Material legacies can degrade resilience

Structure-retaining disturbances promote regime shifts on coral reefs

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1. Disturbances and material legacies

Dead structures of habitat-forming organisms left after disturbance are *material legacies*
- e.g., dead trees, oyster shells, dead coral skeletons, etc.

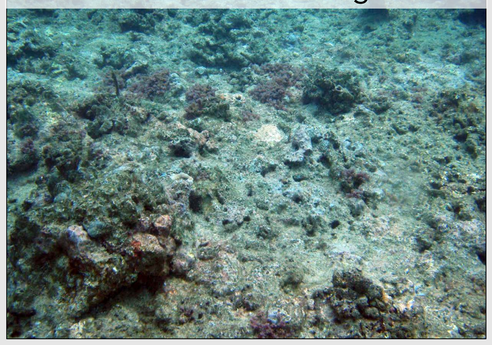
Material legacies can affect processes linked to community assembly and ecosystem recovery:
- Colonization success of new individuals
- Performance of surviving individuals

Different disturbance types can either remove or leave in place material legacies:
- Structure-*removing:* storms, landslides, fires, floods, etc.
- Structure-*retaining:* drought, marine heat waves, predator outbreaks, disease, etc.

Whether either type of disturbance creates more favorable conditions for recovery or facilitates regime shifts to alternative ecosystem states remains an outstanding question.

2. Disturbance types on coral reefs

Structure-removing



- Cyclones and hurricanes kill corals and remove their skeletons from the reef
- The reef is left bare and exposed, allowing herbivores to remove macroalgae, which compete with corals for reef space

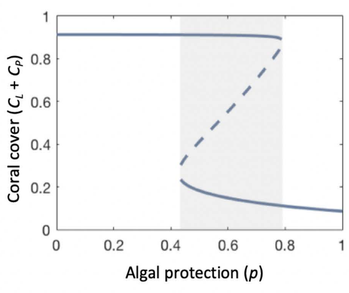
Structure-retaining

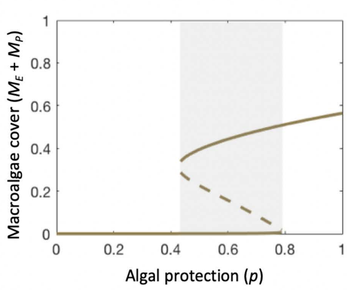
- Thermal bleaching and predator outbreaks kill corals but leave their skeletons intact
- Dead skeletons provide refuge space for macroalgae; this may allow macroalgae to escape control by herbivores and take over as the dominant organism

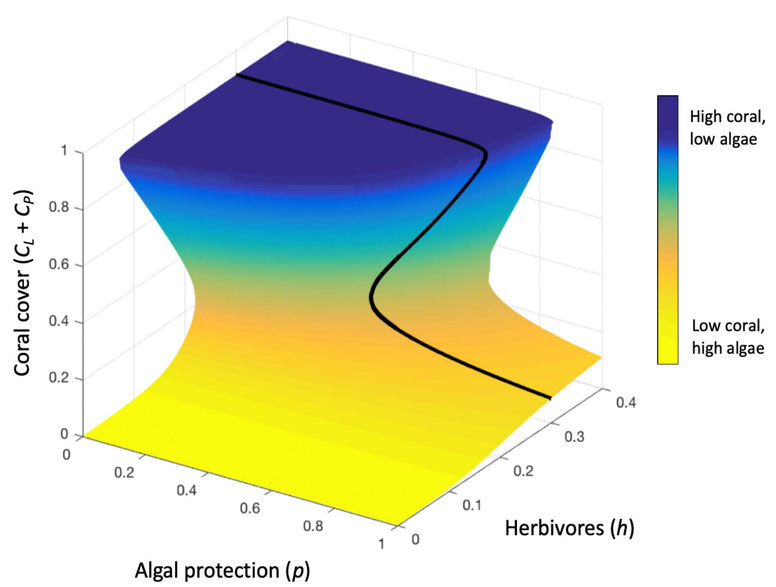
3. Algal protection increases the prevalence of the algae-dominated state

We built a mathematical model of a typical coral reef to:
- simulate cover of live coral and macroalgae that grow on exposed reef or dead coral following disturbances of each type
- test whether either disturbance type facilitates coral recoveries, or instead, regime shifts from coral- to algae-dominance

When dead coral structure provides protection for macroalgae:
- The region of bistability between coral- and algae-dominated states expands
- The algae-dominated state becomes more prevalent, even at high levels of herbivory

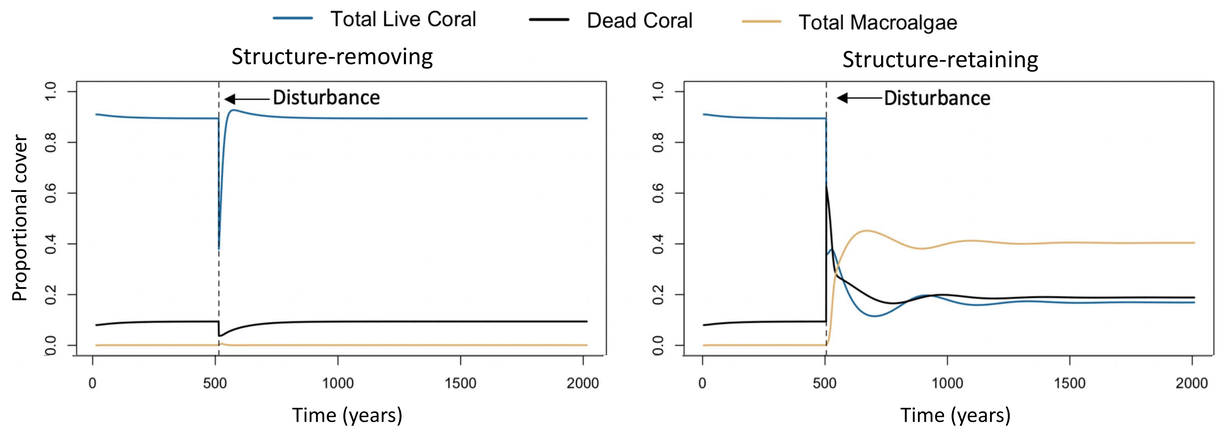






4. Post-disturbance trajectory depends on disturbance type

For the same intensity of disturbance, differing post-disturbance trajectories can arise depending on disturbance type:
- Removal of structure allowed for a rapid recovery to the coral state (left panel)
- Retention of structure caused a coral-macroalgae regime shift (right panel)

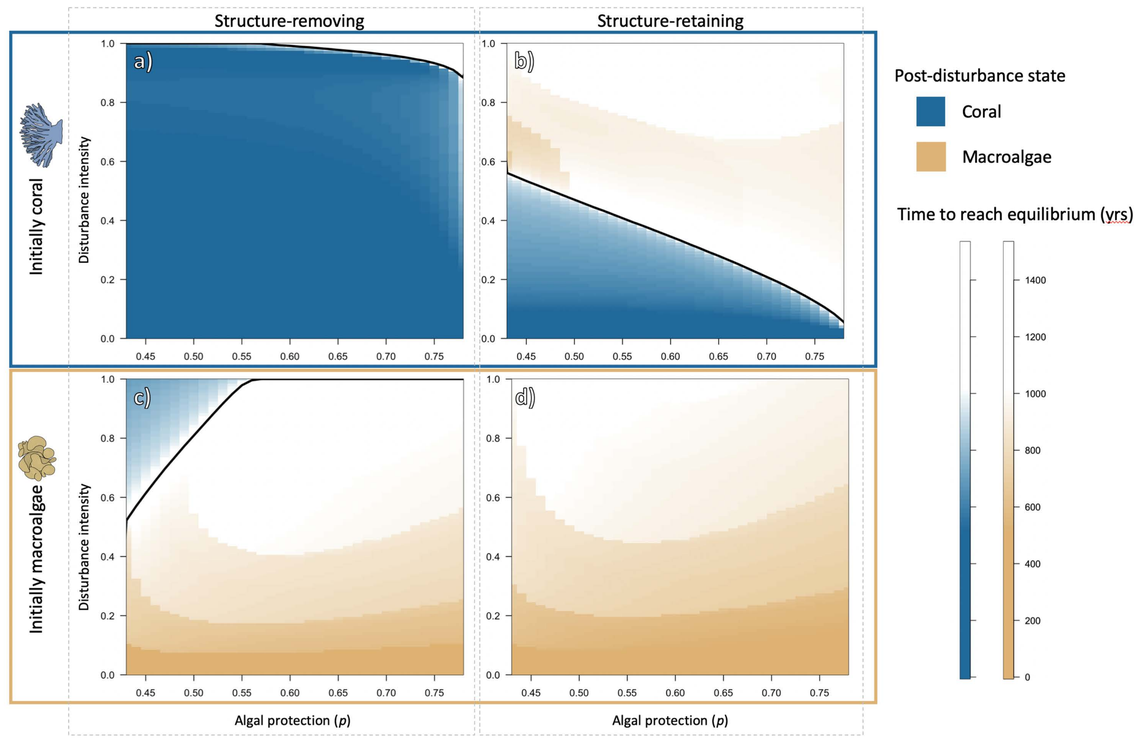


5. The dead skeleton legacy facilitates coral-to-algae regime shifts

Recoveries to the coral state generally occurred when structure is removed
- Regardless of disturbance intensity or level of algal protection

Regime shifts from coral to algae were triggered by structure-retaining disturbances
- The threshold of disturbance intensity required declines as algal protection increased

Shifts from the algae to the coral state are rare
- Only possible with high-intensity structure-removing disturbances at low algal protection
- These shifts did not occur following structure-retaining disturbances



6. Conclusions

Structure-retaining disturbances diminish coral resilience by creating refuge space for algae:
- If the dead skeleton legacy inhibits herbivory (a key recovery process), regime shifts to algae-dominated reefs occur more readily

Identifying how material legacies affect ecosystem recovery may be important to consider in studies of resilience
- Disturbances that generate the dead coral skeleton legacy are becoming more prevalent, posing a management challenge for future coral reefs