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Interesting Images

Branching *Lithophyllum* Coralline Algae: Dominant Reef Builders on Herbivory-Depressed Tropical Reefs after High Coral Mortality

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Abstract: A unique shift in benthic community composition, where scleractinian corals are replaced by coralline algae, has been observed on coral reefs in Guam in the western Pacific. Guam's reefs have been subjected to intense fishing pressure and impaired water quality for decades. Since 2013, heat stress has emerged as an additional major threat to the island's coral reefs. After a severe coral bleaching and mortality event in 2017, branching coralline algae of the genus *Lithophyllum* rapidly overgrew dead coral skeletons of the ecosystem engineer *Acropora abrotanoides* and have since become major components of forereef communities over a broad depth range. By now, the persistence of increased *Lithophyllum* cover meets the temporal criterium of phase shifts, but accurate estimates on the degree of dominance over appropriate spatial scales are lacking due to the absence of reliable baseline data. The ecological impacts of coral reef transitions towards increased coralline cover are unclear. Whereas carbonate budgets and reef growth could remain positive in the long term, the downstream effect of changes in structural complexity, (micro)habitat diversity, and benthic community composition on ecological processes and reef-associated faunal assemblages is unknown.

Keywords: calcifying red algae; climate change; coral bleaching; coral reefs; Corallinales; Guam; Mariana Islands; phase shifts

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In the Mariana Islands, branching *Lithophyllum* species are naturally dominant organisms on shallow forereef systems. Branching *Lithophyllum* species are non-geniculate coralline algae, i.e., members of the red algal order Corallinales that lack non-calcified joints (genicula). The strongly calcified, fruticose plants that branching *Lithophyllum* algae form are morphologically analogous to small, corymbose corals, but these algae are better equipped to deal with the high hydrodynamic force of breaking waves. At the upper limit of their zonation range, branching *Lithophyllum* species grow intermixed with crustose *Porolithon* species in the infralittoral fringe of algal ridges, which define fringing reefs in this ecoregion [1] (Figure 1a). Communities dominated by branching *Lithophyllum* species extend to a subtidal depth of about two meters, where they often form ecological associations with *Pocillopora* and *Goniastrea* corals (Figure 1b,c). Ecological studies suggest that, in the tropics, the branching morphology of these *Lithophyllum* species provides a physical defense against the superficial impact of invertebrate grazing (e.g., by limpets, chitons, and urchins) but not against the deeper grazing scars of parrotfish [2]. Due to the combination of these abiotic and biotic factors, branching *Lithophyllum* species are naturally most abundant from the infralittoral fringe to the upper subtidal of fringing forereefs in the Mariana Islands (Figure 1d).

In Guam, the largest and southernmost island of the Mariana Archipelago, habitat degradation and declines in reef fish populations have intensified in the past decade. Successive large-scale bleaching events, extreme low tides, *Acanthaster planci* outbreaks, and sedimentation stress have significantly reduced coral cover, with certain species suffering severe population declines [3,4]. Historically, fishing pressure on Guam's reefs has been high and the island's reef fish populations are in a near-collapsed state [5]. This downward trend of Guam's reef fish stocks has not been halted, and a 30% reduction in parrotfish biomass was reported for the period between 2011 and 2021 [6]. Reefs with depleted herbivorous fish stocks are more prone to elevated coral mortality and negative coral recovery trajectories following heat stress events [7]. The last Guam-wide bleaching event in 2017 resulted in a mass mortality of the coral ecosystem engineer *Acropora abrotanoides* (Figure 2a–c) along the northern and eastern shores of Guam [4]. Many of the ghost skeletons of this staghorn coral have seen a fast and drastic transformation to branching *Lithophyllum*-dominated assemblages (Figure 2d). Large branching *Lithophyllum* plants have also become more abundant in the deeper subtidal of Guam's forereefs.

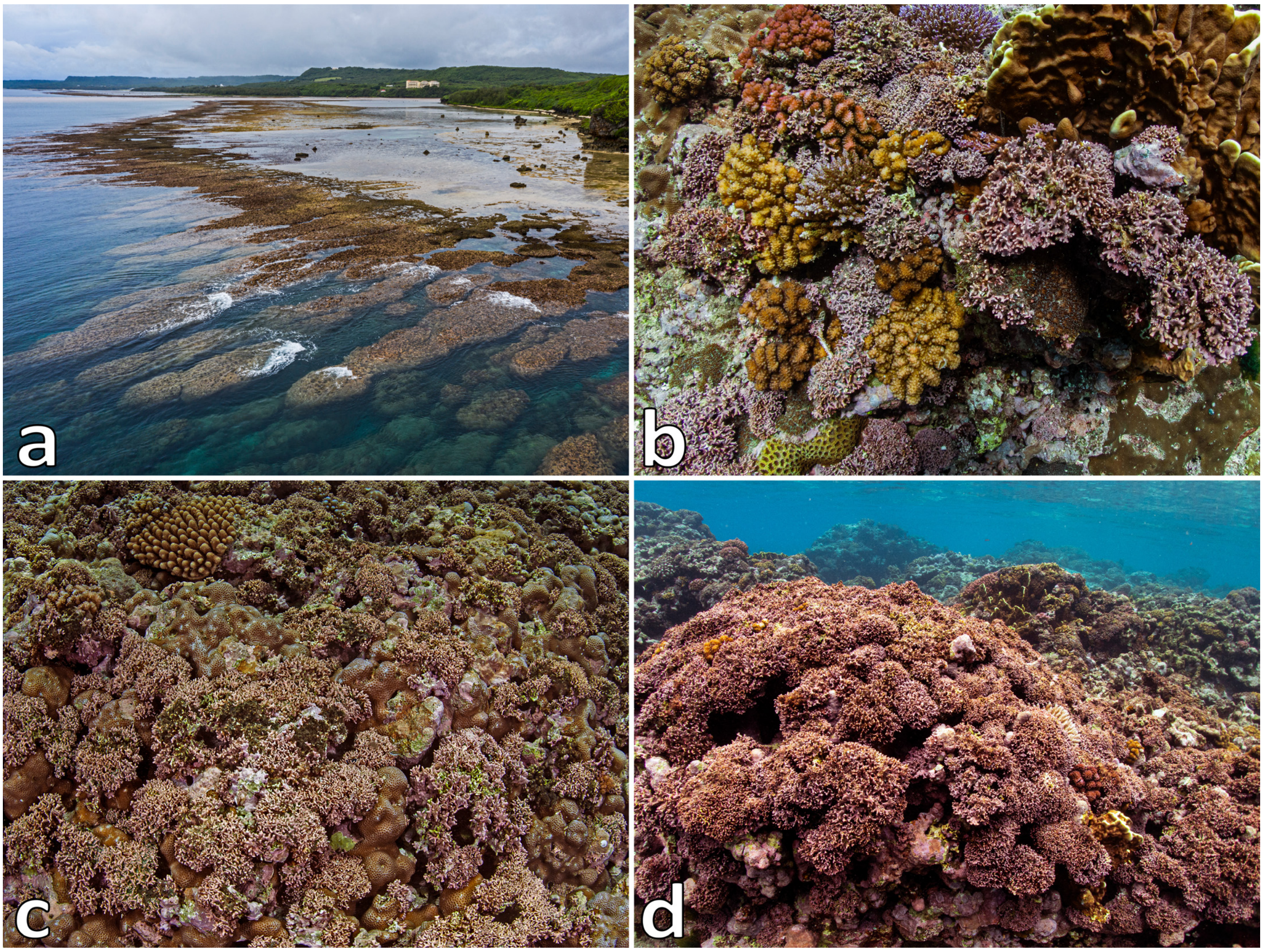

Figure 1. Calcifying red algal communities in Guam, Mariana Islands. (**a**) Algal ridge of a fringing reef along the eastern shores of Guam. Upper subtidal of forereefs, just below the reef crest, with a natural abundance of branching *Lithophyllum* species in an ecological association with the corals (**b**) *Pocillopora* spp. and (**c**) *Goniastrea retiformis*. (**d**) Dense stand of branching *Lithophyllum* in the upper subtidal of Pago Bay.

This phenomenon corresponds to a transition between two net-positive carbonate production states, i.e., primary carbonate production by corals and secondary accretion by calcareous encrusters in the conceptual model of Perry et al. [8]. The effect of the replacement of scleractinian corals by branching *Lithophyllum* algae on the carbonate budget of coral reefs is unknown. *Lithophyllum* species and other coralline algae have been important reef builders in the southern Mariana Islands since the origination of these islands, as evidenced by their continuous and abundant presence in the geological record of limestone deposits since the Eocene [9]. On present-day tropical reefs, coralline algae can also match or surpass the carbonate production of scleractinian corals [10]. However, accurate growth measurements of tropical coralline algae are scarce, which restricts the production of reliable models to evaluate the functional health of reefs in light of ecological, environmental, or climate change [11]. Peak *Lithophyllum* and other calcifying red algal diversity in the Mariana Islands occurred in the early Miocene [9], which corresponds to a sub-epoch of high coral diversity and widespread coral reef development [12]. On a global scale, peak species richness of the family Lithophyllaceae is a recent radiation that experienced a sharp rise in the Pliocene–Pleistocene [13]. Building on these geological trends in morphospecies diversity, recent studies have demonstrated that cryptic diversity is rampant in red algae, including calcifying red algae [14]. Therefore, the local diversity, biogeographic distribution, and ecological characteristics (e.g., zonation, growth rates, etc.) of different branching *Lithophyllum* species need to be resolved to better understand species interactions that drive the observed benthic transitions.

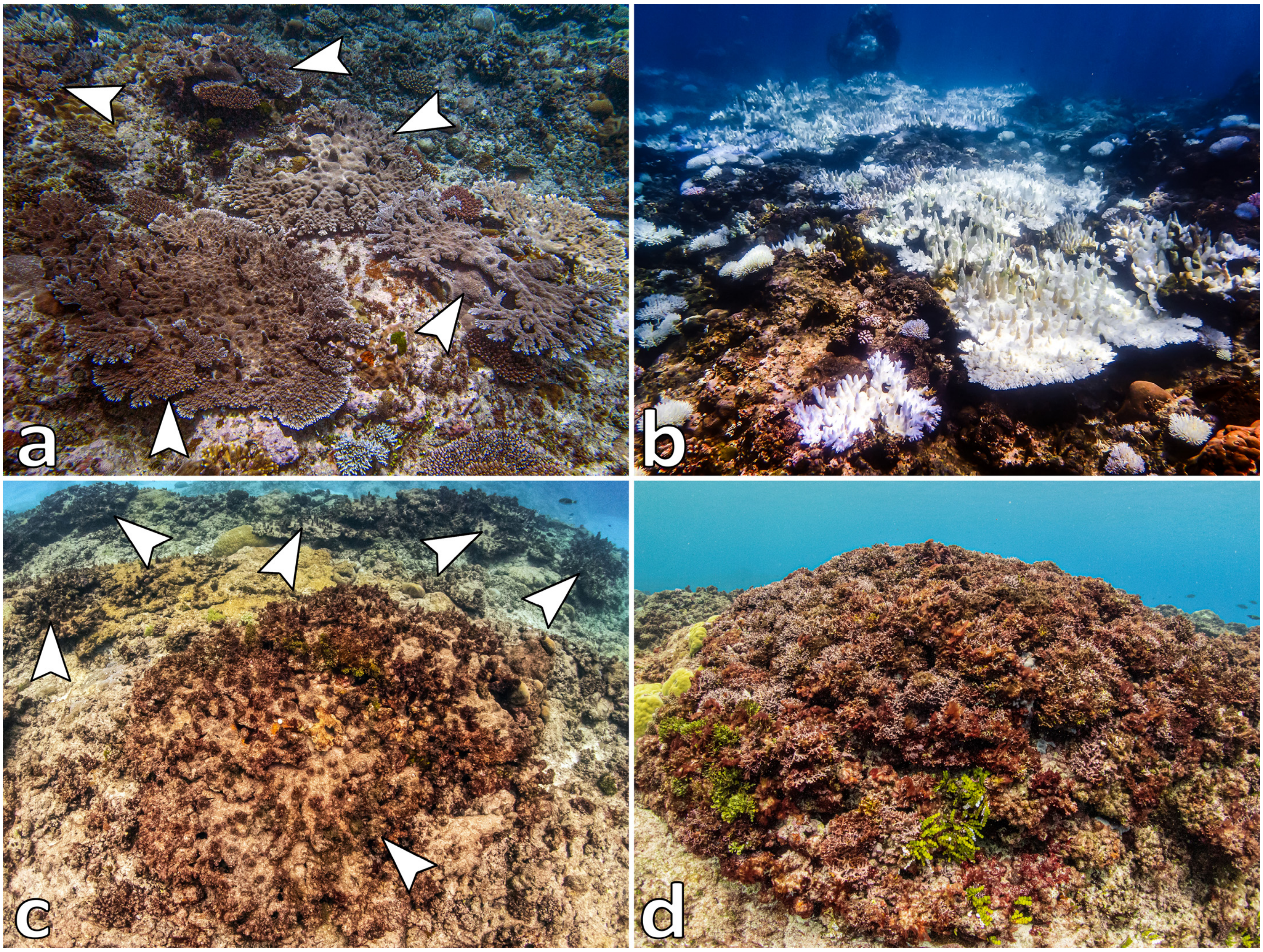

Figure 2. Ecological transition from healthy *Acropora abrotanoides* colonies to *Lithophyllum*-dominated assemblages. (**a**) Healthy colonies of the ecosystem engineer *A. abrotanoides* (arrowheads). (**b**) Bleached *A. abrotanoides* colonies during the island-wide bleaching event in 2017. (**c**) Dead *A. abrotanoides* colonies colonized by pioneer species of cyanobacteria, turf algae, and fleshy macroalgae (arrowheads). (**d**) Branching *Lithophyllum* algae overgrow dead *A. abrotanoides* skeletons and form dense, persistent communities below the upper subtidal on forereefs.

Although branching *Lithophyllum* species are conspicuous as individuals and communities, monitoring data with reliable historical records or baselines on the abundance of these or other calcifying red algae are scarce [15]. Marine monitoring programs in the tropics are often optimized to document coral taxa, and calcifying red algae are often misidentified or binned in broad, non-specific categories (e.g., pavement, etc.). Even if categories like geniculate coralline algae and crustose coralline algae are employed in benthic surveys, branching *Lithophyllum* taxa are not a proper fit with either of these categories, resulting in high observer bias. As such, reliable baseline data on the abundance and persistence of branching *Lithophyllum* taxa are usually non-existent and therefore it is unknown if the observed community transitions are a short-term phenomenon [16] or represent a new type of phase shift on tropical Pacific reefs [17]. This question is relevant because certain species of non-geniculate coralline algae promote coral recovery as they serve as preferred settlement and recruitment substrates for various invertebrate larvae, including scleractinian corals [18]. Although branching *Lithophyllum* species are generally not considered in recruitment studies on crustose coralline algae, we have observed coral recruits on the basal portions of *Lithophyllum* fragments in growth experiments.

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