

Inviolate immigrants drive diversification in the sea

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Understanding how new species arise is central to evolutionary biology, and the study of speciation remains a vibrant frontier (1–5). Although most evolutionary biologists agree that speciation occurs when populations become reproductively isolated from each other—meaning that they do not interbreed when they come into contact or, if they do interbreed, they fail to produce fertile offspring—a major challenge has been to explain how reproductive isolation comes about (5). A recent article in PNAS by Prada and Hellberg (6) addresses this important issue.

The classic scenario for how reproductive isolation arises was articulated by Mayr (7–9). According to Mayr, this process begins when populations become separated from each other, typically by a physical barrier, such as a body of water or an uninhabitable stretch of land. If this barrier prevents populations from exchanging genes, they will inevitably begin to diverge—both genetically and phenotypically—as different patterns of selection, chance events, and mutation act separately on each population. Eventually, as divergence proceeds, some such differences may, purely as an incidental by-product, cause the populations to become reproductively isolated from each other. For example, two populations would be precluded from interbreeding if they evolved divergent mate preferences. This “allopatric” model of speciation (so called, because it assumes that divergence initially arises when populations occur in geographically separate locations; i.e., allopatry) is widely accepted as speciation’s most common route (1, 3, 10).

Problem of Speciation in the Sea

In applying the allopatric model to actual populations, an important question arises: When species occur in (apparently) homogeneous habitat, how will new species arise (if at all)? Because such situations seemingly provide no opportunity for populations to become physically separated, it is unclear how such populations would become reproductively isolated from each other. Perhaps nowhere is this problem more apparent than in ocean-dwelling species, where a

single species may occupy a vast geographical area lacking any obvious physical isolating features. Moreover, many such species possess widely dispersing larval forms, which makes isolation even more difficult to achieve. Nevertheless, ocean-dwelling taxa are often species-rich (11), suggesting that, somehow, speciation has occurred numerous times in such an environment.

Prada and Hellberg’s (6) article provides a resolution to this paradox. The authors sought to explain how reproductive isolation arises in species—corals—that possess features that seemingly render the allopatric model of speciation untenable (12): corals are typically long-lived, geographically widespread, and characterized by widely dispersing larvae. Different species of coral often inhabit different depths, suggesting that populations living at different depths may, in fact, be incipient species (12). Prada and Hellberg (6), therefore, sought to determine if depth could effectively isolate different populations of corals. They did so by focusing on *Eunicea flexuosa*, a species endemic to the Caribbean.

Prada and Hellberg (6) report that *E. flexuosa* occur as two genetically and morphologically divergent lineages: a shallow-water lineage and a deep-water lineage (Fig. 1A). Interestingly, these lineages appear to have exchanged genes since their initial divergence. However, reciprocal transplantation experiments (in which adult colonies of each lineage were transferred to the habitat of the other lineage) indicate that divergent selection maintains the separation between these two lineages. Essentially, colonies from one end of the depth gradient have reduced survival at the opposite end (Fig. 1B), providing evidence of strong selection operating between depths. Presumably such selection arises because corals at different depths experience dramatically different environments (e.g., different light, waves and currents, sediment load, predators and mutualists, and availability and composition of food). Indeed, divergence between populations inhabiting the same geographical location,

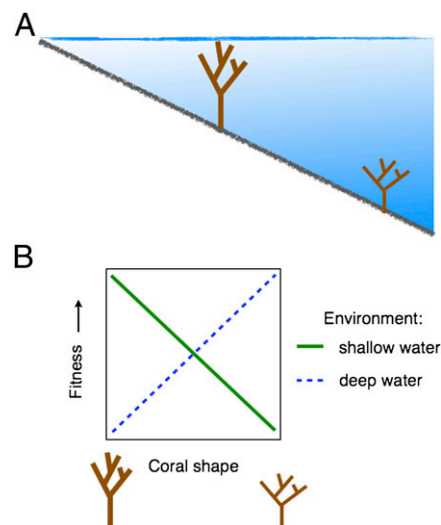


Fig. 1. How do new species form in organisms that occupy habitats where there is (seemingly) little opportunity for barriers to gene flow to arise? (A) *Eunicea flexuosa* corals in the Caribbean occur as two genetically and morphologically distinct lineages: a shallow-water lineage and a deep-water lineage. (B) Divergent selection maintains these two lineages: colonies from one end of the depth gradient have reduced survival at the opposite end. Such immigrant inviability may be crucial in promoting reproductive isolation, especially in long-lived species.

but separated by depth, is greater than that between populations at the same depth, but separated by thousands of kilometers of geography! The authors further suggest that selection against individuals from different depths is enhanced by delayed reproduction. This species takes decades to reach sexual maturity, which provides abundant opportunity for selection to operate. A larva or piece of coral landing at the “wrong” depth cannot reproduce immediately; it must survive there for decades, which (the authors’ reciprocal transplantation experiments demonstrate) is highly unlikely.

Inviolate Immigrants

This study’s greatest contribution is its clear and convincing demonstration that natural selection can act against immigrants into foreign environments, and that such selection

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can serve as an effective barrier to genetic exchange between populations. This process, known as “immigrant inviability,” is expected to occur whenever there is divergent adaptation to different environments (13, 14), and it may be a common and strong component of reproductive isolation and, ultimately, speciation. Indeed, a recent comparative analysis of diverse taxa quantified the various components of reproductive isolation (e.g., habitat/temporal isolation, sexual isolation, genetic incompatibility, natural or sexual selection against hybrids) and found that immigrant inviability is often stronger than these other more commonly considered forms of reproductive isolation (4).

Although immigrant inviability is not an isolating mechanism per se [isolating mechanisms are “biological properties of individuals which prevent the interbreeding of populations that are actually or potentially sympatric” (9)], immigrant inviability may be one of the first barriers to gene flow to arise. Essentially, immigrant inviability is expected to evolve at the same rate as adaptive divergence itself (4). Moreover, immigrant inviability may contribute directly to selection for—and the evolution of—isolating mechanisms, such as traits that restrict dispersal out of natal habitats or mate recognition for one’s own type.

To date, most studies of immigrant inviability have focused on short-lived species, such as insects (13). In contrast, *E. flexuosa* is long-lived, taking 15 y to even begin to reproduce and 30–35 y to reach full maturity. As Prada and Hellberg (6) note, immigrant inviability may be especially effective at isolating divergent populations of such long-lived species because selection can act over a long time period to purge immigrants from a given habitat. The cumulative effects of selection acting over prolonged periods of time can produce almost complete isolation between populations inhabiting different environments. Thus, immigrant viability might play an important role in isolating populations of not only corals, but also those of other long-lived species, such as trees and shrubs.

Plastic Corals

Another interesting feature of *E. flexuosa* is that it harbors environmentally cued, alternative phenotypes. A previous study demonstrated that, when different colonies of the same clone are transplanted at different depths, they facultatively change their form and come to (somewhat) resemble the native coral at their new depth (15). Over the near

term, such developmental plasticity allows a single clone to colonize and survive at different depths. Over the long term, this developmental flexibility may provide both the variation on which divergent selection acts and a mechanism for reproductive isolation.

Indeed, divergence may proceed especially rapidly when populations contain environmentally induced alternative “morphs.” In such a population, a sudden change in the environment (as when these coral land at a new depth) can simultaneously both induce and select for a single alternative morphotype. If there is underlying genetic variation in the degree to which individuals respond to the environmental change [as appears to be present in these corals (15)], this selective process can have important genetic ramifications. In particular, once only a single morph is produced in a population, selection should favor those alleles that regulate the expression of that particular morph. This process—“genetic accommodation” (16)—is a mechanism of evolution in which a novel phenotype (generated either through a mutation or environmental change) is refined into an adaptive phenotype through quantitative genetic changes. When induced phenotypes lose their environmental sensitivity and become expressed constitutively, they are said to undergo an extreme form of genetic accommodation, known as “genetic assimilation” (16, 17). Thus, population differences that initially arose through plasticity might eventually become genetically fixed. Genetic accommodation, following by genetic assimilation, might thereby contribute to the rapid accumulation of genetic differences between populations that, in turn, enhance reproductive isolation (18).

Although Prada and Hellberg’s (6) data are consistent with the above evolutionary scenario, additional information is needed to determine whether or not genetic accommodation/assimilation has actually facilitated divergence in these corals. A difficulty in testing this scenario is that, once populations have become fixed for alternative phenotypes, the evolution of these traits cannot be studied in situ. One way around this problem is to use a phylogenetically informed comparative approach (18). If plasticity has facilitated population divergence, then ancestral lineages should show environmentally contingent divergence. Furthermore, there should be evidence that selection has reduced this plasticity and refined the divergent trait’s expression in more derived lineages. In short, a comprehensive analysis of the evolution of plasticity in this group of corals is needed to evaluate what role, if any, developmental plasticity has played in promoting divergence between lineages at different depths.

Conclusions

Immigrant inviability is a potent isolating filter, particularly in long-lived species that provide abundant opportunity for selection to act before any reproduction takes place. Furthermore, the presence of habitat-dependent alternative phenotypes might represent a critical, early phase in the evolution of reproductive isolation, although this idea requires further attention. Nevertheless, studies such as Prada and Hellberg’s (6) continue to provide critical insights into the evolution of reproductive isolation between populations of widely dispersing species without obvious barriers to interbreeding.

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