RESEARCH ARTICLE

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Do currents shape global patterns of hybrid richness in coral reef fishes?

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[Correction added on 13 October 2022, after first online publication: article title has been updated to include the word 'coral'.]

Abstract

Aim: Our main aim was to identify the distribution of, and potential mechanisms underpinning, hybrid-rich zones – regions with a disproportionate number of unique interspecific hybrids. We investigated whether coral reef fish hybrids coincided with factors such as phylogenetic relatedness, biogeographic barriers, species richness, geographic isolation, endemism, and oceanic currents.

Location: Global.

Time period: Contemporary.

Major taxa studied: Coral reef fishes.

Methods: We conducted a literature review and mapping to assess the taxonomic and global prevalence of hybridisation in coral reef fishes. We then fit Generalised additive models using a full-subsets and Bayesian framework to assess which variables are associated with hybrid-rich zones.

Results: We found 143 unique interspecific coral reef fish hybrids involving 204 species – which accounts for approximately 7% of coral reef fish species, indicating that hybridisation is as common in the sea as it is on land. Characteristic coral reef fish families were not homogeneously represented in our dataset, with particularly colourful groups standing out. Mapping our dataset revealed that coral reef fish hybrids are found worldwide, though some ecoregions (e.g., the Christmas and Cocos (Keeling) Islands, South Kuroshio, Hawaii, and Eastern Philippines) are more hybrid-rich than others. Our analysis revealed that mean surface current velocity, phylogenetic relatedness, and geographic isolation were the best predictors of hybrid richness in a given location.

Main conclusions: Phylogenetic distance between coral reef fish species may serve as a pre-condition for hybridisation to occur, lying between introgression and reproductive incompatibility. We also propose a novel mechanism, with oceanic currents driving long-distance larval dispersal events, transporting stray species to geographically remote sinks to maintain hybrid-rich zones.

KEYWORDS
biogeography, coral reef fishes, dispersal, geographic isolation, hybrid zone, hybridisation, hybrids, phylogenetic distance, surface currents, suture zone

1 | INTRODUCTION

Hybridisation is the interbreeding between genetically distinct individuals belonging to different biological species and evolutionary lineages, producing offspring of mixed descent (Barton & Hewitt, 1985). Historically believed to be rare (Hubbs, 1955), hybridisation is now commonly observed in nature, with 25% of plant and 10% of animal species known to interbreed (Mallet, 2005). Cases of hybridisation offer us 'windows on evolutionary process[es]' (Harrison, 1990) – a unique opportunity to study what lies beneath adaptation, speciation, and reproductive isolation.

After the initial instance of hybridisation, F_1 hybrids may subsequently backcross with parental species, potentially leading to widespread introgression with evolutionary implications for parental species (Bernal et al., 2017). In coral reef fishes, hybrids are commonly detected through their intermediate physical attributes of their parental species, a method that has been supported in many studies by subsequent genetic analyses (e.g., Tea et al., 2020; Yaakub et al., 2006, 2007). However, with the progression of backcrossing, hybrids become morphologically indistinguishable from their parent species, making them difficult to identify (Marie et al., 2007; McMillan et al., 1999; Yaakub et al., 2006). Recent advances in molecular approaches have provided opportunities to discover more of these hybrids.

Beyond the discovery of hybrids and backcrosses, hybridisation can be explored in a geographic context. Restricted regions in which populations of different biological species hybridise and produce viable offspring are called *hybrid zones* (Barton & Hewitt, 1985). *Suture zones* are narrow geographic regions characterised by secondary contact, where multiple pairs of allopatric sister species interbreed (Barton & Hewitt, 1985; Hewitt, 1996; Remington, 1968). Although suture zone theory was initially described in terrestrial systems, where it remains an area of keen exploration (Remington, 1968), studies focused on the marine realm have only gained traction in more recent years (Hobbs et al., 2021). To date, four tropical marine suture or hybrid zones have been described based on coral reef fishes: (a) Christmas and Cocos (Keeling) Islands (DiBattista, Whitney, et al., 2016; Hobbs et al., 2009; Hobbs & Allen, 2014; Marie et al., 2007; Payet et al., 2016; Salas et al., 2020); (b) the Socotra Archipelago (DiBattista et al., 2015); (c) between Papua New Guinea and the Solomon Islands (Gainsford et al., 2015, 2020; Hobbs et al., 2013; McMillan et al., 1999); and (d) Johnston Atoll (Lobel et al., 2020). These are stand-out regions that could have a disproportionate effect on the evolutionary processes of coral reefs as sources or sinks of evolutionary novelty.

While various mechanisms have been identified that may promote the chances of hybridisation, relatively few studies have examined the formation or maintenance of hybrid or suture zones. However, several major potential drivers have been identified: (a) Hybridisation in coral reef fishes has been reported between deeply divergent lineages (Carlon et al., 2021; Tea et al., 2020), but it occurs more readily between closely related species (DiBattista et al., 2015; Montanari et al., 2014, 2016). This suggests that hybridisation may occur due to secondary contact between recently diverged species. (b) The Christmas–Cocos Islands suture zone, for example, is posited to be the product of secondary contact at the Sunda Shelf biogeographic barrier – where closely related Indian and Pacific Ocean populations with Plio-Pleistocene origins meet and interbreed (Marie et al., 2007; Salas et al., 2020). Biogeographic barriers thus represent areas of separation between allopatric and non-allopatric reef fish sister species (Hodge & Bellwood, 2016) and may represent areas in which they meet and hybridise. (c) Many researchers have also suggested that parental species abundances or species rarity may play a large role in promoting interbreeding (DiBattista et al., 2015; Hobbs et al., 2009; Marie et al., 2007; Montanari et al., 2014, 2016; Yaakub et al., 2006). (d) Another ecological factor to consider is species richness. Do species-rich regions have more hybrids simply because a greater number of species increases the chances of interbreeding? Or do regions with low numbers of species coincide with high niche availability for hybrids (Seehausen, 2004)? (e) Geographically isolated locations with variable environmental conditions and (f) endemism may also influence where hybridisation occurs (DiBattista et al., 2015). In the Socotra Archipelago suture zone, for example, where high endemism is observed (DiBattista, Choat, et al., 2016), four of the seven putative hybrids involved endemics (DiBattista et al., 2015). Endemism and geographic isolation have been shown to be tightly linked, such as in the Hawaiian Islands, where remoteness and endemism are high (25% – Randall, 2007). However, geographic isolation alone cannot explain high rates of endemism in some regions. For example, endemism in the Marquesas (11.6% – Randall & Earle, 2000) is explained by ecological conditions distinct to the region in addition to its geographic isolation (Gaither et al., 2015). Consequentially, endemism and geographic isolation should be explored as independent factors. (g) Lastly, specific factors such as the prevailing direction of major currents may facilitate interbreeding, by promoting connectivity and larval dispersal into particular regions (DiBattista et al., 2015; Salas et al., 2020). Therefore, summarising the literature thus far, the following conditions may be associated with marine hybrid or suture zones: genetic relatedness, biogeographic barriers, abundance disparities, species richness, geographic isolation, endemism, and oceanic currents.

With threats to coral reefs climbing, understanding the evolutionary processes that have given rise to their diversity is becoming increasingly urgent, particularly for coral reef fishes, one of the most species rich vertebrate groups in the world. The recent surge in studies of coral reef fish hybridisation has prompted the overarching aim of this study, which is to determine the distribution of, and factors that may underpin geographic variation in hybrid richness. In this study, we addressed the following questions:

1. What is the taxonomic prevalence and geographic distribution of interspecific coral reef fish hybrids on a global scale? and,
2. To what extent does hybrid richness correlate with hypothesised factors driving hybridisation including: genetic relatedness, biogeographic barriers, species richness, geographic isolation, endemism, and oceanic currents?

2 | METHODS

2.1 | Data collection and processing

A systematic literature review was conducted to find all reports of coral reef fish hybrids (Figure 1). To gather these data, we searched Google

Scholar across all years for articles (all text, not including citations) that contained the following terms: "coral reef" AND ("hybrid" OR "introgression" OR "backcross") AND each of the 65 reef-associated fish
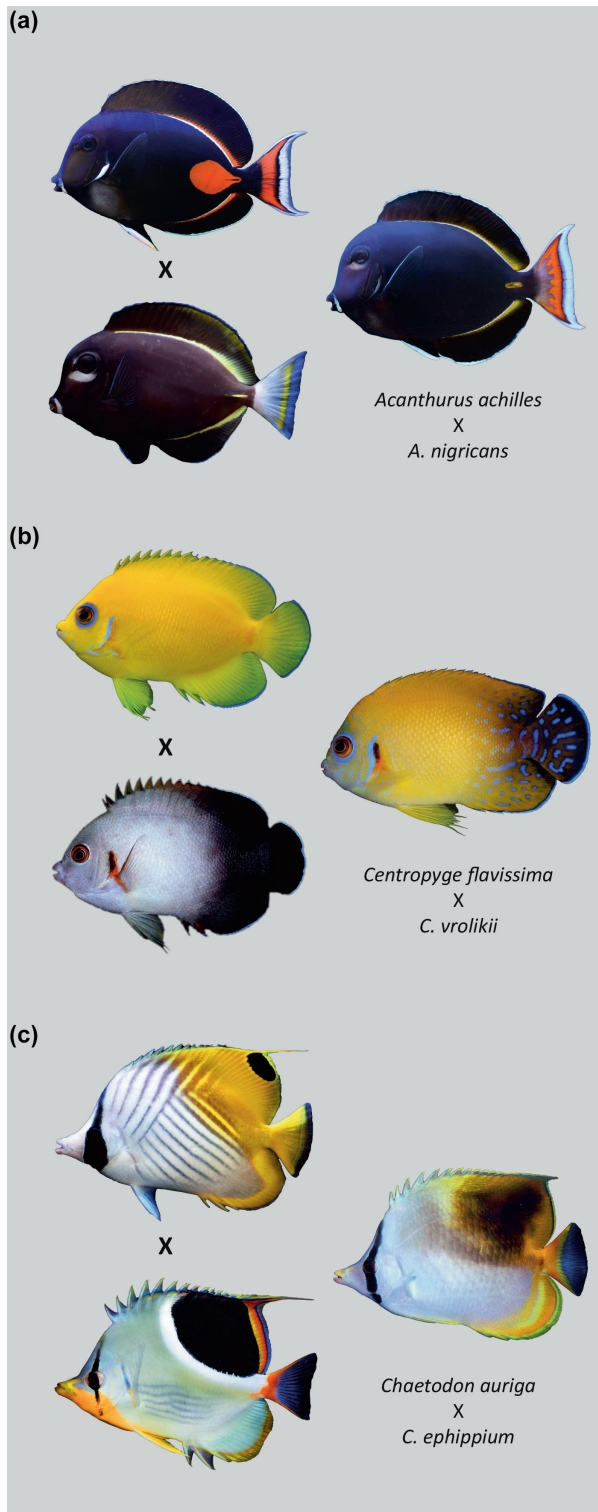

FIGURE 1 Examples of coral reef fish parent species (left) and their respective hybrid (right) exhibiting intermediate phenotypes, that is, colouration and patterns: (a) *Acanthurus achilles* (top) × *Acanthurus nigricans* (bottom), (b) *Centropyge flavissima* (top) × *Centropyge vrolikii* (bottom), and (c) *Chaetodon auriga* (top) × *Chaetodon ephippium* (bottom). All photos provided by Yi-Kai Tea, with permission

families as delineated by Siqueira et al. (2020). Each output was individually searched to retrieve reports on coral reef fish hybridisation. The reference list for each article was then searched for any additional sources that may have been missed from the Google Scholar search (e.g., physical identification books and guides). Only reports of hybrids observed in the wild and that identified the species involved in the cross were included in the dataset. All reported hybrids were included in the database regardless of the method of hybrid detection (e.g., intermediate colouration or genetic markers). The publication dates of the reports from our literature review ranged from 1956 to 2021 – suggesting hybrids from our study are relatively recent, contemporary, phenomena. Our goal was to identify 'unique interspecific hybrids', that is, a hybrid of two distinct species that represents a unique combination within this study.

Data processing involved removing reports that were solely of introgressed or backcrossed individuals, since they start genetically resembling either parent species. These individuals are often only detected using molecular methods due to morphological similarities to their parents (see Introduction). Since molecular advances are recent, backcrossed and introgressed individuals may not be well represented in the literature, and as such, their inclusion in our study may cause sampling bias.

We also designed a systematic method to ensure that all unique interspecific hybrids included in our dataset belonged to 'coral reef fishes'. In our literature review, we searched for reports: (a) containing the term "coral reef" and (b) only of the 65 reef fish families delineated by Siqueira et al. (2020). We then checked that (c) each species involved in an interspecific hybrid pair from our dataset was classified as reef-associated by FishBase (Froese & Pauly, 2022). Finally, (d) we only included hybrids located in tropical ecoregions – within the isocryme of 20°C – which provides a likely measure of the latitudinal distribution limit for tropical marine taxa (Briggs, 1974; Siqueira et al., 2016). Overall, these measures ensure that the hybrids from our study are broadly within the limits of 'coral reef fishes'. Indeed, approximately 86% (175/204) of the hybridising species in our study belong to the conservative 'consensus list' of coral reef fish families (i.e., Acanthuridae, Apogonidae, Blenniidae, Carangidae, Chaetodontidae, Gobiidae, Holocentridae, Labridae, Lutjanidae, Mullidae, Pomacanthidae, Pomacentridae, Serranidae) occurring on coral reefs globally (following Bellwood & Wainwright, 2002 and Siqueira et al., 2021).

2.2 | Taxonomic prevalence and geographic distribution

We summarised the taxonomic prevalence of coral reef fish hybrids in three ways. Firstly, we describe the number of unique interspecific hybrid pairs per family to inform differences in hybrid richness among families. Secondly, we report the number of species involved in hybridisation per family to show whether hybrids are represented by a diversity of species in each family. Finally, we calculate the proportion of hybridising species per family to account for the species richness of each family.

For our geographic distribution and modelling analyses, we use 'the number of unique interspecific hybrids' = 'hybrid richness' as our response variable, since it became apparent that most of the literature did not report the frequency of hybrid occurrences (i.e., how many times a specific hybrid was observed in a given area). 'Hybrid richness', therefore, is the number of unique interspecific hybrids. This means that if a unique interspecific hybrid was reported multiple times within one ecoregion, it would only be counted once – since we are reporting the richness rather than abundance. That given hybrid can also be reported across multiple ecoregions and is included in our dataset so long as it is a unique interspecific hybrid within that ecoregion (Supporting Information Table S1). The term 'hybrid-rich zones' is thus used to describe areas containing a high number of unique interspecific hybrid pairs.

We subsequently mapped the geographic locations of the unique interspecific hybrids to examine the global distribution of hybrid-rich zones. World vector data were plotted and obtained using packages '*sf*' (Pebesma, 2018), '*rnaturalearth*' (South, 2017), '*rnaturalearthdata*' (South, 2017) and '*ggspatial*' (Dunnington, 2021). The central point of hybrid locations was then obtained by calculating the centroid of each ecoregion using the *st_centroid* function from the '*sf*' R package (Pebesma, 2018). This process clustered 160 individual geographic locations of coral reef fish hybrids into 65 marine ecoregions (Spalding et al., 2007). Locations were grouped into ecoregions because hybrid reports from our dataset rarely provided precise geographic coordinates, and locations were inconsistent in their level of specificity, ranging from large to fine spatial scales. For example, hybrid reports have been described at the country level (e.g., Japan), regional level (e.g., South Japan), island chain level (e.g., Ryukyu Islands, South Japan), island level (e.g., Miyako-jima Islands, Ryukyu Islands, South Japan) and in some cases, even down to the reef level (Supporting Information Table S1). By clustering locations into ecoregions, we reduce the inconsistencies associated with the location of each reported hybrid. It also prevents the chance of double counting hybrids, for example in situations where the same interspecific hybrid was identified in both a specific location (e.g., Mombasa, Kenya) and a broad location (e.g., Kenya). We confirmed that ecoregion size (km^2) was not correlated with hybrid richness (Supporting Information Figure S1f).

2.3 | Predicting hybrid richness

Data for each of the hybrid richness predictors were publicly sourced (Table 1) and used to calculate average values at the ecoregion scale. To calculate phylogenetic distances between interspecific hybrids, we used the phylogenetic trees of reef-associated fishes produced by Siqueira et al. (2020). Siqueira et al. (2020) systematically selected which species were kept in the tree by beginning with the list of fish families with reef-associated species from Bellwood and Wainwright (2002). The '*rfishbase*' R package (Boettiger et al., 2012) was then used to calculate the proportion of reef-associated species within each of these families. The chronogram by Rabosky et al. (2018) was subsequently pruned for families with > 20% of reef-associated taxa and used as a backbone tree. Using the Taxonomic Addition for Complete Trees stochastic polytomy resolution algorithm (Chang et al., 2020), missing species were taxonomically assigned into the backbone tree, which resulted in a set of 100 near-complete reef fish trees with 6,257 tips each. Parental species that could not be detected as distinct species in the phylogenetic trees were filtered out of the dataset prior to all covariate calculations. These included crosses between colour morphs (e.g., *Dascyllus trimaculatus* – Salas et al., 2020), cryptic species (e.g., *Ostorhinchus doederleini* – Gerlach et al., 2016), or inconclusive species identifications (e.g., *Cirrhilabrus isosceles* × cf. *lunatus* – Tea et al., 2016). Phylogenetic distances (i.e., the sum of branch lengths separating two species in a phylogeny) between each hybrid parent species pair were measured using the *conphenetic.phylo* function from the '*ape*' R package (Paradis & Schliep, 2019) and subsequently averaged per ecoregion. Averaging phylogenetic distance was required to predict hybrid richness per ecoregion and did not lead to unequal weighting (Supporting Information Figure S2). In addition, ecoregion size (km^2) was not correlated with phylogenetic distance (Supporting Information Figure S1e).

To measure geographic isolation per ecoregion, we first calculated a radius that represented the median distance between all ecoregion centroids in our study. Geographic isolation was then calculated as 'the distance from one ecoregion centroid to the nearest ecoregion centroid ÷ the number of ecoregions within the radius'. Therefore, this metric takes into consideration both geographic distance and isolation from other ecoregions. This

TABLE 1 Data sources for the hybrid richness modelling predictors

Predictor	Data source
Biogeographic barriers	Bellwood and Wainwright (2002); DiBattista, Choat, et al. (2016), Floeter et al. (2008); Hodge and Bellwood (2016); Lessios and Robertson (2006); Luiz et al. (2012); Rocha (2003); Rocha et al. (2007)
Mean current velocity (m/s)	Bio-ORACLE v2.2 (Assis et al., 2018), '*sdmpredictors*' R package v2.10.0 (Bosch & Fernandez, 2021)
Endemics, species richness	Rabosky et al. (2018)
Phylogenetic distances (branch lengths)	Siqueira et al. (2020)

measure appeared to represent isolation well – with Hawaii representing the most remote and Northeast Sulawesi representing the most connected ecoregion. Biogeographic barriers used in our study were based on congruent vicariance events of coral reef fishes (Table 1). Only soft barriers were taken into consideration because hard barriers (e.g., Isthmus of Panama) cannot be physically crossed today and our study focuses only on contemporary hybridisation (i.e., hybrid reports published within the last 65 years). Barriers were plotted using *geom_curve* and *geom_line* functions in R package '*ggplot2*' (Wickham, 2011) and then converted into geographic coordinates. Distance from an ecoregion to a biogeographic barrier was measured as the geographic distance (in kilometres) from the centroid of each ecoregion to the closest point on a barrier using the function *distHaversine* in the '*geosphere*' R package (Hijmans et al., 2019). Mean surface current velocity per ecoregion was extracted from raster data layers (Assis et al., 2018; Bosch & Fernandez, 2021) and represented monthly averages between 2000 to 2014 (Table 1).

Global species richness and endemics data were retrieved from Rabosky et al. (2018). These data are organised as total species or endemic richness values per 150-km^2 geographic grid cell. We first intersected the coordinates from the Rabosky et al. (2018) dataset and our dataset to identify which grid cells were contained within each ecoregion. Mean species and endemic richness values per ecoregion were subsequently calculated (i.e., the sum of grid cell values contained within each ecoregion ÷ the number of grid cells per ecoregion). Endemism was measured as the proportion of endemics (mean) to species richness (mean) per ecoregion. No correlation was detected between species richness and endemism and between ecoregion size (km^2) and the number of endemics, species richness, or endemism (Supporting Information Figure S1). As an alternative to calculating *mean* values of species and endemic richness per ecoregion, we also used the species by ecoregion data from Rabosky et al. (2018) to calculate *total* values of species and endemic richness per ecoregion. Due to a lack of an endemics by ecoregion dataset, the species by ecoregion dataset was used to count the number of endemics per ecoregion. Species were flagged as endemics if they were only found in a single ecoregion. To test the efficacy of using the species and endemic richness *means* per ecoregion based on grid cell data, we replicated the modelling steps below using *total* species and endemic richness values per ecoregion.

We used statistical models to explore the effects of the predictors on the global distribution of hybrid richness – represented by the number of unique interspecific hybrids per ecoregion. Generalised additive models (GAMs) were run using the full-subsets modelling approach (Fisher et al., 2018) to fit models of all possible variable combinations and to explore the relative importance of each covariate. The model, which included all six covariates, was fit using the '*mgcv*' R package (Wood & Wood, 2015). Prior to model fitting, covariates were scaled and log-transformed to reduce skew and achieve normality. Variables were subsequently back-transformed for visualisation purposes. To account for data overdispersion, we fit the GAMs with a negative binomial

distribution and log link function. We used the effective degrees of freedom (edf), a summary statistic estimated from GAMs, to preliminarily detect which covariates exhibited strong, nonlinear relationships with hybrid richness (Hunsicker et al., 2016; Wood, 2006). An edf = 1 is synonymous with a linear relationship, an edf > 1 and ≤ 2 is weakly nonlinear, and an edf > 2 indicates a highly nonlinear relationship (Hunsicker et al., 2016; Zuur et al., 2009). Smoothing functions were fit with a cubic regression spline, restricted to $k = 4$, and were only applied to covariates with an edf > 2 to reduce overfitting and ensure ecological interpretability of the models. Only phylogenetic distance exhibited a highly nonlinear relationship (i.e., edf > 2) with hybrid richness; therefore, all other variables were incorporated into the model as linear predictors.

Candidate model sets were subsequently constructed using the '*FSSgam*' R package (Fisher et al., 2018) and compared using Akaike's information criterion for small sample size (AICc) and AICc weight values (wAICc) (Burnham & Anderson, 2004). The relative importance scores for each covariate were calculated by summing wAICc values across all candidate models containing the variable, with higher scores representing increased predictor importance to the response variable (Burnham & Anderson, 2002; Fisher et al., 2018). Although all predictors were examined, only models with up to five predictor variables were included in any single candidate model to improve the ecological interpretability of our models. Models containing predictors with correlation coefficients (r) ≥ .28 were excluded from the candidate set to prevent collinearity issues among predictor variables (Fisher et al., 2018; Graham, 2003).

We refit the top model from the full-subsets approach (Supporting Information Table S3) for Bayesian inference using the '*brms*' R package (Bürkner, 2021). The GAM incorporated weakly informative priors for the population-level effects and a gamma prior for the estimates of shape. We fit the model with three chains of 15,000 iterations each, including a 7,500 warmup and a thinning rate of 10. Convergence was assessed using the $\hat{R}$ statistic and a visual inspection of trace plots. We found that the chains were well mixed and converged on a stable posterior and that the draws showed no evidence of autocorrelation. The model was validated using '*DHARMa*' residuals (Hartig, 2021) and posterior probability checks. All analyses were conducted within the R 4.1.3 (R Core Team, 2022) Statistical and Graphical Environment.

3 | RESULTS

3.1 | Taxonomic prevalence

We report a total of 143 unique interspecific hybrids involving 17 families, 45 genera and 204 species (Figure 2), with only five (3.5%) of them being intergeneric. Intergeneric hybridisation was observed in three families – Labridae, Lutjanidae and Serranidae. These hybrid reports originated from 101 references published between 1956 and
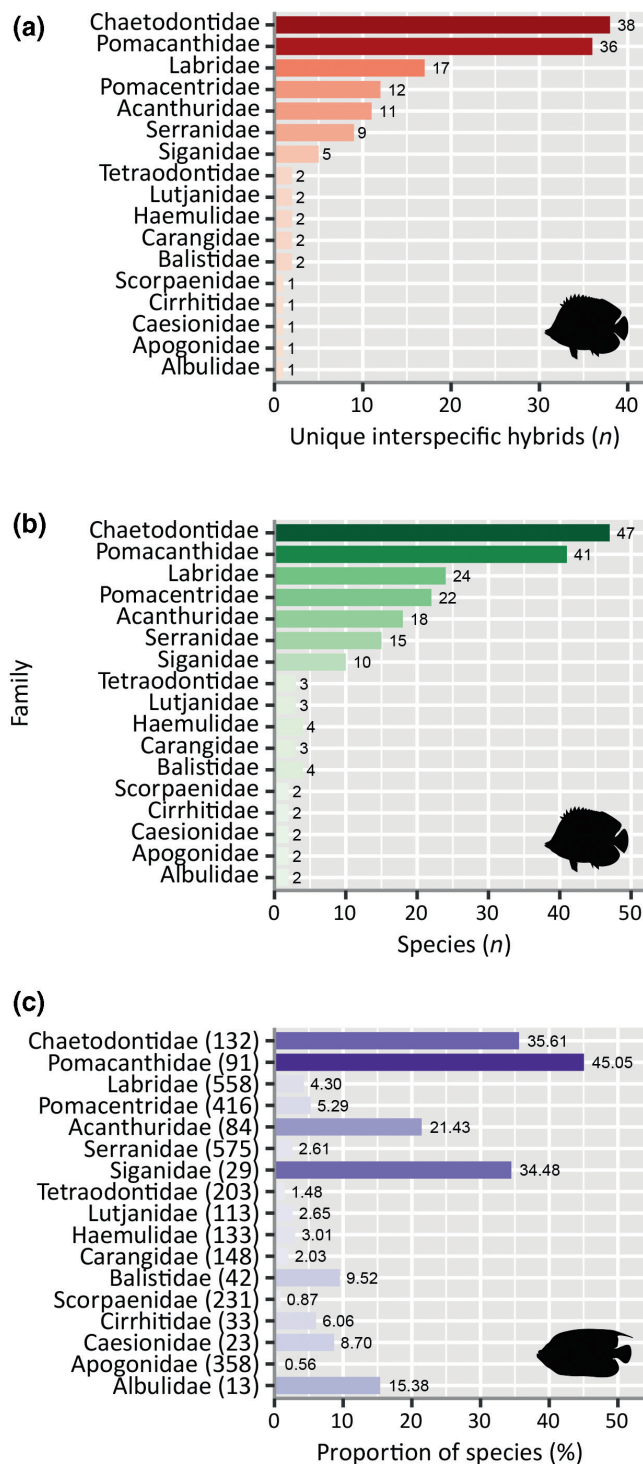
FIGURE 2 (a) The number of unique interspecific hybrids per coral reef fish family, (b) the number of species found to hybridise per family out of 204 species in total, (c) the proportion of species per family involved in hybridisation. The total number of species in each family was obtained from FishBase (Froese & Pauly, 2022) and is shown in parentheses next to each family name in (c). Fish silhouettes were sourced from 'fishualize' (Schiettekatte et al., 2022) and represent the coral reef fish family with the highest count or proportion

2021 (Appendix 1; Supporting Information Table S1). Of the 2,488 reef-associated species in the coral reef fish consensus list families, about 7% (175/2488) are involved in interspecific hybridisation.

The Chaetodontidae and Pomacanthidae have the most repeated interspecific hybrids (Figure 2a) and represent over half (74/143) of the total number of unique interspecific hybrids. Additionally, of the 204 coral reef fish species involved in hybridisation, over 40% (88/204) belong to these two families (Figure 2b). The families with the greatest proportion of species reported to hybridise are the Pomacanthidae, Chaetodontidae and Siganidae (Figure 2c). Only five families – Pomacanthidae, Chaetodontidae, Siganidae, Acanthuridae and Albulidae – have more than 15% of species hybridising per family (Figure 2c).

The species most frequently reported to hybridise ($n \geq 13$) were *Acanthurus nigricans*, *Centropyge vrolikii* and *Centropyge flavissima* (Figure 1) – all of which belong to species complexes (i.e., a group of organisms with uncertain species boundaries). The most widely reported (i.e., the highest number of reported locations, not ecoregions) hybrid crosses were *C. flavissima* × *C. vrolikii* ($n = 11$) (Figure 1b), *Acanthurus achilles* × *A. nigricans* ($n = 8$) (Figure 1a) and *Holacanthus bermudensis* × *Holacanthus ciliaris* ($n = 8$). The majority (87/143) of the unique interspecific hybrids were only reported in a single location.

3.2 | Geographic distribution

Coral reef fish hybrids are found in many locations around the globe, with a total of 229 interspecific hybrids spanning 65 of the 112 tropical ecoregions (Figure 3; Supporting Information Table S2). The four most hybrid-rich zones are the Christmas–Cocos Islands ($n = 19$), Hawaii ($n = 15$), South Kuroshio ($n = 14$) and Eastern Philippines ($n = 13$) (Figure 3). The remaining 61 ecoregions contain ≤9 unique interspecific hybrids each (Figure 3; Supporting Information Table S2).

3.3 | Modelling summary

The top model (i.e., the model with the highest predictive power as selected by AICc) consisted of (a) current velocity, (b) geographic isolation, (c) phylogenetic distance, and (d) biogeographic barriers (Supporting Information Table S3). The second top model contained all the same variables except for biogeographic barriers (Supporting Information Table S3). Both models were equivalent to one another (Supporting Information Table S3), suggesting that the inclusion of biogeographic barriers does not significantly improve the model. The top model was able to explain a fair amount of variability [34% median; 18–48% credible interval (CI)] in the richness of coral reef fish hybrids. Among all variables tested, current velocity was the most important variable, followed by phylogenetic distance and geographic isolation (Figure 4a). Both current velocity (mean estimate = .46; 95% CI = .24 to .70) and geographic isolation (mean estimate = .24; 95% CI = .05 to .44) exhibited a strong positive effect on hybrid richness (Figure 4). Phylogenetic distance, the only covariate fit with a smoother,
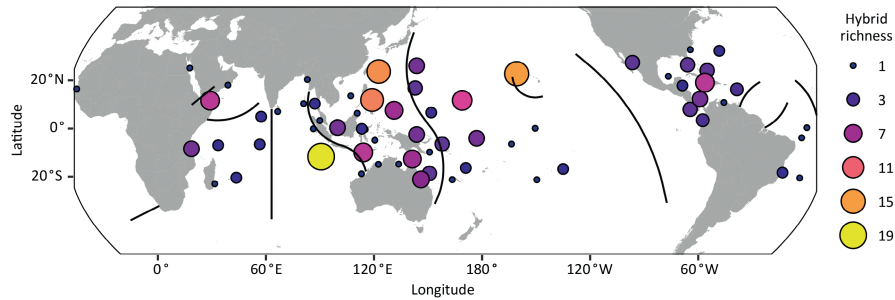
FIGURE 3 The global distribution of hybrid richness (i.e., the number of unique interspecific hybrids) per tropical ecoregion (*n* = 65) with biogeographic barriers (black lines) (details in Table 1). Size and colour of the circles directly correspond to the number of unique interspecific hybrids per ecoregion. World map projection – Robinson projection
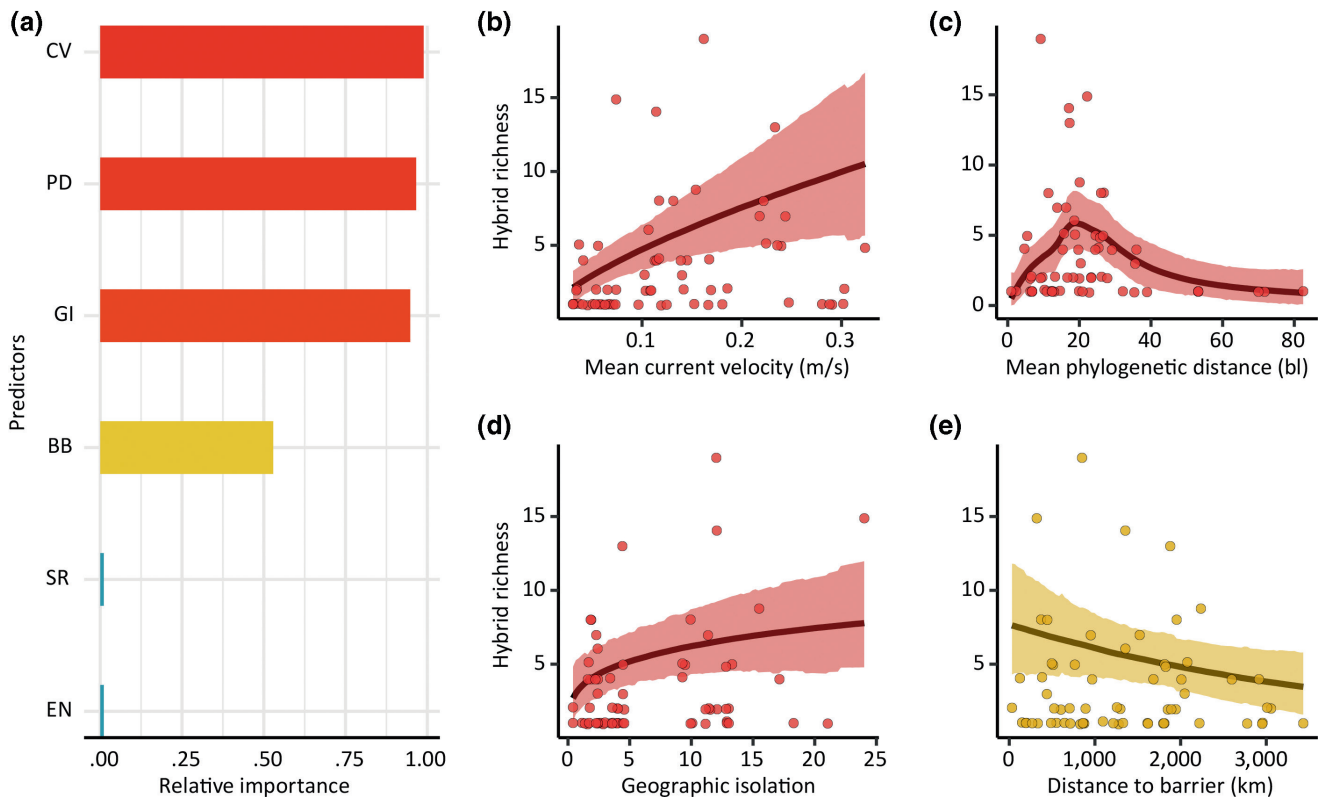

FIGURE 4 (a) Relative importance scores from the full-subsets modelling exploring the influence of six variables: mean surface current velocity (CV), mean phylogenetic distance between hybrid parent species (PD), geographic isolation (GI), distance to biogeographic barriers (BB), mean species richness (SR) and endemism (EN), on hybrid richness. Scores represent summed Akaike's information criterion for small sample size (AICc) weights across the candidate model set. Relationship between hybrid richness and the top model covariates: (b) mean surface current velocity, (c) mean phylogenetic distance between hybrid parent species, (d) geographic isolation and (e) distance to biogeographic barriers; solid lines represent Bayesian mean posterior estimates and shaded regions represent 95% credible intervals

exhibited significant 'wiggliness', suggesting a nonlinear relationship with hybrid richness (Supporting Information Table S4). For phylogenetic distance, hybrid richness increases from 0 to about 20 branch lengths of distance, although with high variability, but drops steadily after reaching a peak at about 20 branch lengths (Figure 4c). This suggests that hybridisation is more likely where parent species are *relatively* closely related, when compared to places with extremely closely or more distantly related species pairs. The distribution of phylogenetic distances between hybrids per ecoregion was indeed significantly smaller compared to null

mean phylogenetic distances per family for species occurring in each ecoregion (Supporting Information Figure S3). Although biogeographic barriers exhibited a negative effect on hybrid richness (mean estimate = −.20; 95% CI = −.44 to .02), the coefficient CI overlaps with zero, suggesting a potentially weaker effect. In addition, biogeographic barriers had the lowest relative importance among all covariates in the top model (Figure 4a). Endemism and species richness were found to be poor predictors and are unlikely to influence hybrid richness (Figure 4a). Overall, our results did not change (Supporting Information Tables S3 and S5; Figure 4 and

Supporting Information Figure S4) regardless of how species richness or endemism was measured (see Methods).

4 | DISCUSSION

4.1 | What is the taxonomic prevalence and geographic distribution of coral reef fish hybrids on a global scale?

Coral reef fishes commonly hybridise, with approximately 7% of species involved in interbreeding, which closely aligns with other terrestrial animal species (10%; Mallet, 2005). Coral reef fish hybrids are also found across the globe, although some ecoregions – namely the Christmas–Cocos Islands, South Japan, Hawaii and Eastern Philippines – stand out as hybrid-rich zones, in alignment with patterns found in Hobbs et al. (2021). Disparities in taxonomic representation of coral reef fish families, however, are evident. Highly species rich families such as the Blenniidae and Gobiidae exhibit no evidence of hybridisation, while less species rich families such as the Chaetodontidae and Pomacanthidae have the most unique interspecific hybrids and numbers of species involved in hybridisation. Detection bias is the most likely explanation for these results (Montanari et al., 2016), with species in both the Chaetodontidae and Pomacanthidae exhibiting bright colours and striking patterns (Figure 1), while blennies and gobies are often small-bodied and cryptic, and thus, easily overlooked (Brandl et al., 2018). The same taxonomic bias is prevalent in terrestrial examples such as in birds of paradise and butterfly groups such as *Heliconius* (Mallet, 2005). Despite substantial development in genetic tools, hybridisation is almost always initially detected using intermediate phenotypes usually based on colours (Figure 1), which, coupled with our taxonomic bias, likely leads to an underestimation in the number of species involved in hybridisation. Despite this sampling bias, hybridisation in coral reef fish appears to be taxonomically widespread and occurs within some of the most species rich families (e.g., Serranidae, Labridae, Pomacentridae, Apogonidae, Scorpaenidae and Tetraodontidae; Froese & Pauly, 2022).

4.2 | What factors are associated with hybrid-rich zones?

4.2.1 | Currents

Oceanic currents, phylogenetic relatedness, and geographic isolation were the only factors that we found to strongly inform patterns of hybrid richness. The inclusion of oceanic currents as one of the three explanatory factors was most unexpected. Currents has only been suggested as a potential mechanism carrying larvae from adjacent areas into hybrid-rich zones by DiBattista et al. (2015) and Salas et al. (2020), but it was never tested. Based on our observations and surface water oceanography, we propose a larval dispersal

model whereby strong currents may transport and trap vagrant coral reef fishes over long distances to specific regions (Figure 5). This potential pathway begins with the North Equatorial Current (NEC), which hits the eastern coast of the Philippines and bifurcates north and south, forming the Kuroshio Current (KC) and Mindanao Current (MC), respectively (Figure 5; Toole et al., 1990).

The MC, Indonesian Throughflow (ITF) and South Equatorial Current (SEC) have the potential to disperse Pacific Ocean larvae to isolated islands of the Indian Ocean such as the Christmas–Cocos Islands. One of the suggested larval dispersal pathways for the ornate spiny lobster, *Panulirus ornatus*, for example, has been described to begin in the east coast of the Philippines, travel through the MC and ITF, out of the Lombok Strait and into the Indian Ocean (Dao et al., 2015). A similar pattern may be occurring for coral reef fish larvae. Salas et al. (2020) proposed that the SEC and the ITF may bring Pacific Ocean *Dascyllus trimaculatus* larvae to the Christmas Islands, resulting in a cross between genetically distinct Pacific and Indian Ocean lineages of the species. The semi-annually reversing South Java Current may also carry Indian Ocean larvae to the Christmas–Cocos Islands through the SEC (Sprintall et al., 1999).

The warm KC has been described as a transport system, carrying tropical fishes from the Philippines and Taiwan to Japan (Kuriiwa et al., 2014). As one of the world's major ocean currents, with the potential of reaching mean maximum daily surface velocities of about 1.2 m/s (Yang et al., 2015), it may have the capacity to reach the Hawaiian Islands through the Kuroshio extension of the North Pacific Current (Hourigan & Reese, 1987) and follow onto the NEC. This pattern of dispersal has been supported by the presence of West Pacific fishes (e.g., *Centropyge interrupta* and *Myripristis murdan* – Pyle, 1999; Mundy, 2005) and limpets (e.g., *Cellana* spp. – Bird et al., 2011) in the north-western Hawaiian Islands. Colonisation into the Hawaiian Islands and Johnston Atoll is more likely to come from the nearest reef habitats in the Northern Line Islands (Wood et al., 2014), where multiple vagrants have been hypothesised to arrive from (Gosline, 1955; Lobel et al., 2020; Randall, 2007). Colonisation pathways into Hawaii from both the West and South Pacific, however, cannot be excluded (Craig et al., 2010).

While currents can promote larval dispersal, they can also act as barriers to dispersal. Highly turbid and fast-moving currents from the Ganges and Indus River systems, for instance, formed the Mid-Indian Ocean Barrier, resulting in genetically distinct populations on each side (Hodge & Bellwood, 2016). Currents, in effect, may trap hybrid-rich zones by impeding larval connectivity and causing isolation between populations. There are also interesting terrestrial parallels. Hewitt (1996) suggested that a hybrid zone could represent stable and long-lived areas of low density or dispersal. For example, for over 25 years, the size and position of *Heliconius* butterfly hybrid zones in the Amazon basin remained stable while located in a region with remarkably high precipitation rates. Rosser et al. (2014) hypothesised that it was in fact the high rainfall that trapped hybrid zones at the base of the Andes mountains, preventing movement of butterflies – in a manner similar to marine currents trapping species on an island. It appears that in both terrestrial and marine habitats,
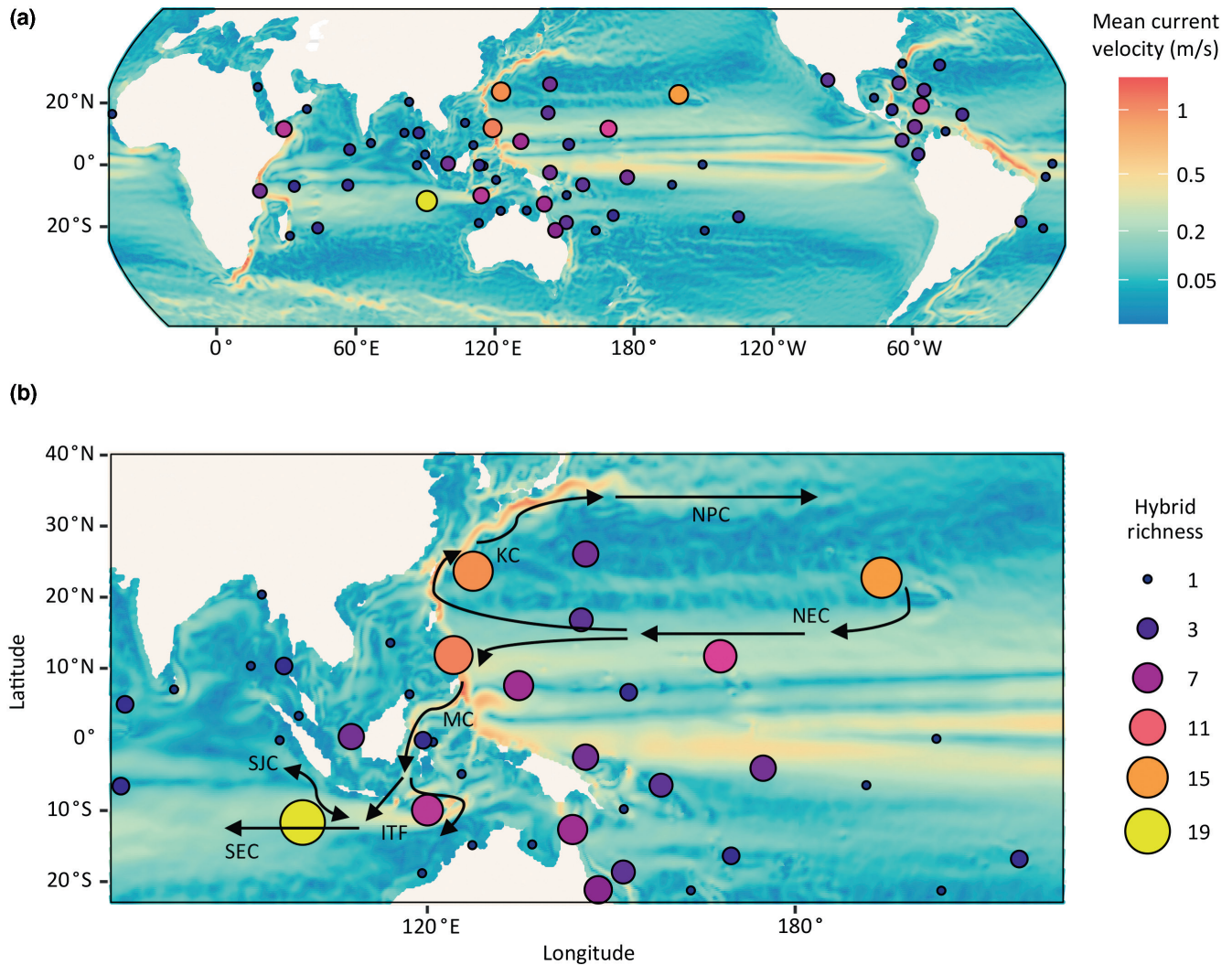
FIGURE 5 (a) The global distribution of hybrid richness in relation to mean surface current velocity (m/s); (b) the hypothesised current pathway dispersing stray coral reef fish to hybrid-rich zones. The North Equatorial Current (NEC) bifurcates north and south at the east coast of the Philippines into both the Kuroshio Current (KC) and the Mindanao Current (MC) (Toole et al., 1990). The KC carries larvae and adults from the Philippines to Japan (Kuriiwa et al., 2014) and can extend its flow to the Hawaiian Islands through the North Pacific Current (NPC), subsequently looping back into the NEC (Hourigan & Reese, 1987). The MC, on the other hand, flows into the Indonesian Throughflow (ITF), which carries Pacific Ocean larvae into the Indian Ocean (Bray et al., 1996) with the potential of reaching the Christmas–Cocos Islands due to the pull of the South Equatorial Current (SEC). Indian Ocean larvae have the potential of reaching the Christmas–Cocos Islands through the South Java Current (SJC). Size and colour of circles directly correspond to the number of unique interspecific hybrids per ecoregion. World map projection – Robinson projection

climatic or environmental factors may shape the position and stability of hybrid-rich zones.

4.2.2 | Isolation

Our results provide support that hybrid richness is also driven by increased geographic remoteness. It is likely that rare, long distance dispersal events shape isolated hybrid-rich zones such as those on the Hawaiian, Christmas and Cocos (Keeling) Islands. For example, *Abudefduf abdominalis* and the invasive *Abudefduf vaigiensis* were transported to the highly remote Johnston Atoll likely through the Northern Line Islands (Lobel et al., 2020). These species now

commonly hybridise in Hawaii (Coleman et al., 2014). This mechanism could also work counterintuitively. Geographically isolated regions may act as sources rather than sinks of larvae, as demonstrated by asymmetric larval export from Hawaii to the West Pacific in *Zebrasoma flavescens* (Eble et al., 2011) and *Scarus rubroviolaceus* (Fitzpatrick et al., 2011). This could help explain patterns of high hybrid richness observed in West Pacific regions such as South Japan and Eastern Philippines (Figures 3 and 5). Overall, the strength and direction of major current systems coupled with the dispersive and long pelagic larval duration of most marine taxa, appear to underpin hybrid-rich zones. In effect, these currents have the potential to 'spray' vagrants to far flung locations where conspecifics may be rare, thereby enhancing the chances for hybridisation.

4.2.3 | Phylogenetic distance

We also found evidence to suggest that phylogenetic distance influences hybrid richness. Specifically, higher hybrid richness was found between species that share a moderately close phylogenetic distance. This is consistent with existing literature. Generally, hybridisation occurs most frequently among closely related species such as incipient species (i.e., those undergoing speciation) or sister taxa (Mallet, 2005). For example, of the 15 hybrid pairs found in the Christmas–Cocos Islands by Hobbs and Allen (2014), nine crosses represented hybridisation between Indian and Pacific Ocean sister species. While hybridisation has been described between distantly related species (Carlon et al., 2021; Tea et al., 2020), there is still a broad agreement that limited genetic distance and potential for heterospecific mating are strongly intertwined. Closely related taxa are more likely to share biological, ecological and behavioural traits, which can increase the probability of interbreeding and production of fertile offspring (Montanari et al., 2014). Furthermore, hybrid viability and fertility are likely to decline with greater evolutionary divergence because of genetic incompatibilities (Abbott et al., 2013). This is supported by laboratory hybridisation experiments, where pre- and post-mating compatibility are negatively correlated with genetic distance and thus time since species divergence (Mallet, 2005). In terrestrial and freshwater systems, divergences in mitochondrial DNA (mtDNA) are generally below 2% for hybridising species (Mallet, 2005). In marine hybrid pairs, mtDNA divergences between species generally range between 2 and 6% (Coleman et al., 2014; DiBattista et al., 2012; DiBattista, Whitney, et al., 2016). Our findings therefore support the hypothesis that heterospecific mating between closely related coral reef fish species is likely the dominant form of hybridisation.

Interestingly, our results exhibit a significant nonlinear pattern between phylogenetic and hybrid richness. Hybrid richness is low when phylogenetic distance is both below and above the peak (Figure 4c). Crosses between very closely related parents may not be detected as hybrids due to a masking effect from introgression and species that are too distantly related are likely to encounter genetic incompatibilities resulting in unsuccessful hybridisation.

4.3 | Future research

A more balanced research effort to include species rich families such as the Blenniidae and Gobiidae is needed to counter the apparent taxonomic bias in the literature. This would allow a more accurate representation of hybrid-rich zones among coral reef fishes. Additionally, most researchers have suggested that disparities in parental abundances (i.e., rarity of a species due to low local population density; Rabinowitz, 1981) promote the chances of interbreeding. However, a lack of data on species-specific coral reef fish abundances at key locations where hybrids are found precluded our ability to include this predictor in our model. To discern whether species rarity is indeed a critical factor in hybrid-rich zones may require more geographically focused research.

5 | CONCLUSIONS

Hybridisation in coral reef fishes is a common, global, phenomenon, although some regions such as the Christmas–Cocos Islands do demonstrate higher hybrid richness relative to other areas. The presence of these hybrid-rich zones suggests that certain regional factors may provide favourable conditions for hybridisation. We found that surface current velocities, phylogenetic distance, and geographic isolation are strongly associated with hybrid-rich regions, whereas variables such as biogeographic barriers, endemism, and species richness were not. The level of phylogenetic relatedness may be a pre-condition for hybridisation to occur, while surface current strength and isolation may create the environmental context of larval dispersal to geographically distant regions, that promote the formation of hybrid-rich zones.

CONFLICT OF INTEREST

We all give consent for publication and declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The datasets generated and analysed during this study are available on Research Data James Cook University (https://doi.org/10.25903/zcn8-nr49). There are no restrictions on data availability. Publicly available datasets for predictor data used in this study are outlined in Table 1 and the hybrid data table is in Supporting Information Table S1 with references located in both Supporting Information Table S1 and the Appendix 1.

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SUPPORTING INFORMATION

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

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APPENDIX 1

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