

# The molecular biogeography of the Indo-Pacific: Testing hypotheses with multispecies genetic patterns

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**Abstract**

**Aim:** To test hypothesized biogeographic partitions of the tropical Indo-Pacific Ocean with phylogeographic data from 56 taxa, and to evaluate the strength and nature of barriers emerging from this test.

**Location:** The Indo-Pacific Ocean.

**Time period:** Pliocene through the Holocene.

**Major taxa studied:** Fifty-six marine species.

**Methods:** We tested eight biogeographic hypotheses for partitioning of the Indo-Pacific using a novel modification to analysis of molecular variance. Putative barriers to gene flow emerging from this analysis were evaluated for pairwise  $\Phi_{ST}$ , and these  $\Phi_{ST}$  distributions were compared to distributions from randomized datasets and simple coalescent simulations of vicariance arising from the Last Glacial Maximum. We then weighed the relative contribution of distance versus environmental or geographic barriers to pairwise  $\Phi_{ST}$  with a distance-based redundancy analysis (dbRDA).

**Results:** We observed a diversity of outcomes, although the majority of species fit a few broad biogeographic regions. Repeated coalescent simulation of a simple vicariance model yielded a wide distribution of pairwise  $\Phi_{ST}$  that was very similar to empirical distributions observed across five putative barriers to gene flow. Three of these barriers had median  $\Phi_{ST}$  that were significantly larger than random expectation. Only 21 of 52 species analysed with dbRDA rejected the null model. Among these, 15 had overwater distance as a significant predictor of pairwise  $\Phi_{ST}$ , while 11 were significant for geographic or environmental barriers other than distance.

**Main conclusions:** Although there is support for three previously described barriers, phylogeographic discordance in the Indo-Pacific Ocean indicates incongruity between processes shaping the distributions of diversity at the species and population levels. Among the many possible causes of this incongruity, genetic drift provides the most compelling explanation: given massive effective population sizes of Indo-Pacific species, even hard vicariance for tens of thousands of years can yield  $\Phi_{ST}$  values that range from 0 to nearly 0.5.

**KEYWORDS**

analysis of molecular variance, biogeographic provinces, biogeographic realms, comparative phylogeography, discordance, dispersal, distance-based redundancy analysis

**1 | INTRODUCTION**

To understand the dynamics of marine systems, biogeographers examine how geography, climate and biotic factors shape biodiversity and evolutionary divergence at scales ranging from genes to species and from ecosystems to continents and globe-spanning oceans. This work is increasing in importance because biogeographic regions defined by species assemblages and climatic/environmental factors provide the foundation to identify patterns of biodiversity and, more recently, to define conservation regions (Ladle & Whittaker, 2011; Margules & Pressey, 2000; Pressey & Bottrill, 2009).

Global biogeographic classification schemes have been developed for terrestrial (Olson et al., 2001), freshwater (Abell, Thieme, Revenga, Bryer, & Kottelat, 2008) and marine (Briggs, 1974; Spalding et al., 2007; Veron, Stafford-Smith, Devantier, & Turak, 2015; Watling, Guinotte, Clark, & Smith, 2013) provinces and vary in levels of detail. Traditionally, these classification systems partition biodiversity based on species distributions and levels of endemism (Abell et al., 2008; Briggs, 1974; Olson et al., 2001). However, many classification systems also consider abiotic factors, dominant habitat, connectivity and geomorphological features (Belanger et al., 2012; Valentine & Jablonski, 2010) and can take a nested hierarchical approach (i.e.

Olson et al., 2001; Spalding et al., 2007). More recently, molecular phylogenies at the species level have also been used to describe biogeographic regions (Cowman, Parravicini, Kulbicki, & Floeter, 2017).

None of these varied approaches includes information below the species level or encompasses the distribution of genetic lineages and spatial structuring of genetic diversity within species. Given that biogeographic barriers occur in regions where geological or environmental variations create filters to species dispersal and connectivity (Avice, 1992), these same processes should shape the distribution of intraspecific genetic diversity and reflect processes, such as speciation, population growth, colonization and dispersal that underlie species distributions. As such, synthesizing biogeographic and phylogeographic patterns provides an ideal way to test whether hypothesized biogeographic breaks correspond to breaks in genetic structure, as would be expected given the mechanisms generally invoked to explain such breaks.

Early efforts to design global marine biogeographic classification schemes were based on the distribution of well-characterized fishes, with endemism being considered as having evolutionary uniqueness. For example, Ekman (1953) described large-scale biogeographic regions and subregions, such as the continental shelf, tropical, temperate and polar waters. Briggs (1974) further divided continental shelves into biogeographic regions that each encompassed provinces defined by 10% endemism in fishes, a criterion that was later adopted by others (Hayden, Ray, & Dolan, 1984). This classification scheme was revised by Briggs and Bowen (2012; fig. 1) who divided the tropical Indo-Pacific into five provinces, including the expansive Indo-Polynesian province that spans from the Maldives to French Polynesia, while assigning each of Hawai'i, the Marquesas, Easter Island and the Western Indian Ocean to the level of province based on the high level of fish endemism found in each. More recent efforts have been driven by the need for fine-scale classification to address regional resource management. Spalding et al. (2007) developed a hierarchical classification system based on data-driven expert opinion for multiple coastal taxa that divided the Indo-Pacific into three realms, which were further subdivided into 25 provinces and 77 ecoregions based on species distributions, dominant habitat type, and geomorphological and oceanographic features. Kulbicki et al. (2013) employed a clustering method based on the dissimilarity of reef fish assemblages to resolve 10 provinces nested within three regions in the Indo-Pacific. Keith, Baird, Hughes, Madin, and Connolly (2013) defined 11 faunal provinces in the tropical Indo-Pacific based on distributions and co-occurrence of range boundaries in corals. Finally, Veron et al. (2015) subdivided the Indo-Pacific into 124 ecoregions in 12 divisions based on the distribution of the habitat-forming scleractinian corals and environmental distinctiveness.

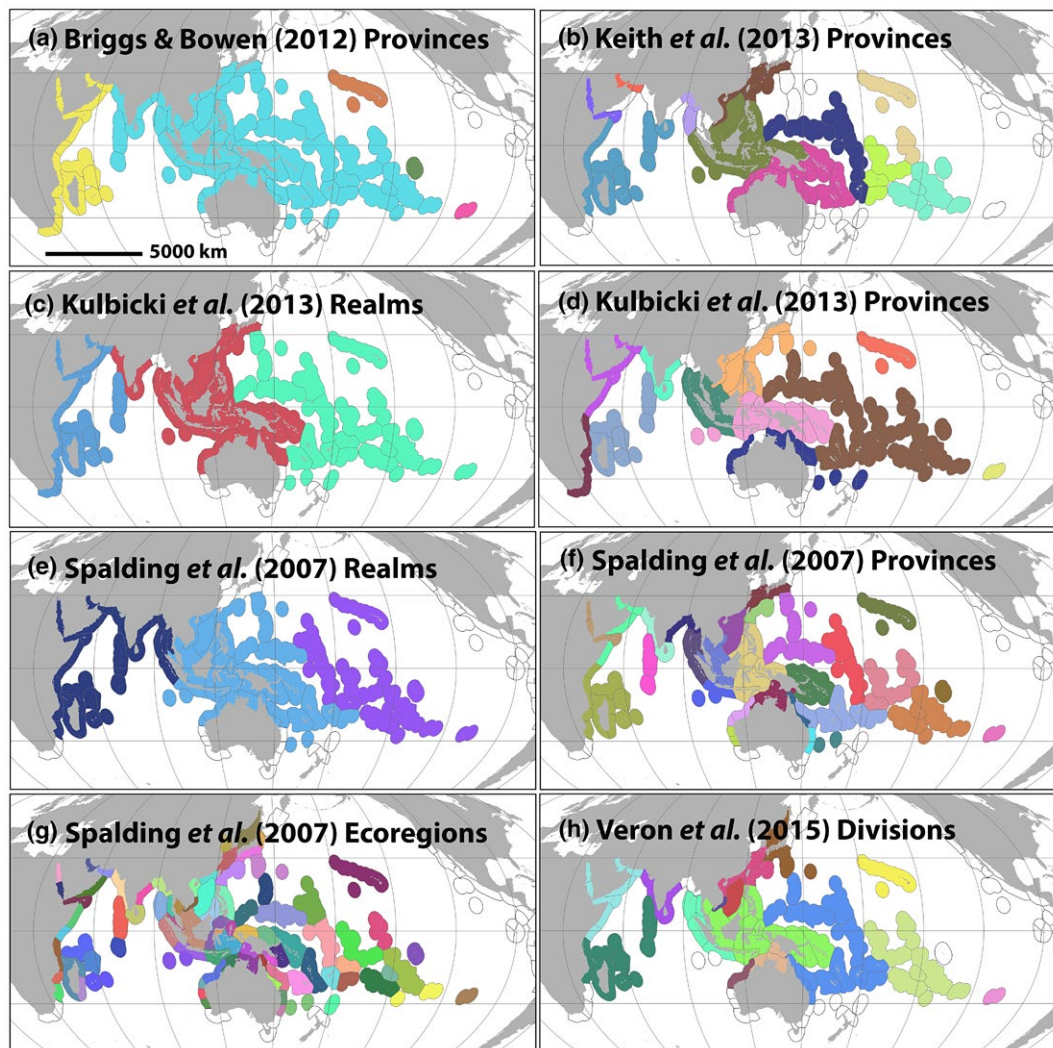
One limitation of the aforementioned regionalization models (Figure 1) is that they are defined by patterns emerging from nearshore species distribution data (Keith et al., 2013; Kulbicki et al., 2013; Veron et al., 2015) and give less consideration to the processes that govern the distribution of marine biodiversity more generally (but see Briggs & Bowen, 2013). Where large-scale geological processes have been taken into account, for example through

application of cladistic biogeography (Pandolfi, 1992), speciation patterns match with these regionalizations (Keith et al., 2013). By focusing on pattern over process, we limit our ability to understand the historical or contemporary causes of biogeographic patterns.

One approach to address such process-related questions in biogeographic regionalization models is through inclusion of data on intraspecific genetic diversity. There are many intriguing questions that might be addressed at the scale of intraspecific genetic diversity patterns: At what spatial and temporal scale does intraspecific genetic variation occur (Benzie, 1999)? Are intraspecific genetic patterns consistent with biogeographic hypotheses showing a coarse-grained nature (Briggs & Bowen, 2013; Huang, Goldberg, Chou, & Roy, 2018; Pandolfi, 1992), or do local environments play a greater role than large-scale geographic regions (Spalding et al., 2007)? Does the observed turnover in species diversity among regions result simply from the vast expanse of open ocean between continents and archipelagos (Vermeij, 1987), or are there barriers to dispersal such as currents (Barber, Cheng, Erdmann, Tenggardjaja, & Ambariyanto, 2011; Trembl, Roberts, Halpin, Possingham, & Riginos, 2015), that act above and beyond the effects of geographic distance? Underlying processes operating across a range of temporal and spatial scales are likely to have an effect on genetic diversity and turnover of haplotypes much as they do on species diversity (Palumbi, 1997).

Phylogeographic studies of marine organisms are notoriously challenging due to large effective population sizes and potentially high rates of larval dispersal among populations (Hellberg, 2009). These traits tend to depress *F*-statistics and related measures of population structure, creating blurred and discordant phylogeographic patterns (Crandall, Frey, Grosberg, & Barber, 2008; Gagnaire et al., 2015; Waples, 1998). Replication of observations is thus key to elucidating shared historical processes (Horne, 2014a). While single-species studies of phylogeography abound in the marine literature (Keyse et al., 2014), and some multispecies regional case studies have been conducted (Barber et al., 2011; Carpenter et al., 2011; Gaither & Rocha, 2013; Ilves, Huang, Wares, & Hickerson, 2010; Kelly & Palumbi, 2010; Liggins, Trembl, Possingham, & Riginos, 2016; Marko et al., 2010; Teske, Von der Heyden, McQuaid, & Barker, 2011; Toonen et al., 2011;), there has never been a multispecies phylogeographic test of biogeographic hypotheses at a global scale.

In this study, we leverage a unique, curated database of genetic data spanning the vast Indo-Pacific region to undertake the largest multispecies phylogeographic study to date. Using data from 56 taxonomically diverse species, representing 4 phyla and 27 families, we investigate which of the biogeographic divisions identified in published marine biogeographic regionalization models are reflected in the distribution of genetic variation below the species level. Concordant phylogeographic patterns across independent species provide evidence for shared evolutionary processes, and divisions between biogeographic regions indicate significant environmental or geographic barriers that could be recapitulated at the population genetic level (Avice, 2000). As such, if the partitions defined by species distributions, major habitat features and oceanography are regarded as first-order approximations of important and enduring barriers to gene flow, then we would expect



**FIGURE 1** Biogeographic regionalizations that were tested using model selection with analysis of molecular variance (AMOVA). Colours represent different regions within a scheme. (a) Briggs and Bowen (2012), endemism in fishes, provinces ( $k = 5$ ); (b) Keith et al. (2013), range boundaries of corals, provinces ( $k = 11$ ); (c) Kulbicki et al. (2013), reef fish species composition, realms ( $k = 3$ ); (d) Kulbicki et al. (2013), provinces ( $k = 10$ ); (e) Spalding et al. (2007), expert opinion, realms ( $k = 3$ ); (f) Spalding et al. (2007) provinces ( $k = 27$ ); (g) Spalding et al. (2007) ecoregions ( $k = 77$ ); (h) Veron et al. (2015), coral distribution, divisions ( $k = 12$ )

concordance between these biogeographic hypotheses and genetic-based population level phylogeography (Bowen et al., 2016; Harvey et al., 2017).

To conduct this analysis, we present a novel analytical framework for phylogeographic hypothesis testing across multiple species. First, we develop a new approach to analysis of molecular variance (AMOVA) set within a comparative framework to rigorously evaluate support for competing biogeographic hypotheses based on how well they explain the distribution of genetic diversity in each species. Second, we statistically evaluate genetic structure generated across divisions among regions (putative barriers) for the two best-supported regionalizations. Finally, we disentangle the relative influences of geographic distance versus impediments to gene flow (historical vicariance, steep environmental gradients, etc.) on evolutionary divergence using distance-based redundancy analysis (Legendre & Anderson, 1999).

## 2 | METHODS

### 2.1 | Data acquisition and quality control: Assembling the DIPnet database

A list of published marine phylogeographic studies from the Indo-Pacific region was compiled in October 2014 during a National Evolutionary Synthesis Center (NESCent) workshop of the Diversity of the Indo-Pacific Network (DIPnet; <http://diversityindopacific.net/>) held in Durham, North Carolina, based on keyword searches of the literature and expert knowledge of working group members. Lead authors on published papers and the heads of research groups known to be actively working in Indo-Pacific phylogeography were also contacted for data. Data were submitted between July 2014 to April 2015 according to instructions developed by the NESCent working group. Each mitochondrial dataset consisted of Sanger



sequence data in FASTA format. Metadata for each sequence were assembled in a spreadsheet template generated using the Biocode Field Information Management System [Biocode FIMS; now available at GeOMe, see Deck et al. (2017)]. Genetic data and associated metadata underwent rigorous quality control during and after submission (Supporting Information Text S1).

## 2.2 | Regionalizations and overwater distances

Sequences for each species and genetic locus combination were assigned group membership using several spatial regionalization schemes (Figure 1). The location of each population sample site (latitude and longitude) in the database was extracted directly or estimated using the geographic place names in the metadata. All individual sample sites were intersected with each regionalization (Figure 1) to assign appropriate group membership to each sample.

Overwater distances between all sampled localities were measured using a simple cost-path algorithm. To simplify this distance calculation, all samples within 10 km were treated as a single mean location (distances between these clustered sites were set to 0) and all locations that fell on land (due to coordinate imprecision or geolocating based on place names) were moved to the nearest water cell, if within 20 km. Overwater distances were calculated between all possible pairs of unique locations. Using a cost surface where water has a cost of one (land cells cannot be crossed), the algorithm effectively finds the shortest geographic distance between points across water cells only. The R package *gdistance* (van Etten, 2017) was used for finding overwater distances. R code for this and all other analyses can be found at <http://dipnet.github.io/popgenDB/>.

## 2.3 | Analysis of molecular variance

We identified the best supported biogeographic regionalization scheme for each species using a novel approach to the hierarchical analysis of molecular variance (Excoffier, Smouse, & Quattro, 1992) model wherein we calculated the Bayesian information criterion (BIC; Schwarz, 1978), based on both  $F_{ST}$  (Weir & Cockerham, 1984) and  $\Phi_{ST}$  (Excoffier et al., 1992) for use in a model selection framework. As results were broadly similar for both statistics, we present results for  $\Phi_{ST}$ , which includes genetic distance between haplotypes (we provide results for  $F_{ST}$ , which is based solely on haplotype frequencies in Supporting Information Text S2). For each species, sampling locations were binned into regions according to each biogeographic regionalization scheme as described above. AMOVA was conducted using the *pegas* package (Paradis, 2010) in R (R Core Team, 2014) for each dataset to estimate the variance components for individuals nested within sampling locations ( $s^2_{err}$ ), sampling locations nested within regions ( $s^2_{loc}$ ), and regions ( $s^2_{reg}$ ). The biogeographic regionalization scheme that was best aligned with the genetic structure of a species-locus combination will result in the greatest amount of variance in the data explained by regions ( $s^2_{reg}$ ) and the least variation explained by samples nested within regions ( $s^2_{loc}$ ) and individuals

nested within samples ( $s^2_{err}$ ). BIC was employed to select the biogeographic regionalization that best explained the genetic structure for each species-locus combination and was calculated as follows (modified from Jombart, Devillard, & Balloux, 2010):

$$BIC = n \ln \left( \frac{s^2_{loc} + s^2_{err}}{n} \right) + k \ln(n) \quad (1)$$

where  $n$  is the number of samples nested within regions and  $k$  is the number of regions. BIC was then converted to relative probability following Johnson and Omland (2004). The regionalization yielding the highest relative probability (lowest BIC) was deemed the best model. We present results for 56 species that had sufficient sampling to test at least five out of the eight biogeographic hypotheses (citations to original datasets can be found in the Appendix).

Our *a priori* model-selection framework is similar to spatial analysis of molecular variance (SAMOVA; Dupanloup, Schneider & Excoffier, 2002) used for detecting patterns of genetic structure *post hoc*, because it employs AMOVA and maximizes  $\Phi_{CT}$ . However, SAMOVA cannot be used to test which regionalization model best explains the data. SAMOVA alters the affiliation of samples to regions, given a pre-determined number of regions. In contrast, our approach penalizes the number of regions by employing BIC, thereby allowing for objective comparison among hypotheses with different numbers of regions in a model selection context.

Cryptic species are often discovered on Indo-Pacific reefs (e.g. Crandall, Frey et al., 2008), and can create a taxonomic bias if not properly accounted for (Knowlton, 1993). To assess the presence of cryptic species in our dataset and their potential effect on our results, we used the software ABGD (0.001 <  $p$  < 0.1, 10 steps, minimum slope increase = 1.5, Jukes-Cantor distances; Puillandre, Lambert, Brouillet, & Achaz, 2012) to partition each species into evolutionarily significant units (ESUs) based on the range of intraclade genetic variation. Model selection was performed on the resultant ESUs, as above.

## 2.4 | Barrier strength analysis

Biogeographic breaks arise for different reasons. While some may be related to distances between suitable habitat being greater than the dispersal capacity of an individual species, others, such as the break at the Sunda Shelf (hereafter referred to as the "Indo-Pacific Barrier"), are related to land barriers created by lowered sea-level stands. To understand the influence of specific biogeographic breaks on the genetic structuring of taxa, we further evaluated the boundaries between regions of the two best-supported models (combining them into a single merged regionalization) with a novel analysis that examines the central tendency of pairwise  $\Phi_{ST}$  values measured across each boundary. We used the *StrataG* R package (Archer, Adams, & Schneiders, 2017) to calculate pairwise  $\Phi_{ST}$  across each putative barrier for 68 species for which a pairwise comparison was possible (some species not amenable to AMOVA were included here; Supporting Information Tables S1, S2). To

evaluate significance, we randomly assigned localities for each of the 68 species to one of two “regions” and estimated pairwise  $\Phi_{ST}$  between these two randomly drawn regions. We replicated this procedure 10 times to create 612 randomized  $\Phi_{ST}$  values (replicates where all localities were assigned to only one region were thrown out). We compared median  $\Phi_{ST}$  values for each putative barrier to the randomized median, with 95% confidence intervals for the medians established by bootstrapping 10,000 datasets, each containing 100 random samples of pairwise  $\Phi_{ST}$  values from the original dataset. *p*-values were calculated as the proportion of bootstrapped medians that were greater than the bootstrapped medians for the randomized datasets.

While pairwise  $\Phi_{ST}$  values in marine systems tend to be low, there is no established set of expectations for these values. So, for comparative purposes, we conducted a simulation of a simple allopatric event in *fastsimcoal* 2.6 (Excoffier & Foll, 2011) that reflects our best understanding of isolation due to low sea level stands during the Last Glacial Maximum (Crandall, Frey et al., 2008): 10,000 generations ago (roughly 10–20 kya for a species with a 1–2 year generation time), a single panmictic population with a half-million effective individuals split into two populations of a quarter-million effective individuals each, which experience no gene flow between them. From this scenario, we generated samples from each of the two populations of 20 non-recombining haploid DNA sequences, 1,000 base pairs in length, with a mutation rate of  $5 \times 10^{-8}$  per base pair per generation [i.e. mitochondrial DNA (mtDNA); Crandall, Sbrocco, DeBoer, Barber, & Carpenter, 2012]. This scenario was simulated 1,000 times, and pairwise  $\Phi_{ST}$  for each iteration was calculated using a batch version of *arlsumstat* (Excoffier & Lischer, 2010).

## 2.5 | Distance-based redundancy analysis

To understand genetic diversification it is important to disentangle differentiation due to distance versus environmental and geographic barriers. To test whether genetic differentiation at regional boundaries was no more than expected based on overwater distance among sampling locations or was higher, possibly being indicative of other evolutionary processes such as historical isolation at low sea-level stands, we used distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999). dbRDA is a multivariate regression method that overcomes the issue of non-independence inherent in Mantel tests and multiple regression with distance matrices (Guillot & Rousset, 2013) through constrained ordination on non-Euclidean distance measures. Here, the distance matrix (pairwise  $\Phi_{ST}$  values between sampled population pairs) was ordinated via multidimensional scaling [MDS: *capscale* function in the R package *vegan* (Oksanen et al., 2017)] to yield population values along orthogonal eigenvectors; these vectors form the response variables in an RDA. Among our predictive variables, the measure of overwater distances was also initially formatted as distance matrices; here again we used ordination to convert these distance matrices to eigenvectors, choosing two dimensions as a reasonable representation of locations along the Earth's surface (employing MDS, with the *cmdscale*

function in *vegan*). To predict the effects of putative barriers between biogeographic regions, we used the merged regionalization from the two best-supported regionalization models. Each region was then defined as a predictor of pairwise  $\Phi_{ST}$ , with localities within each region scored as one, and those outside the region scored as zero. To investigate the effect of distance in the context of barriers we started with a null model of no effect of distance or barriers ( $\Phi_{ST} \sim 1$ ) and used forward model selection to determine the minimal set of predictive variables. We used an adjusted  $R^2$  method appropriate for permuted data (Blanchet, Legendre, & Borcard, 2008) with the *ordiR2step* function in *vegan*. Model significances and significances of the individual MDS terms were assessed using 1,000 ANOVA-like permutations (*anova.cca* function). We carried out dbRDA on 52 species analysed in the AMOVA after removing four species that had fewer than five sample locations.

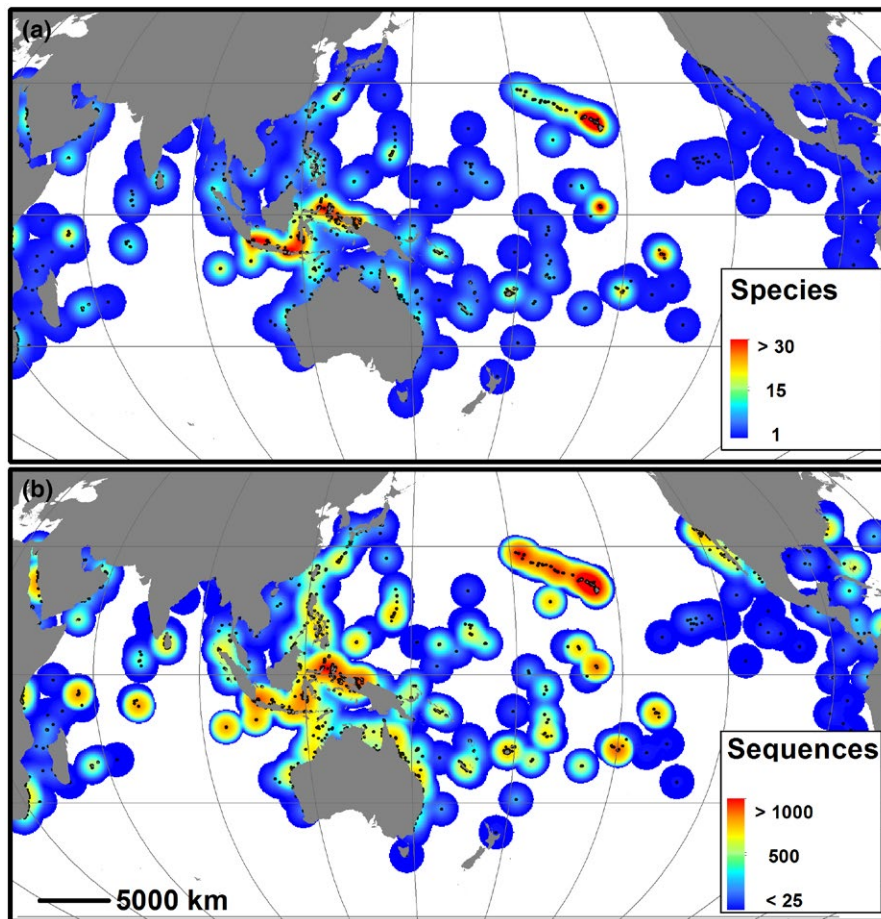
## 3 | RESULTS

### 3.1 | The diversity of the Indo-Pacific database

The DIPnet database represents the largest curated, publicly available collection of mtDNA sequences for phylogeographic comparisons. We received 162 submissions of sequence data, which included over 35,000 sequences. After strict quality control and filtering (see Supporting Information Text S1 for details) the resulting database contained data from 238 marine species (230 from the Indo-Pacific) across the phyla Arthropoda, Chordata, Cnidaria, Echinodermata and Mollusca based on eight mitochondrial gene regions. Data were sourced from 57 Indo-Pacific countries and >1,100 unique localities, spanning the entire Indo-Pacific from the Red Sea to Rapa Nui (Easter Island). Sampling intensity, geographic coverage and completeness of the metadata submissions were variable (Figure 2), and 41 species were represented by more than one genetic marker. In the analyses presented here, we removed one of these markers to avoid pseudo-replication (see Supporting Information Text S1 for removal criteria). The raw sequence files and associated metadata can be searched and downloaded from the Genomic Observatories Metadatabase (GeOMe; <https://www.geome-db.org/>; Deck et al., 2017), an open access repository for geographic and ecological metadata associated with biosamples and genetic data. The trimmed and aligned dataset used here is available at <https://github.com/DIPnet/IPDB>.

### 3.2 | Analysis of molecular variance and pairwise comparisons

AMOVA results showed mixed support for each of the hypotheses that we tested, with most species supporting those with the fewest biogeographic regions (Figures 3 and 4): Spalding et al.'s (2007) realms ( $k = 3$ , supported by 20 species) and Briggs and Bowen's (2012) provinces ( $k = 5$ , supported by 18 species). These two hypotheses were followed by Kulbicki et al.'s (2013) realms ( $k = 3$ , supported by 13



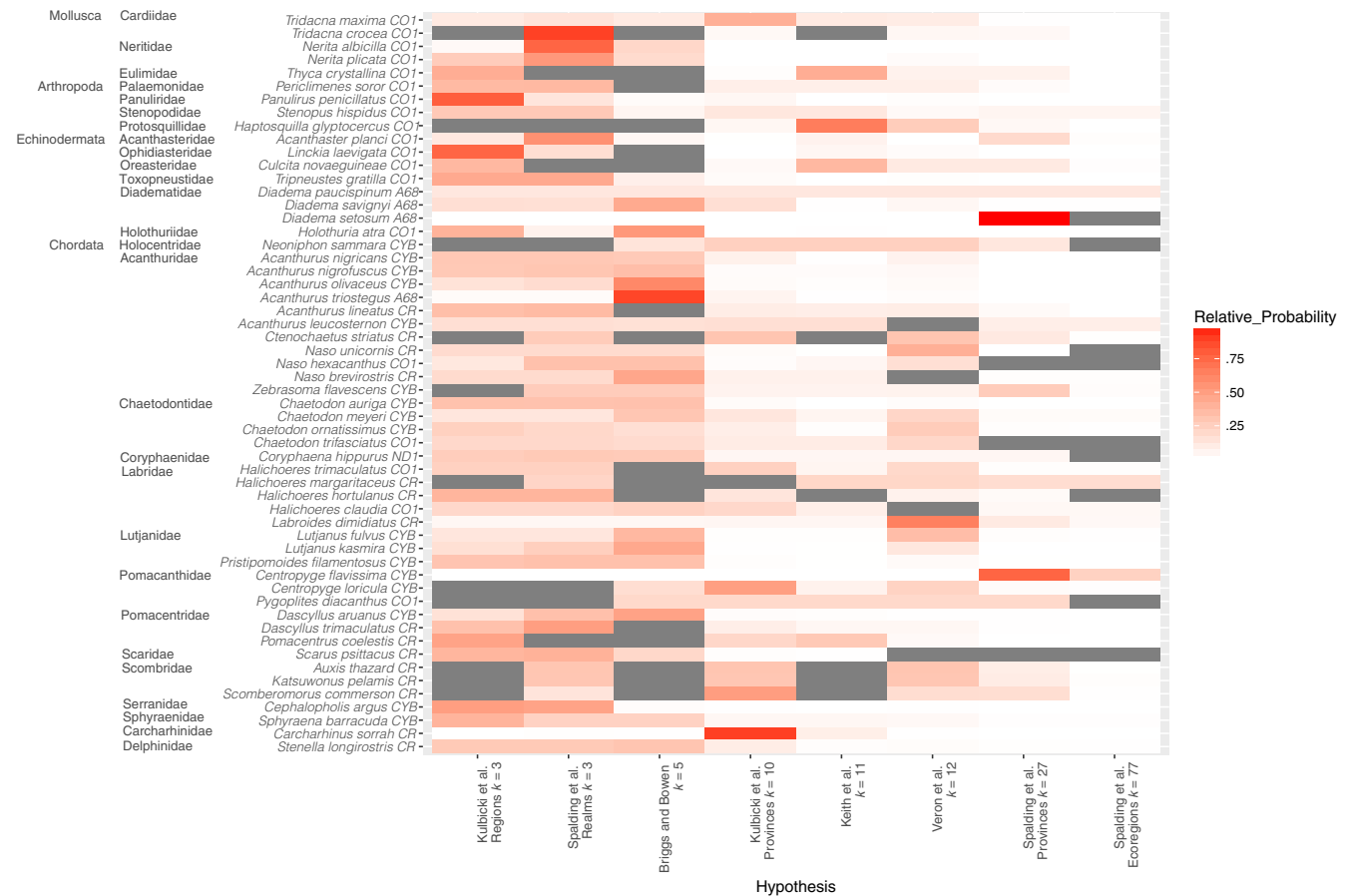
**FIGURE 2** Density maps showing the distribution of species and sequences in the DIPnet database. The total number of species (a) and total number of sequences (b) within a 250-km radius moving window are shown with a linear colour ramp. Sample points are shown as black points. Hotspots are saturated at a maximum value of 30 species (a) and 1,000 sequences (b), although higher values exist. For reference, Hawai'i contains 52 species and 2,300 sequences, a region south of Sulawesi has 32 species and 1,000 sequences, and Fiji contains 18 species and 300 sequences. The scope of the whole database is shown, but analyses were limited to the Indo-Pacific

species) and provinces ( $k = 11$ , supported by 12 species). The hypothesis that received the least support was Spalding et al.'s (2007) ecoregions ( $k = 77$ , supported by one species). Results from AMOVAs based on ESUs identified by ABGD showed an increase in taxa that supported Briggs and Bowen (2012), indicating that Indian and Pacific Ocean populations of some taxa were diagnosed as cryptic species by this algorithm (Supporting Information Text S2). Results were not appreciably different when using  $F_{ST}$  instead of  $\Phi_{ST}$ , nor when using effect size ( $s_{reg}^2$ ),  $\Phi_{CT} = \frac{s_{reg}^2}{s_{tot}^2}$ , or the Akaike information criterion as the criterion for model selection instead of the BIC (Supporting Information Text S2).

### 3.3 | Barrier strength analysis

Results of this analysis are summarized in Figure 5. When each dataset was randomly split into two sets of localities,  $\Phi_{ST}$  ranged between 0 and 0.92, with median pairwise  $\Phi_{ST}$  being 0.003 [95% confidence

interval (CI) 0.0003–0.008, 38% of values were zero]. Median pairwise  $\Phi_{ST}$  between the Western Indian Ocean Province proposed by Briggs and Bowen (2012) and the Western Indo-Pacific Realm proposed by Spalding et al. (2007) was 0.018 (Figure 5; bootstrapped 95% CI 0.000–0.079, 35% zeros), which was not significantly greater than the median of the randomized dataset ( $p = 0.12$ ). Median pairwise  $\Phi_{ST} = 0.021$  between the Western Indo-Pacific and the Central Indo-Pacific Realms of Spalding et al. (the Indo-Pacific Barrier; bootstrapped 95% CI 0.003–0.037, 24% zeros) was significantly greater than the median of the randomized dataset ( $p = 0.025$ ). A similar pattern was observed between the Central Indo-Pacific and the Eastern Indo-Pacific (median pairwise  $\Phi_{ST} = 0.015$ , 95% CI 0.005–0.022, 22% zeros, significant at  $p = 0.01$ ). Barriers delimiting peripheral archipelagos had higher median  $\Phi_{ST}$  and higher variance. The boundary between the Eastern Indo-Pacific and the Hawaiian Province of Briggs and Bowen (2012) had a median pairwise  $\Phi_{ST}$  of 0.051 (95% CI 0.002–0.096, 32% zeros, significant at  $p = 0.046$ ), while a similar comparison with the Marquesan Province had a median pairwise



**FIGURE 3** Heatmap of relative probability scores based on analysis of molecular variance (AMOVA) Bayesian information criterion (BIC) estimates for each of the eight regionalization hypotheses. Grey shading indicates hypotheses that were not testable based on available samples for a particular species and “k” indicates the number of proposed Indo-Pacific biogeographic regions. Hypotheses are arranged in order of increasing number of regions. Locus abbreviations: CO1 = cytochrome oxidase subunit 1; CR = control region; CYB = cytochrome B; ND1 = Nicotinamide adenine dinucleotide (NADH): ubiquinone oxidoreductase subunit 1; A68 = ATPase 6 and 8 region

$\Phi_{ST}$  of 0.028 (95% CI 0.000–0.076, 45% zeros, not significant at  $p = 0.28$ ). The simple simulation of allopatric divergence yielded  $\Phi_{ST}$  values ranging from 0–0.42 with a median pairwise  $\Phi_{ST}$  of 0.023, (95% CI 0.01–0.034, 33% zeros, significantly greater than the median of the randomized dataset at  $p = 0.003$ ). Pairwise values for both  $\Phi_{ST}$  and  $F_{ST}$  are available in Supporting Information Tables S2 and S3, and violin plots of the full distribution of values may be found in Supporting Information Figure S1.

### 3.4 | Distance-based redundancy analysis

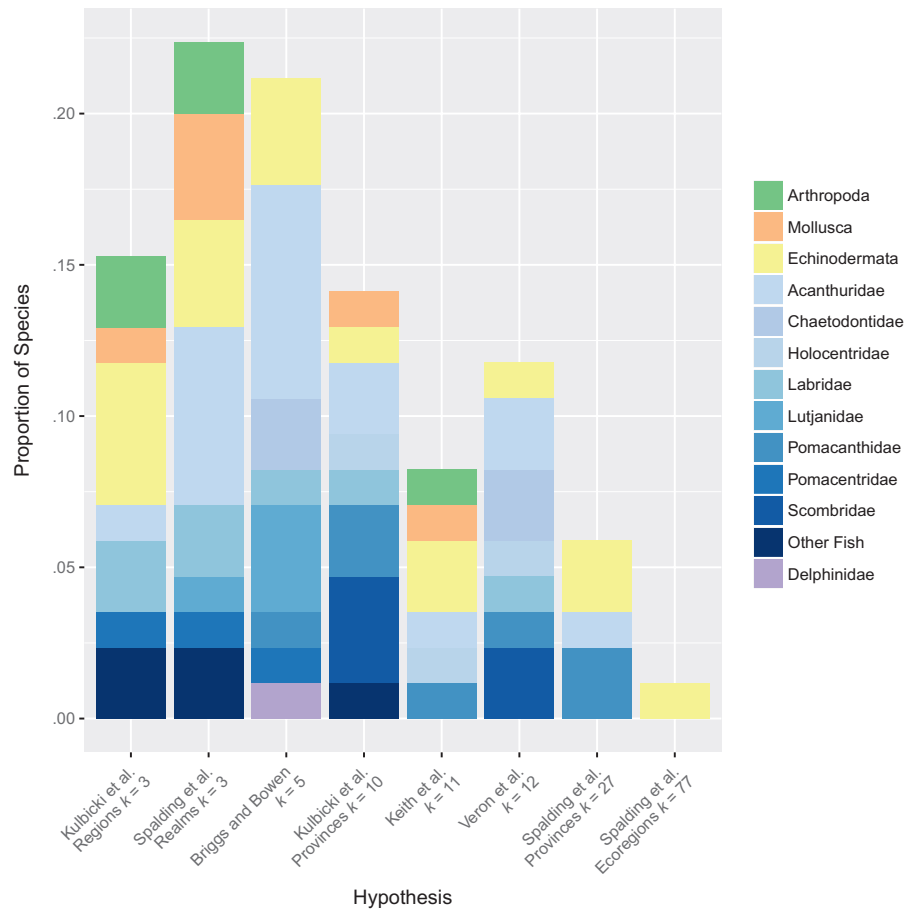
In the dbRDA analysis, 21 out of 52 species (four species had less than five sampling sites and were removed) rejected the null model of no spatial differentiation (Figure 6). Six had significant variance explained only by regional structure, 10 had significant variance explained only by overwater distance (mostly in the zonal, or east–west dimension), and five species had significant variance explained by both regional structure and overwater distance. The percentage of inertia constrained (similar to variance explained) in each model tested was generally less than 25%. Plots of  $\Phi_{ST}$  versus distance for all species can be found in Supporting Information Figure S2.

## 4 | DISCUSSION

Here we conduct comparative phylogeographic analysis of over 50 taxonomically and ecologically diverse marine species distributed across the Indo-Pacific. Novel methodology in a model selection framework returned a diversity of results, as expected when comparing lineages separated by over half a billion years of evolution, but favoured regionalization models with fewer regions. Approximately 60% of the species examined supported biogeographic partitions based on five or fewer regions (Figure 4: Spalding et al.’s Realms, Briggs & Bowen’s Provinces and Kulbicki et al.’s Regions). This result, which is not a statistical artefact as indicated by analyses of multiple alternative criteria in Supporting Information Text S2, suggests that on the scale of the entire Indo-Pacific Ocean, there is only a loose relationship between species distributions and population genetic structure, although there can be more concordance at finer geographic scales (see DeBoer et al., 2014). Kelly and Palumbi (2010) report similar discordance between biogeography and phylogeography at broad spatial scales along the west coast of North America.

Comparative phylogeographic analyses provided broad support for two barriers to gene flow that are well characterized in





**FIGURE 4** Proportional support by species for each regionalization hypothesis, with “k” indicating the number of proposed Indo-Pacific biogeographic regions. Colours depict the taxonomic distribution for each hypothesis—phyla for invertebrates and families for chordates. Hypotheses are arranged in order of increasing number of regions

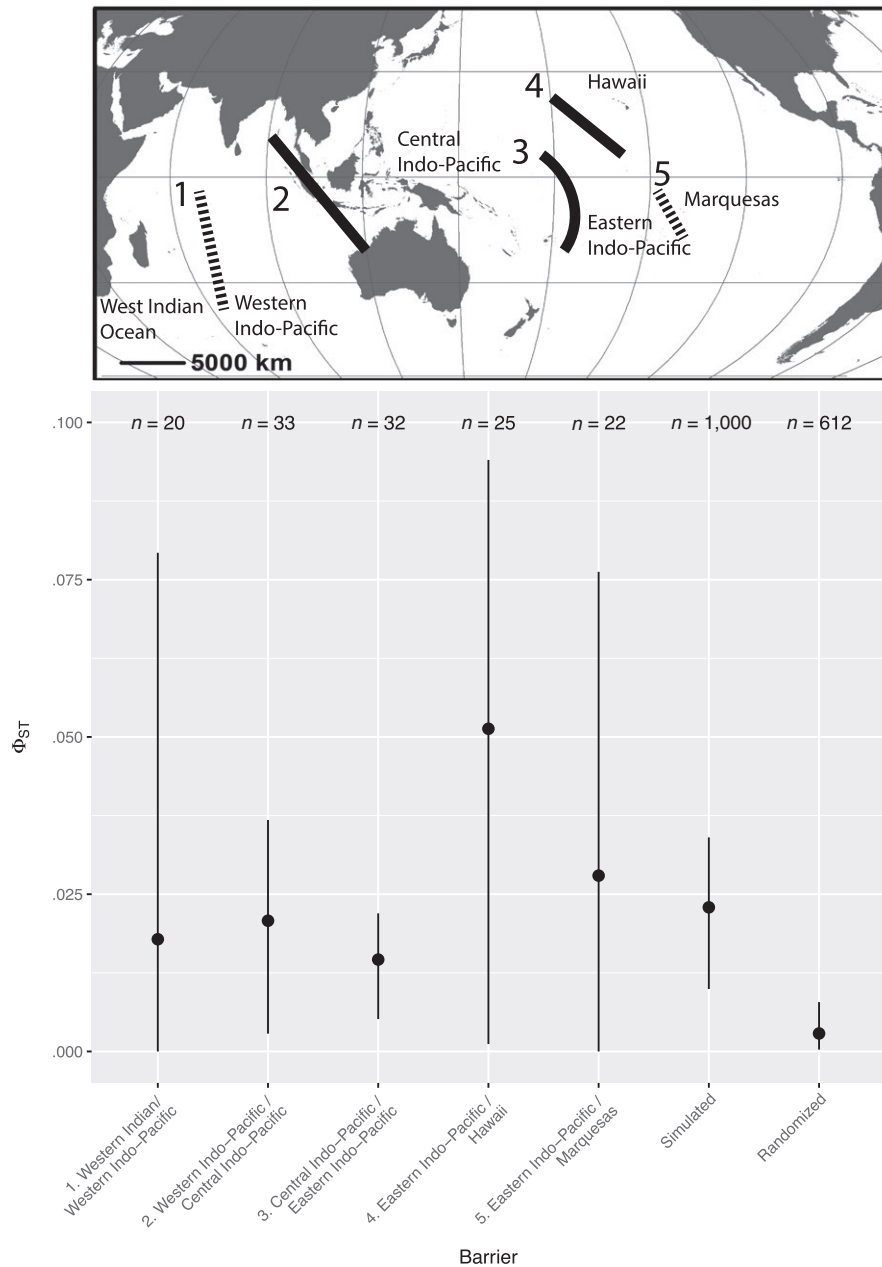
the literature (Figure 5). These barriers are the relative isolation of the Hawaiian Archipelago (Bowen et al., 2016) and the intermittent Indo-Pacific Barrier (Benzie, 1999; Cannon, Morley, & Bush, 2009; Ludt & Rocha, 2014), which is located along the western edge of the Sunda Shelf and has strengthened during low sea-level stands. There is also support for a less appreciated barrier between the continental and uplifted islands of the Central Indo-Pacific and the volcanic island arcs of the Eastern Indo-Pacific (Vermeij, 1987). These three areas of concordant differentiation indicate the presence of broadly acting, pronounced filters to dispersal and gene flow (Avice, 2000) that likely contribute to diversification of Indo-Pacific marine fauna.

Despite the clear presence of filters in the Indo-Pacific region, the distribution of pairwise  $\Phi_{ST}$  (Figure 5) with respect to each of these barriers was relatively low (in comparison to values obtained for terrestrial species; Medina, Cooke, & Ord, 2018) as expected from a fluid environment with high potential for significant dispersal (Riginos, Crandall, Liggins, Bongaerts, & Tremblay, 2016). Median values ranged between 0.018 and 0.051 and many species registered little or no genetic turnover across each barrier (22% to 45% with  $\Phi_{ST} = 0$ ). However, three of these median values were significantly greater than what would be found if populations were randomly distributed. Typically, such limited genetic structure might be overlooked in a

single-species study. However, the comparative approach taken in this study allowed emergent patterns to materialize, highlighting the value of large comparative datasets, particularly in high dispersal, high gene flow systems [see Paulay and Meyer (2002) for counterexamples from marine species with low dispersal capability].

#### 4.1 | Origins of discordance between biogeography and phylogeography

Although there was modest concordance between phylogeographic patterns and regionalization models with the fewest partitions, there was substantial discordance among species. The biogeographic classifications comprising fewer regions seem to reflect the influence of broad-scale physical processes that have separated geographic regions over time. In contrast, regionalizations with higher numbers of regions may reflect local-scale environmental differences that may have only manifested over recent time-scales or else have affected species differently. Our results indicate that, at least for putatively neutral loci at a local scale, these contemporary environmental differences may not contribute much to genetic structuring in Indo-Pacific species (Benzie, 1999; Horne, 2014b, although see DeBoer et al., 2014), a pattern consistent with data at the genomic scale as well (Gaither et al., 2015).

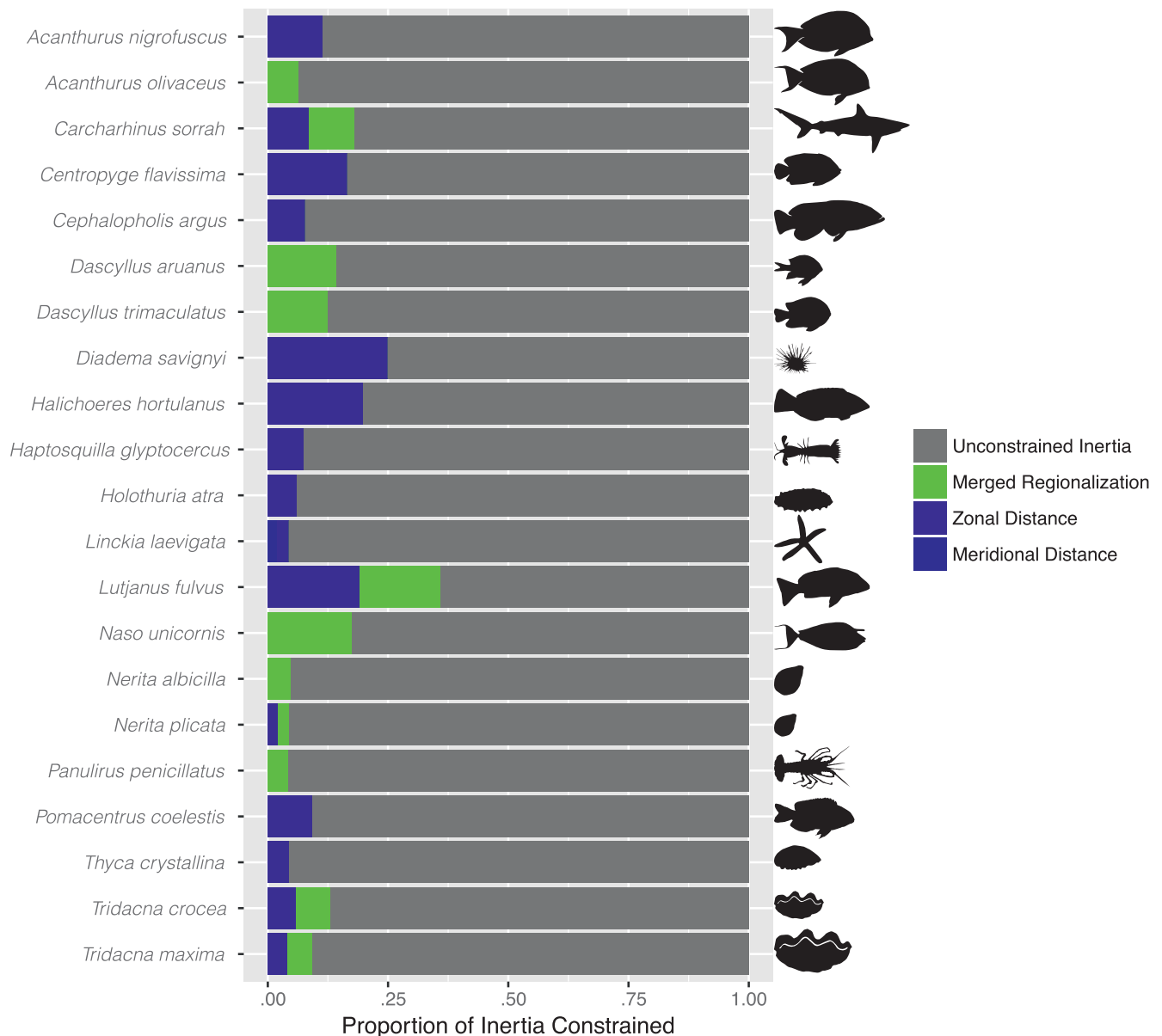


**FIGURE 5** Median and 95% bootstrapped confidence intervals for pairwise  $\Phi_{ST}$  calculated between each of six regions of the merged regionalization. Also depicted are the same values for 1,000 datasets simulated under a scenario of allopatric divergence starting 10,000 generations ago, as well as a randomized dataset in which population samples were randomly allocated to one of two regions. Each putative barrier between regions is drawn as a black line on the map, with solid lines depicting barriers with median  $\Phi_{ST}$  that is significantly greater than random expectation

Another explanation for the differences among Indo-Pacific species in the degree of genetic structure and best-supported regionalization could reflect the dynamic nature and geographic variability of evolutionary and ecological processes, including rates of species origin, survival and export (Cowman & Bellwood, 2013). For example, the shallow shelves of the Indo-Malay-Philippine Archipelago that Spalding (2007) breaks into more than 20 ecoregions experienced pronounced changes in sea level (Voris, 2000). These cycles of exposure and flooding tend to homogenize the distribution of genetic variation on continental shelves (Benzie, 1999; Crandall,

Sbrocco et al., 2012) and could also modify species distributions or drive local extinctions that impact biogeographic regionalization models. Combined, these processes could result in a decoupling between contemporary environments and species distributions used in biogeographic models and non-equilibrium patterns of genetic variation.

Another potential source of discordance are sampling biases. There is a clear lack of co-sampling among the disparate research groups that contributed data. Figure 2 shows clear hotspots in investigator effort, a pattern previously highlighted by Keyse et al. (2014).



**FIGURE 6** Proportion of constrained inertia in ordinated pairwise  $\Phi_{ST}$  values that can be attributed to either overwater distance (zonal or meridional components) or to putative barriers to gene flow hypothesized by the merged regionalization. Results are only shown for species that rejected the null model of no relationship between  $\Phi_{ST}$  and distance and barriers. Silhouettes of taxa were traces by P. F. Cowman from photos found on reeplifsurvey.com, sealifebase.org and fishesofaustralia.com.au

As noted above, average genetic structure was relatively low, requiring comparison of large numbers of taxa to elucidate regional concordance. Given variation in sampling effort across the Indo-Pacific region, it is possible that increased sampling (and increased sample sizes) could result in more support for more highly subdivided regionalizations. Similarly, there is a sampling bias in Indo-Pacific phylogeography toward widely distributed taxa with planktotrophic larvae, and our analysis strengthened that bias by tending to select well-sampled species with large ranges. More geographically distributed data are needed from species with limited dispersal capability (e.g. Meyer, Geller, & Paulay, 2005).

Rather than being a sampling artefact, simulated allopatric divergence scenarios over 10,000 generations (Figure 5) suggest that the

absence of stronger concordance between biogeographic regionalizations and phylogeographic patterns may simply be a function of genetic drift. These simulations yielded  $\Phi_{ST}$  distributions similar to empirical data observed across each putative barrier, including 33% of the iterations measuring  $\Phi_{ST} = 0$ . This result suggests that, given realistic coalescent effective sizes for Indo-Pacific species of 100,000 individuals or more (Crandall, Frey et al., 2008; Crandall, Jones et al., 2008), genetic drift is often too weak to establish much genetic structure over the time-scales of historical environmental fluctuations that are several orders of magnitude smaller than the effective sizes of Indo-Pacific species (Pillans, Chappell, & Naish, 1998).

When genetic drift does establish genetic structure, there can be enormous variance in magnitude. The simulated values of  $\Phi_{ST}$

ranged from 0 to 0.42, providing further insight into the overall lack of concordance in our AMOVA results. For populations of any given Indo-Pacific species that have been allopatrically isolated for 10,000 generations,  $\Phi_{ST}$  can range between 0 and almost 0.5, with a high probability that it will be 0. Marine genetic structure is blurred by the stochasticity of genetic drift (Hellberg, 2009). These results highlight the challenge of identifying biogeographic processes and patterns in marine systems using single-species studies, and the power of large-scale comparative phylogeographic meta-analyses.

## 4.2 | Distance or barriers?

Our results from dbRDA demonstrate that, while there is much stochasticity in pairwise  $\Phi_{ST}$  values, distance is the most important predictor of genetic differentiation at the scale of the Indo-Pacific based on the variables that we included in our models. Overall, only 40% of species that we tested rejected the null model of no effect of distance or barriers, and only 29% included distance in the best dbRDA model. This may seem low, given that species dispersal via pelagic larvae should be expected to conform to a model of isolation-by-distance (IBD), but it is comparable to the proportion of species demonstrating IBD across all marine species (c. 33%; Selkoe & Toonen, 2011; Selkoe et al., 2016). It may be that mtDNA is not well suited to detection of IBD due to rampant selection along its non-recombining length (Teske et al., 2018), or the relationship may simply be obscured by genetic drift as discussed above.

While dbRDA is able to deal with non-independence in genetic and geographic distances, it appears to sacrifice some power to do so, as there were several species that displayed trends in  $\Phi_{ST}$  versus overwater distance but did not reject the null model (see Supporting Information Figure S2). While distance was the most important variable, there were still 21% of species for which the merged amalgamation of the Briggs & Bowen and Spalding regionalizations constrained some proportion of model inertia. This indicates that physical barriers (such as the Sunda Shelf) or environmental barriers/filters, while potentially important locally, may play a more limited role in genetic differentiation across the broader Indo-Pacific.

## 4.3 | Conclusions

In conclusion, our large-scale phylogeographic survey of the Indo-Pacific yields inconsistent support for various biogeographic hypotheses, with most species supporting relatively coarse-grain biogeographic divisions. A simple interpretation of this result would be that the Indo-Pacific is well connected by propagule-mediated gene flow (Mora et al., 2012). However, our simulation results show that *F*-statistics are often an unreliable indicator of divergence processes when the effective size of a species significantly surpasses the time-scale of divergence. In other words, most species in the Indo-Pacific are likely out of equilibrium with respect to gene flow and genetic drift (Hellberg, 2009), with the broad similarities in allele frequencies across the region likely reflecting historical processes including extinction-recolonization dynamics (Horne, 2014b), or ongoing gene flow that is evolutionarily significant but not ecologically relevant (Crandall, Tremblay,

& Barber, 2012; Crandall, Toonen, ToBo Laboratory, & Selkoe, 2019; Matias & Riginos, 2018). Hence, there may be more isolation among Indo-Pacific reefs than is indicated in our results.

Despite leveraging the largest phylogeographic dataset to date, our analysis was somewhat hampered by a lack of taxonomic coordination and overlap among sample locations (Keyse et al., 2014). Future studies in the region would profit from a coordinated sampling strategy, wherein principal investigators agree to co-sample a fixed set of taxa throughout the Indo-Pacific, including the collection of extensive georeferenced metadata to accompany each sample. Future seascape genetic studies in the Indo-Pacific will also benefit from the addition of thousands of loci generated by massively parallel methods (Gaither et al., 2015; Saenz-Agudelo et al., 2015), which can be used with analyses based on coalescent simulations and linkage equilibrium in addition to allele frequencies to resolve genetic structure over much shorter time-scales (Crandall et al., 2019; Crandall, Tremblay et al., 2012; Matias & Riginos, 2018).

The current dataset forms the core of the Genomic Observatories Metadatabase (GeOME; Deck et al., 2017), which facilitates coordinated sampling strategies and metadata collection and curation. GeOME creates a permanent link between occurrence metadata and genetic sequences (both FASTA and FASTQ formats) submitted to the International Nucleotide Sequence Database Collaboration (i.e. National Center for Biotechnology Information, NCBI; European Molecular Biology Laboratory, EMBL; DNA Data Bank of Japan, DDBJ). GeOME is a searchable database thereby allowing researchers to determine sample coverage in terms of both taxonomy and geography. We also make available our analysis pipeline (<https://github.com/DIPnet/popgenDB>) in support of multispecies comparative phylogeography initiatives.

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## DATA ACCESSIBILITY

All empirical genetic data are available in the Genomics Observatories Metadatabase (GeOME; <https://www.geome-db.org/query>). The trimmed and aligned dataset used in the paper is available on GitHub (<https://github.com/DIPnet/IPDB>) and Dryad (<https://doi.org/10.5061/dryad.30326v6>). Code and simulated datasets are available in a separate GitHub repository (<https://github.com/DIPnet/popgenDB>).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

## BIOSKETCH

Founded in 2012, the Diversity of the Indo-Pacific Network (DIPnet) was created to advance genetic diversity research in the Indo-Pacific Ocean by aggregating published population genetic data into a searchable database so that original datasets can be utilized to address questions concerning conservation of marine biodiversity. It is our aim to promote collaboration, increase research capacity in Indo-Pacific countries and advocate best practices for conducting biodiversity research. Please visit our website at <http://diversityindopacific.net>.

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## APPENDIX: DATA SOURCE CITATIONS

### Citations to original datasets of species depicted in Figure 3.

- Tridacna maxima*—small giant clam  
DeBoer, T. S., Naguit, M. R. A., Erdmann, M. V., Ablan, M. C. A., Ambariyanto, Carpenter, K. E., ..., Barber, P. H. (2014). Concordance between phylogeographic and biogeographic boundaries in the Coral Triangle: Conservation implications based on comparative analyses of multiple giant clam species. *Bulletin of Marine Science*, 90(1), 277–300. <https://doi.org/10.5343/bms.2013.1003>
- Tridacna crocea*—boring giant clam  
DeBoer, T. S., Naguit, M. R. A., Erdmann, M. V., Ablan, M. C. A., Ambariyanto, Carpenter, K. E., ..., Barber, P. H. (2014). Concordance between phylogeographic and biogeographic boundaries in the Coral Triangle: Conservation implications based on comparative analyses of multiple giant clam species. *Bulletin of Marine Science*, 90(1), 277–300. <https://doi.org/10.5343/bms.2013.1003>
- Nerita albicilla*—blotched nerite  
Crandall, E. D., Frey, M. A., Grosberg, R. K., & Barber, P. H. (2008). Contrasting demographic history and phylogeographical patterns in two Indo-Pacific gastropods. *Molecular Ecology*, 17(2), 611–626. <https://doi.org/10.1111/j.1365-294X.2007.03600.x>
- Nerita plicata*—ribbed nerite  
Crandall, E. D., Frey, M. A., Grosberg, R. K., & Barber, P. H. (2008). Contrasting demographic history and phylogeographical patterns



- in two Indo-Pacific gastropods. *Molecular Ecology*, 17(2), 611–626. <https://doi.org/10.1111/j.1365-294X.2007.03600.x>
- Thyca crystallina*—parasitic snail
- Crandall, E. D., Jones, M. E., Muñoz, M. M., Akinronbi, B., Erdmann, M. V., & Barber, P. H. (2008). Comparative phylogeography of two seastars and their ectosymbionts within the Coral Triangle. *Molecular Ecology*, 17(24), 5276–5290. <https://doi.org/10.1111/j.1365-294X.2008.03995.x>
- Sepioteuthis lessoniana*—bigfin reef squid
- Cheng, S. H., Anderson, F. E., Bergman, A., Mahardika, G. N., Muchlisin, Z. A., Dang, B. T., ... Barber, P. H. (2014). Molecular evidence for co-occurring cryptic lineages within the *Sepioteuthis* cf. *lessoniana* species complex in the Indian and Indo-West Pacific Oceans. *Hydrobiologia*, 725(1), 165–188.
- Periclimenes soror*—commensal shrimp
- Crandall, E. D., Jones, M. E., Muñoz, M. M., Akinronbi, B., Erdmann, M. V., & Barber, P. H. (2008). Comparative phylogeography of two seastars and their ectosymbionts within the Coral Triangle. *Molecular Ecology*, 17(24), 5276–5290. <https://doi.org/10.1111/j.1365-294X.2008.03995.x>
- Panulirus penicillatus*—pronghorn spiny lobster
- Iacchei, M., Gaither, M. R., Bowen, B. W., & Toonen, R. J. (2016). Testing dispersal limits in the sea: Range-wide phylogeography of the pronghorn spiny lobster *Panulirus penicillatus*. *Journal of Biogeography*, 43(5), 1032–1044. <https://doi.org/10.1111/jbi.12689>
- Stenopus hispidus*—banded coral shrimp
- Dudoit, A., Iacchei, M., Coleman, R. R., Gaither, M. R., Browne, W. E., Bowen, B. W., & Toonen, R. J. (2018). The little shrimp that could: phylogeography of the circumtropical *Stenopus hispidus* (Crustacea: Decapoda), reveals divergent Atlantic and Pacific lineages. *PeerJ*, 6:e4409.
- Haptosquilla glytocercus*—mantis shrimp
- Barber, P. H., Erdmann, M. V., & Palumbi, S. R. (2006). Comparative phylogeography of three codistributed stomatopods: Origins and timing of regional lineage diversification in the Coral Triangle. *Evolution*, 60, 1825–1839.
- Acanthaster planci*—crown of thorns seastar
- Vogler, C., Benzie, J., Barber, P. H., Erdmann, M. V., Ambariyanto, Sheppard, C., ... Wörheide, G. (2012). Phylogeography of the Crown-of-Thorns Starfish in the Indian Ocean. *PLoS ONE*, 7(8), e43499. <https://doi.org/10.1371/journal.pone.0043499>
- Vogler, C., Benzie, J., Tenggardjaja, K., Barber, P. H., & Wörheide, G. (2013). Phylogeography of the crown-of-thorns starfish: genetic structure within the Pacific species. *Coral Reefs*, 32(2), 515–525. <https://doi.org/10.1007/s00338-012-1003-z>
- Linckia laevigata*—blue seastar
- Crandall, E. D., Trembl, E. A., Liggins, L., Gleeson, L., Yasuda, N., Barber, P. H., ... Riginos, C. (2014). Return of the ghosts of dispersal past: Historical spread and contemporary gene flow in the blue sea star *Linckia laevigata*. *Bulletin of Marine Science*, 90(1), 399–425. <https://doi.org/10.5343/bms.2013.1052>
- Culcita novaeguineae*—pincushion seastar
- Yasuda, N., Taquet, C., Nagai, S., Fortes, M., Suharsono, Susanto, H. A., Phongsuwan, N., Nadaoka, K. (2014) Genetic structure of *Culcita* sp. pincushion starfish in the Coral Triangle. *Proceedings of International Coral Reef Symposium*, 25A
- Tripneustes gratilla*—collector sea urchin
- Lessios, H., Kane, J., & Robertson, D. (2003). Phylogeography of the pan-tropical sea urchin *Tripneustes*: Contrasting patterns of population structure between oceans. *Evolution*, 57(9), 2026–2036.
- Liggins, L., Gleeson, L., & Riginos, C. (2014). Evaluating edge-of-range genetic patterns for tropical echinoderms, *Acanthaster planci* and *Tripneustes gratilla*, of the Kermadec Islands, southwest Pacific. *Bulletin of Marine Science*, 90(1), 379–397. <https://doi.org/10.5343/bms.2013.1015>
- Diadema paucispinum*—long-spined sea urchin
- Lessios, H., Kessing, B., & Pearse, J. (2001). Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. *Evolution*, 55(5), 955–975.
- Diadema savignyi*—long-spined sea urchin
- Lessios, H., Kessing, B., & Pearse, J. (2001). Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. *Evolution*, 55(5), 955–975.
- Diadema setosum*—long-spined sea urchin
- Lessios, H., Kessing, B., & Pearse, J. (2001). Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. *Evolution*, 55(5), 955–975.
- Echinothrix diadema*—blue-black urchin
- Lessios, H., & Robertson, D. (2006). Crossing the impassable: Genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2201–2208.
- Holothuria atra*—black sea cucumber
- Skillings, D. J., Bird, C. E., & Toonen, R. J. (2011). Gateways to Hawai'i: Genetic population structure of the tropical sea cucumber *Holothuria atra*. *Journal of Marine Biology*, 2011, 1–16. <https://doi.org/10.1155/2011/783030>
- Neoniphon sammara*—Sammara squirrelfish
- DiBattista, J. D., Berumen, M. L., Gaither, M. R., Rocha, L. A., Eble, J. A., Choat, J. H., ... Bowen, B. W. (2013). After continents divide: Comparative phylogeography of reef fishes from the Red Sea and Indian Ocean. *Journal of Biogeography*, 40(6), 1170–1181. <https://doi.org/10.1111/jbi.12068>
- Acanthurus nigricans*—black surgeonfish
- DiBattista, J. D., Whitney, J., Craig, M. T., Hobbs, J.-P. A., Rocha, L. A., Feldheim, K. A., ... Bowen, B. W. (2016). Surgeons and suture zones: Hybridization among four surgeonfish species in the Indo-Pacific with variable evolutionary outcomes. *Molecular Phylogenetics and Evolution*, 101, 203–215. <https://doi.org/10.1016/j.ympev.2016.04.036>
- Acanthurus nigrofusus*—brown surgeonfish
- Eble, J. A., Rocha, L. A., Craig, M. T., & Bowen, B. W. (2011). Not all larvae stay close to home: Insights into marine population connectivity with a focus on the brown surgeonfish (*Acanthurus nigrofusus*). *Journal of Marine Biology*, 2011, 1–12. <https://doi.org/10.1155/2011/518516>
- Acanthurus olivaceus*—orangeband surgeonfish
- Gaither, M. R., Bernal, M. A., Coleman, R. R., Bowen, B. W., Jones, S. A., Simison, W. B., & Rocha, L. A. (2015). Genomic signatures of geographic isolation and natural selection in coral reef fishes. *Molecular Ecology*, 24(7), 1543–1557. <https://doi.org/10.1111/mec.13129>
- Acanthurus triostegus*—convict tang
- Liggins, L., Trembl, E. A., Possingham, H. P., & Riginos, C. (2016). Seascape features, rather than dispersal traits, predict spatial genetic patterns in co-distributed reef fishes. *Journal of Biogeography*, 43(2), 256–267. <https://doi.org/10.1111/jbi.12647>
- Acanthurus lineatus*—striped surgeonfish
- Paul Barber—unpublished data
- Acanthurus leucosternon*—powderblue tang
- DiBattista, J. D., Whitney, J., Craig, M. T., Hobbs, J.-P. A., Rocha, L. A., Feldheim, K. A., ... Bowen, B. W. (2016). Surgeons and suture zones: Hybridization among four surgeonfish species in the Indo-Pacific with variable evolutionary outcomes. *Molecular Phylogenetics and Evolution*, 101, 203–215. <https://doi.org/10.1016/j.ympev.2016.04.036>
- Acanthurus achilles*—Achilles tang
- DiBattista, J. D., Whitney, J., Craig, M. T., Hobbs, J.-P. A., Rocha, L. A., Feldheim, K. A., ... Bowen, B. W. (2016). Surgeons and suture zones: Hybridization among four surgeonfish species in the Indo-Pacific with variable evolutionary outcomes. *Molecular Phylogenetics*



- and Evolution, 101, 203–215. <https://doi.org/10.1016/j.ympev.2016.04.036>
- Arothron meleagris*—guineafowl puffer
- Lessios, H., & Robertson, D. (2006). Crossing the impassable: Genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2201–2208.
- Ctenochaetus striatus*—striated surgeonfish
- Paul Barber—unpublished data
- Naso unicornis*—bluespine unicornfish
- Horne, J. B., van Herwerden, L., Choat, J. H., & Robertson, D. R. (2008). High population connectivity across the Indo-Pacific: Congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution*, 49(2), 629–638. <https://doi.org/10.1016/j.ympev.2008.08.023>
- Naso brevirostris*—short-nosed unicornfish
- Horne, J. B., van Herwerden, L., Choat, J. H., & Robertson, D. R. (2008). High population connectivity across the Indo-Pacific: Congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution*, 49(2), 629–638. <https://doi.org/10.1016/j.ympev.2008.08.023>
- Zebrasoma flavescens*—yellow tang
- Eble, J. A., Toonen, R. J., Sorenson, L., Basch, L. V., Papastamatiou, Y. P., & Bowen, B. W. (2011). Escaping paradise: Larval export from Hawaii in an Indo-Pacific reef fish, the yellow tang *Zebrasoma flavescens*. *Marine Ecology Progress Series*, 428, 245–258. <https://doi.org/10.3354/meps09083>
- Chaetodon auriga*—threadfin butterflyfish
- DiBattista, J. D., Waldrop, E., Rocha, L. A., Craig, M. T., Berumen, M. L., & Bowen, B. W. (2015). Blinded by the bright: a lack of congruence between colour morphs, phylogeography and taxonomy for a cosmopolitan Indo-Pacific butterflyfish, *Chaetodon auriga*. *Journal of Biogeography*, 42(10), 1919–1929. <https://doi.org/10.1111/jbi.12572>
- Chaetodon lunula*—raccoon butterflyfish
- DiBattista, J. D., Rocha, L. A., Hobbs, J., He, S., Priest, M. A., Bowen, B. W., & Berumen, M. L. (2015). When biogeographical provinces collide: Hybridization of reef fishes at the crossroads of marine biogeographical provinces in the Arabian Sea. *Journal of Biogeography*, 42, 1601–1614.
- Chaetodon meyeri*—scrawled butterflyfish
- DiBattista, J. D., Rocha, L. A., Craig, M. T., Feldheim, K. A., & Bowen, B. W. (2012). Phylogeography of two closely related Indo-Pacific butterflyfishes reveals divergent evolutionary histories and discordant results from mtDNA and microsatellites. *Journal of Heredity*, 103(5), 617–629. <https://doi.org/10.1093/jhered/ess056>
- Chaetodon ornatissimus*—ornate butterflyfish
- DiBattista, J. D., Rocha, L. A., Craig, M. T., Feldheim, K. A., & Bowen, B. W. (2012). Phylogeography of two closely related Indo-Pacific butterflyfishes reveals divergent evolutionary histories and discordant results from mtDNA and microsatellites. *Journal of Heredity*, 103(5), 617–629. <https://doi.org/10.1093/jhered/ess056>
- Chaetodon trifasciatus*—melon butterflyfish
- Waldrop, E., Hobbs, J. P. A., Randall, J. E., DiBattista, J. D., Rocha, L. A., Kosaki, R. K., ... & Bowen, B. W. (2016). Phylogeography, population structure and evolution of coral-eating butterflyfishes (Family Chaetodontidae, genus *Chaetodon*, subgenus *Corallochaetodon*). *Journal of Biogeography*, 43(6), 1116–1129. <https://doi.org/10.1111/jbi.12680>
- Forcipiger flavissimus*—longnose butterflyfish
- Lessios, H., & Robertson, D. (2006). Crossing the impassable: Genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2201–2208.
- Cirrhitichthys oxycephalus*—coral hawkfish
- Lessios, H., & Robertson, D. (2006). Crossing the impassable: Genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2201–2208.
- Coryphaena hippurus*—common dolphinfish
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