Trait similarity in reef fish faunas across the world's oceans

Matthew McLean[a,1], Rick D. Stuart-Smith[b], Sébastien Villéger[c], Arnaud Auber[d], Graham J. Edgar[b], M. Aaron MacNeil[a,e], Nicolas Loiseau[c], Fabien Leprieur[c,f], and David Mouillot[c,f]

[a]Department of Biology, Dalhousie University, Halifax, NS, Canada, B3H 4R2; [b]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia; [c]MARBEC, Univ Montpellier, CNRS, Institut Français de Recherche pour l'Exploitation de la Mer, IRD, 34095 Montpellier, France; [d]Institut Français de Recherche pour l'Exploitation de la Mer, Unité Halieutique de Manche et mer du Nord, 62321 Boulogne-sur-Mer, France; [e]Ocean Frontier Institute, Dalhousie University, Halifax, NS, Canada, B3H 4R2; and [f]Institut Universitaire de France, 75005 Paris, France

Edited by Nils Chr. Stenseth, University of Oslo, Oslo, Norway, and approved February 10, 2021 (received for review June 15, 2020)

Species' traits, rather than taxonomic identities, determine community assembly and ecosystem functioning, yet biogeographic patterns have been far less studied for traits. While both environmental conditions and evolutionary history shape trait biogeography, their relative contributions are largely unknown for most organisms. Here, we explore the global biogeography of reef fish traits for 2,786 species from 89 ecoregions spanning eight marine realms with contrasting environmental conditions and evolutionary histories. Across realms, we found a common structure in the distribution of species traits despite a 10-fold gradient in species richness, with a defined "backbone" of 21 trait combinations shared by all realms globally, both temperate and tropical. Across ecoregions, assemblages under similar environmental conditions had similar trait compositions despite hosting drastically different species pools from separate evolutionary lineages. Thus, despite being separated by thousands of kilometers and millions of years of evolution, similar environments host similar trait compositions in reef fish assemblages worldwide. Our findings suggest that similar trait-based management strategies can be applied among regions with distinct species pools, potentially improving conservation outcomes across diverse jurisdictions.

biogeography | community assembly | functional ecology | macroecology | phylogenetics

Biogeographic patterns reflect how past and current environmental conditions along with evolutionary history have shaped biodiversity, ecosystem functioning, and the ecosystem services human societies depend on. While biogeography has historically focused on species composition (1), species traits (morphological, physiological, or behavioral features of organisms) are increasingly recognized as the main drivers of community assembly and ecosystem functioning (2–5). Trait composition has been shown to mediate species' interactions (6), shape ecological niches (7), determine species' responses to environmental fluctuations (8), and govern species' influences on key ecological processes like nutrient cycling (9, 10) and biomass production (11).

Large-scale variation in trait composition is shaped by biotic (e.g., trophic interactions) and abiotic constraints (e.g., environmental filtering) under the influence of evolutionary and biogeographic processes (i.e., speciation, extinction, and immigration), yet global patterns and processes in trait biogeography are poorly known for most organisms. In marine ecosystems, how environmental constraints and evolutionary history have shaped species diversity has been broadly debated (12, 13), and recent studies suggest that both adaptation to regional climate (14) and geographical expansion of clades (15) have influenced global patterns in marine biodiversity. On shallow rocky and coral reefs, large-scale environmental gradients and evolutionary history have led to ocean basins with vastly different species richness and composition (13, 16), yet the distribution and drivers of associated trait composition are still unclear.

Here, using data collected through the Reef Life Survey (RLS) (17) (http://www.reeflifesurvey.com/) from 89 ecoregions spanning eight marine realms in both temperate and tropical oceans, we examined global biogeographic patterns in reef fish trait composition and evaluated whether trait composition is shaped primarily by the environment, taxonomic relatedness, or evolutionary history. Specifically, we examined patterns of species distribution in trait space relative to environmental conditions and taxonomic and phylogenetic composition.

We explicitly considered two spatial scales—marine realms and marine ecoregions—for which we examined distinct questions. Marine realms are large areas of ocean basins for which "biotas are internally coherent at higher taxonomic levels, as a result of a shared and unique evolutionary history" (18) and are shaped by major differences in environmental regimes and historical or broadscale isolation. Given their distinct biotas, environmental regimes, species richness, and evolutionary histories, we began by examining how realms differed in trait composition and redundancy. For instance, we examined whether temperate and tropical oceans contained similar trait diversity and trait proportions and whether certain trait combinations existed in all realms. We next examined ecoregion-scale patterns to assess regional variation in trait composition and redundancy and whether trait composition varied predictably within realms. Ecoregions are smaller areas of "relatively homogeneous species composition," (18) which are shaped by distinct oceanographic and environmental conditions. We hypothesized that regional species assemblages

Significance

Biogeography has focused extensively on species identities, yet global patterns in species traits (morphological, physiological, or behavioral features) are not well known, including whether they are shaped by modern environmental conditions or by shared evolutionary history. Our global analysis of nearly 3,000 reef fish species found a consistent variety of traits across ocean basins worldwide, including a backbone of 21 trait combinations common to all oceans. At the regional scale, we found that fish assemblages in similar environments had similar trait compositions despite being separated by up to 100 degrees of latitude and hosting different species with distinct evolutionary histories. Thus, environmental conditions have likely shaped global patterns in reef fish traits regardless of geography, species identity, or evolutionary history.

Author contributions: M.M., R.D.S.-S., S.V., A.A., G.J.E., M.A.M., N.L., F.L., and D.M. designed research; M.M. performed research and analyzed data; and M.M., R.D.S.-S., S.V., A.A., G.J.E., M.A.M., N.L., F.L., and D.M. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

[1]To whom correspondence may be addressed. Email: mcleamj@gmail.com.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2012318118/-/DCSupplemental.

Published March 15, 2021.

Downloaded by guest on January 7, 2022

would show similar trait composition under similar environmental conditions worldwide regardless of species composition or shared evolutionary history.

Results

A Global "Backbone" of Reef Fish Traits. To quantify the distribution of reef fish traits, we first created a multidimensional trait space of 2,786 reef fish species (using principal coordinates analysis, PCoA) according to five categorical traits. Trait variation among species was primarily explained by water-column position (benthic, demersal, site-attached pelagic, or mobile pelagic), gregariousness (solitary, paring, or schooling), and active period (diurnal or nocturnal). Along the first axis, there was a clear gradient from benthic to pelagic species, and solitary and nocturnal species were distinguished from schooling and diurnal species (Fig. 1 *A* and *C*). Species also varied largely in diet, with invertivores being distinct from planktivores and piscivores along the first axis. Along the second axis, species primarily varied in body size, with a clear gradient from small to large species.

Across five tropical and three temperate marine realms, we found a common pattern in the distribution of species in trait space despite a 10-fold gradient in species richness (Fig. 1*D*). In all realms, species clustered in the same area of trait space and occupied similar ranges of the overall space (Fig. 1*D*). The proportions of different trait categories were also strikingly similar across realms (*SI Appendix*, Fig. S1). Thus, reef fish trait composition appears remarkably consistent worldwide when considered at the scale of marine realms, despite major differences in species number and identity. Across realms, species richness ranged from 6 to 54% of the observed global pool, whereas the number of functional entities (i.e., unique trait combinations) ranged from 24 to 77%, indicating that species-poor realms maintain disproportionately high trait diversity (*SI Appendix*, Table S1). Mouillot et al. (19) previously found that the breadth of reef fish traits was consistent across the tropics, with a ninefold gradient in species richness corresponding to only a threefold gradient in the number of functional entities. Here, we extend those patterns to temperate oceans, showing astonishing similarity between reef fish faunas worldwide despite drastic differences in species richness, environmental regimes, and habitat types (i.e., coral versus rocky substrates). Together, these findings show that key ecological functions are retained, even in species-poor realms, through high differentiation and limited redundancy that capture the overall breadth of reef fish traits (19).

We next identified functional entities shared by all marine realms, both temperate and tropical (Fig. 1*B*). A total of 21 entities (of 356 in the global species pool) define a common "backbone" (20) in trait space filled by reef fishes from all ocean basins. These 21 core entities encompass a broad range of trait values, including a variety of body sizes, behaviors, and diets (*SI Appendix*, Fig. S2). In particular, the most common backbone traits were invertivorous diet, demersal water-column position, diurnal active period, solitary behavior, and small to medium body size, most frequently represented by families such as wrasses, sea basses, groupers, damselfishes, and gobies. We also identified specific backbones for temperate and tropical realms, which revealed consistent ecological structuring within temperate (42 entities) and tropical (45 entities) oceans (Fig. 1*B* and *SI Appendix*, Fig. S2). However, null models revealed that the numbers of shared functional entities within the global and tropical backbones were lower than expected by random (*SI Appendix*, Fig. S3). This suggests that similar trait distributions across realms were not due to identical functional entities but rather similar trait proportions. Hence, similar overall trait composition can arise from a variety of functional entities, depending on their relative frequencies, particularly when functional entities share multiple traits in common. Furthermore, this result indicates that intense filtering by environmental and ecological constraints has limited the number of viable functional entities that can persist in all ocean basins.

Latitudinal Similarity in Reef Fish Traits. To evaluate similarity in species assemblage trait composition at the regional scale, we examined trait space patterns across 89 ecoregions globally. We generated probability densities of PCoA 1 and PCoA 2 scores (i.e., species distributions on the first and second axes of trait space) for regional species pools and calculated the centroid position (i.e., mean value along each axis, *SI Appendix*, Fig. S4) for each ecoregion, as well as species richness and the number of functional entities. Across ecoregions, we found that PCoA 1 centroids had a clear unimodal relationship with latitude, being similar in temperate regions in both hemispheres and converging toward the equator (Fig. 2), highlighting similar trait compositions at similar latitudes worldwide. Linear models of PCoA 1 centroids using the absolute value of latitude revealed that including hemisphere as a predictor added no explanatory power (latitude: $R^2 = 0.327$; latitude + hemisphere: $R^2 = 0.332$), further demonstrating latitudinal similarity regardless of hemisphere. Reef fish assemblages in temperate ecoregions were distinguished from those in tropical ecoregions along the first axis of trait space (Figs. 1 and 2), with temperate ecoregions more characterized by benthic, solitary, nocturnal, and invertivore species and tropical ecoregions more characterized by demersal, pairing, diurnal, and grazer species (*SI Appendix*, Fig. S5 and Table S2). PCoA 2 centroids also showed a unimodal relationship with latitude, indicating that body sizes were larger at higher latitudes and that temperate regions were more characterized by piscivores (Fig. 2*C* and *SI Appendix*, Fig. S5).

We further found that both species richness and the number of functional entities were lowest at temperate latitudes and increased toward the equator; however, species richness increased 2.5 times faster than the number of functional entities (2.8 species versus 1.1 functional entities per degree latitude; *SI Appendix*, Fig. S6). Thus, as species richness increased, an average of 2.5 species were packed into existing functional entities before a new functional entity emerged. Together, these results indicate that as species richness increases in the tropics, species are packed into existing functional entities, increasing redundancy rather than extending the breadth of trait space (19, 21).

To determine if trait similarity resulted from shared species composition (taxonomy) or evolutionary history (phylogeny), we examined dissimilarity patterns between realms and between ecoregions. We defined trait dissimilarity as the Euclidean distance between species-pool centroids in the first four dimensions of trait space and defined taxonomic and phylogenetic dissimilarity as the turnover component of pairwise Jaccard dissimilarity (22). While both taxonomic and phylogenetic dissimilarity are naturally bounded between 0 and 1, trait dissimilarity (distance between ecoregion centroids) has no intrinsic upper limit. We therefore used a null model approach to define the maximum expected trait dissimilarity between realms under random assembly (see *Materials and Methods*). For consistency, this approach was also used for both taxonomic and phylogenetic dissimilarity. We found that marine realms were highly similar in trait composition but highly dissimilar in taxonomic and phylogenetic composition, suggesting that common trait distributions are not a result of shared species or evolutionary histories (Fig. 3). We also found that when ecoregions became farther apart in latitude, they became more dissimilar in taxonomic and phylogenetic composition. However, trait composition was not related to latitudinal distance since both geographically near and far ecoregions had similar trait compositions. Thus, ecoregions separated by up to 100 degrees of latitude displayed equivalent trait compositions despite hosting radically different species pools from separate evolutionary lineages (Fig. 4 and *SI Appendix*, Fig. S7).

Downloaded by guest on January 7, 2022

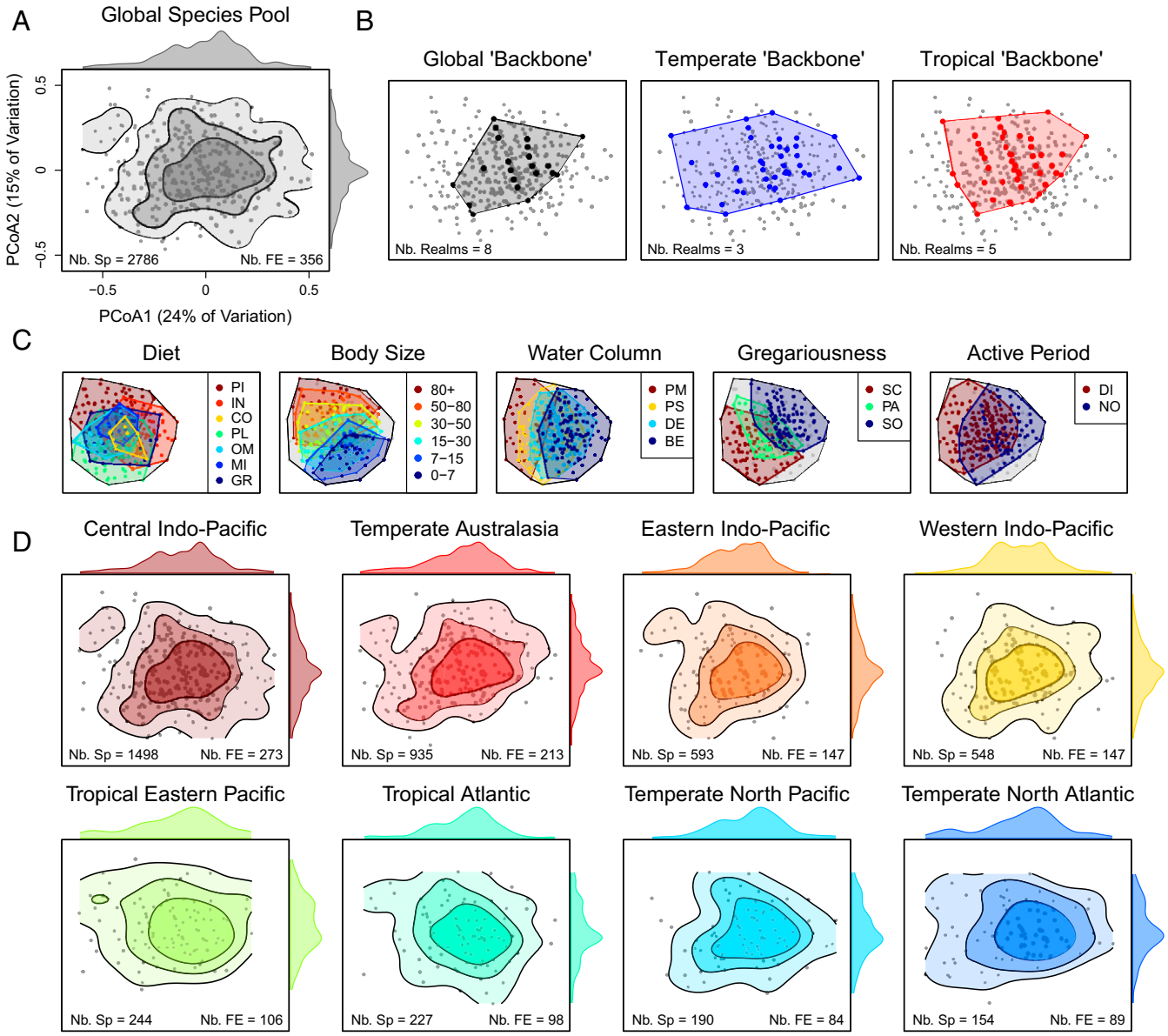


Fig. 1. Trait space for the global pool of 2,786 reef fish species and for each of the eight marine realms. (*A*) The first two axes of trait space for the global species pool showing 50, 75, and 95% contours of species density, along with marginal distributions of PCoA 1 and PCoA 2 scores. (*B*) The common "backbone" of 21 functional entities shared by all realms globally, as well as the temperate and tropical backbones. (*C*) Convex hulls showing the distribution of trait categories within the trait space for each of the five categorical traits. Diet: PI, piscivore; IN, invertivore; CO, corallivore; PL, planktivore; OM, omnivore; MI, microphage; and GR, grazer. Water column: PM, pelagic mobile; PS, pelagic site-attached; DE, demersal; and BE, benthic. Gregariousness: SC, schooling; PA, pairing; and SO, solitary. Active period: DI, diurnal; and NO, nocturnal. (*D*) The first two axes of trait space for each of the eight marine realms showing 50, 75, and 95% contours of species density, along with marginal distributions of PCoA 1 and PCoA 2 scores. The total number of observed species and functional entities for the global species pool and for each marine realm are indicated in the bottom left and bottom right corners of each plot; realms are ordered by descending number of species. While all species are plotted, species belonging to the same functional entity (i.e., having identical trait values) are superimposed.

Environment Shapes Trait Composition. Debate over the relative influences of contemporary environmental conditions and shared evolutionary history has focused extensively on species composition rather than trait composition (13, 16). Therefore, to determine if trait similarity was more strongly driven by environmental conditions than by taxonomic or phylogenetic composition, we evaluated the relationship between trait dissimilarity and taxonomic, phylogenetic, and environmental dissimilarity using multiple regression of distance matrices (MRM) (23). We defined environmental dissimilarity as the Euclidean distance between ecoregions according to mean sea-surface temperature (SST), SST range, nitrate, phosphate, and net primary productivity (see *Materials and Methods*). We found that environmental dissimilarity was the primary driver of trait dissimilarity (effect size = 0.60 ± 0.01 and $R^2 = 0.56$), while taxonomic (effect size = 0.09 ± 0.02 and $R^2 = 0.20$) and phylogenetic dissimilarity (effect size = 0.11 ± 0.02 and $R^2 = 0.24$) added little explanatory power (all variables together $R^2 = 0.58$; Fig. 4).

Trait similarity among geographically distant assemblages inhabiting similar environmental conditions could arise through both environmental filtering—in which regional trait composition is filtered from the realm pool—and evolutionary convergence—in

Downloaded by guest on January 7, 2022

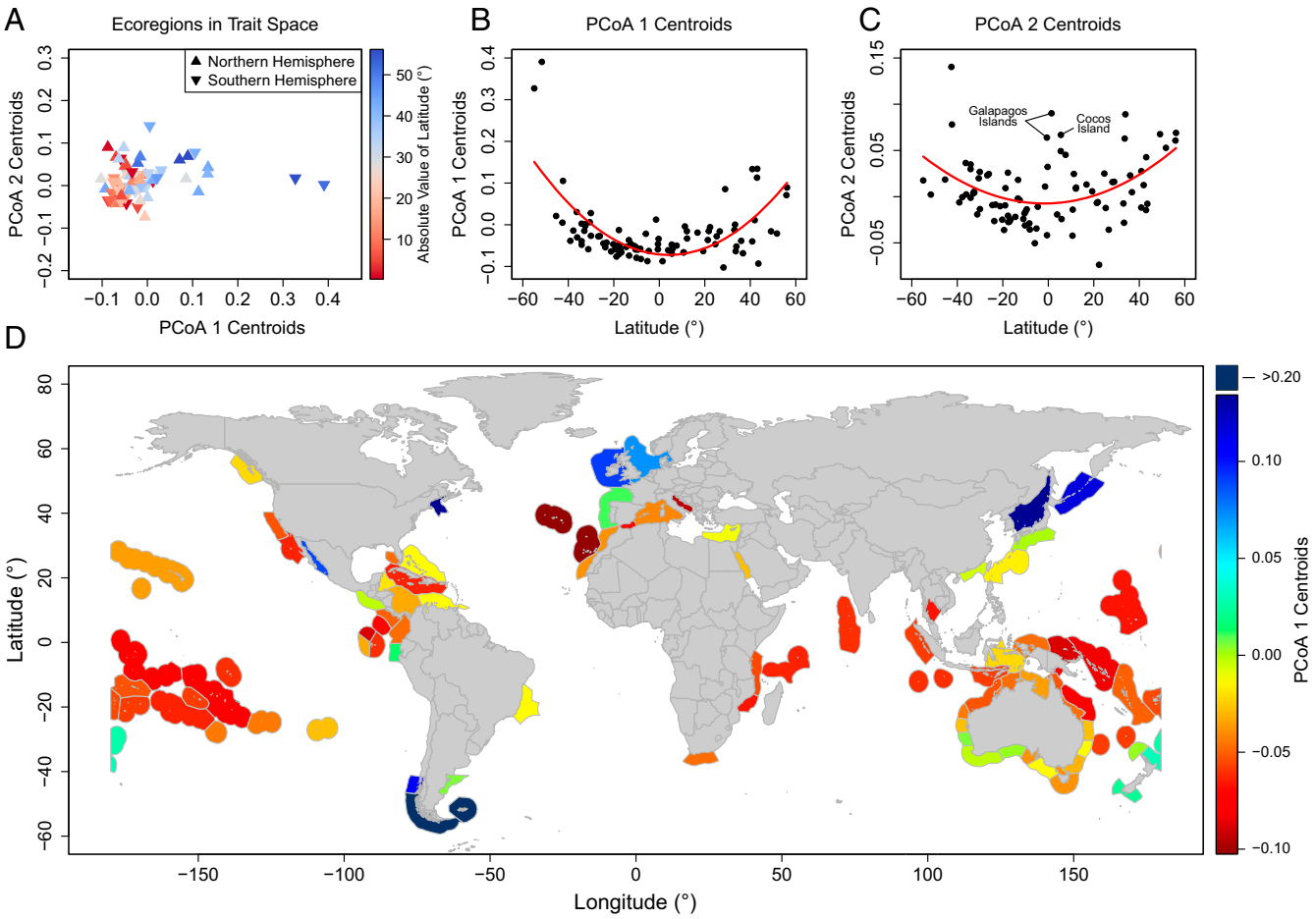


Fig. 2. Latitudinal patterns in trait space centroids for reef fish assemblages from 89 global ecoregions. (*A*) The centroid position of each ecoregion in trait space colored by the absolute value of latitude per ecoregion. (*B*) PCoA 1 centroid of each ecoregion plotted against latitude. (*C*) PCoA 2 centroid of each ecoregion plotted against latitude. The Galapagos Islands and Cocos Island are indicated as outliers. In *B* and *C*, red lines indicate the best fits from second-order polynomial regressions, which are shown for visualization. (*D*) Global map of the 89 ecoregions colored by PCoA 1 centroid values.

which species with distinct trait combinations independently evolve in response to similar environmental pressures (24, 25). Both processes have likely contributed to contemporary patterns in trait composition yet disentangling their relative effects is challenging and contentious (25). Therefore, to assess the likelihood of convergent evolution in shaping spatial trait similarity among assemblages, we tested whether the observed relationship between trait dissimilarity and taxonomic, phylogenetic, and environmental dissimilarity was different from expected under neutral evolution by simulating trait dissimilarity according to a Brownian model of evolution. Following Mazel et al. (25), we simulated species' positions on the first axis of trait space, recalculated trait dissimilarity between ecoregions, recalculated the relationship between trait dissimilarity and taxonomic, phylogenetic, and environmental dissimilarity, and compared null expectations to the observed relationship. We also calculated the magnitude of difference in observed versus expected trait dissimilarity between ecoregions [i.e., standardized effect size (SES), termed "phylogenetically standardized trait distance" in Mazel et al. (25)]. We found a positive, albeit weak, relationship (slope = 0.036; *SI Appendix*, Fig. S8) between SES and environmental dissimilarity, with 9% of ecoregion pairs sharing more similar trait compositions than expected under neutral evolution. More importantly, we found that the observed relationship between trait dissimilarity and environmental dissimilarity was stronger ($R^2 = 0.45$) than expected under neutral evolution (mean of R^2 null distribution = 0.21, 95% = 0.43; *SI Appendix*, Fig. S9), whereas the relationship between trait dissimilarity and both taxonomic and phylogenetic dissimilarity did not differ from neutral expectation (observed taxonomic dissimilarity: $R^2 = 0.06$, mean of R^2 null distribution = 0.08, 95% = 0.13; observed phylogenetic dissimilarity: $R^2 = 0.08$, mean of R^2 null distribution = 0.12, 95% = 0.21; *SI Appendix*, Fig. S9).

Discussion

Our results show that similar trait compositions have arisen among reef fish faunas worldwide in response to contemporary environmental conditions rather than shared evolutionary history (14, 26–28). Across marine realms, we found a common pattern in the distribution of reef fish species in trait space, indicating a wide range of shared functional roles despite major differences in species richness and composition, evolutionary history, and environmental regimes (19). For instance, the distribution of species in trait space was highly similar between the Central Indo-Pacific and Temperate Northern Pacific despite fundamentally different habitats (i.e., coral versus rocky substrates) and a near 10-fold difference in species richness. These results suggest that shallow reefs have been shaped by consistent environmental and ecological pressures, hosting a similar range of trait combinations at different levels of redundancy, with a common backbone of functional entities worldwide. This is a key discovery highlighting that universal ecological roles exist on shallow reefs globally and have been filled by a diversity of species and evolutionary lineages.

Downloaded by guest on January 7, 2022

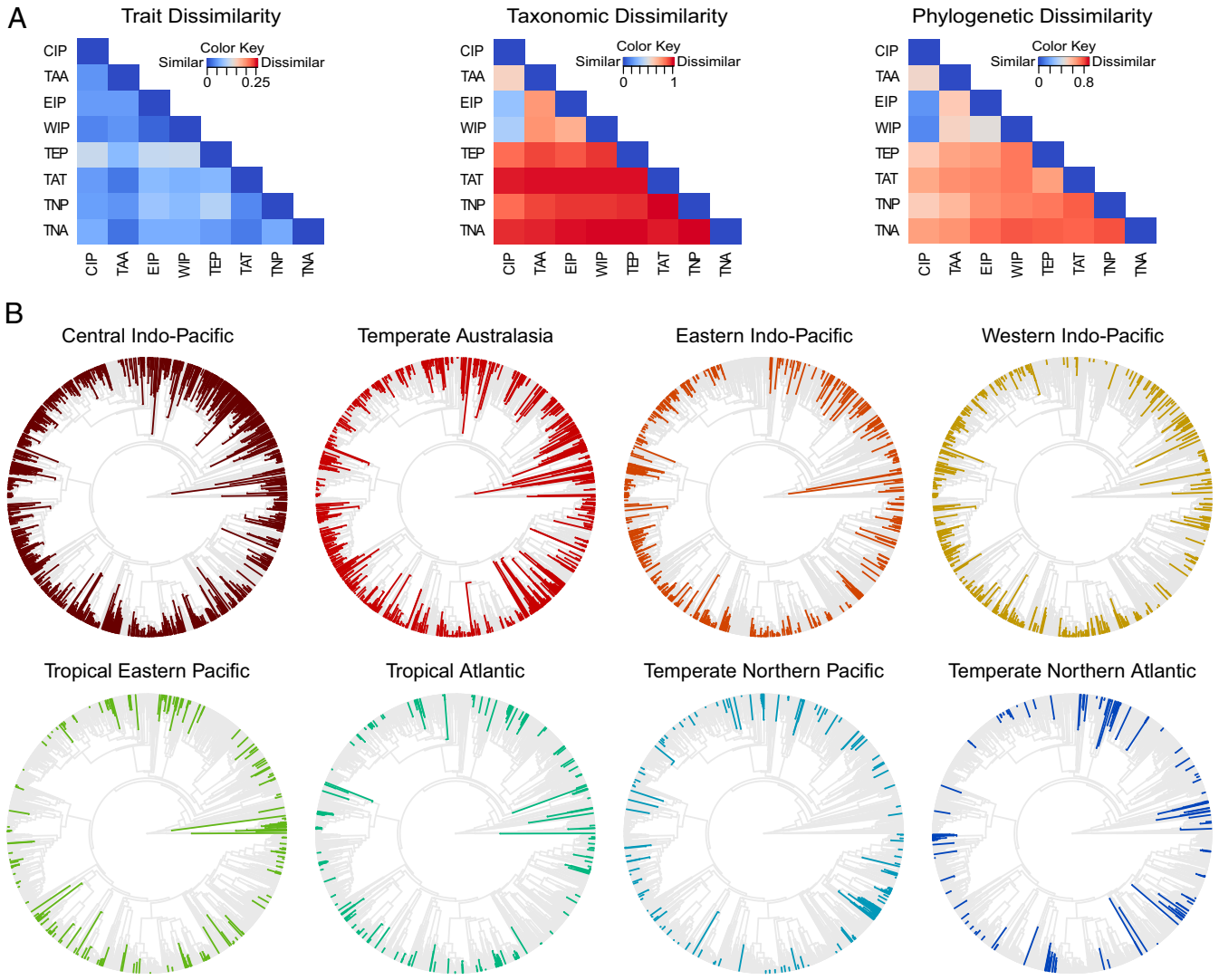


Fig. 3. Heatmaps of trait, taxonomic, and phylogenetic dissimilarity across marine realms, along with phylogenetic trees for species pools from each realm. (*A*) Heatmaps of trait, taxonomic, and phylogenetic dissimilarity across realms; blue indicates high similarity whereas red indicates high dissimilarity. CIP, Central Indo-Pacific; TAA, Temperate Australasia; EIP, Eastern Indo-Pacific; WIP, Western Indo-Pacific; TEP, Tropical Eastern Pacific; TAT, Tropical Atlantic; TNP, Temperate Northern Pacific; and TNA, Temperate Northern Atlantic. Trait dissimilarity was calculated as the Euclidean distance between realm centroids in the first four dimensions of trait space. Taxonomic and phylogenetic dissimilarity were calculated as the turnover component of pairwise Jaccard dissimilarity. (*B*) Phylogenetic trees for each of the eight marine realms; species present in each realm are colored, whereas absent species are gray.

Several hypotheses have attempted to explain global patterns in reef fish diversity, with debate over the importance of evolutionary history versus contemporary environmental variation. For instance, the center-of-origin hypothesis suggests that the greater diversity of reef fishes in the Indo-Australian Archipelago arises from higher rates of speciation (ref. 16, but see ref. 29), while the "climate stability" and "time for speciation" hypotheses suggest that higher diversity results from greater environmental stability during the Quaternary (30) and older colonization events, providing more time for in situ diversification (31). Other hypotheses suggest that reef fish diversity is driven by contemporary gradients in productivity and energy availability (32). While existing evidence supports a mixture of evolutionary and environmental mechanisms in shaping reef fish species diversity (13), there is little knowledge on how these patterns and processes extend to trait composition.

Across ecoregions, we found that reef fish assemblages displayed similar trait compositions in similar environments, with little influence of shared evolutionary history. This pattern could result from evolutionary convergence, environmental filtering, or a combination of both. Only 9% of ecoregion pairs showed greater trait similarity than expected by neutral evolution (*SI Appendix*, Fig. S8), providing little evidence for evolutionary convergence in shaping trait similarity among distantly related reef fish assemblages. However, the observed relationship between trait dissimilarity and environmental dissimilarity was stronger than expected under neutral evolution, providing evidence for environmental filtering (*SI Appendix*, Fig. S9). Similarly, Mazel et al. (25) found that trait similarity between most mammal assemblages did not differ from neutral expectation, concluding that evolutionary convergence may be an important process shaping trait similarity in certain regions only (e.g., Australia). Overall, our results suggest that trait composition arises independently of taxonomic diversity and is primarily driven by contemporary environmental filtering that operates similarly across oceans and evolutionary lineages (33).

This study not only reveals the importance of the environment in shaping trait assembly in reef fishes but also implies that trait composition could be substantially modified by future environmental

Downloaded by guest on January 7, 2022

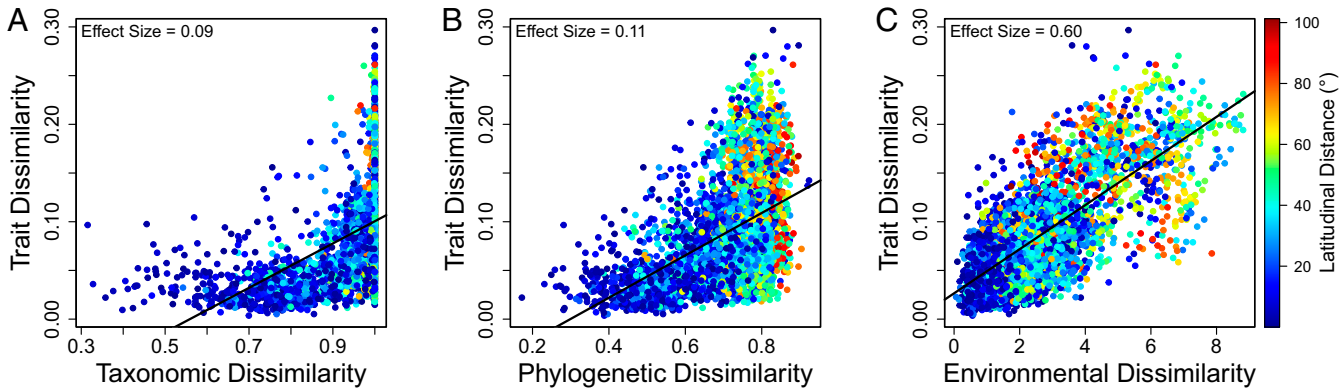


Fig. 4. Trait dissimilarity in relation to taxonomic, phylogenetic, and environmental dissimilarity between ecoregions. (*A*–*C*) Environmental dissimilarity had the strongest influence on trait dissimilarity between ecoregions; although trait dissimilarity increased with taxonomic and phylogenetic dissimilarity, many latitudinally distant regions had similar trait compositions despite highly dissimilar taxonomic and phylogenetic compositions. Points in all panels are pairwise comparisons between ecoregions and are colored by latitudinal distance between ecoregions. Lines are best fits from simple linear regressions.

changes. Environmentally driven trait similarity supports a "periodic table of niches" (27), which hypothesizes that predictable community configurations should arise in response to similar environmental conditions through common responses to environmental filtering. Therefore, the predictability of reef fish trait composition could be key for anticipating future changes in ecosystem functioning and ecosystem services under climate change and human development (34, 35). Our results also imply that trait-based resource management strategies can be applied among regions with distinct species pools (36). Thus, trait-based approaches could improve conservation outcomes across diverse jurisdictions by identifying trait compositions associated with high-functioning reefs and favorable ecosystem states (37). Given the link between environmental conditions and reef fish trait composition, future climate change will profoundly alter the ecological roles sustained by reef fishes, threatening the current livelihoods of millions of people (38). Uncovering links between reef fish traits and ecosystem resilience will be key to maintaining functional reefs in an era dominated by human impacts.

Materials and Methods

Fish Survey Methods. Fish data were collected through the RLS, a standardized monitoring program that surveys fish communities on coral and rocky reefs worldwide (www.reeflifesurvey.com). RLS was chosen for this study because 1) all surveys follow a standardized protocol, and patterns between different biogeographic regions are readily comparable; 2) RLS is conducted uniquely on shallow reef habitats; and 3) RLS has extensive spatial coverage, including both temperate and tropical regions. RLS is comprised of teams of professional scientists and trained recreational divers who complete underwater visual censes of fish communities using 50 × 10 m belt transects. On each transect, divers record the species identity, abundance, and estimated size of all fishes encountered within 5 m of either side of the transect. For full details refer to Edgar and Stuart-Smith (17). For this study, fish data were compiled from 10,913 transects (conducted between 2006 and 2018), encompassing 2,786 taxa from 89 marine ecoregions spanning 10 marine realms (two realms were not included in realm-level analyses, see *Traits, Trait Space, and Common Trait Backbones*). Of the 2,786 observed taxa, 2,582 were recorded at species level, with the remaining recorded primarily at genus level (162 at genus level and 43 at family level); however, for simplicity we refer to all taxa as species throughout the paper. Ecoregions and realms were defined according to the Marine Ecoregions of the World categorization (18), which was also used to classify ecoregions as temperate or tropical. For this study, we considered species occurrences and did not integrate abundance or biomass. Species occurrences were chosen to examine trait composition and redundancy within different realms and biogeographic regions and to identify how these patterns are shaped by environmental conditions and evolutionary history. Species occurrences reveal changes in trait composition due to differences in the existence or redundancy (number of species) of functional entities (i.e., unique trait combinations), whereas species abundances can lead to drastically different trait compositions even when species pools have identical trait spaces. For instance, substantial variation exists in species evenness between temperate and tropical realms, which has strong implications for trait distribution among individuals (39). All indices and metrics throughout the manuscript were therefore calculated using presence/absence data; however, sensitivity tests were performed using species abundances (see *Sensitivity of Results to Occurrence versus Abundance Data*).

Traits, Trait Space, and Common Trait Backbones. We compiled five categorical traits for each of the 2,786 species in the data set, which were chosen to describe life history, trophic ecology, habitat preference, and behavior. While we recognize that these traits only represent a small portion of the true multidimensional species niche, they are recognized proxies of fish functions (5) and have been used to examine reef fish biogeographic patterns (19, 38, 39) and impacts on ecosystem functioning (40). Diet characterized species' main food items and was coded using seven trophic categories: grazer, microphage (feeding on cyanobacteria and microorganisms), planktivore, omnivore, corallivore, invertivore, and piscivore. Microphage was chosen in lieu of "scraping herbivore" or "excavator" based on recent reviews by Clements et al. (41) and Bellwood et al. (42). Water-column position was coded using four ordered categories: benthic (sedentary on the bottom), demersal (swimming near the bottom), pelagic site attached (swimming off the bottom within a reef), and pelagic mobile (swimming off the bottom between reefs). Active period was coded as either diurnal (active during the day) or nocturnal (active during the night). Gregariousness was coded using three ordered categories: solitary, pairing (or sometimes forming small schools), and schooling. Body size was coded using six ordered categories: 0 to 7 cm, 7.1 to 15 cm, 15.1 to 30 cm, 30.1 to 50 cm, 50.1 to 80 cm, and >80 cm. Trait data came from Stuart-Smith et al. (39), the majority of which were derived from FishBase and expert knowledge. The multidimensional trait space was created by applying PCoA to a Gower similarity matrix of the species × traits table and was primarily examined by plotting the first two Principal Coordinate axes (43), which cumulatively explained 39% of the total variance. Trait space was additionally examined using the third and fourth Principal Coordinates axes which together explained 25% of the total variance (*SI Appendix*, Figs. S10 and S11). Thus, the first four axes of trait space accounted for 64% of overall variation, and because a test of mean absolute deviation (44) identified four axes as the optimal number for describing trait space, additional axes were not examined.

While we analyzed trait biogeography by considering single trait values for each species, it should be noted that trait–environment relationships operate at the scale of individuals, and substantial trait variation may exist within species (45). Traits may also be highly plastic and can evolve in response to environmental or ecological pressures (46). In turn, this intraspecific variability can influence ecosystem functioning (47). Here, we were unable to integrate intraspecific trait variability due to insufficient data; however, by using broad categorical traits (e.g., diet, water-column position, and size bin) rather than highly specific continuous traits (e.g., length at maturity and fecundity), we capture the ecological profile of adult individuals.

To evaluate reef fish trait composition globally, we began by examining the distribution of species within trait space for three temperate and five tropical marine realms. Temperate South America and Temperate Southern

Downloaded by guest on January 7, 2022

Africa were not included in realm-level analyses due to low and patchy sampling effort, as few sites and ecoregions have been sampled within these realms. For instance, only 25 species have been observed in Temperate Southern Africa in comparison to 154 species in Temperate North Atlantic, the most species-poor realm included. Thus, we were not able to confidently assess trait-space patterns for Temperate South America and Temperate Southern Africa. However, the individual ecoregions sampled within these realms were included in ecoregion-level analyses, which were separate from realm-level analyses. We calculated 50, 75, and 95% density contours for each realm based on the position and density of species in trait space using the R package emdbook (48) function HPDregionplot. We then generated probability density plots of PCoA 1 and PCoA 2 scores for all species in each realm to further examine the distribution of species along each of the trait-space axes. To examine which traits were most responsible for trait-space structure and to examine how species were distributed according to their trait combinations, we plotted convex hulls of each trait category within the trait space.

Functional entities refer to unique combinations of trait categories, that is, the number of functional entities for a given species pool is the total number of combinations of the different trait categories present (19). Species in the same functional entity also occupy identical positions in trait space. Here, the 2,786 species and five traits considered led to 1,008 possible trait combinations, of which 356 were realized in the global species pool. Common trait "backbones" were calculated by identifying functional entities that were shared by assemblages in 1) all realms, 2) temperate realms only, and 3) tropical realms only. Temperate Australasia is considered a temperate realm but borders the Great Barrier Reef along the east coast of Australia and has been extensively sampled by the RLS program, leading to high species richness and similarities to Indo-Pacific realms. We therefore examined how temperate and tropical backbones changed if we reclassified Temperate Australasia as a tropical realm or if we removed it entirely. In both cases, there was little change, as reclassifying Temperate Australasia as tropical reduced the tropical backbone from 45 to 43 functional entities and removing it from temperate realms expanded the temperate backbone from 42 to 44 entities.

Null Models. Several null models were used throughout this study to assess the sensitivity of results and to identify whether results could have arisen because of chance (random assembly) or from confounding patterns like latitudinal gradients in species richness. These null models all use the approach of randomizing species composition across assemblages (realms or ecoregions) while maintaining observed species richness and species occurrence frequency, using the "independent swap" algorithm (49) in the R package picante (50). We chose to randomize species composition among assemblages rather than randomize species-trait values to avoid creating species with ecologically unfeasible trait combinations.

Null Models for Trait Backbones. To determine whether the number of shared functional entities comprising global, temperate, and tropical backbones was different from expected by chance, we randomly shuffled species composition between realms while maintaining initial species richness and species occurrence frequency and calculated the number of shared functional entities. We repeated this process 999 times to build null distributions of shared functional entities and compared the actual observed numbers of functional entities to the null distributions. Both the global and tropical backbones contained fewer shared functional entities (global = 21 and tropical = 45) than 95% of the null distribution (global null 5% = 26 and tropical null 5% = 50), while the temperate backbone contained fewer entities than 90% of the null distribution but not fewer than 95% (temperate = 42 and temperate null 5% = 40; *SI Appendix*, Fig. S3).

PCoA Centroids, Species Diversity, and Functional Entities across Ecoregions. PCoA centroids refer to the central positions of species pools within trait space and reflect the mean trait values of the observed species. PCoA centroids were therefore calculated for each ecoregion as the mean positions of observed species pools on each of the PCoA axes (*SI Appendix*, Fig. S4). To calculate PCoA centroids and functional entities for each ecoregion while accounting for uneven sampling effort across regions, we randomly selected six transects per ecoregion to generate species pools, calculated metrics for the resulting species pools, repeated this process 99 times with replacement, and calculated mean values for the 99 repetitions. For PCoA centroids, in each of the 99 repetitions, the ecoregion centroid value was calculated as the mean centroid of the six transects. We chose six transects because it was the most common number of transects performed within any ecoregion, that is, the mode. The mode was chosen in lieu of mean or median because the distribution of sampling effort (number of transects per ecoregion) was highly skewed, with few ecoregions containing disproportionate numbers of transects (*SI Appendix*, Table S3). Transects were randomly sampled with replacement because some ecoregions had fewer than six transects; however, we tested the robustness of these choices (see below).

To help visualize latitudinal similarity in ecoregion centroids, we used second-order polynomial linear regressions. However, the purpose of these regression models was primarily visualization—providing a trend line to highlight the unimodal latitudinal pattern in ecoregion centroids (and additionally for a null model, see *Null Model for the Influence of Species Richness*). Yet, we do note that the relationship between PCoA 1 centroids and latitude was substantially better fit by a second order polynomial regression ($R^2 = 0.46$ and Akaike Information Criterion [AIC] = −254.8) than by a simple linear regression ($R^2 = 0.007$ and AIC = −203.4). To provide quantitative evidence for latitudinal similarity in trait composition, we also used simple linear regressions of PCoA 1 centroids in functional of the absolute value of latitude and examined whether including hemisphere as a predictor improved explanatory power.

To test the robustness of the number of transects and procedure used to calculate ecoregion centroids, we recalculated PCoA 1 centroids and reexamined latitudinal similarity patterns by randomly selecting 1, 5, 10, 15, and 20 transects per ecoregion instead of 6. This was done first with replacement and no deletion, second with replacement but after deleting all ecoregions with less than the selected number of transects, and third without replacement after deleting all ecoregions with less than the selected number of transects. Latitudinal trait similarity was robust to all choices except deleting ecoregions with fewer than 20 transects, because this removed over 40% (38 of 89) of ecoregions (*SI Appendix*, Fig. S12).

Magnitude of Variation in PCoA Centroids across Ecoregions. As visible in Fig. 2*A*, distances between ecoregion centroids were much smaller than the extent of the overall trait space, implying that variation across ecoregions was limited. However, the extent of the trait space is defined by the maximum distance between the most dissimilar individual functional entities, which is an inappropriate context for evaluating variation among regional species assemblages. To determine the expected maximum distance between ecoregion centroids, we randomly shuffled species composition among ecoregions while maintaining initial species richness and species occurrence frequency and calculated the maximum distance between ecoregions in the first four dimensions of trait space. We repeated this process 999 times to build a null distribution of expected maximum distances between ecoregion centroids. The maximum null value was 0.60, substantially lower than the maximum distance between any two functional entities (1.24). The actual observed value of maximum distance between ecoregion centroids (0.550) was greater than 95% of the null distribution (95 null = 0.549), demonstrating that ecoregions displayed substantial variation in trait composition that was greater than expected under random assembly (*SI Appendix*, Fig. S13).

Contribution of Traits to Latitudinal Patterns in PCoA Centroids. To examine the contribution of each trait to latitudinal patterns in PCoA 1 centroids, and to examine the distinction between temperate and tropical ecoregions, we calculated average trait values per ecoregion as the proportions of different trait categories present in each species pool using the R package FD (51) function functcomp. We then calculated Pearson correlations between PCoA centroid values and trait values for each ecoregion, and we used multiple factor analysis (MFA) to examine associations between traits and ecoregions. MFA is a modified PCoA that can account for categorical data and therefore give equal weighting to traits with different numbers of categories, for example, diet, which has seven categories, is not overweighted. Associations between traits and temperate versus tropical ecoregions were assessed by the contributions of trait values to the first and second axes of the MFA analysis (*SI Appendix*, Fig. S5). MFA was conducted using the R package FactoMineR (52) function MFA.

Trait Dissimilarity between Marine Realms. In this study, trait dissimilarity was calculated as the Euclidean distance between species-pool centroids in the first four dimensions of trait space, which is not bounded by an upper limit of 1. To define the expected upper limit of trait dissimilarity between marine realms, we randomly shuffled the species composition of each realm while maintaining initial species richness and species occurrence frequency and recalculated the Euclidean distance between realms. We repeated this process 999 times and calculated the maximum trait dissimilarity between realms across the 999 repetitions. The observed maximum value (0.26) was then used to define the upper limit of trait dissimilarity between realms in

Downloaded by guest on January 7, 2022

Fig. 3*A*. This procedure was chosen to provide a conservative estimate of maximum dissimilarity between realms, rather than defining maximum dissimilarity between two species in the trait space (the theoretical maximum distance between assemblages that would each have only one of these two extreme species). For consistency, this procedure was also applied to taxonomic and phylogenetic dissimilarity, which resulted in a maximum taxonomic dissimilarity of 1 and a maximum phylogenetic dissimilarity of 0.91.

Influences of Taxonomic, Phylogenetic, and Environmental Dissimilarity. To evaluate taxonomic and phylogenetic dissimilarity, we use the additive partitioning of pairwise Jaccard dissimilarity proposed by Baselga (22) for taxonomy and adapted by Leprieur et al. (53) for phylogeny, which decomposes beta diversity into nestedness and turnover components. Because we were interested in knowing whether similarity in trait composition resulted from similarity in species composition or evolutionary lineages, we focused on taxonomic and phylogenetic turnover—dissimilarity that occurs when species or lineages present in one region are absent in another region but are replaced by other species or lineages not found in the first region independently of the difference in species richness. As with PCoA centroids, we randomly selected six transects per ecoregion to generate species pools, calculated taxonomic and phylogenetic turnover for the resulting species pools, repeated this process 99 times, and calculated mean values for the 99 repetitions. Phylogenetic trees were derived from the R package fishtree (54), and taxonomic and phylogenetic turnover were calculated using the R package betapart (55). For this analysis, two ecoregions with only five species present in the phylogeny (Malvinas/Falklands and Channels/Fjords of Southern Chile) were removed. Environmental dissimilarity between ecoregions was calculated according to SST mean and range, nitrate, phosphate, and net primary productivity. Following extensive discussion among coauthors, these environmental variables were chosen based on existing knowledge of reef fish functional responses to environmental gradients (56). However, we tested the sensitivity of results to the choice of environmental variables, including adding pH and salinity (see *Sensitivity of Results to the Choice of Environmental Variables*). Data for mean SST and SST range were obtained from the National Oceanic and Atmospheric Administration Coral Reef Watch (57). Data for nitrate and phosphate were obtained from the Bio-ORACLE environmental data set (58). Net primary productivity data were derived from the standard Vertically Generalized Production Model (59). We calculated mean values of environmental variables per ecoregion and standardized them (using the R function scale) before calculating Euclidean distances between all pairs of ecoregions. As for realms, we calculated trait dissimilarity between ecoregions as the Euclidean distance between ecoregion centroids in the first four dimensions of trait space. We then used MRM [R package ecodist (60) function MRM (23)] to quantify the relative influences of taxonomic, phylogenetic, and environmental dissimilarity on trait dissimilarity. Because trait dissimilarity and environmental dissimilarity were not bounded between 0 and 1, all distance matrices were normalized between 0 and 1 prior to analysis. Because the MRM function does not allow direct model assessment, we assessed model quality and assumptions (e.g., residual normality) by performing a standard multiple linear regression with distance matrices as vectors, which provides equivalent results to the MRM function (*SI Appendix*, Fig. S14).

Brownian Motion Null Models. To compare observed results to those expected under neutral evolution, we simulated trait dissimilarity using Brownian motion. A Brownian motion model was first fit to the observed phylogeny and the corresponding sigma value was used for the simulations. Following Mazel et al. (25), we simulated species' positions on the first axis of the trait space (PCoA 1) using the R package geiger (61). We repeated this process 999 times and, in each repetition, we recalculated trait dissimilarity (distance between ecoregion centroids) and reexamined the relationship between trait dissimilarity and taxonomic, phylogenetic, and environmental dissimilarity to develop null distributions of R^2 values between variables. We then compared observed R^2 values, also calculated using trait dissimilarity on the first PCoA axis only, to the null distributions to determine whether the observed relationship was stronger than neutral expectations. We also calculated the magnitude of difference between observed and expected trait dissimilarity [i.e., SES, termed "phylogenetically standardized trait distance" in Mazel et al. (25)] as observed dissimilarity—mean expected dissimilarity/SD of expected dissimilarities—and examined the linear relationship between SES and environmental dissimilarity. Ecoregion pairs were considered more similar or less similar than expected if observed dissimilarity was less than or greater than 97.5% of simulated dissimilarity values (two tails used to allow for both "convergent" and "divergent" pairs). We simulated species' positions on the first axis only because PCoA axes are perfectly uncorrelated by construction and simulating multiple PCoA axes under Brownian motion would induce strong correlations, leading to bias in the neutral data (see ref. 25).

Sensitivity of Results to the Choice of Traits. We tested whether latitudinal similarity in PCoA 1 centroids was robust to the choice and number of traits by deleting each trait, one at a time, recalculating PCoA 1 centroids for each ecoregion, and reexamining latitudinal patterns. Latitudinal similarity was again robust to all choices (and in some cases became more pronounced), indicating that the results were not dictated by any single trait but rather the overall composition of traits (*SI Appendix*, Fig. S15).

Sensitivity of Results to Extreme PCoA Centroid Values. We tested whether latitudinal similarity in PCoA 1 centroids as well as the relationship between trait dissimilarity and environmental dissimilarity were robust to removing extreme centroid values—highly positive PCoA 1 centroids at high latitudes (i.e., ecoregions with the highest leverage). We sequentially removed each of the top 15 ecoregions with the highest PCoA 1 centroid values and reexamined latitudinal patterns for the remaining PCoA 1 centroids, as well the relationship between trait dissimilarity and environmental dissimilarity. However, only 13 ecoregions were removed for assessing the relationship between trait dissimilarity and environmental dissimilarity, because Malvinas/Falklands and Channels/Fjords of Southern Chile were not included in the original MRM analysis (see *Influences of Taxonomic, Phylogenetic, and Environmental Dissimilarity*). Latitudinal similarity in PCoA 1 centroids (i.e., unimodal relationship between centroids and latitude) was again robust to removing ecoregions with the most extreme values; however, the unimodal pattern became less pronounced as ecoregions were removed (*SI Appendix*, Fig. S16). The strong linear relationship between trait dissimilarity and environmental dissimilarity was highly robust and remained clear even with 13 ecoregions removed. (*SI Appendix*, Fig. S17).

Sensitivity of Results to the Choice of Environmental Variables. We tested whether the results of the MRM analysis were robust to the choice of environmental variables used to calculate environmental dissimilarity. We removed each environmental variable, one at a time, recalculated environmental dissimilarity, and reran the MRM analysis. We also tested the effect of adding pH and salinity, both individually and together. Salinity data were obtained from the MULTIOBS_GLO_PHY_REP_015_002 database (62) available through Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=MULTIOBS_GLO_PHY_REP_015_002), and pH data were derived from the Norwegian Earth System Model forced ocean simulation (63). Again, the results were robust to all combinations of environmental variables, with mean effect sizes (across all models) of 0.60 (±0.03) for environmental dissimilarity, 0.13 (±0.04) for phylogenetic dissimilarity, and 0.09 (±0.04) for taxonomic dissimilarity (*SI Appendix*, Table S4).

Sensitivity of Results to Family-Level Taxonomic Dissimilarity. Because not all taxa included in this study were identified to species level, and because different species in the same family may have similar traits, we tested whether results of the MRM analysis were robust to calculating taxonomic dissimilarity at the family level rather than species level. Thus, we recalculated taxonomic dissimilarity between ecoregions and reran the MRM analysis modeling trait dissimilarity in function of family-level taxonomic dissimilarity, phylogenetic dissimilarity, and environmental dissimilarity. Again, results were robust with effect sizes of 0.54 for environmental dissimilarity, 0.11 for phylogenetic dissimilarity, and 0.09 for taxonomic dissimilarity.

Null Model for the Influence of Species Richness. We tested whether latitudinal similarity in PCoA centroids could have resulted from latitudinal patterns in species richness using two null models where we randomly shuffled species composition among ecoregions while maintaining initial species richness and species occurrence frequency. We therefore shuffled species composition, recalculated PCoA centroid values for each ecoregion, and calculated the strength (R^2 value) of the relationship between randomized PCoA 1 centroid values and latitude using 1) second-order polynomial regression and 2) simple linear regression with the absolute value of latitude. We repeated this process 999 times to build null distributions of R^2 values and compared observed R^2 values to the null distributions. R^2 values from both observed models were greater than 95% of the values in the null distributions, indicating that latitudinal trait similarity was not a result of latitudinal patterns in species richness alone (*SI Appendix*, Fig. S18).

Downloaded by guest on January 7, 2022

Sensitivity of Results to Occurrence versus Abundance Data. In this study, we used species occurrences rather than species abundances (see *Fish Survey Methods*). To determine whether results were robust to this choice, we recalculated PCoA 1 centroids for all ecoregions as abundance-weighted centroids and tested the correlation between the original centroid values and the abundance-weighted centroid values. We then reran the MRM analysis in which trait dissimilarity was calculated as the Euclidean distance between abundance-weighted ecoregion centroids in the first four dimensions of trait space, and taxonomic turnover was calculated with species abundances using Bray–Curtis dissimilarity. The Pearson's correlation value between the original (occurrence-based) PCoA 1 centroid values and the abundance-weighted PCoA 1 centroid values was 0.97, demonstrating that trait similarity was robust to both species' occurrences and abundances. Effect sizes from the MRM analysis, and R^2 values from individual regressions, using species abundances were nearly identical to those of the original occurrence-based analysis (Original analysis: environmental dissimilarity: effect size = 0.60 and R^2 = 0.56; taxonomic dissimilarity: effect size = 0.09 and R^2 = 0.20; phylogenetic dissimilarity: effect size = 0.11 and R^2 = 0.24. Abundance-based analysis: environmental dissimilarity: effect size = 0.51 and R^2 = 0.56; taxonomic dissimilarity: effect size = 0.003 and R^2 = 0.12; phylogenetic dissimilarity: effect size = 0.15 and R^2 = 0.28), again demonstrating that results were robust to both occurrence and abundance data.

Sensitivity of Results to the Trait Dissimilarity Metric. We examined whether results were robust to how trait dissimilarity was quantified by rerunning the MRM analysis using functional beta diversity from Chao et al. (64) instead of distances between ecoregion centroids in trait space, where functional beta diversity is calculated as a generalized version of pairwise Rao's quadratic entropy between assemblages. In agreement with the original MRM analysis, and individual regressions, environmental dissimilarity had the highest effect size (0.31) and individual R^2 value (0.28), while taxonomic and phylogenetic dissimilarity had weaker effect sizes (taxonomic: −0.012; phylogenetic: −0.002) and R^2 values (taxonomic: 0.04; phylogenetic: 0.06) and added little explanatory power (R^2 full model: 0.281).

Data Availability. RLS data are freely available and can be accessed at https://reeflifesurvey.com/. Reef fish trait data are freely available and can be accessed at http://www.fishbase.org. Reef fish phylogenies are freely available through the R package fishtree (42). All environmental data came from freely available public sources (see *Materials and Methods*).

ACKNOWLEDGMENTS. We thank all RLS divers worldwide whose data collection efforts made this study possible. This research used the National Collaborative Research Infrastructure Strategy-enabled Integrated Marine Observing System infrastructure for database support and storage. This research was funded through the 2017–2018 Belmont Forum and BiodivERsA REEF-FUTURES project under the BiodivScen ERA-Net COFUND program along with the French National Research Agency, the Natural Sciences and Engineering Research Council (Grant No. RGPBB/525590), the Canada Research Chairs Program, and the Ocean Frontier Institute.

1. C. Violle, P. B. Reich, S. W. Pacala, B. J. Enquist, J. Kattge, The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 13690–13696 (2014).
2. S. Díaz, M. Cabido, Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* **16**, 646–655 (2001).
3. F. de Bello *et al*., Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.* **19**, 2873–2893 (2010).
4. M. F. Rosenfield, S. C. Müller, Plant traits rather than species richness explain ecological processes in subtropical forests. *Ecosystems (N. Y.)* **23**, 52–66 (2020).
5. S. Villéger, S. Brosse, M. Mouchet, D. Mouillot, M. J. Vanni, Functional ecology of fish: Current approaches and future challenges. *Aquat. Sci.* **79**, 783–801 (2017).
6. C. Fortunel, R. Valencia, S. J. Wright, N. C. Garwood, N. J. B. Kraft, Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest. *Ecol. Lett.* **19**, 1062–1070 (2016).
7. N. J. B. Kraft, R. Valencia, D. D. Ackerly, Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* **322**, 580–582 (2008).
8. M. McLean *et al*., Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. *Glob. Change Biol.* **25**, 3424–3437 (2019).
9. J. E. Allgeier, C. A. Layman, P. J. Mumby, A. D. Rosemond, Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Glob. Change Biol.* **20**, 2459–2472 (2014).
10. A. Norkko, A. Villnäs, J. Norkko, S. Valanko, C. Pilditch, Size matters: Implications of the loss of large individuals for ecosystem function. *Sci. Rep.* **3**, 2646 (2013).
11. C. Roscher *et al*., Using plant functional traits to explain diversity-productivity relationships. *PLoS One* **7**, e36760 (2012).
12. D. P. Tittensor *et al*., Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1101 (2010).
13. T. Gaboriau *et al*., Ecological constraints coupled with deep-time habitat dynamics predict the latitudinal diversity gradient in reef fishes. *Proc. Biol. Sci.* **286**, 20191506 (2019).
14. G. J. Edgar *et al*., Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. *Sci. Adv.* **3**, e1700419 (2017).
15. D. Jablonski *et al*., Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 10487–10494 (2013).
16. C. Mora, "Large-scale patterns and processes in reef fish richness" in *Ecology of Fishes on Coral Reefs*, C. Mora, Ed. (Cambridge University Press, 2015), pp. 88–96.
17. G. J. Edgar, R. D. Stuart-Smith, Systematic global assessment of reef fish communities by the Reef Life Survey program. *Sci. Data* **1**, 140007 (2014).
18. M. D. Spalding *et al*., Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience* **57**, 573–583 (2007).
19. D. Mouillot *et al*., Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 13757–13762 (2014).
20. B. Bramon Mora, D. Gravel, L. J. Gilarranz, T. Poisot, D. B. Stouffer, Identifying a common backbone of interactions underlying food webs from different ecosystems. *Nat. Commun.* **9**, 2603 (2018).
21. A. L. Pigot, C. H. Trisos, J. A. Tobias, Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proc. Biol. Sci.* **283**, 20152013 (2016).
22. A. Baselga, Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **19**, 134–143 (2010).
23. J. W. Lichstein, Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecol.* **188**, 117–131 (2007).
24. G. H. Orians, "Convergent evolution at the community level" in *Coevolution*, D. J. Futuyama, M. Slatkin, Eds. (Sinauer Associates, 1983), pp. 431–458.
25. F. Mazel *et al*., The geography of ecological niche evolution in mammals. *Curr. Biol.* **27**, 1369–1374 (2017).
26. L. M. Bower, K. O. Winemiller, Fish assemblage convergence along stream environmental gradients: An intercontinental analysis. *Ecography* **42**, 1691–1702 (2019).
27. K. O. Winemiller, D. B. Fitzgerald, L. M. Bower, E. R. Pianka, Functional traits, convergent evolution, and periodic tables of niches. *Ecol. Lett.* **18**, 737–751 (2015).
28. R. E. Drenovsky, A. Khasanova, J. J. James, Trait convergence and plasticity among native and invasive species in resource-poor environments. *Am. J. Bot.* **99**, 629–639 (2012).
29. D. L. Rabosky *et al*., An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395 (2018).
30. L. Pellissier *et al*., Quaternary coral reef refugia preserved fish diversity. *Science* **344**, 1016–1019 (2014).
31. E. C. Miller, K. T. Hayashi, D. Song, J. J. Wiens, Explaining the ocean's richest biodiversity hotspot and global patterns of fish diversity. *Proc. Biol. Sci.* **285**, 20181314 (2018).
32. D. J. Currie *et al*., Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.* **7**, 1121–1134 (2004).
33. D. Bellwood, P. Wainwright, C. Fulton, A. Hoey, Assembly rules and functional groups at global biogeographical scales. *Funct. Ecol.* **16**, 557–562 (2002).
34. M. McLean *et al*., Fish communities diverge in species but converge in traits over three decades of warming. *Glob. Change Biol.* **25**, 3972–3984 (2019).
35. I. Trindade-Santos, F. Moyes, A. E. Magurran, Global change in the functional diversity of marine fisheries exploitation over the past 65 years. *Proc. Biol. Sci.* **287**, 20200889 (2020).
36. L. A. K. Barnett, N. S. Jacobsen, J. T. Thorson, J. M. Cope, Realizing the potential of trait-based approaches to advance fisheries science. *Fish Fish.* **20**, 1034–1050 (2019).
37. A. J. Woodhead, C. C. Hicks, A. V. Norström, G. J. Williams, N. A. J. Graham, Coral reef ecosystem services in the Anthropocene. *Funct. Ecol.* **33**, 1023–1034 (2019).
38. J. E. Cinner *et al*., Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* **368**, 307–311 (2020).
39. R. D. Stuart-Smith *et al*., Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* **501**, 539–542 (2013).
40. F. Micheli *et al*., High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biol. Conserv.* **171**, 186–194 (2014).
41. K. D. Clements, D. P. German, J. Piché, A. Tribollet, J. H. Choat, Integrating ecological roles and trophic diversification on coral reefs: Multiple lines of evidence identify parrotfishes as microphages. *Biol. J. Linn. Soc. Lond.* **120**, 729–751 (2017).
42. D. R. Bellwood, R. P. Streit, S. J. Brandl, S. B. Tebbett, The meaning of the term 'function'in ecology: A coral reef perspective. *Funct. Ecol.* **33**, 948–961 (2019).
43. D. Mouillot, N. A. J. Graham, S. Villéger, N. W. H. Mason, D. R. Bellwood, A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**, 167–177 (2013).
44. E. Maire, G. Grenouillet, S. Brosse, S. Villéger, How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob. Ecol. Biogeogr.* **24**, 728–740 (2015).
45. J. E. Allgeier, T. C. Adam, D. E. Burkepile, The importance of individual and species-level traits for trophic niches among herbivorous coral reef fishes. *Proc. Biol. Sci.* **284**, 20170307 (2017).
46. J. A. Sheridan, D. Bickford, Shrinking body size as an ecological response to climate change. *Nat. Clim. Chang.* **1**, 401–406 (2011).

Downloaded by guest on January 7, 2022

47. S. Des Roches *et al*., The ecological importance of intraspecific variation. *Nat. Ecol. Evol.* **2**, 57–64 (2018).
48. B. M. Bolker, *Ecological Models and Data in R* (Princeton University Press, 2008).
49. N. J. Gotelli, Null Model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621 (2000).
50. S. W. Kembel *et al*., Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464 (2010).
51. E. Laliberté, P. Legendre, B. Shipley, M. E. Laliberté, *Package 'FD* (Meas. Funct. Divers. Mult. Traits Tools Funct. Ecol, 2014).
52. F. Husson, J. Josse, S. Le, J. Mazet, M. F. Husson, Package 'FactoMineR.' *Package FactorMineR* (2020).
53. F. Leprieur *et al*., Quantifying phylogenetic beta diversity: Distinguishing between 'true' turnover of lineages and phylogenetic diversity gradients. *PLoS One* **7**, e42760 (2012).
54. J. Chang, D. L. Rabosky, S. A. Smith, M. E. Alfaro, An r package and online resource for macroevolutionary studies using the ray-finned fish tree of life. *Methods Ecol. Evol.* **10**, 1118–1124 (2019).
55. A. Baselga, C. D. L. Orme, betapart: An R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–812 (2012).
56. J. E. Duffy, J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, G. J. Edgar, Biodiversity enhances reef fish biomass and resistance to climate change. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6230–6235 (2016).
57. G. Liu *et al*., Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA coral reef Watch. *Remote Sens.* **6**, 11579–11606 (2014).
58. L. Tyberghein *et al*., Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Glob. Ecol. Biogeogr.* **21**, 272–281 (2012).
59. M. J. Behrenfeld, P. G. Falkowski, Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* **42**, 1–20 (1997).
60. M. W. Pennell *et al*., Geiger v2.0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* **30**, 2216–2218 (2014).
61. S. C. Goslee, D. L. Urban, The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.* **22**, 1–19 (2007).
62. B. B. Nardelli, A novel approach for the high-resolution interpolation of in situ sea surface salinity. *J. Atmos. Ocean. Technol.* **29**, 867–879 (2012).
63. Ø. Seland *et al*., The Norwegian Earth System model, NorESM2 - Evaluation of theCMIP6 DECK and historical simulations. *Geosci Model Dev Discuss* **2020**, 1–68 (2020).
64. A. Chao *et al*., An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. *Ecol. Monogr.* **89**, e01343 (2019).

Downloaded by guest on January 7, 2022