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Ancient coastal forests reborn as modern marine blue carbon ecosystems

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Abstract

Sea-level rise and coastal erosion can submerge terrestrial carbon-rich landscapes, yet the ecological fate and climate significance of such blue-carbon deposits remain largely unknown. We report the discovery of submerged peat reefs in the shallow coastal waters of the Bazaruto Archipelago, Mozambique, relict of ancient coastal forests now transformed into benthic marine habitats. Radiocarbon (^{14}C) dating reveals ages spanning ~300 to ~5000 years BP, indicating mid- to late-Holocene origins as coastal peat swamps subsequently submerged by rising seas. The peat contains up to 40% organic carbon by weight, representing a substantial blue-carbon stock, and $\delta^{13}C$ values around -27‰ confirm a predominantly terrestrial plant origin for this carbon. Peat reefs are shallower and exhibit greater variability in temperature, salinity, oxygen, pH□□□□□, light, and tidal exposure than adjacent hard coral reefs, influencing biological structure and habitat function. Biodiversity surveys across multiple scales (benthic quadrats, invertebrate, small fish, and megafauna transects) show that these peat reefs support a rich and distinctive assemblage of marine life, significantly different from nearby hard coral reefs. The peat substrate is colonized by diverse sessile and mobile invertebrates providing structural complexity for fish communities and as nursery habitat, with richness comparable to nearby hard coral reefs. Importantly, overlapping communities highlight ecological connectivity across reef types (41 and 44 small fish/megafauna species shared), even as habitat composition differs markedly: unlike adjacent hard coral reefs dominated by reef-building corals, peat reefs host no living corals and are instead characterized by seagrass patches, macroalgae, sponges, and detritus-based food webs. Our findings illustrate how ancient terrestrial ecosystems can persist and support contemporary ecological functions, and the ecological reinvention of Earth's landscapes under shifting sea levels. This underscores how substrate-driven ecosystem baselines shape biodiversity, calling for the inclusion of such relict ecosystems in emerging conservation frameworks and blue-carbon strategies.

Introduction

Coastal blue-carbon ecosystems, such as mangrove forests, seagrass meadows, and salt marshes, play a critical role in long-term carbon sequestration (1). These vegetated habitats, alongside coastal forests and sand dunes vegetation, accumulate thick organic soils and peat deposits that lock away vast stores of carbon over millennia (2). However, much less attention has been paid to what happens when such carbon-rich peat deposits become submerged and transformed into marine habitat as sea levels change. Peat reefs are an emerging example of this habitat transition, wherein relict peat from ancient coastal wetlands and forests now forms solid substrate in the marine environment (3). Globally, peat reefs remain largely undocumented and understudied despite their potential significance as blue-carbon reservoirs and biodiversity hotspots (4). Only a handful of cases have been noted in the literature (5, 6, 7), and there is little information on the extent or ecology of these subtidal peat habitats. This paucity of research leaves a clear gap in our understanding of peat reefs as a distinct class of blue-carbon ecosystem.

In this context, the Bazaruto Archipelago (Mozambique), in the Western Indian Ocean (WIO) region, provides an opportunity to study marine peat reefs for the first time in a tropical setting. To our knowledge, this archipelago and adjacent shoreline host the first case study targeting the ecology and ecosystem function of a peat reef system (Figure 1). Bazaruto is renowned for its diverse marine habitats, including coral reefs, mangroves, mudflats, sand dunes, and seagrass beds, which collectively support a rich assemblage of marine life (8). Within this mosaic, we identified a variety of peat reef formations (Figure 1, 2), representing a previously unrecognized component of the blue-carbon ecosystem seascape. Investigating these peat reefs offers a novel window into how buried terrestrial carbon deposits can be “recycled” into functional marine ecosystems.

Marine peat reefs are products of long-term coastal change and erosion (5). During periods of sea-level rise and shoreline advance, former terrestrial peatlands can become submerged, and once wave action removes overlying sediments, ancient peat layers are exposed as semi-hard substrate on the seafloor. Notably, post-glacial marine transgressions flooded vast coastal peatlands, leaving behind relict “submerged forests” (Figure 1, 2), peat deposits and tree stumps now visible in the intertidal or subtidal zone (9). What was once waterlogged soil in a coastal swamp can thus be transformed into a reef-like platform in the ocean. This phenomenon exemplifies Earth’s capacity to reconfigure ecosystems through habitat transitions, turning buried terrestrial substrates into novel marine habitats over geological time. The preserved peat in these formations remains highly organic (10), reflecting its origin as a terrestrial carbon sink, yet it now exists in an entirely marine context.

Once established underwater, peat reefs effectively serve as new foundations for marine life, much like traditional rock or coral reefs (11). Their irregular surfaces and crevices provide attachment sites and shelter for diverse benthic organisms (6). Field observations in temperate systems have documented submerged peat reefs being rapidly colonized by seaweed, bivalves, and reef-associated invertebrates (5, 6). For instance, blocks of salt-marsh peat in Cape Cod estuaries were found to host abundant algal mats and harbored juvenile American lobsters at densities comparable to those of typical cobble nursery grounds (6). These peat outcrops may also support mussels, shrimps, and other crustaceans that use the peat structure for feeding, breeding, and refuge. By introducing relatively hard and structurally complex substrate where only soft sediment (e.g., sand and mud) existed before, peat reefs expand the available habitat for benthic communities and fishes, potentially bolstering local biodiversity and fisheries productivity.

In tropical settings such as the Bazaruto Archipelago seascape, the ecological role of peat reefs may extend to larger fauna. Complex reef structures attract and support elasmobranchs, fish, and reptiles by providing foraging grounds, shelter, and nursery areas (12, 13). The archipelago’s existing coral and rocky reefs, for example, are critical for sustaining fish populations and for providing refuge to endangered species like marine turtles, reef sharks, and dugongs that frequent these habitats (8). By analogy, the newly discovered peat reefs likely offer comparable ecosystem services, functioning as underwater “oases” for marine life in a similar manner (14). In augmenting the seascape’s structural complexity, peat

reefs may also enhance trophic connectivity among adjacent habitats (mangroves, seagrasses, sand banks and coral reefs), creating additional linkages in coastal food webs (15).

Here, we present the first quantitative ecological assessment of such tropical peat reefs, comparing their benthic structure, invertebrate and fish communities, and megafauna presence with adjacent coral reef systems in the Bazaruto Archipelago (Figure 1). We further characterize their physicochemical regimes, sediment composition/age, and exposure patterns to evaluate their functional position in the coastal ecosystem mosaic. These peat reefs are not static remnants, but dynamic-transient platforms undergoing episodic exposure and burial under the influence of seasonal swells, tropical cyclones, and tidal extremes. Our findings suggest that these habitats, once considered relicts, are instead active participants in ecosystem restructuring under sea-level rise (8, 16), offering new transient substrate for colonization, foraging, and nursery use by both pelagic and benthic species, including juvenile sharks, turtles, and reef-associated fish. Over time, such peat formations may become increasingly relevant as the coastline erodes and unveils previously buried terrestrial carbon reservoirs (14). We argue that this process constitutes a form of ecosystem “rebirth,” whereby Earth’s capacity for ecological recycling is realized through the “reactivation” of submerged blue-carbon substrates. By bridging terrestrial peat formation processes with marine ecological function, this study contributes a novel perspective on habitat transitions in a warming and rising ocean. Furthermore, it emphasizes the importance of recognizing and protecting unconventional blue-carbon ecosystems that contribute meaningfully to biodiversity, carbon storage, and trophic connectivity across the land-sea interface.

Results

Geospatial and geomorphological context of tropical peat reef formations

The distribution of shallow peat reef structures along the coastline of the Bazaruto Archipelago, Mozambique, with transient field-verified peat reefs and satellite-identified peat structures (Fig. 1), reveal a mosaic-like irregular pattern. Peat reefs were observed both in intertidal and subtidal zones, occurring as patchy, elongated formations along sandy stretches of the coast (Fig. 2). The conceptual reconstruction suggests a Holocene trajectory of landscape transformation, where initial coastal forest/vegetation zones and sediment-rich plains transitioned into peat-forming environments due to shoreline recession and sea-level rise (8, 16). The schematic model (Fig. 1C) outlines a three-phase evolution: (1) sediment and dune formation (~ 10,000 years BP), (2) mid-Holocene forest submergence and peat accumulation (~ 5,000 years BP), and (3) modern exposure and reworking of peat layers into structurally complex, carbon-rich reef habitats. These formations now serve as novel benthic substrates, potentially extending blue-carbon functionality from landward systems into the marine domain.

Coral reef sites exhibit high structural complexity typical of fringing reefs, with diverse hard coral assemblages and reef-associated fauna (Fig. 2). In contrast, the surveyed peat reefs reveal a heterogeneous mix of exposed peat substrata, carbonate-free rocky patches, macroalgae, seagrasses,

and benthic invertebrate cover. Underwater quadrat images and satellite overlays highlight the physical contrast between reef types, with peat reefs lacking live hard coral but supporting dense biological growth in crevices and surface irregularities. Satellite imagery confirms the presence of unsurveyed peat reef formations across additional coastal segments (Fig. 2), reinforcing the broader distribution and ecological relevance of these features in the Bazaruto Archipelago.

Seawater time-series data

Short-term environmental variability differed markedly between hard coral and peat reef sites. At the coral reef (Fig. 3A), 15-minute interval measurements over a 5-day deployment showed relatively stable seawater temperatures ranging between 26.8–27.6°C, with moderate diel variability. Light intensity displayed a cyclical pattern consistent with daylight cycles, peaking near 6,000 lux. In contrast, the peat reefs (Fig. 3B) showed broader fluctuations in temperature and light intensity over a 15-day deployment. Temperature profiles at 1-minute intervals across peat reefs revealed more dynamic thermal regimes, with daily oscillations spanning 24.5–28.6°C. Light intensity reached values exceeding 40,000 lux in the most exposed sites, likely reflecting shallower depths (2–4 m) and greater exposure to incident light in peat reef areas relative to the deeper coral reef site (12–22 m).

Discrete physicochemical measurements

Seabed measurements collected across all sites revealed differences in physicochemical conditions between hard coral and peat reefs (Fig. 3). The coral reef site showed relatively uniform profiles, with salinity around 35.3 psu, temperatures averaging 27.0°C, pHtotal values between 7.95–8.10, and dissolved oxygen (DO) ranging from 5.4–5.8 mg L^{-1}. In peat reef environments, salinity values remained variable (35-35.8 psu), while temperatures also fluctuated substantially (26.8–30.2 ºC). pHtotal values were generally consistent (7.9-8.0), though slightly more variable than in coral sites. DO levels in peat reefs showed greater fluctuations (6–8 mg L^{-1}), potentially linked to tidal exposure and organic matter decomposition dynamics.

Geochemical and stable isotope signatures

Surface and core sediment samples from the peat reefs displayed distinct geochemical profiles (Fig. 3B). Nitrogen (N) and carbon (C) content were very high in peat reef sediments, with C values reaching ~ 2.5% and N values around 0.3–0.4%, suggesting organic-rich substrates. Stable isotope ratios of $\delta^{13}C$ were negative in peat reefs (-21‰ to -26‰), consistent with terrestrial C_3 plant origin, while $\delta^{15}N$ values ranged from 0.5‰ to 2.5‰, suggesting minimal marine nitrogen input and a legacy of organic matter from coastal vegetation.

Habitat/substrate composition

Benthic quadrat surveys revealed clear compositional differences between coral and peat reef habitats. Individual quadrats (*n* = 134) showed high live coral cover (primarily Poritidae, Acroporidae, and Pocilloporidae) in coral reef sites, while peat reefs were dominated by macroalgae, seagrasses, and exposed peat substrate (Fig. 4A). Stacked barplots highlighted the uniformity of benthic composition within reef types and the heterogeneity between them. Mean cover data aggregated by site (Fig. 4B) confirmed that coral reefs had significantly higher live coral cover (~60–70%), while peat reefs showed greater abundance of macroalgae (~25–30%), seagrass (~20%), and structurally distinct substrates such as exposed peat, dead shells, and carbonate-free structures. Live hard or soft coral was totally absent in peat sites (0%). Heatmap visualization (Fig. 4C) emphasized dominant habitat-forming elements by reef type. Coral reefs exhibited strong live coral dominance (up to 41.1%), whereas peat reefs showed high mean cover of macroalgae (up to 27.6%), seagrass (20.2%), and peat substrate (29.4%). Cluster analysis based on Bray-Curtis distances grouped quadrats strongly by habitat (Fig. 4A), indicating consistent within-habitat similarity and between-habitat dissimilarity. Principal Coordinates Analysis (PCoA; Bray-Curtis distance) revealed distinct separation between coral and peat reef benthic assemblages (Figure S2). ANOSIM confirmed this separation (R = 0.531, $p = 0.001$), and PERMANOVA showed that ~30.6% of the variation in benthic composition was explained by habitat type ($R^2 = 0.306$, $p = 0.001$). SIMPER analysis identified the benthic categories contributing most to dissimilarity: exposed peat substrate, macroalgae, and seagrass were dominant in peat reefs, while live coral categories (Merulinidae, Poritidae, Acroporidae) accounted for most of the coral reef structure (Figure S3).

Invertebrate community structure

Invertebrate counts revealed strong differences in abundance and taxonomic composition between habitats (Fig. 5A). Peat reefs supported higher total invertebrate counts compared to the coral reef. Coral reef surveys recorded 28 species, while individual peat reefs hosted 12–14 species each. Diversity indices (Shannon H' and dominance index d) indicated more even assemblages at the coral reef ($H' = 1.88$, $d = 0.58$) compared to the peat reefs ($H' = 0.82–1.31$, $d = 0.61–0.79$), where dominance was higher. Stacked barplots showed that coral reef assemblages were more taxonomically balanced, while peat reefs were dominated by echinoderms, bivalves, and barnacle-like crustaceans. Peat reefs lacked cnidarians and sponges, and coral reef-specific taxa (e.g., demosponges, ascidiaceans) were not recorded at peat sites. Heatmaps of species and family proportions (Fig. 5B) confirmed distinct community profiles. Coral reefs hosted multiple unique families not observed in peat reefs, while peat reefs were dominated by fewer, more abundant taxa. Venn diagrams showed no species overlap between habitats; only 5 of 13 total families were shared. SIMPER analysis showed that unidentified oyster and barnacle species, along with *Biemna humilis* and *Clavelina* spp., contributed most to community differences (Figure S3). These were especially dominant in peat reefs. Dendrograms based on Bray-Curtis dissimilarity revealed clear separation by habitat at both species and family levels (Fig. 5C). PCoA plots showed moderate group separation, (Figure S2) supported by ANOSIM results: R = 0.124 ($p = 0.013$) at species level and R = 0.144 ($p = 0.022$) at family level. PERMANOVA indicated that

reef type explained 52.6% of species-level and 55.5% of family-level variation in assemblage structure ($p < 0.05$ in both cases).

Small fish community structure

Coral reefs supported markedly higher small fish (fish < 20 cm total length) abundance than peat reefs (Fig. 6A), especially in the < 5 cm and 5–10 cm size classes. Coral sites had 54 recorded species (H' = 2.35), with moderate dominance (d = 0.45). Peat reef diversity was slightly higher (26–36 species; H' = 2.80–3.21), but individual abundance was lower, and communities were taxonomically skewed toward a few dominant families. Family-level composition differed between habitats (Fig. 6A). Coral reefs were dominated by Pomacentridae, Labridae, and Chaetodontidae, while peat reefs hosted higher proportions of Nemipteridae, Lethrinidae, and Sciaenidae. Venn diagrams (Fig. 6B) showed broad taxonomic overlap: 41 species and 18 families were shared, with peat reefs hosting 18 exclusive species compared to 14 species in coral reefs. Heatmaps showed that key differences in relative abundance were linked to specific families, such as higher Pomacentridae dominance in coral reefs and a broader spread of families in peat reef systems (Fig. 6B). Hierarchical clustering grouped coral reef surveys distinctly from peat reef surveys (Fig. 6C), but overlap was more pronounced than in invertebrates or benthic cover. SIMPER analysis identified *Ostorhynchus apogonides* and *Pempheris schwenkii* as key contributors to coral-peat dissimilarity (Figure S3). These two species alone accounted for over 60% of the Bray-Curtis distance. Multivariate tests showed moderate but non-significant separation between habitats. PCoA results suggested weak clustering by reef type. ANOSIM returned R = 0.50 for both species and family level comparisons ($p > 0.25$), and PERMANOVA showed low explanatory power (R^2 = 0.126–0.450, $p > 0.25$).

Megafauna community structure

Megafauna (animals > 20 cm total length) counts were highest at the coral reef reference site, with considerably lower total observations across all peat reef sites (Fig. 7A). Coral reef surveys recorded 25 species, while peat reef sites recorded 6–11 species each. Shannon diversity was highest in the coral reef (H' = 2.00) and progressively lower across peat reefs (H' = 1.42–1.77), while dominance indices (Berger-Parker d) were elevated in the peat reefs, reflecting strong contributions from a few abundant taxa. Community composition showed clear shifts between reef types. Heatmaps revealed higher species richness and greater evenness at the coral reef site, with *Lutjanus kasmira* dominating the peat reef assemblages (Fig. 7B). Venn diagrams showed no exclusive coral species or families, and a high degree of overlap (44 shared species; 23 shared families), suggesting broad-scale ecological connectivity. Hierarchical clustering (Bray-Curtis dissimilarity) indicated distinct site groupings by reef type, with coral reef samples forming a separate cluster from peat reef sites (Fig. 7C). However, results from PERMANOVA and ANOSIM were not statistically significant ($p > 0.05$), despite high R values (R = 1.000), suggesting that the observed separation may reflect limited sampling or within-group variability

rather than consistent structural divergence. SIMPER analysis identified key discriminating species, with *L. kasmira* and *Scaridae spp.* contributing the most to dissimilarity.

Discussion

Functional habitat differentiation

Our comparative analyses demonstrate clear structural and functional differences between local coral reefs and the newly described tropical peat reef habitats. Benthic quadrat surveys confirmed that the coral reef surveyed in the Bazaruto Archipelago is dominated by scleractinian coral framework (high live hard coral cover; 8, 17), whereas peat reefs consist of a peat-macroalgae-seagrass matrix with markedly lower/absent live hard coral cover. In peat reef plots, fleshy macroalgae (e.g. *Sargassum*, *Ulva*) and seagrass (e.g. *Halodule*, *Thalassia*) were significantly more diverse and abundant than on coral reefs (absent), which were instead characterized by calcifying organisms (hard corals, crustose coralline algae) and lower macroalgal biomass. This sharp contrast in benthic composition indicates distinct foundational structures: coral reefs are built by biogenic calcium carbonate, while peat reefs provide a transient substrate derived from ancient coastal peat deposits (14). The different physical structures likely drive differences in resource availability and microhabitats, resulting in divergent community assemblages between the two habitat types.

Invertebrate communities showed the most pronounced differentiation between coral and peat reef habitats. Benthic invertebrates (such as echinoderms, crustaceans, and mollusks) exhibited statistically significant differences in abundance and composition linked to habitat type. Multivariate analyses support this: PERMANOVA and ANOSIM tests on invertebrate assemblages revealed a significant habitat effect ($p < 0.01$), and a PCoA ordination showed distinct clustering of coral-reef versus peat-reef invertebrate samples. For example, corals and their obligate associates (e.g. certain coral-dwelling decapods and obligate corallivorous gastropods) were far more prevalent on hard coral reefs, whereas peat reefs supported more detritivores and algal grazers adapted to the rich organic and algal substrata (18). These findings suggest that sessile and site-attached organisms respond strongly to the underlying habitat structure and benthic flora. By contrast, the assemblages of small reef fish and mobile megafauna were more variable between the two habitats, with no clear-cut separation in multivariate space (PERMANOVA $p > 0.05$). Small fish surveys indicated broadly overlapping species pools, and large motile fauna (e.g. sharks, rays, turtles) were observed using both habitat types. The weaker differentiation in these groups reflects their mobility and opportunistic foraging behavior, many fish and megafauna range across habitat patches in search of food or shelter, reducing community dissimilarity between coral and peat reefs (19, 20). Our results indicate strong functional habitat differentiation at the level of benthos and sessile communities, contrasted by a greater integration of highly mobile fauna across the seascape.

Peat reefs as functional refuges and extensions

Despite structural differences, tropical peat reefs emerge as important functional extensions of the coral reef ecosystem. Species overlap was considerable; we recorded at least 41 small reef fish species common to both coral and peat habitats, as well as 44 shared megafauna species, demonstrating that many reef-associated organisms readily utilize peat reef areas. Rather than isolated anomalies, peat reefs serve as complementary habitats that broaden the overall reef system's ecological scope (21) by enhancing connectivity between patches. Notably, we encountered numerous juvenile fishes on peat reefs, including juveniles of species typically associated with coral reefs (e.g. lutjanids, haemulids, pomacentrids). This suggests a nursery function analogous to that of seagrass beds or mangroves, whereby structurally complex peat reef areas provide shelter and foraging opportunities for the early life stages of reef fishes. Similar cross-habitat life-cycle linkages are well documented in tropical seascapes, many reef fishes recruit in vegetated or algal nurseries and later migrate to adult reef habitats (19, 22). In our study, peat reefs featured patches of seagrass within the peat matrix, likely offering food for herbivores and refuge from predators. Herbivorous megafauna such as green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*), both present in the Bazaruto region and seen around the peat areas occasionally, could also use the peat habitats for feeding on the seagrass patches. The occurrence of these iconic grazers underlines the role of peat reefs as viable foraging grounds that extend beyond the limits of hard-bottom coral areas.

Tropical peat reefs also appear to function as refuge habitats for certain taxa. We noted a high abundance of spiny lobsters (*Panulirus spp.*) and other cryptic invertebrates sheltering within crevices of consolidated peat blocks (23). These peat formations create complex three-dimensional structures, including undercut ledges and cavities, analogous to rock or coral crevices (24). Such features are likely to protect small fauna from predators and harsh environmental conditions, offering similar services to rocky reefs or mangrove root habitats do. Indeed, temperate latitude studies have shown that peat reefs (formed from eroded saltmarsh peat) can serve as critical nursery and refuge habitat for juvenile lobsters and fishes (6, 23). Our findings suggest a comparable mechanism in the tropics: the peat reef provides physical refuge and feeding habitat for species that also exploit nearby coral reefs. In essence, peat reefs enlarge the functional footprint of the reef ecosystem, creating a mosaic of interconnected habitat patches. This fine-scale habitat heterogeneity likely underpins the high species overlap we observed, as organisms move among patches to exploit different resources (25). Physical exposure regimes are a key structuring mechanism: many peat reef sites in our study were shallow (0–5 m depth) and could be subject to tidal exposure, seasonal desiccation, and transient existence. Intertidal peat reef flats, for example, experience periodic air exposure and high temperature/light conditions at low tide, which few live corals can tolerate. Instead, hardy macroalgae, seagrasses, and invertebrates adapted to variable conditions thrive there, providing sustenance for mobile consumers at high tide. In subtidal peat reefs (deeper sections not exposed to tides), conditions are more stable, but even these areas are influenced by seasonal changes (e.g. monsoonal turbidity or storm surge). These findings align with the notion that mosaic seascapes comprising multiple habitats can support greater diversity and serve complementary ecosystem roles (26). Peat reefs, though atypical in origin, fit into this seascape concept as yet another habitat type that reef-associated species have learned to exploit.

Connectivity, patch dynamics, and ecosystem resilience

The dynamic nature of peat reef habitats highlights processes of connectivity and patch dynamics that may enhance ecosystem resilience (21, 27). Unlike relatively static hard coral frameworks that accrete in place, peat deposits are relict and subject to ongoing erosion and redistribution since their presence is transient in origin. We observed evidence of habitat turnover: portions of peat reef were actively eroding at seaward edges, breaking off peat blocks that can be transported by waves and currents. This process creates open space for new colonization while potentially seeding other areas with peat fragments that create new habitat. Such cycles of disturbance and renewal are reminiscent of patch dynamics in other ecosystems, where periodic physical perturbation prevents stagnation and promotes landscape-level heterogeneity (28). In the peat reef context, abrasion by seasonal storms can cause localized mortality of sessile organisms (e.g., breakage of weak peat sections). However, these disturbances effectively "reset" portions of the habitat, allowing for subsequent recolonization by fast-growing algae, seagrass, and benthic invertebrates once conditions ameliorate. We postulate that this recurrent clearing and regrowth cycle maintains a high turnover of niches, potentially supporting a higher beta-diversity and preventing any one functional group (e.g. a single coral or algal species) from completely monopolizing the space (29). The result is a more mixed and possibly more resilient community, as resources and biomass are distributed across a variety of organisms with different vulnerabilities. This mechanism aligns conceptually with the intermediate disturbance hypothesis (28, 30), wherein moderate levels of disturbance foster greater diversity and ecosystem stability. While live hard coral cover on peat reefs is absent, their biotic community may be more tolerant of environmental swings, a trait that could become increasingly valuable as climate change intensifies disturbance regimes on tropical coasts.

Crucially, tropical peat reefs illustrate how ancient terrestrial carbon can be "repurposed" into a marine ecological framework in response to sea-level rise (31). The peat underlying these reefs is a remnant of an old coastal forest, wetland or mangrove forest, now submerged and transformed into a new type of reef substrate. During the Holocene sea-level transgressions, vast areas of coastal peat across the globe were inundated and reworked by the sea (5). In the Bazaruto Archipelago and adjacent shorelines, ongoing sea-level rise and coastal erosion continue to expose buried peat layers (8, 16), essentially recruiting them into the marine environment as structural habitat. This represents a form of "ecosystem rebirth": the organic foundation of a long-gone peat swamp finds a second life as the backbone of a marine reef community. Such transitions from terrestrial to marine ecosystems underscore the resilience of coastal systems, the capacity to reorganize and maintain ecological function in the face of environmental change. The concept is analogous to submerged "Pleistocene forests" or peat beds that have been documented in other regions and later colonized by marine life (e.g. submerged mangrove peat in the Caribbean supporting seagrass and algal communities) (32, 33). Rather than viewing the erosion of peat as a simple loss of land or carbon, our study suggests it can also be viewed as a natural recycling process that fuels new ecosystem development. The connectivity between peat reefs and adjacent habitats is central to this process: tidal fluxes and mobile fauna transfer energy, nutrients, and propagules between peat reefs, coral reefs, and seagrass beds, enhancing the overall resilience of the

coastal seascape (21, 33). If one habitat type is degraded (for instance, coral reefs suffering bleaching events), the presence of alternative refugia like peat reefs could help sustain populations of certain non-coral species in the interim, thus contributing to the stability and resilience of the wider ecosystem. Our findings therefore emphasize that habitat connectivity and the availability of “backup” habitats (34) are critical components of resilience in tropical coastal ecosystems.

Broader implications: blue carbon, coastal resilience, and overlooked habitats

Tropical peat reefs highlight a yet unrecognized aspect of blue-carbon systems. Coastal peat deposits are among the planet’s richest carbon stores, tropical peat swamps can accumulate over 1,000–2,000 Mg C per hectare below ground (31, 35). When such peat deposits become submerged and persist in the marine realm, they effectively continue to sequester carbon on geologic timescales, provided the peat remains waterlogged and only slowly decomposes. In our study area, the peat forming the reef substrate is Pleistocene-Holocene in origin (radiocarbon dates from similar coastal peat in the region range from ~ 6,000–7,000 years BP; 5). The fact that this peat has endured and still supports a living community implies a form of long-term carbon storage in situ. This is a notable addition to the blue-carbon paradigm, which traditionally focuses on living vegetated habitats like mangroves, seagrass meadows, and salt marshes. We propose that tropical peat reef complexes should also be considered in coastal carbon assessments: they represent the legacy carbon of ancient wetlands now serving as marine habitat. In essence, peat reefs are a bridge between “green” carbon of terrestrial peatlands and “blue” carbon of marine systems. Furthermore, the biological community on peat reefs (especially seagrasses and macroalgae) can capture additional carbon via primary production, some of which may become buried in the peat matrix or adjacent sediments. By contrast, disturbance of peat reefs (for example by dredging or excessive peat mining) could lead to remineralization of this stored carbon and release of CO_2 and nutrients into coastal waters. A recent estimate suggests that loss of vegetated coastal ecosystems globally emits on the order of 0.15–1.02 Pg CO_2 annually (36); while peat reefs were not explicitly included in such analyses, their carbon stock and vulnerability deserve attention in the same context.

The existence of tropical peat reefs underscores the resilience and adaptive reorganization potential of coastal ecosystems under pressure from sea-level rise and shoreline change (37). As sea levels accelerate upward and shorelines erode, we are likely to see more examples of terrestrial ecosystems transitioning to novel marine habitats. These transitional systems, which might include submerged peat reefs, drowned forests, or relict mangrove peat banks now colonized by marine life, have largely been overlooked in research and management. Incorporating such “cryptic” habitats into coastal resilience planning is important. They can enhance coastal protection and provide alternative habitat for species displaced by the loss or degradation of traditional coral reefs. Their contribution to biodiversity and ecosystem services (fisheries, carbon sequestration, nutrient cycling) should be recognized in coastal management and conservation strategies. For example, coastal zone plans in Mozambique and beyond

could inventory peat outcrops and include them as important ecological features, particularly in regions where coral reef health is declining.

This study represents, to our knowledge, the first ecological characterization of tropical marine peat reef habitats. The novelty of these systems means they have likely been underreported and undervalued. Similar habitats might exist in other tropical regions with extensive coastal peatlands (e.g. Southeast Asia, the Caribbean, West Africa), but they remain undocumented in the scientific literature. By demonstrating that tropical peat reefs support complex food webs and serve functions comparable to classic shallow-water habitats (coral reefs, seagrass beds, etc.), we highlight a gap in our ecosystem understanding. Future research should investigate the distribution of peat reefs or submerged peat banks, their formation processes, and their ecological trajectories under ongoing environmental change. Addressing these questions will improve our capacity to forecast coastal ecosystem changes and harness natural resilience mechanisms.

In conclusion, tropical peat reefs in the Bazaruto Archipelago exemplify an ecosystem born from transformation, a fusion of ancient organic matter and modern marine life. They differ from hard coral reefs in structural composition and community makeup, yet they function as integral parts of the coastal seascape, offering refuge, nursery habitat, and feeding grounds for a variety of species. Their dynamic, patchy nature may confer a degree of resilience through continual renewal and connectivity with adjacent habitats. From a broader perspective, peat reefs remind us that as climates warm and seas rise, ecosystems will not only suffer losses but may also reinvent themselves in surprising ways. Recognizing and studying these novel systems will be crucial for holistic coastal conservation, climate change adaptation, and the preservation of biodiversity and blue-carbon assets in the Anthropocene.

Methods

Study site and context

The work was conducted in 2023 as a sub-project under the BCSS Ocean Observatory platform (MCTES license 002/IICDTI/BCSS/MCTES/2023, INAMAR license 1437/INAMAR/MA/2021; https://bcssmz.org/, https://bcssmz.org/ocean-observatory-public-database/;38-40), which provides open-access time-series data within the Mozambique Exclusive Economic Zone (EEZ) and the Mozambique Channel/Bazaruto Archipelago. All field surveys took place in the southern side of the San Sebastian Peninsula, in the greater Bazaruto Archipelago area, outside Marine Protected Areas (MPAs) (Fig. 1). The Bazaruto Archipelago includes fringing and deep coral reefs, sand banks, and subtidal blue carbon peat reefs located along a dynamic coastline shaped by Holocene sea-level change and shoreline retreat. Stratigraphic and conceptual reconstructions (Fig. 1) indicate that peat reef formation and burial over time were followed by erosion and exposure under rising sea levels. This landscape supports a mosaic of forest, shoreline, and coral-peat reef interactions, with evidence of habitat overlap, species exchange, and extreme erosional changes driven by annual cyclones (Fig. 2).

Peat reefs sampling

Surface and core sediments were collected from three subtidal peat reefs. Each reef was gridded (10x10 m), and between 5 and 10 surface samples (depth = 1 cm) were taken using randomized 20 cm² grabs (Fig. 3). At each site, one deep core was extracted using a stainless-steel hollow corer (5 cm diameter), manually driven to a depth of 50 cm during SCUBA diving. Cores were recovered vertically and immediately sectioned onsite. Subsamples were dried upon arrival at the Bazaruto Center for Scientific Studies (BCSS) on Benguerra Island, using a Cole-Parmer StableTemp oven with laminar flow at 60°C for 48 hours. Dried samples were then shiped to University of La Coruña (Spain) for stable isotopes analyses, and to the Curt-Engelhorn-Center Archaeometry gGmbH (Germany) for radiocarbon (^{14}C) age determination.

Stable isotopes analytics

The determination of $\delta^{15}N$ and $\delta^{13}C$ was carried out in University of La Coruña (Spain) by combustion using a FlashEA1112 elemental analyzer (ThermoFinnigan) coupled via a Conflo IV interface to a DeltaV Advantage isotope ratio mass spectrometer (Thermo Scientific). Samples were weighed into tin capsules using a UMX-2 microbalance (Mettler Toledo). Results for $\delta^{15}N$ and $\delta^{13}C$ are expressed in ‰ relative to atmospheric nitrogen (Air) and Vienna Pee Dee Belemnite (VPDB), respectively. For each analytical sequence, the following secondary standards were used for $\delta^{15}N$ calibration: USGS 40 (-4.52‰), USGS 41a (+ 47.55‰), IAEA-N-1 (+ 0.4‰), IAEA-N-2 (+ 20.3‰), and USGS 25 (-30.4‰). For $\delta^{13}C$, the standards used were: USGS 40 (-26.39‰), USGS 41a (+ 36.55‰), NBS 22 (-30.031‰), and USGS 24 (-16.049‰). Analytical precision (standard deviation) was assessed using acetanilide as a laboratory standard, yielding ± 0.15‰ (n = 10).

Age determination

The samples age was determined by radiocarbon (^{14}C), and it was conducted at the Curt-Engelhorn-Center Archaeometry gGmbH (Germany). The samples were pre-treated using the ABA-Method (Acid/Base/Acid, HCl/NaOH/HCl). The insoluble fraction was used for further treatment. The remaining sample material was combusted to CO_2 in an Elemental Analyzer (EA). CO_2 was then converted catalytically to graphite. ^{14}C was analyzed using a MICADAS-type AMS system in-house. The isotopic ratios $^{14}C/^{12}C$ and $^{13}C/^{12}C$ of samples, calibration standard (Oxalic Acid-II), blanks and control standards were measured simultaneously in the AMS. ^{14}C-ages were normalized to $\delta^{13}C$=-25‰ (41) and calibrated using the dataset IntCal20 and software SwissCal (L.Wacker, ETH-Zürich). Calibration graphs (Figure S1) were generated using the software OxCal (small deviations between SwissCal and OxCal results are possible). The ^{14}C ages were given in BP (before present) meaning years before 1950AD. In order to provide absolute calendar dates, the ^{14}C ages needed to be calibrated. The results of the calibration are shown using the 68% probability (1σ) and 95% probability (2σ) of the ^{14}C ages, respectively. The $\delta^{13}C$ value was obtained from the isotope determination in the AMS system with a typical uncertainty of 2‰. This value may be influenced by isotope fractionation in the ion source and during graphitization and is only used for fractionation correction. Hence, this value is not comparable to the one obtained in a stable isotope IRMS and should not be used for further data interpretation.

Coral and peat reef surveys

Ecological surveys were conducted via scuba diving across coral and peat reef sites to assess benthic structure and faunal communities. Standardized protocols were applied across all sites to ensure comparability of results. Survey methods included benthic quadrats for habitat characterization, invertebrate line transects, small fish counts, and megafauna counts following standardized methods at the BCSS Ocean Observatory (https://doi.org/10.82174/bcssmz.ocean.observatory.research.themes.methodology,

https://doi.org/10.82174/bcssmz.ocean.observatory.timeseries.underwater.activity.survey.megafauna). Each survey targeted a distinct component of the reef community and was conducted under comparable daylight and tidal conditions. Data collection was stratified by habitat type to enable direct comparisons of assemblage structure, functional groups, and species presence across contrasting reef systems. Detailed protocols for each survey component are provided in the following subsections.

Quadrats

As the analysis focused solely on habitat structure, soft and hard corals, and substrate types, other organisms such as sponges and ascidians were not recorded and were labeled according to the substrate on which they were located. A 30 m transect line was laid across each habitat, and every 5 m, two photo quadrats were taken, one on either side of the transect line (coral reef: 100×100 cm; peat reef: 50×50 cm). In the laboratory, all photo quadrats were individually reviewed to obtain an initial understanding of species diversity on both coral and peat reefs. A comprehensive list of familia/species and functional groups was compiled using local field guides (42). Corals were identified to the family level, with soft and hard corals distinguished. Substrate types were categorized as dead coral, rock, sand, peat, dead shells, and rubble (defined as loose pieces larger than 2 cm), mostly composed of rocks and coral fragments. Each quadrat was analyzed using PhotoQuad software, with uniform point generation at a density of one point per cm^2 (coral reef: 100 points; peat reef: 50 points). Each point was systematically labeled based on the established species and substrate library. Uniform sampling was used instead of random or stratified methods to ensure equal selection probability across all points. Quality control measures were used to ensure data accuracy and reliability, including double-checking labels and correcting identified errors.

Invertebrates

Invertebrate counts were conducted along a 30 m belt transects laid across each reef habitat. All visible invertebrates were recorded on underwater slates within a 2 m width on either side of the transect line, resulting in a total survey area of 120 m^2 per transect. Surveys were conducted by two observers (scuba diving) swimming in parallel, each covering one side of the transect. Coral reef sites were surveyed on five separate occasions, with counts from both observers combined for each date. For peat reefs, a single survey was conducted per reef, combining counts from both observers. All invertebrates

encountered were identified to the genus and species level (when possible) in situ or through photographic confirmation where needed.

Small fish

Small fish (teleost fish < 20 cm total length) were surveyed using a stationary visual census method adapted for subtidal habitats. Two surveyors positioned themselves at 4 m intervals along an 8 m transect line laid perpendicular to the reef habitat, starting from a central point. Each survey consisted of two consecutive 5-minute observation periods. During the first 5 minutes, surveyors rotated slowly in place and recorded all observed fish species on underwater slates. In the second 5 minutes, surveyors again rotated slowly, counting the number of individuals per species and estimating their size range. Upon completing each transect, the survey line was rotated 90° clockwise from the previous orientation, and the procedure was repeated. A total of four such rotational transects were conducted per survey location, allowing for a broad spatial sampling footprint around the fixed monitoring site.

Megafauna

Marine megafauna (any animal including teleost fish > 20 cm total length) were surveyed in coral and peat reefs through visual scuba diving transects targeting 46 pre-determined species representing key indicators of ecosystem health used in the BCSS Ocean Observatory diving surveys (

https://doi.org/10.82174/bcssmz.ocean.observatory.timeseries.underwater.activity.survey.megafauna). Each survey followed a fixed 30-minute transect, starting from a standardized point (station latitude/longitude) and proceeding in a straight line parallel to the coastline, heading north. Two divers swam in parallel, maintaining a 5 m distance from each other, and recorded all observed target species within their visual range (left/right side) using underwater slates.

Coral and peat reef seawater time-series and discrete sampling

Environmental conditions at coral and peat reefs were monitored using fixed moorings equipped with HOBO Pendant® sensors programmed at 1-minute and 15-minute intervals. Deployments lasted between 5 and 15 days, capturing short-term variability in seabed temperature and light. Sensors included the ONSET HOBO Pendant® UA-002-64 and/or MX2202 models. The UA-002-64 uses a precision thermistor to measure temperature from − 20°C to 70°C (accuracy ± 0.53°C at 25°C; resolution 0.14°C), and a silicon photodiode to detect relative light intensity (not lux-calibrated), suitable for tracking diel light/dark cycles. Complementary discrete measurements of temperature (-5 to 70°C; resolution 0.1°C; accuracy ± 0.2°C), salinity (0 to 70 ppt; resolution 0.01 ppt; accuracy ± 0.1 ppt), dissolved oxygen (0 to 50 mg L^{-1}; resolution 0.1% air saturation; accuracy ± 2%), and pH_{total} (0 to 14 units, 0.01 units, ± 0.2 units) were collected around the coral and peat reef areas using a ProQuatro YSI multiparameter probe, calibrated every three months.

Software and statistical data handling/graphics

All data analyses were conducted primarily in R-Studio (v2022.02.3), with statistical testing, community analysis, and visualization performed using the *vegan*, *tidyverse*, and *ggplot2* packages. Bray-Curtis dissimilarity matrices were computed using the *vegdist()* function, and multivariate differences among reef types were assessed using ANOSIM, SIMPER, and PERMANOVA functions within the *vegan* package. Dendrograms, Principal Coordinates Analysis (PCoA) ordinations, and heatmaps were generated using *ggplot2*, *factoextra*, and *pheatmap*, respectively. Venn diagrams were created using *VennDiagram*, and color scaling was adjusted with *RColorBrewer*. Exploratory data handling and figure prototyping were supported in Python (v3.8) using *pandas*, *seaborn*, and *matplotlib*, and selective matrix validation and comparative plotting were performed in MATLAB R2020b. All final figures were assembled and standardized for publication in Adobe Illustrator CS6. Prior to analysis, all datasets were screened for completeness, checked for normality and variance homogeneity where relevant, and inspected for outliers using platform-specific diagnostics.

Declarations

Author Contribution

All authors contributed to the interpretation of the results and provided feedback to the paper. M.L., J.S., A.J., M.C., and A.L. designed the project. M.L., J.S., A.J., M.J.G., M.G., M.C., and A.L. conducted the fieldwork and collected samples. M.L. wrote the paper with all co-authors' comments.

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Data Availability

The databases are open-access and available from the corresponding author. Original data were derived from the BCSS Ocean Observatory (https://bcssmz.org/) in DOI links https://doi.org/10.82174/bcssmz.ocean.observatory.data.access and https://doi.org/10.82174/bcssmz.ocean.observatory.data.repository, where data are permanently archived under citable DataCite DOIs.

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Figures

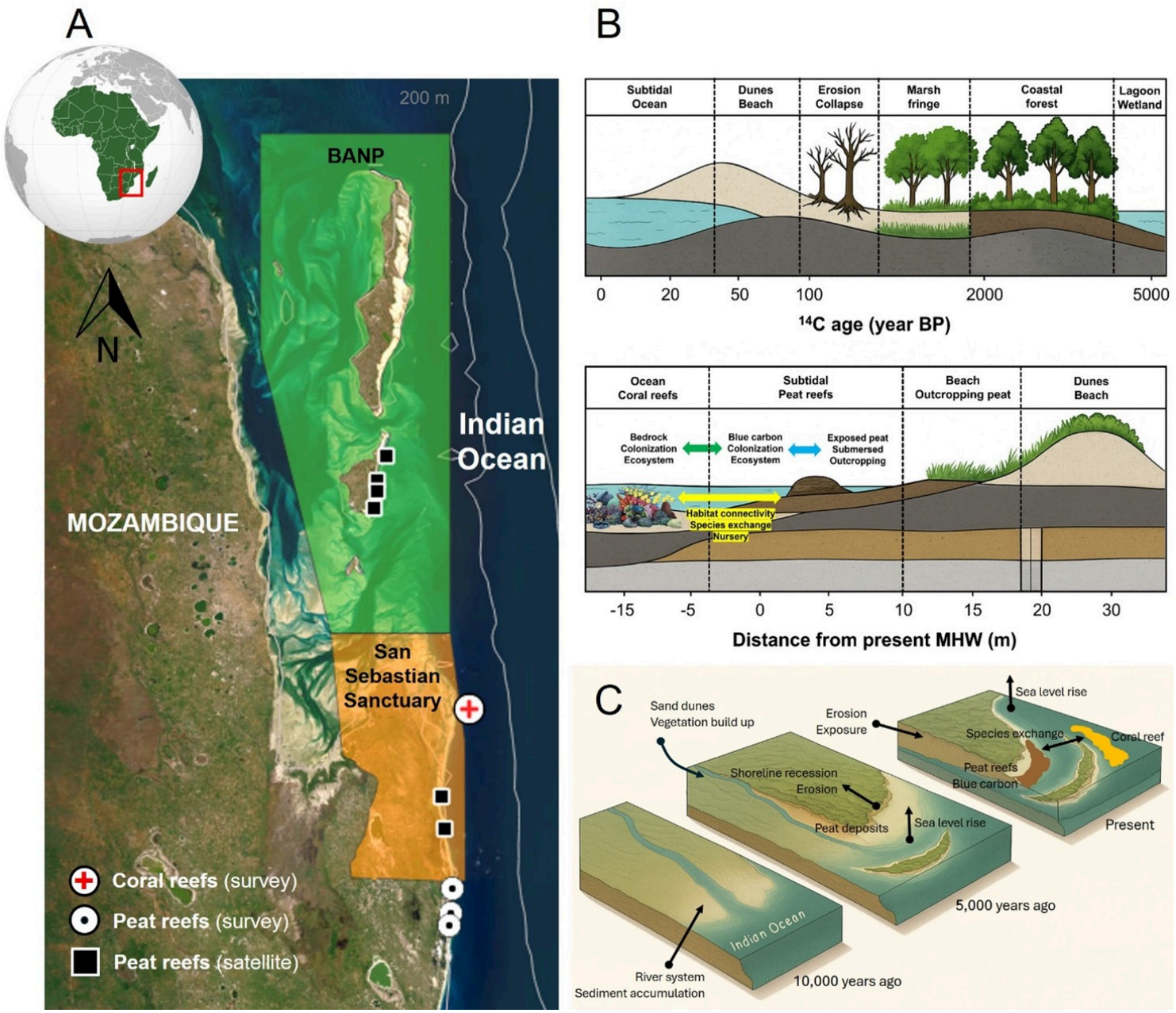


Figure 1

Distribution and identified processes of blue-carbon peat reefs formation in the Bazaruto Archipelago, Mozambique. (A) Location of physically surveyed and satellite-identified (no in situ survey/data) peat reef features along the southern coast of the Bazaruto Archipelago, including surveyed coral reef reference site. All physical field surveys were conducted outside the boundaries of Marine Protected Areas (MPAs). (B) Conceptual cross-sections illustrating (top) the Holocene progression of shoreline vegetation zones inferred from radiocarbon-dated peat cores, and (bottom) the current spatial arrangement of ecological habitats from subtidal coral reefs to peat reefs to terrestrial dune systems. Peat reefs, both exposed and submerged, represent relict shorelines that now function as novel hard-bottom substrates. (C) Three-stage conceptual model of coastal evolution. Initially, riverine sediment accumulation formed extensive coastal plains and dune fields (~10,000 years ago). Rising sea level led to shoreline retreat, forest submergence, and peat deposition in the mid-Holocene (~5,000 years ago).

Continued transgression transformed these deposits into peat habitats and colonizable reef substrates, facilitating habitat connectivity and species exchange with coral reefs until the present day. All basemap and satellite imagery was legally obtained from publicly/licensed sources via Google Earth (Imagery ©2023 Maxar Technologies) and ESRI (contributors: Maxar, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, GEBCO, and the GIS User Community).

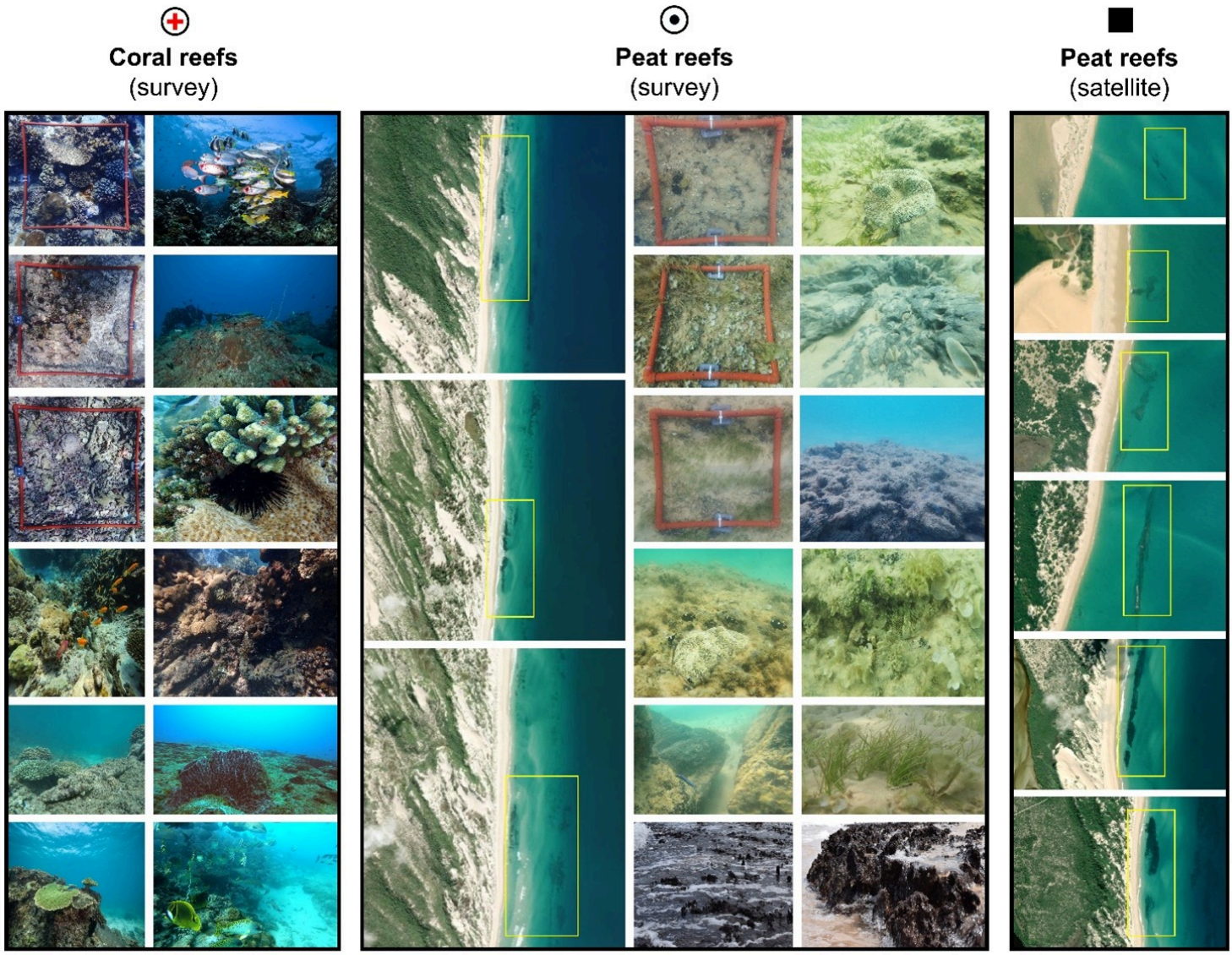


Figure 2

Visual comparison of blue-carbon peat reef and coral reef habitats. Hard coral reef reference site (left column) displays the diverse systems typical of fringing reefs in the region. Surveyed peat reefs (central column) are shown through paired satellite images, underwater quadrat photographs (1×1 m), and close-up benthic views, illustrating the structural heterogeneity and biological complexity. Satellite imagery (right column) highlights peat reef structures identified from satellite imagery (available in public forum) as means of habitat example (no physical survey/data obtained). Together, these visuals support the classification of shallow peat reefs as ecologically relevant benthic habitats distinct from traditional coral systems. All basemap imagery was legally obtained from publicly/licensed sources via Google

Earth (Imagery ©2023 Maxar Technologies) and ESRI (contributors: Maxar, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).

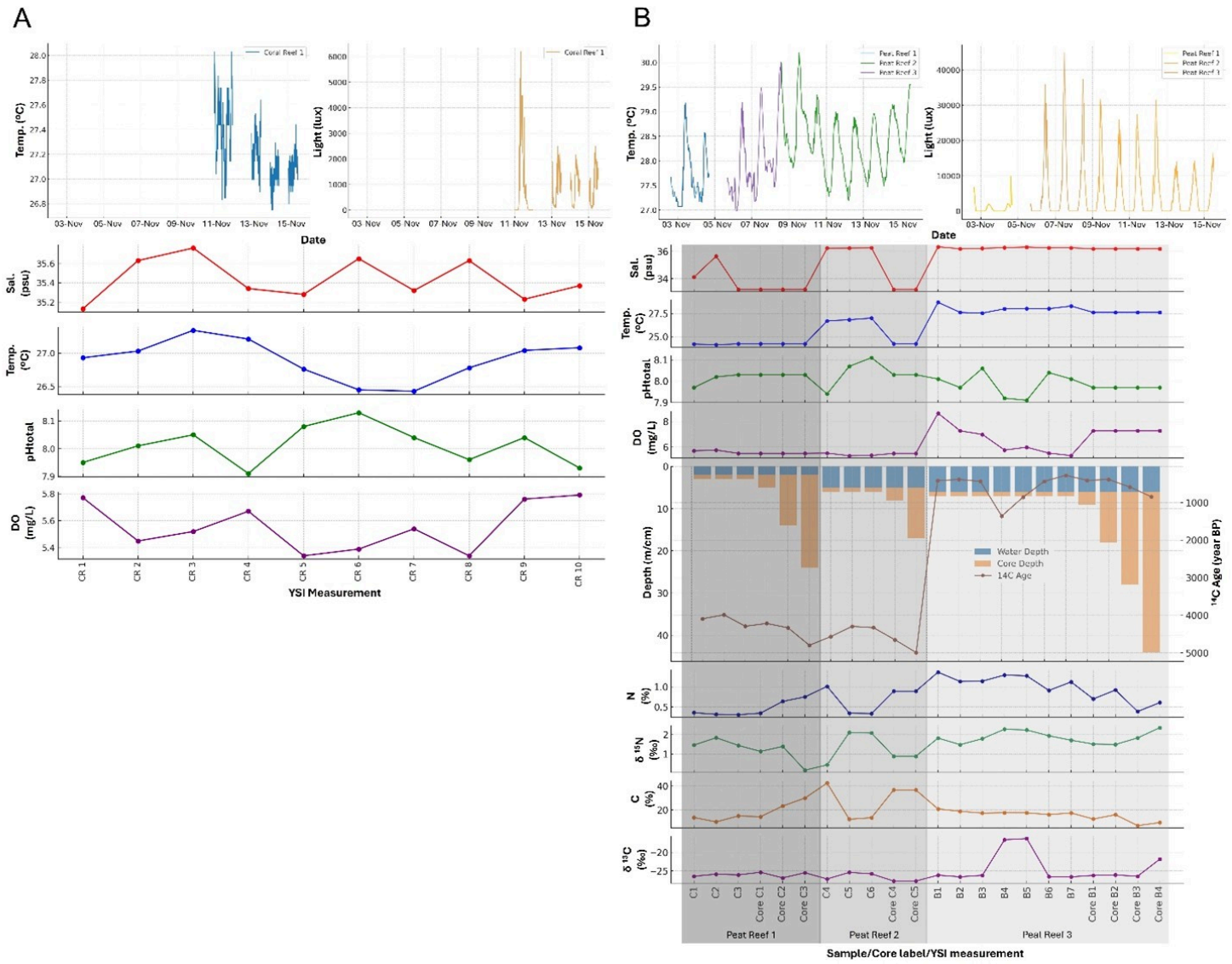


Figure 3

Environmental, oceanographic, and geochemical in the hard coral and blue-carbon peat reef systems. (A) Coral reef time-series data (15-min intervals) of seawater temperature and light intensity collected over a 5-day period to characterize environmental variability at the site (11 to 16 m). Discrete seabed physicochemical measurements (*n* = 10) were obtained from seawater column profiles across reef areas, quadrats, and sampling sites. (B) Peat reefs time-series data (1-min and 15-min intervals) of seawater temperature and light intensity collected over a 15-day period to characterize environmental variability at the sites. Discrete seabed physicochemical measurements (*n* = 22) were obtained from water column profiles across peat reef areas, quadrats, and sampling sites. Water depth (2, 5, 6 m) and subsurface core depth are shown for each location, along with associated radiocarbon (^{14}C) ages. Sediment (substrate) geochemical and isotopic parameters from surface and core samples include nitrogen and carbon content, and stable isotope signatures of $\delta^{15}N$ and $\delta^{13}C$.

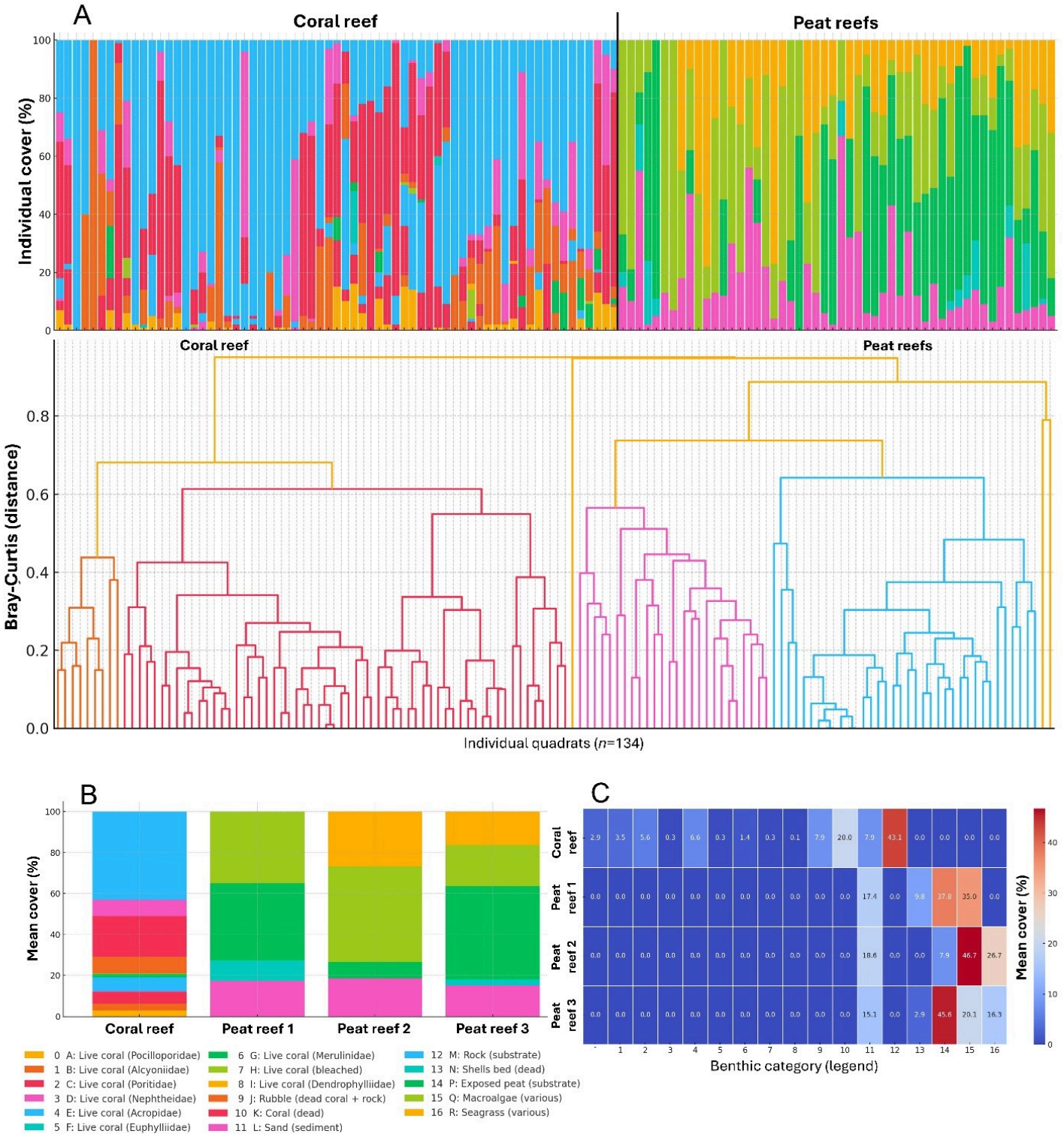


Figure 4

Benthic habitat structure in the hard coral and blue-carbon peat reef systems. (A) Stacked bar plots showing percent cover of benthic categories across individual quadrats, grouped by reef sites. Each bar represents one quadrat; color segments indicate individual benthic categories. Also included Bray-Curtis similarity dendrogram, with clustering reflecting variation in benthic composition, with clear grouping by habitat type. (B) Mean percent cover of benthic categories aggregated by reef site (Coral reef, Peat reef

1-3), highlighting differences in dominant components such as live coral, macroalgae, and substrate. (C) Heatmap of mean percent cover (%) for each benthic category across reef sites. Color scale reflects category dominance, from low (blue) to high (red) mean cover. Numerical values within cells indicate the exact mean % cover. Legend below panels lists each benthic category (A-R/1-16) with corresponding group identity and description.

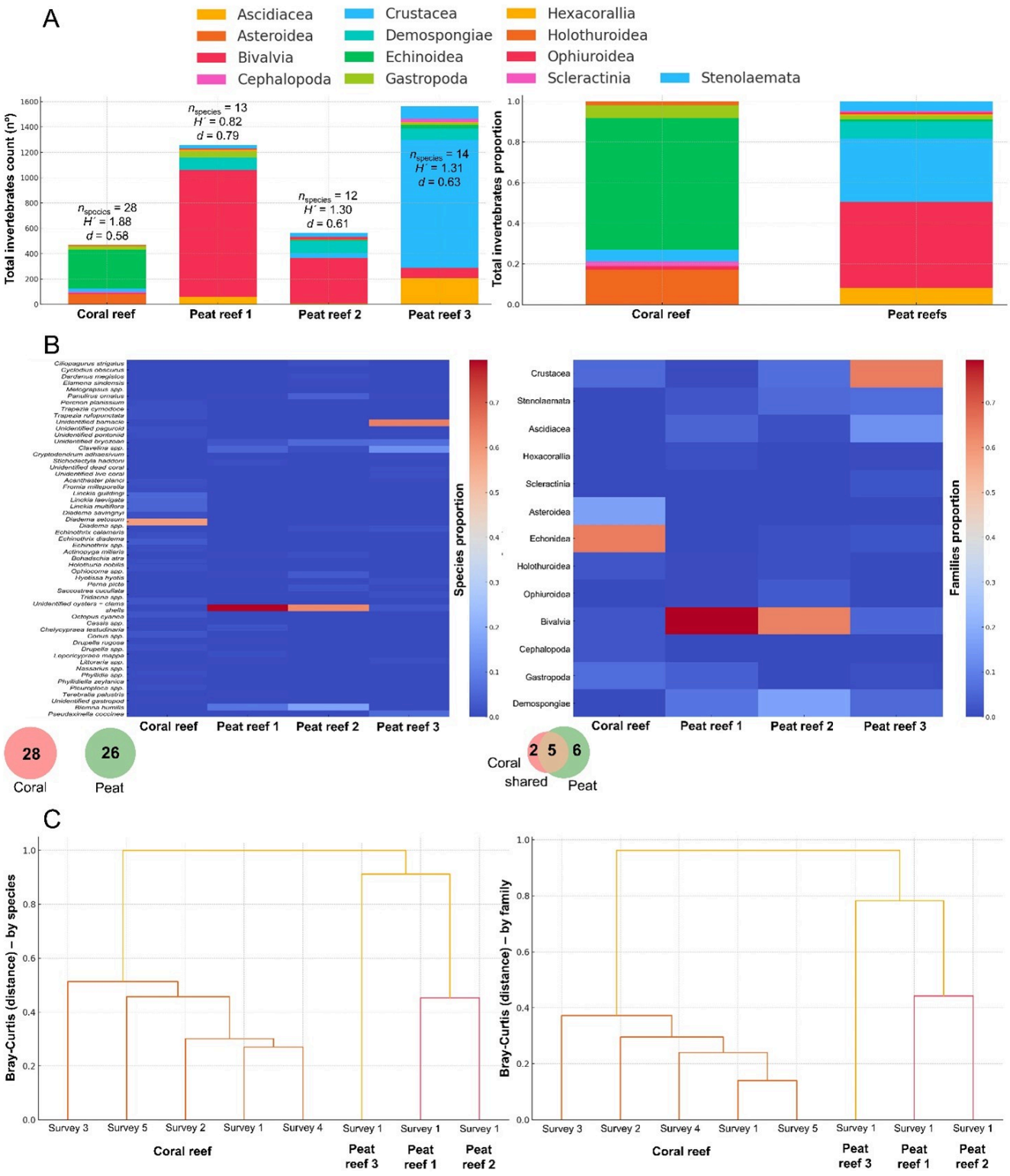


Figure 5

Benthic invertebrates' community structure in the hard coral and blue-carbon peat reef systems. (A) Stacked bar plots show total abundance and proportional representation of major taxonomic families. Diversity metrics per site are included (species nº, Shannon-diversity index *H´*, and Berger-Parker dominance index *d*). (B) Heatmaps representing invertebrate's species- and family-level proportional abundances. Also included are Venn diagrams showing partitioning of exclusive and shared species (coral=28, peat=26, shared=0) and families (coral=2, peat=6, shared=5). (C) Dendrograms showing hierarchical clustering of surveys based on Bray-Curtis dissimilarity.

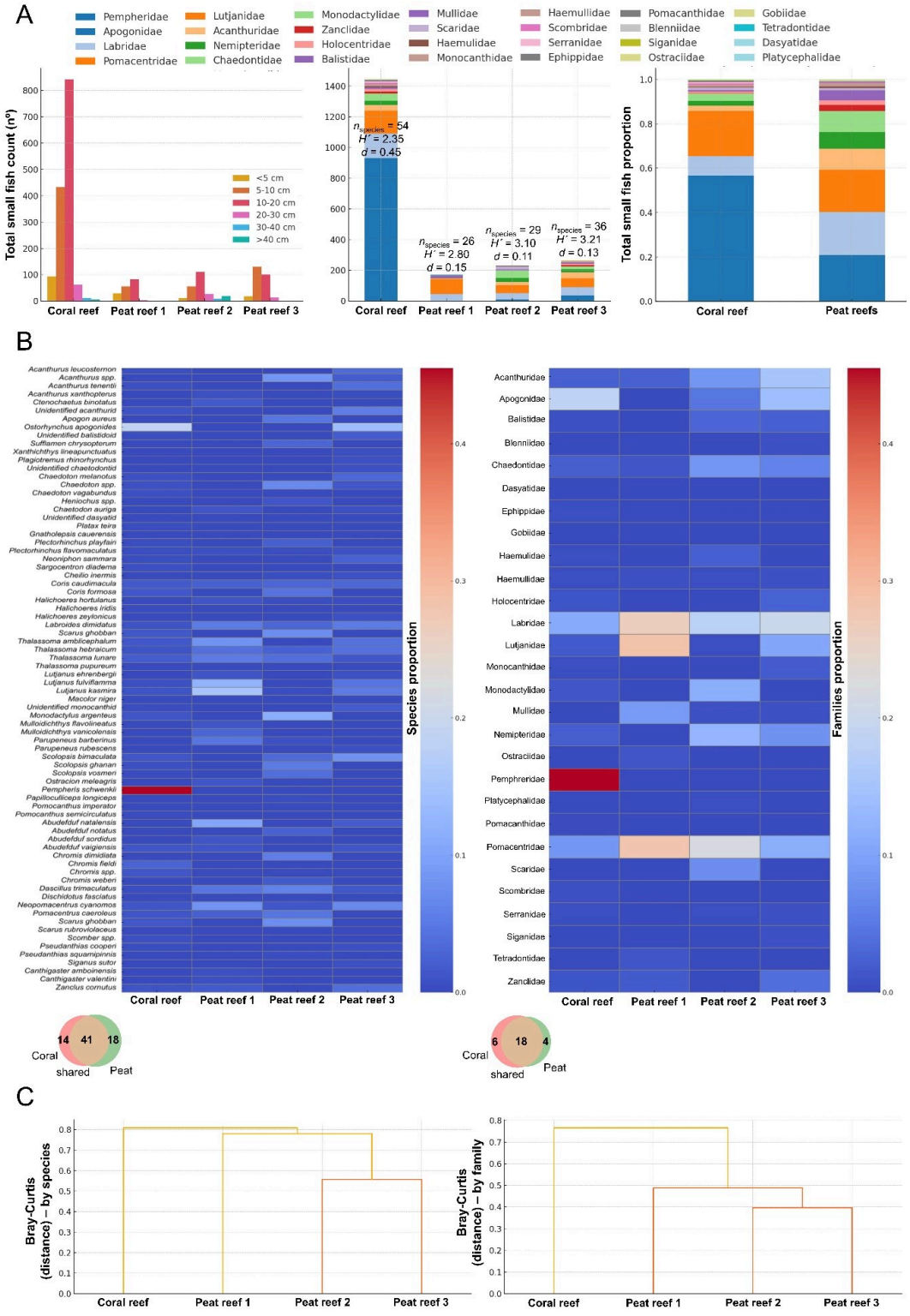


Figure 6

Small fish structure in hard coral and blue-carbon peat reef systems. (A) Stacked bar plots show counts per size class, total abundance per site, and relative family-level composition. Diversity metrics per site are included (species nº, Shannon-diversity index *H´*, and Berger-Parker dominance index *d*). (B) Heatmaps showing proportional abundance of species and families. Also included are Venn diagrams showing partitioning of exclusive and shared species (coral=14, peat=18, shared=41) and families (coral=6, peat=4, shared=18). (C) Dendrograms showing hierarchical clustering of surveys based on Bray-Curtis dissimilarity.

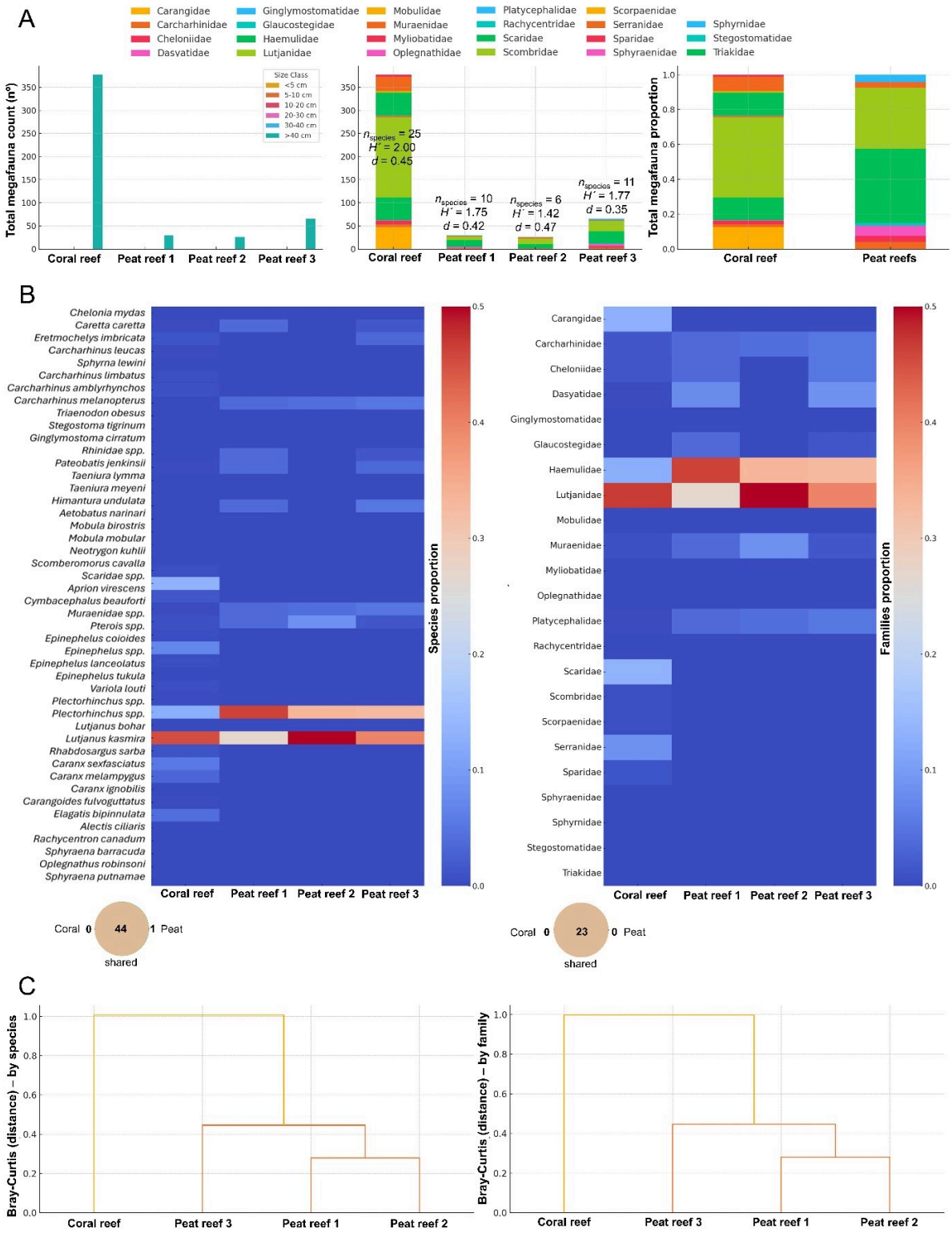


Figure 7

Megafauna structure in the hard coral and blue-carbon peat reef systems. (A) Stacked bar plots show counts per size class, total abundance per site, and relative family-level composition. Diversity metrics per site are included (species nº, Shannon-diversity index *H´*, and Berger-Parker dominance index *d*). (B) Heatmaps showing proportional abundance of species and families. Also included are Venn diagrams showing partitioning of exclusive and shared species (coral=0, peat=1, shared=44) and families (coral=0,

peat=0, shared=23). (C) Dendrograms showing hierarchical clustering of surveys based on Bray-Curtis dissimilarity.

Supplementary Files

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