

- 162, 1602–1616.e1606. <https://doi.org/10.1053/j.gastro.2021.12.288>.
- Balda, M.S., and Matter, K. (2016). Tight junctions as regulators of tissue remodelling. *Curr. Opin. Cell Biol.* 42, 94–101. <https://doi.org/10.1016/j.ceb.2016.05.006>.
- Beal, R., Alonso-Carriazo Fernandez, A., Grammatopoulos, D.K., Matter, K., and Balda, M.S. (2021). ARHGEF18/p114RhoGEF coordinates PKA/CREB signaling and actomyosin remodeling to promote trophoblast cell-cell fusion during placenta morphogenesis. *Front. Cell. Dev. Biol.* 9, 658006. <https://doi.org/10.3389/fcell.2021.658006>.
- Beutel, O., Maraspin, R., Pombo-Garcia, K., Martin-Lemaire, C., and Honigsmann, A. (2019). Phase separation of zonula occludens proteins drives formation of tight junctions. *Cell* 179, 923–936. e11. <https://doi.org/10.1016/j.cell.2019.10.011>.
- Capaldo, C.T., and Nusrat, A. (2015). Claudin switching: physiological plasticity of the tight junction. *Semin. Cell. Dev. Biol.* 42, 22–29. <https://doi.org/10.1016/j.semcdb.2015.04.003>.
- Gonzalez-Mariscal, L., Raya-Sandino, A., Gonzalez-Gonzalez, L., and Hernandez-Guzman, C. (2018). Relationship between G proteins coupled receptors and tight junctions. *Tissue Barriers* 6, e1414015. <https://doi.org/10.1080/21688370.2017.1414015>.
- Haas, A.J., Zihni, C., Krug, S.M., Maraspin, R., Otani, T., Furuse, M., Honigsmann, A., Balda, M.S., and Matter, K. (2022). ZO-1 guides tight junction assembly and epithelial morphogenesis via cytoskeletal tension-dependent and -independent functions. *Cells* 11, 3775. <https://doi.org/10.3390/cells11233775>.
- Hashimoto, Y., Greene, C., Munnich, A., and Campbell, M. (2023). The CLDN5 gene at the blood-brain barrier in health and disease. *Fluids Barriers CNS* 20, 22. <https://doi.org/10.1186/s12987-023-00424-5>.
- Larre, I., Ponce, A., Franco, M., and Cereijido, M. (2014). The emergence of the concept of tight junctions and physiological regulation by ouabain. *Semin. Cell. Dev. Biol.* 36, 149–156. <https://doi.org/10.1016/j.semcdb.2014.09.010>.
- Otani, T., and Furuse, M. (2020). Tight junction structure and function revisited. *Trends Cell. Biol.* 30, 805–817. <https://doi.org/10.1016/j.tcb.2020.08.004>.
- Piontek, J., Krug, S.M., Protze, J., Krause, G., and Fromm, M. (2020). Molecular architecture and assembly of the tight junction backbone. *Biochim. Biophys. Acta. Biomembr.* 1862, 183279. <https://doi.org/10.1016/j.bbamem.2020.183279>.
- Schwayer, C., Shampour, S., Pranjić-Ferscha, K., Schauer, A., Balda, M., Tada, M., Matter, K., and Heisenberg, C.P. (2019). Mechanosensation of tight junctions depends on ZO-1 phase separation and flow. *Cell* 179, 937–952.e18. <https://doi.org/10.1016/j.cell.2019.10.006>.
- Tsukita, S., Tanaka, H., and Tamura, A. (2019). The claudins: from tight junctions to biological systems. *Trends Biochem. Sci.* 44, 141–152. <https://doi.org/10.1016/j.tibs.2018.09.008>.
- Varadarajan, S., Stephenson, R.E., and Miller, A.L. (2019). Multiscale dynamics of tight junction remodeling. *J. Cell Sci.* 132, jcs229286. <https://doi.org/10.1242/jcs.229286>.
- Vasileva, E., and Citi, S. (2018). The role of microtubules in the regulation of epithelial junctions. *Tissue Barriers* 6, 1539596. <https://doi.org/10.1080/21688370.2018.1539596>.
- Zihni, C., Mills, C., Matter, K., and Balda, M.S. (2016). Tight junctions: from simple barriers to multifunctional molecular gates. *Nat. Rev. Mol. Cell Biol.* 17, 564–580. <https://doi.org/10.1038/nrm.2016.80>.

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The rising threat of peyssonnelioid algal crusts on coral reefs

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For more than a century, coral reefs have been exposed to increasing anthropogenic disturbances that have profoundly altered their community structure. These perturbations continue to challenge coral reefs in new ways as ecological paradigms are recast in the Anthropocene Epoch¹. In recent decades, macroalgal blooms have blighted Caribbean reefs², but the appearance of aggressive peyssonnelioid algal crusts (PAC) that are rapidly increasing in abundance to become dominant members of the benthos on Caribbean and Indo-Pacific reefs is a novel phenomenon in tropical seas³. By pre-empting vacant space, overgrowing corals, deterring the settlement of coral larvae, and favouring a phase transition from coral to algae⁴, PAC are likely to accelerate the decline in dominance of corals on global reefs (Figure 1).

Macroalgae are ubiquitous throughout the world's oceans, and on coral reefs multiple taxa are increasingly playing negative ecological roles, with fleshy macroalgae outcompeting scleractinian corals through overgrowth, abrasion, allelopathy, and shading⁵. PAC, however, are becoming a newly dominant group of crustose algae on coral reefs, and while formerly restricted to trivial abundances³, they are increasing in range and local abundance on shallow reefs where they have the potential to create a resilient benthic algal community^{3,4}. In the Caribbean, PAC became conspicuous on the reefs of St. John, US Virgin Islands, around 2012, and by 2019 they covered 47–64% of benthic space at three-meters depth. In the tropical Pacific at Guam, the significant prevalence of PAC prompted a diversity investigation that revealed 48 peyssonnelioid species, yet could not validate the only *Peyssonnelia* species that was previously reported for the island⁶.

PAC within the red algal family Peyssonneliaceae are composed of multiple genera containing a high

diversity of species of non-calcified or aragonite-calcifying organisms, but their identification and taxonomy has remained difficult because of their morphologically-simple crusts, variable colouration, and commonly sterile thalli (i.e., an absence of data on possibly diagnostic reproductive features). Consequently, PAC may be confused for similar looking seaweeds, including crustose coralline algae, fleshy macroalgal crusts, and turf algal communities. Most functional groups to which PAC have been assigned during surveys are prone to being biologically incorrect, thereby decreasing the accuracy with which the cover of PAC and other macroalgae on tropical and subtropical reefs is estimated.

PAC are native inhabitants of tropical reefs, but their recent rise to spatial prominence in this ecosystem is novel^{3,4}. In the Caribbean, they can overgrow live corals^{3,4} and pre-empt vacant space created by disturbances such as frequently-occurring hurricanes⁴. As PAC may be unaffected by ocean acidification⁷, they may function as winners on future reefs exposed to more acidic seawater. While PAC appear to be avoided by grazing fishes, they are consumed by the sea urchin *Diadema antillarum* to create PAC-free halos in which coral recruitment is elevated⁸, although these halos may disappear with the recent population collapse of *Diadema*. Of great relevance in a global context characterized by declines in coral recruitment and flattening of reef structures is the paucity of coral recruits on top of PAC⁴, possibly because the microbiome of PAC repels invertebrate larvae⁹. Rapidly spreading crusts of PAC have also been appearing throughout the tropical Indo-Pacific, as in the Caribbean. PAC have also become prominent components of reefs in Hawai'i, the Mariana Islands, the Marshall Islands, the South China Sea and Vanuatu, where they overgrow dead corals on reefs affected by coastal runoff and have increased after coral mortality events¹⁰.

PAC outbreaks appear to be a rapidly developing crisis on coral reefs worldwide, where they are exploiting the ecological legacies of decades of reef degradation. Critically, PAC appear to be less negatively affected than scleractinian corals by prevailing climatic conditions⁶. While the proliferation of other functional groups (e.g., macroalgae²) on tropical reefs provides well-known



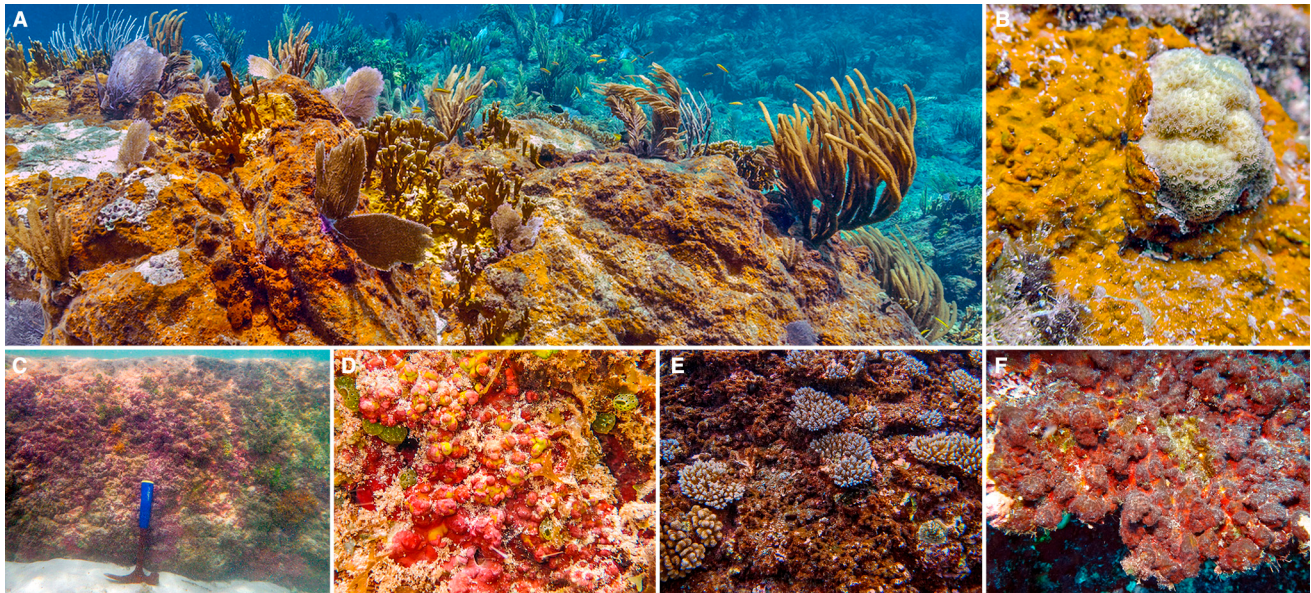


Figure 1. Examples of peyssonnelioid algal crust outbreaks in the Caribbean and Pacific.

(A) Peyssonnelioid algal crusts (PAC) overgrowing igneous rocks, stony corals, soft corals (~20 cm high for scale), and sponge at ~5 m depth in St. John (2017). (B) PAC overgrowing *Porites astreoides* (~3 cm diameter) at ~5 m depth in St. John (2017). (C) *Ramicrusta asanitensis* covering micro-atolls at Asanite Cove, Guam (hammer for scale). (D) Close up of *R. asanitensis* in Guam after removing a fine layer of sediment. (E) *Peyssonnelia* sp. carpeting vast expanses of reef tract on Majuro Atoll, Marshall Islands. (F) Close up of the *Peyssonnelia* sp. from Majuro Atoll.

examples of the consequences of anthropogenic disturbances, the ecological consequences of PAC outbreaks may be more severe than their high coverage alone portends. Through increased ecological resilience, restricted herbivory, and active deterrence of sessile invertebrate recruitment, PAC may represent an ecological process intensifying the hysteresis preventing a reversal of the ecological transition favouring macroalgal dominance over reef corals.

The recent increases in cover and distribution of PAC on tropical reefs demonstrate their capacity to accelerate the restructuring of tropical benthic habitats. PAC are an ecological surprise arriving late to the scene of widespread ecosystem degradation of coral reefs in the Anthropocene Epoch. Within this seascape, PAC may serve as an opportunistic ‘ecological catalyst’ that could hasten the global demise of corals on reefs under accelerating climate change. To understand this rapidly emerging threat, timely answers must urgently be sought in response to crucial issues regarding: the ability for early detection of PAC outbreaks at local-to-regional scales; the description of species-specific impacts of PAC in mediating phase transitions of benthic

communities; and the capacity of tropical reefs to maintain resilience to PAC outbreaks. Suitable progress in these areas will only be obtained by a well-funded synergy of ecological, phylogenetic, and multi-omic studies that must start with the ability to quickly and accurately identify the taxa driving the global advance of PAC.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas, J., van de Leemput, I.A., Lough, J.M., Morrison, T., *et al.* (2017). Coral reefs in the Anthropocene. *Nature* 546, 82–90.
- Roff, G., and Mumby, P.J. (2012). Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.* 27, 404–413.
- Pueschel, C.M., and Saunders, G.W. (2009). *Ramicrusta textilis* sp. nov. (Peyssonneliaceae, Rhodophyta), an anatomically complex Caribbean alga that overgrows corals. *Phycologia* 48, 480–491.
- Edmunds, P.J., Zimmerman, S.A., and Bramanti, L.A. (2019). A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands. *Coral Reefs* 38, 1329–1341.
- McCook, L.J., Jompa, J., and Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* 19, 400–417.
- Mills, M.S., Deinhart, M.E., Heagy, M.N., and Schils, T. (2022). Small tropical islands as hotspots of crustose calcifying red algal diversity and endemism. *Front. Mar. Sci.* 9, 898308.
- Dutra, E., Koch, M., Peach, K., and Manfrino, C. (2016). Tropical crustose coralline algal individual and community responses to elevated pCO₂ under high and low irradiance. *ICES J. Mar. Sci.* 73, 803–813.
- Stockton, L., and Edmunds, P.J. (2021). Spatially aggressive peyssonnelid algal crusts (PAC) constrain coral recruitment to *Diadema* grazing halos on a shallow Caribbean reef. *J. Exp. Mar. Biol. Ecol.* 541, 151569.
- Wilson, B., Fan, C.M., and Edmunds, P.J. (2020). An unusual microbiome characterises a spatially-aggressive crustose alga rapidly overgrowing shallow Caribbean reefs. *Sci. Rep.* 10, 20949.
- Grady B.W., Kittle, R.P., III, Pugh, A., Lamson, M.R., Richards, J.L., Fredericq, S., McDermid, K.J., Allen, Q., and Asner, G.P. (2022). Long-term ecological monitoring of reefs on Hawai’i Island (2003–2020): Characterization of a common cryptic crust, *Ramicrusta hawaiiensis* (Peyssonneliales, Rhodophyta). *Front. Mar. Sci.* 9, 1009471.

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