

# Coral reefs as novel ecosystems: embracing new futures

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The composition and functions of many ecosystems are changing, giving rise to the concept of novel ecosystems. Although some coral reefs are becoming non-coral systems, others are becoming novel coral-dominated ecosystems driven principally by differential species responses to climate change and other drivers, but also due to species range shifts at higher latitudes, and in some cases introduced species. Returning many coral reefs to pristine baselines is unrealistic, whereas embracing novel futures enables more pragmatic approaches to maintaining or re-building the dominance of corals. Coral reefs are changing in unprecedented ways, providing the impetus to improve our understanding of reef compositions that may dominate in the future, explore new management approaches, assess changes in ecosystem services, and investigate how human societies can adapt and respond to novel futures.

## Addresses

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## Introduction

Many drivers of ecosystem change, such as harvesting, climate change and the introduction of invasive species, lead to non-random species loss or alterations in abundance [1–3]. In the field of community ecology, there is a long history investigating these types of changes. Some changes lead to persistent new ecosystem configurations, which have been referred to as *novel ecosystems* [4,5<sup>••</sup>]. Novel ecosystems have been broadly defined as changes in species composition, relative abundances, interactions and ecosystem functions, although they have also sometimes been used to describe even more dramatic ecosystem

change related to threshold-driven regime shifts [5<sup>••</sup>]. The novel ecosystem concept, which has similarities to the no-analog community literature in paleoecology [6], explicitly recognizes that many ecosystems are changing and are unlikely to return to historic conditions. Importantly, these novel configurations may still provide valuable goods and services to society, and consequently there is a need to understand the properties of these emerging ecosystems [6] and determine the most appropriate management in the new ecosystem contexts [7]. The majority of work on novel ecosystems has focussed on the terrestrial realm, where land-use change, restoration, introduced species, and differential responses of species to climate change have given rise to novel ecosystem configurations in many locations [5<sup>••</sup>,6]. Given the substantial changes for a range of coastal marine ecosystems [8], there is a need to evaluate whether the novel ecosystem concept is applicable and useful in the marine environment (e.g. [9]). Here, we evaluate the concept using coral reefs as a focal ecosystem.

## Novel coral reef ecosystems

Coral reefs had relatively stable community compositions through the Pleistocene [10], but have now become substantially altered by humans through a range of direct anthropogenic drivers and global climate change, rendering a return to pristine coral reef configurations unlikely [11,12,13<sup>•</sup>]. Although a handful of large remote unpopulated wilderness areas remain in very good condition [14], around one-third of the world's coral reefs have been severely degraded by overfishing and pollution, some of which have undergone regime shifts to alternate non-coral states (e.g. [11,15,16<sup>•</sup>]). Some predictions suggest that climate change could lead to complete degradation of all coral reefs [12,17]. Yet on many reefs, coral reef species are responding differentially to a range of drivers, including climate change [18,19<sup>••</sup>] and may persist as altered coral-dominated systems (e.g. [13<sup>•</sup>,19<sup>••</sup>,20<sup>••</sup>,21,22]). We define novel coral ecosystems as changes in species configurations, interactions and functions, but systems still within the parameter space of calcifying coral-dominated reefs. In doing so, we differentiate between heavily degraded reefs that have undergone a regime shift to a non-coral ecosystem (e.g. from hard corals to seaweed) [20<sup>••</sup>], and reefs that remain in a calcifying condition but have shifted in composition and function.

Human alteration of coral reef ecosystems has a long history (e.g. [15]) and has been causing novel species dominance and interactions on many reefs for some time.

Moreover, there are three principal mechanisms why novel coral reef ecosystems are becoming increasingly commonplace: introduced species; species range shifts; and asymmetrical species responses to climate change and other common disturbances.

Introduced species have not been a widely recognized problem for coral reefs, although they are becoming an issue in some locations. In the few examples where introduced species are becoming dominant components of non-native coral reefs, they tend to be contributing to further decline of already vulnerable systems. The red macroalgae, *Gracilaria salicornia*, was introduced to Hawaiian coral reefs in the 1970s. It is a strong competitor for space and is altering the 3-dimensional and compositional make up of some reefs, smothering many sessile benthic organisms including corals [23]. Perhaps the best known contemporary species introductions on coral reefs are the Indo-Pacific lionfish, *Pterois volitans* and *Pterois miles*, which have spread across much of the Caribbean since their first detection in the early 1990s [24] (Figure 1a). The lionfish are competitors and voracious predators of native fishes on Caribbean reefs [25]. Although these introduced species examples are negative and likely reinforcing pathways to non-coral states, it is possible that other introductions will contribute to novel coral-dominated assemblages, indicating we should evaluate the impacts of introduced species on coral reefs on a case-by-case basis.

Contemporary range shifts of coral reef species are becoming more common as climate change alters sea water temperatures and other environmental conditions (e.g. currents). Dramatic range shifts in coral reef organisms are being documented at higher latitudes, leading to novel ecosystem compositions, where tropical and temperate reef organisms co-inhabit stretches of coastline and new ecological interactions unfold. For example, reef corals in Japan have been extending their range northward at rates of up to 14 km/yr, generating novel 3-dimensional structures on these coastlines [26•] (Figure 1b). Commensurate with these shifting coral species, associated mobile organisms, such as obligate coral dwelling crabs, are also extending their ranges northward [27]. In south-east Australia, corals previously restricted to the Great Barrier Reef are now expanding south to the Solitary Islands, between Sydney and Brisbane [28]. Similarly, tropical fish species are mixing with temperate fish species down the coast beyond Sydney leading to novel compositions and interactions [29]. Temperature induced coral range extensions are also occurring in the Caribbean, with *Acropora* corals reported north of their expected range on the Florida peninsula and northern Gulf of Mexico [30]. These examples suggest the emergence of entirely new communities with species expanding to higher latitudes where they have been absent in recent geological time periods. As these

range shifts are occurring at the marginal edges of coral reef growth, they may not be highly diverse and productive ecosystems, but will undoubtedly lead to changing ecosystem dynamics.

Novel ecosystems can also emerge in situations where species composition and abundances change in persistent and predictable ways, for example through responses to climate change and other anthropogenic drivers [5•,6]. Indeed, the composition of the vast majority of coral reefs is unfolding in novel ways. *Acropora palmata* and *A. cervicornis* used to be dominant components of Caribbean coral reefs [10] (Figure 1c). However, overfishing, disease, coral bleaching and recruitment failure have greatly reduced their abundance and it is very unlikely they will come to dominate Caribbean reefs again in the future. In some locations, reductions in these corals have led to increases in the abundance of corals such as *Agaricia* [31] and thus novel coral-dominated assemblages [32]. However, for many Caribbean reefs, the loss of previously dominant corals has resulted in long-term live coral loss, net carbonate erosion and degradation to alternate non-coral states [19•,33,34]. Substantial alterations in coral reef assemblages are also unfolding on Indo-Pacific coral reefs. Some Indo-Pacific species of corals are far more susceptible than others to temperature induced coral bleaching and mortality (e.g. [18,35]), and similar species-specific responses to ocean acidification are also apparent [19•,36]. A range of other common impacts to reef corals also result in non-random effects, including crown-of-thorns starfish predation [37], storms [38], fishing [39] and sedimentation [40], and the influence of these drivers may interact in unexpected ways. The winner and loser dynamics from these disturbances are 2-fold processes; differential mortality as well as differences in recovery potential among coral taxa [19•,41•]. The influence of these benthic changes is shaping novel reef fish assemblage structure, with small bodied species and those specialized on certain types of coral for food, shelter or settlement most effected [42,43]. Furthermore, a different suite of the fish community is non-randomly influenced by fishing, with vulnerability mediated by life history traits such as late maturation, slow growth and large body size [42]. Taken together, these non-random disturbance responses and recovery patterns are leading to different species abundances, compositions, structures and functions, some of which can persist on decadal time scales [44,45] (Figure 1d).

### Is the novel ecosystem concept useful for coral reefs?

The novel ecosystem concept has been largely developed in terrestrial ecology, highlighting a need for some caution in its application to the marine environment, but also an opportunity for application of ideas between terrestrial and marine ecology [46]. One obvious difference is the emphasis on invasive species in causing novel ecosystems

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