The origins of tropical marine biodiversity

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Recent phylogeographic studies have overturned three paradigms for the origins of marine biodiversity. (i) Physical (allopatric) isolation is not the sole avenue for marine speciation: many species diverge along ecological boundaries. (ii) Peripheral habitats such as oceanic archipelagos are not evolutionary graveyards: these regions can export biodiversity. (iii) Speciation in marine and terrestrial ecosystems follow similar processes but are not the same: opportunities for allopatric isolation are fewer in the oceans, leaving greater opportunity for speciation along ecological boundaries. Biodiversity hotspots such as the Caribbean Sea and the Indo-Pacific Coral Triangle produce and export species, but can also accumulate biodiversity produced in peripheral habitats. Both hotspots and peripheral ecosystems benefit from this exchange in a process dubbed biodiversity feedback.

The enigma of speciation in the sea

Over half a century ago Ernst Mayr posed the question of whether speciation is fundamentally different in the sea [1]. On the basis of studies of sea urchins, he concluded that the process was the same in marine and terrestrial faunas, but this controversy flared across ensuing decades. Much of the debate centered on the relative importance of genetic isolation versus dispersal in a scientific era in which physical (allopatric) barriers were regarded as the primary, if not exclusive, starting point for speciation [2,3]. There are few obvious physical barriers in the ocean, and dispersal is extensive in this transglobal aquatic medium; two factors that should reduce opportunities for allopatric speciation [4]. Yet tropical reefs host biodiversity that rivals that in rainforests. Coral reefs cover less than 0.1% of the ocean floor [5], but their fish communities include approximately one-third of the recognized marine species. In these circumstances it is impossible to reconcile the prevailing beliefs about speciation by allopatric isolation with the plethora of closely related species living together in the sea.

If cessation of gene flow by geographic isolation is the key to terrestrial speciation, then intuitively the processes leading to speciation should be different between marine and terrestrial habitats. Most marine organisms move little as juveniles and adults, so connectivity must be through pelagic (oceanic) stages such as larvae, and in some cases this dispersal can be extensive. Whereas some reef fauna show self-recruitment over small geographic ranges [6], the majority have oceanic dispersing larvae that can contribute substantially to connectivity among regions [7]. Marine biotas show a broad range of dispersal capabilities [8], from crawl-away larvae to pelagic dispersal that is at least an order of magnitude greater than the

Glossary

Biodiversity feedback: biogeographic model with biodiversity hotspots acting as both Centers of Speciation and Centers of Accumulation and/or Overlap.

Biodiversity hotspot: region with especially high levels of biodiversity as measured by species numbers and levels of endemism. Conservation of biodiversity hotspots should aim at preserving not just species diversity but also the mechanisms underlying biodiversity production.

Center of Accumulation model: this model suggests that the high number of species in the Coral Triangle results from speciation in peripheral locations with subsequent dispersal of novel taxa into the Coral Triangle. The long history of the Pacific archipelagos, some of which date to the Cretaceous, the possibility of isolation in these peripheral habitats, and current and wind patterns that favor dispersal towards the Coral Triangle have been suggested as a mechanism.

Center of Overlap model: this model suggests that the high species diversity in the Coral Triangle is in part due to overlap of distinct faunas from the Pacific and Indian Oceans. The hypothesis is based on the premise that the isolating mechanism is the Indo-Pacific Barrier, which separates the Pacific and Indian Oceans during low sea-level stands, with the faunas of these oceans diverging during periods of isolation.

Center of Speciation model: also known as the Center of Origin, this biogeographic model suggests that tropical biodiversity hotspots including the Coral Triangle are exporters of species, possibly driven by the fracture of populations that result from geologic complexity and habitat heterogeneity coupled with intense competition.

Coral Triangle: epicenter of marine biodiversity, with over 2700 species of shore fishes and 600 species of corals, that extends from the Philippines, eastern Indonesia and New Guinea southeast to the Solomon Islands (see Figure 1 in main text).

Evolutionary graveyard: the premise that depauperate peripheral habitats act solely as sinks of biodiversity and contribute little to overall species richness.

Gametic recognition proteins (GRP): cell surface proteins that mediate the interactions between gametes with incompatibility, resulting in unsuccessful fertilization. Rapid evolution of GRPs is thought to be an important driver of speciation in some taxa.
capabilities of pollen-dispersing terrestrial biotas [9]. For example, moray eels (family Muraenidae) show high population genetic connectivity across two-thirds of the planet, from Africa to Central America [10], unicornfishes (Naso spp.) show no genetic isolation across the Indian and Pacific Oceans [11], and even the diminutive pygmy angel-fishes (genus Centropyge) show high genetic connectivity across thousands of kilometers [12]. To the extent that dispersal and gene flow influence speciation, the process cannot be the same on land and sea, or must work on vastly different scales. Here we review recent work indicating that (i) speciation in the sea can proceed without absolute barriers to gene flow, (ii) peripheral habitats such as the Hawaiian Archipelago and Red Sea can produce and export new species, and (iii) exchange of biota among extremely competitive hotspots and depauperate peripheral areas is a process that enhances species numbers and ecosystem resilience in both areas, which we term the biodiversity feedback model (see Glossary) [13]. This synthesis arises primarily from efforts to resolve the origins of marine biodiversity hotspots, including three apparently overlapping hypotheses reviewed in the next section.

### Biodiversity hotspots

John Briggs has been the primary advocate of marine centers of speciation, among which the Coral Triangle in the Indo-Pacific (also known as Indo-Australian Archipelago or Indo-Malayan Triangle, the area between Indonesia, New Guinea, and the Philippines in Figure 1) and the Caribbean Sea in the Atlantic are cradles for new species that radiate out and replace older species [14]. Under this model, intense competition in highly diverse habitats yields new species with greater fitness than their predecessors. A combination of physical and ecological partitioning is probably the most effective means to establish new species. Therefore, isolated populations within the Coral Triangle might be the precursors of speciation and subsequent radiations [15–17].

The distribution of reef fishes is consistent with this model [18] and it is apparent that much of the biodiversity in peripheral archipelagos has arrived from the central Indo-Pacific [19]. Recent evidence indicates that two reef-associated sharks (Sphyraena lewini and Triakodon obesus) radiated from the central Indo-Pacific to attain broad or global distributions [20,21]. Two new reviews provide concordant assessments for the Coral Triangle hotspot, including a long history of species accumulation beginning in the Miocene [20–12 million years ago (mya)] and subsequent export of biodiversity in the Pliocene, Pleistocene, and Holocene (7 mya to the present) [22,23].

A corollary of the Center of Speciation hypothesis is that areas peripheral to biodiversity hotspots are evolutionary graveyards, where colonizers arrive and evolve into endemic species, but never radiate beyond their new home. This is supported by studies of the isolated Hawaiian fauna, including fish, corals, and other invertebrates [24–26]. Recent studies have prompted a reappraisal of this corollary, which we examine below.

A primary alternative to the Center of Speciation hypothesis is a Center of Accumulation, in which new species arise in peripheral habitats such as oceanic archipelagos and accumulate in the center of the range because of prevailing currents [27,28]. Support for this model comes from several phylogeographic studies (see below). Budd and Pandolfi note that morphological novelty is highest at the edge of coral species distributions, consistent with the Center of Accumulation model [29].

A related model is the Center of Overlap, in which isolated faunas of the Indian and Pacific Oceans are codistributed in the area of overlap, including the Coral Triangle. The biogeographic case for Center of Overlap includes the many sister species with Pacific and Indian Ocean distributions that overlap at the boundary of these oceans [30]. Gaither et al. observed two mtDNA lineages in the grouper Cephalopholis argus corresponding to Indian and Pacific Oceans but overlapping in the boundary regions between these oceans (including the Coral Triangle; Figure 1) [31].

Overall, there is substantial evidence in support of all three processes according to recent phylogeographic studies of tropical marine fauna [13,22,33]. Whereas the Center of Speciation model involves speciation without complete

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**Figure 1.** Biogeographic provinces of the tropical West Atlantic and Indo-Pacific (indicated in blue) [23,33]. The Biodiversity Feedback model indicates that biodiversity flows out from the Coral Triangle (light blue in central Indo-Pacific) to peripheral habitats in Hawaii, the East Pacific, Red Sea, and elsewhere. In the Atlantic, Caribbean fauna can colonize the depauperate coastline of Brazil. Species diverging in these peripheral habitats can subsequently radiate back out to enhance overall biodiversity [22,23].
geographic isolation (allopatry), the other two models include some level of allopatric isolation, which raises the question as to whether isolation plays a leading role in marine speciation.

**Speciation without geographic barriers**

Speciation via allopatry, as proposed by Dobzhansky [34] and Mayr [2], continues to be the dominant paradigm in evolutionary biology [35]. By contrast, molecular phylogenies of marine organisms provide many examples of sister taxa with distributions that are adjacent (parapatric), overlapping, or even identical (sympatric). In a growing body of literature, non-allopatric speciation is inferred from phylogenetic data combined with distribution data and ecological partitions (Box 1). Examples of sympatric sister species have been documented in a diversity of taxa including East Pacific fishes [36], North Atlantic snails [37], and Caribbean sponges [38]. Among the most intriguing examples are sympatric species that seem to maintain separate identities despite ongoing gene flow, including Pacific pygmy angelfishes (Centropyge flavissima complex) [12], Caribbean hamlets (genus Hypoplectrus) [39], and sea stars (Linckia multiflora and Linckia laevigata) [40] (Figure 2). These may represent the earliest stages of speciation.

In addition to overlapping sister species, numerous examples have emerged of sister species with adjacent distributions. Caribbean gobies (genus Elacatinus) have several color morphs with parapatric distributions, for which coloration differences might facilitate assortative

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**Box 1. Cases of non-allopatric speciation**

**Caribbean and East Pacific reef fish, collectively known as grunts (genus Haemulon), show numerous examples of sympatric sister species [50]. Vocalization may be key to mate recognition in the darkness as these fishes spawn at night. It is suspected that sexual selection on the basis of vocal cues promotes reproductive isolation among sister species. Photo: L.A. Rocha.**

**West Pacific reef fishes include several examples of sympatric sister species characterized by habitat shifts, including gobies (Gobiodon spp.) [99]. In this case, sympatric speciation has been accompanied by a host shift between Acropora corals. Photo: P.L. Munday.**

**Hawaiian limpets (Cellana spp.) comprise three sympatric sister species that partition along ecological lines into upper, middle, and lower intertidal zones. Habitat partitioning is thought to be caused by desiccation, thermal tolerance, and/or predation avoidance mechanisms, and reproductive isolation may be accomplished by the timing of genetic release [91]. Photo: C.L. Bird.**

**The brooding coral Seriatopora histrix shows genetic partitions between adjacent habitat types on the Great Barrier Reef [98], prompting the authors to conclude that “adaptation to the local environment has caused ecological divergence of distinct genetic groups within S. histrix.” Photo: J. Sprung.**

**Caribbean wrasses (Halichoeres spp.) reveal intraspecific genetic partitions between adjacent and ecologically distinct habitats, but high genetic connectivity between similar habitats separated by thousands of kilometers [95]. Photo: L.A. Rocha.**

**Nudibranchs (genus Phestoila) form a close bond with their scleractinian coral host, feeding, reproducing, and requiring host-specific chemical cues for settlement. Phylogenetic analyses revealed several incidences of host-shifting accompanied by speciation [89]. Photo: R. Williams.**

**The Caribbean sponge Chondrilla caribensis has two ecotypes, one proposed ancestral ecotype adapted to reef habitats and another specialized for mangrove habitats. These ecotypes, long described as a single species, have been distinguished on the basis of morphology and genetics [96]. Photo: K. Ruetzler.**

**The Caribbean basslet Gramma dejongi has a restricted geographic range completely encompassed by the widespread sister species G. loreto. In describing this species, Victor and Randall note that G. dejongi has a narrower depth range than G. loreto [97]. Photo: B. Victor.**

**Sister species of brown algae (genus Fucus) segregate along a steep intertidal gradient despite ongoing hybridization. Common garden experiments show that physiological resistance to desiccation in each species is commensurate with intertidal exposure time [94]. Photo: K.R. Nicastro.**
mating at range boundaries [41]. The *Dascyllus trimaculatus* species complex of four closely related Pacific damselfishes has parapatric distributions [42]. Particularly interesting cases of parapatry include highly mobile marine vertebrates with ecotypes that segregate into adjacent (often inshore and offshore) morphotypes, a phenomenon observed in marine mammals [43,44], sharks [45], and manta rays [46]. These species are all capable of vast dispersal and yet retain genetic partitions along ecological boundaries.

These and many other examples have prompted researchers to resurrect ecological factors as primary drivers in marine speciation [47]. This Darwinian view of selection driving speciation is a marked departure from the era of vicariant biogeography, when speciation was defined in terms of geography and physical isolation [3]. Clearly, a single model of speciation via allopatric isolation is insufficient to describe the diversity of species in the sea. The combination of hard, soft, or intermittent barriers (such as oceanic currents, water masses, expanses of deep ocean, or land masses exposed during glaciation) and ecological differences between adjacent areas represents a middle ground between speciation in sympatric or allopatric isolation, a very fertile circumstance for speciation in the sea [4,48].

A counterargument to these cases of apparent sympatric speciation is based on allopatric speciation with subsequent range expansion and secondary contact. Under this scenario, speciation occurs in isolation but then species ranges expand to overlap [49]. This explanation of historical changes in geographic distribution is very difficult to disprove, and is almost certainly correct in some cases. Isolation followed by secondary contact can explain diversification within the Coral Triangle for less dispersive

![Figure 2. Sister species with overlapping distributions that maintain striking color differences despite apparent gene flow: (a) *Hypoplectrus puella* and (b) *Hypoplectrus gemma* in the Caribbean Sea [39]; (c) *Centropyge vrolikii* and (d) *Centropyge flavissima* in the West Pacific [12]; and (e) *Linckia multiflora* and (f) *Linckia laevigata* in the West Pacific [40]. Photos: L.A. Rocha and G. Paulay.](image-url)
species (e.g., the clownfish Amphiprion ocellaris) [16]. It is harder, however, to fit this hypothesis to recently derived species (such as the grunts, Haemulon spp.) in which many sister species have entirely overlapping distributions [50].

Several research groups have concluded that sympatric (or parapatric) speciation is faster than the allopatric alternative [35,51], averaging approximately 200,000 years versus 2.7 million years in Drosophila, presumably because selection can establish a reproductive barrier more rapidly than random genetic drift due to physical isolation [52,53]. Rapid evolution of gametic recognition proteins (bindins) can facilitate the final stages of reproductive isolation [54]. Examples of rapid speciation include marine snails [55], seastars [56], and marine fishes [57]. Recent modeling studies indicate that the more rapid speciation in sympatry or parapathy is likely driven by a combination of sexual selection (mate recognition and assortative mating) combined with adaptive natural selection for alternative habitats [58].

Peripheral habitats can export new species
The Center of Speciation versus Center of Accumulation and/or Overlap hypotheses cast oceanic islands in opposing roles. In the Center of Speciation model, islands are evolutionary dead ends, whereas in the Center of Accumulation and/or Overlap, islands are engines of biodiversity production. Recent studies have evaluated these alternatives. Although some ocean island endemics appear to be relic populations of previously widespread species [19], many have become established recently (neo-endemic; e.g., Thalassoma spp.) [32], with their presence demonstrating evolutionary innovation around oceanic islands.

Accumulated evidence indicates that areas peripheral to biodiversity hotspots are exporting genetic and biological diversity [59]. The ember parrotfish (Scarus rubroviolaceus) occurs throughout the Indo-Pacific, but population genetic data indicate that larval export from Hawaii is an order of magnitude greater than import [60], and this ratio is even higher for the deepwater crimson jobfish Pristipomoides filamentosus [61] and the lollyfish sea cucumber Holothuria atra [62]. The bullethead parrotfish (Chlorurus sordidus) has three distinct mtDNA lineages corresponding to the Indian Ocean, the West Pacific, and Hawaii. However, fish collected in the Northwestern Mariana Islands (westward and down-current from Hawaii) have the Hawaiian lineage, indicating a period of extended Hawaiian isolation followed by more recent larval export [63]. Migration estimates for the Indo-Pacific yellow tang (Zebrasoma flavescens) are similar to those for the ember parrotfish, with a prevailing pattern of larval export from Hawaii [64]. Moreover, yellow tang ecology, historical demography, and phylogenetics point to a Hawaiian origin for this widely distributed reef fish. Hence, Hawaii is both a source and recipient of Indo-Pacific marine diversity.

The Red Sea can also export unique genetic lineages to adjacent regions. Despite a volatile geological history characterized by intermittent isolation and multiple salinity crises, mtDNA distributions of widespread reef fish species indicate that some species originate in the Red Sea with subsequent export to the Indian Ocean [65].

Isolated archipelagos and peripheral seas are not the only sources conveying species into areas of higher biodiversity. The continental coastlines of the Indo-Pacific and Atlantic can also provide evolutionary novelties. The parrotfish genus Scarus includes two basal lineages (Scarus zuñar and Scarus collana) endemic to the coastlines of the northern Indian Ocean and Red Sea [66]. The continental reefs of the tropical eastern Pacific have contributed at least 23 species to the Central Pacific [67]. Much of the reef fauna of the eastern tropical Pacific are derived from the central Indo-Pacific, involving migration events across the vast open ocean between the Central and East Pacific (Figure 1). However, phylogeographic studies indicate recent or ongoing connections in both directions [68]. In the tropical Atlantic, the Caribbean is recognized as a biodiversity hotspot with approximately 814 reef fishes, and the Brazilian coastline is a depauperate outpost of this fauna with approximately 471 species [69]. Most of the Brazilian fauna is derived from the Caribbean, but Brazil also exports both genetic diversity and fish species back into the Caribbean [13].

These studies demonstrate that isolated islands, marginal seas, and peripheral coastlines are not evolutionary graveyards for marine fauna. We anticipate that with more investigations, the number of examples of biodiversity export from peripheral areas will grow. Clearly, biodiversity production in tropical seas does not fall easily into a model of a Center of Speciation, Accumulation, or Overlap, but requires a more inclusive model that incorporates all of the observed patterns.

Biodiversity feedback: a new paradigm
In recent years a number of phylogeographic studies have tested whether the youngest lineages or species are in biodiversity hotspots (favoring Center of Speciation) or in peripheral habitats (favoring Center of Accumulation and/or Overlap). The results have been mixed. Barber et al. support a Center of Speciation on the basis of the genetic architecture of mantis shrimp (Stomatopods) [15], and similar patterns have been reported for mangroves (Rhizophoraceae) [70] and turban snails (Gastropoda) [71]. Teske et al. support the Center of Accumulation model on the basis of seahorse (Hippocampus spp.) phylogenetics [72]. In a survey of eight fishes, four corals, and one mollusk, Halas and Winterbottom observed evidence for both hypotheses [73]. Phylogeographic patterns in wrasses (Halichoeres spp. and Thalassoma spp.) also support both models [32,74]. These studies laid the foundations for the current synthesis, with the recognition that these models are not mutually exclusive. The new biodiversity feedback model [13] incorporates elements of all three previous models (Box 2).

There is no question that allopatric speciation occurs in the sea, and many examples have emerged from phylogeographic studies [75]. It is also clear that rare dispersal events to oceanic archipelagos, followed by isolation and speciation, are an important evolutionary process responsible for the high level of endemism in remote archipelagos [76,77]. The paradigm shift here is that these marine species can sometimes radiate further and escape the evolutionary dead end of peripheral isolation. In Hawaii,
Marine versus terrestrial speciation

It remains to be seen whether biodiversity feedback is operating in terrestrial hotspots, but our focus remains on the tropical reef ecosystems that are the heart of marine biodiversity. In a departure from our illustrious predecessors, new research indicates that speciation has a different blend of processes in the sea. As noted by Dawson and Hamner [87], there is no hard dichotomy between speciation mechanisms in marine and terrestrial spheres; diversification is proceeding along both geographic and ecological partitions. However, the greater dispersal ability of most marine organisms reduces the prevalence of the former and tips the balance towards the latter. This contrast is clearly illustrated in the natural history of the Hawaiian Islands. Above the waterline, hundreds of terrestrial species have radiated from single rare colonization events. Examples range from flowering plants to insects to birds, and the footprints of allopatric speciation are strong [88]. Below the waterline, however, allopatric divergence is apparent in low-dispersal species, but radiations within the archipelago have a stronger ecological component [89–91]. Another important distinction is that Hawaii exports marine biodiversity, whereas exports of terrestrial diversity are virtually unknown. Hence, it is apparent that the origins and maintenance of biodiversity are starkly different in the sea, as is the prevalence of various mechanisms of speciation.

Concluding remarks

Two decades of phylogeographic research indicate that both allopatric and sympatric speciation is occurring in marine ecosystems, with the combination of ecological divergence and partial isolation (parapatry) perhaps offering the richest opportunities for diversification. Marine biodiversity hotspots are wellsprings that export species, but isolated archipelagos, marginal seas, and depauperate coastlines also contribute to overall biodiversity. Furthermore, the interaction between hotspots and peripheral habitats can boost biodiversity in both. The Indo-Pacific hotspot with the greatest diversity has a halo of archipelagos in both the Indian Ocean and (especially) the Pacific Ocean. The Caribbean hotspot has no halo, but has demonstrated feedback with depauperate Brazilian reefs [13]. Under this biodiversity feedback model, the islands that surround the central Indo-Pacific Coral Triangle are essential to the processes that support the highest marine biodiversity on the planet.

Although phylogeographic and phylogenetic studies set the stage for this paradigm shift, the field is entering a vast new stage of exploration. It is now possible to read entire genomes and divide genomes into arrays of neutral loci and regions under selection [58]. In abundant cases of suspected speciation by natural selection in sympatry (versus allopatry and secondary contact), genomics will reveal which loci are under selection and whether these are responsible for evolutionary divergences that are the foundation of biodiversity. New coalescent modeling approaches hold promise for revealing the timing of the cessation of gene flow and the relative roles of drift and selection responsible for evolutionary divergences [92]. It is certain that paradigms will fall, new ones will rise, and science will take a giant step towards the resolution of

the yellow tang [64], lollyfish [62], bullethead parrotfish [63], and ember parrotfish [60] have exported genetic and biological diversity, and export of biodiversity to the Coral Triangle has been shown for the lemon damselfish (Pomacentrus moluccensis) [78]. Rather than being an evolutionary graveyard, peripheral habitats can export biodiversity.

The ecological component of speciation

Although isolation can explain much of marine biodiversity, there is growing recognition that speciation in the sea can also occur in the presence of gene flow. The consensus is that this occurs when divergent selection overwhelms the homogenizing effect of gene flow [79,80].

New species can arise through intense competition in biodiversity hotspots, and these may constitute the majority of novel evolutionary lineages. However, new species are also evolving under conditions of ecological release in the depauperate archipelagos that surround biodiversity hotspots. In the Coral Triangle, a carnivorous grouper (family Epinephelidae) might overlap with over 100 other grouper species, in particular 15 members of the widespread genus Cephalopholis with similar ecology and diet [81]. Under such conditions, there is a premium on habitat partitioning and specialization that leads to rapid speciation, with subsequent radiation of the fitter species into new areas. In the peripheral archipelago of Hawaii, an introduced grouper (C. argus) has to contend with no other members of the genus and only one other member of the taxonomic family [82], so that ecological release has allowed expansion of niche breadth [83]. This pattern is consistent with the ecological opportunity hypothesis proposed by Simpson [84] and recently supported by empirical studies [85,86]. The intense competition in the center, in conjunction with ecological release at the periphery, results in biodiversity feedback that produces more species than either process could alone.
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Darwin’s mystery. Furthermore, it is apparent that if human minds can conjure a plausible speciation mechanism, then nature can probably provide an example, and perhaps more as yet undreamed.

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