

Prioritizing phylogenetic diversity to protect functional diversity of reef corals

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Abstract

Aim: The ecosystem functions and services of coral reefs are critical for coastal communities worldwide. Due to conservation resource limitation, species need to be prioritized to protect desirable properties of biodiversity, such as functional diversity (FD), which has been associated with greater ecosystem functioning but is difficult to quantify directly. Selecting species to maximize phylogenetic diversity (PD) has been shown to indirectly capture FD in certain other taxa but not corals. Here, we test this hypothesis, the “phylogenetic gambit”, on corals within global marine protected areas (MPAs).

Location: Global coral reefs.

Methods: Based on the global distributions of reef corals, a complete species-level phylogeny and trait data, we compared the FD of coral assemblages within MPAs when selected to maximize PD versus FD for assemblages selected randomly. The relationships between PD and FD were also tested as predictors of surrogacy. We then used coral FD and PD to perform spatial prioritization of reefs for protection and assessed the congruence between the two approaches.

Results: Selecting assemblages to maximize PD captured significantly more FD than a random subset of species for 83.1% of all selection scenarios across MPAs and would protect on average 18.7% more FD than random selection. Spatial prioritization analyses showed some mismatches between PD- and FD-optimized planning units, particularly in the Tropical Western Atlantic, but the high degree of overlap between the optimizations for other reef regions lends further credence to the PD-maximizing strategy in conserving coral FD.

Main Conclusions: A PD-maximizing strategy generally protects greater FD of coral assemblages relative to random selection of species, suggesting that the “phylogenetic gambit” is valid for reef corals. There are risks, however, and the mismatches between PD-maximized and FD-maximized MPA networks highlight specific shortcomings of the PD-maximization approach. Nevertheless, in data-deficient circumstances, maximizing PD may provide a viable alternative.

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KEYWORDS

biogeography, conservation prioritization, coral reefs, ecosystem functioning, evolutionary diversity, functional traits, marine protected areas, Scleractinia

1 | INTRODUCTION

Biodiversity loss threatens the functioning of ecosystem processes that depend upon the persistence of species assemblages and the functions they provide (Díaz & Cabido, 2001; Díaz et al., 2007; McGill et al., 2006; Tilman et al., 1997). Species contribute unequally to ecosystem functioning and drive ecosystem properties more variably than can be predicted by species richness alone (Maureaud et al., 2019; Tilman et al., 1997; Wardle et al., 1997). These contributions are underlain by the diversity of functional traits exhibited by species in a community (Díaz & Cabido, 2001; Tilman et al., 1997). The functional diversity (FD) of a community—quantified by the range of trait states and values represented in the community—has been linked to higher ecosystem functioning, and the potential value of the ecosystem services provisioned (Díaz et al., 2007; Funk et al., 2017; Lavorel & Garnier, 2002; Tilman et al., 1997; Violle et al., 2007; but see van der Plas et al., 2020). To preserve the wide-ranging natural benefits of biodiversity (Tucker et al., 2019), conservation research has increasingly been focussed on understanding and measuring species traits with the objective of preserving FD (Barnosky et al., 2011; Cadotte et al., 2011; Isbell et al., 2017; Mouillot et al., 2014; Vane-Wright et al., 1991).

Given that conservation resources are generally limited, it is becoming apparent that even within protected areas, not all species can be effectively conserved, necessitating that we prioritize among them. A wide range of criteria have been proposed and applied for species' prioritization, including threat levels, genetic diversity, cultural importance and potential contributions to ecosystem function (Bottrill et al., 2008; Vane-Wright et al., 1991). FD is often used as a proxy and maximized to retain the greatest diversity of traits within an assemblage (Mazel et al., 2018; Tilman et al., 1997). Higher assemblage FD may also preserve the evolutionary potential of the participating clades, as greater variability of traits would generally result in more stable communities and thus less local extinction (Faith, 1992; Tucker et al., 2019; Walsworth et al., 2019; Winter et al., 2013). However, owing to our limited understanding of the relative importance of traits in various contexts (Cadotte et al., 2011; Díaz et al., 2013), and how FD varies spatially and between clades, directly computing FD might not always be feasible (Etard et al., 2020; Madin, Hoogenboom, et al., 2016; Májeková et al., 2016; Mazel et al., 2018; Pakeman, 2014).

These challenges have since prompted some to view phylogenetic diversity (PD)—computed as the sum of all branch lengths from a common root (Faith, 1992), specifically PD_F —as a proxy for FD (reviewed in Tucker et al., 2019). Maximizing PD as a conservation strategy has been advocated widely (Cadotte, 2013; Daru et al., 2019; Forest et al., 2007; Mooers et al., 2005; Pollock et al., 2017; Thuiller et al., 2015) and has formed the basis for conservation initiatives

such as the EDGE (Evolutionarily Distinct and Globally Endangered) of Existence programme (Isaac et al., 2007). The International Union for the Conservation of Nature (IUCN) has also embraced the use of PD as a metric to inform conservation (IUCN, 2019), particularly for identifying evolutionarily significant assemblages and ecosystems (IUCN, 2016; Keith et al., 2015). The emphasis on PD follows the hypothesis that trait similarities reflect evolutionary relatedness among species. Additionally, PD is favoured as a biodiversity measure because of the relative ease of attaining the necessary data, often in the form of a DNA-based phylogeny, to compute it.

The supposed relationship between PD and total FD has led to the hypothesis that maximizing PD would also maximize the diversity of form and function (Cadotte et al., 2008; Faith, 1992; Mazel et al., 2018; Winter et al., 2013), implying that PD could be an efficient criterion for conserving FD without having to quantify species traits. This approach has been dubbed the “phylogenetic gambit” by Mazel et al. (2018), which refer to the use of PD as a surrogate for trait diversity where information is scant or unavailable (Bottrill et al., 2008; Mouillot et al., 2014; Vane-Wright et al., 1991). To assess the effectiveness of the “phylogenetic gambit”, Mazel et al. (2018) quantified the strength of maximizing PD of an assemblage as a surrogate for maximizing FD in mammals, birds and tropical reef fishes with the following metric:

$$S_{PD-FD} = \frac{\text{maxPD} - \text{randomFD}}{\text{maxFD} - \text{randomFD}}$$

where maxPD represents the FD of a PD-maximized assemblage, maxFD is the FD of a FD-maximized assemblage and randomFD is the FD of randomly sampled species, all from the same species pool and of the same richness. While Mazel et al. (2018) found that in the majority (88%) of selection scenarios, PD did capture more known FD than would be expected whether species assemblages were randomly selected and variation in outcomes was high. In the worst-case scenario, maximizing PD performed up to 85% worse than random selection, suggesting that a PD-maximizing strategy could be detrimental toward achieving conservation outcomes in some instances (Mazel et al., 2018). Nevertheless, the conservation of understudied ecosystems containing taxa whose traits are mostly uncharacterized could benefit from a PD-maximizing strategy.

Reef corals of the order Scleractinia constitute one such group that could benefit from a PD-maximizing strategy if the conservation objective is to maximize FD of coral reefs. Amidst elevated threats to reefs and limited resources, it is possible that only a subset of reef corals within an assemblage may be conserved or restored (Carpenter et al., 2008; Huang, 2012; Huang & Roy, 2015). Selecting species in a way that maximizes FD may be the best way to preserve the ecosystem function of reefs (Bellwood et al., 2004; Darling et al., 2012, 2013). Indeed and importantly,

preserving coral FD has been shown to improve the resilience of reefs against climate change (Walsworth et al., 2019). While generating complete data on coral species to directly maximize FD is certainly possible, it would require considerable research effort. Given the urgency to prioritize species facing increasing levels of threat (Bellwood et al., 2004; Walsworth et al., 2019), were the “phylogenetic gambit” be valid for corals, maximizing PD would be a viable conservation strategy.

The conservation of coastal and marine ecosystems has been identified as one of the targets of the United Nations (UN) Sustainable Development Goal (SDG) 14, “Life below water” (United Nations, 2015). As of 2019, 17% of coastal and marine areas under national jurisdiction has been accorded some degree of protection, exceeding the target of protecting 10% of coastal waters by 2020 (United Nations, 2020). However, it has been suggested that despite the extensive coverage of marine protected areas (MPAs), the global MPA network is not adequately protecting marine biodiversity (Agardy et al., 2011; Daru & le Roux, 2016; Hargreaves-Allen et al., 2011). Relatedly, efficiency is an important factor to consider in conservation planning (Possingham et al., 2006). The use of proxy variables as biodiversity indicators may prove simpler and more cost-effective than collecting extensive data on species and communities (Caro, 2010; Svitok et al., 2018). If areas with higher PD are found to also have relatively high measured FD, key areas to be chosen as MPAs can be identified by a PD-maximization strategy, i.e. using only data on species identity and phylogeny.

Therefore, our aims in this study are to (1) assess the efficacy of a strategy that prioritizes coral assemblages based on PD, with the goal of maximizing coral FD within reefs bounded by MPAs and (2) investigate the spatial patterns of such a PD-maximizing strategy on conserving FD and how S_{PD-FD} might be associated with the spatial overlap between PD and FD of corals. Specifically, we assessed the relative gains in FD by maximizing PD (S_{PD-FD}) as opposed to directly optimizing FD for the purposes of marine conservation. To investigate this, the performance of PD as a surrogate for FD was measured against directly maximizing FD as an upper-limit and random species selection as the lower limit for subsets of varying proportions of species richness. We then carried out a spatial prioritization procedure to optimize the global MPA network based on the objectives of maximizing local FD in one set of scenarios and maximizing local PD in another set, subject to other constraints including fishing volume as a proxy of opportunity cost, habitat connectivity, and exposure to anthropogenic threats. We perceive the mismatches between PD-maximized and FD-maximized networks to be examples highlighting shortcomings of the PD-maximizing strategy. Furthermore, while it would be expected that areas with higher S_{PD-FD} would have fewer mismatches, there are exceptions that can help inform MPA planning to better capture coral FD. More generally, until complete species trait data are available, particularly for data-deficient regions, it is important to determine whether maximizing PD is an efficient measure for coral conservation.

2 | METHODS

2.1 | Species distributions across MPAs

Spatial analyses were performed with QGIS v3.16.2 (QGIS Development Team, 2020), and computation and statistical analyses were performed with R v4.0.2 (R Core Team, 2020). Spatial information on protected areas was collected from the World Database on Protected Areas (WDPA; UNEP-WCMC & IUCN, 2020). This dataset was subsequently trimmed by excluding areas on land and those which did not include a coastal habitat—defined as those found outside of the continental shelf, i.e. >200-m depth (Lucieer et al., 2019) and beyond the deepest reef corals (Rouzé et al., 2021). This yielded a database of MPAs ($n = 3625$; area = 942,568 km²), which were then overlaid with the distributions of 805 coral species derived from Mouillot et al. (2016) to obtain presence/absence data within protected coral reefs. The dataset was further trimmed to include only those MPAs that contained at least five species of scleractinian corals for which data for at least four traits of interest were available (see below), resulting in a final dataset of 215 MPAs covering 159,851 km². Species distribution data across 141 reef ecoregions defined by the Coral Geographic Database (Veron et al., 2009, 2011) were also compiled.

2.2 | Phylogenetic and trait data

Phylogenetic data used for the computation of PD were based on a published set of 1000 Bayesian supertrees containing 805 reef coral species obtained from Huang and Roy (2015) and Mouillot et al. (2016). All analyses that required PD to be quantified were repeated across all 1000 supertrees to account for phylogenetic uncertainty. PD_F (Faith, 1992) was computed using the R package ‘picante’ (Kembel et al., 2010) for all the species within each MPA and ecoregion with each supertree. The difference between the PD_F of an MPA or ecoregion and PD_F of a random assemblage of species as a proportion of the PD_F within said MPA or ecoregion was computed as PD_{excess} , a richness-independent measure. Because the random assemblages were drawn from the global species pool, PD_{excess} would generally be negative since actual communities tended to be more phylogenetically clustered than random assemblages with the same richness (Huang & Roy, 2015).

Trait data were obtained from the Coral Trait Database compiled by Madin, Anderson, et al. (2016). Eight traits were chosen for analysis representing the major trait categories of morphology, biomechanics, physiology and reproduction, all of which are known to be crucial for explaining phenotypic variation in reef corals (Darling et al., 2012, 2013; Hartmann et al., 2017; Madin, Hoogenboom, et al., 2016; Wong et al., 2018) (Table 1). The trait data were then used to compute the functional distances between species using Gower’s dissimilarity index to summarize the trait space in fewer dimensions with principal coordinate analysis (PCoA). Sufficient PCoA axes were retained to capture 70% of total initial variability. Only 379 species with data available for at

TABLE 1 The eight traits used to characterize species function in reef corals

Trait	Description	Data type	References
Growth form	Branching, plating or domed form	Categorical	Darling et al. (2012)
Colonicity	Solitary or colonial	Categorical	Darling et al. (2012)
Colony size	Largest recorded size of colony in cm	Continuous	Darling et al. (2012)
Growth rate	Average monthly growth rate in mm month ⁻¹	Continuous	Darling et al. (2012)
Skeletal density	Average density of CaCO ₃ skeleton in g cm ⁻³	Continuous	Darling et al. (2012)
Reproductive mode	Brooding or broadcast spawning	Categorical	Hartmann et al. (2017)
Sexual system	Gonochoric or hermaphroditic	Categorical	Hartmann et al. (2017)
Symbiont transfer mode	Horizontal or vertical	Categorical	Hartmann et al. (2017)

Note: Trait data were obtained from the Coral Trait Database (Madin, Anderson, et al., 2016).

least four of the eight traits were considered. Functional diversity for each MPA and ecoregion was estimated using the index of functional richness (FRic) (Cornwell et al., 2006; Villéger et al., 2008), which measures the convex hull volume defined by the species at its vertices in the multidimensional trait space based on the PCoA (Cornwell et al., 2006). FRic was computed using the R package 'FD' (Laliberté & Legendre, 2010). Negative PCoA eigenvalues were resolved with the 'Cailliez' correction method (Gower & Legendre, 1986). FD_{excess} , the total FD within each assemblage relative to a random assemblage of species with the same species richness, was also computed for each MPA and ecoregion (analogous to PD_{excess} above; similarly, generally negative).

Linear regressions between PD_F and FRic, and between PD_{excess} and FD_{excess} were performed for assemblages in all MPAs and ecoregions. We also fitted a locally estimated scatterplot smoothing (LOESS) curve to these relationships to visualize the degrees to which they deviated from being linear.

2.3 | PD as a surrogate for FD

For each MPA, at five different proportions of total species richness (0.1, 0.3, 0.5, 0.7 and 0.9), PD was maximized for a subset of species within the MPA using the approach from Mazel et al. (2018). This was calculated by maximizing the PD for the subset of species within the MPA using the greedyMMD algorithm (see Supporting Information) and then computing the FD (as FRic) of this PD-maximized subset (see Bordewich et al., 2008). It is rare that there is a single unique subset of species that maximizes PD for a given tree (Mazel et al., 2018), and in order to account for this uncertainty, for each pool of species within an MPA, 10 replicate PD-maximizing subsets of species were generated for each proportion and each of the 1000 Bayesian supertrees. The final maxPD value represents the average of the total FRic (hereafter FD) calculated across the 10 generated sets across all 1000 supertrees.

Functional diversity maximization (based on FRic) was performed for subsets of species at five different proportions of total species richness (0.1, 0.3, 0.5, 0.7 and 0.9) within each MPA community to derive maxFD. Also based on Mazel et al. (2018), the approach iteratively selected the species in the trait space that was furthest away from

the centroid of the existing set of species to be added to the maxFD assemblage. To provide a null hypothesis against which maxPD and maxFD can be compared, we computed randomFD as the average FD of randomly sampled species within each MPA (10,000 times) at each proportion of selected species (0.1, 0.3, 0.5, 0.7 and 0.9).

For each MPA, at the proportions of species selected (0.1, 0.3, 0.5, 0.7 and 0.9), we quantified the strength of PD as a surrogate for FD using S_{PD-FD} (Mazel et al., 2018). PD would be a perfect surrogate for FD whether S_{PD-FD} has a value of one. Positive S_{PD-FD} would indicate that maximizing PD is a better strategy for conserving FD than random selection. Consequently, S_{PD-FD} of 0 would indicate that the PD-maximization scheme does not do better than randomly selecting species, and negative S_{PD-FD} would indicate that it fares more poorly than random. A two-sample t-test was also performed for each MPA at every proportion of species conserved to directly compare maxPD with randomFD.

2.4 | Spatial conservation prioritization

We performed spatial conservation planning to obtain six global MPA network scenarios that optimized local diversity—three that were PD-maximized and three that were FD-maximized—with the same area as the existing global MPA network. Our planning units (PUs) were $0.5^\circ \times 0.5^\circ$ grid cells, which were filtered for those which contained reefs (IMaRS-USF & IRD, 2005; Spalding et al., 2001; UNEP-WCMC, WorldFish Centre, WRI, & TNC, 2010). These PUs were then further filtered to include only those which were within exclusive economic zones to ensure that they fell within national jurisdiction. The resulting pool contained 3780 PUs occupying a total area of 11,262,900 km². As our focus was on reef conservation, rather than reallocating the entire 17% of marine and coastal areas that are currently designated as MPAs, only the total area of protected reefs within MPAs was considered. To determine the target area of reefs to be conserved, the PUs were overlaid on the map of MPAs (UNEP-WCMC & IUCN, 2020), with intersecting PUs summed to attain the total area of reef-containing PUs to be conserved, which was found to be 3,833,334 km² (~14% of global MPA area).

To maximize habitat connectivity and minimise exposure to anthropogenic threats, the original pool of PUs was filtered to exclude those

which did not contain either mangrove or seagrass habitat and those which contained the centroids of cities with populations exceeding 300,000. This trimmed the number of PUs to 1858 with a total area of 5,550,160 km². Proximity to mangrove or seagrass areas was included as a selection criterion as these habitats are important contributors of reef ecosystem functioning (Martin et al., 2015; Olds et al., 2013; Unsworth et al., 2008). It has been demonstrated that mangrove and seagrass habitats can enhance the performance of reserves up to 1 km away (Grober-Dunsmore et al., 2007; Martin et al., 2015). Ensuring the connectivity of protected reefs with these other habitats would thus ensure long-term reef resilience while better meeting conservation goals (Magris et al., 2017; Martin et al., 2015). The urban human population was included as a selection criterion to account for the threats of human impact (Agardy et al., 2011; Ban & Klein, 2009), following that human activity has been found to have negative implications on reef health (Mora, 2008). While studies have found that reef degradation is not necessarily correlated with local human population density (Bruno & Valdivia, 2016), urban settlements remain a potential threat to coastal habitats and challenge to MPA management (Heery et al., 2018). Spatial data for mangrove and seagrass habitats were obtained from the UNEP-WCMC (Giri et al., 2011; UNEP-WCMC & Short, 2020), and population data were obtained from the United Nations, Department of Economic and Social Affairs, Population Division (2019).

For spatial optimization, the PUs were selected by integer linear programming performed in Gurobi v9.1 (Beyer et al., 2016), constrained by fishing volume and the area of each planning unit (Table 2). For each objective of FD or PD, the selection scheme was

TABLE 2 Objectives, criteria and constraints of the optimization to select planning units (PUs) to be established as marine protected areas (MPAs)

Objective	Optimization equation
Maximize functional diversity (FD)	maximise $\sum_{i=1}^N FD_i x_i$
Maximize phylogenetic diversity (PD)	maximise $\sum_{i=1}^N PD_i x_i$
Constraint	Criterion
Fishing volume (FV)	Subject to $\sum_{i=1}^N \frac{FV_i x_i A_i}{TA} < k_z$ $z \in \{25, 50, 75\}$
Total area (TA)	Subject to $\sum_{i=1}^N A_i x_i \leq TA \text{ km}^2$

Note: FV denotes the annual fishing volume within a planning unit (PU), A denotes the area of a PU and TA denotes the total area of reef to be conserved. x_i is a binary variable that represents whether a planning unit i is selected. k represents the fishing volume in tons at the z -th percentile for $0.5^\circ \times 0.5^\circ$ grids within exclusive economic zones (EEZs). Note that PUs which did not contain either mangrove or seagrass habitat and those which contained the centroids of cities with populations exceeding 300,000 were excluded to maximize habitat connectivity and minimise exposure to anthropogenic threats, respectively.

run thrice constrained by the 75th, 50th and 25th percentiles of global fishing volume as a proxy for the opportunity cost incurred by designating a particular area as an MPA, representing the lost profits as a result of fishery restrictions (Ban & Klein, 2009; Magris et al., 2017). Global annual fishing volume data were obtained from Sea Around Us (Pauly et al., 2021).

The PD-maximizing and FD-maximizing schemes at each quartile of fishing volume were then compared to determine whether maximizing known local PD would result in the protection of similar areas as directly maximizing known local FD. Specifically, PUs were classed into four categories, (1) selected by both FD- and PD-maximizing schemes, (2) selected by only the FD-maximizing scheme, (3) selected by only the PD-maximizing scheme and (4) selected by neither scheme. The proportion of each type of PU within the 215 MPAs was then computed to test the linear relationship between S_{PD-FD} and the tendency for the PD- and FD-maximizing schemes to select differing sets of PUs within each MPA.

3 | RESULTS

3.1 | PD as a surrogate for FD

As expected from their strong correlation with species richness, PD_F and FD computed for all 215 MPAs were positively correlated ($R^2 = .8764$; $p < .001$) (Figure 1a; Table S1). However, and importantly, the excess of PD and FD for each MPA—the relative PD and FD an MPA has to a random assemblage of the same size, or PD_{excess} and FD_{excess} , respectively—were also positively correlated ($R^2 = .7112$; $p < .001$) (Figure 1b). At the ecoregion level, PD_F and FD were positively correlated ($R^2 = .8348$; $p < .001$) (Figure 1c; Table S2), and PD_{excess} and FD_{excess} had a significant but much weaker positive relationship ($R^2 = .4189$; $p < .001$) (Figure 1d), likely because of their nonlinear relationship at this scale. LOESS curves illustrated that FD and FD_{excess} reached maximum values faster than PD and PD_{excess} , respectively; species in the most diverse regions contributed more PD without concomitantly increasing convex hull volume.

Across five different proportions of species selected, we found with S_{PD-FD} that a PD-maximized assemblage of species contained 18.7% (\pm SD 26.6%) on average more FD than randomly selected species assemblages selected from the same MPA. While computed surrogacy values were generally positive, there were considerable variations among MPAs and proportions of species selected, with maxPD preserving between 34.9% less and 71.2% more FD (5th and 95th percentiles, respectively) than randomly selecting a pool of species at the same richness for all proportions conserved (Figure S1). In fact, the full range of values were between -279.8% and $+95.6\%$ relative to random (Table S3). S_{PD-FD} values were mostly positive and increased on average with more species conserved (Figure 2; Figure S1). There was no consistent relationship between S_{PD-FD} and species richness across all proportions of species richness conserved ($R^2 < .2$).

On average, maximizing PD (maxPD) consistently preserved more FD than a random selection of species (randomFD) (Figure 3).

Conserving 0.3 of species richness had the greatest proportion of MPAs (90.2%; 194 out of 215 MPAs) where maximizing PD (maxPD) conserved significantly more FD than random selection ($p < .05$). This was followed by conserving 0.1 of richness at 88.7% of MPAs, 0.9 of richness at 84.2%, 0.5 of richness at 80.5% and 0.7 of richness at 73.0%.

S_{PD-FD} differed substantially among MPAs, and values were spatially clustered, likely due to shared species pools (Figure 4). Generally, the Tropical Northwestern Atlantic, Tropical Southwestern Atlantic and the Polynesian Islands had the highest S_{PD-FD} values, followed by the Red Sea and Gulf of Aden, and the Arabian Sea and finally the Central Indo-Pacific. Negative S_{PD-FD} values were clustered around Cape Verde, Sahelian Upwelling, the Gulf of Guinea and the Tropical Eastern Pacific.

3.2 | Spatial conservation prioritization

Filtering the original pool of 3780 PUs to meet the criteria of connectivity and distance from cities yielded 1858 PUs with a total area of 5,550,160 km², on which integer linear programming was carried out to maximize PD or FD. A large majority of the selected planning units were common to both the PD- and FD-maximized networks across the three constraints based on global fishing volume (75th, 50th and

25th percentiles). At the 75th percentile, there were 1088 planning units (58.6%) that were common to both networks, with a total area of 3,231,380 km². At the 50th percentile, there were 447 planning units (24.1%) that were common to both networks, with a total area of 1,325,560 km². At the 25th percentile, there were 184 planning units (9.9%) that were common to both networks, with a total area of 544,683 km², a decrease suggesting fishing pressure was a strong driver of covariance. In both the FD- and PD-maximizing schemes, the PUs selected were largely concentrated around five marine realms—Western Indo-Pacific (Figures S2 and S3), Central Indo-Pacific (Figure S4), Temperate Australasia (Figure S5), Eastern Indo-Pacific (Figure S6) and Tropical Atlantic (Figure S7). Specifically, the most prominent clusters of selected PUs were found in the provinces and ecoregions of Tropical Northwestern Atlantic, Banda Sea, Lesser Sunda, Northeast Sulawesi, Sahul Shelf and Northeast Australian Shelf.

Mismatches in PU selection between the two maximization schemes were few and geographically distinct, as outlined in the Supporting Information (Figures S2–S7). Notably, PD-maximized PUs that were not FD-maximized were clustered in the Tropical Northwestern Atlantic, Tropical Eastern Pacific and Galapagos (Figure S7).

The PUs selected by maximizing only FD varied among the three constraining levels of global fishing volume (Figure 5a–d), while PUs selected by maximizing only PD were more similar across the

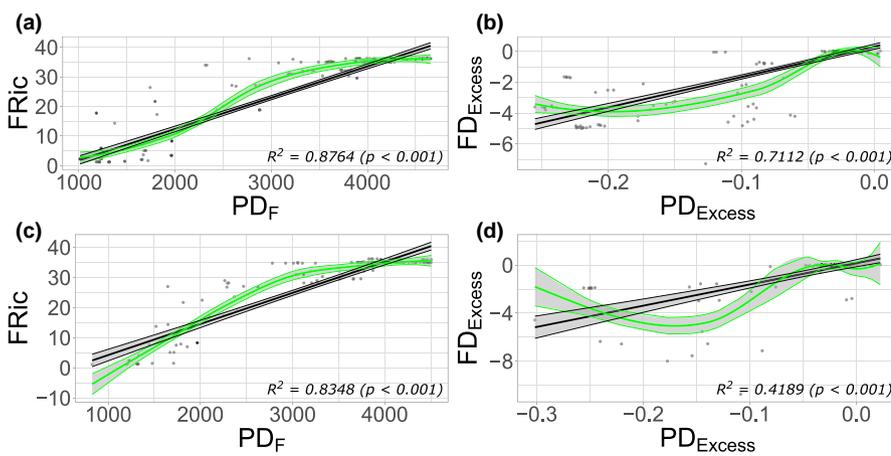


FIGURE 1 Linear regression (in black, with R^2 and p values) and locally estimated scatterplot smoothing (LOESS) curve (in green) between Faith's (1992) phylogenetic diversity (PD_F) and functional richness (FRic) as a measure of functional diversity (FD) (a, c), and between PD_{excess} and FD_{excess} (excess of PD_F and FD relative to expected values, respectively) (b, d), for assemblages within 215 marine protected areas (a, b) and 137 ecoregions (c, d)

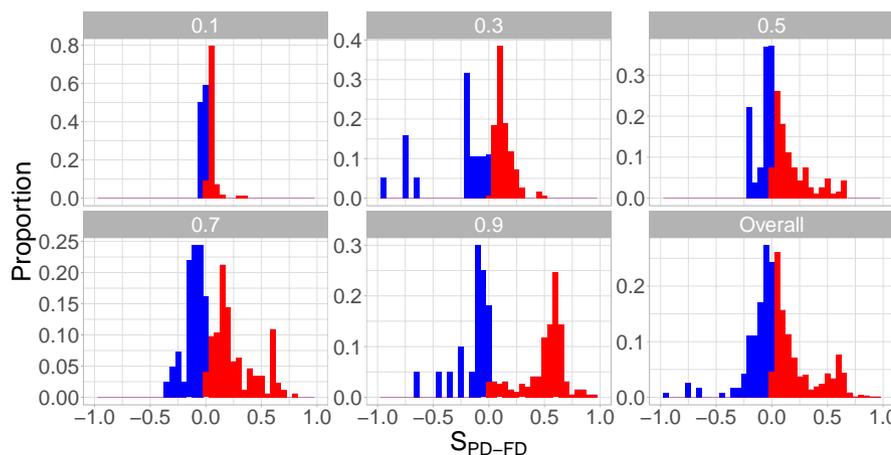


FIGURE 2 Density distributions of S_{PD-FD} , defined as the strength of the PD_F -maximizing function (maxPD) as a surrogate for directly maximizing functional diversity (FD), for conserving five different proportions of total richness (0.1, 0.3, 0.5, 0.7 and 0.9) in 215 marine protected areas. Negative S_{PD-FD} values are indicated in blue while positive S_{PD-FD} values are indicated in red

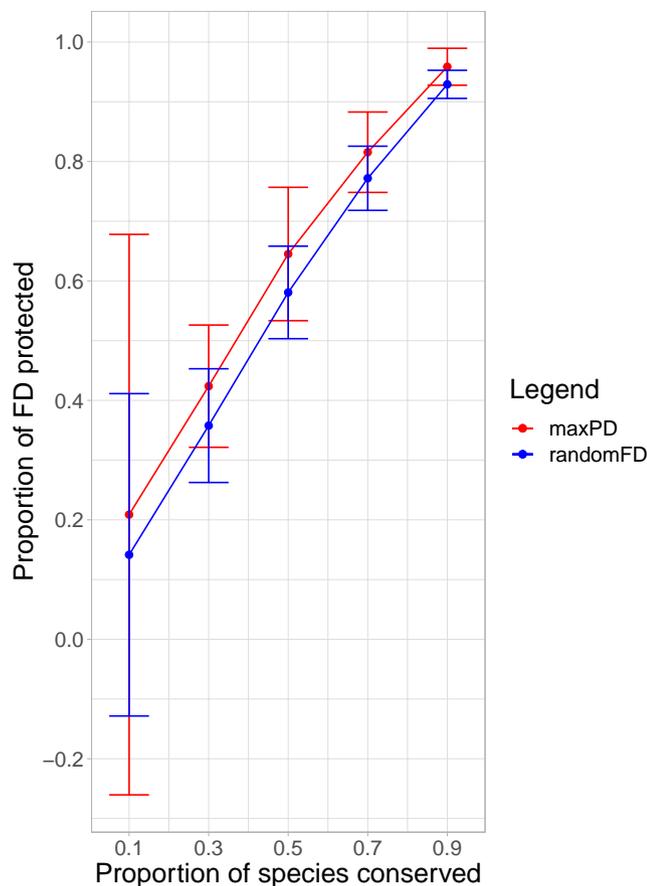


FIGURE 3 Comparing between maxPD (FD conserved through maximizing PD for a subset of species) and randomFD (FD conserved through randomly selecting a subset of species) for conserving five different proportions of total richness (0.1, 0.3, 0.5, 0.7 and 0.9) in 215 marine protected areas. Error bars represent standard deviation. FD, functional diversity; PD, phylogenetic diversity

three constraining values of fishing volume. Most MPAs contained a relatively low proportion of mismatched PUs except for those in the marine provinces of Tropical Northwestern Atlantic, Tropical Eastern Pacific and Galapagos, which consistently had relatively high proportions of mismatched PUs across all three constraining values of fishing volume. The PUs selected by maximizing only PD were also more commonly found within MPAs with higher S_{PD-FD} (at 0.5 of species richness conserved), while PUs selected by maximizing only FD were more commonly found within MPAs where S_{PD-FD} was lower but still positive (Figure 5d).

We failed to detect consistent, significant relationships between S_{PD-FD} and the proportion of mismatched PUs within MPAs across all constraints of global fishing volume, regardless of species richness conserved (Figures S8–S10). There were also no significant, consistent relationships between S_{PD-FD} and the proportion of PUs selected by maximizing only FD or only PD. The trends were all negative for MPAs constrained by the 25th percentile of global fishing volume, but they were not statistically significant ($p > .05$; Figure S10).

4 | DISCUSSION

Species are rarely given equal attention for conservation; resource limitation often does not allow all species in a community to be targeted for protection (Vane-Wright et al., 1991). The interest in prioritizing species based on PD is due in part to its potential to preserve trait diversity, which is regarded as a benefit on its own but also underlies other benefits to humanity (Tucker et al., 2019). Beyond the possibility that prioritizing based on PD could result in the conservation of more traits (and thus more FD), there is no known direct ecological benefit for doing so (Winter et al., 2013). Indeed, while there is commonly a strong positive correlation between PD and FD (mediated by species richness) (e.g. Flynn et al., 2011; Lososová et al., 2016; Wong et al., 2018), it has been shown that maximizing PD is not necessarily a good proxy for maximizing FD (Devictor et al., 2010; Gerhold et al., 2015; Mazel et al., 2017, 2018; Pollock et al., 2017; Srivastava et al., 2012). Here, to test the “phylogenetic gambit” for reef corals, we assess the performance of a PD-maximizing strategy to preserve FD relative to arbitrarily selecting species. Critically, we evaluate the risks of this strategy by investigating the mismatches between PD-maximized and FD-maximized MPA networks and highlighting scenarios where this approach could fall short. Deficiency of coral trait data will continue to be a major limitation in FD studies, so it is important to understand the circumstances in which protecting PD could still lead to gains in FD.

4.1 | PD as a surrogate for FD

Overall, maximizing PD outperforms random selection and is a viable option for maximizing FD. Indeed, S_{PD-FD} values are positive on average (mean 18.7%) showing that a PD-maximizing strategy generally performs better than random selection. This is comparable with the average S_{PD-FD} of 18% for vertebrates obtained by Mazel et al. (2018). Across the different proportions of species conserved, S_{PD-FD} is mostly positive with values generally increasing with a higher proportion of species conserved (Figure 2), suggesting that a PD-maximizing strategy is more viable when a greater proportion of species to be conserved is considered. In the best-performing case, a PD-maximizing strategy relative to randomly selecting (maxPD) could result in FD gains by as high as 95.6%, again comparable with the maximum S_{PD-FD} of 92% obtained by Mazel et al. (2018).

However, in the worst-case scenario, maxPD performs 279.8% worse than random selection and is more severe than the corresponding scenario in Mazel et al. (2018), where the poorest performance of maxPD was 85% worse than random selection. This situation occurs when randomFD performs nearly as well as directly maximizing FD while a PD-maximizing strategy (maxPD) severely underperforms. It should be noted that the worst case in this study is an isolated one, at 0.1 of species richness conserved at a single Hawaiian MPA. There are three selection scenarios where S_{PD-FD} values are lower than -100% , two at 0.1 of richness conserved (inclusive of the worst-case scenario)

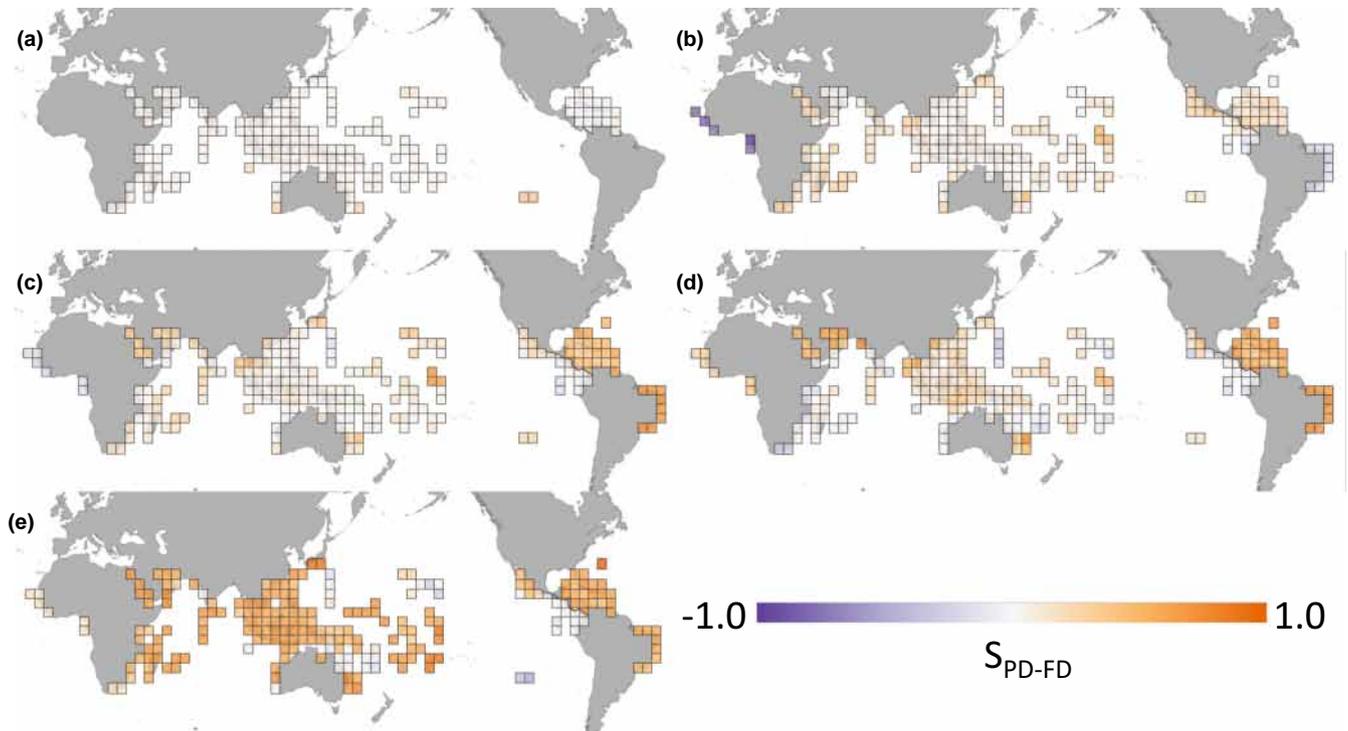


FIGURE 4 Spatial distribution of S_{PD-FD} , defined as the strength of the PD-maximizing function (maxPD) as a surrogate for directly maximizing functional diversity (FD), for conserving 0.1 (a), 0.3 (b), 0.5 (c), 0.7 (d) and 0.9 (e) of species richness in 215 marine protected areas

and one at 0.3 of richness conserved. These extreme selection scenarios where maxPD performs exceptionally poorly are likely a result of the MPAs being species-poor; selections at the corresponding richness result in only three species. Of course, when very few species are to be prioritized, quantifying FD directly would be feasible.

Interestingly, maxPD protects significantly more FD than randomFD in 863 out of all 1038 selection scenarios (83.1%), much higher than the 64% of cases in Mazel et al. (2018). This suggests that maxPD may be a more reliable conservation strategy for reef corals compared with the mammals, birds and labrid fishes tested by Mazel et al. (2018). Such a strategy would benefit the ecosystem functioning of reefs if these traits do indeed confer ecosystem functions. However, there are also 81 selection scenarios where maxPD protects significantly less FD, and on average 24.8% worse, than randomFD, meaning there are potential risks in adopting a PD-maximizing strategy, as highlighted in the selection scenarios where maxPD protects less FD than randomFD, sometimes considerably so. To manage these risks, there is a need to better understand the factors affecting S_{PD-FD} , so that the suitability of a PD-maximizing strategy can be assessed for specific areas.

There is considerable spatial variation in the strength of PD as a surrogate for FD and variation in S_{PD-FD} values between assemblages. It is important to note that PD and FD are strongly correlated at both the MPA and ecoregion levels (Figure 1a,c), a pattern that is congruent with findings in the literature (see Devictor et al., 2010; Safi et al., 2011; Wong et al., 2018). However, the precision of this relationship is not universal and could be associated with the varying strengths of the phylogenetic signal among the selected traits

(Cadotte & Tucker, 2018; Flynn et al., 2011). Furthermore, while maxPD may be able to select species assemblages that outperform random selection in protecting FD, it still falls short of directly maximizing FD, evident in the small average S_{PD-FD} of 18.7%, meaning the assemblage of species selected by maxPD likely differ substantially from the species that contribute most to the known FD of the entire assemblage.

Mazel et al. (2018) found that the strength of PD as a surrogate for FD decreases with increasing total richness, making maxPD a viable conservation strategy for species-poor clades and regions. However, reef corals show a distinct result. While species richness is correlated with S_{PD-FD} , the strength and direction of the relationship are highly variable. In the cases of richness conserved at 0.1, 0.3 and 0.9, higher richness appears to predict higher S_{PD-FD} values while the opposite is true for richness conserved at 0.5 and 0.7 (Figure S1). Furthermore, as conserving 0.1, 0.3 and 0.9 of species richness are associated with a higher likelihood that maxPD would conserve significantly more FD than random selection, adopting a PD-maximizing approach to prioritize the lowest and highest proportions of species in diverse areas may yield greater FD gains. Overall, however, the effect size of species richness on S_{PD-FD} is relatively small, and given the lack of a consistent relationship between them (even as S_{PD-FD} generally increases with higher proportion of richness conserved), it is unlikely that species richness alone can inform the validity of using an area-specific PD-maximizing strategy.

Many underlying factors such as climate change, herbivory and habitat complexity could affect coral assemblages nonrandomly,

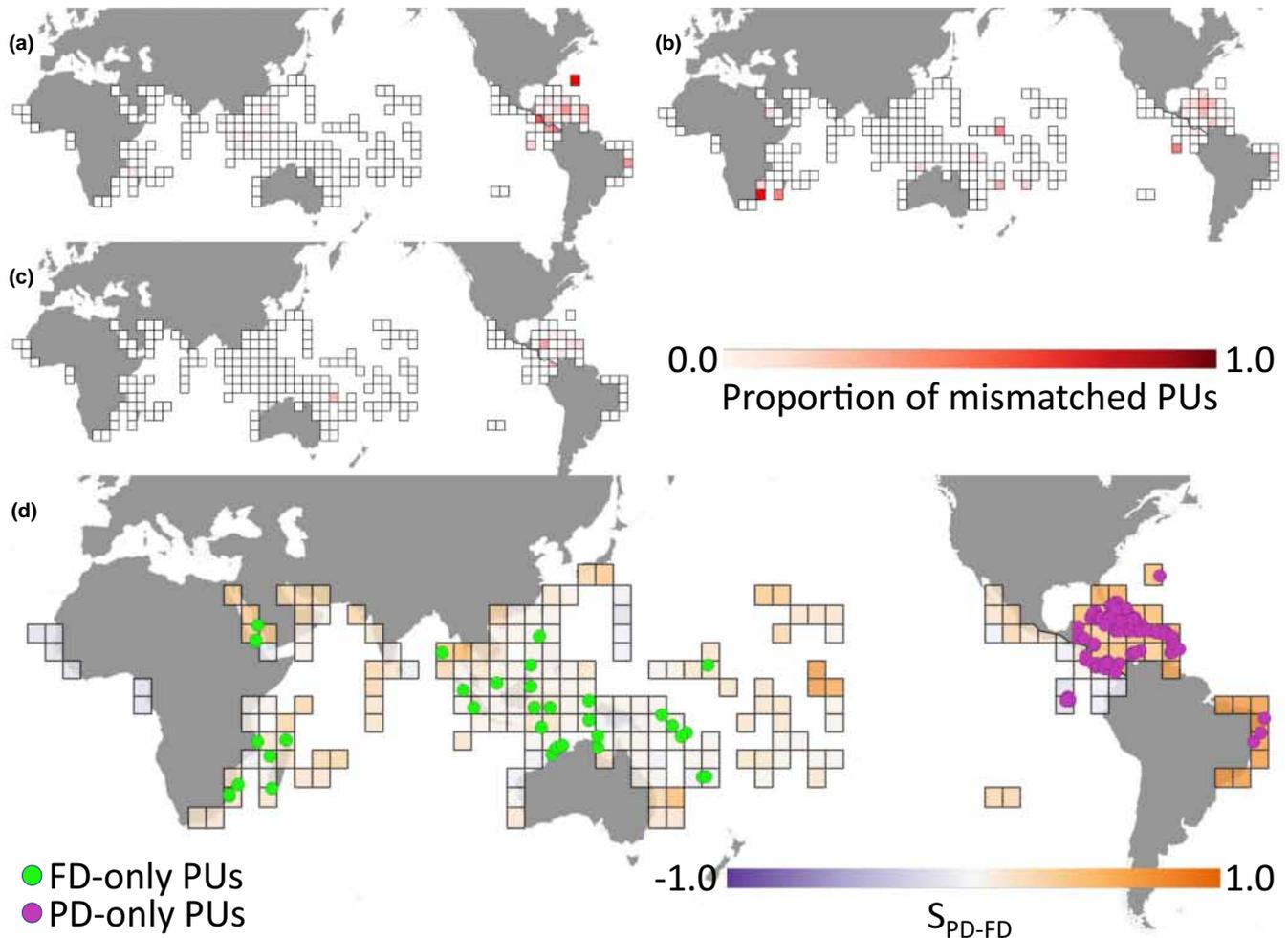


FIGURE 5 Proportion of mismatched planning units (PUs) selected based on either the phylogenetic diversity (PD)- or functional diversity (FD)-maximizing scheme (but not both), constrained at 75th (a), 50th (b) and 25th (c) percentiles of global fishing volume. Spatial distribution of S_{PD-FD} (at 0.5 of species richness conserved) (d), showing the mismatched PUs aggregated across all three fishing volumes

resulting in disproportionate PD and FD losses (Altman-Kurosaki et al., 2021; Madin et al., 2008; van Woesik et al., 1999). These factors could select for particular species, removing certain traits over others and thereby decreasing the overall FD of an assemblage. A PD-maximizing strategy would thus vary in its ability to capture FD depending on how each of these factors impacts different geographic regions following prioritization and protection. As illustrated by the nonrandom spatial patterns of S_{PD-FD} (Figure 4), the biogeography of reef corals has strong and semi-independent effects on both trait and species compositions (Huang et al., 2016; McWilliam et al., 2018) and so plays a major role in how evolutionary history and ecosystem functioning relate to each other (Khalil et al., 2018; McLean et al., 2021; Violle et al., 2014), further explaining the challenge of finding precise relationships between biodiversity indices and S_{PD-FD} . Thus, further studies are required to explore the link between community structure and S_{PD-FD} . While these caveats highlight the potential risks of a PD-maximizing strategy, our findings suggest that in most circumstances, this approach protects greater FD relative to random selection of species.

4.2 | Spatial congruence between PD- and FD-maximizing strategies

Given how PD and FD are positively correlated (Figure 1), it is unsurprising that a large majority of PUs have been selected by both the PD- and FD-maximizing schemes across all three constraining levels of fishing (Figure 5; Figures S2–S7). The large degree of overlap suggests that, in the absence of data for computing FD, a spatial PD-maximizing strategy is a viable proxy for conserving FD. Nevertheless, there remain mismatched PUs selected only by either of the prioritization schemes (Figure 5). The PUs selected only by the FD-maximizing scheme are geographically distinct from those selected by the PD-maximizing scheme, the latter of which are consistently concentrated in the Tropical Northwestern Atlantic with some found in the Tropical Southwestern Atlantic. However, PUs chosen by maximizing only FD are generally not found within the same MPAs across the three constraining levels of fishing, indicating that the selection of PUs to maximize FD is sensitive to this constraint. This could be attributed to FD being more evenly distributed in space as

compared to PD, with the Tropical Western Atlantic having unusually high PD and furthermore at risk of losing disproportionate levels of PD with coral extinctions (Huang & Roy, 2015). A PD-maximizing strategy could therefore result in the over-representation of specific marine provinces in the global MPA network.

Nevertheless, species in the Tropical Western Atlantic represent some of the most phylogenetically unique corals globally, including several placed among the top 20 species based on evolutionary distinctiveness (i.e. *Stephanocoenia intersepta*, *Montastraea cavernosa*, *Helioseris cucullata*, *Siderastrea* spp.) (Curnick et al., 2015; Redding et al., 2015). Caribbean corals within the region are also at high risk of extinction (e.g. critically endangered *Acropora cervicornis* and *A. palmata*, and endangered *Orbicella* spp.) (Carpenter et al., 2008; Huang, 2012), as the reefs have experienced dramatic declines since the 1980s with a coral-to-macroalgal community phase shift that persists till today (Gardner et al., 2003; Hughes, 1994; Jackson et al., 2014). Therefore, while a PD-maximizing strategy would not capture the most functionally diverse PUs, it could help protect corals in a biogeographically unique and threatened reef region (Briggs, 1974; Huang & Roy, 2015; Jackson et al., 2014).

While PUs selected only by the PD-maximizing strategy coincide with areas having higher S_{PD-FD} values in the Tropical Western Atlantic (Figure 5), those selected by maximizing only FD are more dispersed geographically. There are also few mismatched PUs within MPAs having exceptionally low or negative S_{PD-FD} , with limited associations between S_{PD-FD} and the proportion of PUs selected by maximizing only PD or FD (Figures S8–S10). While it may appear suitable for areas with higher S_{PD-FD} to use a PD-maximizing approach to conserve FD, this strategy may be counterproductive since it does not always guarantee the selection of fewer FD-PD mismatched PUs or more FD-maximized PUs. Therefore, directly maximizing FD would yield greater conservation gains in the long run and remains the most conservative approach. As biodiversity and socioeconomic levels vary geographically, the burden of establishing MPAs may fall on jurisdictions within a select few ecoregions. Rather than expand MPA coverage independently and regionally, nations should aim to prioritize protection at the global level and to address potential inequities through financing mechanisms and other means (Pollock et al., 2017; Sala et al., 2021).

To increase habitat connectivity, the co-occurrence of either mangrove forests or seagrass beds is a precondition for a particular PU to be selected. Therefore, PUs in the resultant optimized networks mostly cover coastal reefs and omit oceanic reefs. We note that many oceanic reefs have high S_{PD-FD} and even outsized FD (Figures 4–5), so they may need to be prioritized separately or with more ecologically relevant conditions of habitat connectivity (Balbar & Metaxas, 2019; McMahon et al., 2012). Our spatial optimization also follows the premise that areas under anthropogenic threats from urban areas should be avoided as protected areas. However, it can be argued that areas facing the greatest anthropogenic impacts should be prioritized instead (Mazor et al., 2021; Nelson & Burnside, 2019). Establishing MPAs in heavily fished regions could also be used as a fisheries management tool (Sala et al., 2021). Regardless,

careful planning is an integral part of effective conservation, and similar methodologies that are data-driven and guided by the most relevant metrics should be applied when identifying areas to expand the global MPA network.

5 | CONCLUSION

In this study, we show that a prioritization strategy that maximizes PD is viable for reef coral assemblages as it results in 18.7% more known FD (measured as assemblage-level FRic) on average relative to random selection of species. However, as there are instances where this strategy preserves significantly less FD than even random choice, especially when just a few species are to be prioritized, the PD-maximizing strategy is not one that comes without risks. We note that our comparisons with random subsets of species serve primarily as a conceptual test, and gains in FD may be more realistically benchmarked with species selection based on real-world priorities (e.g. Huang & Roy, 2013). This is an important area of work.

In the long-term, research efforts should characterize traits and understand their roles in the natural functioning of ecosystems. Even for corals, which are relatively well-studied, only about half of the species have data for four or more of the eight traits considered. More complete trait data would enable FD to be computed with greater accuracy, enabling studies on whether FD based on a subset of traits predicts FD overall and potentially negating the need to use PD as a proxy for conservation prioritization. More generally, the spatial optimization approaches based on FD and PD we have developed here could serve as a framework for the future expansion of the MPA network to better meet desired conservation outcomes associated with reef ecosystem functioning.

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CONFLICT OF INTEREST

The author declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All datasets and R scripts are available at Zenodo (<https://doi.org/10.5281/zenodo.6331588>).

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BIOSKETCH

The sCAP (Conservation and Phylogeny) working group was assembled at sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research, and comprises researchers in conservation, phylogenetic metrics, macroevolution, trait evolution, trait diversity and ecosystem function. sCAP aims to test the conservation value of phylogenetic diversity and the assumptions behind the use of phylogenetic metrics for conservation and management.

Author contributions: C. Chisholm, M. Winter and D. Huang conceptualised the study. All authors contributed to the study design, methodology and data consolidation. L.W.K. Ng and C. Chisholm led the data analyses. L.W.K. Ng and D. Huang led the writing of the manuscript. All authors contributed to the review and editing of the final manuscript.

SUPPORTING INFORMATION

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