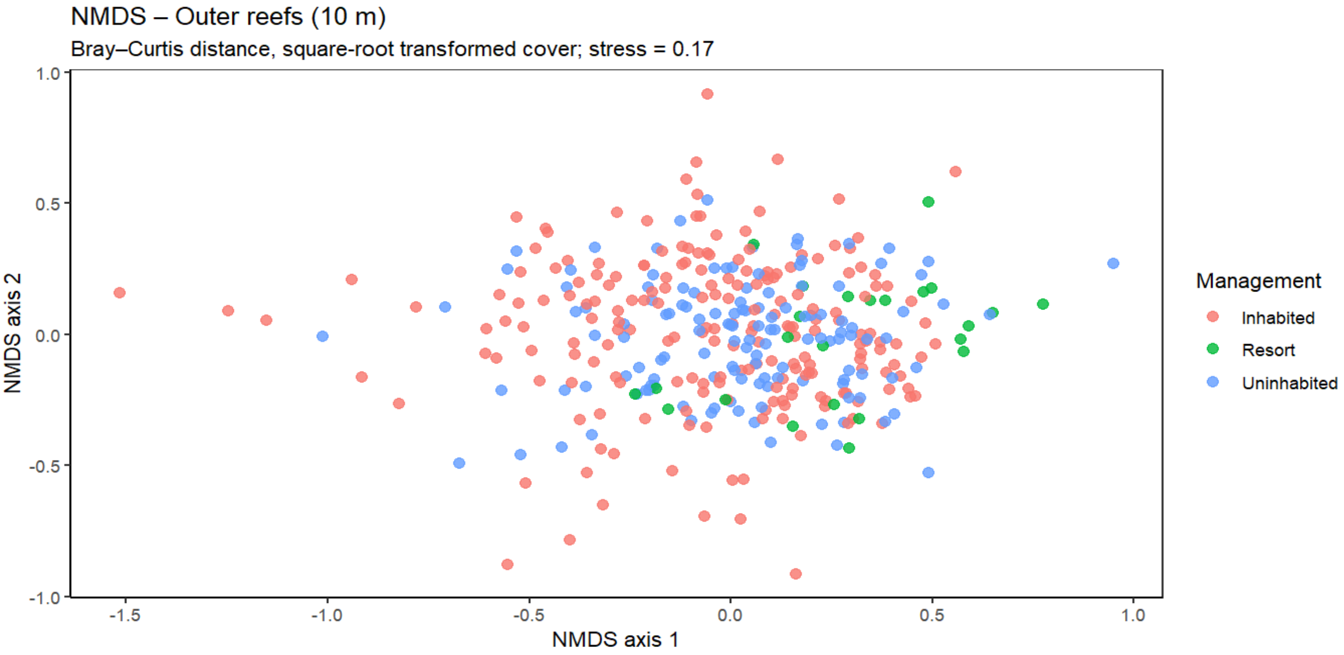


*Figure 36 NMDS ordination of benthic community composition for outer reefs at 10 m depth based on Bray–Curtis dissimilarity of square-root transformed cover data (stress = 0.17). Points represent samples colored by management category (inhabited = red, resort = green, uninhabited = blue).*

PERMANOVA analysis revealed a significant influence of management on benthic community composition at outer reef sites at 10 m depth (p = 0.001). Nevertheless, the proportion of variance explained by management was low ($R^2 = 0.041$), although greater than that recorded at Flat (Table 48).

Significant PERMDISP results (p = 0.001) indicate that multivariate dispersion varies among management categories, suggesting that the observed patterns are partly driven by high within-group variability rather than clear separation between groups (Table 49).

*Table 48 PERMANOVA results for samples collected at 10 m depth on outer reefs, highlighting a significant effect of management on multivariate structure. The $R^2$ value indicates a low proportion of explained variability. The bold values indicate significance ($p<0.005$).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 1.529 | 0.04171 | 7.7692 | **0.001** |
| Residual | 357 | 35.118 | 0.95829 | | |
| Total | 359 | 36.647 | 1.00000 | | |

*Table 49 PERMDISP test results for samples collected at 10 m depth on outer reefs, highlighting significant differences in within-group dispersion among management groups.*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 0.1000 | 0.049999 | 5.3328 | **0.003** |
| Residuals | 357 | 3.3471 | 0.009376 | | |

Analysis of multivariate dispersion shows that resort sites exhibit the lowest average dispersion value (0.278), indicating a comparatively homogeneous benthic community structure, whereas the other management categories are characterized by greater internal variability (Table 50). These differences among management groups are confirmed by a significant ANOVA of betadisper distances (p = 0.005), demonstrating that dispersion varies significantly across the groups considered (Table 51).

*Table 50 Betadisper analysis of multivariate within-group dispersion for Resort, Inhabited, and Uninhabited sites. Values represent the mean distance to the group median; lower values indicate greater homogeneity in community structure.*

**BETADISPER**

Average distance to median:

| Inhabited | Resort | Uninhabited |
|---|---|---|
| 0.3116 | 0.2786 | 0.2779 |

*Table 51 Results of the ANOVA applied to Betadisper distances, showing significant differences in within-group dispersion among the analyzed site categories (p = 0.005). The bold values indicate significance (p<0.005).*

| **ANOVA** | | | | | |
|---|---|---|---|---|---|
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| Groups | 2 | 0.1000 | 0.049999 | 5.3328 | **0.005** |
| Residuals | 357 | 3.3471 | 0.009376 | | |

At 20 m depth, the NMDS ordination (stress = 0.16) indicates considerable overlap among management groups, suggesting weak differences in benthic community composition on outer reefs. Inhabited sites show higher variability, while resort and uninhabited sites largely coincide in ordination space. Overall, these patterns suggest that natural environmental factors have a stronger influence than management on benthic community structure at this depth (Figure 37).

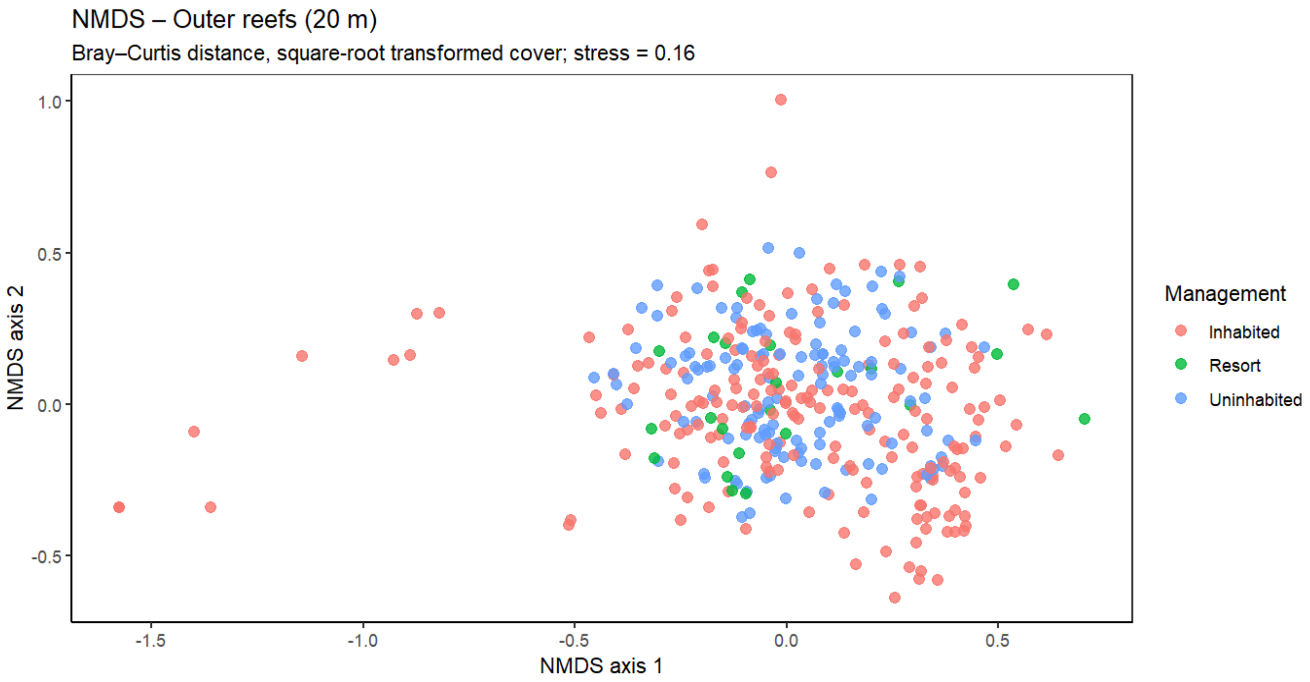


*Figure 37 NMDS ordination of benthic community composition for outer reefs at 20 m depth based on Bray–Curtis dissimilarity of square-root transformed cover data (stress = 0.16). Points represent samples colored by management category (inhabited = red, resort = green, uninhabited = blue).*

PERMANOVA results indicate that management has a statistically significant effect on benthic community composition at outer reef sites at 20 m depth (p = 0.001). However, management explains only a very small fraction of the total variation ($R^2 = 0.025$), and this effect is weaker than that observed at shallower depths (Table 52).

PERMDISP results were statistically significant (p = 0.001), demonstrating that multivariate dispersion differs among management groups and suggesting that the detected community patterns are influenced more by within-group heterogeneity than by clear differences between groups (Table 53).

*Table 52 PERMANOVA results for samples collected at 20 m depth on outer reefs, highlighting a significant effect of management on multivariate structure. The R² value indicates a low proportion of explained variability. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | R² | F | Pr(>F) |
|---|---|---|---|---|---|
| Management | 2 | 0.874 | 0.02488 | 4.5548 | **0.001** |
| Residual | 357 | 34.263 | 0.97512 | | |
| Total | 359 | 35.138 | 1.00000 | | |

*Table 53 PERMDISP test results for samples collected at 20 m depth on outer reefs, highlighting significant differences in within-group dispersion among management groups. The bold values indicate significance (p<0.005).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 2 | 0.3372 | 0.16860 | 13.182 | **0.001** |
| Residuals | 357 | 4.5659 | 0.01279 | | |

Results from the PERMDISP analysis show that uninhabited sites are associated with the lowest average dispersion (0.248), indicating a relatively homogeneous benthic community structure, while the remaining management categories display greater internal variability (Table 54). These differences are corroborated by a significant ANOVA on betadisper distances (p < 0.001), demonstrating that dispersion varies significantly among the management groups considered (Table 55).

*Table 54 Betadisper analysis of multivariate within-group dispersion for Resort, Inhabited, and Uninhabited sites. Values represent the mean distance to the group median; lower values indicate greater homogeneity in community structure.*

**BETADISPER**

Average distance to median:

| Inhabited | Resort | Uninhabited |
|---|---|---|
| 0.3127 | 0.2715 | 0.2484 |

*Table 55 Results of the ANOVA applied to Betadisper distances, showing significant differences in within-group dispersion among the analyzed site categories (p <0.001). The bold values indicate significance (p<0.005).*

| **ANOVA** | | | | | |
|---|---|---|---|---|---|
| **Source** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| Groups | 2 | 0.3372 | 0.16860 | 13.182 | **<0.001** |
| Residuals | 357 | 4.5659 | 0.01279 | | |

Figure 38 illustrates multivariate dispersion of benthic communities, expressed as the distance of samples from group centroids in Bray–Curtis dissimilarity space, and highlights differences in within-group variability across management regimes as well as along depth and reef typology gradients, indicating non-uniform patterns of intra-group variability across contexts.

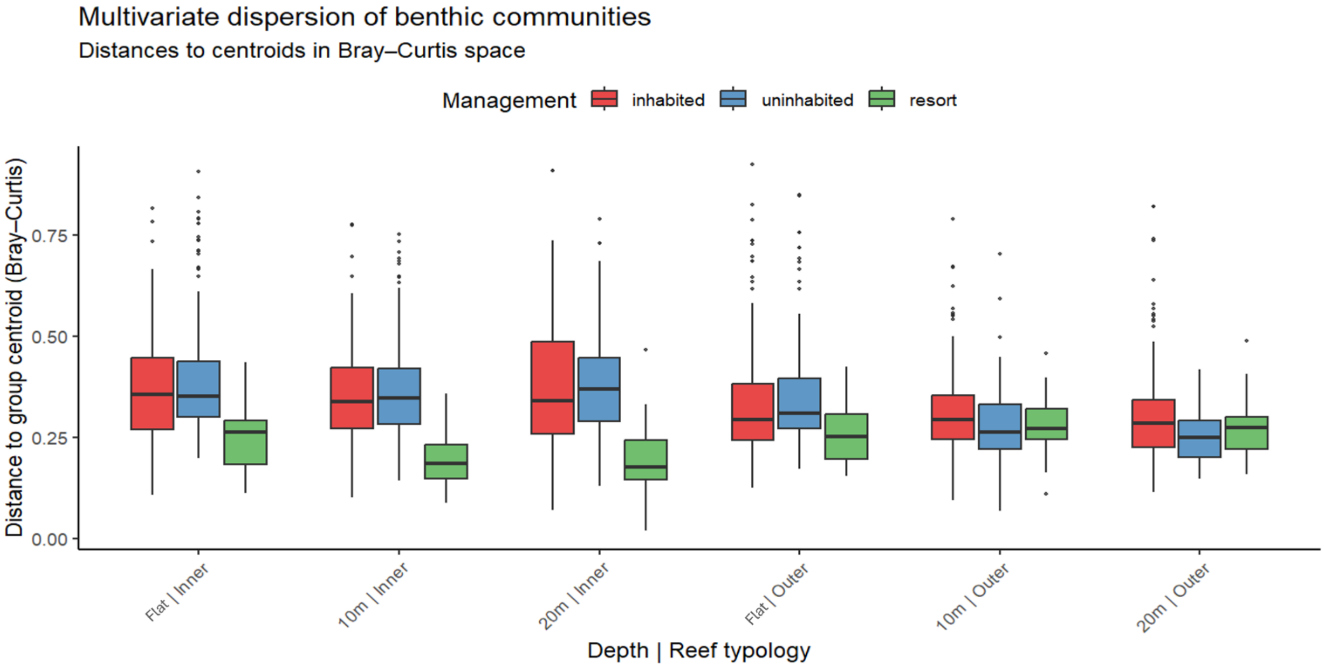


*Figure 38 Multivariate dispersion of benthic communities across management regimes, reef typologies, and depth strata. Boxplots show distances of samples to group centroids in Bray–Curtis space.*

An overview of coral community composition across management regimes, reef typology and depth is shown in Figure 39. Mean coral cover varied across management categories and depth strata, with clear differences between inner and outer reef typologies. Across all conditions, coral assemblages were dominated by massive and encrusting growth forms, while branching *Acropora* contributed variably depending on management regime and depth. This figure provides a descriptive summary of observed community patterns and is intended to support subsequent multivariate and mixed-model analyses.

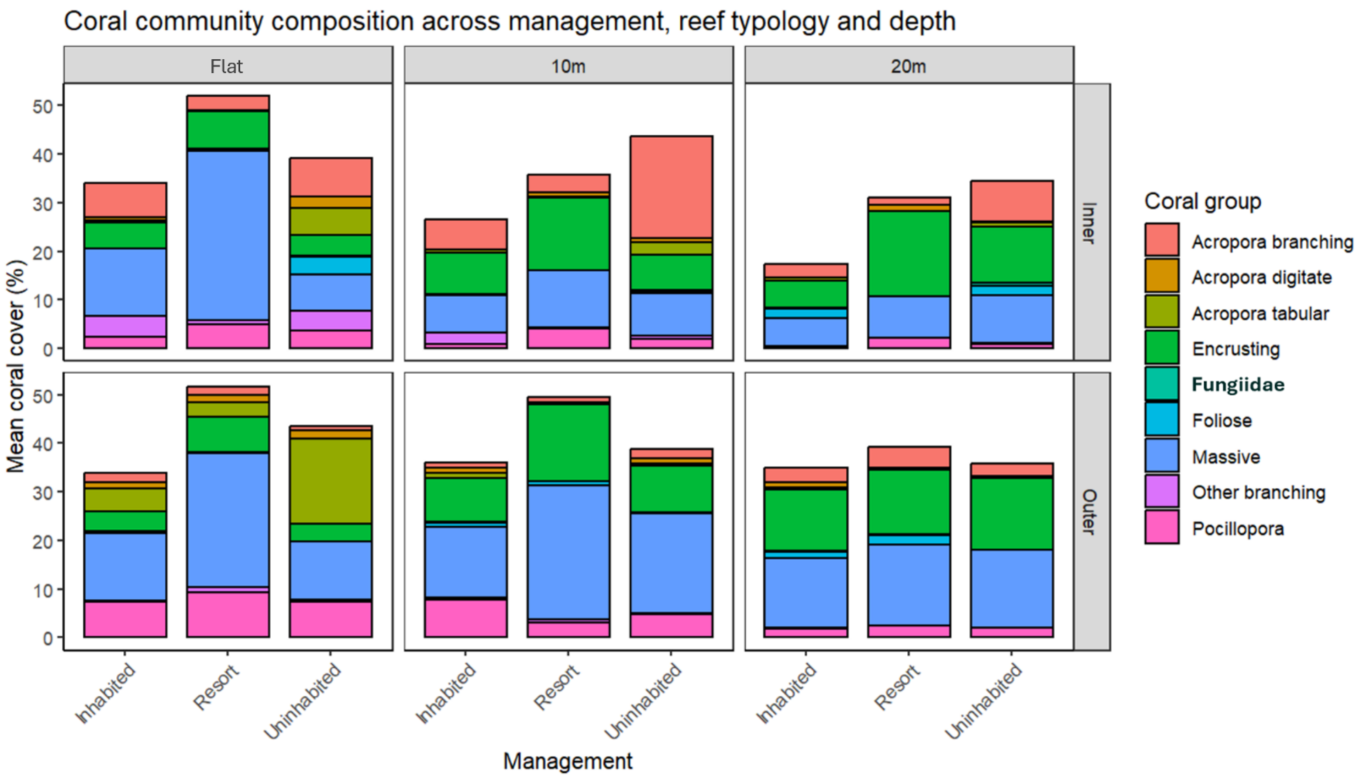


*Figure 39 Observed coral community composition expressed as mean coral cover (%) by coral growth form across management regimes, reef typology and depth.*

A linear mixed-effects model (LMM) was used to examine the effects of management regime, reef typology, and depth on total live coral cover, with atoll included as a random effect. Total live coral cover was significantly affected by management, reef typology, and depth, with a significant three-way interaction indicating that management effects differed between lagoon and ocean reefs and across depths ($p < 0.001$) (Table 56).

*Table 56 Results of a linear mixed-effects model testing the effects of management, reef typology (inner vs outer), depth, and area on total live coral cover, with atoll included as a random intercept. Fixed effects were assessed using Type III ANOVA with Satterthwaite's approximation. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| Management | 8.4640 | 4.2320 | 2 | 2135.99 | 54.7220 | **< 0.001** |
| Typology | 0.8357 | 0.8357 | 1 | 2209.02 | 10.8066 | **0.00103** |
| Depth | 2.9647 | 1.4823 | 2 | 2203.85 | 19.1676 | **< 0.001** |
| Area | 0.3283 | 0.1642 | 2 | 7.38 | 2.1228 | 0.18695 |
| Management:Typology | 0.7943 | 0.3971 | 2 | 2116.78 | 5.1353 | **0.00596** |
| Management:Depth | 0.3785 | 0.0946 | 4 | 2203.85 | 1.2236 | 0.29866 |
| Typology:Depth | 0.5938 | 0.2969 | 2 | 2203.85 | 3.8391 | **0.02166** |
| Management:Typology:Depth | 1.9313 | 0.4828 | 4 | 2203.85 | 6.2430 | **< 0.001** |

Predicted cover of sensitive corals (*Acropora spp*. and *Pocillopora spp.*), based on estimated marginal means from the linear mixed-effects model, varied across management regimes, reef typology and depth. Model-based predictions revealed contrasting patterns in sensitive coral cover within inner reefs across management regimes (Figure 40). Inner reefs under inhabited management exhibited consistently low predicted cover of sensitive corals, with a pronounced decline at 20 m depth. Differently, higher sensitive coral cover was observed under uninhabited and resort management regimes, with a marked peak at 10 m depth, indicating a depth-dependent effect of management (Management × Depth; $p < 0.001$; Table 57). In contrast, outer reefs exhibited substantially higher sensitive coral cover in shallow waters, followed by a pronounced decline at 10–20 m across management regimes. The significant three-way interaction detected by the linear mixed-effects model (Management × Typology × Depth; $p < 0.001$) (Table 57), indicates that management effects on sensitive coral cover vary between reef typologies and across depths, consistent with the patterns shown by model-based predictions.

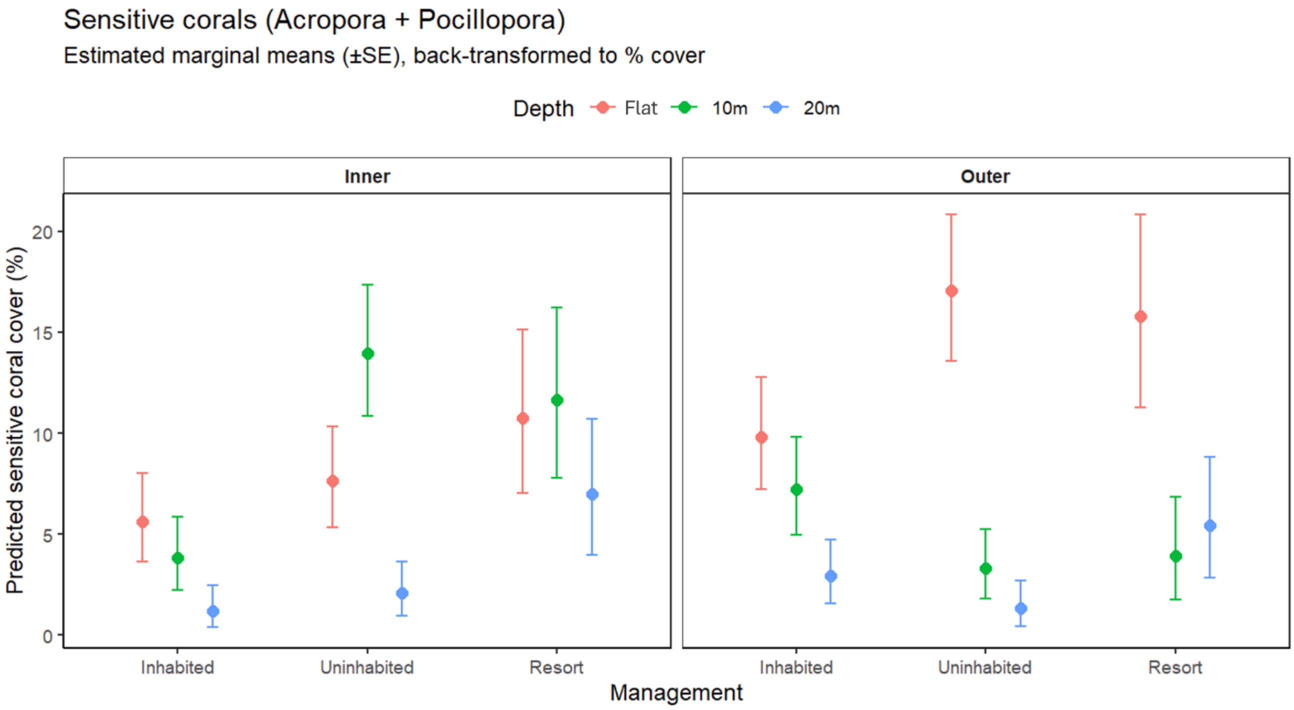


*Figure 40 Estimated marginal means (± SE) of sensitive coral cover (%) predicted by the linear mixed-effects model across management regimes, reef typology and depth.*

*Table 57 Type III ANOVA results from the linear mixed-effects model testing the effects of management, reef typology (inner vs outer), depth, and their interactions on sensitive coral cover (Acropora + Pocillopora). Degrees of freedom were estimated using Satterthwaite's approximation. The bold values indicate significance (p<0.005).*

| **ANOVA** | | | |
|---|---|---|---|
| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
| Management | 4.5610 | 2 | 0.102232 |
| Typology | 9.7572 | 1 | **0.001786** |
| Depth | 26.1374 | 2 | **<0.001** |
| Area | 2.6347 | 2 | 0.267840 |
| Management:Typology | 3.2784 | 2 | 0.194138 |
| Management:Depth | 24.8861 | 4 | **<0.001** |
| Typology:Depth | 0.2514 | 2 | 0.881872 |
| Management:Typology:Depth | 44.3527 | 4 | **<0.001** |

Figure 41 presents predicted resistant coral cover (Massive coral and Encrusting coral), expressed as estimated marginal means (± SE) from the linear mixed-effects model, across management regimes, reef typology and depth. Model-based predictions indicate that resistant corals (massive and encrusting morphologies) maintain relatively high and stable cover across management regimes and depth strata. Overall cover was higher and more persistent across depths, with weak depth-related gradients, particularly in outer reefs where peak values occurred at intermediate depths. In inner reefs, resistant coral cover increased from inhabited to uninhabited and reached the highest values in resort areas (Figure 41).

Resistant corals (massive and encrusting morphologies) exhibited a response pattern distinct from sensitive taxa, with higher overall cover and greater persistence across depth strata, indicating reduced sensitivity to depth-related gradients. Differences among management regimes were comparatively small and smooth, while the influence of reef typology was weak and non-significant (Management × Typology; $p = 0.283$). Although management effects remained significant ($p < 0.001$), resistant coral cover persisted across depth strata and management regimes, suggesting that stress-tolerant coral forms buffer disturbance and dominate under higher-pressure conditions, whereas sensitive taxa benefit disproportionately from effective management (Table 58).

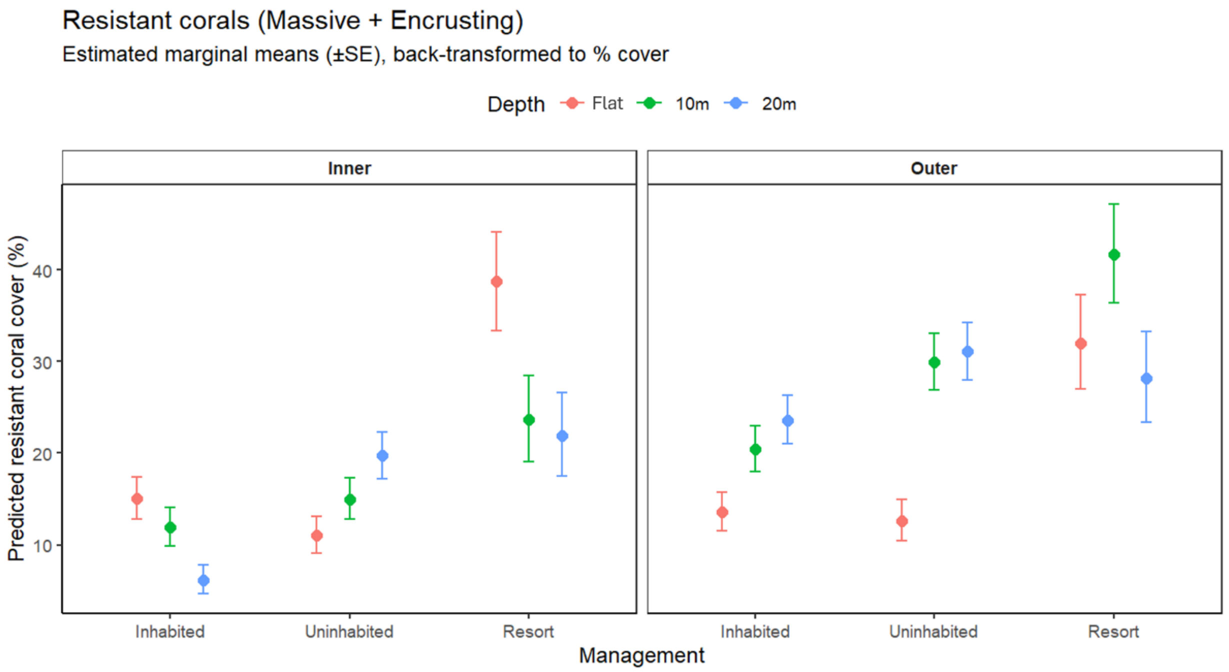


*Figure 41 Estimated marginal means (± SE) of resistant coral cover (%) predicted by the linear mixed-effects model across management regimes, reef typology and depth.*

*Table 58 ANOVA results from the linear mixed-effects model testing the effects of management, reef typology (inner vs outer), depth, and their interactions on resistant coral cover (Massive + Encrusting). Degrees of freedom were estimated using Satterthwaite's approximation. The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | $\chi^2$ | Df | Pr(>$\chi^2$) |
|---|---|---|---|
| Management | 41.7110 | 2 | **<0.001** |
| Typology | 0.7110 | 1 | 0.398792 |
| Depth | 35.8508 | 2 | **<0.001** |
| Area | 0.6162 | 2 | 0.734844 |
| Management:Typology | 2.5227 | 2 | 0.283274 |
| Management:Depth | 70.4360 | 4 | **<0.001** |
| Typology:Depth | 66.1693 | 2 | **<0.001** |
| Management:Typology:Depth | 20.6471 | 4 | **<0.001** |

Model-based predictions showed clear differences in abiotic cover (sand, rock, coral rubble and dead corals) among management categories, along with consistent changes across depth strata. Abiotic cover was generally higher in inner reefs and increased with depth, reaching maximum values at 20 m, particularly under inhabited management. In contrast, outer reefs showed lower and more stable abiotic cover across depth strata, with weaker differences among management regimes (Figure 42).

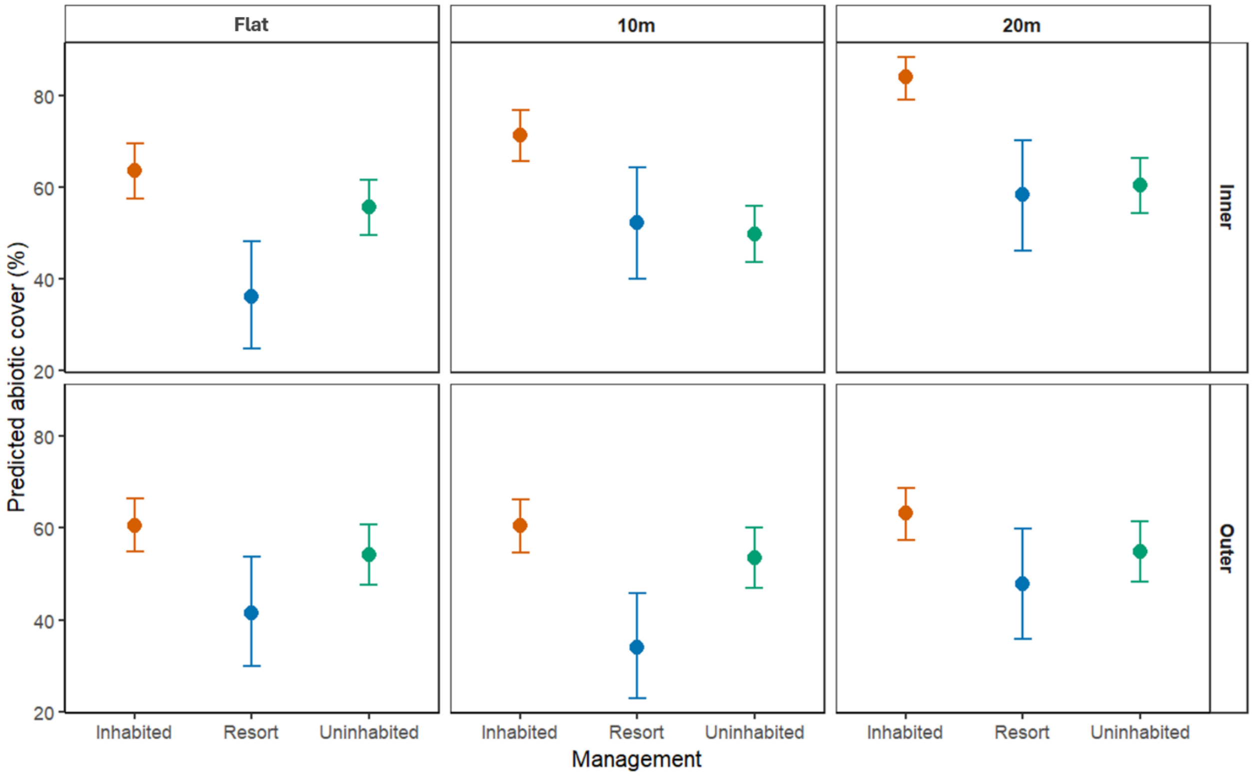


*Figure 42 Estimated marginal means (± SE) of abiotic cover (%) predicted by the linear mixed-effects model across management regimes, reef typology and depth.*

Abiotic cover was strongly affected by management regime ($p < 0.001$) and differed between reef typologies, with additional variation across depth. Importantly, a significant three-way interaction (Management × Typology × Depth; $p < 0.001$) (Table 59) indicated that the effects of management on abiotic cover varied depending on reef location (lagoon vs ocean) and depth. This result highlights that the accumulation of abiotic substrates is shaped by the combined influence of reef typology and depth, with patterns differing among management regimes.

*Table 59 ANOVA results from the linear mixed-effects model testing the effects of management, reef typology (inner vs outer), depth, and their interactions on abiotic components (Sand, Rock, Coral rubble and Dead Coral). Degrees of freedom were estimated using Satterthwaite's approximation. The bold values indicate significance (p<0.005).*

| **ANOVA** | | | |
|---|---|---|---|
| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
| Management | 22.2816 | 2 | **<0.001** |
| Typology | 0.9574 | 1 | 0.32784 |
| Depth | 60.6181 | 2 | **<0.001** |
| Area | 8.9032 | 2 | **0.01166** |
| Management:Typology | 0.9512 | 2 | 0.62151 |
| Management:Depth | 25.0785 | 4 | **<0.001** |
| Typology:Depth | 25.8480 | 2 | **<0.001** |
| Management:Typology:Depth | 12.4564 | 4 | **0.01426** |

Figure 43 illustrates shifts in substrate composition (sand–rock–rubble) across management regimes, reef typology and depth, with inner reefs generally characterized by higher proportions of sand and rubble, whereas outer reefs are predominantly rock-dominated.

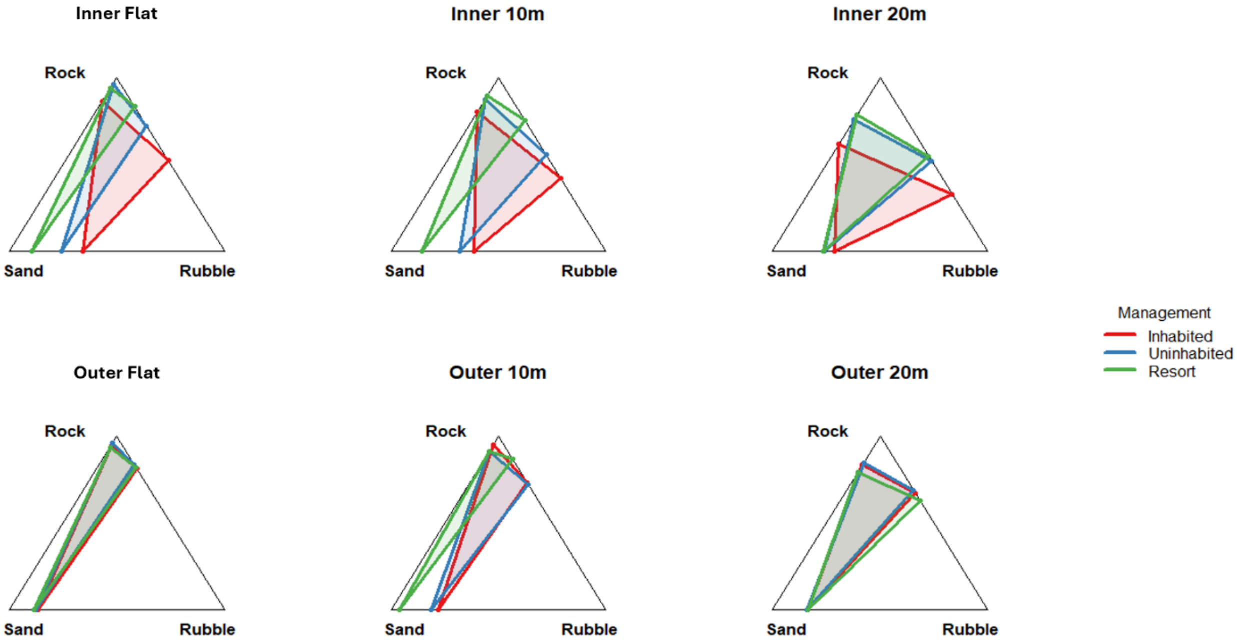


*Figure 43 Ternary plots showing substrate composition (sand, rock and rubble) across management regimes (inhabited, uninhabited and resort), reef typology (inner vs outer reefs) and depth (Flat, 10 and 20 m).*

Model-based predictions indicated that macroalgal cover did not exhibit a simple or uniform response to management regime, nor did it show a clear and consistent difference between lagoon and ocean reefs or a strong regional signal (Figure 44).

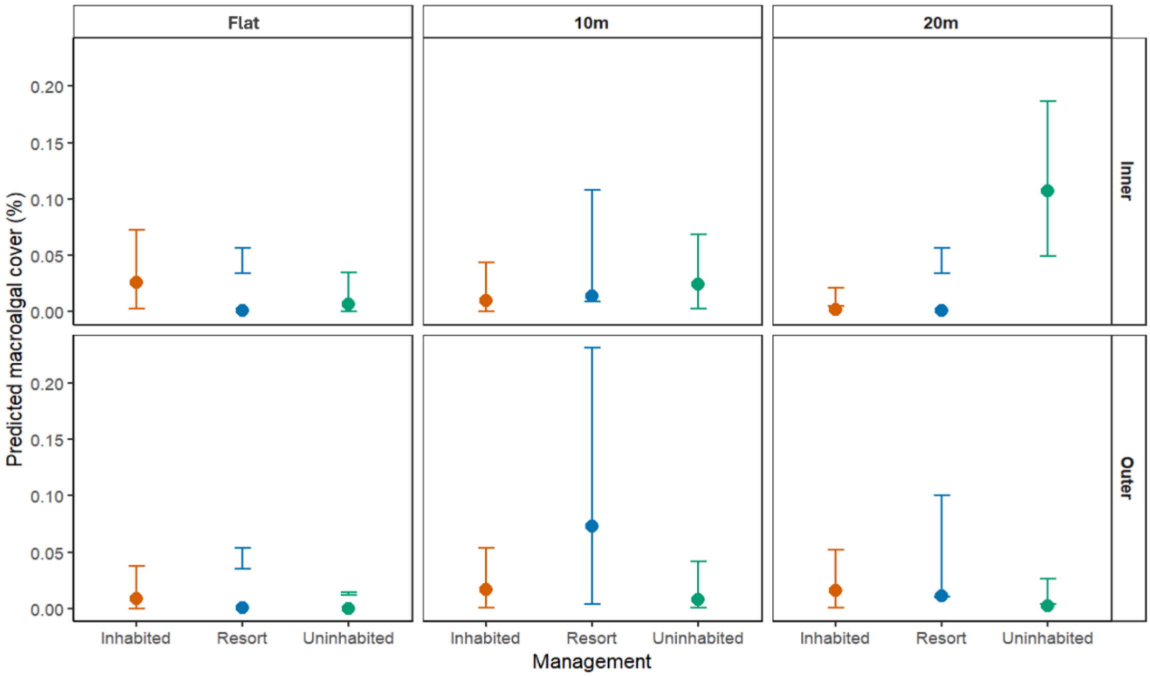


*Figure 44 Estimated marginal means (± SE) of Macroalgae cover (%) predicted by the linear mixed-effects model across management regimes, reef typology and depth.*

These results suggest that macroalgae do not track human pressure in a linear manner. Although no significant main effect of management was detected, significant interaction terms revealed that management-related differences in macroalgal cover varied between reef typologies and across depth strata (Management × Typology × Depth; $p < 0.001$) (Table 60).

*Table 60 ANOVA results from the linear mixed-effects model testing the effects of management, reef typology (inner vs outer), depth, and their interactions on Macroalgae. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
|---|---|---|---|
| Management | 4.3248 | 2 | 0.11505 |
| Typology | 1.8107 | 1 | 0.17842 |
| Depth | 5.3945 | 2 | 0.06739 |
| Area | 0.9788 | 2 | 0.61298 |
| Management:Typology | 0.7939 | 2 | 0.67236 |
| Management:Depth | 28.5687 | 4 | **<0.001** |
| Typology:Depth | 4.9257 | 2 | 0.08519 |
| Management:Typology:Depth | 12.2149 | 4 | **0.01582** |

## *4.5 ATOLL BENTHIC COMMUNITY COMPOSITION*

PERMANOVA revealed significant differences in coral community composition among atolls, with significant two-way (p = 0.001) and three-way interactions (Atoll x Typology x Depth; p = 0.001), indicating that these differences vary across reef typology and depth strata (Table 61) However, PERMDISP indicated significant differences in multivariate dispersion among groups (p <0.001) (Table 62) suggesting that PERMANOVA results may reflect both shifts in community composition and differences in within-group variability.

*Table 61 Results of PERMANOVA testing differences in coral community composition among atolls, reef typology (inner vs outer) and depth, including two-way and three-way interactions, based on Bray–Curtis dissimilarities. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | R² | F | Pr(>F) |
|---|---|---|---|---|---|
| Atoll | 10 | 38.53 | 0.11104 | 36.9915 | **0.001** |
| Typology | 1 | 14.87 | 0.04285 | 142.7570 | **0.001** |
| Depth | 2 | 16.87 | 0.04861 | 80.9616 | **0.001** |
| Atoll:Typology | 7 | 17.06 | 0.04917 | 23.3982 | **0.001** |
| Atoll:Depth | 20 | 20.16 | 0.05809 | 9.6762 | **0.001** |
| Typology:Depth | 2 | 3.74 | 0.01077 | 17.9376 | **0.001** |
| Atoll:Typology:Depth | 14 | 9.23 | 0.02659 | 6.3273 | **0.001** |
| Residual | 2175 | 226.56 | 0.65289 | | |
| Total | 2231 | 347.02 | 1.00000 | | |

*Table 62 Results of PERMDISP assessing homogeneity of multivariate dispersion among groups used in the PERMANOVA, based on Bray–Curtis distances. The bold values indicate significance (p<0.005).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 56 | 6.821 | 0.12180 | 7.9907 | **0.001** |
| Residuals | 2175 | 33.152 | 0.01524 | | |

Subsequently, analyses were conducted separately by reef typology to examine how community composition varied within each habitat.

NMDS ordination of inner reef benthic communities (stress = 0.16) showed substantial overlap among atolls, with no clear separation along either ordination axis, suggesting limited regional structuring of community composition (Figure 45).

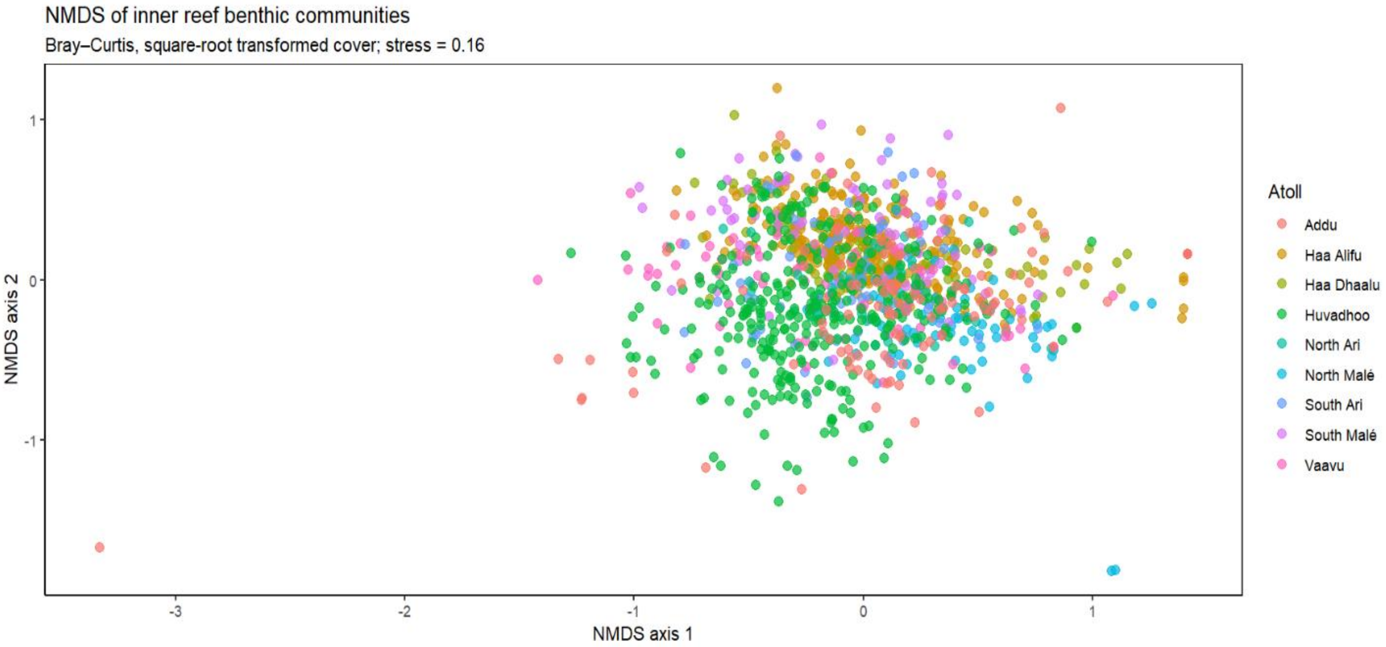


*Figure 45 NMDS ordination of inner reef benthic communities based on square-root transformed cover and Bray–Curtis dissimilarities (stress = 0.16). Points are colored by atoll.*

Benthic community composition of inner reefs differed significantly among atolls (PERMANOVA, $p = 0.001$), with atoll explaining 17.1% of the total variation, exceeding the effect of depth (5.1%) (Figure 63). Multivariate dispersion also differed significantly among atolls, indicating variable within-atoll heterogeneity in community structure (PERMDISP, $p = 0.001$) (Fugure 64). This was confirmed by the associated ANOVA on dispersion ($p < 0.001$) (Figure 65).

*Table 63 Results of PERMANOVA testing differences in benthic community composition among atolls and across depth, based on Bray–Curtis dissimilarities. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | R² | F | Pr(>F) |
|---|---|---|---|---|---|
| Atoll | 8 | 35.462 | 0.17121 | 31.40 | **0.001** |
| Depth | 2 | 10.636 | 0.05135 | 37.68 | **0.001** |
| Residual | 1141 | 161.033 | 0.77744 | | |
| Total | 1151 | 207.131 | 1.00000 | | |

*Table 64 Results of PERMDISP assessing homogeneity of multivariate dispersion among groups used in the PERMANOVA. The bold values indicate significance (p<0.005).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 8 | 1.2335 | 0.15419 | 7.6098 | **0.001** |
| Residuals | 1143 | 23.1593 | 0.020262 | | |

*Table 65 ANOVA results testing differences in multivariate dispersion among groups, associated with the PERMDISP analysis. The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 8 | 1.2335 | 0.15419 | 7.6098 | **<0.001** |
| Residuals | 1143 | 23.1593 | 0.02026 | | |

NMDS ordination of outer reef benthic communities (stress = 0.178) showed substantial overlap among atolls, with no clear separation along ordination axes, although greater dispersion was observed compared to inner reefs (Figure 46).

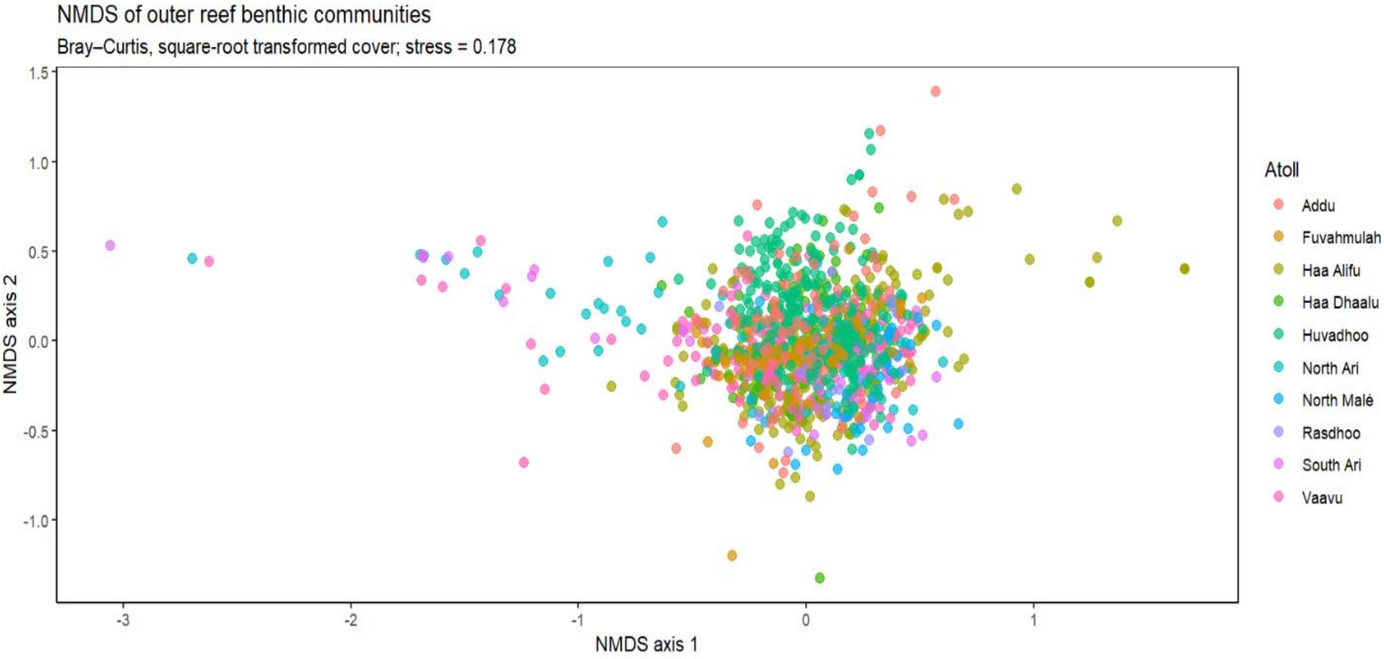


*Figure 46 NMDS ordination of outer reef benthic communities based on square-root transformed cover and Bray–Curtis dissimilarities (stress = 0.178). Points are colored by atoll.*

Outer reef benthic communities showed significant differences among atolls (PERMANOVA, p = 0.001) (Table 66), with atoll explaining 16.3% of the variation, comparable to inner reefs. Depth accounted for an additional 6.7% of variation. PERMDISP indicated significant heterogeneity in multivariate dispersion among atolls (p = 0.001) (Table 67), as confirmed by the associated ANOVA (p < 0.001) (Table 68).

*Table 66 Results of PERMANOVA testing differences in benthic community composition among atolls and across depth, based on Bray–Curtis dissimilarities. The bold values indicate significance (p<0.005).*

**PERMANOVA**

Permutation N: 999

| Source | Df | Sum Of Sqs | R² | F | Pr(>F) |
|---|---|---|---|---|---|
| Atoll | 9 | 23.117 | 0.16316 | 25.15 | **0.001** |
| Depth | 2 | 9.472 | 0.06686 | 46.366 | **0.001** |
| Residual | 1068 | 109.091 | 0.76998 | | |
| Total | 1079 | 141.680 | 1.00000 | | |

*Table 67 Results of PERMDISP assessing homogeneity of multivariate dispersion among groups used in the PERMANOVA. The bold values indicate significance (p<0.005).*

**PERMDISP**

Permutation N: 999

| Source | Df | Sum Sq | Mean Sq | F | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 9 | 1.5229 | 0.169214 | 12.563 | **0.001** |
| Residuals | 1070 | 14.4124 | 0.013469 | | |

*Table 68 Results of PERMDISP assessing homogeneity of multivariate dispersion among groups used in the PERMANOVA. The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| Groups | 9 | 1.5229 | 0.169214 | 12.563 | **<0.001** |
| Residuals | 1070 | 14.4124 | 0.013469 | | |

Figure 47 presents coral assemblages across Maldivian atolls, stratified by reef typology and depth. Substantial spatial variation was observed, with clear differences in the relative dominance of branching (e.g., *Acropora*), massive, and encrusting growth forms among atolls. Shallow inner reefs were typically characterized by higher proportions of branching and tabular Acropora, whereas outer reefs were more commonly dominated by massive and encrusting corals, especially at greater depths.

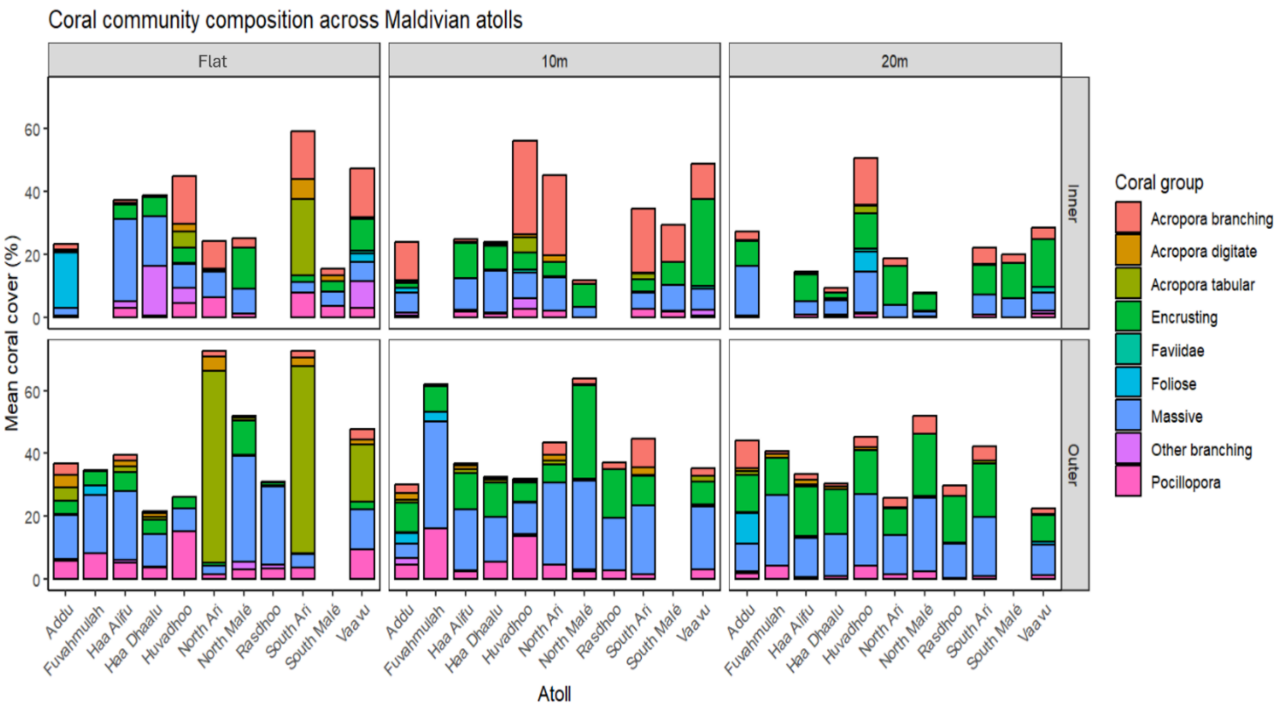


*Figure 47 Stacked barplots showing the mean percentage cover of major coral groups across Maldivian atolls, stratified by reef typology (inner vs outer reefs) and depth (Flat, 10 and 20 m).*

Total live coral cover in inner reefs varied significantly among atolls, revealing marked spatial heterogeneity. Some atolls exhibited consistently higher coral cover than others (Figure 48).

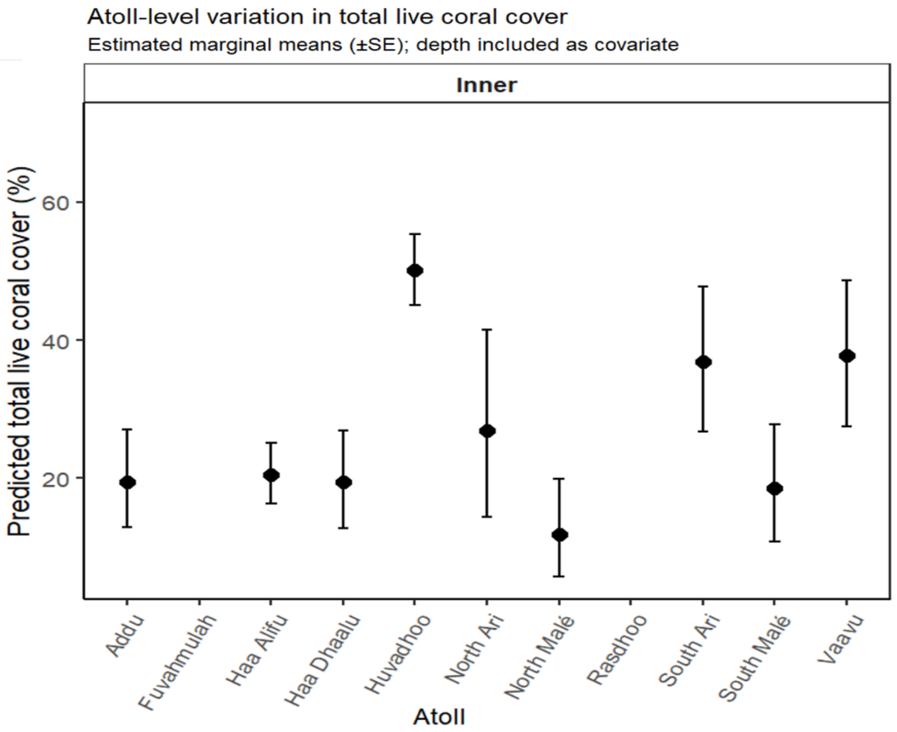


*Figure 48 Atoll-level variation in total live coral cover (%) in inner reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

The analysis of the fixed effects indicates that depth partially influences the live coral cover component in inner reef. No significant differences were observed at 10 m compared to the reference depth ($p = 0.083$), whereas a significant decrease was detected at 20 m (Estimate = −0.169; $p < 0.001$), indicating lower values at greater depth. Regarding atoll effects, most atolls did not differ significantly from the reference ($p > 0.05$). The only exception was Huvadhoo, which showed significantly higher values ($p = 0.005$) (Table 69).

*Table 69 Fixed effects estimate from the linear mixed-effects model evaluating the effects of depth and atoll on the live coral cover. The bold values indicate significance (p<0.005).*

**SUMMARY**

**Fixed effects:**

| **Source** | **Estimate** | **Std. Error** | **df** | **t value** | **Pr(>\|t\|)** |
|---|---|---|---|---|---|
| Atoll Haa Alifu | 1.31E-02 | 1.09E-01 | 2.30E+01 | 0.120 | 0.90559 |
| Atoll Haa Dhaalu | 1.32E-03 | 1.32E-01 | 2.30E+01 | 0.010 | 0.99208 |
| Atoll Huvadhoo | 3.30E-01 | 1.08E-01 | 2.30E+01 | 3.067 | **0.00546** |
| Atoll North Ari | 8.75E-02 | 1.87E-01 | 2.30E+01 | 0.469 | 0.64333 |
| Atoll North Malé | -1.05E-01 | 1.48E-01 | 2.30E+01 | -0.713 | 0.48317 |
| Atoll South Ari | 1.96E-01 | 1.48E-01 | 2.30E+01 | 1.327 | 0.19761 |
| Atoll South Malé | -6.88E-03 | 1.48E-01 | 2.30E+01 | -0.047 | 0.96320 |
| Atoll Vaavu | 2.10E-01 | 1.48E-01 | 2.30E+01 | 1.424 | 0.16776 |
| Depth 10m | -3.33E-02 | 1.92E-02 | 1.12E+03 | -1.734 | 0.08315 |
| Depth 20m | -1.69E-01 | 1.92E-02 | 1.12E+03 | -8.787 | **<0.001** |

Total live coral cover in inner reefs varied significantly across atolls ($p = 0.008$) after controlling depth and regional factors. Coral cover decreased markedly with increasing depth ($p < 0.001$), while area did not contribute significantly to explaining additional variability. Site was included as a random effect to account for repeated observations within locations (Figure 70).

*Table 70 Table Type III ANOVA results for total live coral cover in inner reefs, showing significant effects of atoll and depth, but not area. Site was fitted as a random effect. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| Atoll | 1.9981 | 0.24977 | 8 | 23 | 3.5291 | **0.00833** |
| Depth | 6.1312 | 3.06560 | 2 | 1118 | 43.3161 | **<0.001** |
| Area | | | | | | |

Figure 49 shows clear variation in total live coral cover among atolls in outer reefs. Some atolls (e.g., North Malé and South Ari) exhibit higher coral cover, while others (e.g., Haa Dhaalu) display lower values, indicating marked spatial heterogeneity across locations.

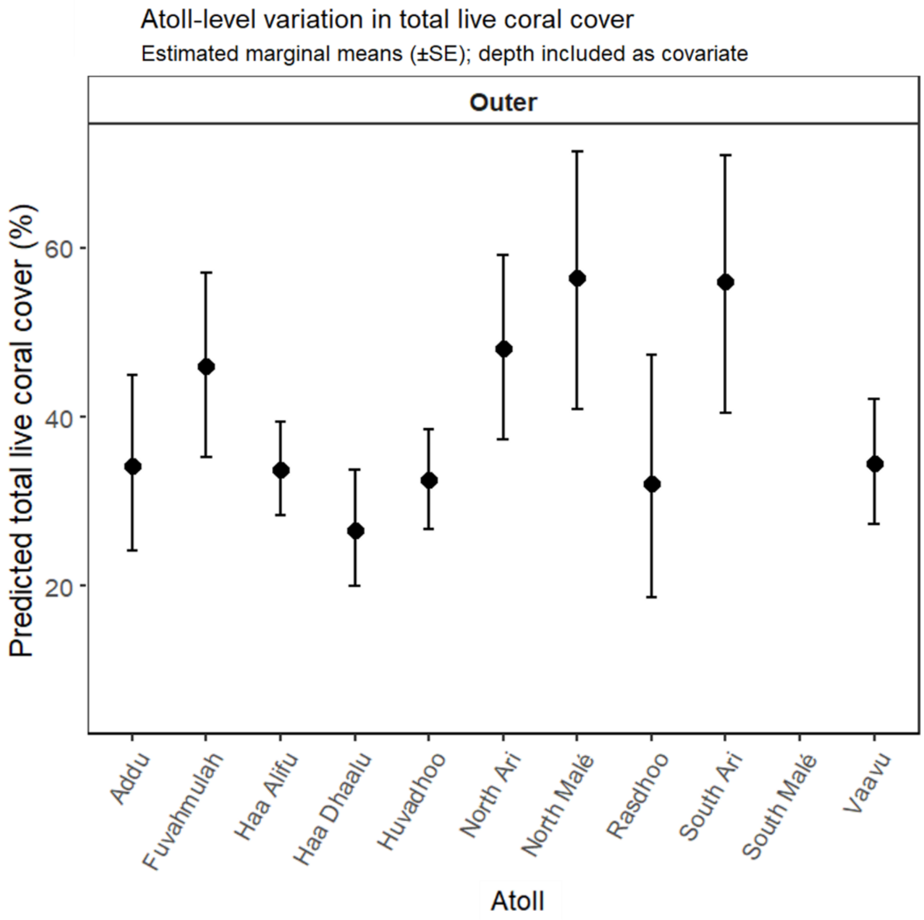


*Figure 49 Atoll-level variation in total live coral cover (%) in inner reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

The analysis of the fixed effects indicates that depth has a limited effect on the live coral cover component in outer reef. No significant differences were observed at 10 m compared to the reference depth (p = 0.479), whereas a significant decrease was detected at 20 m (Estimate = −0.042; p = 0.010), indicating lower values at greater depth. Regarding atoll effects, none of the atolls showed significant differences compared to the reference atoll (all p-values > 0.05), suggesting no significant spatial variation among atolls (Table 71).

*Table 71 Fixed effects estimate from the linear mixed-effects model evaluating the effects of depth and atoll on the live coral cover. The bold values indicate significance (p<0.005).*

**SUMMARY**

**Fixed effects:**

| Source | Estimate | Std. Error | df | t value | Pr(>\|t\|) |
|---|---|---|---|---|---|
| Atoll Fuvahmulah | 1.19E-01 | 1.50E-01 | 2.00E+01 | 0.792 | 0.4379 |
| Atoll Haa Alifu | 7.77E-03 | 1.21E-01 | 2.00E+01 | 0.064 | 0.9493 |
| Atoll Haa Dhaalu | -8.33E-02 | 1.30E-01 | 2.00E+01 | -0.640 | 0.5296 |
| Atoll Huvadhoo | -2.01E-02 | 1.23E-01 | 2.00E+01 | -0.163 | 0.8720 |
| Atoll North Ari | 1.45E-01 | 1.50E-01 | 2.00E+01 | 0.962 | 0.3474 |
| Atoll North Malé | 2.27E-01 | 1.84E-01 | 2.00E+01 | 1.231 | 0.2326 |
| Atoll Rasdhoo | -2.38E-02 | 1.84E-01 | 2.00E+01 | -0.129 | 0.8986 |
| Atoll South Ari | 2.18E-01 | 1.84E-01 | 2.00E+01 | 1.184 | 0.2501 |
| Atoll Vaavu | 5.58E-03 | 1.30E-01 | 2.00E+01 | 0.043 | 0.9662 |
| Depth 10m | -1.16E-02 | 1.64E-02 | 1.05E+03 | -0.708 | 0.4794 |
| Depth 20m | -4.22E-02 | 1.64E-02 | 1.05E+03 | -2.573 | **0.0102** |

On outer reefs, total live coral cover (including bleached colonies) did not differ significantly among atolls once depth and site-level variability were accounted for (p = 0.52). Coral cover showed a weak but significant decline with increasing depth (p = 0.03), while no additional effect of broad geographic area was detected. Site identity was included as a random effect to account for within-site replication (Table 72).

*Table 72 Table Type III ANOVA results for total live coral cover in outer reefs, showing significant effects of depth, but not atoll or area. Site was fitted as a random effect. The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | Sum Sq | Mean Sq | NumDF | DenDF | F value | Pr(>F) |
|---|---|---|---|---|---|---|
| Atoll | 0.40591 | 0.045101 | 9 | 20 | 0.9316 | **0.51976** |
| Depth | 0.34206 | 0.171031 | 2 | 1048 | 3.5326 | **0.02958** |
| Area | | | | | | |

A factorial ANOVA was performed to evaluate the effects of Atoll, Typology, and Depth on the response variable. While only Atoll showed a significant main effect (p = 0.039), significant interaction terms were detected between Atoll and Typology (p = 0.0035), Atoll and Depth (p < 0.001), and in the three-way interaction among Atoll, Typology, and Depth (p < 0.001), indicating that the effect of typology across depth gradients varies among atolls, thereby highlighting spatial heterogeneity in the observed patterns and preventing independent interpretation of lower-order effects (Table 73).

*Table 73 Factorial ANOVA results showing a significant effect of atoll and significant interactions among atoll, typology, and depth, including the three-way interaction, indicating that patterns vary across atolls. The bold values indicate significance ($p<0.005$).*

| **ANOVA** | | | |
|---|---|---|---|
| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
| Atoll | 19.0944 | 10 | **0.039079** |
| Typology | 1.3506 | 1 | 0.245172 |
| Depth | 0.4348 | 2 | 0.804600 |
| Area | | | |
| Atoll:Typology | 21.1562 | 7 | **0.003546** |
| Atoll:Depth | 201.6605 | 20 | **<0.001** |
| Typology:Depth | 3.0973 | 2 | 0.212534 |
| Atoll:Typology:Depth | 94.0692 | 14 | **<0.001** |

Figure 50 shows moderate variation in abiotic substrate cover among atolls in the inner sites, with some atolls displaying higher predicted values than others.

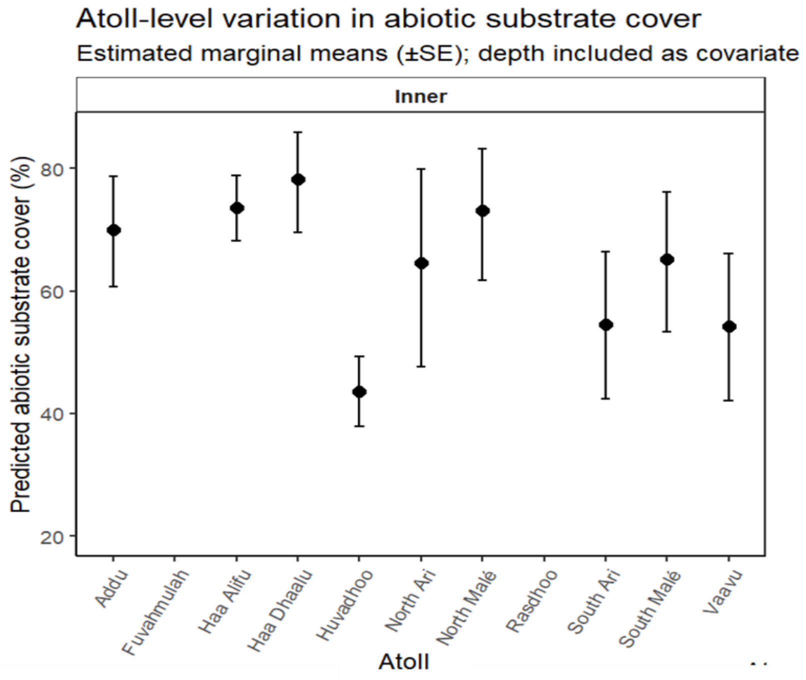


*Figure 50 Atoll-level variation in abiotic substrate cover (%) in inner reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

Depth significantly influences the abiotic component. In particular, a significant increase was observed at 20 m (Estimate = 0.141; $p < 0.001$), indicating higher values at greater depth. Regarding atoll effects, most atolls did not differ significantly from the reference atoll ($p > 0.05$). The only exception was Huvadhoo, which exhibited significantly lower values ($p = 0.0378$) (Table 74).

*Table 74 Fixed effects estimate from the linear mixed-effects model evaluating the effects of depth and atoll on the abiotic substrate component. The bold values indicate significance (p<0.005).*

**SUMMARY**

**Fixed effects:**

| Source | Estimate | Std. Error | df | t value | Pr(>\|t\|) |
|---|---|---|---|---|---|
| Atoll Haa Alifu | 0.04013 | 0.12508 | 23 | 0.321 | 0.7512 |
| Atoll Haa Dhaalu | 0.09406 | 0.15085 | 23 | 0.624 | 0.5391 |
| Atoll Huvadhoo | -0.27151 | 0.12317 | 23 | -2.204 | 0.0378 |
| Atoll North Ari | -0.05853 | 0.21333 | 23 | -0.274 | 0.7863 |
| Atoll North Malé | 0.03435 | 0.16866 | 23 | 0.204 | 0.8404 |
| Atoll South Ari | -0.16145 | 0.16866 | 23 | -0.957 | 0.3484 |
| Atoll South Malé | -0.05198 | 0.16866 | 23 | -0.308 | 0.7607 |
| Atoll Vaavu | -0.16393 | 0.16866 | 23 | -0.972 | 0.3412 |
| Depth 10m | 0.01746 | 0.01983 | 1118 | 0.880 | 0.3788 |
| Depth 20m | 0.14128 | 0.01983 | 1118 | 7.125 | **<0.001** |

On inner reefs, abiotic substrate cover (including dead corals, rubble, sand, and rock) increased significantly with depth (*p* < 0.001). Differences among atolls were weak and marginally non-significant (*p* = 0.063), while no additional effect of broad geographic area was detected. Site identity was included as a random effect to account for within-site replication (Table 75).

*Table 75 Table Type III ANOVA results for abiotic substrate component in inner reefs, showing significant effects of depth, but not atoll or area. Site was fitted as a random effect. The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | Sum Sq | Mean Sq | NumDF | DenDF | F value | Pr(>F) |
|---|---|---|---|---|---|---|
| Atoll | 1.35170 | 0.16897 | 9 | 23 | 2.2381 | 0.06251 |
| Depth | 4.55640 | 2.27818 | 2 | 1118 | 30.1761 | **<0.001** |
| Area | | | | | | |

Figure 51 shows a moderate variation in abiotic substrate cover among atolls; however, the differences between them do not appear particularly pronounced. However, the overlap of error bars suggests that differences among atolls are not strongly pronounced (Figure 51).

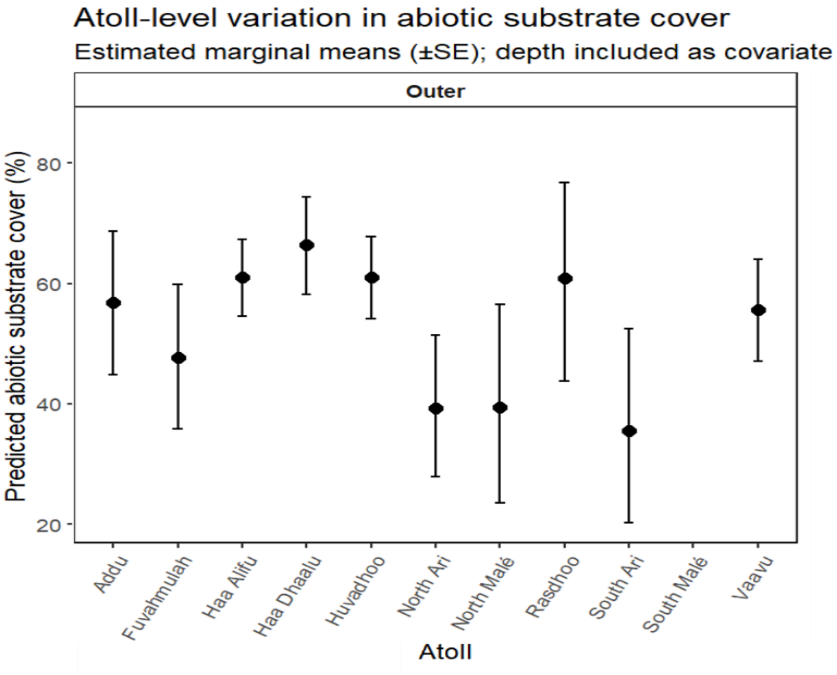


*Figure 51 Atoll-level variation in abiotic substrate cover (%) in outer reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

The analysis of the fixed effects indicates that depth does not significantly influence the abiotic component, as neither 10 m ($p = 0.593$) nor 20 m ($p = 0.177$) differ significantly from the reference depth, but it continues to increase with depth. Similarly, no significant differences were detected among atolls (all p-values > 0.05), suggesting limited spatial variation in the abiotic component across atolls (Table 76).

*Table 76 Fixed effects estimate from the linear mixed-effects model evaluating the effects of depth and atoll on the abiotic substrate component.*

**SUMMARY**

**Fixed effects:**

| **Source** | **Estimate** | **Std. Error** | **df** | **t value** | **Pr(>\|t\|)** |
|---|---|---|---|---|---|
| Atoll Fuvahmulah | -9.22E-02 | 1.56E-01 | 2.00E+01 | -0.592 | 0.561 |
| Atoll Haa Alifu | 4.20E-02 | 1.25E-01 | 2.00E+01 | 0.337 | 0.740 |
| Atoll Haa Dhaalu | 9.89E-02 | 1.35E-01 | 2.00E+01 | 0.733 | 0.472 |
| Atoll Huvadhoo | 4.24E-02 | 1.27E-01 | 2.00E+01 | 0.333 | 0.742 |
| Atoll North Ari | -1.77E-01 | 1.56E-01 | 2.00E+01 | -1.135 | 0.270 |
| Atoll North Malé | -1.76E-01 | 1.91E-01 | 2.00E+01 | -0.924 | 0.366 |
| Atoll Rasdhoo | 4.08E-02 | 1.91E-01 | 2.00E+01 | 0.214 | 0.833 |
| Atoll South Ari | -2.17E-01 | 1.91E-01 | 2.00E+01 | -1.137 | 0.269 |
| Atoll Vaavu | -1.25E-02 | 1.35E-01 | 2.00E+01 | -0.093 | 0.927 |
| Depth 10m | -8.46E-03 | 1.58E-02 | 1.05E+03 | -0.534 | 0.593 |
| Depth 20m | 2.14E-02 | 1.58E-02 | 1.05E+03 | 1.352 | 0.177 |

On outer reefs, abiotic substrate cover did not differ significantly among atolls (p = 0.46), nor did it vary with depth (p = 0.15). No additional effects of geographic area were detected. Site identity was included as a random effect to account for within-site replication (Table 77).

*Table 77 Table Type III ANOVA results for abiotic substrate component in outer reefs, showing effects of depth, atoll and area. Site was fitted as a random effect.*

| **ANOVA** | | | | | | |
|---|---|---|---|---|---|---|
| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
| Atoll | 0.41343 | 0.045936 | 9 | 20 | 1.0173 | 0.4593 |
| Depth | 0.17081 | 0.085407 | 2 | 1048 | 1.8914 | 0.1514 |
| Area | | | | | | |

The ANOVA shows a significant effect of atoll (p = 0.039), while typology (p = 0.245) and depth (p = 0.805) are not significant. However, the interaction between atoll and typology is highly significant (p = 0.0035), indicating that the effect of typology varies among atolls (Table 78).

*Table 78 Factorial ANOVA results showing a significant effect of Atoll and significant interactions among Atoll and Typology. The bold values indicate significance (p<0.005).*

| **ANOVA** | | | |
|---|---|---|---|
| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
| Atoll | 19.0944 | 10 | **0.039079** |
| Typology | 1.3506 | 1 | 0.245172 |
| Depth | 0.4348 | 2 | 0.804600 |
| Area | | | |
| Atoll:Typology | 21.1562 | 7 | **0.003546** |

Figure 52 shows the estimated marginal means of sensitive coral cover in the inner sites, highlighting marked variability among atolls. Some atolls display very low values, while others show considerably higher cover.

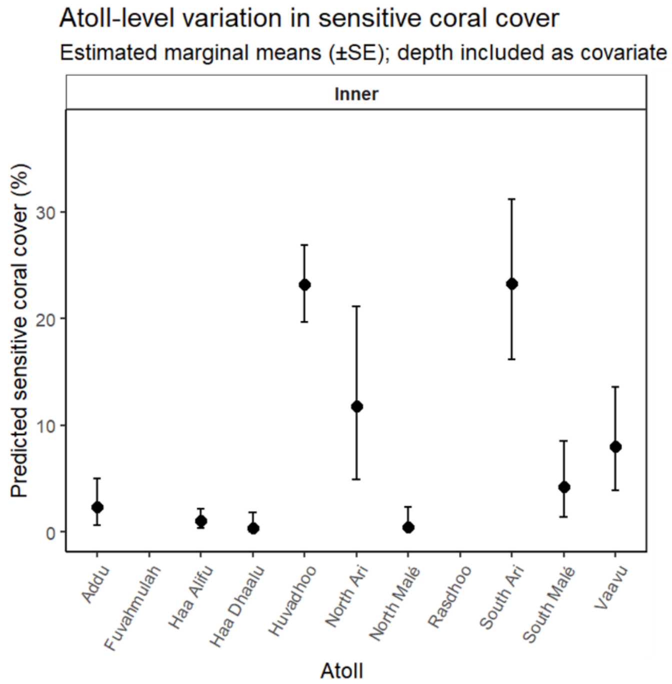


*Figure 52 Atoll-level variation in sensitive coral cover (%) in inner reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

The ANOVA results confirm this pattern: on inner reefs, sensitive coral groups (*Acropora* and *Pocillopora*) differed significantly among atolls (p < 0.001) and exhibited a strong depth-related decline (p < 0.001). This indicates that the distribution of sensitive corals varies significantly both among atolls and along the depth gradient (Table 79).

*Table 79 Table Type III ANOVA results for sensitive coral cover in inner reefs, showing effects of depth, atoll and area. Site was fitted as a random effect. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| Atoll | 2.2468 | 0.28085 | 8 | 23 | 6.8002 | **<0.001** |
| Depth | 5.5928 | 2.79638 | 2 | 1118 | 67.7083 | **<0.001** |
| Area | | | | | | |

Figure 53 illustrates the estimated marginal means of sensitive coral cover on outer reefs, showing clear differences among atolls. Some atolls exhibit relatively low predicted cover, whereas others display substantially higher values, indicating pronounced spatial variability.

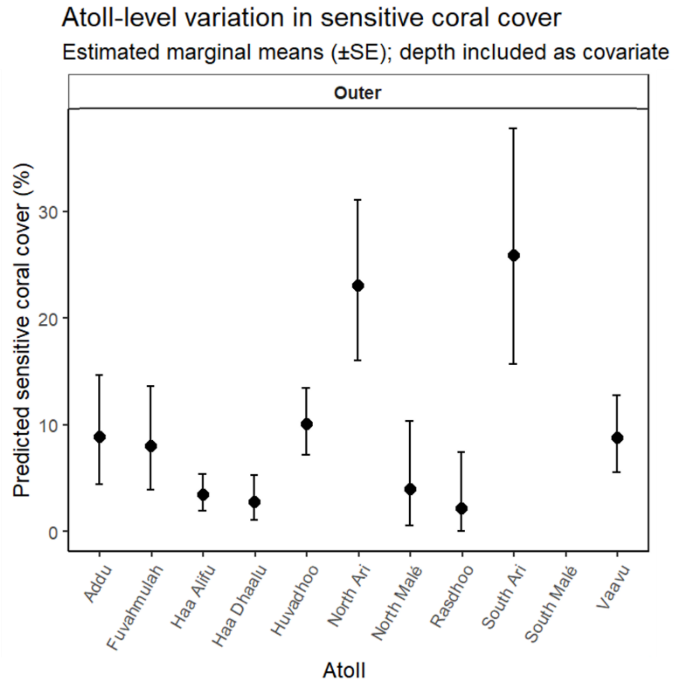


*Figure 53 Atoll-level variation in sensitive coral cover (%) in outer reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

The ANOVA reveals significant effects on outer reefs, with sensitive coral groups differing among atolls (p = 0.020) and showing a pronounced effect of depth (p < 0.001). These results indicate that sensitive coral cover varies significantly across atolls and is strongly influenced by the depth gradient (Table 80).

*Table 80 Table Type III ANOVA results for sensitive coral cover in outer reefs, showing effects of depth, atoll and area. Site was fitted as a random effect. The bold values indicate significance (p<0.005).*

**ANOVA**

| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| Atoll | 1.2957 | 0.1440 | 9 | 20 | 2.9697 | **0.02043** |
| Depth | 7.9532 | 3.9766 | 2 | 1048 | 82.0305 | **<0.001** |
| Area | | | | | | |

The ANOVA shows that the interaction between atoll and typology is not significant (p = 0.120), indicating that the influence of typology remains consistent across atolls (Table 81).

*Table 81 Factorial ANOVA results showing a significant effect of atoll, depth and interaction among atoll and typology. The bold values indicate significance (p<0.005).*

**ANOVA**

| Source | $\chi^2$ | Df | Pr(>$\chi^2$) |
|---|---|---|---|
| Atoll | 21.178 | 10 | **0.01989** |
| Typology | 0.787 | 1 | 0.37502 |
| Depth | 52.883 | 2 | **<0.001** |
| Area | | | |
| Atoll:Typology | 11.463 | 7 | 0.11965 |

Figure 54 presents the estimated marginal means of resistant coral cover across inner reefs, showing some variation among atolls. While certain atolls display lower predicted values and others higher ones, overall differences appear relatively modest.

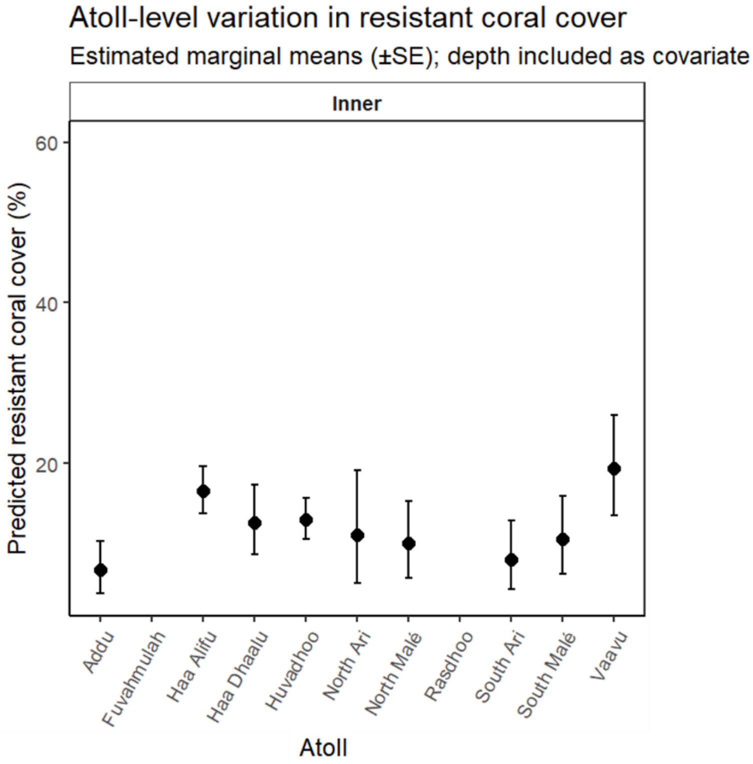


*Figure 54 Atoll-level variation in resistant coral cover (%) in inner reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

In contrast, resistant coral groups (Massive and Encrusting forms) did not show significant differences among atolls (p = 0.36) nor along the depth gradient (p = 0.62). These results indicate limited spatial and bathymetric structuring in resistant coral cover (Table 82).

*Table 82 Table Type III ANOVA results for resistant coral cover in outer reefs, showing effects of depth, atoll and area. Site was fitted as a random effect.*

**ANOVA**

| Source | Sum Sq | Mean Sq | NumDF | DenDF | F value | Pr(>F) |
|---|---|---|---|---|---|---|
| Atoll | 0.55911 | 0.069889 | 8 | 23 | 1.1599 | 0.3637 |
| Depth | 0.05672 | 0.028358 | 2 | 1118 | 0.4706 | 0.6247 |
| Area | | | | | | |

Figure 55 illustrates the estimated marginal means of resistant coral cover on outer reefs, highlighting variability among atolls. While some atolls show comparatively low predicted cover, others exhibit markedly higher values, suggesting a moderate degree of spatial variation.

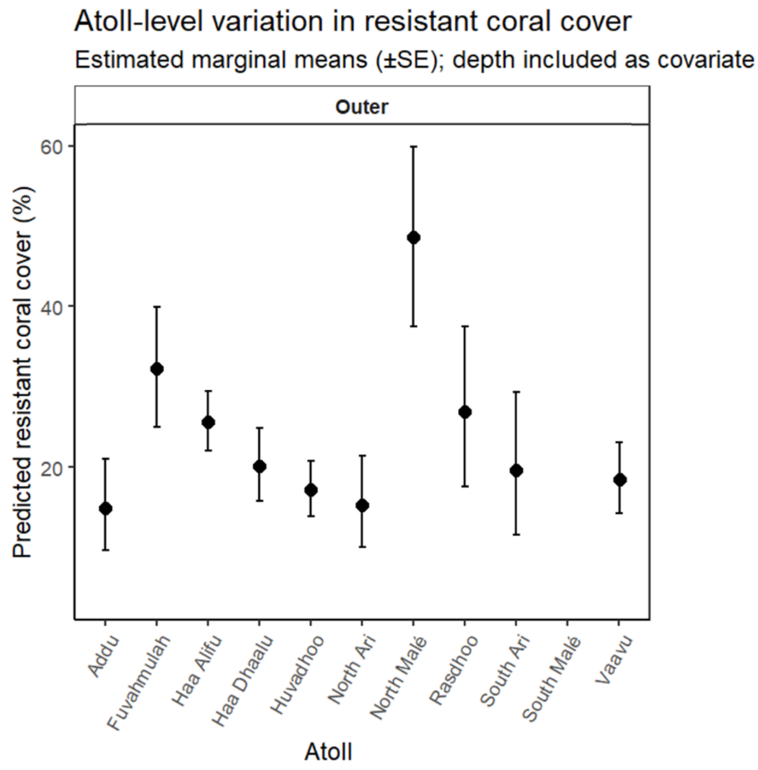


*Figure 55 Atoll-level variation in resistant coral cover (%) in outer reefs. Points represent model-predicted values, with error bars indicating ± standard error. Depth was included as a covariate in the model.*

The ANOVA showed that resistant coral groups (massive and encrusting forms) on outer reefs did not differ significantly among atolls ($p = 0.30$), but were strongly influenced by depth ($p < 0.001$) (Table 83).

*Table 83 Table Type III ANOVA results for resistant coral cover in outer reefs, showing effects of depth, atoll and area. Site was fitted as a random effect. The bold values indicate significance (p<0.005).*

| **ANOVA** | | | | | | |
|---|---|---|---|---|---|---|
| **Source** | **Sum Sq** | **Mean Sq** | **NumDF** | **DenDF** | **F value** | **Pr(>F)** |
| Atoll | 0.4256 | 0.04729 | 9 | 20 | 1.3013 | 0.2963 |
| Depth | 5.1868 | 2.59339 | 2 | 1048 | 71.3626 | **<0.001** |
| Area | | | | | | |

The ANOVA indicates that the interaction between atoll and typology is not significant (p = 0.070), suggesting that the effect of typology does not differ among atolls (Table 84).

*Table 84 Factorial ANOVA results showing a significant effect of atoll, depth and interaction among atoll and typology. The bold values indicate significance (p<0.005).*

| **ANOVA** | | | |
|---|---|---|---|
| **Source** | **$\chi^2$** | **Df** | **Pr(>$\chi^2$)** |
| Atoll | 68.6347 | 10 | **<0.001** |
| Typology | 1.6623 | 1 | 0.197299 |
| Depth | 241.4551 | 2 | **<0.001** |
| Area | | | |
| Atoll:Typology | 13.0792 | 7 | 0.070203 |

# 5 DISCUSSIONS

From a methodological perspective, *CoralNet* proved to be a reliable and scalable annotation platform for large benthic image datasets. The strong agreement observed between automated (*Coralnet*) and manual (*Photoquad*) classifications confirms previous validation studies demonstrating that deep learning–based approaches can achieve accuracy comparable to expert annotation while substantially reducing processing time (Beijbom *et al.,* 2015; Williams *et al.,* 2019; González-Rivero *et al.,* 2020). Although manual tools such as *PhotoQuad* allow more detailed control during annotation, *CoralNet* represents an effective balance between precision and analytical scalability, enabling consistent and reproducible high-throughput reef monitoring.

The benthic communities' composition results revealed a clear spatial structuring across the Maldivian archipelago, confirming that reef condition is not ecologically homogeneous. The regional differentiation is driven not only by taxonomic composition but also by changes in substrate configuration and structural complexity.
A latitudinal component appears to underpin part of this variability. McClanahan *et al.* (2014) documented a clear gradient across the Western Indian Ocean, with benthic richness and diversity increasing toward lower southern latitudes, a pattern that is partially reflected within the Maldivian archipelago. However, large-scale geographic gradients often interact with local environmental filtering processes, including hydrodynamic exposure and reef geomorphology, which can modulate community structure at smaller spatial scales (Huston, 1985; Mumby & Steneck, 2008). Therefore, spatial variability in the Maldives should be interpreted as the outcome of both regional positioning and local environmental drivers. The 2016 bleaching event further highlighted spatial heterogeneity. Although it affected the entire archipelago, recovery trajectories differed among regions (Germani *et al.,* 2025). In the central atolls, Pisapia *et al.* (2016) reported marked declines in branching corals following bleaching, with recovery dominated by slower-growing, stress-tolerant taxa. More recent assessments indicate a shift toward massive and encrusting forms despite partial coral cover recovery (Pisapia *et al.,* 2025). Such post-disturbance shifts toward stress-tolerant morphologies are consistent with broader Indo-Pacific observations of bleaching-driven community reassembly (Darling *et al.,* 2012). Recurrent thermal stress events are known to favour taxa with conservative life-history strategies, potentially reducing long-term structural complexity even when coral cover partially rebounds (Hughes

*et al.,* 2018). Although few data are available in the post 2016 bleaching event, Northern atolls are historically characterized by stronger hydrodynamic exposure, which may limit carbonate accretion and influence community structure. Persistent wave energy and water movement can act as environmental filters, favoring robust and low-profile coral morphologies while constraining the persistence of delicate branching forms (Gischler *et al.,* 2014; McClanahan & Muthiga, 2014; Ibrahim *et al.,* 2017). However, spatial patterns should be interpreted cautiously, as monitoring effort is uneven across the archipelago, with central atolls historically more intensively surveyed than northern ones. Overall, the southern Maldivian atolls exhibit variable post-bleaching trajectories. Earlier assessments reported high survival of massive corals and relatively rapid recovery after past disturbances (Zahir *et al.,* 2009). However, the 2016 event caused substantial declines in structurally complex taxa such as branching and tabular *Acropora*, whereas stress-tolerant genera such as *Porites* proved more resistant (Ibrahim *et al.,* 2017). Intense hydrodynamic exposure and steep reef morphology further influence benthic structure, often favouring rubble-dominated substrates and reducing three-dimensional complexity (Perry & Alvarez-Filip, 2019). These dynamics illustrate how disturbance legacy and physical setting interact to shape present-day community patterns. Spatial variability is not solely driven by latitudinal gradients but is strongly structured by depth and reef typology. Depth represents the main structuring factor of benthic variability across the Maldivian reefs. Along the depth gradient, a marked shift was observed from coral-dominated assemblages in shallow waters to increasingly abiotic-dominated substrates at greater depths. This transition was particularly evident in northern atolls, where coral cover declined more sharply with increasing depth. Similar depth-related structuring of benthic assemblages has been widely documented in Indo-Pacific reef systems, where light attenuation and hydrodynamic gradients strongly regulate coral dominance and substrate composition (Laverick *et al.,* 2020). Vertical gradients can influence thermal variability and sediment dynamics, further contributing to compositional differentiation.

Reef typology further shaped community patterns. Inner reefs exhibited higher compositional heterogeneity, whereas outer reefs appeared more homogeneous, likely reflecting their continuous exposure to oceanic hydrodynamics. Persistent hydrodynamic forcing can promote environmental filtering, leading to more uniform assemblages dominated by stress-tolerant morphologies (McClanahan & Muthiga, 2014; Montefalcone *et al.,* 2020). In terms of functional composition, outer reefs were generally dominated by massive and encrusting corals, although central atolls, particularly South Ari, showed notable abundances of tabulate *Acropora*. Conversely, inner reefs, especially in the southern region, supported greater structural diversity, with a stronger representation of branching forms. Northern reefs were comparatively less heterogeneous and more characterized by stress-tolerant coral morphologies, suggesting that repeated disturbance and physical forcing may have reinforced compositional filtering over time. Mean live hard coral cover across the archipelago ranged approximately between 30% and 40%, with slightly higher values observed on outer reefs compared to inner systems. These values exceed the national average reported immediately after the 2016 bleaching event (approximately 19–20%), indicating a substantial recovery in coral cover in the years following the disturbance. However, increases in coral cover do not necessarily imply full ecosystem recovery (Dryden *et al.,* 2020). Shifts toward stress-tolerant taxa may indicate long-term changes in structural complexity and carbonate production capacity (Perry & Alvarez-Filip, 2019). Functional reassembly rather than full restoration may therefore characterize post-bleaching reef trajectories (Zampa *et al.,* 2023).

The functional indices adopted in this study move beyond a purely taxonomic description of community composition and allow reef condition to be interpreted in structural and geomorphological terms.

The CAPI (Coral–Algae Predominance Index) reveals a vertical reorganization of benthic communities, where coral dominance in shallow habitats progressively gives way to greater macroalgal presence at depth, indicating a strong environmental control on community structure. Within this framework, live coral cover represents the current biological contribution to carbonate production and reef framework accretion, whereas increased macroalgal abundance is widely interpreted as a signal of potential transitions toward alternative benthic states under declining coral dominance. (Hughes *et al.,* 2007). Increased macroalgal cover is often associated with reduced herbivory or chronic disturbance and may inhibit coral recruitment, thereby influencing long-term recovery trajectories (Graham *et al.,* 2015).

The BAI (Biotic–Abiotic Index) reveals a gradual increase in abiotic substrates, such as coral rubble and sand, along the bathymetric gradient. This trend is especially evident in the inner reefs of the northern atolls, where the predominance of unconsolidated material suggests diminished framework stability and potential functional weakening.

The RCI (Reef Consolidation Index) serves as a proxy for substrate consolidation, capturing the balance between carbonate production and framework erosion and, consequently, the long-term stability of the reef structure. Lower values observed at greater depths within inner reef environments suggest reduced consolidation, while outer reefs display comparatively higher structural integrity. Because reef persistence relies on accretion consistently outpacing erosion, recurrent disturbances can disrupt this equilibrium, potentially driving systems toward net erosional states (Perry *et al.,* 2013). The three indices reveal a coherent, spatially structured reef state across the Maldives. Northern inner reefs and southern outer reefs are characterized by lower substrate consolidation and a higher abiotic component, with increased coral rubble at depth and reduced coral cover in shallow zones. In contrast, central outer reefs and southern inner reefs appear more biologically stable, showing more consolidated substrates and higher live coral cover. These patterns highlight the combined influence of cross-shelf (inner-outer) gradients and latitudinal variation in shaping reef condition. A better understanding of current movements and oceanographic dynamics would help clarify the mechanisms underlying these patterns.

Consistent with previous research in the Maldives, reefs adjacent to resort islands generally exhibit higher coral cover than those near inhabited islands (Moritz *et al.,* 2017). However, the present results indicate that this contrast is not purely quantitative. Rather than representing a simple increase in overall coral abundance, the difference reflects shifts in life-history composition and functional structure, pointing to a subtle but significant management-related effect on benthic assemblages. The “resort effect” identified by Moritz *et al.* (2017) in North Ari Atoll was attributed to reduced fishing pressure and localized management practices. The current findings support this interpretation, suggesting that the observed pattern is driven primarily by lower levels of chronic local stress rather than by active ecological enhancement. In contrast, reefs exposed to coastal modification and sediment inputs, typically found in inhabited islands, show increased abiotic cover and signs of structural degradation (Nepote *et al.,* 2016). These reefs are subject to sustained anthropogenic disturbance and are therefore more frequently dominated by stress-tolerant massive and encrusting taxa, consistent with disturbance-driven environmental filtering processes documented in the Maldives (Nepote *et al.,* 2016).

Importantly, these findings do not imply that resorts inherently improve reef ecosystems or that tourism functions as a conservation tool. Instead, they indicate that reduced chronic stress allows disturbance-sensitive taxa to persist. This management-related effect interacts strongly with reef typology and depth, both of which structure coral and abiotic distribution patterns. Sensitive taxa are more abundant on outer reefs of resort and uninhabited islands, likely reflecting lower anthropogenic pressure combined with enhanced hydrodynamic flushing. Branching genera such as *Acropora* and *Pocillopora* dominate shallow waters and decline with depth on outer reefs, whereas inner reefs exhibit a more gradual compositional shift along the depth gradient. Massive corals display higher cover on outer reefs, consistent with greater substrate stability and exposure-mediated filtering. The abiotic component increases with depth and reaches its highest levels near inhabited islands, where live coral cover, both sensitive and resistant, is markedly reduced. In contrast, macroalgae show no consistent management-related pattern, suggesting that algal dynamics are primarily governed by local environmental conditions rather than by management status alone.

After identifying a clear latitudinal differentiation in benthic community structure, a finer-scale analysis at the atoll level revealed that spatial variability is more strongly structured by atoll identity than by broad regional grouping. This hierarchical organization is consistent with previous evidence indicating that coral reef systems exhibit pronounced spatial heterogeneity operating across relatively small ecological scales (Levin, 1992). From a management perspective, these findings suggest that conservation strategies should not be uniformly applied across extensive geographic sectors, such as the entire northern Maldives. Instead, the marked heterogeneity observed among atolls highlights the value of local-scale prioritization. Spatially explicit conservation frameworks emphasize the identification and protection of reef areas that function as resilient hotspots or maintain relatively high coral cover and structural complexity (Mumby & Steneck, 2008; Game *et al.,* 2009). Within this context, specific islands or reef sectors, where disturbance-sensitive taxa persist or coral cover remains comparatively elevated, may represent more effective conservation targets than broad regional designations. Although mean live coral cover declined consistently with increasing depth, variability among atolls indicates that local environmental conditions and disturbance histories strongly modulate these depth-related trends. This supports the view that reef resilience is unevenly distributed, reinforcing the need to prioritize locally robust reef sectors capable of sustaining recovery processes (Graham *et al.,* 2013; Hughes *et al.,* 2018).

# 6 CONCLUSIONS

By combining methodological comparison with ecological analysis, this thesis aimed to clarify how reef condition and resilience are structured across the Maldivian archipelago. From an analytical standpoint, the validation of *CoralNet* alongside traditional *PhotoQuad* analysis shows that scalable automated approaches can reliably support regional reef assessments. Beyond representing a technical improvement, the capacity to standardize and expand monitoring is essential for adaptive, evidence-based management in the context of accelerating climate change. Ecologically, the outcomes of this thesis challenge simplified views of Maldivian reefs as uniformly degraded or resilient. Instead, the archipelago emerges as a spatially structured system where ecological conditions and recovery vary across environmental and geographic gradients, and where resilience operates as a process contingent upon the interaction between climate-driven disturbances and local pressures. In this framework, coral cover alone proves to be an incomplete indicator of ecosystem condition, as reef persistence depends on maintaining structural consolidation and a balance between carbonate accretion and erosion. Some coral assemblages retain framework integrity despite moderate coral cover, whereas others with comparable levels exhibit reduced structural stability. This distinction is critical, as three-dimensional complexity underpins biodiversity support, habitat provision, and coastal protection. The uneven distribution of ecosystem conditions across atolls further indicates that repeated bleaching events do not operate in isolation. Their effects are mediated by local environmental settings and anthropogenic pressures. Coral communities exposed to lower chronic disturbance appear better positioned to sustain recovery, while those subjected to cumulative stress display greater ecological instability. In this perspective, resilience should be understood as dynamic and conditional rather than inherent or guaranteed. Although recent recovery trajectories suggest a capacity for partial ecological reorganization, the progressively shortening intervals between thermal anomalies raise serious concerns. If recovery windows continue to shorten, even structurally robust carbonate frameworks may experience declining accretion potential and long-term geomorphological weakening.

Ultimately, safeguarding Maldivian coral ecosystems requires moving beyond single-metric evaluations toward spatially explicit, function-based approaches. Prioritizing reef sectors that retain structural integrity and recovery capacity is essential. In a rapidly warming ocean, the persistence of these systems will depend on recognizing that resilience is spatially uneven and increasingly fragile.

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