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Perspective

Will coral reefs survive by adaptive bleaching?

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Some reef-building corals form symbioses with multiple algal partners that differ in ecologically important traits like heat tolerance. Coral bleaching and recovery can drive symbiont community turnover toward more heat-tolerant partners, and this 'adaptive bleaching' response can increase future bleaching thresholds by 1–2°C, aiding survival in warming oceans. However, this mechanism of rapid acclimatization only occurs in corals that are compatible with multiple symbionts, and only when the disturbance regime and competitive dynamics among symbionts are sufficient to bring about community turnover. The full scope of coral taxa and ecological scenarios in which symbiont shuffling occurs remains poorly understood, though its prevalence is likely to increase as warming oceans boost the competitive advantage of heat-tolerant symbionts, increase the frequency of bleaching events, and strengthen metacommunity feedbacks. Still, the constraints, limitations, and potential tradeoffs of symbiont shuffling suggest it will not save coral reef ecosystems; however, it may significantly improve the survival trajectories of some, or perhaps many, coral species. Interventions to manipulate coral symbionts and symbiont communities may expand the scope of their adaptive potential, which may boost coral survival until climate change is addressed.

Introduction

Coral reef ecosystems are declining rapidly due to human influence, with ocean warming causing more frequent and severe coral bleaching and mortality worldwide [1,2]. Until action to limit warming is taken on a global scale, corals must navigate challenging future environments through mechanisms of acclimatization and adaptation, and potential human interventions to accelerate these processes [3–5]. One mechanism by which some corals might rapidly acclimatize to rising temperatures is through changes in the composition of their Symbiodiniaceae communities. Through 'adaptive bleaching' [6–8], heat-sensitive Symbiodiniaceae may be replaced or outcompeted by more heat-tolerant types, thereby increasing the thermal tolerance of the coral holobiont. Such shifts toward heat-tolerant symbionts have been observed in some corals during natural bleaching events [9–11] and field and laboratory manipulations [12–14], and have been shown to increase bleaching thresholds by 1–2°C [13,15]. While bleaching may promote rapid turnover in symbiont dominance, changes in community composition may also gradually and dynamically track the environment [16,17], suggesting 'symbiont shuffling' is a general mechanism of acclimatization to environmental change [18]. Here, 'shuffling' is used to describe any change in symbiont community composition regardless of mechanism, though scientists have historically distinguished changes in the relative abundance of existing symbionts ('shuffling') from the acquisition of new symbionts from the environment ('switching') [19]. While both mechanisms may play important roles in the various ecological contexts described here, they can be impossible to distinguish in the field; therefore, 'shuffling' is used in a general sense to encompass both mechanisms and shift focus to the ecology of symbiont community changes.

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Ecological scope of symbiont shuffling

The scope for adaptive symbiont shuffling to improve coral reef survival depends on understanding when and where it occurs. Even though corals commonly host multiple symbionts at background

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levels [20,21], many exhibit high specificity and fidelity to a single symbiont type [22] and may not be capable of shuffling [23]. Others have highly flexible symbioses, such as *Orbicella* spp. in the Caribbean, which routinely shift toward dominance by the thermally tolerant symbiont *Durusdinium trenchii* after bleaching and recovery [10,24–26]. Several other Caribbean species undergo similar shifts to *D. trenchii* [14], while others may shift to dominance by more tolerant *Symbiodinium* [27] or *Breviolum* species [28]. Shuffling toward heat-tolerant symbionts after bleaching has also been observed throughout the Indo-Pacific [9,11,29–31], suggesting it is a widespread phenomenon. Nevertheless, shuffling is much rarer in other well-studied species despite the prevalence of background symbionts [32,33]. The reason why dynamic, multi-partner symbiont assemblages occur in some coral species but not others remains poorly understood, though it may relate to variation in symbiont acquisition strategies [34,35] and the genetic architecture of symbiont recognition and immune pathways [36,37]. A better understanding of these constraints and mechanisms will be gained by studying symbiont shuffling in a wider range of host species, which should be a priority for future research.

While host-symbiont specificity may set the biological capacity for symbiont shuffling, its actual occurrence is an ecological outcome dependent on interactions between symbionts and the environment. Resources such as light and nutrients may limit symbiont growth and determine competitive outcomes among symbionts [38,39], while physical stressors and disturbance can further affect competitive hierarchies and drive successional changes in symbiont community structure [40,41]. For example, shuffling to tolerant symbiont dominance is more likely in corals that bleach more severely (reducing self-shading), and recover in a warmer environment [26], since higher light and temperature give stress-tolerant symbionts a greater competitive advantage as they repopulate the host. The difference in stress tolerance between co-occurring symbionts also determines the community trajectory through a disturbance event, with more evenly matched competitors changing less in relative abundance compared with symbionts with very different levels of tolerance, which may experience complete turnover in dominance [14]. Finally, minimum threshold abundances may also be needed in order for a symbiont to rise to dominance after bleaching [42]. In this way, symbionts' physiological traits and relative abundances, along with the environment and disturbance regime, drive variable community trajectories that sometimes result in changes in the dominant symbiont, and sometimes do not.

As reefs enter unprecedented environments and disturbance regimes, symbiont shuffling remains difficult to predict, but is likely to become even more prevalent. For example, repeated disturbances may incrementally increase background levels of tolerant symbionts such that they surpass minimum thresholds to rise to dominance after multiple bleaching events [43]. Furthermore, as tolerant symbionts increase in prevalence in coral hosts and the environment, they may be more readily available for uptake by bleached corals [44,45], leading to recovery with these symbionts in even more cases. While more research into these metacommunity feedbacks linked to symbiont availability and acquisition is needed to better predict the prevalence of symbiont shuffling (including long-term monitoring of its actual occurrence in the field), modeling studies indicate that if it is sufficiently widespread, coral cover decline may be delayed by several decades [46,47], helping to buy additional time to mitigate climate change.

Leveraging symbiont shuffling in interventions

Dynamic symbiont communities may also be leveraged in interventions to boost reef resilience, by incorporating directed symbiont manipulations into reef restoration and conservation actions [5,48]. For example, corals propagated in field or land-based nurseries could be manipulated to host tolerant symbionts prior to out planting, though to date such directed manipulations have only been performed in the laboratory (e.g. [14]). Tolerant symbionts could also be introduced into large, valuable colonies on the reef via grafting, where extracted tissue plugs are manipulated in the lab to host tolerant symbionts and re-implanted to the parent colony [49]. Seeding reef environments with thermotolerant symbionts could also boost their availability for uptake by bleached corals (e.g. [44]), but seeding approaches may be most effective in early coral life stages when symbionts are acquired from the environment. For example, rearing *O. faveolata* recruits in proximity to adult corals hosting *D. trenchii* increases uptake of these tolerant symbionts during symbiosis establishment [50], and such manipulations could be integrated into existing coral restoration approaches that rear and out-plant sexual recruits to reefs [51,52]. Finally, the scope of any of these manipulations could be further increased with the use of symbionts evolved or engineered to be compatible with more hosts [53], and/or better cope with climate change stressors [54].

Tradeoffs and limitations of symbiont shuffling

The scope for tolerant symbionts to improve coral reef survival also depends on their net effect on coral performance, including potential tradeoffs, and the longevity of any positive impacts. One primary limitation is the transient nature of shuffling to heat-tolerant symbionts, since subsequent reversion toward less tolerant types may occur over months to years [24,25,55]. However, as both baseline temperatures and the frequency of bleaching events (now averaging every 6 years [1]) continue to increase, associations with heat-tolerant symbionts are likely to become more persistent, and more beneficial. Yet, tradeoffs of these associations may also occur, such as reduced carbon translocation and calcification of corals hosting thermally tolerant symbionts [56–61], which could reduce reef growth and ecosystem resilience [62]. Other physiological tradeoffs associated with thermotolerant symbionts could include reduced reproductive output [58], or increased disease susceptibility [63]. However, such metabolic costs of stress-tolerance are likely to vary across distinct host-symbiont associations [61,64], with some heat-tolerant symbionts potentially having no negative tradeoffs. Any tradeoffs will also depend on the environment, and growth disadvantages of heat-tolerant symbionts at cooler temperatures may be eliminated or reversed as temperatures rise [65,66]. Therefore, the benefits of heat-tolerant symbionts are likely to exceed their costs, with this advantage increasing as oceans continue to warm.

Conclusion

The survival of some corals may benefit from adaptive bleaching and symbiont shuffling, with these outcomes governed by host-symbiont compatibility, disturbance ecology, symbiont availability, and metacommunity dynamics. Given these various biological and ecological constraints, symbiont shuffling alone cannot ensure the survival of coral reef ecosystems. Indeed, many coral species may not be capable of changing symbiont partners, while those that are may only do so when conditions are 'just right' to promote community turnover and persistence. Nevertheless, symbiont shuffling may positively influence the survival trajectories of some, and perhaps many, coral species under continued warming, with its effects amplified by more frequent bleaching and strengthened metacommunity feedbacks. Research on symbiont community dynamics in a broader range of coral taxa, as well as in field settings, will be critical to understand and predict the cases in which symbiont shuffling may boost coral survival. In the meantime, interventions that leverage symbiont community manipulations should also be considered to maximize their potential benefits until climate change stressors are mitigated.

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Competing Interests

The author declares that there are no competing interests associated with this manuscript.

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