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Biogeography and evolution of reef fishes on tropical Mid-Atlantic Ridge islands

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With their simplified and isolated communities, oceanic islands are considered 'natural laboratories' for biogeographic and evolutionary studies. Along the Mid-Atlantic Ridge (MAR), St Paul's Rocks, Ascension and St Helena islands are nearly equidistant from South America and Africa. While St Paul's Rocks is typically associated with the Brazilian Province, Ascension and St Helena are commonly treated as a unified biogeographical entity despite being separated by approximately 1300 km of open ocean. Using an expert-validated, rigorously curated dataset on Atlantic reef fishes, we demonstrate that these three islands constitute a cohesive biogeographic unit, sharing 46 species found nowhere else in the Atlantic. By integrating time-calibrated phylogenies and distributional data, we reconstructed dispersal routes of 88 MAR fishes, revealing predominant western Atlantic origins and a pronounced eastern influence among endemics. Divergence estimates for two Ascension endemics may predate the islands' emergence, highlighting the potential roles of seamounts and eustatic sea-level changes in shaping biotic persistence and diversification. Trait analysis revealed that MAR fishes are typically larger, occupy wider depth ranges and are more often pelagic spawners and rafters than MAR endemics and their coastal counterparts. Our findings underscore the complex biogeographic and evolutionary processes structuring the reef fish communities of the tropical MAR islands.

1. Introduction

Biogeography seeks to explain spatial patterns of biodiversity by assessing the distributions of organisms. This interdisciplinary field draws on ecology, geology and palaeontology to uncover the evolutionary and ecological mechanisms underlying regional differences and similarities [1–3]. In the marine realm, biogeographic barriers are often subtler than on land, as the fluid nature of the environment, combined with the pelagic larval stage common in many species, enables strong connections across vast distances. In this context, oceanic islands emerge as compelling research subjects, often considered 'natural laboratories' for biogeographic, ecological and evolutionary studies due to their isolation, small size and often well-known geological histories [4–6]. Studies on these environments can offer critical insights into ecological and evolutionary processes and community assembly across space and time. Many oceanic islands are classified as unique provinces

within greater biogeographic areas, following the threshold of >10% endemism proposed by Briggs [4], a parameter still widely applied [1,3].

In the Atlantic, St Paul's Rocks (0°55' N, 29°21' W), Ascension (7°58' S, 14°23' W) and St Helena (16°00' S, 5°45' W) are highly isolated oceanic islands of great biogeographic interest. They are located in the Mid-Atlantic Ridge (MAR), central to the coasts of South America and Tropical Eastern Africa [7] (electronic supplementary material, table S1), prompting questions about the origins of their biotic composition and evolutionary history. Ascension and St Helena are volcanic islands that surfaced around 1.15 million years ago (Ma) and 15 Ma, respectively, and are known as two of the remotest islands in the world. Their pronounced isolation has contributed to a depauperate shallow fish fauna, with 116 species recorded for Ascension and 95 for St Helena [8]. St Paul's Rocks, one of the smallest and most isolated archipelagos, originated around 9 Ma and, although often viewed as an impoverished outpost of the Brazilian marine fauna, also hosts species absent from nearby coasts yet present on other Atlantic islands, with a total of 70 reef fish species [7,9–11].

Thousands of kilometres separate these three islands within the tropical Atlantic, where biogeographic barriers of distinct orders act as possible boundaries for genetic connectivity, such as distance, sea currents, temperature and salinity. Surface currents generally flow from the eastern Atlantic towards the MAR, potentially transporting larvae [3]. However, faunal affinities for many reef groups are stronger with the western Atlantic (e.g. [12–15]), supported by palaeontological [13] and phylogeographic [16] evidence, indicating a prevailing west-to-east dispersal. Another dispersal route seems to connect the Indian Ocean to the tropical Atlantic, possibly via the Cape of Good Hope [3,17,18], transported by the Agulhas leakage during interglacial periods [18,19]. Although currents seem to facilitate mainly larval dispersal [7,20], other studies highlight the importance of various additional biological attributes for fishes dispersing to oceanic islands and the differences between this group and insular endemic species (e.g. [21,22]).

Notably, factors beyond pelagic larval duration are equal or better predictors of reef fish geographic range size, such as adult body sizes, schooling behaviour and period of activity [23]. Larger range sizes and the ability to raft enhance the odds of reaching remote locations, while pelagic larval development (instead of demersal) is an important feature for crossing soft barriers [24]. Furthermore, environmental factors ('habitat similarity', such as similar surface temperatures and water turbidity) promote the settlement, maintenance and connectivity of species and populations among insular and coastal areas (e.g. Greater Caribbean and Brazilian oceanic islands), as well as connecting different islands [10]. Historical, oceanographical and geological factors, including seamounts and sea-level fluctuations, further shape insular community assembly [25]. Given their distinct geological ages, extreme isolation and geographic position, the MAR islands offer a valuable case study for understanding transatlantic dispersal and how traits and phylogenetic history influence species' responses to biogeographic filters.

Here, we examine the evolutionary history and biogeographical patterns of three MAR islands, focusing on (i) historical connections, (ii) biogeographic affinities of their reef fish assemblages, and (iii) contrasts in life-history traits among Atlantic, MAR and MAR endemic fishes. We identify the MAR islands as a single biogeographic entity with 17 fish species shared exclusively among two or more of the islands and three endemics common to all. Leveraging a comprehensive dataset covering distributions and life-history traits for 1637 Atlantic reef fishes, we explore how species attributes may influence their geographic ranges and the emergence of insular endemism. Our analyses encompass ancestral areas, haplotype networks and biogeographical patterns of over half of the fish species that occur on the MAR islands, shedding light on the influence of both the western and eastern Atlantic in the community composition of these isolated habitats. By integrating expert-curated data and molecular analyses, our findings provide valuable insights into macroecological and evolutionary dynamics that shape reef fish diversity in one of the Atlantic's most isolated marine systems.

2. Material and methods

(a) Species distributions and life-history traits

We gathered presence–absence data for 73 families of reef-associated fishes, encompassing 1637 species in 26 distinct biogeographical units within the Atlantic Basin (electronic supplementary material, table S2), thus building a comprehensive Atlantic fish database [8]. We followed Floeter *et al.*'s definition for 'reef fish' [3], including any shallow (<100 m) tropical/subtropical benthic or benthopelagic fishes that consistently associate with hard substrates of coral, algal or rocky reefs or occupy adjacent sandy substrate. All distributions were strictly verified by the authors and double-checked with online databases and available literature (peer-reviewed regional checklists and scientific papers). Life-history traits were compiled using personal data, online databases and published sources (e.g. [10,21,26,27]). Carefully curating the aforementioned data was a crucial step in mitigating issues associated with using information from unfiltered online databases, as discussed by Chollett & Robertson [28] and Nori *et al.* [29].

(b) Cluster analysis

We used presence–absence information for 1637 reef fish species to perform a bootstrapped cluster analysis (999 replicates) with Euclidean distance matrix, Sørensen similarity coefficient and UPGMA as the clustering method, selected based on the highest degree of reliability of the clustered branches, and cophenetic correlation value [30] (figure 1). Here, *p*-values for cluster nodes were calculated using bootstrap resampling (999 replicates) with the 'Pvclust' package [31]. To preclude possible bias related to species misidentification and differences in the sampling effort among the studied areas, we also performed the same cluster analyses using genus distribution (electronic supplementary material, figure S1). Invasive, introduced and undescribed

species were excluded. Areas encompassed by the Guiana and Amazonian coasts, South European Atlantic Shelf and Saharan Upwelling [32] were excluded from ensuing analyses, given the unavailability of polished data on reef fish distributions, along with overall habitat dissimilarity compared with adjacent studied regions.

(c) Taxonomic selection: phylogenies

We compiled molecular phylogenies with estimations of divergence time, including species endemic to at least one of the MAR islands. Six phylogenies met these requirements (*Chaetodon*, *Chromis*, *Priolepis*, *Scartella*, *Sparisoma* and *Thalassoma* [33–38]). Since the *Chaetodon* and *Chromis* tree files were not available from the original publications, we compiled the sequences available in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and re-ran the divergence time analyses, reaching results congruent with those recovered by the original publications.

(d) Molecular phylogenies and haplotype networks

When phylogenies lacked an estimate of the divergence time, sequences and topology were used for subsequent analysis; that is, we used the ‘sibling species’ relationships found in the topologies to perform the analysis of divergence time. When sister-pairs molecular phylogenetic studies were unavailable, we pursued the sequences of target species in GenBank and Barcode of Life Data System (<http://www.boldsystems.org/>) to perform analyses of divergence time between clades. We also generated novel genetic sequences for species of *Prognathodes* and *Stegastes*, which were previously unrepresented in genetic databases (electronic supplementary material, table S3). Therefore, divergence dates were calculated for five sister-pairs of MAR endemics and their closest relatives (genera *Chaetodon*, *Chromis*, *Ophioblennius*, *Prognathodes* and *Stegastes*) using BEAST 2.6.3 [39], with a relaxed lognormal clock and the Calibrated Yule Model as priors. Substitution models were estimated using jModelTest2 [40]. Secondary calibration points provided by Rabosky *et al.* [41] or by time-tree phylogenies of the target group were also considered. In multi-locus analyses with both mtDNA and nuDNA, the genes were individually partitioned, thereby enabling the specification of independent substitution models for each partition (electronic supplementary material, table S5). In single-locus mtDNA analyses, we employed a strict molecular clock, applying mutation rates derived from the literature: 0.02 for the COI gene, 0.025 for CytB and 0.035 for the control region [42,43]. At least two independent Markov chain Monte Carlo (MCMC) simulations were implemented for each analysis. The MCMC chain length was refined to be sufficient once all convergence statistics of effective sample sizes were >200, sampling trees at every 0.01% generation of the chain length. The run parameters were accessed in Tracer 1.7 [44], and the log and tree files were combined in LogCombiner [39]. The target tree was summarized in TreeAnnotator [39] after excluding 20% burning from each run. In the analyses, divergence dates were considered only when a clear phylogenetic separation was discernible between the MAR and eastern or western Atlantic populations (i.e. clearly distinct clades with geographical structure and absence of shared haplotypes between them). When different clades were not distinguishable for those regions, indicating an absence of isolation between populations from the MAR and eastern or western Atlantic, the divergence date was computed as zero, regardless of the estimated crown age (e.g. *Centropyge* [17]). This also applies to cases when there was no separation between different islands. To discern finer details of population connectivity, we constructed haplotype networks using the TCS algorithm [45] implemented in PopArt [46] for *Ophioblennius* and *Stegastes* species (figure 2).

(e) Ancestral areas

We estimated the ancestral geographic range of 10 MAR lineages for which we were able to obtain or build phylogenetic trees (genera *Chaetodon*, *Chromis*, *Ophioblennius*, *Prognathodes*, *Scartella*, *Sparisoma* and *Thalassoma*; figure 3; electronic supplementary material, figure S14) with the R package ‘BioGeoBEARS’ [47]. In cases of comprehensive phylogenies, the trees were pruned by selecting the clade that included the MAR fishes. The analysis performed in ‘BioGeoBEARS’ is a result of three different models to assess the biogeographic history of the species: dispersal–vicariance analysis (DIVALike), Bayesian analysis of biogeography (BayArea-like model) and dispersal–extinction–cladogenesis (DEC model [48]). We performed six non-stratified and six time-stratified analyses using each model (i.e. DEC, DIVA and BayArea), including those with founder-event jump dispersal (e.g. ‘DEC+j’ model). We designated 10 biogeographic regions for this analysis (modified from [1,32,49]; electronic supplementary material, figure S2).

(f) Functional space

To estimate functional diversity, we used six life-history traits compiled for Atlantic reef fish [8]: maximum total adult body length and depth range, spawning method, schooling behaviour, diet and rafting ability (see figure 4 legend for spawning and dietary classes). Fishes were arranged into functional entities (unique trait combinations), and for this purpose, we grouped the numerical traits ‘maximum body length’ and ‘maximum depth’ into categories following Mouillot *et al.* [50] and Halpern & Floeter [51], respectively. Variations in trait composition for each group of species occurrence (MAR endemics, MAR fishes and Atlantic fishes) were evaluated using principal coordinate analysis with Gower dissimilarity matrix [52]. Functional indexes (functional evenness, richness and diversity; electronic supplementary material, table S6) and the quality of functional spaces (electronic supplementary material, figure S3) were calculated using the ‘mFD’ R package [53], and geometric polygons for each group were created using convex hulls with R package ‘geometry’ [54].

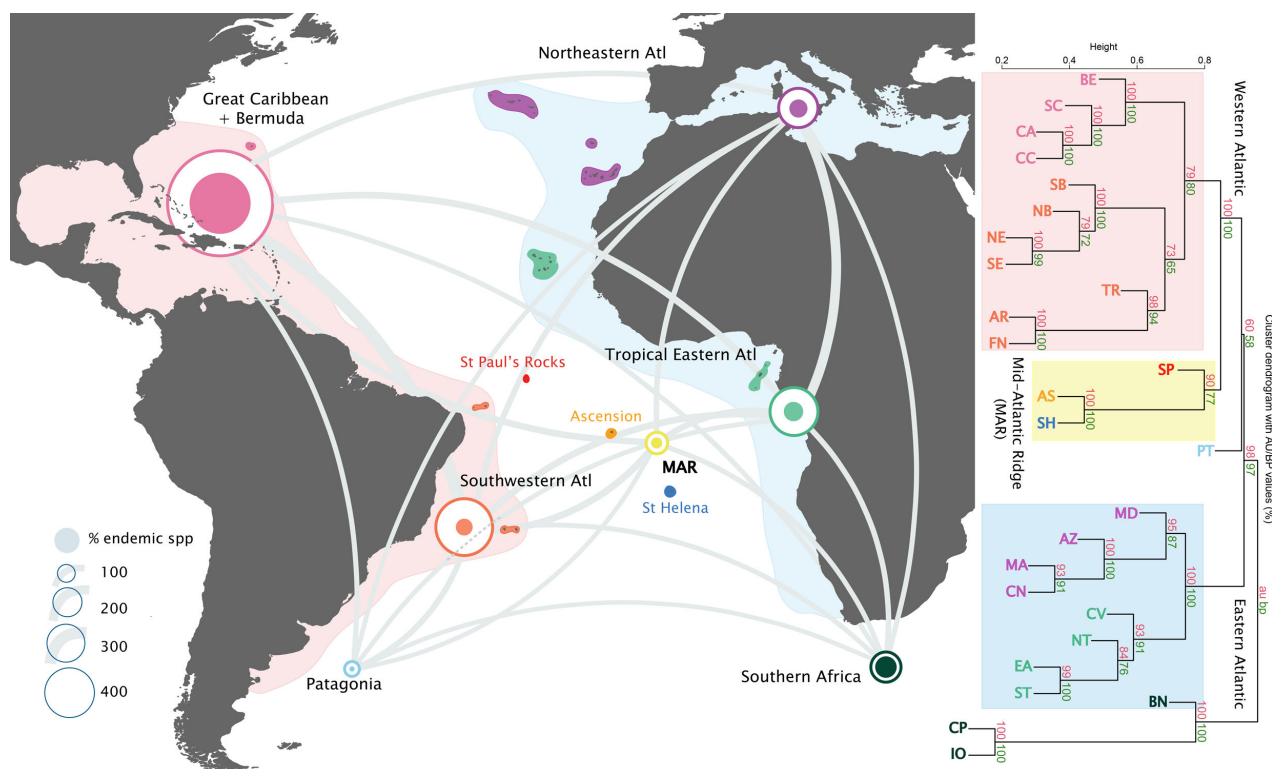


Figure 1. Map of the Atlantic Ocean outlining the western (pink) and eastern (blue) coasts and the tropical islands of the MAR combined in yellow. Outer circles are sized according to the number of fish species present in each Atlantic region, and internal circles are proportional to the number of endemics in each region. The internal circle of South Africa represents Indo-Pacific species absent in the Atlantic or endemic species for the area. The number of species shared among the areas is shown by the width of the grey lines connecting them. On the right side, bootstrapped cluster analysis shows the biogeographic clustering within the Atlantic. The circles in the map and acronyms in the dendrogram are coloured according to significant groups. Red numbers on the nodes represent approximately unbiased p -values ('au'), and green numbers are the bootstrap probability value ('bp') for each cluster. The two-letter acronyms in the dendrogram refer to the 26 units used for compiling reef fish distributions (electronic supplementary material, table S2).

3. Results

St Paul's Rocks, Ascension and St Helena formed a statistically supported cluster (figure 1), with Ascension and St Helena more similar to each other than either is to St Paul's Rocks. The MAR ichthyofauna showed greater affinity with the western Atlantic, particularly the Brazilian Province and Greater Caribbean, sharing 44 species exclusively. We found that 11 fish species occur only in the MAR islands and eastern Atlantic regions; 74 are amphi-Atlantic and 44 are MAR endemics (three of which occur across all three islands; electronic supplementary material, table S7).

Ancestral area reconstructions (figure 3), haplotype networks (figure 2) and published phylogenies allowed us to trace the dispersal routes of 88 MAR fishes (electronic supplementary material, figures S5–S13, table S8). Approximately 70% of the non-endemics reached the MAR islands via dispersal routes traced to the western Atlantic, with some using Brazilian islands as stepping stones. About 22% of the species came from the eastern Atlantic, predominantly from the Tropical Eastern Atlantic, while approximately 8% were traced back to the Indian Ocean. Among MAR endemics, over half had western Atlantic origins, while the eastern Atlantic and the Indian Ocean contributed approximately 37% and approximately 11%, respectively. Two endemic species from Ascension showed divergence times that potentially predate the island's emergence: *Scartella nuchifilis* (3.1 Ma, 1.0–5.2 Ma 95% HPD) marginally overlaps the time of island formation.

Molecular and network analyses also resolved the biogeographic positions of MAR endemics *Prognathodes dichrous*, *Stegastes lubbocki*, *S. sanctaehelenae* and *Ophioblennius* aff. *atlanticus*. The closest relatives of the first three were located in the western Atlantic, while the latter aligned with an eastern lineage. This *Ophioblennius*, endemic to the MAR islands, has been recognized as a new species but is still awaiting formal description [16]. We found clear biogeographical compartmentalization between *Stegastes pictus* and *S. lubbocki* and *S. sanctaehelenae*, which configures distinct Brazilian (including Vitória-Trindade seamounts) and Ascension and St Helena haplogroups (figure 2). Even though the Brazilian coast, along with seamounts and the islands of Trindade and Martin Vaz, appears quite separated for *S. pictus*, either these areas remain connected, as shown by Trindade and Martin-Vaz haplotypes appearing in the larger circle along with the Brazilian coast and seamounts, or those are ancestral haplotypes.

Concerning life-history traits (figure 4), among the Atlantic reef fish species that do not occur on any MAR island (herein ATL fishes), nearly 6% of them have a relatively higher dispersal ability due to their documented rafting behaviour while juveniles or adults, whereas approximately 13% of MAR endemics and approximately 31% of MAR fishes possess rafting abilities. We also examined spawning behaviour, finding that approximately 70% of ATL fishes and 51% of MAR endemics are pelagic spawners, while approximately 28% and approximately 43% of them, respectively, are demersal spawners. In contrast,

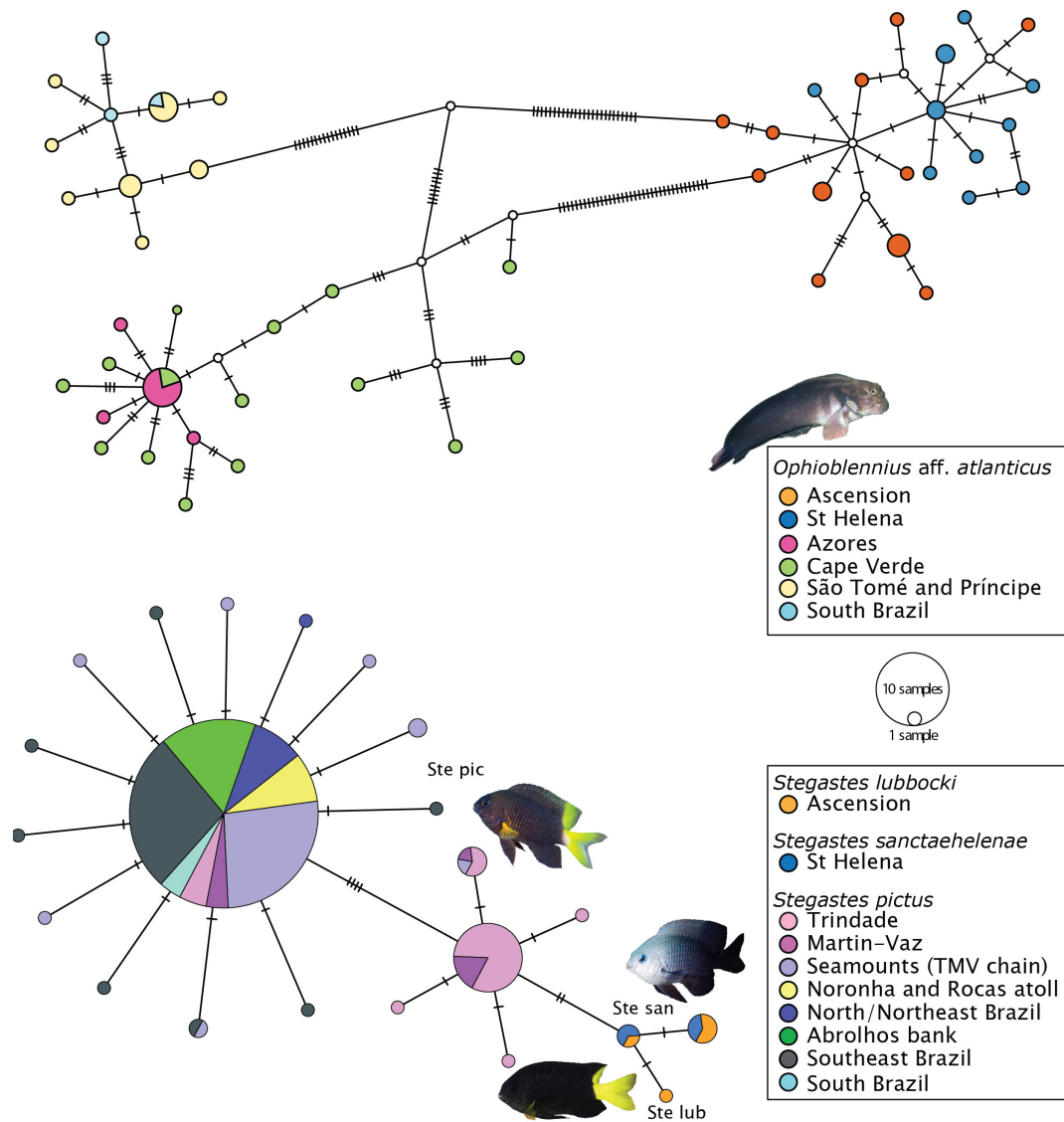


Figure 2. Haplotype networks of *Ophioblennius* and *Stegastes* clades containing endemic species of the tropical Mid-Atlantic Ridge (MAR) islands. Each circle represents a unique haplotype of the mitochondrial gene CytB, with the circle size proportional to the number of individuals sharing that haplotype. Hatch marks indicate mutational steps between haplotypes.

approximately 82% of the fish present in at least one of the MAR islands and elsewhere are pelagic spawners, with only 9.56% being demersal. We also compiled the maximum recorded depth and body length for species found in these three biogeographic scales and observed that the larger maximum adult size is found for MAR fishes, while MAR endemics are smaller-bodied. MAR fishes are able to inhabit deeper waters than both MAR endemics and ATL fishes.

By organizing species into functional entities within a functional space, we found that both MAR endemics and MAR fishes represent a subset of the overall Atlantic reef fish functional space, but nearly one-third of the MAR endemic species have functional aspects that are not presented in the overall MAR fish community (figure 4). Furthermore, compared with widespread Atlantic species, MAR fishes and MAR endemics exhibit higher functional evenness but lower functional richness and divergence (electronic supplementary material, table S6).

4. Discussion

The reef fish communities across St Paul's Rocks, Ascension and St Helena form a unique biogeographic group, distinct from other coastal and insular areas on both sides of the Atlantic. Despite prevailing westbound surface currents reaching the MAR islands, facilitating larval dispersal from the eastern Atlantic [7,9], the overall insular ichthyofauna displays a stronger affinity to the western biota. This tendency probably stems from the fact that both primary and secondary centres of diversity in the Atlantic, notably the Greater Caribbean [55] and the Brazilian Province [10], are in the western Atlantic. It is commonly perceived that dispersal primarily occurs from the more diverse regions to peripheral ones with less diverse biotas, even stochastically, when current directions do not favour such paths [56]. However, the contribution of endemic lineages increases from the east (and also from the Indian Ocean) relative to the western Atlantic. This result suggests that favourable currents could allow weaker dispersers to reach the MAR islands, contributing to speciation.

In previous studies, Ascension and St Helena were grouped and showed a closer affinity either to the eastern Atlantic [3] or the western Atlantic [57], whereas St Paul's Rocks was consistently associated with the Brazilian Province. However, our

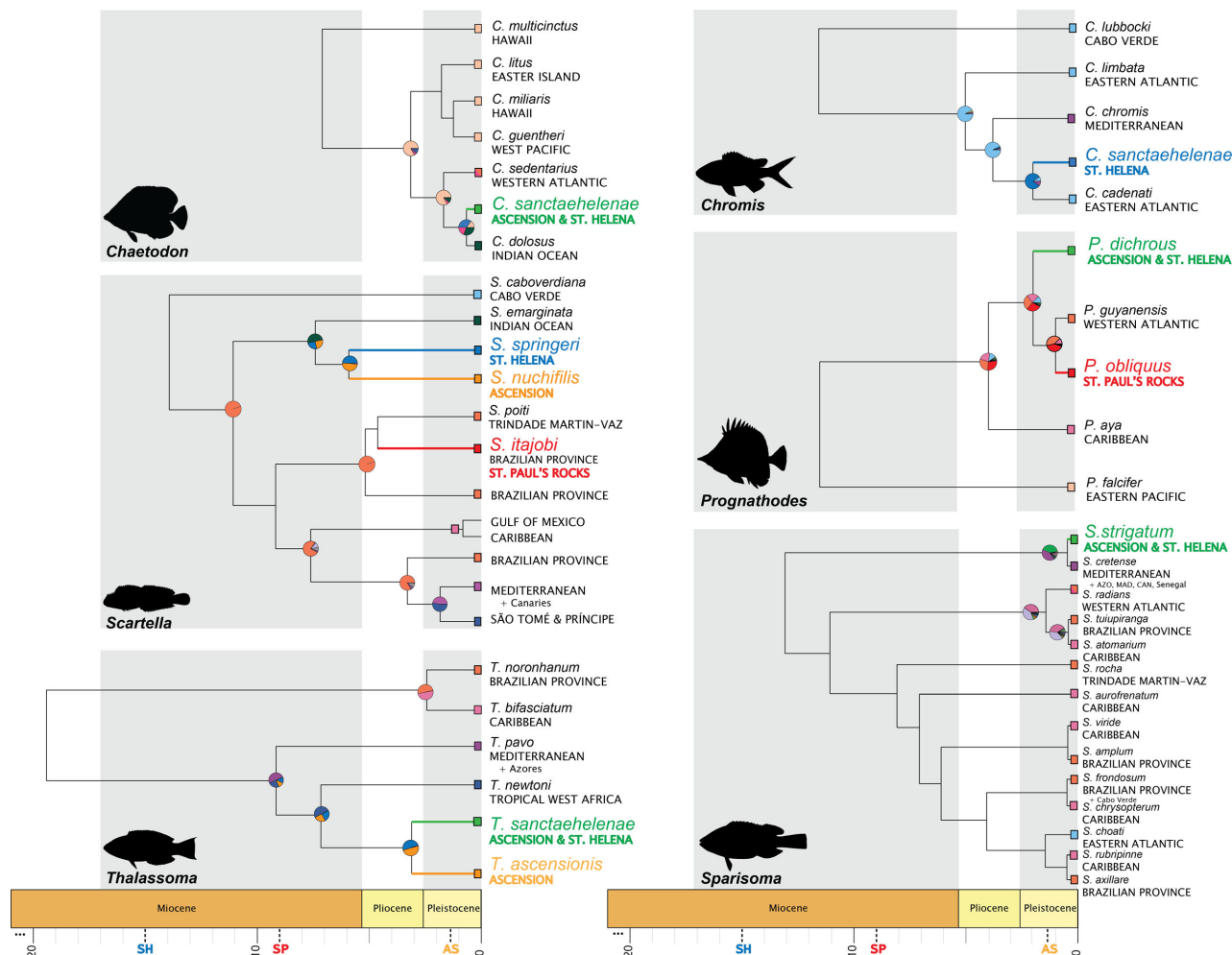


Figure 3. Ancestral area reconstructions over chrono-phylogenies for clades containing species from the tropical MAR islands of the following genera: *Chaetodon*, *Scartella*, *Thalassoma*, *Chromis*, *Prognathodes* and *Sparisoma*. Pie charts represent the probability of ancestral geographic origins for each node. Species found in St Paul's Rocks are highlighted in red, Ascension endemics are shown in yellow and St Helena endemics in blue, while species present in both Ascension and St Helena appear in green. Time scale in millions of years before the present.

analyses support the three tropical MAR islands as a coherent biogeographic unit, sharing 84 species, including 25 present at all three islands and 44 MAR endemics. Notably, three endemic species (*Bodianus insularis*, *Pontinus nigropunctatus* and *Scorpaenodes insularis*) occur across all three islands, underscoring a unique 'MAR signature'. Additionally, each island harbours distinctive endemics or closely related taxa, such as *T. ascensionis* and *T. sanctaehelenae* and *Scartella springeri* and *S. nuchifilis* (figure 3), further distinguishing the islands. The genus *Prognathodes* is a notable example of the MAR signature, comprising closely related species connecting all three islands: *P. obliquus* at St Paul's Rocks and *P. dichrous* at Ascension and St Helena (figure 3). Common traits such as small island size, extreme isolation and nutrient-poor oceanic conditions likely enhance faunal similarity and reinforce the MAR's distinctive identity.

Scientific attention toward the MAR and other remote tropical Atlantic islands has intensified over the past decade, highlighted by increased expeditions, systematic data collection and the subsequent discovery of new species and range extensions [10,11]. Biogeographic surveys in such peripheral regions yield essential data for clarifying marine evolutionary processes [58], revealing previously unrecognized biodiversity and enriching our understanding of large-scale biogeographic patterns. While Robertson [59] showed that most island endemics originate from regionally diverse reef fish families, we found that MAR endemics are not predominantly from the richest regional families (electronic supplementary material, figure S4). Instead, biodiversity patterns vary across spatial scales, with different families dominating among endemic, MAR and Atlantic species pools, emphasizing the impact of ecological filters and biogeographic barriers.

Briggs [56] predicted that Ascension and St Helena would share four times more species with the western than with the eastern Atlantic. Using our updated dataset, we find that the MAR islands share approximately 39% more species with the western (118) than with the eastern (85) Atlantic. However, when we consider only those species found in the MAR and on one side of the Atlantic basin but not the other, the pattern aligns closely with Briggs' forecast: 44 species are shared exclusively with the western, and 11 with the eastern Atlantic, roughly 300% more species in favour of the west. Dispersal route reconstruction (electronic supplementary material, figure S5, table S8) reinforces this asymmetry: we traced 60 non-endemic MAR species back to western sources but only 19 to eastern ones, indicating a 3.2-fold stronger western influence on colonization pathways. Taken together, these results underscore that stochastic dispersal from biodiversity-rich western centres, rather than advection from peripheral provinces, dominates community assembly on these remote Mid-Atlantic islands.

The greater faunistic affinity of the MAR islands with the western Atlantic is also observed for other taxonomic groups (e.g. [12,15]) and supported by paleontological findings [13]. In addition to historical biogeography, habitat similarity seems to be a factor that could enforce this pattern, as the eastern Atlantic is predominantly composed of unconsolidated substrate in high turbidity waters, with depauperate coral communities that do not form biogenic reefs [60]. Habitat similarity and relative reef area have been identified as prominent factors influencing the colonization of oceanic islands by reef species [23], as these characteristics affect the size of source populations and consequently increase the likelihood of propagules reaching these remote systems [6].

Of the 44 MAR endemic fish species, we inferred potential biogeographic origins for 27 via ancestral area analyses, haplotype networks and species distribution patterns, identifying the western Atlantic as the likely source for over half. This aligns with previous research on marine invertebrates, such as the sea urchins *Echinometra lucunter* [61] and *Diadema antillarum* [62], as well as the coral *Favia gravis*, which are more closely related to western Atlantic clades. That is also the case for *Octopus insularis* [63], where phylogeographic data highlight seamounts and surface currents as crucial drivers of population structure in the tropical Atlantic. This work provides the first report on the origins of *Prognathodes obliquus* (St Paul's Rocks) and *P. dichrous* (Ascension and St Helena), both derived from western Atlantic lineages. These butterflyfishes, which primarily inhabit mesophotic reefs, exemplify the shared diversification history between shallow and mesophotic reef biodiversity. Furthermore, we detected a recent history of colonization of Ascension and St Helena from the Brazilian Province for the genus *Stegastes*, with an estimated divergence time of approximately 0.3 Ma. Regarding the Brazilian endemic damselfish *Stegastes pictus*, two lineages have been identified: one endemic to the Trindade-Martin-Vaz insular complex (including some seamounts) and another widespread along the Brazilian coast and Vitória-Trindade Chain. While the widespread *S. pictus* lineage utilizes the seamounts to reach Trindade from the Brazilian coast [64], an older endemic lineage used Trindade as an evolutionary stepping stone to reach Ascension (*S. lubbocki*) and St Helena (*S. sanctaehelenae*). Therefore, in addition to the prevalent propagule pressure driven by large populations in centres of diversity, this example emphasizes the importance of stepping stones for colonization and diversification processes on oceanic islands, which involves smaller founder populations that are already adapted to oceanic conditions. Interestingly, despite the presence of an endemic parrotfish at Trindade (*Sparisoma rocha*), which theoretically has greater dispersal potential due to its pelagic spawning, the congeneric endemic from St Helena (*S. strigatum*, rare in the warmer waters of Ascension) is most closely related to the temperate Mediterranean and Northeastern Atlantic species, *S. cretense*.

We identified dispersal routes linking 10 MAR endemic species to the eastern Atlantic, including *T. ascensionis* and its sister species *T. sanctaehelenae*. Although these taxa are distinct in mitochondrial DNA [65], hybridization has been reported (*T. sanctaehelenae* was found in Ascension, likely because of human transport [66]). Additionally, 19 non-endemic MAR fishes were traceable to eastern Atlantic origins, such as *Xyrichtys sanctaehelenae* [67]. Regarding other groups, the mollusc sister species *Echinolittorina miliaris* (Ascension) and *E. helenae* (St Helena) are closely related to *E. granosa* from the eastern Atlantic, suggesting an insular origin linked to a region where the genus exhibits minimal diversity [14]. Notably, some clades, such as the temperate-affiliated *Diplodus*, are more diverse in the eastern than in the western Atlantic. Despite its peripheral status, the eastern Atlantic retains lineages with deep evolutionary roots, tracing back to the Tethys Sea and its former Indo-Pacific connections. Floeter *et al.* [3] identified 18 eastern Atlantic fish genera with Indo-Pacific affinities that are absent from both the western Atlantic and the Tropical Eastern Pacific—potentially reflecting either historical connectivity via southern Africa or the persistence of Tethyan relicts.

A less conventional route to the MAR islands involves east-to-west migration from the Indian Ocean around the Cape of Good Hope. During interglacial periods, the Agulhas leakage may intermittently facilitate such dispersal into the South Atlantic [18,19]. Indicative cases include *Helcogramma ascensionis*, a MAR endemic and the sole Atlantic representative of an otherwise Indo-Pacific genus [68,69], as well as *Decapterus muroadsi* and *Uraspis helvola*, both recorded at Ascension and St Helena, with distributions spanning the Indo-Pacific [68]. Endemic species such as *Centropyge resplendens* and *Chaetodon sanctaehelenae*, along with *Gnatholepis thompsoni*, widespread in the Tropical Atlantic, likewise point to Indo-Pacific affinities [17,18,33,70]. Additional genera (e.g. *Cirrhitus*, *Girella* and *Prionurus*) display disjunct distributions across the Indo-Pacific, eastern Atlantic and tropical eastern Pacific, yet are absent from the western Atlantic. This pattern suggests that the MAR islands can act as gateways for colonization into the Atlantic or act as museums, preserving relic populations that survived extinction events in the western Atlantic. The Indian Ocean link is especially evident in the biogeographic origins of both the youngest (*C. sanctaehelenae*) and oldest (*S. nuchifilis*) MAR endemics. For both species, best-fitting models in 'BioGeoBEARS' support DEC scenarios, consistent with island radiations via peripatric speciation [6,71].

Oceanic islands harbour both genetic novelties, in the form of neo-endemics, and genetic conservatism, represented by palaeo-endemics that persist after extinction elsewhere, occasionally exporting lineages back to biodiversity centres [64]. We identified two endemic species from Ascension whose divergence times appear to predate the island's emergence, supporting the hypothesis that older, now-submerged seamounts and past sea-level fluctuations have facilitated lineage persistence through deep geological time. While older endemic species often display traits conducive to ecological speciation and early colonization, the prevalence of younger endemics in the MAR islands indicates shorter life cycles and higher turnover of endemic species with limited dispersal, evidenced by population bottlenecks and negative growth [6]. However, the unique geological and evolutionary history of the MAR islands, combining both older (approx. 15 Ma) and younger (approx. 1.5 Ma) islands with intermediate seamounts, makes the evolutionary history of the MAR endemics more complex.

The extreme isolation imposes strong dispersal constraints, reflected by diverse functional traits among younger MAR endemics. Interestingly, certain ancient lineages, such as the *Scartella* species, demonstrate unexpectedly low dispersal potential, suggesting that palaeo-endemism in the MAR is less about initial colonization capability and more about maintaining small, specialized populations in low-competition environments shaped by stringent dispersal filters. The restricted geographical

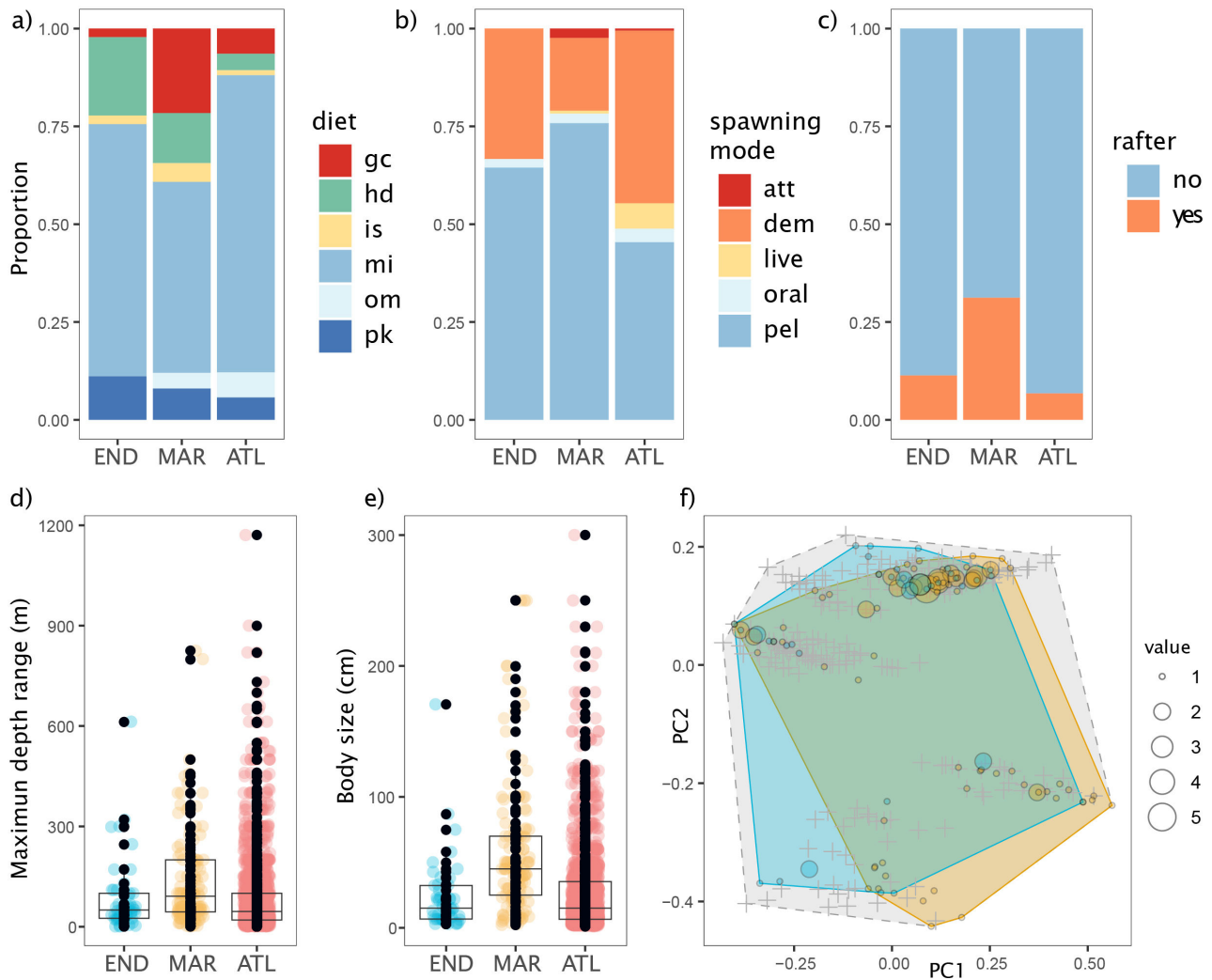


Figure 4. Functional trait comparisons among ATL fishes (Atlantic reef fishes not found on MAR islands), MAR fishes (species occurring on MAR islands but not endemic) and MAR endemics (species endemic to MAR islands). (a) Diet composition grouped into six categories: gc, generalized carnivores; hd, herbivores/detritivores; is, sessile invertivores; mi, mobile invertivores; om, omnivores; pk, planktivores. (b) Spawning modes: att, attached; dem, demersal; live, livebearers; oral, oral; pel, pelagic. (c) Proportion of species with documented rafting ability (yes/no). (d,e) Box plots of maximum adult body length and maximum recorded depth, respectively. (f) Functional space. The grey background represents all functional entities of Atlantic reef fishes, the orange polygon represents MAR fishes and the blue polygon represents MAR endemics; green overlap indicates shared functional space between MAR and END-fishes. Circles represent species grouped by unique trait combinations (functional entities), with size proportional to the number of species per entity; grey crosses represent Atlantic species not found on MAR islands.

extent of single-island endemics could be related to their relatively young age and recent establishment or a reflection of a range reduction caused by extinction processes in other areas [2,72]. For instance, Delrieu-Trottin *et al.* [33] observed that all Rapa Nui's small-range endemics were neo-endemics, whereas species whose distributions were restricted to the broader area of the southern subtropical Pacific had varied divergence times.

Nevertheless, the restricted distribution could also represent the remnants of ancestral species with broader distributions. In the Vitória-Trindade Chain, a volcanic ridge of seamounts and islands in the South Atlantic, Pinheiro *et al.* [6] found three cases of species predating the studied insular complex, paralleling our observations in Ascension (*S. nuchifilis* and *T. ascensionis*). These ancient lineages may have initially colonized now-submerged seamounts that once provided suitable shallow-water habitats [25,73]. Alternatively, they might have dispersed from nearby islands such as St Helena, subsequently diverging through allopatric speciation facilitated by intervening seamounts [35], exemplified by *T. ascensionis*/*T. sanctaehelenae* and *Ophioblennius* aff. *atlanticus*. Additionally, seamounts likely acted as drivers of diversification, particularly during the Pleistocene, when fluctuations in sea level periodically exposed these features, creating new opportunities for speciation via vicariance and enhanced dispersal [6,64,74]. Seamounts such as Grattan, Cardno and Bonaparte, situated between Ascension and St Helena, could have supported lineage diversification, contributing to the high species overlap and cohesive MAR identity [75].

Life-history traits further distinguish MAR island assemblages from the broader Atlantic ichthyofauna. MAR fishes tend to be larger bodied and capable of inhabiting deeper waters compared with both MAR endemics and Atlantic species that have not reached the islands. These attributes likely enhance reproductive output and facilitate crossing biogeographic barriers, resembling patterns observed in amphi-Atlantic species [23]. Most MAR fishes exhibit pelagic spawning and rafting capabilities, extending larval dispersal potential [21]. Conversely, MAR endemics typically feature demersal spawning, limited rafting potential and smaller body size, increasing their susceptibility to isolation and divergence (e.g. [6,59]). Thus, stochastic colonization events likely delivered their ancestors to the MAR islands, where isolation drove subsequent differentiation.

MAR endemics represent a relatively small subset of the MAR biota, and given that St Paul's Rocks, Ascension and St Helena are among the world's most functionally vulnerable oceanic islands [76], these endemics are likely further susceptible to environmental pressures. We found that each functional entity present in the Atlantic comprises, on average, four species, whereas the average functional entity for MAR endemics and MAR fishes is composed of only 1.19 and 1.32 species, respectively. In the Atlantic, half the functional entities are made up of a single species. However, for MAR endemics and MAR fishes, the proportions are higher, with around 83% and 77% of functional entities, respectively, represented by one species. The presence of a single species per entity likely represents a unique combination of traits, highlighting the functional vulnerability of these insular fish assemblages. In the event of a disturbance, these unique trait combinations cannot be replaced by other species, leaving them more susceptible to local functional extinctions [50]. Our functional metrics support these findings, with MAR assemblages displaying higher functional evenness but lower richness and divergence relative to widespread Atlantic species (electronic supplementary material, table S6). This indicates that, despite evenly distributed roles, reduced trait diversity and niche variation could impair long-term ecosystem resilience [77].

In this study, we synthesized multiple datasets and analytical approaches to establish a comprehensive biogeographic and ecological framework. Oceanographic conditions, ecological factors and physiological traits, such as dispersal potential, body size and spawning mode, interact intricately, influencing colonization processes, endemism and the assemblage structure of fishes on remote islands. Widespread Atlantic species that also inhabit the MAR islands tend to be larger bodied, more frequently pelagic spawners and often capable of rafting, which enhances their dispersal potential, as well as post-dispersal persistence. In contrast, MAR endemic fishes, characterized by smaller body sizes and demersal spawning, exhibit limited dispersal, reinforcing their restricted distributions. While numerous species may physically reach the MAR islands, successful colonization, population establishment and subsequent diversification depend profoundly on species-specific ecological traits and environmental interactions. Additionally, historical colonization via submerged seamounts, the establishment of populations on older islands as stepping stones or the survival of relict species with historically broader distributions may explain endemic lineages older than their current habitats. These turnover processes offer valuable insights into the complex interplay between dispersal, persistence and endemism, highlighting the complexity and temporal depth underpinning the evolutionary dynamics of isolated oceanic ecosystems.

Ethics. Collecting permits: Fernando de Noronha, SISBIO 64991-3; St Paul's Rocks, SISBIO 41327-12 and 58069-1; Trindade, SISBIO 12786-1 and 20880-2; Ascension, Conservation Department ERP-2015-09; St Helena, EPO Research Licence 2023/SRE/01.

Data accessibility. The complete dataset used in this study is publicly available at Zenodo [8]. All DNA sequences are available in the electronic supplementary material [78].

Declaration of AI use. We have used AI-assisted technologies exclusively for grammar and style checks.

Authors' contributions. I.C.: conceptualization, data curation, formal analysis, writing—original draft, writing—review and editing; G.S.A.: data curation, formal analysis, writing—review and editing; F.C.S.: formal analysis, writing—review and editing; Y.R.K.: formal analysis, writing—review and editing; C.R.R.: formal analysis; H.T.P.: formal analysis, writing—review and editing; L.R.: writing—review and editing; S.R.F.: conceptualization, data curation, funding acquisition, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

- Briggs JC, Bowen BW. 2013 Marine shelf habitat: biogeography and evolution. *J. Biogeogr.* **40**, 1023–1035. (doi:10.1111/jbi.12082)
- Cowman PF, Parravicini V, Kulbicki M, Floeter SR. 2017 The biogeography of tropical reef fishes: endemism and provinciality through time. *Biol. Rev.* **92**, 2112–2130. (doi:10.1111/brv.12323)
- Floeter SR *et al.* 2008 Atlantic reef fish biogeography and evolution. *J. Biogeogr.* **35**, 22–47. (doi:10.1111/j.1365-2699.2007.01790.x)
- Briggs KC. 1974 *Marine zoogeography*. New York, NY: McGraw-Hill.
- MacArthur RH, Wilson EO. 1967 *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Pinheiro HT, Bernardi G, Simon T, Joyeux JC, Macieira RM, Gasparini JL, Rocha C, Rocha LA. 2017 Island biogeography of marine organisms. *Nature* **549**, 82–85. (doi:10.1038/nature23680)
- Edwards A, Lubbock R. 1983 Marine zoogeography of St Paul's Rocks. *J. Biogeogr.* **10**, 65–72.
- Cord I *et al.* 2025 Atlantic reef fishes: distributions and life-history traits (Version 2) [Dataset]. Zenodo. (doi:10.5281/zenodo.15636151)
- Edwards A, Lubbock R. 1983 The ecology of Saint Paul's Rocks (Equatorial Atlantic). *J. Zool.* **200**, 51–69. (doi:10.1111/j.1469-7998.1983.tb06108.x)

10. Pinheiro HT *et al.* 2018 South-western Atlantic reef fishes: zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean. *Divers. Distrib.* **24**, 951–965. (doi:10.1111/ddi.12729)
11. Pinheiro HT *et al.* 2020 Fish biodiversity of Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge, Brazil: new records and a species database. *J. Fish Biol.* **97**, 1143–1153. (doi:10.1111/jfb.14484)
12. Joyeux JC, Floeter SR, Ferreira CEL, Gasparini JL. 2001 Biogeography of tropical reef fishes: the South Atlantic puzzle. *J. Biogeogr.* **28**, 831–841. (doi:10.1046/j.1365-2699.2001.00602.x)
13. Vermeij GJ, Rosenberg G. 1993 Giving and receiving: the tropical Atlantic as donor and recipient region for invading species. *Am. Malacol. Bull.* **10**, 181–194.
14. Williams ST, Reid DG. 2004 Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* **58**, 2227–2251. (doi:10.1111/j.0014-3820.2004.tb01600.x)
15. Wirtz P. 2003 New records of marine invertebrates from São Tomé Island (Gulf of Guinea). *J. Mar. Biol. Assoc. UK* **83**, 735–736. (doi:10.1017/s0025315403007720h)
16. Muss A, Robertson DR, Stepien CA, Wirtz P, Bowen BW. 2001 Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution* **55**, 561–572. (doi:10.1111/j.0014-3820.2001.tb00789.x)
17. Bowen BW, Muss A, Rocha LA, Grant WS. 2006 Shallow mtDNA coalescence in Atlantic pygmy angelfishes (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *J. Hered.* **97**, 1–12. (doi:10.1093/jhered/esj006)
18. Rocha LA, Robertson DR, Rocha CR, Van Tassell JL, Craig MT, Bowen BW. 2005 Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish. *Mol. Ecol.* **14**, 3921–3928. (doi:10.1111/j.1365-294X.2005.02698.x)
19. Baraf LM, Pratchett MS, Cowman PF. 2019 Ancestral biogeography and ecology of marine angelfishes (F: Pomacanthidae). *Mol. Phylog. Evol.* **140**, 106596. (doi:10.1016/j.ympev.2019.106596)
20. Gamoyo M, Obura D, Reason CJC. 2019 Estimating connectivity through larval dispersal in the Western Indian Ocean. *J. Geophys. Res.* **124**, 2446–2459. (doi:10.1029/2019jg005128)
21. Luiz OJ, Allen AP, Robertson DR, Floeter SR, Madin JS. 2015 Seafarers or castaways: ecological traits associated with rafting dispersal in tropical reef fishes. *J. Biogeogr.* **42**, 2323–2333. (doi:10.1111/jbi.12574)
22. Mora C, Trembl EA, Roberts J, Crosby K, Roy D, Tittensor DP. 2012 High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography* **35**, 89–96. (doi:10.1111/j.1600-0587.2011.06874.x)
23. Luiz OJ, Allen AP, Robertson DR, Floeter SR, Kulbicki M, Vigliola L, Becheler R, Madin JS. 2013 Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proc. Natl Acad. Sci. USA* **110**, 16498–16502. (doi:10.1073/pnas.1304074110)
24. Luiz OJ, Madin JS, Robertson DR, Rocha LA, Wirtz P, Floeter SR. 2012 Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. *Proc. R. Soc. B* **279**, 1033–1040. (doi:10.1098/rspb.2011.1525)
25. Mazzei EF *et al.* 2021 Mechanisms of dispersal and establishment drive a stepping stone community assembly on seamounts and oceanic islands. *Mar. Biol.* **168**, 1–11. (doi:10.1007/s00227-021-03919-7)
26. Froese R, Pauly D (eds). 2023 FishBase. [Version 06/2023]. See <http://www.fishbase.org>.
27. Quimbayo JP, Silva FC, Mendes TC, Ferrari DS, Danielski SL, Bender MG, Parravicini V, Kulbicki M, Floeter SR. 2021 Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. *Ecology* **102**, e03298. (doi:10.1002/ecy.3298)
28. Chollett I, Robertson DR. 2020 Comparing biodiversity databases: greater Caribbean reef fishes as a case study. *Fish Fish.* **21**, 1195–1212. (doi:10.1111/faf.12497)
29. Nori J *et al.* 2023 Contrasting biogeographical patterns of threatened vertebrates on islands emerge from disparities between expert-derived maps and Global Biodiversity Information Facility data. *J. Biogeogr.* **50**, 418–427. (doi:10.1111/jbi.14545)
30. Galili T. 2015 dendextend: an R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics* **31**, 3718–3720. (doi:10.1093/bioinformatics/btv428)
31. Suzuki R, Shimodaira H. 2006 Pvcust: an R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics* **22**, 1540–1542. (doi:10.1093/bioinformatics/btl117)
32. Spalding MD *et al.* 2007 Marine ecoregions of the World: a bioregionalization of coastal and shelf areas. *BioScience* **57**, 573–583. (doi:10.1641/b570707)
33. Delrieu-Trottin E, Brosseau-Acquaviva L, Mona S, Neglia V, Giles EC, Rapu-Edmunds C, Saenz-Agudelo P. 2019 Understanding the origin of the most isolated endemic reef fish fauna of the Indo-Pacific: coral reef fishes of Rapa Nui. *J. Biogeogr.* **46**, 723–733. (doi:10.1111/jbi.13531)
34. McCord CL, Nash CM, Cooper WJ, Westneat MW. 2021 Phylogeny of the damselfishes (Pomacentridae) and patterns of asymmetrical diversification in body size and feeding ecology. *PLoS One* **16**, e0258889. (doi:10.1371/journal.pone.0258889)
35. Quintão TL, Andrades R, Macieira RM, Loss AC, Joyeux JC. 2022 The evolutionary history of *Priolepis* (Gobiidae) in the Atlantic Ocean. *Mar. Biol.* **169**, 1–17. (doi:10.1007/s00227-022-04082-3)
36. Araujo GS, Vilasboa A, Britto MR, Bernardi G, von der Heyden S, Levy A, Floeter SR. 2020 Phylogeny of the comb-tooth blenny genus *Scartella* (Blenniiformes: Blenniidae) reveals several cryptic lineages and a trans-Atlantic relationship. *Zool. J. Linn. Soc.* **190**, 54–64. (doi:10.1093/zoolinnean/zl142)
37. Siqueira AC, Bellwood DR, Cowman PF. 2019 Historical biogeography of herbivorous coral reef fishes: the formation of an Atlantic fauna. *J. Biogeogr.* **46**, 1611–1624. (doi:10.1111/jbi.13631)
38. Araujo GS, Rocha LA, Lastrucci NS, Luiz OJ, Di Dario F, Floeter SR. 2022 The Amazon-Orinoco Barrier as a driver of reef-fish speciation in the Western Atlantic through time. *J. Biogeogr.* **49**, 1407–1419. (doi:10.1111/jbi.14398)
39. Bouckaert R *et al.* 2019 BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* **15**, e1006650. (doi:10.1371/journal.pcbi.1006650)
40. Darriba D, Taboada GL, Doallo R, Posada D. 2012 jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* **9**, 772–772. (doi:10.1038/nmeth.2109)
41. Rabosky DL *et al.* 2018 An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395. (doi:10.1038/s41586-018-0273-1)
42. Reece JS, Bowen BW, Smith DG, Larson A. 2010 Molecular phylogenetics of moray eels (Muraenidae) demonstrates multiple origins of a shell-crushing jaw (*Gymnomuraena*, *Echidna*) and multiple colonizations of the Atlantic Ocean. *Mol. Phylogenet. Evol.* **57**, 829–835.
43. Lessios HA. 2008 The Great American Schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annu. Rev. Ecol. Evol. Syst.* **39**, 63–91. (doi:10.1146/annurev.ecolsys.38.091206.095815)
44. Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018 Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**, 901–904. (doi:10.1093/sysbio/syy032)
45. Clement M, Posada DCKA, Crandall KA. 2000 TCS: a computer program to estimate gene genealogies. *Mol. Ecol.* **9**, 1657–1659. (doi:10.1046/j.1365-294x.2000.01020.x)
46. Leigh JW, Bryant D. 2015 popart: full-feature software for haplotype network construction. *Methods Ecol. Evol.* **6**, 1110–1116. (doi:10.1111/2041-210x.12410)
47. Matzke NJ. 2013 *BioGeography with Bayesian (and likelihood) evolutionary analysis in R scripts*. Berkeley, CA: University of California.

48. Ree RH, Smith SA. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**, 4–14. (doi:10.1080/10635150701883881)
49. Cord I *et al.* 2022 Brazilian marine biogeography: a multi-taxa approach for outlining sectorization. *Mar. Biol.* **169**, 1–13. (doi:10.1007/s00227-022-04045-8)
50. Mouillot D *et al.* 2014 Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl Acad. Sci. USA* **111**, 13757–13762. (doi:10.1073/pnas.1317625111)
51. Halpern BS, Floeter SR. 2008 Functional diversity responses to changing species richness in reef fish communities. *Mar. Ecol. Prog. Ser.* **364**, 147–156. (doi:10.3354/meps07553)
52. Laliberté E, Legendre P. 2010 A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305. (doi:10.1890/08-2244.1)
53. Magneville C *et al.* 2022 mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography* **2022**. (doi:10.1111/ecog.05904)
54. Grassman R, Gramacy RB, Sterratt DC. 2011 Package 'geometry'. See <http://geometry.r-forge.r-project.org/>.
55. Rocha LA, Rocha CR, Robertson DR, Bowen BW. 2008 Comparative phylogeography of Atlantic reef fishes indicates both origin and accumulation of diversity in the Caribbean. *BMC Evol. Biol.* **8**, 1–16. (doi:10.1186/1471-2148-8-157)
56. Briggs JC. 1995 *Global biogeography*. Amsterdam, The Netherlands: Elsevier.
57. Kulbicki M *et al.* 2013 Global biogeography of reef fishes: a hierarchical quantitative delineation of regions. *PLoS One* **8**, e81847. (doi:10.1371/journal.pone.0081847)
58. Santos MEA, Wirtz P, Montenegro J, Kise H, López C, Brown J, Reimer JD. 2019 Diversity of Saint Helena Island and zoogeography of zoantharians in the Atlantic Ocean: jigsaw falling into place. *System. Biodivers.* **17**, 165–178. (doi:10.1080/14772000.2019.1572667)
59. Robertson DR. 2001 Population maintenance among tropical reef fishes: inferences from small-island endemics. *Proc. Natl Acad. Sci. USA* **98**, 5667–5670. (doi:10.1073/pnas.091367798)
60. Laborel J. 1974 West African reef corals: an hypothesis on their origin. In *Proc. of the Second Int. Coral Reef Symposium*, vol. **1**, pp. 425–443, Brisbane, Australia: Great Barrier Reef Committee.
61. Mccartney MA, Keller G, Lessios HA. 2000 Dispersal barriers in tropical oceans and speciation in Atlantic and eastern Pacific sea urchins of the genus *Echinometra*. *Mol. Ecol.* **9**, 1391–1400. (doi:10.1046/j.1365-294x.2000.01022.x)
62. Lessios HA, Kessing BD, Pearse JS. 2001 Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution* **55**, 955–975.
63. Lima FD, Leite TS, Haimovici M, Nóbrega MF, Oliveira JEL. 2014 Population structure and reproductive dynamics of *Octopus insularis* (Cephalopoda: Octopodidae) in a coastal reef environment along northeastern Brazil. *Fish. Res.* **152**, 86–92. (doi:10.1016/j.fishres.2013.08.009)
64. Simon T *et al.* 2021 Comparative phylogeography of reef fishes indicates seamounts as stepping stones for dispersal and diversification. *Coral Reefs* **41**, 551–561. (doi:10.1007/s00338-021-02178-8)
65. Costagliola D, Robertson DR, Guidetti P, Stefanni S, Wirtz P, Heiser JB, Bernardi G. 2004 Evolution of coral reef fish *Thalassoma* spp. (Labridae). 2. Evolution of the eastern Atlantic species. *Mar. Biol.* **144**, 377–383. (doi:10.1007/s00227-003-1200-y)
66. Wirtz P, Bingeman J, Bingeman J, Fricke R, Hook TJ, Young J. 2014 The fishes of Ascension Island, central Atlantic Ocean—new records and an annotated checklist. *J. Mar. Biol. Assoc. UK* **97**, 783–798. (doi:10.1017/s0025315414001301)
67. Wirtz P, Ferreira CEL, Floeter SR, Fricke R, Gasparini JL, Iwamoto T, Rocha L, Sampaio CLS, Schliewen UK. 2007 Coastal fishes of São Tomé and Príncipe islands, Gulf of Guinea (Eastern Atlantic Ocean)—an update. *Zootaxa* **1523**, 1–48. (doi:10.11646/zootaxa.1523.1.1)
68. Brown J, Beard A, Clingham E, Fricke R, Henry L, Wirtz P. 2019 The fishes of St Helena Island, central Atlantic Ocean—new records and an annotated check-list. *Zootaxa* **4543**, 151–194. (doi:10.11646/zootaxa.4543.2.1)
69. Edwards AJ. 1990 *Fish and fisheries of saint helen island*. Newcastle upon Tyne, UK: Centre for Tropical Coastal Management Studies, for the Education Department of the Government of Saint Helena.
70. Bellwood DR, Klanten S, Cowman PF, Pratchett MS, Konow N, Van Herwerden L. 2010 Evolutionary history of the butterflyfishes (F: Chaetodontidae) and the rise of coral feeding fishes. *J. Evol. Biol.* **23**, 335–349. (doi:10.1111/j.1420-9101.2009.01904.x)
71. Matzke NJ. 2014 Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* **63**, 951–970. (doi:10.1093/sysbio/syu056)
72. Willis JC. 1922 *Age and area—a study in geographical distribution and origin of species*. Cambridge, UK: Cambridge University Press.
73. Peluso L, Tascheri V, Nunes FLD, Castro CB, Pires DO, Zilberberg C. 2018 Contemporary and historical oceanographic processes explain genetic connectivity in a Southwestern Atlantic coral. *Sci. Rep.* **8**, 1–12. (doi:10.1038/s41598-018-21010-y)
74. Delrieu-Trottin E, Hubert N, Giles EC, Chifflet-Belle P, Suwalski A, Neglia V, Rapu-Edmunds C, Mona S, Saenz-Agudelo P. 2020 Coping with Pleistocene climatic fluctuations: demographic responses in remote endemic reef fishes. *Mol. Ecol.* **29**, 2218–2233. (doi:10.1111/mec.15478)
75. Trunov IA. 2006 Ichthyofauna of seamounts around the island of Ascension and St. Helena Island (Atlantic Ocean). *J. Ichthyol* **46**, 493–499. (doi:10.1134/S0032945206070010)
76. Ferraris DS, Floeter SR, Leprieur F, Quimbayo JP. 2023 A trait-based approach to marine island biogeography. *J. Biogeogr.* **50**, 528–538. (doi:10.1111/jbi.14549)
77. Villéger S, Mason NWH, Mouillot D. 2008 New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301. (doi:10.1890/07-1206.1)
78. Cord I, Gabriel SA, Silva FC, Yan RK, Claudia RR, Pinheiro HT *et al.* 2025 Supplementary material from: Biogeography and evolution of reef fishes on tropical Mid-Atlantic Ridge islands. Figshare. (doi:10.6084/m9.figshare.c.7882003)