Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs

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Ecosystem engineers that create habitats facilitate the coexistence of many interacting species. This biotic response to habitat engineering may result in non-intuitive cascading interactions, potentially including feedbacks to the engineer. Such feedback mechanisms, either positive or negative, may be especially important for the maintenance of biogenic habitats and their community-wide facilitation. Here, we describe the complex interactions and feedbacks that link marine habitat-forming engineers, the reef-building corals, and a group of herbivores, the parrotfishes; the latter pre- venting the overgrowth of macroalgae, a major competitor of corals. Using density data of eight parrotfish species on a Caribbean reef, we first describe the form of the response of parrotfish abundance to increasing topographic complexity generated by coral growth. Topographic complexity enhanced parrotfish abundance by promoting habitat suitability, but the shape (linear vs asymptotic) and strength of this response varied across species and size. Parrotfish grazing intensity, estimated from data on abundance and species-, size- and life phase-specific grazing rates also increased with topographic complexity despite an increase in the surface area over which parrotfish graze. Depending on fish species, this functional response was found to be linear or asymptotic. Using a simple analytical model we then explored the effects of topographic complexity and fishing pressure on coral-algal competition, with particular emphasis on the implications of non-linearities in the intensity of grazing. Simulations demonstrate that fishing and habitat degradation impair the performance of grazing, but that an asymptotic response of grazing intensity to topographic complex- ity increases the ecological resilience of coral reefs. Parrotfish and corals are mutually beneficial by creating a loop of positive, indirect feedbacks that maintain their own structure and function: coral growth promotes habitat suitability for parrotfish, concordantly enhancing grazing intensity, which in turn facilitates coral growth by reducing competitive exclusion by macroalgae. We conclude that the resilience of biogenic habitats is enhanced by non-linear biotic responses exclusion by macroalgae. We conclude that the resilience of biogenic habitats is enhanced by non-linear biotic responses to engineering and by the emergence of reciprocal facilitation linking habitat engineering and response organisms.

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