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PERSPECTIVE

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The Habitat Persistence Hypothesis: a new perspective on the distribution of coral-reef organisms

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Abstract

We propose and define the "Habitat Persistence Hypothesis" (HPH) to explain the biogeographical distributions of organisms (especially fishes, invertebrates and algae) inhabiting tropical coral reefs. Both published and unpublished sources indicate that species occurring on deep coral reefs show higher rates of endemism and a less apparent biodiversity gradient across the Pacific Ocean than their counterparts inhabiting shallow coral reefs. The HPH accounts for these biogeographical differences by stipulating that deep reefs are relatively unaffected by sea level changes associated with glacial-interglacial cycles. Shallow-reef habitats may persist across sea level changes in regions with sloped bathymetry (e.g., continental regions and large islands), but are largely extirpated in regions with steep bathymetry (e.g., coral atolls). The HPH suggests that regions with habitat persistence are characterized by higher rates of endemism, and that patterns of attenuating diversity with increasing distance from centers of species richness are shaped by relatively recent recolonization of less persistent habitats from regions with greater habitat persistence. Whereas most existing hypotheses that attempt to explain biogeographical patterns observed on coral reefs (especially in the Indo-Pacific region) rely on observations limited to shallow (<30 m) coral-reef habitat and invoke processes operating on speciation time-scales ($10^7 – 10^8$ yr), the HPH incorporates patterns observed within the remaining 80% of coral-reef habitat (30 – 150 m) and invokes processes operating on time scales associated with sea-level changes ($10^5 – 10^6$ yr). The HPH posits seven specific predictions about coral-reef biogeography that can be directly tested to distinguish it from previous hypotheses. Our intention is to describe the rationale and qualitative support for the HPH with the hope of providing a framework for accumulating sufficient quantitative data to test the predictions, which we anticipate will require decades of robust field surveys.

Highlights

- A novel hypothesis is presented to account for patterns of geographic distribution of marine organisms inhabiting both shallow and deep coral-reef habitats.
- In contrast to most existing hypotheses of tropical marine biogeography, the basis for the hypothesis reflects decades of published and unpublished data and observations across the entire depth range of coral-reef habitats (0-150m).
- The hypothesis posits that differences in large-scale biogeographic patterns between shallow- and deep-reef organisms is at least partly driven by the effects of sea-level changes associated with glacial cycles on persistence of shallow vs. deep habitats in areas with sloped vs. steep bathymetry.
- The hypothesis implies that much of the shallow-reef distributions observed today are the result of processes happening on timescales of tens of thousands of years (glacial cycles) rather than hundreds of thousands or millions of years (evolution and/or plate tectonics).
- Apparent increased rates of local endemism among species inhabiting deep habitats and shallow habitats in areas of sloped bathymetry (compared to shallow habitats in areas of steep bathymetry) are the result of habitat persistence allowing commensurate persistence of isolated populations for timescales sufficient to allow for evolutionary divergence.

Keywords: biodiversity hotspot, center of origin, Coral Triangle, coral reef, dispersal, endemism, marine, mesophotic coral ecosystems, sea level change, speciation

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Introduction

Much has been written about the observed distribution patterns of organisms inhabiting tropical coral reefs. Coral-reef biodiversity peaks in the western equatorial regions of the three major tropical oceans, with attenuating diversity along eastward and latitudinal gradients (Briggs 1974, Veron 1995, Myers 1999, Mora et al. 2003, Bellwood and Meyer 2009, Carpenter and Springer 2005). This pattern is most evident in the Pacific Ocean (Fig. 1). There is far less agreement on hypothesized mechanisms to explain the origin and causes of this general pattern (Bowen et al. 2013, Gaither and Rocha 2013, Bellwood et al. 2015). A thorough review of the various hypotheses is beyond the scope of this work; however, the different perspectives can be broadly clustered into several categories, including *vicariance models* (Springer 1982, Paulay 1990, Pandolfi 1992, Santini and Winterbottom 2002), *centers of origin* (Briggs 2003, Carpenter et al. 2011, Barber et al. 2011, Cowman and Bellwood 2013, Tornabene et al. 2015), *centers of accumulation* (Ladd 1960, Jokiel and Martinelli 1992, Budd and Pandolfi 2010), *regions of overlap* (Woodland 1983, Hobbs et al. 2008, Gaither and Rocha 2013), *centers of survival* (McCoy and Heck 1976, Barber and Bellwood 2005, Cowman and Bellwood 2013), and *models based on environmental and ecological parameters* (Vermeij 1978, Fraser and Currie 1996, Bellwood and Hughes 2001, Renema et al. 2008, Brown 2014).

No clear consensus has emerged for any of these hypotheses, and most recent treatments acknowledge that elements of several hypotheses are likely at play (Randall 1998, Wilson and Rosen 1998, Bernardi et al. 2004, Allen and Erdmann 2012, Bowen et al. 2013, Hodge et al. 2014, Bellwood et al. 2015, Bowen et al. 2016). These different biogeographical hypotheses are supported by varying degrees of empirical evidence, but in some cases different hypotheses have similar or congruous predictions, so it is not always clear which alternative biogeographical mechanism best explains the available evidence. Moreover, available evidence is fragmentary, and in some cases woefully lacking. Even for the most studied coral-reef organisms (fishes, scleractinian corals), accurate distribution patterns are not uniformly available. Comprehensive regional inventories of species exist only for a few localities (particularly throughout the Pacific and Indian Oceans), and even the fishes and corals are plagued by incomplete or unstable taxonomy (Forsman et al. 2010, Gaither et al. 2015). Perhaps the most significant limitation of existing hypotheses for coral-reef biogeography is that the vast majority of the documented patterns of species distributions, “hotspots”, endemism, and general diversity have been limited to observations of species occurring on the shallowest 30 m of coral-reef habitat, primarily due to the depth limitations of conventional SCUBA technology (Parrish and Pyle 2002, Pyle 2019a). Despite the limited knowledge of deep-reef habitats, hermatypic corals have been found at 98 m in the tropical Atlantic (Hartman 1973, Fricke and Meischne 1985, Appeldoorn et al. 2019, Frade et al. 2019, Francini-Filho et al. 2019, Reed et al. 2019, Slattery and Lesser 2019), 145 m in the Red Sea (Fricke and Schuhmacher 1983, Eyal et al. 2019), 165 m in Hawaiʻi and Johnston Atoll (Kahng and Maragos 2006, Pyle et al. 2016, Spalding et al. 2019a), and 172 m in the Gambier archipelago (Rouzé et al. 2021). Nearly 100% coral cover has been reported at 70 m on the Great Barrier Reef (Hopley et al. 2007, Bridge et al. 2012, 2019) and in Hawaiʻi (Pyle et al. 2016, Spalding et al. 2019a), and up to 60% coral cover at 60 – 75 m at Pulley Ridge in the Gulf of Mexico (Jarrett et al. 2005, Reed et al. 2019). Photosynthetic algae have been observed at similar or deeper depths (Littler et al. 1985, Hills-Colinvaux 1986, Wagner et al. 2011, Spalding et al. 2019b), and fish species on reef habitats down to about 150 m belong almost exclusively to families typical of shallower coral-reef environments (Pyle 1996, Tornabene et al. 2016, Baldwin et al. 2018, Pyle et al. 2019b). Thus, the evidence about distribution patterns of coral-reef organisms is based on incomplete species inventories with inadequate taxonomic resolution and limited to approximately one-fifth of coral-reef habitat. It should, therefore, come as no surprise that mechanisms underlying coral-reef biogeographical patterns remain unresolved.

Over the past three decades, the authors and collaborators have conducted dozens of surveys of deep coral-reef habitat (mesophotic coral ecosystems [MCEs]; 30 – 150 m; see Hinderstein et al. 2010; Baker et al. 2016, Kahng et al. 2017, Loya et al. 2019) at numerous localities throughout the tropical Pacific (Fig. 1) (e.g., Pyle 1996, 2000, Wagner et al. 2014, Kane et al. 2014, Pyle et al. 2016, Coleman et al. 2018). These surveys (which serve as the basis for a large-scale biogeographical analyses currently in development) have revealed two qualitative patterns among species inhabiting deep-reef habitats that were both unexpected, and inconsistent with patterns observed among shallow-reef habitats (i.e., the patterns upon which virtually all biogeographical hypotheses of coral-reef organisms are based). First, species restricted to deep reefs tend to have smaller geographical ranges (on average) than species restricted to shallow reefs, which also means that *a greater proportion of species on deep reefs are endemic to specific geographical regions* (Pyle 1996, Pyle 2000, Kane et al. 2014, Pyle et al. 2016, Pyle and Copus 2019). Second, the general pattern of high diversity in the Indo-Australian Archipelago (IAA), with attenuating diversity eastward across the tropical Pacific – well documented for many groups of organisms inhabiting shallow coral reefs – *does not appear to exist among organisms inhabiting deep coral reef environments* (Pyle 2000, Pyle and Copus 2019). Hence the emerging picture for reef biodiversity may include higher species diversity on shallow reefs, but higher endemism on deep reefs (Kane et al. 2014, Kosaki et al. 2016).

Herein we describe a generalized hypothesis to explain patterns of coral-reef biogeography including distribution patterns observed throughout the entire depth range of coral-reef habitats. We do not represent this model as “the” explanation for patterns of species richness and endemism on coral reefs; rather, we introduce it as another possible mechanism shaping

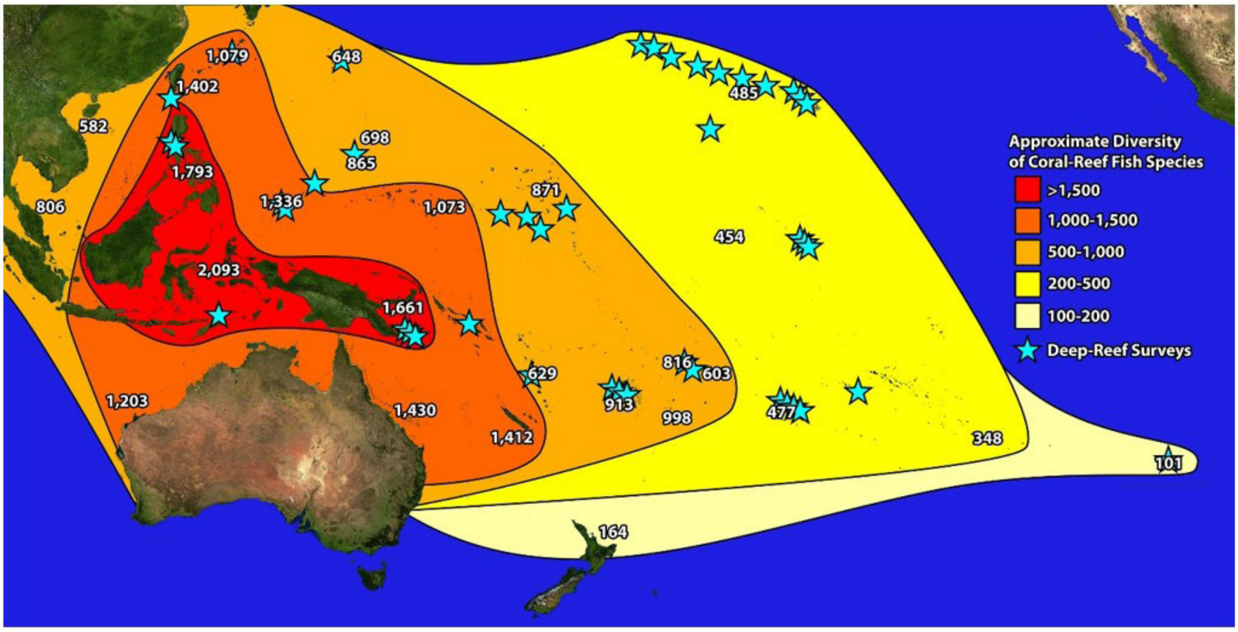

Figure 1. Map of the tropical Pacific, showing the generalized pattern of eastward attenuation of shallow-reef fish species diversity. Colored regions represent approximate areas for different levels of diversity (1,500+ species, 1,000–1,500 species 500-1,000 species, 200-500 species, and 100-200 species), based on numbers of reef-associated fish species reported in FishBase[1] (overlayed numbers). Locations where qualitative observations of MCE habitat have been made during the past three decades by authors and collaborators are represented by blue stars.

biodiversity patterns as they currently exist on coral reefs worldwide. Moreover, the model is rudimentary. The dynamics that have led to modern-day distribution patterns of coral reef biodiversity are likely almost as diverse as the organisms themselves. In our ongoing efforts to evaluate this model, we expect to find exceptions and idiosyncratic distribution patterns (as is the case for all generalized models of biogeography). Although this perspective was largely inspired by observations of species distributions on deep coral reefs throughout the Pacific (to be published elsewhere), its greatest implications relate to mechanisms affecting the distribution patterns of shallow-reef species. The section that follows represents a formal description of a novel biogeographical hypothesis relating to distribution patterns of coral-reef organisms, based on the relative persistence of habitat over evolutionary time-scales. Although the hypothesis itself is very general and may apply to biogeographic patterns in any environment involving different degrees of habitat persistence over time, herein we focus particularly on what is likely to be among the most important factors influencing persistence of coral-reef habitat: changes in sea level in response to glacial-interglacial cycles and the corresponding influence of differing bathymetric profiles.

The aim of this paper is not to "prove" the application of the hypothesis with respect to coral-reef ecosystems; rather our intention is to clearly define the hypothesis, including a clear articulation of both the premises that under-pin it, and the specific predictions that result from it. The conclusions here are based primarily on the distribution patterns of fishes in part because they are the best-studied group of marine organisms across both shallow and MCE depths. However, many (if not most) marine organisms share similar life-history traits and are likely subject to similar factors in shaping broad distribution patterns, so we extend this hypothesis to potentially apply to all major groups of coral-reef-associated organisms. Data necessary to support or refute the hypothesis – including for fishes, invertebrates and algae – will only come from decades of future research involving careful documentation of biogeographic patterns, depth distributions, and ecology of species throughout many locations, and across the entire depth range of coral-reef ecosystems.

The Habitat Persistence Hypothesis

The general concepts behind the Habitat Persistence Hypothesis (HPH) were first outlined in the context of explaining biological diversity, richness and endemism of coral-reef fishes at Johnston Atoll (Kosaki et al. 1991). It was later developed into a generalized model, initially proposed as the "Center of Refuge" hypothesis (Pyle 2005). However, that label was easily confused with the "area of refuge" hypothesis (McCoy and Heck 1976, Paulay 1990, Bellwood and Hughes 2001, Carpenter and Springer 2005), as well as hypotheses about deep coral reefs serving as ecological refugia for shallow reefs (Hughes and Tanner 2000, Riegl and Piller 2003, Bongaerts et al. 2010, Hinderstein et al. 2010, Kahng et al. 2014, Baker et al. 2016, Semmler et al. 2016, Smith et al. 2016, Bongaerts and Smith 2019, Bloomberg and Holstein 2021). A brief description of the HPH, as fully described and articulated herein, is included in Pyle and Copus (2019).

The underlying premise of the HPH is that the persistence of habitat over ecological and evolutionary timescales is correlated with the persistence of populations (or lack thereof) over those timescales, and broadly influences both the biogeographic distribution of organisms and their associated patterns of evolution. Herein we provide a comprehensive description of the HPH in the context of tropical coral-reef ecosystems, with particular emphasis on the effects of sea-level changes and their impacts on habitat persistence in regions with different bathymetric profiles. We acknowledge that latitudinal compression (shrinking of the tropics) also influenced species distributions during glacial cycles. However, the extent of compression is controversial, whereas sea level changes are more tightly constrained and a more tangible hook upon which to hang a hypothesis. We include a detailed description of six premises and seven predictions related to the HPH in this context, as well as a discussion of key areas for future testing and other implications.

Premises

The six basic premises of the HPH in the context of coral-reef ecosystems, as illustrated in part in Fig. 2, are as follows:

1. *Relative sea level has changed throughout oceanic regions on a global scale*

During the last glacial maximum (LGM), a period that lasted from approximately 26.5 until 19 – 20 thousand years ago (ka), global eustatic sea level (ESL; changes in ocean volume) was approximately 125-130 m lower than it is today (Fairbanks 1989, Pillans et al. 1998, Peltier and Fairbanks 2006, Clark et al. 2009, Rohling et al. 2014, Lambeck et al. 2014, Yokoyama et al. 2018). Fluctuations in relative sea-level (RSL) of approximately the same magnitude (depending on specific regional and local factors such as tectonic uplift and subsidence, glacial isostatic adjustments [GIA] etc that affect RSL compared to ESL) have occurred throughout tropical regions in association with glacial-interglacial cycles at approximately 100-ka intervals during the mid-to-late Pleistocene (Hanebuth et al. 2000, Voris 2000, Bintanja et al. 2005, Bintanja and van de Wal 2008, Rohling et al. 2009, Elderfield et al. 2012, Lambeck et al. 2014). Although frequency and magnitude of past sea-level changes (as well as differences between ESL and RSL) vary, the core principles of the HPH apply regardless and are particularly applicable to how biogeographic patterns have been shaped since the LGM (as well as other previous glacial and interglacial periods).

2. *Falling RSL results in more substantive loss of shallow-reef habitats where existing bathymetry is steep or vertical, than in regions where existing bathymetry allows lateral habitat shifts as RSL falls*

As illustrated schematically in Fig. 2, many oceanic atolls and islands are characterized by steep or vertical bathymetry extending downward hundreds of metres (hereinafter referred to as "steep bathymetry"). By contrast, many continental islands (e.g., the IAA) and large volcanic archipelagos within Oceania (e.g., Marquesas Islands, Hawaiian Archipelago, and Fiji Islands; see Cabioch et al. 2008, SOEST 2014, Pyle 2019b, respectively) have more gradually sloping bathymetry and/or shelves spanning the upper 150 – 200 m (hereinafter referred to as "sloped bathymetry"). As RSL falls, shallow-reef habitats such as mangroves, lagoons, patch reefs, barrier reefs, spur and groove habitats, and shallow fore-reefs (among others) disappear from oceanic atolls and islands with steep bathymetry (Wise and Schopf 1981, Kosaki et al. 1991, Valentine and Jablonski 1991, Nunn 1998, Camoin et al. 2001, 2012, Dickinson 2004, Lisiecki and Raymo 2005, Norris and Hull 2011, Woodroofe and Webster, 2014, Camoin and Webster 2015, Ludt and Rocha 2015, et al. 2021). Conversely, such shallow-reef habitats are more likely to shift along bathymetric contours (and thereby persist across glacial cycles) in regions with sloped bathymetry (Abbey et al. 2011, Webster et al. 2018; see Fig. 2a-c).

Although examples of both sloped and steep bathymetry can be found within many archipelagos and other similarly-sized geographic regions (e.g., Toomey et al. 2013), the important factor for the purposes of the HPH is the presence of substantial sloped bathymetry within a relatively small (~10's – 100's of km) geographic scale; such that shallow-reef habitats persist within the geographic range of reef-dwelling populations. Several studies have also explored the influence of varying substrate slopes on coral reef development on both oceanic islands (Webster et al. 2007) and continental margins (Webster et al. 2018, Esat et al. 2022). In both cases, reef development in response to sea level fall and rise on steep bathymetry leads to narrower reefs (and likely compressed associated habitats) compared with sloped bathymetry. It should also be noted that a *rise* in RSL can lead to a *loss* of shallow-reef habitat at coral atolls, in cases where the rise exceeds the rate at which corals and other reef-building organisms can grow vertically – the "Darwin Point" (Grigg 1982, Webster et al. 2004, Woodroofe and Webster, 2014, Sanborn et al. 2017). In such cases, the resulting submerged reef ("drowned atoll") will also lack the suite of shallow-reef habitats as described above. Conversely, a *fall* in RSL can lead to *restoration* of shallow-reef habitat in areas with submerged reefs and seamounts (Pinheiro et al. 2017, Webster et al. 2018). However, these examples are not as likely to have as broad-scale impact on species distribution as RSL drops that reduce the availability of shallow-reef habitats throughout regions with steep bathymetry.

3. *Loss of shallow-reef habitats leads to extirpation of populations of reef-associated species that require such habitats for part of their life cycles*

Classic island biogeography theory maintains that increased rates of local extinction will result from a decrease in habitat area (MacArthur and Wilson 1967), and this applies to marine environments as

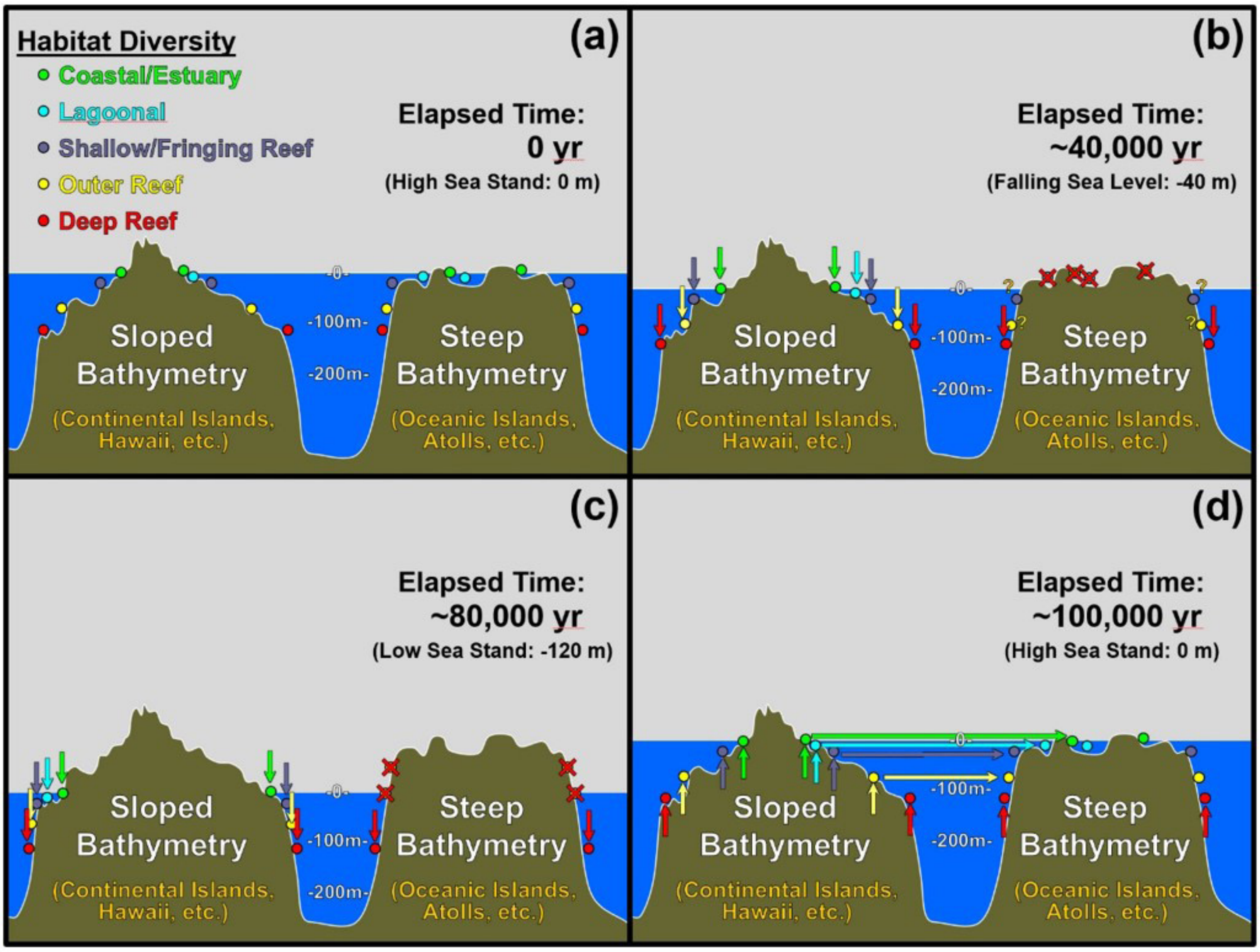

Figure 2. A diagrammatic representation of the mechanism underlying the Habitat Persistence Hypothesis, showing the effects of different phases of a single glacial cycle and associated changes in relative sea level (RSL) on shallow and deep coral-reef habitats (and associated species assemblages) at locations with different bathymetric profiles. a) At the end of an interglacial high RSL, shallow- and deep-reef habitats exist at all localities. b) As RSL drops, shallow and deep habitats shift along the bathymetric contours of localities with sloped bathymetry, but disappear from localities with steep bathymetry. c) During periods of low RSL, most shallow and deep habitats persist at localities with sloped bathymetry, but only deep-reef habitats persist at localities with steep bathymetry. d) After high RSL is restored, shallow-reef habitats at localities with steep bathymetry are likewise restored, and these habitats are recolonized from source populations that persisted across all phases of the glacial cycle at localities with gradually sloping bathymetry. Thus, biogeographical patterns among shallow-reef organisms on many islands with steep bathymetry are more likely shaped by relatively recent dispersal from regions with persistent shallow habitat, whereas patterns of deep-reef organisms are shaped proportionally more by speciation processes operating on longer time scales. Diagrams modified from Pyle 2005.

well (Pinheiro et al. 2017, Hachich et al. 2020). Many marine species require shallow ecosystems for some or all of their life cycles, depend on shallow ecosystems for food or habitat, and/or rely on cues associated with shallow-reef habitats for larval settlement (among other possible dependencies). During low RSL, shallow-reef habitat in the Pacific was reduced by approximately 90%, and in the Gulf of Mexico and Caribbean Sea by as much as 92% (Bellwood et al. 2015, Ludt and Rocha 2015). Complete or near-complete loss of these shallow-reef habitats in regions with steep bathymetry would likely lead to the demise of local populations of many reef-associated species (Kosaki et al. 1991, Nunn 1998, Ludt and Rocha 2015). By contrast, populations of reef-associated species are more likely to persevere across glacial cycles at regions with sloped bathymetry, where shallow-reef habitats are more likely to persist (Myers 1999, Tager et al. 2010).

4. *Restoration of high RSL generally leads to restoration of shallow-reef habitats in regions with steep bathymetry*

As RSL rises from the deglacials into the inter-glacial periods, the various shallow-reef habitats are restored at locations with steep bathymetry (Fig. 2d). The current shallow-reef habitats (< 30 m) at oceanic atolls and islands have existed for only about ~8–9 ka, as the sea surface approached modern levels (Dickinson 2004). We presume that in regions with sloped bathymetry, shallow-reef habitats are able to persist by shifting along bathymetric contours upward with the rising RSL. Certain exceptions to this are known to exist (e.g., Webster et al. 2010); but in general, most locations relevant to the HPH have remained geologically stable at least since the LGM (e.g., Tager et al. 2010).

5. *Natural restoration of shallow-reef habitats in regions with steep bathymetry allows recolonization of previously extirpated species from regions where shallow-reef habitats persist*

As the geomorphological structure of shallow-reef habitats are restored with rising sea level, the potential to support previously extirpated species is likewise restored. Over time, these restored habitats are recolonized via dispersal from populations inhabiting regions with sloped bathymetry, where the shallow habitats (and the associated species) persist (Fig. 2d). Patterns of recolonization vary among species, depending on many factors (e.g., larval duration and other factors affecting dispersal potential, habitat specificity, restoration of ecological networks, oceanographic patterns, stochastic factors, distance from source, etc.), with some species able to recolonize relatively quickly across broad geographical ranges, and others less so.

6. *Deep-reef habitats and associated organisms are likely to persist, regardless of bathymetric profile*

Deep-reef habitats should persist during all sea-level states regardless of whether the bathymetry is steep or sloped, because in most cases these habitats are already situated along mostly vertical bathymetry (Abbey et al. 2013; Fig. 2). Indeed, Velasco-Lozano et al. (2020) found that deep-reef fish assemblages in the eastern Pacific were "more ecologically intact than those around the [nearby] continental islands". Exceptions include regions where deep-reef habitat is dramatically reduced or eliminated during low RSL, such as certain regions around the Arabian Peninsula (DiBattista et al. 2018) and IAA (Myres 1999). In the majority of locations (especially around oceanic islands), however, we presume that a lowering of RSL by 120 m or more would not fundamentally change the geologic structure or other environmental parameters of these habitats in most cases. As RSL falls and rises, these deep-reef habitats should simply move up and down the steep slopes or vertical drop-offs, maintaining the same depth, habitat, and geophysical characteristics. Of course, species inhabiting deep reefs may be subject to local extirpation similar to shallow-reef species if they require shallow ecosystems for a part of their life cycles, depend on shallow ecosystems for food, and/or rely on cues associated with shallow-reef habitats for larval settlement (among other possible habitat dependencies).

In the context of these six premises, we hypothesize that the biogeographical patterns of shallow coral-reef ecosystems (i.e., the basis for most existing alternative hypotheses about coral-reef biogeography) are strongly shaped by *relatively recent (~10^5 – 10^6 yr) recolonization from regions across glacial-interglacial cycles and associated RSL changes*. Specifically, certain regions (e.g., continental margins, the IAA, and major archipelagos such as the Hawaiian Archipelago, Fiji Islands and Marquesas Islands) allow shallow-reef habitats and their associated species to persist across multiple glacial-interglacial cycles. This pattern has been documented at Papua New Guinea (region of sloped bathymetry), where every one of 76 coral, calcareous red algae, and foraminifera taxa persisted across both high and low sea-level stands during the past ~416 kyr (Tager et al. 2010). Populations in these regions serve as source populations that recolonize similar shallow-reef habitats in regions with steep bathymetry. Deep-reef habitats, by contrast, would persist at most localities across glacial cycles, regardless of the bathymetric profile. Thus, many deep-reef species assemblages would not be shaped by the same cyclical extirpation/recolonization process that shapes shallow-reef assemblages, and, therefore, should reveal different biogeographical patterns. Fig. 2 illustrates the hypothesized process with respect to RSL across a single glacial cycle.

A fundamental difference between the HPH and most other coral-reef biogeographic hypotheses is that the latter invoke processes that occur across "evolutionarily significant time" (i.e., 10^7 – 10^8 years), whereas the HPH invokes processes that occur across "ecologically significant time" (i.e., 10^5 – 10^6 years) (Veron 1995). Premise 5 of the HPH presumes that many (if not most) coral-reef organisms are capable of long-distance dispersal to varying degrees, and that the process of recolonization of shallow-reef habitats in regions with steep bathymetry is driven largely by dispersal from regions with sloped bathymetry.

Predictions

Many of the existing hypotheses that attempt to explain the distribution of shallow-reef organisms yield overlapping predictions, confounding attempts to interpret which hypothesis best explains any given set of evidence. Here we assert seven specific predictions that result from the HPH, most of which do not overlap the predictions from other diversity-gradient hypotheses.

1. *There should be proportionally higher rates of endemism in regions where habitats persist across evolutionary time-scales, than in regions where habitats are eliminated during low RSL*

If species that require shallow-reef habitats are more likely extirpated from islands with steep bathymetry, then populations of these species resulting from rare or infrequent (>100 ka) colonization events are less likely to persist across evolutionary time scales. Consequently, they have a much shorter timeframe to diverge into unique (endemic) species. Instead, the shallow-reef habitats of islands with steep bathymetry should harbour proportionally more species that have been recolonized since the current high sea-level stand was re-established. By contrast, regions with sloped bathymetry that favour shallow-reef habitat persistence should have proportionally higher rates of endemism among species that require shallow-reef habitats (compared to regions with steep-slope bathymetry), because populations resulting from rare colonization events at localities with sloped bathymetry are more likely to persist across evolutionary time scales, and thus have a longer timeframe to evolve into distinct species. Similarly, if deep-reef habitats persist through changing RSL due to glacial cycles at most localities (regardless of bathymetric profile), then novel populations of deep-reef species resulting from rare colonization events are more likely to persist across evolutionary time scales, and thus ultimately evolve into distinct species. Differences in rates of endemism between deep-reef species and shallow-reef species in regions with sloped or steep bathymetry would be most pronounced when comparing species that are exclusive to each respective habitat depth (i.e., species restricted to deep reefs vs. species restricted to shallow reefs).

2. *There should be more examples of closely-related "species complexes" and "incipient species" in regions where habitats persist across evolutionary time-scales, than in regions where habitats are eliminated during low RSL*

In the same way that higher rates of endemism are predicted for persistent habitats, examples of species "complexes" (i.e., closely-related but taxonomically distinct sibling species) and "incipient species" (i.e., species with geographical variation and/or recognized as distinct at the subspecific level) are more likely to be present in regions with persistent habitat (deep-reef habitats and shallow-reef habitats in regions with sloped bathymetry). By contrast, if species restricted to shallow reefs in regions with steep bathymetry are primarily represented by recent recolonizations, then there should be fewer examples of recent and incipient speciation.

3. *There should be greater average population genetic structure among species in persistent habitats, than in regions where habitats are eliminated during low RSL*

If shallow populations in regions with steep bathymetry are largely the product of recent recolonization, then such species should tend to have greater propensity for dispersal and, therefore, greater average gene flow. Consequently, there should be relatively low population genetic structure, on average, among species restricted to shallow-reef habitats in regions with steep bathymetry across geographical ranges (a possible signature of recent colonization). This pattern has been reported for shallow-reef species distributed across the Central-West Pacific (Craig et al. 2007, Reece et al. 2011, DiBattista et al. 2012; Gaither et al. 2015). By contrast, species capable of inhabiting deep-reef habitats, which are more likely to persist at most localities regardless of bathymetric profile, should include a mixture of species with high dispersal potential and gene flow, and species with lower dispersal potential and gene flow. Therefore, species inhabiting deep-reef habitats should tend to show greater population structure, on average, across their geographical ranges, and a higher proportion of genetic signatures consistent with older, more stable populations, compared with shallow-reef species in regions with steep bathymetry.

4. *There should be lower average genetic diversity among populations of shallow-reef species in regions with steep bathymetry, relative to conspecifics in regions with sloped bathymetry, or among populations of deep-reef species*

For genetic loci that are not under strong selection, genetic diversity is a function of effective population size (N_e), the mean number of successfully reproducing adults averaged across thousands of generations (Gillespie 2004). However, N_e is based on a harmonic mean, which is strongly influenced by population bottlenecks. If contemporary populations of species restricted to shallow-reef habitats in regions with steep bathymetry are the result of relatively recent recolonization (or persistence in small refugia), then the average genetic diversity should be lower, relative to populations that have persisted in sloped bathymetry or deep habitats. Indeed, some fish populations in shallow lagoon habitats around oceanic islands show genetic signatures of recent colonization (Fauvelot et al. 2003, Thacker 2004, Ludt et al. 2012).

5. *Genetic signals of recent population expansions should be less common in regions where habitats persist across evolutionary time-scales, than in regions where habitats are eliminated during low RSL*

Population expansion during the last 20 ka will leave distinctive genetic signatures that include an overabundance of closely-related haplotypes (Fu and Li 1993, Delrieu-Trottin et al. 2017). If species restricted to shallow reefs in regions with steep bathymetry are experiencing population expansions following RSL rise, we expect that these populations should have significant negative values of Fu's F_S statistic (Fu 1997). By contrast, populations on deep reefs and shallow reefs with sloped bathymetry should tend to have equilibrium N_e values. This expectation was tested on three deepwater snappers (*Etelis spp.*), and mtDNA networks did not indicate older more-stable populations (Andrews et al. 2020), however these species are not mesophotic, living at depths of greater than 200 m.

6. *There should be less eastward attenuation of diversity among species in persistent habitats, compared with regions where habitats are eliminated during low RSL*

Regions with sloped bathymetry (e.g., east Africa and Madagascar, the IAA, Caribbean, eastern Brazil) tend to dominate in the western parts of the three major tropical oceans, whereas central and more eastern regions (particularly in the Pacific) tend to be dominated by oceanic islands and coral atolls with steep bathymetry. According to the HPH, the pattern of eastward diversity attenuation of shallow-reef species is largely the result of recolonization of oceanic atolls and islands with steep bathymetry. If deep-reef habitats are more persistent across longer time periods at oceanic atolls and islands, then there should be less-pronounced habitat loss and species extirpation from deep-reef habitats following RSL drops. Instead, the distribution pattern among deep-reef organisms should show a more homogeneous pattern of diversity across large geographical areas.

7. *There should be an attenuation of diversity among shallow-reef species in regions with steep bathymetry correlating with increasing distance from regions with sloped bathymetry*

Most biogeographical hypotheses concerning coral-reef organisms focus on patterns of diversity as they relate to regions with high diversity (e.g., the IAA, western Indian Ocean, Caribbean). By contrast, the HPH focuses on patterns of diversity as they relate to regions with habitat persistence. Although regions with high diversity are mostly congruous with regions of hypothesized habitat persistence, there are key exceptions. Specifically, within the Pacific Ocean, the HPH predicts that certain regions with sloped bathymetry (e.g., the Hawaiian Archipelago, Fiji Islands, Marquesas Islands, Rapa Nui [Easter Island]) are also characterized by persistent shallow-reef habitat. Rather than patterns of distribution radiating only from “hotspots” of shallow-reef diversity, the HPH predicts patterns of distribution of shallow-reef organisms that radiate from regions with shallow-reef habitat persistence. As such, we predict that shallow-reef species assemblages on oceanic atolls and islands with steep bathymetry will be most similar to those at nearby localities with sloped bathymetry (including certain archipelagos without high diversity).

Discussion

Testing the predictions of the Habitat Persistence Hypothesis requires relatively complete inventories of, and collected samples from, both shallow and deep species assemblages at multiple localities across large geographical regions – to assess patterns of diversity attenuation, establish rates of endemism (i.e., endemics can only be asserted as such when their absence from adjacent localities can be confidently established), and assess population genetic features. It is difficult enough to amass this level of quantitative data among shallow-reef assemblages; to do so among deep-reef species requires many field expeditions using advanced diving technologies, submersibles, or remote survey technologies. Direct, quantitative evidence to test these predictions is so far lacking. However, based on our preliminary observations across the Pacific (Fig. 1), in combination with other published and unpublished data, we present two qualitative but coherent patterns in support of the HPH.

The first (and least quantified) observation is that deep-reef fish communities appear no more diverse in terms of species richness within the IAA (e.g., Indonesia, Philippines, New Guinea) and other western-Pacific localities (e.g., Ryukyu Islands, Taiwan, Palau, Vanuatu, Fiji), than they do in Central Pacific regions (e.g., Kiritimati, Cook Islands, Society Islands) (Prediction 6).

The second pattern we have observed supports Prediction 1: proportionally higher rates of endemism among deep-reef species compared to endemism among shallow-reef species (Pyle 2000, Kane et al. 2014, Kosaki et al. 2016, Pyle et al. 2016, see Fig. 3). Fig. 4 shows a comparison of species overlap among both deep- and shallow-reef fish species between Palau, Papua New Guinea and Fiji, based on unpublished data. Species overlap is nearly ten times greater among shallow reef fishes than among deep-reef fishes. Reduced species overlap indicates more restricted distributions, and thus higher rates of endemism.

Although the concept behind the HPH was inspired by observations made throughout the tropical Pacific, the principles should also apply to the Indian Ocean and potentially the tropical Atlantic Ocean as well (perhaps to a much lesser extent). This may be observed when comparing regions with complex bathymetry within the upper 200 m (e.g., eastern African continent, Madagascar in the Indian Ocean; eastern American continent, Caribbean, and eastern Brazil in the Atlantic Ocean) to regions with primarily vertical bathymetry across this depth range (e.g., Chagos Archipelago, Maldives in the Indian Ocean; Bermuda, Ascension, St. Helena, and St. Paul’s Rocks in the Atlantic Ocean). The application of the HPH within the tropical Atlantic is limited. The entire Caribbean is comparable in both scale and general bathymetric characteristics to the IAA, and as such, we would not expect the predictions of the HPH to be borne out within the Caribbean any more than we would expect them to be within the IAA. The important comparison in terms of the HPH is between continental regions (IAA; Caribbean) versus oceanic islands and atolls within the same ocean. As noted above, only a few isolated oceanic islands exist within the tropical Atlantic, so while it is possible that the mechanisms of the HPH may have influenced the broader distribution of species in parts of the tropical Atlantic, the potential for testing the predictions is far lower than in the Pacific and Indian Oceans. Nevertheless, a comparison of the broader Caribbean with oceanic islands such as Bermuda, Ascension, St. Helena, St. Paul’s Rocks and Rocas Atoll could prove insightful, as shallow-reef habitat in the latter localities would be reduced to a narrow band along the sloping sides of these islands (Armstrong and Singh 2011, Locke et al. 2013, Amado-Filho et al. 2016, Rosa et al. 2016). Similar comparisons could be made in reef areas associated with the coast of South America (Cordeiro et al. 2015, Pinheiro et al. 2015a, 2015b, Simon et al. 2016, de Oliveira Soares 2018). Indeed, both Ascension and St. Paul’s Rocks harbour a number of endemic species, most of which are known to inhabit deeper-reef environments. Below we provide some considerations for gathering and analyzing evidence in the context of the HPH.

Figure 3. The highest rates of marine endemism on Earth are found among MCEs. Every fish species in this image, taken during surveys at 90m depth off Kure atoll, is endemic to the Hawaiian Archipelago. Multiple quantitative surveys of this and nearby MCE habitat yielded 100% endemism (Kosaki et al. 2016). Photo: R. L. Pyle.

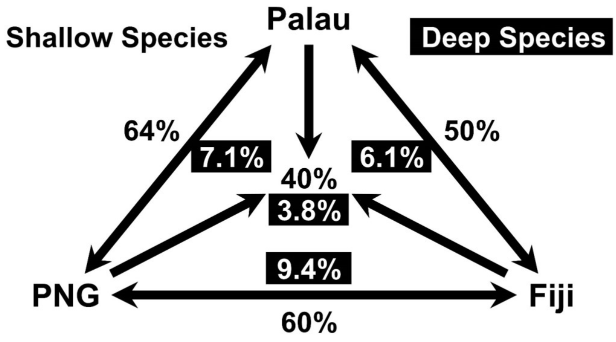

Figure 4. Comparison of species overlap between Palau, Papua New Guinea (PNG) and Fiji for shallow-reef fishes and deep-reef fishes. Less species overlap among deep-reef species implies higher rates of endemism. Modified from Pyle (2005), and based on unpublished data from fish collections on MCEs made by co-author Pyle and collaborators, and unpublished data on diversity of shallow-reef species from G.R. Allen for Palau and PNG, and from D.W. Greenfield for Fiji. These data are not represented as support for the HPH, but rather as part of the rational basis for formulating and proposing the hypothesis.

Key Locations for Future Testing

We have identified several key locations where robust documentation from existing and future studies of both deep and shallow species assemblages would allow direct tests of patterns predicted by the HPH and other biogeographical hypotheses.

One example, for which extensive data has already been published, involves the Hawaiian Archipelago. The bathymetry of most of the Archipelago is very well established (Miller et al. 2006, Hawaiʻi Mapping Research Group 2015, PIBHMC 2015), and the distribution of many reef-associated organisms (particularly fishes) inhabiting both shallow and deep coral reefs are well documented (Mundy 2005, Randall 2007, Pyle et al. 2016, Spalding et al. 2016a). The bathymetry throughout most of this archipelago is dominated by gradual slopes and/or near-horizontal shelves, with evidence that shallow shoreline habitats (such as spur-and-grooves) existed at lower sea levels (Stearns 1978, Fletcher and Sherman 1995, Webster et al. 2009, Faichney et al. 2010, 2011). Indeed, ancient and drowned shorelines and habitat features that formed during periods of lower RSL often now serve as primary structure for habitat at much greater depths (Pyle et al. 2016, Currey-Randall et al. 2017). High rates of shallow-reef endemism among Hawaiian species, as well as even higher rates of endemism among deep-reef species (Kane et al. 2014, Kosaki et al. 2016, Pyle et al. 2016, Fukunaga et al. 2016, 2017, Spalding et al. 2019a Friedlander et al. 2020) support Prediction 1. Comparisons have already been made to nearby Johnston Atoll, a coral atoll with near-vertical bathymetry, which initially inspired the HPH (Kosaki et al. 1991, Wagner et al. 2014). Johnston Atoll has fewer total species of reef and shore fishes (323 vs. 622 in Hawaiʻi) and only one endemic fish species (*Centropyge nahackyi* Kosaki 1989, occasionally reported from Hawaiʻi), in contrast to about 25% endemism among reef and shore fishes in the Hawaiian Archipelago (Kosaki et al. 1991, Randall 2007, Wagner et al. 2014, Pyle et al. 2016). However, this comparison is confounded by the much smaller size of Johnston Atoll. In terms of genetic diversity, Johnston Atoll and Hawaiʻi have similar levels of mtDNA variability in a number of reef fishes, including *Centropyge loriculus* (Günther, 1874) (Schultz et al. 2007), *Chaetodon multicinctus* Garrett, 1863 (Craig et al. 2010), *Zebrasoma flavescens* (Bennett, 1828) (Eble et al. 2011), and *Halichoeres ornatissimus* (Garrett, 1863) (Ludt et al. 2012). However, the surgeonfish *Acanthurus nigroris* Valenciennes, 1835 (DiBattista et al. 2011) has significantly lower mtDNA haplotype diversity at Johnston Atoll (h = 0.22) versus Hawaiʻi (h= 0.52), consistent with Prediction 4. Notably, this species may be the best test of HPH predictions, because it shows strong isolation between Johnston Atoll and Hawaiʻi (most of the others do not), indicating independent population trajectories. Similar comparisons between Hawaiian reef populations and those at Johnston Atoll could be made with populations occurring at Minami Tori-Shima (formerly Marcus Island).

Another example is the Marquesas Islands, which are similar to the Hawaiian Archipelago both in terms of bathymetric profile (Cabioch et al. 2008) and shallow-reef endemism (Kulbicki 2007, Moolenbeek et al. 2008, Delrieu-Trottin et al. 2015). Unlike the Hawaiian Archipelago, the deep-reef communities of the Marquesas have not yet been well documented. Doing so would allow testing of HPH predictions. In particular, the proximity of the Marquesas to the Society Islands (dominated by atolls and islands with steep bathymetry) will allow robust testing of Prediction 7, especially given that the HPH predicts patterns that contrast with other coral-reef biogeographical hypotheses.

The third example involving the IAA, Palau, and Fiji is represented in Fig. 4 (see also Pyle and Copus 2019). Preliminary data reveal greater overlap among shallow-reef fish species between localities compared with deep-reef species (and, hence, higher endemism among deep reefs). Palau is a group of islands with mostly vertical bathymetry, and is less than 1,000 km north and east of the IAA. Fiji is a group of islands with sloped bathymetry, and is more than 3,000 km east of the IAA. Traditional hypotheses of coral-reef biogeography would predict much greater biological affinity between the IAA and Palau among both shallow- and deep-reef species relative to Fiji, based on geographical proximity. The HPH predicts that more shallow-reef species would persist in the IAA and Fiji across glacial cycles relative to Palau (which the HPH would predict is still being recolonized from the IAA after shallow-reef habitat loss during the LGM). Indeed, patterns of gorgonian coral distributions including the IAA and eastward locations across the Pacific show species richness attenuation for shallow-reef species, but not deep-reef species, which is consistent with Prediction 7 of the HPH (Rowley et al. 2019, Sánchez et al. 2019). More comprehensive surveys of both deep- and shallow-reef species of these regions would allow effective testing of such HPH predictions.

The fourth example would involve a comparison of both deep and shallow species at Rapa Nui (Easter Island), with nearby Pitcairn and Rapa islands, and the Tuamotu Archipelago. The bathymetry of Rapa Nui, Pitcairn and Rapa is sloped, so shallow-reef habitats are more likely to persist across glacial cycles than shallow-reef habitats within the Tuamotu Archipelago. Several recent studies have focused on marine biodiversity and associated biogeographic implications at Rapa Nui, including species inhabiting MCEs (Easton et al. 2017, Delrieu-Trottin et al. 2019, Hoeksema et al. 2019, Mecho et al. 2019, Friedlander et al. 2021, Liggens et al. 2021, Mah 2021). The results of these studies reveal patterns that are consistent (or, at least, not inconsistent) with the predictions of the HPH. As with the Marquesas, a comprehensive comparison of both shallow and deep species at these localities would represent an effective test of all of the HPH predictions, especially Prediction 7.

The fifth example involves uplifted islands. One of the premises of the HPH is that at times of lower RSL there will be a loss of shallow-reef habitats in regions with steep bathymetry, which in turn results in the loss of species that require shallow-reef habitats for part of their life cycles. Several islands throughout the Pacific (e.g., Henderson, Makatea, Niue, Fais, Hallmann et al. 2021) are geologically anomalous in that they are uplifted relative to the current high sea-level stand, and thus represent what many islands and atolls throughout the Pacific would look like during periods of lower sea level (McNutt and Menard 1978). Comprehensive surveys of uplifted Pacific islands should result in reduced numbers of species compared to nearby islands that are not uplifted (and therefore maintain the full complement of shallow reef habitats).

Finally, seamounts may represent other useful examples in terms of their availability as coral-reef habitat and stepping-stones during periods of lower RSL (Galbraith et al. 2021). Among those listed in the Global Seamount Database (Kim and Wessel 2011), 645 seamounts within tropical latitudes reach depths shallower than 300 m of the current sea surface level (and thus the lower limits of coral-reef habitat, 150 m, during the lowest sea-level stands). It is possible that some of these seamounts may have played a role in facilitating dispersal of deep-reef species, and possibly to a lesser degree shallow-reef species during low sea-level stands. Seamounts may have allowed deep-reef habitat to persist in regions where shallow reef habitat did not exist during the Pleistocene, and as such may have played a role in Predictions 1 and 2.

Species Classes

To test the predictions of the HPH, it is helpful to distinguish several classes of species with respect to the habitats they occupy. Evidence supporting or refuting predictions comparing shallow-reef species to deep-reef species should be most apparent in species restricted to each of these respective habitats. In particular, species that are restricted to shallow-reef habitats are most likely to demonstrate patterns of local extirpation during low RSL and subsequent recolonization in regions with steep bathymetry during high RSL. Likewise, species restricted to deep-reef habitats are less likely to be impacted by changes in RSL, and should reflect fundamentally different distributional and genetic patterns across their geographical ranges, compared to species restricted to shallow reefs.

Evidence supporting or refuting predictions of the HPH will be less apparent when considering species that occupy both shallow- and deep-reef habitats. For such depth generalists, the persistence of deep-reef habitats would reduce the probability of extirpation from regions with steep bathymetry during low RSL; but populations in regions with steep bathymetry may nevertheless be more heavily impacted by changes in RSL than they would be in regions where both shallow and deep habitats persist. Therefore, we expect a mixture of evidence from species with broad depth ranges.

Another important class of species to consider when evaluating the HPH predictions is the set of species that inhabit rocky shorelines. Although the bulk of habitat that is expected to persist across glacial cycles in regions with steep bathymetry involves habitat below a depth of about 30 m, the foundation of the HPH concerns habitat persistence. One such habitat that we would expect to persist in all tropical regions (including those with steep bathymetry) is rocky shoreline, including intertidal and shallow subtidal habitats. Species inhabiting rocky shoreline habitats would be expected to have patterns concordant with species inhabiting deep-reef habitats, including regions with steep bathymetry. Documenting rocky shoreline habitats and associated species at uplifted islands (see fifth case study above) would help reveal which specific species are most likely to be included within this class.

Alternate Hypotheses

Clearly, the HPH does not account for all biogeographical patterns in reef-associated species. Under a strict interpretation of the HPH, if shallow-reef habitat in the Hawaiian Archipelago has persisted for as long as shallow-reef habitats within the IAA, then we would expect the same level of diversity among shallow-reef species. Clearly this is not the case: the shallow coral-reef biodiversity within the IAA is five to six times greater than that of the Hawaiian Archipelago (Randall 2007, Allen and Erdmann 2012). The discrepancy in total diversity is no-doubt a result of multiple factors, such as much larger total habitat area (at all sea levels), greater overall diversity of habitat types within IAA (Woodland 1990, Randall 1998), overlapping of species from the Indian Ocean and Pacific Ocean (Gaither and Rocha 2013), historical factors (Cowman and Bellwood 2013, Hodge et al. 2014), and many other processes operating on both evolutionary and ecological time scales.

The HPH shares some characteristics with the ‘Center of Survival’ hypothesis (McCoy and Heck 1976, Bellwood and Hughes 2001). A key difference between HPH and ‘Center of Survival’ is that the latter assumes that survival is contingent on large swaths of appropriate habitat: larger habitats are a buffer against extinction, a key link between biogeography and conservation (Rosenzweig 1999, Staude et al. 2020). Accordingly, discussions about centers of survival (e.g. Barber and Bellwood 2005, Cowman and Bellwood 2013) focused on the IAA, maintaining that lower extinction rates are (at least partially) responsible for high biodiversity. The HPH is a more generalized explanation that applies to the IAA as well as other regions in all tropical seas where differences in *habitat persistence* (both geographically and across depths) show different levels of endemism and genetic signatures of persistence (e.g. Cowman et al. 2017).

It is not clear how extensively the principles of the HPH may be operating in continental margins in the eastern tropical oceans (in terms of serving as persistent source populations to recolonize nearby islands with steep bathymetry); other factors operating in eastern oceans, such as annual temperature cycles and oceanic current patterns, geological history, the distribution and paucity of oceanic islands and atolls with steep bathymetric profiles, and a multitude of other factors lead us to believe that the principles of the HPH may apply less extensively within the eastern oceans. Moreover, the HPH is primarily focused on coral-reef habitats and their associated organisms. While scleractinian corals flourish in eastern oceans, the nature and extent of coral-reef ecosystems are dramatically different from those of western and central tropical oceans (Hollarsmith et al. 2020, Velasco-Lozano et al. 2020).

As stated earlier, we do not represent the HPH as “the” explanation for patterns of biological diversity, richness and endemism on coral reefs. However, the HPH addresses patterns of endemism and the general pattern of eastward attenuation of shallow-reef species diversity across all three tropical oceans, which are the major patterns that have shaped biogeographical hypotheses for coral-reef organisms.

HPH Application to Alternate Environments

Although the HPH was conceived and formulated in response to observed biogeographic patterns of organisms within coral-reef ecosystems, its general principles apply to any environment. We would expect analogous biogeographic patterns to exist among organisms in other marine and terrestrial ecosystems that have experienced differences in degrees of broad-scale habitat persistence across ecological and evolutionary timescales. For example, Jacquet et al. (2015) found that climatic oscillations over the Pleistocene probably played a major role in shaping the genetic diversity within a species complex of African Shrews, which may be analogous to the effects of sea level cycles on tropical coral reefs. Genetic diversity in temperate continental fauna of the Northern Hemisphere is undoubtedly shaped by cyclic intrusions of ice sheets, a conclusion that applies to both freshwater and terrestrial organisms (Bernatchez and Wilson 1998, Hewitt 2004). Meseguer and Condamine (2020) found higher rates of extirpation and extinction of reptiles in temperate latitudes, when habitats turned from “hothouse to icehouse”. In this regard, HPH may link well with ‘time for speciation’ hypotheses, which posit that greater diversity in tropical versus temperate climates is because temperate habitat lacks the stability and timeframe necessary for new species to emerge (Stephens and Wiens 2003; Egan et al. 2022). In a meta-analysis of ray-finned fishes (Percomorpha), Miller et al. (2018) found support for ‘time for speciation’ in marine faunas. A detailed review of the potential relevance of the HPH to other environments and evolutionary models is beyond the scope of this paper; however, it is likely that the general principles outlined in the premises and predictions described herein could be adjusted for any environments (terrestrial or marine) where heterogeneous habitat persistence may have played a role in shaping biogeographic and evolutionary patterns.

Summary

According to the HPH as applied to tropical coral-reef ecosystems, most coral-reef habitats (both shallow and deep) tend to persist across glacial cycles and associated changes in RSL in regions with sloped bathymetry within the upper 200 m, because these habitats are likely to shift along the bathymetric profile during periods when RSL changes. In regions characterized by steep or vertical bathymetry (e.g., oceanic islands and atolls), deep-reef habitats (which already exist on vertical or near-vertical bathymetry) persist by shifting up and down with changes in RSL; whereas many shallow-reef habitats (and the associated organisms that require them) disappear or are greatly reduced during low RSL. Speciation is more likely to occur in regions where habitat persists across evolutionary time scales – an expected feature of most deep coral reefs and those shallow reefs that exist in regions with sloped bathymetry. By contrast, populations of shallow-reef organisms are less likely to persist in regions characterized by steep bathymetry (such as many oceanic islands and atolls), and therefore biogeographical patterns are more likely to be shaped by relatively recent recolonizations from regions with persistent shallow-reef habitat during the past ~10 ka (i.e., ecological time scales). Thus, the HPH posits that much of the pattern of eastward attenuation in species diversity observed in tropical oceans is shaped by patterns of relatively recent recolonization, rather than patterns of speciation. The generality of this pattern needs to be tested with a wide range of vertebrate, invertebrate and phycological organisms. Whereas most other hypotheses concerning coral-reef biogeography are based only on shallow-reef species, the HPH is more consistent with observed distribution patterns of species throughout the entire depth range of coral-reef habitat. A series of predictions resulting from the HPH can be tested through more complete documentation of distribution patterns of both shallow- and deep-reef species distributions, and associated patterns of genetic diversity and phylogeography.

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Author Contributions

Copus coordinated the overall manuscript ideas; Copus, Pyle, Bowen and Kosaki all contributed to the core biodiversity and biogeography ideas, based on existing literature and their own personal observations; Webster provided essential geological context with respect to historical sea-level changes and their likely effect on coral-reef habitat. All authors contributed to the writing.

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