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Global change ecology

Accepting the loss of habitat specialists in a changing world

Global warming is irrevocably changing coastal marine communities, resulting in community reorganisations that favour generalist fishes that are able to associate with degraded or novel habitats.

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Specialist species are uniquely adapted, typically rare, and often can particularly pique our curiosity about the living world. In the marine realm, specialist species include marine iguanas, coconut crabs, sea turtles, anemonefish, and sea horses. Writing in *Nature Ecology & Evolution*, Stuart-Smith et al.¹ report detailed evidence from reef fishes in tropical and temperate ecosystems that suggests we may be losing specialists as their habitats homogenise under the anthropogenic pressures of human use and climate change.

Some species of fish specialise to use a specific type of habitat to hide, feed, interact, and reproduce, while others – the generalists – are less picky². Stuart-Smith and colleagues present a Species Generalisation Index (SGI), based on global observations of how fish species associate with different habitat types. The index reveals how fishes are responding to acute and ongoing anthropogenic impacts, such as pollution or heat-stress events induced by climate change, that result in declines of habitat quality and diversity. Not all species of habitat-building corals and kelp can withstand stress events, and this leads to a homogenisation and simplification of marine habitats. It is no surprise that the fish communities that associate with these degraded reef habitats also change²; Stuart-Smith and colleagues now show that this habitat simplification leads to a shift in the fish community that favours generalist species (Figure 1). In line with global temporal patterns observing turnover towards generalists³, these transitioning coral reef fish community also don't necessarily show species loss, but turnover.

Not only do acute disturbance events homogenise reef habitats – habitats are also changing gradually as the planet warms. Such transitions can lead to reduced diversity and cover of habitat engineers of coastal marine ecosystems, such as scleractinian corals (Fig. 1a) and kelp (Fig. 1b). In particular, tropical coral reef species are increasingly invading higher latitude subtropical and temperate reefs. This process is called tropicalisation, where temperate kelp-dominated systems transition to systems supporting coral communities or barrens (habitats that lack structural species, or are dominated by a single taxon). In particular, increased abundances of algae-eating herbivores, together with intense fishing pressure on the natural enemies of such herbivores, facilitate the transition of temperate kelp reefs to

barrens. Sometimes these barrens persist, but new coral habitat builders can also establish in these areas. Both barrens and subtropical coral communities allow novel associations of generalist fishes with these simplified habitats. Stuart-Smith et al. show that tropical fish species with generalist habitat requirements can establish further into subtropical and temperate reefs than specialists, consistent with the known notion of tropical coral communities at high latitudes being simplified versions of their tropical counterparts, due to environmental filtering⁴.

Habitat simplification leads to a contraction in the functional trait space of associated species. This means that the fish communities present in novel high-latitude coral habitats and degraded tropical reefs are characterised by a reduced suite of traits. For example, fishes able to tropicalise by expanding their ranges into warming temperate regions possess certain enabling traits related to dispersal, feeding, and morphology⁵. These traits may be characteristic of generalist species, as flexibility in life history strategies and plasticity in behaviour exhibited by generalists are likely to also work well across a wide range of habitats, including degraded ones. The ability of a species to associate with habitat signifies a trait known to be important, but has been elusive in quantitative terms. The SGI now further illustrates how habitat homogenisation results in fish community simplification, with the loss of species that have evolved specialised trait combinations.

The loss of specialists may impact on energy and nutrient cycling on reefs. Certain fish families have more specialists than others, but many specialists have small body sizes. A key family with mostly specialists are the Gobiidae, and Stuart-Smith and colleagues find that they are among the most heavily impacted group in terms of the loss of specialists. This group contains over 2000 of mostly tiny species, with many more still undescribed. Other small fish taxa, such as the Blenniidae, Pomacentridae and Apogonidae, although supporting both specialists and generalists, contain some of the most specialised species. Small fish species are a major contributor to reef energy turnover⁶. With ongoing habitat homogenisation we might thus well be losing the engines of marine productivity and energy provisioning⁶, an issue which is important to test in the future.

What do these findings mean for the management and conservation of reef biodiversity? Increasingly, anthropocene ecosystem changes are irreversible⁷. Such changes mean that a conservation goal of achieving the persistence of all biodiversity and function is no longer realistic, requiring new conservation thinking. With broad scale reef habitat homogenisation, tropicalisation and associated novel fish communities already occurring (Fig. 1), conservation science clearly needs to redefine goals to embrace and better evaluate the role of generalist fishes in reef ecosystems, as well as their importance and relevance for people. On the other hand, global change pushes us to reconsider the conservation paradigm of preserving all species⁸. In line with typical triage approaches in emergency medicine, we may need to triage specialist fishes when needing to choose priorities given finite conservation resources⁹. Further, given the specialists' habitat specificity and the predicted declines of coral reef⁷ and kelp ecosystems¹⁰, we lack feasible actions for manage the "individual requirements of specialist species"¹ and preserving them functionally on large reef scales. Yet we still do not know which particular ecosystem services are associated with what specialists, or whether reef systems can persist without the evolutionary and adaptive potential embodied in

specialists. Remaining refuges may still allow us to answer these questions, but for the majority of shallow reef ecosystems, the increasing dominance of generalist fishes is part of the ongoing reorganisation of ocean communities for which suitable conservation interventions are not available.

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Figure 1. Changing habitats and loss of specialists.

Many marine habitats and their associated fish communities are transforming from highly complex heterogeneous to degraded homogeneous states. Examples include (a) simplifying coral reefs and (b) tropicalising kelp reefs. Stuart-Smith *et al.*¹ provide widespread evidence that fish communities associating with each habitat state transition from those containing both generalists and specialists (left panels) to those dominated by generalists (right panels), where species richness and abundance do not necessarily change but trait distributions contract. Further, the authors show that coral reef communities can sometimes recover, with specialist species re-establishing.

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