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Patterns of taxonomic and functional diversity in the global cleaner reef fish fauna

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Abstract

Aim: Several drivers explain the global distribution of all reef fish. However, whether these drivers also explain the distribution and traits of a functional subgroup involving cleaner fishes remain unclear. Here we examine the variation in traits of cleaner fishes and test whether historical, environmental, ecological and geographical drivers are correlated with cleaner species richness and abundance at global reefs.

Location: Tropical and subtropical reefs.

Taxon: Actinopterygii.

Methods: We tested whether species traits and trait space vary between facultative (*i.e.* species that clean only during the juvenile stages or sporadically) and dedicated (*i.e.* species that clean during their whole lives) cleaner types. We compiled data from local checklists (relative richness) and belt transects (standardized richness and abundance). We built four models to test whether past and current isolation (*i.e.* distance from Quaternary refugia and biodiversity centres), sea temperature, primary productivity, local species pool and abundance of potential clients influenced the relative richness and abundance of cleaners.

Results: Facultative cleaners had high trait variability that contributed disproportionally to the trait space, whereas dedicated cleaners exhibited low trait variability. Cleaner species richness was higher in the Indo-Pacific and Caribbean provinces, but the relative richness and standardized abundance of cleaners were higher in the Atlantic (*i.e.* North Eastern and Southwestern) and Eastern Pacific. Isolation influenced the relative richness of facultative cleaners, whereas the distance to Quaternary refugia, sea temperature and isolation influenced the relative richness of dedicated cleaners. Local species richness and standardized abundance of cleaner fish exhibited a strong relationship with regional diversity. The standardized abundance of both facultative and dedicated cleaners was influenced by the abundance of potential clients and the local species pool.

Main conclusions: The small trait space occupied by cleaner fishes may reflect their restricted origin among lineages of reef fishes. Differences in the relative richness and standardized abundance of cleaner fishes across marine realms suggest a strong influence on biogeographical history. Our results also indicate that cleaner fishes originated mostly in peripheral areas in high latitudes due to the absence of dedicated cleaners. Our results imply that cleaner fishes do not follow the pattern of main centres of origin described for reef fishes due to opportunistic cleaning behaviour that originated with higher frequency at locations with low species richness.

KEYWORDS
dedicated cleaners, diversity gradient, facultative cleaners, marine mutualism, marine realms, relative species richness, standardize abundance, trait species

1 | INTRODUCTION

Organisms live in complex networks of ecological interactions that influence their ecosystem functioning and community structure (Mougi & Kondoh, 2012). Unravelling the processes that determine the interactions among organisms, such as competition, predation and mutualism is one of the major challenges in ecology (Cantor et al., 2018; Guimarães et al., 2016). Mutualisms are positive interactions which involve multiple levels of biological organization and benefit participating species with resources, such as food and protection (Guimarães et al., 2007; Quimbayo et al., 2018; Trøjelsgaard et al., 2015). Much research on marine mutualistic interactions has been conducted at the local scale (*e.g.* Grutter, 2005; Ollerton et al., 2007). However, whether mutualistic interactions are influenced by past evolutionary history, current environmental conditions or the traits of species remains to be determined (Grutter, 2005; Guimarães et al., 2016). This information is important to understand whether the patterns observed at the local scale are due to local community dynamics or biogeographical processes that act over large spatial and long temporal scales. Here, we tackle this issue investigating one of the most remarkable models of mutualism in the marine environment—cleaning interactions—which occurs when a 'cleaner' species (fishes and crustaceans) removes ectoparasites and dead or diseased tissues from the body surface of other marine animals, the 'clients' (Côté, 2000).

Marine cleaning interactions are important because they increase fish abundance and promote species diversity in local fish communities through the removal of parasites, favouring the concentration of a large number of species around the cleaner species (Côté, 2000; Grutter et al., 2003; Waldie et al., 2011). Furthermore, the presence of cleaner species helps to maintain diverse fish communities by attracting large and non-reef species (O'Shea et al., 2010; Quimbayo et al., 2017). In marine tropical and subtropical habitats, about 208 fishes and 51 shrimps species are reported as cleaners and are either classified as facultative or dedicated cleaners (Côté, 2000; Vaughan et al., 2017). Facultative cleaners clean only during the juvenile stage or sporadically, whereas dedicated cleaners clean throughout their lives (Vaughan et al., 2017). This classification can provide insights on the evolution, degree of specialization and the foraging niches occupied by each type of cleaner species in communities (Floeter et al., 2007; Sazima, Guimarães, Reis, & Sazima, 2010). For instance dedicated cleaners have elongated bodies, aposematic colorations and lateral body stripes whereas facultative cleaners display a high morphological and coloration diversity, which vary according to their ontogenetic development stage (Baliga & Law, 2016; Baliga & Mehta, 2019; Cheney et al., 2009; Côté & Soares, 2011). Our understanding of cleaning behaviour comes mainly from a restricted number of species, whereas analyses built upon a broad range of cleaner species are lacking (Baliga & Mehta, 2019; Quimbayo et al., 2018). In particular, data to solve two main questions are scarce: (a) how do behavioural, dispersal and colonization traits vary between both types of cleaner fishes (facultative and dedicated)?; and (b) what is the multidimensional trait space (*i.e*. a space calculated from the combination of the species traits, where the axes are traits along which species are placed according to their trait values; Mouillot et al., 2013) occupied by each type of cleaner fish, given that this ecological group represents only a small fraction of the global reef fish species richness (Kulbicki et al., 2013; Parravicini et al., 2013; Vaughan et al., 2017)? Answering these questions can shed light on the ecological and evolutionary processes that influence the maintenance of this marine mutualism on a global scale.

In the last decades, we have begun to better understand the global patterns and drivers of the distribution of richness and abundance of reef fishes, as well as to identify the processes that modulate them (Barneche et al., 2019; Bellwood & Meyer, 2009; Parravicini et al., 2013; Yancovitch Shalom et al., 2020). For instance, hotspots of both richness and abundance of reef fishes occur in the Indo-Australian Archipelago and the Caribbean (Bellwood & Meyer, 2009; Floeter et al., 2008; Yancovitch Shalom et al., 2020). Historical (Pellissier et al., 2014), environmental (Barneche et al., 2016), geographical (Kulbicki et al., 2015; Parravicini et al., 2013) and physiological (Barneche et al., 2016) processes have been proposed as mechanisms that explain these patterns. As a consequence, such processes may influence species occurrence, their abundance and the biotic interactions (Vázquez et al., 2007). Regarding marine cleaning interactions, cleaner fish richness increases rapidly in tropical areas (Baliga & Mehta, 2019), and the local abundance of clients can influence cleaning frequency (Quimbayo et al., 2018; Quimbayo et al., 2017). Despite the latter advances revealing some drivers of cleaner distribution, the extent to which these historical, environmental, ecological and geographical drivers can influence the biotic interactions; or how the global distribution of reef fishes determine the presence of cleaner fishes remain to be formally investigated (Albouy et al., 2019; Fontoura et al., 2020; Longo et al., 2019; Quimbayo et al., 2018). Here, we combined four empirical datasets to investigate how the relative richness and abundance of cleaner reef fishes may vary with a range of explanatory factors. Below, we outline how we investigated this general hypothesis in several different ways.

Facultative cleaner species originated independently in several reef fish lineages and differ in their degree of specialization to attract clients. On the other hand, dedicated species are restricted exclusively to three genera and have a high degree of specialization (Baliga & Mehta, 2019; Gingins & Bshary, 2016). Therefore, we tested the hypothesis that facultative cleaners have a higher variability of traits and occupy a larger fraction of the multidimensional trait space than dedicated cleaners. To test this hypothesis, we first compared nine traits of facultative and dedicated cleaner fishes (Baliga & Mehta, 2019; Gingins & Bshary, 2016). Second, since facultative cleaners have a higher body size and therefore a higher dispersion than dedicated small cleaners (Luiz et al., 2013), we tested whether traits related to dispersal and colonization vary according to regional species pool and if evolutionary and historical processes influence the trait species distribution. Third, we compared the multidimensional trait space occupancy of each type of cleaner and how much of the multidimensional trait space built from all cleaner species is occupied by each type of cleaner fish. This allowed us to test the degree of overlap between facultative and dedicated cleaners. Fourth, we tested whether the multidimensional trait space varies among a subset of fish families that contain the highest number of cleaner species. Here, considering that some of the families with cleaner species (*i.e*. Labridae, Pomacentridae, Chaetodontidae) comprise a vast combination of traits (Mouillot et al., 2014), and that cleaner species only represent a small subset of these families (Baliga & Mehta, 2019), we tested the prediction that cleaner fishes would have a lower occupancy in the multidimensional trait space than non-cleaner species and that the trait space occupied by facultative cleaners would be larger than that of dedicated cleaners due to their lower richness. Finally, we investigated whether historical, environmental, ecological and geographical factors influence the relative local richness and abundance of cleaners. We hypothesized that cleaner fishes follow the same global distribution patterns of reef fishes, and that cleaners are influenced by the same historical, environmental, ecological and geographical factors that other reef fishes are influenced by (Baliga & Mehta, 2019; Kulbicki et al., 2013). Specifically, we tested whether the relative local richness and abundance of cleaner fishes are concentrated in the Indo-Australian Archipelago and the Caribbean. Our study provides a new view of how species traits vary between facultative and dedicated cleaners, as well as how historical, environmental, ecological and geographical factors may determine the macroecological patterns of cleaner fishes distribution at a global scale.

2 | MATERIALS AND METHODS

2.1 | Distributional datasets

We compiled two extensive distributional datasets for this study: one consists of reef fish species occurrence records from species checklists for 290 locations distributed throughout 17 regions and 28 marine biogeographical provinces (Kulbicki et al., 2013; Spalding et al., 2007), in tropical, subtropical and temperate marine areas. This dataset was compiled by the GASPAR (General Approach to Species-Abundance Relationships) research group (Kulbicki et al., 2013; Parravicini et al., 2013) and consists of records for 7129 species belonging to 1454 genera and 247 families. The second dataset consists of abundance data of reef fishes compiled from 13,050 underwater visual censuses (UVCs) which were conducted using belt transects across 110 tropical locations. The final dataset consists of 2523 species from 552 genera and 119 families (Barneche et al., 2018; Quimbayo et al., 2019).

2.2 | Cleaner fishes dataset

We compiled a third dataset containing the most recent list of cleaner fishes, by combining four reviews on marine cleaning interactions (Baliga & Mehta, 2019; Côté, 2000; Quimbayo et al., 2018; Vaughan et al., 2017) and a systematic review of recent literature (Table S1). We also used search engines (Web of Science, Scopus and Google Scholar) to search for studies and grey literature on cleaner fishes. We used combinations of the following search terms, in English, Portuguese, French and Spanish: cleaner fish, cleaning interactions, cleaning symbiosis, cleaning mutualism, facultative cleaner, dedicated or obligate cleaner. Each cleaner fish was classified in one of the two types (facultative vs. dedicated) according to their dependence and time spent during cleaning interactions (Figure 1; Côté, 2000; Vaughan et al., 2017). Facultative cleaners clean only during their juvenile stage or sporadically and dedicated cleaners clean during their entire lives (Côté, 2000; Vaughan et al., 2017). A caveat about this classification is that cleaner fishes do not always follow this classification since there are different levels of specialization between both discrete groups. However, this arrangement allows us to test general hypotheses surrounding the varying degrees of cleaning behaviour.

2.3 | Species traits of cleaner fishes

A fourth dataset was assembled by classifying all reef fish species from our distributional datasets according to seven species traits (five discrete and two continuous) and two distributional parameters (Table S1). These species traits have been successfully used to describe the functional role of reef fish assemblages at different scales (D'agata et al., 2014; Parravicini et al., 2014; Quimbayo et al., 2019). The discrete traits were defined using the properties defined by Mouillot et al. (2014), whereas continuous traits were compiled from FishBase (Froese & Pauly, 2020; Parravicini et al., 2014; Quimbayo et al., 2021). We considered body size, depth range, pelagic larval duration (PLD) and geographical range index, because they are traits related to dispersal and colonization capacity (Luiz et al., 2013; Parravicini et al., 2014). The nine traits (and trait classification) and the rationale for their use are summarised below:

FIGURE 1 Illustrative examples of dedicated (a–c) and facultative (d–f) cleaner fish and their clients, including shapes, colours, relative sizes and behaviours. (a) *Labroides dimidiatus* and *Cirrhilabrus humanni*; (b) *Labroides pectoralis* and *Macolor macularis*; (c) *Elacatinus phthirophagus* and *Cephalopholis fulva*; (d) *Thalassoma noronhanum* and *Acanthurus chirurgus*; (e) *Pomacanthus paru* and *Carangoides bartholomaei*; (f) *Cochleoceps orientalis* and *Upeneichthys lineatus*. Photographs by R. Smith – OceanRealmImages.com (a, b, f), I. Sazima (c, e) and J.P. Quimbayo (d)

1. Mobility (sedentary/mobile/very mobile): Cleaner species considered as sedentary were ones that remain in a restrict area less than 3 m^2 where they establish cleaning stations (*e.g. Elacatinus* spp.); mobile cleaners were ones that remain in an area of more than 50 m^2 and can also establish cleaning stations (*e.g. Labroides* spp.) and very mobile cleaners were ones that frequently change reefs or travel large distances daily (*e.g. Caranx* spp.).
2. Activity period (diurnal/nocturnal/both): diel activity was selected because cleaner fishes often attract potential clients by visual cues during the day (Vaughan et al., 2017). However, a few cleaners have nocturnal habits (*e.g. Siphamia tubifer*) and may avoid competition with diurnal cleaners (Côté, 2000).
3. Level in water (bottom/low/high): cleaners that are more associated with the substratum attend different clients as compared to cleaners that remain in either low or higher positions in the water column (Johnson & Ruben, 1988; Quimbayo, Nunes, et al., 2017). For instance we considered cleaner gobies *Elacatinus* spp. as bottom-associated because they remain on the substratum. Cleaners that attended their clients some metres above the bottom, such as cleaner wrasses *Labroides* spp. were considered to occupy a low-level water position. Cleaners that attend their clients in the water column (*i.e.* several metres from the bottom), such as *Caranx* spp. were considered as high-level water position.
4. Size group [solitary, pair, small (3–20), medium (21–50), large (>50 individuals)]: the number of cleaner fish can influence the efficiency of cleaning services and the level of attention of clients (Côté, 2000; Quimbayo, Nunes, et al., 2017).
5. Diet was categorized into seven groups according to food items composition as defined by Mouillot et al. (2014): herbivores-detritivores (feed upon turf and filamentous algae and/or detritus), macroalgae-feeders (large fleshy algae and/or seagrass), sessile invertebrate feeders (corals, sponges, ascidians), mobile invertebrate feeders (benthic prey, such as crabs and molluscs), planktivores (small organism in the water column), piscivores (fishes and cephalopods) or omnivores (both plant/algae and animal material).
6. Body size (maximum total length reported in centimetres; Froese & Pauly, 2020): cleaner fishes of different sizes may target different clients (Baliga & Mehta, 2016; Côté, 2000; Floeter et al., 2007).
7. Depth range: records of cleaning symbiosis range mostly between 1 and 30 m depth, although several cleaner fishes are known to clean below 30 m (Sazima, Grossman, & Sazima, 2010). Thus, we retained the minimum and maximum depth of occurrence of each species.
8. Pelagic larval duration: the distribution of reef fishes can be influenced by pelagic larval-stage duration (Luiz et al., 2013), a trait used to help to explain the presence or absence of cleaner species (Walsh et al., 2017).
9. Geographical range index: number of geographical cells (based upon a 5° × 5° sized latitude and longitude grill pattern) where the species occur. Each cell corresponding to approximately an area 550 × 550 km at the equator.

For each species trait, we compared the proportion of dedicated and facultative cleaners and non-cleaner species within families in which cleaners occur. Additionally, we compared the multidimensional functional space occupied by each type of cleaner in each of the families with the highest numbers of cleaner species. This multidimensional functional space was built from a principal coordinates analysis using a Gower's distance dissimilarity matrix, which allows mixing qualitative and quantitative data (Podani & Schmera, 2006). We examined the quality of functional space that would reflect our life-history trait space, using the quality_funct_space R function. As expected, the quality of representation increased with the number of axes (Figure S1; Maire et al., 2015). We kept only the first four axes for the convenience of graphical representation and because they represented more than 70% of the explained variance in the data. Finally, we estimated the functional volume occupied by each type and the most important families, using the multidimFD R function (Mouillot et al., 2013).

2.4 | Explanatory factors

For each location reported in the first two datasets (*i.e.* species occurrence records from species checklists and abundance data from UVCs), we compiled a set of historical, environmental, ecological and geographical factors to examine their influence on the relative richness and standardized abundance of cleaner fishes. We considered a historical factor to be the distance of isolation from the nearest coral reef refugia across the Quaternary period (see Pellissier et al., 2014 for further details) in order to evaluate whether the Quaternary climatic oscillations left an imprint on the global distribution of cleaner fishes, as already found for many tropical reef fishes families (Ottimofiore et al., 2017; Pellissier et al., 2014). We used the Bio-ORACLE database (Tyberghein et al., 2012) to obtain data for the following contemporary environmental factors between 2002 and 2009: annual minimum sea surface temperature (in degrees Celsius) and primary productivity (mean surface chlorophyll *a* concentration) both estimated from satellite imaging. These two environmental factors have been found to influence the metabolism of ectothermic species, and therefore population abundance and community biomass patterns at large spatial scales. We considered as ecological factors the total local species richness extracted from checklists (Kulbicki et al., 2013) and the relative richness and abundance of potential clients (*i.e.* all the non-cleaner species that were recorded during the UVCs) extracted from the first datasets mentioned above in Section 2.1 (Barneche et al., 2018, 2019; Quimbayo et al., 2019). These factors were found to modulate both the presence of cleaner fishes and the frequency of the cleaning interactions (Quimbayo et al., 2012; Quimbayo, Nunes, et al., 2017). Finally, we used current isolation and the distance from the main centres of biodiversity as geographical factors. Isolation was defined as the minimum distance (km) from the nearest continental coast. Isolated locations harbour only a subset of reef fish species from the regional pool

(Bender et al., 2017). The distance from biodiversity centres was measured, assuming them to be Panama for the Eastern Pacific (Parravicini et al., 2013), the Caribbean for the Atlantic (Floeter et al., 2008) and the Indo-Australian Archipelago for the rest (Kulbicki et al., 2013).

2.5 | Data analysis

The relative richness of facultative and dedicated cleaners were calculated for each location as the ratio between cleaner richness and the total local species pool calculated from checklists. Standardized richness and abundance were calculated using the minimum number of fish individuals by location. To do this, we first identified the location with the smallest abundance (*i.e.* 424 individuals) and restricted this value in the other locations in order to standardize the sampling effort. Subsequently, we used the multiple combinations of transects to compose the minimum number of fish individuals by location to calculate the standardized richness and abundance of both types of cleaners and non-cleaner species (*i.e.* potential clients). This procedure was repeated 999 times to ensure that all belt transects from each location were used at least one resulting in mean richness and abundance values for a given sample size. This procedure is analogous to individual-based rarefaction curves, which allow comparisons between richness and abundance observed in the UVCs while controlling for the minimum number of individuals (Gotelli & Colwell, 2001). We adopted this standardization procedure because the number and sample area of belt transects varied among the 110 tropical locations in our dataset.

We employed general linear models (GLMs) to compare local species richness observed in each dispersal and colonization trait between cleaner fishes and non-cleaners, as well as according to realm. To examine potential collinearity among the different drivers (*e.g.* historical, environmental, ecological and geographical), we used Pearson's correlation, considering a correlation coefficient $r < |\pm 0.70|$ as a cut-off value for retaining predictors in the models, since values below this threshold in practice are unlikely to involve multicollinearity in models (Dormann et al., 2013). We scaled all predictors to a mean of zero and to unity standard deviation to enable the direct comparison among effect sizes. Additionally, we calculated the variance inflation factor (VIF) using the vif R function from the '*car*' package (Fox & Weisberg, 2019) to ensure that predictors were not correlated with each other, considering a value <3 as a cut-off (Tables S6 and S7; Dormann et al., 2013). We did not observe any important correlations or VIF values >3 across our candidate covariates, thus we maintained all the predictor variables in our analysis (Figures S2 and S3).

We built four models that were divided into two groups. In the first group, we built two generalized linear mixed models (GLMMs) assuming a Binomial distribution with a logit link to investigate how the relative richness of facultative and dedicated cleaners (*i.e.* a proportion) were influenced by past and current isolation (*i.e.* distance from refugia, biodiversity centres and isolation), sea temperature, primary productivity and local species pool. In the second group of models, we built linear mixed models LMMs with a Gaussian distribution to examine how the standardized abundance of both types of cleaners are influenced by the same predictor variables listed above for the first group of models, with the addition of the standardized richness and abundance of potential clients observed in the UVCs transects. The Gaussian distribution was justified as standardized richness and abundance involved mean continuous estimates obtained from the standardizing procedure used to control for the heterogeneous sample size of fish assemblages. We considered biogeographical province as a random factor in all models to account for the residual variation that could be associated with the historical and evolutionary processes of each province (Kulbicki et al., 2013; Spalding et al., 2007). All models were built using the glmer and lmer R functions from the package '*lme4*' (Bates et al., 2015). We evaluated the significance of all predictors using likelihood ratio tests (LRTs) using the drop1 R function, which drops non-significant ($p > 0.05$) individual predictors from the full model and calculates significant differences in model fit based on chi-squared distributions (Dormann et al., 2013).

Finally, we used the geographical coordinates of each location and residual values of each model to estimate Moran's *I* index using the inverse of the Euclidean distance among locations as weights. Overall, Moran's *I* indicated no spatial autocorrelation in the model residuals built from relative richness of cleaner fishes estimated from species checklists (facultative cleaner $I = -0.021 \pm 0.013$, $p = 0.05$; dedicated cleaner $I = -0.007 \pm 0.013$, $p = 0.38$; Figures S4 and S5a,b); and models residuals built for the relative abundance of cleaner fishes estimated from belt transects (facultative cleaner $I = -0.005 \pm 0.03$, $p = 0.59$; dedicated cleaner $I = -0.012 \pm 0.03$, $p = 0.91$; Figures S5c,d and S6). This index was estimated used the Moran.I R function from the '*ape*' package (Paradis & Schliep, 2019). All figures were constructed using the '*rgdal*' (Bivand et al., 2020), '*pgirmess*' (Giraudoux, 2018) and 'ggplot2' (Wickham, 2016) packages, and all the analyses were performed in the R environment, v 4.0.2 (R Core Team, 2020).

3 | RESULTS

3.1 | Species traits and multidimensional trait space occupied by cleaner fishes

We detected significant differences in species traits between cleaner and non-cleaner fishes (Figure 2). Facultative cleaners tended to be mobile, formed groups of various sizes, had varied diets and occupied higher levels in the water column (Figure 2a–e). In contrast, dedicated cleaners were mainly sedentary, bottom dwellers, had diurnal habits, formed mainly small groups and were exclusively mobile invertebrate feeders. Non-cleaner species were mainly sedentary, bottom dwellers, had diurnal habits, formed groups of various

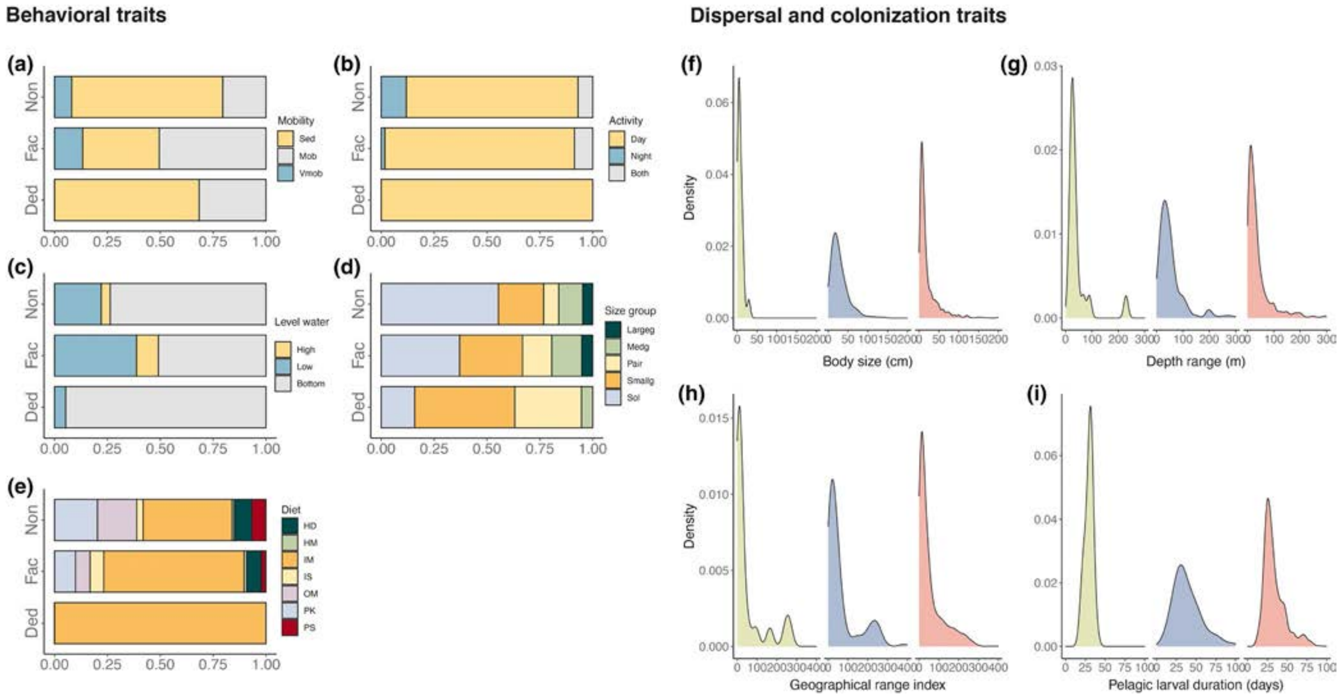

FIGURE 2 Comparison between behavioural, dispersion and colonization traits of cleaner and non-cleaner fish. The behavioural traits are as follows: (a) Mobility: sedentary (Sed), mobile (Mob) and very mobile (Vmob); (b) Activity: day, night and both; (c) Level water: bottom, high and low; (d) Size group: solitary (Sol), pair (Pair), small (Smallg: 3–20), medium (Medg: 21–50) and large (Largeg: >50 individuals). Diet: herbivores-detritivores (HD), macroalgal-feeder (HM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK), piscivores (PS) and omnivores (OM). Density plots of dispersion and colonization traits are: (f) Body size (cm); (g) Depth range (m); (h) Geographical range index; (i) Pelagic larval duration (days). The green color in the figures f to g, represents the dedicated cleaners, the blue color the facultative cleaners and red color the non-cleaners fish.

sizes and presented a great range of diets. The average body size of facultative cleaners and non-cleaners was on average four times larger (mean ± SD = 28 ± 21.57 and 20 ± 27.4 cm respectively) than dedicated cleaners, which had an average of 6.5 cm (2.3–15 cm; Figure 2f). Facultative cleaners and non-cleaner species occupied a depth range from 0 to 300 m, whereas dedicated cleaners were recorded down to 90 m depth (Figure 2g). Both cleaner types presented a similar pattern of geographical range, in which most species had a restricted distribution and a second mode with species occurring in *ca*. 250 5° × 5° cells; however, facultative cleaners presented a higher maximum distribution with species occurring in up to 400 5° × 5° cells. Non-cleaners presented only one distributional mode and had maximum values similar to those of dedicated cleaners (Figure 2h; Table S1). Finally, we observed a higher mean (± SD) PLD for facultative and non-cleaner species (40.2 ± 19.55 and 34.32 ± 17.74 respectively) than that for dedicated cleaners (mean ± SD = 29.82 ± 4.46; Figure 2i). All cleaners occupied 39% of the total multidimensional trait space based on the families in which cleaners are reported (Figure 3). However, facultative cleaners occupied 38.96% of the total trait space (99% of the cleaners' trait space), whereas dedicated cleaners only occupied 0.04% or 1% of the entire cleaners trait space (Figure 3; Figure S7). We observed that 11 families had a higher number of cleaner species, but none of them filled more than 10% of the total multidimensional trait space (Figure 3). For instance, the family with the highest number of facultative and dedicated cleaners (Labridae) occupied 1.46% of the total multidimensional trait space (Figure 3a; Supporting information S7a), whereas the family with the highest number of dedicated species (Gobiidae) occupied only 0.006% of the space (Figure 3b; Table S2 and Figure S7).

3.2 | Relationships between dispersal and colonization traits and local species pool

The average body size between cleaner species and non-cleaner varied significantly (GLM: *p*-value <0.01; Table S3). There was a positive and significant correlation between the body size of both facultative and dedicated cleaners and local species pool (Figure 4a). There were no differences in the average body size of facultative cleaners according to realm (Figure 4b; Table S4). However, dedicated cleaners showed variation among realms, with the Atlantic and Eastern Pacific being the realms with a smaller average body size of dedicated cleaners compared with the rest (Figure 4c; GLM: *p*-value <0.01; Table S4). Fish PLD varied among cleaner species and non-cleaners (GLM: *p*-value <0.01; Table S3). Moreover, the PLD of facultative cleaners was positively correlated with local richness, reaching an asymptote beyond approximately 500 species, whereas PLDs of dedicated cleaners were constant and PLDs of non-cleaners were longest at low local richness (Figure 4d). We also found differences in the PLD of facultative cleaners across realms (GLM: *p*-value

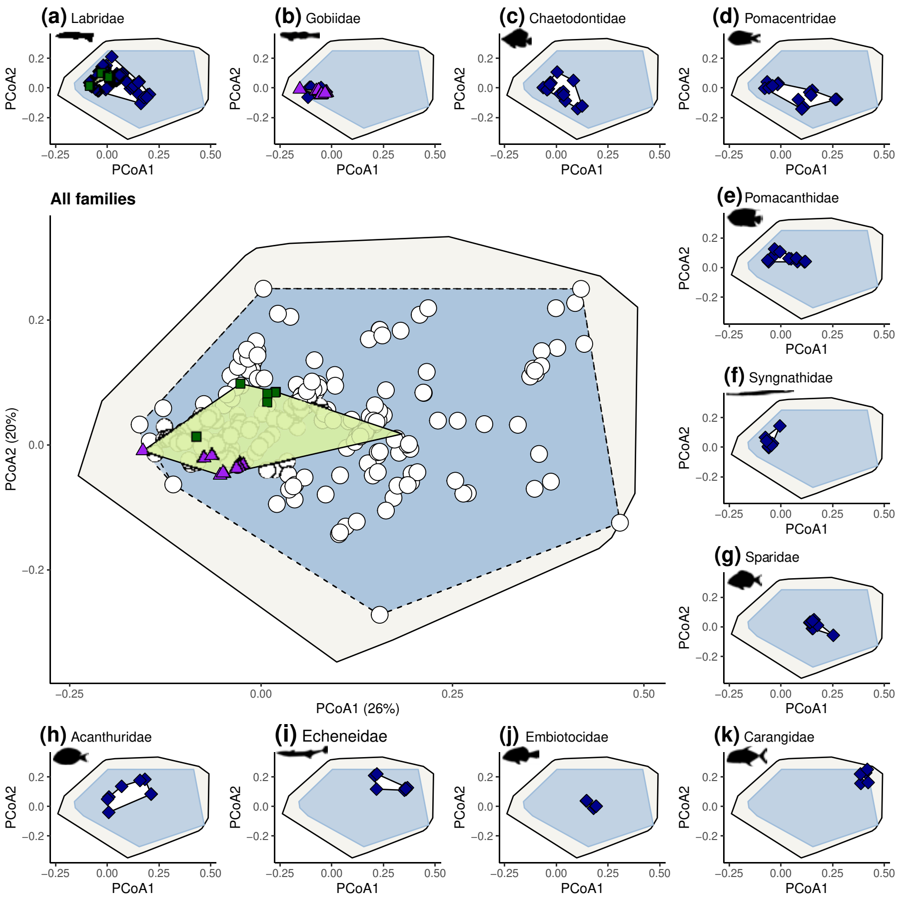

FIGURE 3 Multidimensional functional space occupied by cleaner fish and the 11 families grouping 76% of global cleaner richness. Central plot: the grey polygon represents all species (i.e. cleaner and non-cleaner fishes), whereas the blue polygon represents the trait space occupied by all cleaner fish. The black dashed line represents the trait space occupied by facultative cleaners, while the white circles are the exact position of facultative cleaners. The light green polygon represents the trait space occupied by dedicated cleaners; the dark green squares are Labridae (six species) and the purple triangles are Gobiidae (12 species). Peripheral plots: The grey polygon represents all species (cleaner and non-cleaner fish), whereas the blue polygon represents the trait space occupied by all cleaner fishes. The white polygon represents the trait space occupied by facultative cleaners belonging to 11 families and the blue diamonds their exact position in the trait space. Plots show the first and second axes derived from a Principal Coordinate Analysis (PCoA) performed on ten life-history traits. Plots with third and fourth axes are in Figure S6

<0.01; Table S3), which decreased with local richness in the Pacific and Indian realms and increased in the Atlantic and Eastern Pacific (Figure 4e). In contrast, the PLD of dedicated cleaners was shorter in the Atlantic, and longer in the Indian and Pacific realms (Figure 4f). In sites that are characterized by low local richness, both facultative and dedicated cleaners occurred in shallower waters than did other species (Figure 4g; GLM: *p*-value <0.01; Table S3). Facultative cleaners showed differences in PLD among realms (GLM: *p*-value <0.01; Table S4) and their PLD correlated negative with the increase in the local species pool (Figure 4h). In contrast, dedicated cleaners did not exhibit differences in their PLD in relation to the local species pool (Figure 4h; GLM: p-value <0.01; Table S4). Finally, both cleaners and non-cleaners exhibited the same pattern in the relationship between geographical range and local richness, but cleaners displayed larger geographical ranges for a given local richness level (Figure 4j; GLM: *p*-value <0.01; Table S3). The geographical range between both types of cleaners varied among realms, being consistently narrower in the Atlantic and Eastern Pacific than in the Indian and Pacific realm for both the type of cleaners (Figure 4k-i; GLM: *p*-value <0.01; Table S4).

3.3 | Biogeographical patterns of the relative richness of cleaner fishes from checklists and drivers

We found 253 marine cleaner fish species belonging to 44 families (Table S1), with 92.5% being facultative ($n = 234$) and 7.5% being dedicated ($N = 18$). Twenty-five percent ($N = 11$) of families accounted for 76% of the cleaner species (both dedicated and facultative). Labridae had the most, with 88 cleaner species, followed by Gobiidae (18 species), Chaetodontidae (16 species), Pomacentridae (14 species), Pomacanthidae (13 species), Syngnathidae and Sparidae (9 each), Acanthuridae (8 species), Embiotocidae (6 species) and Carangidae (5 species; Table S2). In contrast, dedicated cleaners belonged to only two families. Gobiidae was the most speciose, with 12 dedicated cleaners, whereas Labridae had six species (Table S2).

The hotspots of cleaner richness were detected mainly in locations from the Indo-Pacific and Caribbean (Figure 5a; Table S5). There was a positive relationship between total cleaner species richness recorded in the checklists and local species pool (Figure S8a). There was a higher relative richness of cleaner fishes in the Atlantic and Eastern Pacific than in the Indian and Pacific realms (Figure 5b), and the relative richness of cleaner decreased with the increase in total species pool (Table S5). The relative richness of all cleaners ranged from 1% to 21%, but seldom reached values higher than 15%, except in oceanic islands from the Western Atlantic and Eastern Pacific, whereas islands from other realms exhibited lower values (Figure 5b). The relative richness of facultative cleaners followed the same pattern observed for all cleaner species, that is with higher values in the Atlantic and Eastern Pacific (Figure 5c). On the other hand, the relative richness of dedicated cleaners did not show any strong biogeographical distributional pattern and only eight locations had values higher than 0.012 (Figure 5d).

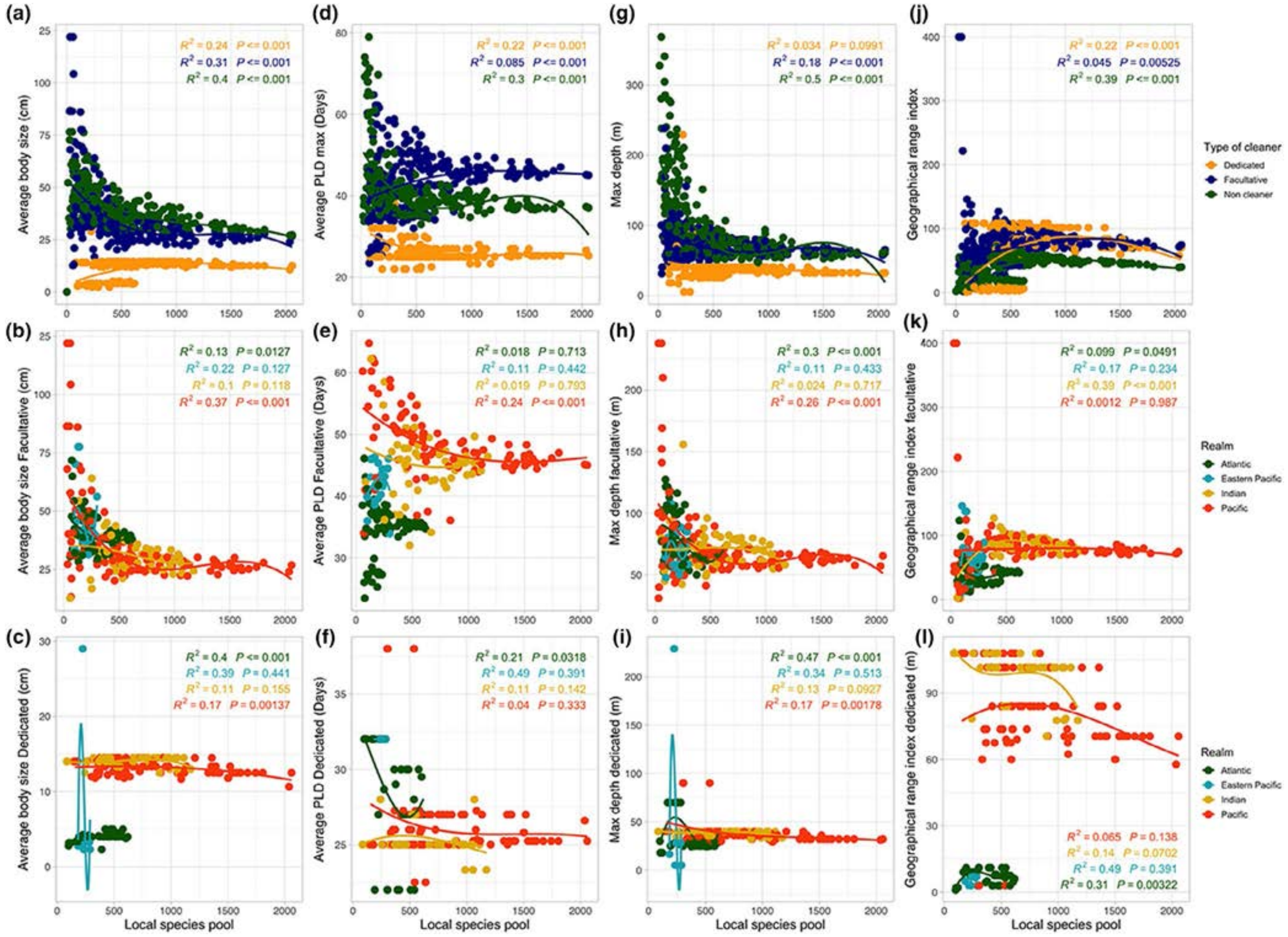

FIGURE 4 Linear correlations between dispersal and colonization traits and local fish species pool. Dispersal traits: (a) Average body size according to the type of cleaner and non-cleaner species; (b) average body size of facultative cleaners according to realm; (c) average body size of dedicated cleaners according to realm; (d) average maximum pelagic larval duration (PLD) according to the type of cleaner and non-cleaner species; (e) average maximum pelagic larval duration (PLD) of facultative cleaners according to realm; (f) average maximum pelagic larval duration (PLD) of dedicated cleaners according to realm; (g) average maximum depth according to type of cleaner and non-cleaner species; (h) average maximum depth of facultative cleaners according to realm; (i) average maximum depth of dedicated cleaners according to realm; (j) geographical range index according to type of cleaner and non-cleaner species; (k) geographical range index of facultative cleaners according to realm; (l) geographical range index of dedicated cleaners according to realm

The relative richness of facultative cleaners increased with distance from the Quaternary coral reef refugia and isolation, whereas local species richness had a negative effect. The minimum sea surface temperature was the only factor that influenced positively the relative richness of dedicated cleaners (Figure 6; Table S6). It should be noted that the relative richness of all cleaners had different relationships to latitude according to realms (Figure S9). In the Atlantic and Eastern Pacific, the relative richness of cleaners increased as northern latitudes increased and decreased as southern latitudes, whereas in the Indian and Pacific realm it exhibited an opposite pattern (Figure S8). Sites with SST lower than 23°C never had more than two dedicated cleaner species, whereas facultative cleaners were found between 7 and 29°C (Figure S10). In other words, all sites with three or more dedicated cleaners were found in tropical waters with SST above 23°C (Figure S10b). Sites located <100 km from a refugia always had two or more dedicated cleaners.

3.4 | Biogeographical patterns of the standardized richness and abundance from belt transects and drivers

We did not observe any global pattern of distribution of the standardized richness of cleaner species estimated from UVCs (Figure 7a–c). On the other hand, the standardized abundance of all cleaners and facultative cleaners was higher in the Atlantic and Eastern Pacific than in other realms, ranging from 1 to 208 individuals (mean ± SD =128.9 ± 38 and 91 ± 24 individuals respectively [Figure 7d,e]). The average standardized abundance of dedicated cleaners also varied among realms, with it being higher in the Atlantic (1.76 ± 2.83 individuals) and lower in the Eastern Pacific (0.002 ± 0.004; Figure 7f). We did not detect any geographical pattern in the distribution of the relative abundance of dedicated cleaners, but, among the 110

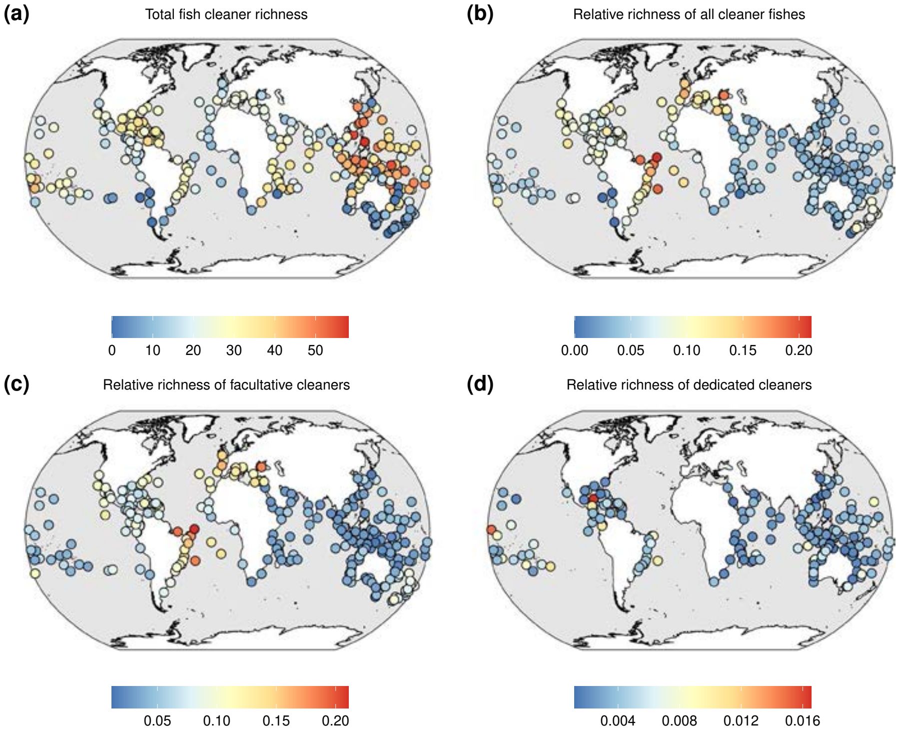

FIGURE 5 Robinson projection: Global gradient maps of (a) total cleaner fish richness, (b) relative richness of all cleaner fishes estimated from the ratio between cleaner fish richness and the total local species pool calculated from checklists; (c) relative richness of facultative cleaners; and (d) relative richness of dedicated cleaners across 290 localities. Cells with warm colours represent hotspots

tropical locations, Turks and Caicos Islands in the Caribbean, and Ilha Grande and Arraial do Cabo in the Western Atlantic had the highest relative abundances for both types of cleaner species (Figure 7d–f).

The standardized abundance of facultative cleaners estimated from UVCs was negatively influenced by minimum SST, the local species pool and the standardized abundance of potential clients observed in the UVCs (Figure 6; Table S7). The standardized abundance of dedicated cleaners estimated from UVCs was positively influenced by the local species pool but negatively by the standardized abundance of potential clients observed in the UVCs (Figure 6; Table S5).

4 | DISCUSSION

We compiled and combined different datasets to explore macroecological patterns of cleaner reef fish fauna at a global scale. Our results revealed a high disparity in traits between facultative and dedicated cleaners, which together occupied less than 39% of the multidimensional trait space of the reef fish families in which they occur. Dedicated cleaners only occupied less than 1% of the functional trait space. Other studies in tropical and subtropical reefs show they contribute disproportionately to maintaining healthy reef fish communities (Côté, 2000), controlling parasite populations (Grutter, 2002) and influencing local reef species richness and abundance (Grutter et al., 2003; Waldie et al., 2011). We observed a wide variation in the dispersal and colonization capacity of cleaners according to the biogeographical realm. Our results also suggest that history left a strong imprint on the distribution of cleaner fish richness at a global scale. Furthermore, cleaner fish richness followed a pattern similar to that observed for the entire reef fish fauna, with hotspots in the Indo-Pacific and Caribbean provinces (Parravicini et al., 2013). However, the relative richness, compared to all fish species, of both facultative and dedicated cleaners had its highest peaks at high latitude locations which are characterized by low species richness. We also noted that the highest standardized abundance, adjusted to the local abundance of all species, of facultative cleaners was concentrated in the Atlantic and Eastern Pacific, whereas for dedicated cleaner it showed no clear pattern of distribution. The peak observed in both relative richness and standardized abundance may be associated with the high contribution of cleaner fish species in the local pool and the abundance of these poorer regions. On the other hand, we observed that the relative richness and standardized abundance of cleaner fishes were influenced by the same drivers proposed for the total reef fish fauna. Thus, our study provides a new view of how species traits vary between facultative and dedicated cleaners, as well as how historical, environmental, ecological and geographical factors may determine the macroecological patterns of cleaner fishes distribution at the global scale.

4.1 | Species traits and multidimensional trait space occupied by cleaner fishes

We found that traits differed between cleaners and other reef fishes and also between facultative and dedicated cleaners. When combined, cleaners occupied 39% of the multidimensional trait space of the reef fish families in which they occur, whereas when separated into cleaning types, dedicated cleaners occupied less than 1% of the entire cleaners' trait space. Thus, these results confirm our first hypothesis that facultative cleaners exhibit a higher variation in their traits than dedicated cleaners. This reflects the larger number of facultative compared with dedicated species and differences in their evolutionary histories given that each biogeographical realm has only a single genus of dedicated cleaners (*i.e. Elacatinus* spp.

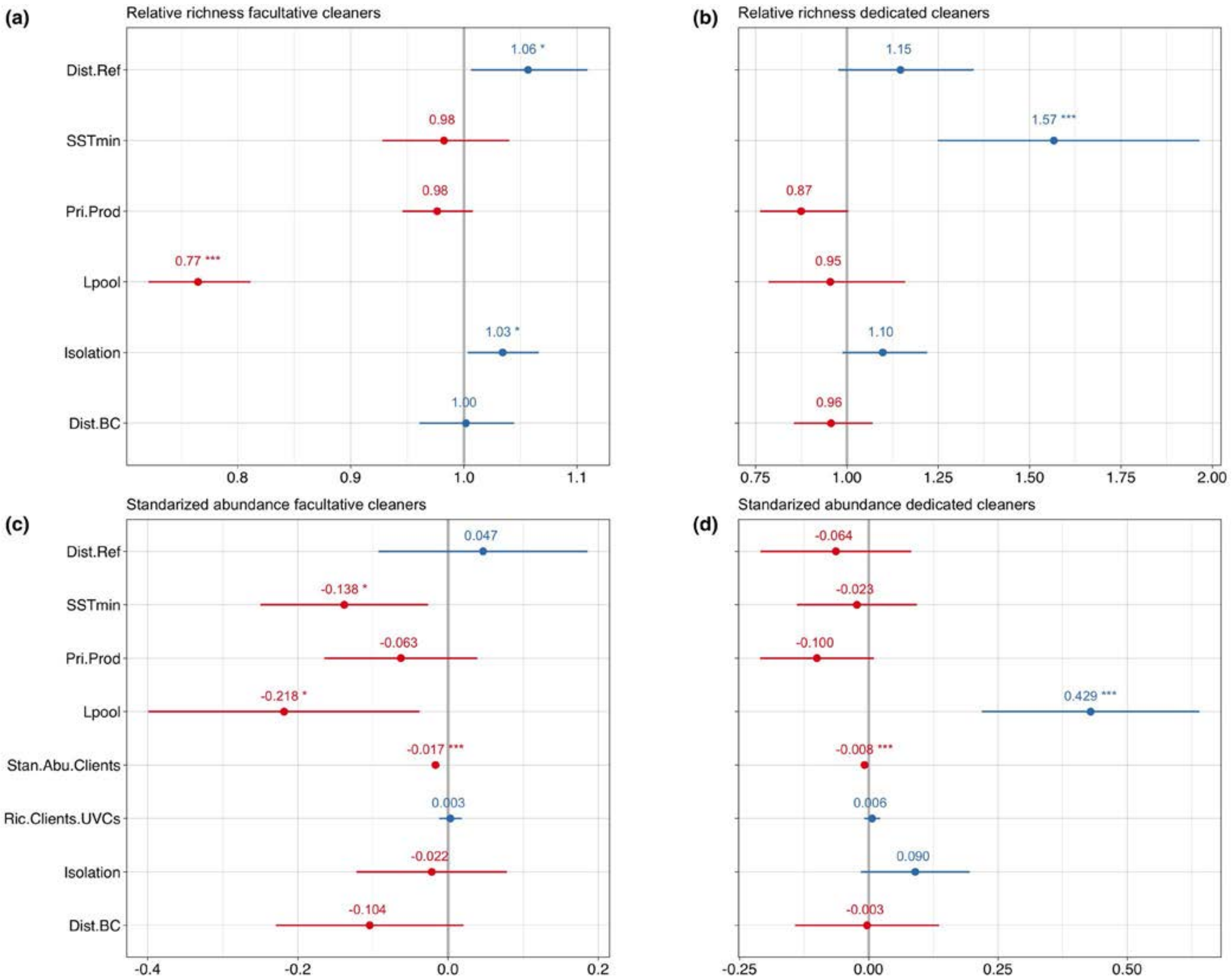

FIGURE 6 Mean effects of historical (Dist. Ref: distance from refugia), environmental (SSTmin: annual minimal sea surface temperature, Pri. Prod: primary productivity), ecological (Lpool: Local species pool extracted from checklist, Ric. Clients: relative richness of potential clients, Stan. Abu. Clients: relative abundance of potential clients) and geographical (Isolation: isolation from the coast, Dist.BC: distance from centre of biodiversity) factors on the relative richness (a, b) and standardized abundance (c, d) of cleaner fish. Values are standardized as effect sizes, circles represent mean parameter estimates and the lines represent 95% confidence intervals. All the effect sizes in blue represent positive relationships and the ones in red negative relationships. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

[Atlantic realm], *Tigrigobius* spp. [Eastern Pacific realm] and *Labroides* spp. [Indo-Pacific realm; Baliga & Mehta, 2019; Huie et al., 2020]).

The trait space occupied by both facultative and dedicated cleaners (38.96% and 0.04% respectively) indicates that, overall, this ecological group is highly specialized and is more densely packed in the trait space than non-cleaner species (61%). These results confirm our hypothesis that cleaner fishes occupy only a small fraction of the available multidimensional trait space occupied by the fish lineages in which they originated. Furthermore, the high specialization of dedicated cleaners influences cleaning mutualism networks (Guimarães et al., 2007; Quimbayo et al., 2018; Sazima et al., 2010), and therefore explain the trait space occupied by this cleaner group. The disproportional packing of cleaner species in the trait space supports the idea of a high functional redundancy among cleaners, at least at the resolution we can target with our trait categories. Higher than expected functional redundancy is also reported for reef fishes in species-poor provinces (Mouillot et al., 2014), freshwater fishes (Toussaint et al., 2016) and corals (McWilliam et al., 2018). Dedicated cleaners evolved between 8 and 12 Myr, whereas the first transition to facultative cleaners began much earlier at 20 Myr (Baliga & Mehta, 2019). This may explain the difference in the level of dependence of each cleaner type in obtaining food via cleaning interactions (Vaughan et al., 2017). Dedicated cleaners required more time to developed more specialized morphological and behavioural adaptations to attract the attention of clients than did facultative cleaners, due to the latter's higher dependency on cleaning interaction to obtain food (Côté, 2000). Thus, our results confirm that dedicated cleaners have a lower phylogenetic trait divergence than do facultative cleaners (Baliga & Mehta, 2019), as the latter have had more opportunity to diversify and develop a wider range of traits.

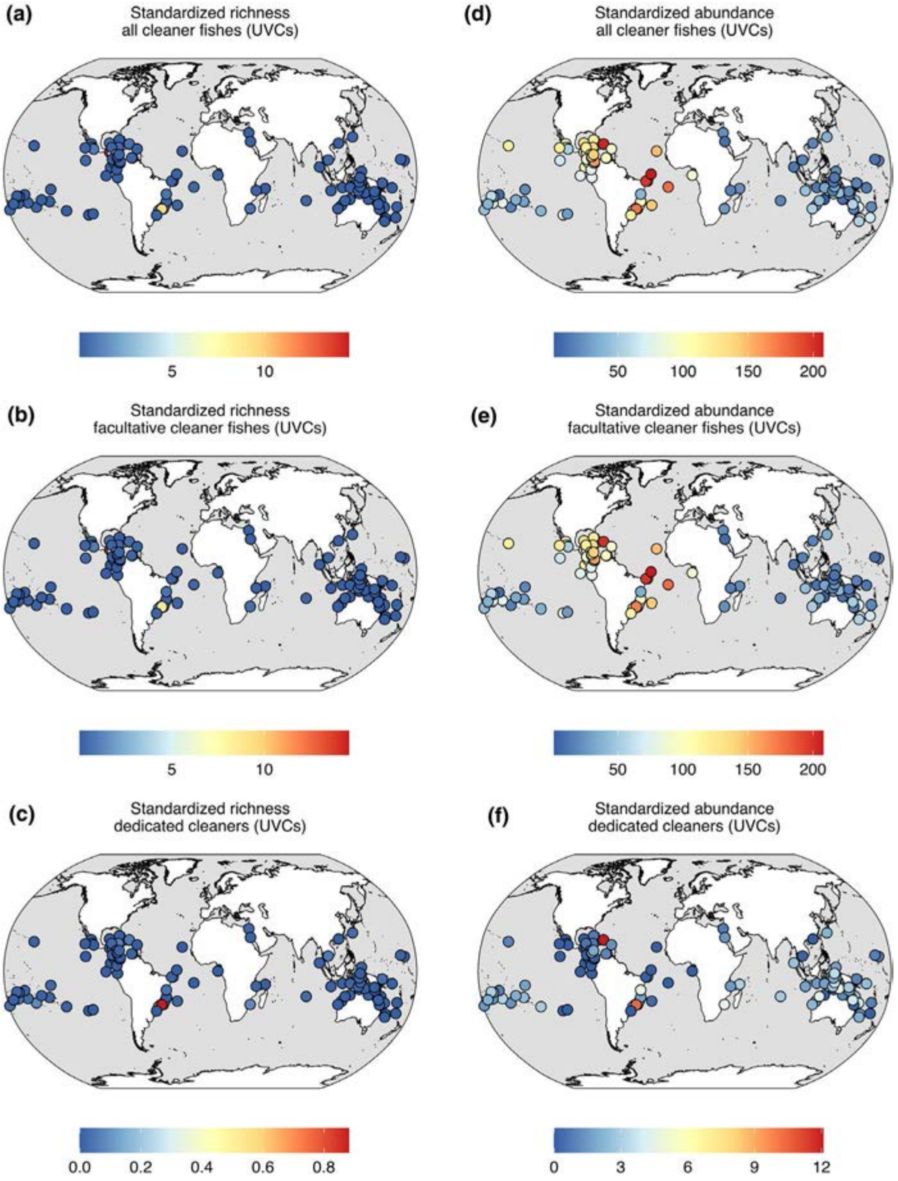

FIGURE 7 Robinson projection: Global gradient maps of standardized cleaner richness (a) and standardized abundance calculated from the selection of the minimum number of fish individuals by location observed in underwater visual census (b); standardized richness (c) and abundance (d) of facultative cleaners; standardized richness (e) and abundance (f) of dedicated cleaner across 109 tropical localities

Our results indicate that dedicated cleaners are mainly sedentary, diurnal and remain mostly near the bottom. This may explain their development of aposematic coloration, which involves a lateral body stripe to increase chromatic contrast between the cleaners and the background (Cheney et al., 2009; Lettieri et al., 2009). On the other hand, the broad diet of facultative cleaners corroborates their low dependency on cleaning interactions to obtain food when compared with dedicated cleaners (Côté, 2000). However, further studies exploring in more detail the diet of both facultative and dedicated cleaners are necessary to understand the ecological niche occupied by each type of cleaner. The size of facultative cleaners did not differ from non-cleaners, and was on average four times larger than that of dedicated cleaners, indicating that small size is a critical trait for dedicated cleaners. The convergence of small body size in dedicated cleaners from different families has been suggested as a key condition for establishing cleaning interactions, as it allows them to clean clients' external openings, such as mouth and gills (Baliga & Mehta, 2019). Moreover, dedicated cleaners occupy mostly shallow areas and have both narrower geographical ranges and lower dispersal capacities than facultative cleaners. Dedicated cleaner gobies (*e.g. Elacatinus* spp.) do not occur at the isolated island of Bermuda probably due to low PLD (Taylor & Hellberg, 2005; Walsh et al., 2017). These results are consistent with previous studies showing that reef fish species with small body size, specialized diet and short PLD often have narrow geographical ranges (Luiz et al., 2013). Thus, our results indicate that dedicated cleaners have a lower phylogenetic trait divergence than facultative cleaners, the latter having more opportunity to diversify and develop a wider range of traits.

4.2 | Relationships among dispersal and colonization traits and regional pool

However, our analysis of the relationships between traits related to dispersal and colonization capacities and regional diversity indicates that these capacities are very different across realms. The Eastern

Pacific and Atlantic, for example, display similar patterns whereas the Indo-Pacific usually display opposite patterns. Luiz et al. (2013) found that for all fish species pooled there was a correlation between PLD, species size and geographical range, which varied across realms, with a steeper gradient in the Indo-Pacific. Here, however, we found that cleaners, despite being smaller and living in shallower water than non-cleaner species, also can exhibited larger geographical ranges. Thus, one prediction is that cleaners should therefore have longer PLDs. This is indeed the case in regions with high richness (regional richness >500 species), but the opposite in species-poor regions. The change to the opposite pattern in the relationship between PLD and regional diversity of cleaners versus non-cleaners when 500 total species was reached is striking. Our results show that this is due to differences among realms, with completely different dispersal strategies and evolutionary histories for cleaners in the Atlantic and the Indo-Pacific. Minimum SST seems to play the same role in these differences, with a congruence of results across realms for SST below 20°C. This indicates a different evolutionary history of cleaners in cold-temperate waters versus tropical waters, as well as differences in evolutionary history linked to realms (Atlantic-Eastern Pacific vs. Indo-Pacific). Hence, the same ecological function is ensured by cleaner fishes with great differences in their dispersal and colonizing capacities depending on the realm and temperature. Similar ecological convergence with major differences in life-history strategies across regions is illustrated for terrestrial vertebrates (Belmaker & Jetz, 2015) meaning that an ecological function does not necessarily constrain the same traits and that multiple combinations of traits may insure the same role.

4.3 | Biogeographical patterns of the relative richness of cleaner fishes from checklists and drivers

We recorded cleaner fishes in all marine realms, but the hotspots of total cleaner richness were located in tropical areas of the Indo-Australian Archipelago (IAA) and the Caribbean. This result is consistent with our hypothesis that the total cleaner fish richness should follow the same distribution described for all reef fishes (Bellwood & Meyer, 2009; Floeter et al., 2008). Evidence suggests that the IAA and the Caribbean are likely the main centres of origin, accumulation and overlap of reef fish fauna (Bowen et al., 2013), which can be explained by (i) old colonization processes linked to tectonic plate movements during the last 50 Myr (Leprieur et al., 2016), (ii) the formation of refugia in the IAA during the Quaternary glaciations (Pellissier et al., 2014), and the large past and current reef area (Parravicini et al., 2013). Overall, our results provide evidence that evolutionary history also left a strong imprint on the distribution of the main facultative cleaner richness at a global scale.

Bellwood and Hughes (2001) found that for 13 major reef fish families, the relative contribution of each family to total richness was nearly constant beyond 200 species in the species pools. Likewise, Knowlton (2001) proposed that major functions should be represented by a similar proportion of the species pool from one region to another. Our results are not consistent with this hypothesis and show that the relative richness of facultative cleaners differs among regions, being higher in SW Atlantic, Mediterranean and NW Atlantic locations. These results also contradict our hypothesis that the relative richness of facultative cleaners is higher in locations with high diversity. In the Mediterranean, cleaners compose on average 12% of the fish fauna with a peak of 17.5%, whereas they compose on average only 5% of the local fish fauna in the Indo-Pacific, with a maximum of 10%. In this sense, the high isolation and the absence of dedicated cleaners in the Mediterranean would favour the concentration of facultative cleaners. Similar examples can also be observed in Bermuda where the absence of dedicated cleaners favour the development of cleaning interactions by other species which are classified as facultative cleaners (Walsh et al., 2017). Somewhat similar principles may apply for the high relative richness of facultative cleaners around the Atlantic oceanic islands—which exhibit limited the colonization of reef fish species from the mainland, including cleaners due to its high isolation from the coast (Hachich et al., 2020). We suggest that the absence of dedicated cleaners in these peripheral locations opens the niche space for other fish species to explore cleaning as an alternative feeding strategy.

The relative richness of dedicated cleaners did not follow any pattern already described for reef fishes (Parravicini et al., 2013), which may be related to the low number of dedicated cleaners worldwide, only 18 species, too few to show a clear pattern (Vaughan et al., 2017). The highest relative richness of dedicated cleaners was found near refugia and at high SST (>23°C). The proximity of refugia correlates with the lower dispersal capacities of dedicated cleaners. High SST may be a pre-requisite for high parasite prevalence (Klaus Rohde & Heap, 1998), a requirement for the presence of permanent cleaning activities (Grutter, 1996). Moreover, the restricted geographical distribution of dedicated cleaners in tropical locations in the Indo-Pacific and Caribbean may favour strong intra and interspecific competition which, in turn, favour some species within clades to explore the cleaning role (Baliga & Mehta, 2019). For instance, the cleaning behaviour in Labridae is derived from corallivory (Floeter et al., 2018), whereas in Gobiidae it is derived from trophic generalists (Huie et al., 2020). Both the Indo-Pacific and Caribbean are tropical regions characterized by high temperatures and high richness that may both act upon the relative richness of dedicated cleaners, probably through the higher net diversification in tropical regions (Siqueira et al., 2016). The positive effect of distance from refugia and isolation on the relative richness of dedicated cleaners does not support our initial hypothesis. This result may be related to the distribution of all dedicated cleaners from the genus *Labroides* in the Indo-Pacific realm, which also includes greatly isolated locations, such as the Hawaiian Archipelago, Reunion or Chagos Islands (Baliga & Mehta, 2019).

4.4 | Biogeographical patterns of the standardized richness and abundance from belt transects and drivers

The standardized abundance of cleaners observed in the UVCs was influenced exclusively by environmental and ecological factors.

However, the effect of each factor differed among realms and between the type of cleaner species. For instance facultative cleaners showed hotspots in the Atlantic and Eastern Pacific realms. This suggests a strong pattern in the distribution of facultative cleaners and contradicts our initial hypothesis which predicted a higher abundance in the Indo-Pacific. This may be associated with the high contribution of facultative cleaners in the local abundance of reef fishes. For instance facultative cleaners such as *Thalassoma noronhanum*, *T. adscensionis*, *T. lucasanum*, *Johnrandallia nigrirostris* and *Stegastes santicpauli* account for about 15% of the total abundance in several locations in the Atlantic and Eastern Pacific (Krajewski & Floeter, 2011; Longo et al., 2015; Luiz et al., 2015; Quimbayo et al., 2019).

The negative effect of environmental and ecological factors on the standardized abundance of facultative cleaners indicates that these species are modulated independently by the factors that determine the global patterns of abundance of reef fishes. Moreover, the high peaks in standardized abundance of facultative cleaners indicate that they arise more frequently in the absence of the dedicated cleaners (Narvaez et al., 2015; Quimbayo et al., 2012; Walsh et al., 2017). Dedicated cleaners are probably very efficient and may hinder the diversification of facultative cleaners. However, when dedicated cleaners are absent the number of facultative cleaner species increases maintaining a similar level of cleaning activity. Thus, we suggest that the contribution of facultative cleaners in the standardized abundance is dependent on low local species richness and the absence of dedicated cleaners, a situation that favours the exploration of cleaning behaviour by less specialized species.

We observed no pattern in the distribution of the standardized abundance of dedicated cleaners at a global scale. Contrary to facultative cleaners, the abundance of dedicated cleaners was not related to local or regional diversity. Dedicated cleaners had their highest standardized abundances in few locations with low local species pool but abruptly declined in high diversity sites. Several hypotheses can be inferred from this observation. The resource of these dedicated cleaners (parasite load of client or total amount of available parasites) is probably linked to total fish abundance, which is in turn linked to total regional diversity (Parravicini et al., 2013). The narrow geographical distribution of dedicated cleaners in tropical areas can be linked to high SST and low isolation from the refugia as these influence past and current diversity hotspots (Pellissier et al., 2014). Thus, dedicated cleaners of the genus *Tigrigobius* are restricted to the Eastern Pacific (Huie et al., 2020; Quimbayo & Zapata, 2018), *Elacatinus* to the Western Atlantic (Dunkley et al., 2019; Johnson & Ruben, 1988; Sazima et al., 2000; Whiteman & Côté, 2002), and *Labroides* to the Indo-Pacific (Sims et al., 2014). On the other hand, sampling of dedicated cleaners using UVCs may tend to underestimate the abundance of cryptobenthic species such as small benthic cleaners. Moreover, due to the lack of effect of the standardized abundance of potential clients on the standardized abundance of dedicated cleaners, we propose that dedicated species naturally have a low abundance that may be associated with a dilution phenomenon as these species occur in locations recognized as reef fish abundance hotspots (Yancovitch Shalom et al., 2020).

5 | CONCLUSION

Our study is the first integrative analysis exploring the variation in species traits, the patterns of distribution of cleaner fishes and their historical, environmental, ecological and geographical drivers across tropical and subtropical regions. The great variation of species traits between facultative and dedicated cleaners reflects both their different evolutionary history and their varying degree of specialization. However, this variability represents only a small fraction of the vast combination of reef fish traits. On the other hand, our results show that the relative richness and standardized abundance of cleaners are heterogeneously distributed across the marine realms. However, dedicated cleaners are concentrated mainly in tropical areas. Thus, the cleaner fish fauna characterizes a conspicuous example of the importance of considering ecological interactions to better understand the global patterns of distribution of reef fish fauna.

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DATA AVAILABLILITY STATEMENT

Data can be found at the Zenodo repositories: http://doi.org/10.5281/zenodo.1484591 (abundance data); http://doi.org/10.5281/zenodo.4455016 (species traits).

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