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Similar levels of trophic and functional diversity within damselfish assemblages across Indo-Pacific coral reefs

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Abstract

1. Understanding the forces that influence the dynamics of communities is a key challenge to undertake in changing environments. Despite recent advances in coral reef community ecology, a more comprehensive knowledge about processes (niche-related traits and phylogenies) driving the composition of reef fish community is needed.
2. Here, we conducted a quantitative comparison of these processes in damselfish assemblages that belong to three distinct Indo-Pacific coral reefs differing in taxonomic composition, morphology and degree of human disturbance.
3. We compiled a dataset of eight categorical variables to estimate functional diversity of damselfish assemblages and a second one of stable isotope ratios to evaluate isotopic diversity, a proxy of trophic diversity. Both datasets represent the eco-functional diversity and provide insights into niche-related traits. Indices were then computed to grasp complementary facets of this diversity: the size of multidimensional space (richness), the partitioning of niches (divergence) and the regularity in the distribution of niches (evenness) within each space. We also tested whether functional and trophic traits displayed some evolutionary niche conservatism.
4. We found that functional richness was influenced by the number of species and functional entities (unique combination of trait values), and that the portions of the functional spaces filled by assemblages mainly overlapped. Functional divergence and evenness indices were similarly high. For trophic diversity, the isotopic richness remained equivalent, while the two other indices were of high values and did not significantly differ. Both functional and trophic traits did not display any phylogenetic conservatism.
5. We demonstrated consistent levels of eco-functional diversity in Indo-Pacific coral reef damselfishes. Each assemblage hosted species whose niches were highly differentiated and evenly distributed in eco-functional spaces of similar sizes, albeit the extent of functional space varied with the species richness. Assemblages also tended to share similar functional attributes. The inconsistent phylogenetic structures of eco-functional traits and the similarity in diversity

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indices suggest that the assemblage composition of damselfishes is mainly driven by niche-related processes rather than by phylogenetic relatedness. Our work helps to determine which mechanisms shape coral reef fish biodiversity and more particularly assemblages issued from replicated events of ecological radiation.

KEYWORDS
community assembly, coral reef fishes, diversity indices, functional traits, phylogenetic comparative methods, repeated adaptive radiation, species niche, trophic diversity

1 | INTRODUCTION

In the face of environmental changes, understanding how communities assemble and the underlying mechanisms are important challenges to undertake (Cavender-Bares, Keen, & Miles, 2006). Community composition is mostly driven by niche-related factors (following local environmental filters and the principle of competitive exclusion) and by phylogenetic relatedness among organisms (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Cavender-Bares et al., 2006). These factors are critical to investigate because they provide insights about how species diversity is maintained and how community processes are shaped across space and time.

Competitive exclusion and limiting similarity favour the coexistence of species that differ along some axes of the niche (Schoener, 1974). A species' niche was formally conceptualized as an n-dimensional hyper volume defined by all resources exploited by a given population (Hutchinson, 1957). Some dimensions (i.e. the origin of food and trophic interactions) can be appraised with stable isotope ratios, which are commonly used as proxies of trophic diversity (Bearhop, Adams, Waldron, Fuller, & Macleod, 2004; Layman et al., 2012). When isotopic axes also reflect other environmental variables (e.g. habitat use; Fry, 2002; Quevedo, Svanbäck, & Eklöv, 2009), they can be considered as indicators of ecological diversity.

By analogy with the n-dimensional niche concept, functional diversity is also represented by the distribution of species in a multidimensional space whose axes characterize functional features, which are diverse variables embodying the life strategy of organisms (Mouchet, Villéger, Mason, & Mouillot, 2010; Villéger, Mason, & Mouillot, 2008). Both trophic and functional diversities represent the overall eco-functional diversity and are commonly quantified with several indices that reflect complementary facets of the distribution of organisms in a multidimensional space (Mouchet et al., 2010). The richness index depicts the amount of isotopic or functional space occupied by a given species' assemblage (Cucherousset & Villéger, 2015; Villéger et al., 2008). Divergence and evenness are two indices that measure, respectively, the repartition (defined as the distance from the centre of the multidimensional space) and the regularity in the distribution of species within this space (Cucherousset & Villéger, 2015; Villéger et al., 2008).

Phylogenetic relatedness is also a key factor that affects community composition and can impact niche partitioning. Two scenarios have been proposed: (1) phylogenetically related species co-occur more often in the niche space because they share similar eco-functional trait values (due to environmental filtering) and may suggest a niche conservatism or, in contrast, (2) their similarity causes them to compete more strongly, resulting in competitive exclusion and indicative of a niche lability during evolution (Li, Ives, & Waller, 2017; Losos et al., 2003). Among various evolutionary patterns, repeated events of adaptive radiation are crucial to investigate as they may be responsible for a significant portion of diversity on Earth (Mahler, Ingram, Revell, & Losos, 2013). They consist of replicated sets of descendants that have evolved separately in multiple isolated areas, but display similar morphological, ecological and/or behavioural characteristics. These repeated events of adaptive radiation have been beautifully illustrated by *Anolis* lizards in the Caribbean Archipelago (Losos, Jackman, Larson, Queiroz, & Rodriguez-Schettino, 1998) and cichlids in the African Great Lakes (Cooper et al., 2010; Muschick, Indermaur, & Salzburger, 2012). The evolutionary history of damselfishes (Pomacentridae) is a rare example of the occurrence of an iterative ecological radiation in the ocean (Frédérich, Sorenson, Santini, Slater, & Alfaro, 2013). Damselfishes have experienced many repeated convergences wherein subclades radiated across similar trophic strategies (i.e. pelagic foragers, benthic feeders and an intermediate group) and similar morphologies (Cooper & Westneat, 2009; Frédérich, Cooper, & Aguilar-Medrano, 2016; Frédérich et al., 2013). The case of clownfishes (Amphiprionini), a tribe within the Pomacentridae, further illustrates this process of diversification with a main clade that radiated first in the Indo-Australian Archipelago, followed by a second one with analogous ecological requirements that occurred independently along the East African coast (Litsios, Pearman, Lanterbecq, Tolou, & Salamin, 2014).

Using phylogenetic comparative methods, the aforementioned examples (e.g. Frédérich et al., 2013; Litsios et al., 2014; Losos et al., 1998) emphasize the presence of evolutionary convergences with combined ecological and morphological traits of taxa. Nevertheless, many other aspects of these replicated sets of lineages remain unexplored. For example, little is known about the functional diversity of assemblages including convergent lineages that emerged from iterative processes of ecological radiation, or which of the niche-related processes and phylogenetic conservatism are the major factors shaping these assemblages.

In the present study, we seek to further quantify factors driving community composition by comparing damselfish assemblages that have evolved separately in three different coral reefs varying in taxonomic composition, morphology and degree of human disturbance. As species may respond differently to environmental conditions, we hypothesize that differences exist in the three complementary facets (i.e. richness, divergence and evenness) of trophic and functional diversity among assemblages. We also tested whether the studied eco-functional traits display evolutionary conservatism. The expected corollary is that closely related species should be eco-functionally more similar than distantly related ones.

2 | MATERIALS AND METHODS

2.1 | Taxa sampling

We selected three coral reef ecosystems (Madagascar, Dongsha and Moorea) located in the Indo-Pacific ocean realm (Figure 1a).

2.1.1 | Madagascar

A sampling campaign was conducted in November 2005 at the Great Reef of Toliara (GRT) in the southwest of Madagascar (23°36′S; 43°66′E) in the Indian Ocean. The GRT is a barrier reef 19 km long with a width between 1 and 3 km, bordered by two rivers at each side and located 2 km seaward of Toliara. Its lagoon reaches on average 10 m depth and is partially covered with seagrass beds (Andréfouët et al., 2013; Harmelin-Vivien, 1981). Sampling of damselfishes occurred on the inner reef slope of the barrier reef, where substantial coverage of living corals remained (Figure 1a). As our sampling did not include any damselfishes from the outer slope of the GRT, they are hereafter referred as “Madagascar lagoon.” The GRT is an important fishing ground and a harvest place for invertebrates. Among others, overfishing and sewage discharges were responsible for a loss of about 40%–80% of the coral coverage over a period of 50 years (Andréfouët et al., 2013).

2.1.2 | Dongsha

In May–June 2015, we conducted a sampling expedition in Dongsha Atoll (20°35′N; 116°55′E) in the South China Sea. The ring-shaped atoll is about 25 km in diameter and consists of a submerged barrier reef encircling a semi-enclosed lagoon of 10 m depth (Li, Lee, Tew, & Fang, 2000). The inner side of the arc-shaped barrier reef is also covered by abundant seagrass beds. We sampled damselfishes within the lagoon (i.e. around the island, in coral patches and on the reef flat) and also on the outer slope of the barrier reef (Figure 1a). When the damselfish assemblage included species sampled across the whole reef system (including the lagoon and the outer reef), we referred to it as “Dongsha whole reef.” However, when it only comprised species from sites within the lagoon, it was named “Dongsha lagoon.” Dongsha Atoll is the first marine national park of Taiwan and became a marine protected area in 2007 where visits are only granted for researchers and the army (Li et al., 2000).

2.1.3 | Moorea

In 2014, we carried out a field campaign in Moorea Island, situated in the South Pacific Ocean (17°30′S; 149°50′W). The lagoon comprises coral patches in between sand banks and a fringing reef shaped as a wall (mean depth of 7 m). The barrier reef is made of a crest and a steep slope bathed by the South Pacific Ocean and was hereafter referred as the outer reef. Sampling mostly took place in coral reefs on the north coast where it started from the beach shore (i.e. fringing reef) until the outer slope of the barrier reef (Figure 1a). When the damselfish assemblage included species from all reef zones (fringing reef, reef flat and outer reef), we referred it as “Moorea whole reef.” When the assemblage only consisted of species from the fringing reef and the reef flat, it was named “Moorea lagoon.”

During the respective sampling campaigns, damselfishes were caught with the use of anaesthetics (i.e. quinaldine or clove oil with concentration of >40 and >60 mg/L, respectively) while snorkelling and scuba diving. Fishes were euthanized by an overdose (>400 mg/L) of MS-222 (tricaine-methanesulfanate). Sampling was conducted in accordance to the European Directive 2010/63/EU following the guidelines from the Animal Ethics Committee of ULg (Belgium), and under the laws and regulations of Madagascar, Taiwan and French Polynesia.

2.2 | Functional dataset

With a multi-tiered approach utilizing scientific articles, online databases and field observations, we collected environmental, biological and behavioural information for the 55 studied damselfish species. These data were summarized into eight categorical traits that describe the main facets of the functional diversity of damselfishes (see Appendix S1 in Supporting Information for their relevance and Table S1). (1) Fish size was coded using three ordered categories: 3.9–7.5 cm, 7.6–14.0 cm and >14.1 cm. (2) The position of fish along the water column was coded using three main categories: on or close to the substratum for species staying permanently on the bottom or at an approximate distance of 0.5–1.0 m, mid water to surface, and finally, both when species exploit the entire water column. (3) Microhabitat requirements were sandy areas, dead corals or rocks, corals (O) for damselfishes having obligated relationships with their live coral or anemone hosts and corals (F) for species with facultative or opportunist relationships with corals. (4) The group type and territoriality were coded simultaneously: group type consisted of four categories, whereas territoriality was coded as present or absent. The classification for the group size was solitary (exclusively alone), small (a dozens of individuals) and large groups (>12 individuals). (5) Farming activity was simply coded as present or absent. (6) The intensity of wave exposure was categorized as follows: zero to low, moderate and moderate to high. (7) There were four categories for the maximum depth: ≤6, ≤20, ≤40 and >40 m. (8) Sex change at the adult stage (including protandrous and protogynous sex changers) was coded as present or absent.

This set of eight functional traits and their respective number of categories yield a number of unique combinations of trait values called functional entities (FEs) (Mouillot et al., 2014; Villéger, Novack-Gottshall, & Mouillot, 2011). The number of FEs was calculated for each damselfish assemblage. These traits also constitute the basis to compute other indices of functional diversity.

2.3 | Stable isotope dataset

Samples of damselfish epaxial tissue were dried for 48 h at 60°C and ground into a homogeneous fine powder. Stable isotope ratios of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}/N) were measured with an isotope ratio mass spectrometer (IsoPrime100, Isoprime, UK) coupled in continuous flow to an elemental analyzer (vario MICRO cube, Elementar, Germany). Isotope ratios were conventionally expressed as δ values in ‰ (Coplen, 2011). Certified reference materials from the International Atomic Energy Agency (IAEA, Vienna, Austria) were sucrose (IAEA-C6, δ^{13}C = −10.8 ± 0.5%‰; *M* ± *SD*) and ammonium sulphate (IAEA-N$_2$, δ^{15}N = 20.3 ± 0.2%‰). Both these

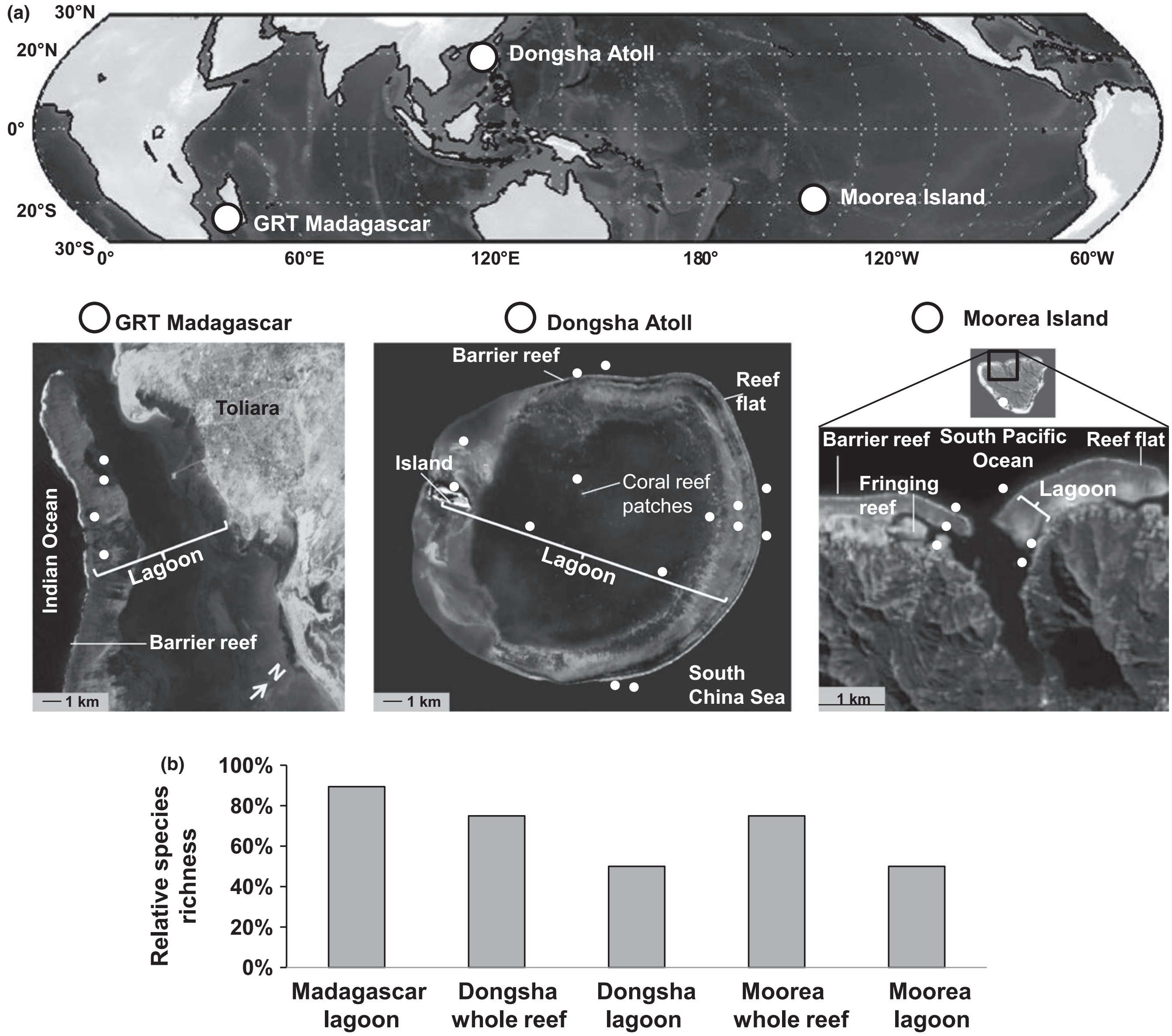

FIGURE 1 (a) Map and pictures of the three coral reef ecosystems where sampling campaigns were conducted: the Great Reef of Toliara (GRT) in Madagascar (only sites in the lagoon), Dongsha Atoll and Moorea Island. Local sampling sites within each coral reef are indicated by white-filled circles. (b) Histograms show the relative species richness for each damselfish assemblage, which is the ratio between the number of species sampled and the maximum number of species recorded at each reef

reference materials were calibrated against the international references Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. Hundreds of replicate assays of internal laboratory standards indicate precisions (*SDs*) of ±0.2 ‰ for δ^{13}C and ±0.3 ‰ for δ^{15}N.

This methodology was applied on damselfish individuals from Dongsha (whole reef and lagoon) as well as on individuals from the lagoon of Madagascar and the whole reef of Moorea (comprising its lagoon), although the isotopic data of the last two coral reefs were already used in Frédérich, Fabri, Lepoint, Vandewalle, and Parmentier (2009) and in Gajdzik, Parmentier, Sturaro, and Frédérich (2016), respectively.

2.4 | Statistical analyses to measure functional and trophic diversity

For each damselfish assemblage (whole reef or lagoon), functional and trophic diversity were estimated on functional traits and stable isotope ratios, respectively. Following the multifaceted framework of functional ecologists (Mouchet et al., 2010), we decomposed these diversities into three complementary components: richness, divergence and evenness.

Richness component is the total extent of multidimensional space utilized by species. We applied FRic (functional richness) and IRic (isotopic richness) indices (Cucherousset & Villéger, 2015; Villéger et al., 2008).

Divergence quantifies the distribution of species within the multidimensional space. FDiv (functional divergence) and IDiv (isotopic divergence) approach zero when species are close to the centre of gravity, whereas they equal one when species are located on the edges of the space (Cucherousset & Villéger, 2015; Villéger et al., 2008). The higher the values of these indices, the more species' niches are differentiated in the multidimensional space (Cucherousset & Villéger, 2015; Mouchet et al., 2010; Villéger et al., 2008).

Evenness characterizes the regularity in the distribution of species along the shortest tree linking all of them. FEve (functional evenness) and IEve (isotopic evenness) approach zero when species are packed within a small region in the multidimensional space, whereas they are maximized (i.e. closer to one) by an even distribution of species in this space (Cucherousset & Villéger, 2015; Villéger et al., 2008). The higher the values of these indices, the more its indicates a limitation in functional or trophic similarity, probably achieved through niche complementarity (Cucherousset & Villéger, 2015; Mouchet et al., 2010; Villéger et al., 2008).

FRic, FDiv and FEve were computed using the *MultidimFD* function (Maire, Grenouillet, Brosse, & Villéger, 2015; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Villéger et al., 2008) in R (R Core Team 2017). Pairwise functional distances between species were computed using the Gower's distance and then, a principal coordinates analysis (PCoA) was applied on this distance matrix (e.g. Mouillot et al., 2014). As suggested by the quality test performed with the *quality_funct_space* function (Maire et al., 2015), we used species' coordinates on the four principal axes of the PCoA through our analyses. The functional dissimilarity among damselfish assemblages was then explored by examining whether assemblages occupied different portions of the total functional space. It was performed on the two-dimensional functional space (i.e. PCoA 1 and PCoA 2) with the R-package spatstat.utils v.1.7-1 and corresponds to the functional dissimilarity index (Villéger et al., 2011). High values (closer to one than zero) mean that species' assemblages tend to occupy different portions of the functional space and have dissimilar functional attributes (Villéger et al., 2011).

IRic, IDiv and IEve were calculated with commands derived from the script "SI _ DIV" (Cucherousset & Villéger, 2015) in R (R Core Team 2017). These three indices are computed with scaled, unitless coordinates (from zero to one) of species from a two-dimensional isotopic space. The standardization of our stable isotope dataset allowed us to compare different assemblages of damselfishes. To assess potential inter-assemblage differences in each of these three indices, we performed Monte Carlo simulations with 10^4 iterations following the framework described as follows. In each iteration, we re-calculated the mean scaled isotopic values by adding random error (assuming Gaussian distributions) based on the scaled standard deviations of isotopic ratios for each species composing each assemblage. We then computed the IRic, IDiv and IEve indices (as described above) and we took the standard deviation of these indices across the 10^4 iterations to estimate their uncertainties. Finally, we calculated *z*-scores (i.e. the probability that the mean of each index is different) to test whether significant differences were found among species' assemblages based on the means and standard deviations of these indices (IRic, IDiv and IEve) from the Monte Carlo simulations.

2.5 | Phylogenetic signals of functional and trophic traits

To evaluate the influence of phylogenetic processes on community composition of damselfishes, we tested whether functional and trophic traits showed phylogenetic signals, which are defined as the statistical dependence among species' trait values due to their phylogenetic relatedness (Revell, Harmon, & Collar, 2008). We used the time-calibrated phylogeny described in Frédérich et al. (2013), providing an estimate of the evolutionary relationships among damselfish taxa. All the studied species were found in that phylogeny, except for *Pomacentrus aquilus*. Given the similarity in body shape and colour pattern (i.e. dark colour with an ocellus on the dorsal fin), the phyletic position of *Pomacentrus adelus* was used for *P. aquilus*. Using the Bayesian posterior distribution generated by BEAST v.1.8 (Drummond & Rambaut, 2007), we randomly sampled 100 trees that were pruned to match the species of each damselfish assemblage. This method allows the inclusion of uncertainty in tree topology and branch length for the calculation of phylogenetic signals.

We performed phylogenetic signal tests, separately, on the four-dimensional space built with functional traits and on the two-dimensional space based on scaled isotope ratios (i.e. trophic traits) for each lagoonal assemblage (Madagascar, Dongsha and Moorea) because all studied reefs possess a lagoon. The calculation of these signals (K_{mult}) were conducted using the R-package geomorph v.3.0.3 with 10^5 iterations (Adams, 2014; Adams & Otárola-Castillo, 2013). A $K_{mult} > 1$ indicates a stronger resemblance of species than expected under a Brownian Motion model of evolution (i.e. random walk), with a presumed corollary that traits are phylogenetically conserved. In contrast, a $K_{mult} < 1$ suggests a greater malleability of traits during evolution with less phylogenetic structure (Adams, 2014).

3 | RESULTS

3.1 | Species richness and taxonomic composition

We caught 583 damselfish individuals belonging to 55 species. During three respective sampling campaigns, 17 species were collected in the lagoon of Madagascar (Frédérich et al., 2009), 33 species in the whole reef of Dongsha (22 for its lagoon; present study) and 21 species in the whole reef of Moorea (14 for its lagoon; Gajdzik et al., 2016) (Table S2 in Appendix S1). According to species checklists, the maximum number of pomacentrid species is 19 for the GRT at Madagascar (Harmelin-Vivien, 1981), 44 for Dongsha (Chen, Jan, Huang, Kuo, & Shao, 2011) and 28 for Moorea (Brooks, 2016). Across the different damselfish assemblages, the relative species richness (i.e. the ratio between the number of species sampled and the maximum number of species recorded at each reef) ranged between 89% and 75% for, respectively, the lagoon of Madagascar and the whole reef of Dongsha or Moorea (Figure 1b). It reached 50% for the lagoons of Dongsha and Moorea. Five species were common to the whole reefs of Dongsha and Moorea, whereas three species were found in common among the three lagoonal assemblages. This represented between 14% and 24% of species shared among the three studied coral reefs.

3.2 | Evaluation of functional and trophic diversity

Although sampling effort and timing of fieldwork varied, we found that the diversities of lagoonal assemblages mimicked those of the whole reef, except the values of FRic for Dongsha.

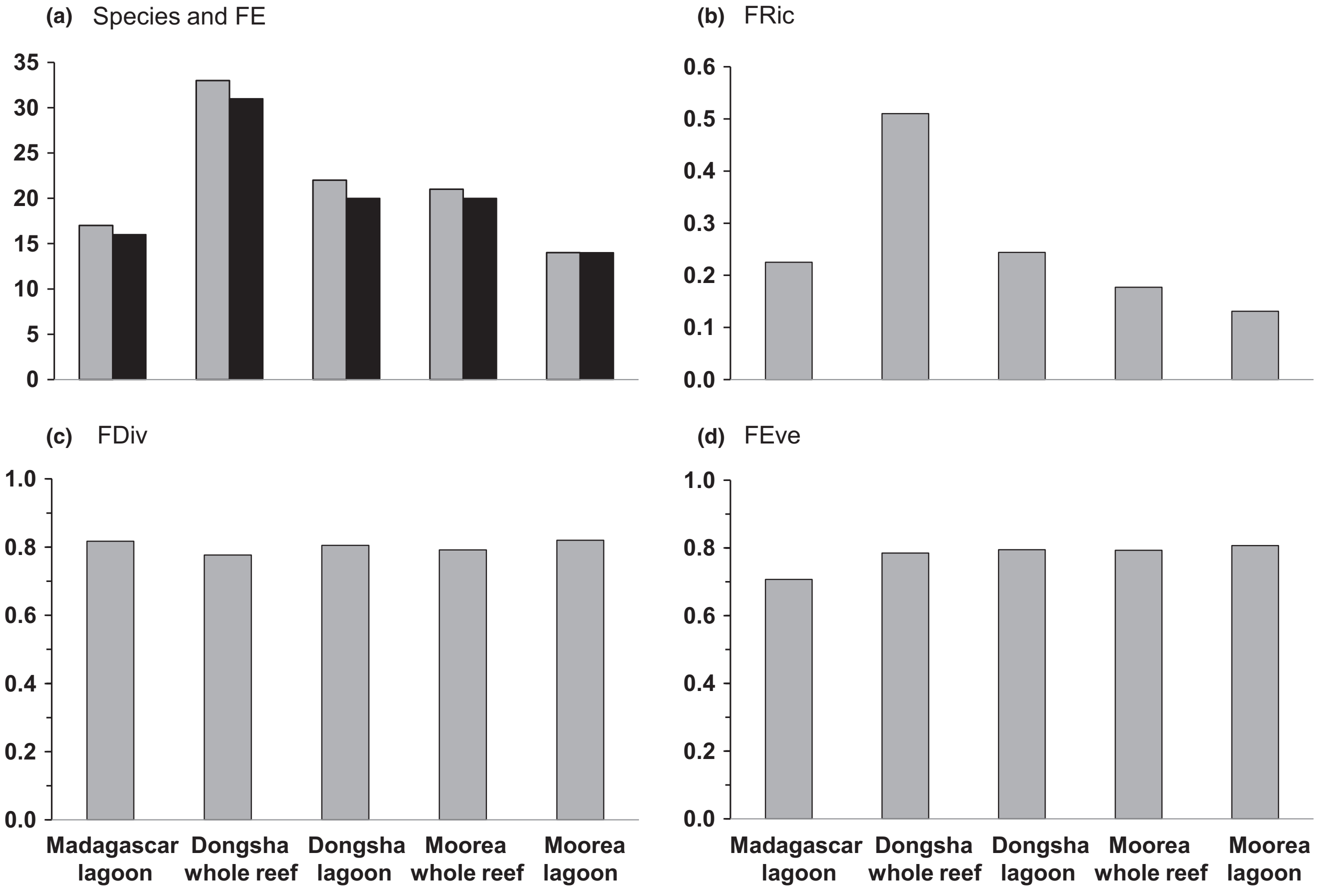

FIGURE 2 Histograms showing diverse indices that reflect complementary facets of functional diversity of damselfish assemblages. (a) Species richness (dark grey) and functional entities (black) (i.e. FEs, unique combination of trait values), (b) functional richness (FRic, the smallest functional space filled by species composing each damselfish assemblage), (c) functional divergence (FDiv, how far species are located from the centre of the functional space) and (d) functional evenness (FEve, how regularly species are distributed in the functional space). *Y*-axes of histograms represent either the number of species/FE for each assemblage or the value of indices computed on four PCoA axes from a principal coordinate analysis applied on functional traits (see Materials and Methods)

3.2.1 | Richness

The number of FEs almost equated to the number of species (Figure 2a) and influenced the size of functional space (FRic), which was more than two times bigger for the whole reef of Dongsha (0.51) than the size of all other assemblages (Figure 2b). Although functional dissimilarity was the smallest when comparing whole reef and lagoonal assemblages, almost all values were <0.50 (Table S3 in Appendix S1) and this indicated that species' assemblages appeared rather functionally similar than dissimilar. No significant differences were found among all IRics and they largely overlapped, i.e. the 95% confidence interval (CI_{95}) ranged from 0.46 to 0.73 for the lagoon of Madagascar and from 0.56 to 0.80 for the whole reef of Dongsha (Figure 3a). The graphical representations of IRics were not identical among reef locations or reef zones (Figure 4a), although IRics displayed somewhat similar mode values, from 0.52 to 0.68 (Figure 3a).

3.2.2 | Divergence

FDivs remained quite similar and varied from 0.78 to 0.82 for the whole reef of Dongsha and the lagoon of Moorea, respectively (Figure 2c). This indicated that species were highly differentiated in the functional space. The distribution of species' isotopic niches in Dongsha showed a more centred dispersion in the isotopic space than the two other reef locations whose species' niches were mainly located on the edges of the convex hull (Figure 4b). Even though the dispersion of isotopic data visually fluctuated among reef locations, all IDivs did not significantly differ and largely overlapped, i.e. CI_{95} = (0.66; 0.75) for the whole reef of Moorea and CI_{95} = (0.68; 0.81) for the lagoon of Moorea (Figure 3b). Their mode values (0.70–0.75) were closer to one than zero, implying a relative high degree of differentiation in trophic niches.

3.2.3 | Evenness

FEves varied slightly among damselfish assemblages with the smallest value for the lagoon of Madagascar (0.71) and the highest one for the lagoon of Moorea (0.81; Figure 2d). Their values were closer to one than zero, which indicated that assemblages were rather characterized by an even distribution of species in the functional space. The shape of neighbouring-trees, representative of IEves, quite differed among all different assemblages. For Madagascar and Moorea, the tree was elongated with fewer branches than Dongsha whose form was more aggregated with many branches (Figure 4c). Nevertheless, IEves did not significantly differ and largely overlapped (Figure 3c): CI_{95} = (0.64; 0.78) for the whole reef in Moorea and CI_{95} = (0.71; 0.83) for the whole reef in Dongsha. Mode values of IEves (0.71–0.78) were closer to one than zero, suggesting a regular distribution of trophic niches.

3.3 | Phylogenetic signals of functional and trophic traits

The calculation of phylogenetic signals suggested no evolutionary conservatism in functional and trophic traits for each assemblage (Table 1). For the assemblage of Dongsha, the non-significant *p*-values indicated an absence of phylogenetic signal in the data. On the other hand, the assemblages of Madagascar and Moorea showed a significant degree of phylogenetic structure for these traits ($p < .05$, Table 1). However, all K_{mult} values were not >1, which meant that close relatives were not more similar in functional and trophic trait values than distant relatives under a Brownian motion model.

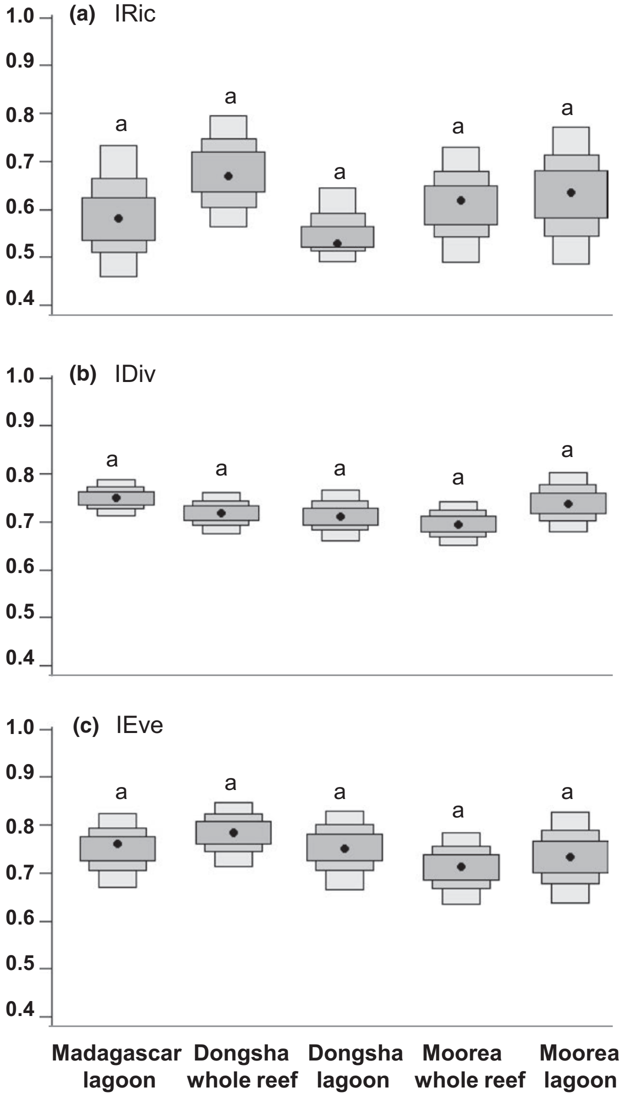

FIGURE 3 Three components of isotopic diversity of damselfish assemblages evaluated with scaled stable isotope ratios, which represent their trophic diversity: (a) isotopic richness (IRic, the smallest isotopic space filled by species composing each damselfish assemblage), (b) isotopic divergence (IDiv, how far species are located from the centre of the isotopic space) and (c) isotopic evenness (IEve, how regularly species are distributed in the isotopic space). IRic, IDiv and IEve were calculated with 10^4 Monte Carlo simulations. The same letters on top of each index indicate that the levels of the variables did not have significantly different values of IRic, IDiv and IEve ($p > .05$). All indices show 50%, 75% and 95% confidence intervals from dark to light grey respectively. Mode values are indicated by a black dot

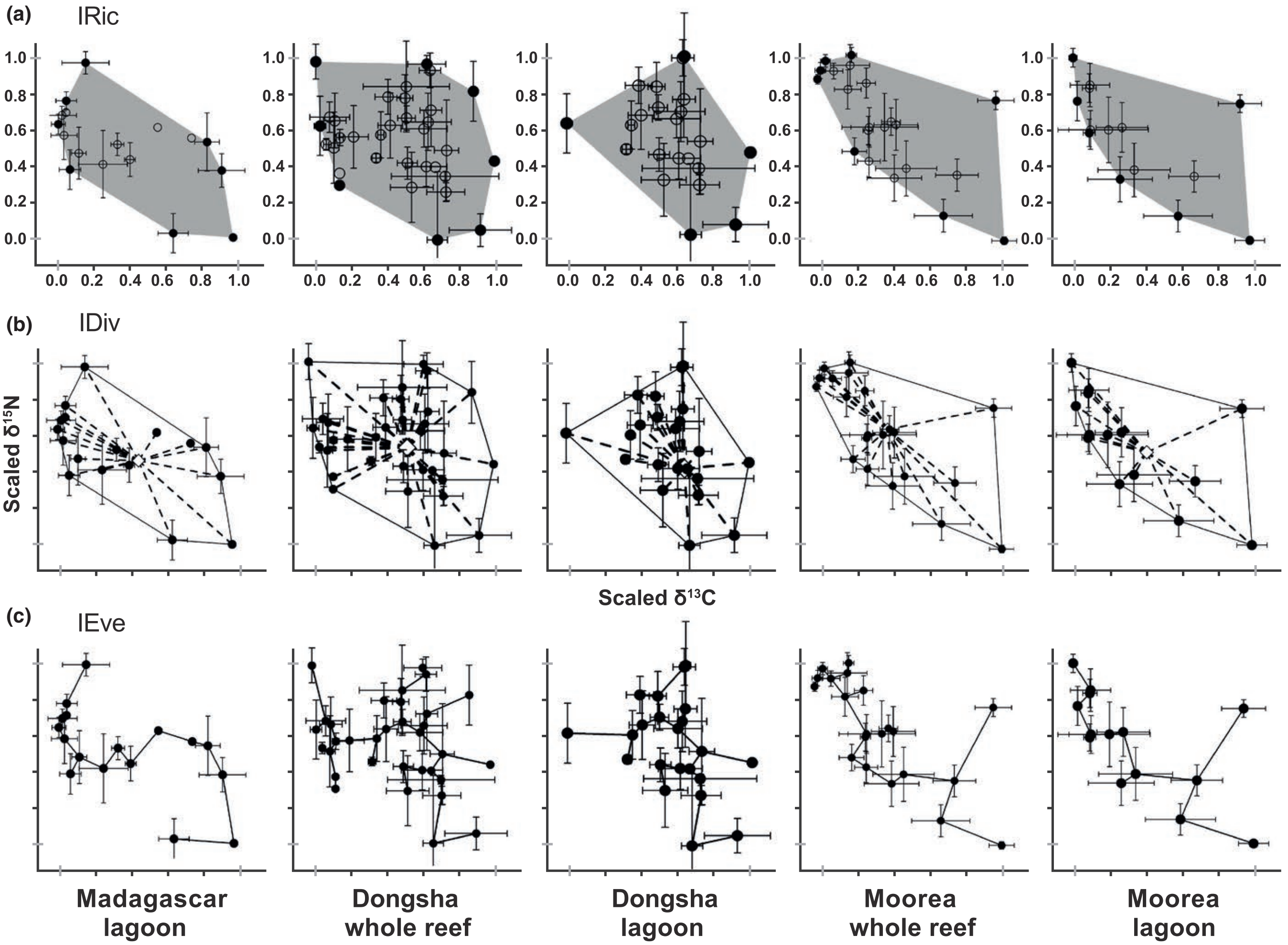

FIGURE 4 Biplots of mean scaled δ^{13}C and δ^{15}N of damselfish species from each assemblage that represent the three components of isotopic diversity (proxy of trophic diversity). (a) Isotopic richness (IRic, the smallest isotopic space filled by species composing each damselfish assemblage), (b) isotopic divergence (IDiv, how far species are located from the centre of the isotopic space) and (c) isotopic evenness (IEve, how regularly species are distributed in the isotopic space)

4 | DISCUSSION

We provide evidence of similar trophic and functional diversity of damselfish assemblages from three distinct Indo-Pacific coral reefs. In spite of some differences in phylogenetic structures among reefs, our results did not support any phylogenetic conservatism for functional and trophic traits.

4.1 | Consistent levels of eco-functional diversity in regionally distinct damselfish assemblages

We demonstrated that a higher species richness does not ineluctably imply the occupancy of a wider trophic space. Despite comprising the highest proportion of pomacentrids, the damselfish assemblage in Dongsha occupied a trophic space of a similar size as those from the two other reefs (IRics; Figure 3a) that have 1.5–2.3 times fewer species. Likewise, the poorest lagoonal assemblage with 14 species (Moorea) fills the same amount of trophic space as the richest lagoon with 22 species (Dongsha). Three different scenarios may induce such similarity in the size of trophic space. (1) Following the niche variation hypothesis, species of depauperate assemblages may expand their niches due to a release from interspecific competition, which can be associated with an increase in variation among individuals (Costa, Mesquita, Colli, & Vitt, 2008). (2) Species may also show some trophic plasticity by adapting their ecological strategy to current environmental conditions, for example versatility in resource requirement induced by an increased availability of scarce resources (Berg & Ellers, 2010). (3) Apart from trophic requirements, species may differ along other axes of the niche (Schoener, 1974). For example, a spatial partitioning of the same resources may allow the coexistence of more species without necessarily increasing the trophic space. For example, *Anolis* lizards feed on similar sized-prey but perched on tree branches at various heights (Schoener, 1974) or pelagic-feeding damselfishes hunt zooplankton (e.g. *Chromis* spp.) although they forage in different reef locations, fringing or barrier reefs (Gajdzik et al., 2016). Likewise, a partitioning of same resources on a diel temporal scale may also contribute to such similarity (Kronfeld-Schor & Dayan, 2003), with an expected corollary

TABLE 1 Outcomes of the phylogenetic signal analysis (K_{mult}) of functional and trophic traits for each lagoonal assemblage of damselfishes

	K_{mult} of functional traits			K_{mult} of trophic traits		
Reef site	***M* ± *SD***	**Median**	***p***	***M* ± *SD***	**Median**	***p***
Madagascar lagoon	0.66 ± 0.05	0.66	2.7×10^{-2}	0.74 ± 0.04	0.74	.03
Dongsha lagoon	0.43 ± 0.05	0.44	.09	0.33 ± 0.03	0.33	.45
Moorea lagoon	0.91 ± 0.05	0.92	4.0×10^{-4}	0.70 ± 0.06	0.71	.02

Shown are the mean values with standard deviations (*SD*) and associated *p*-values, and the median values obtained across our sample of 100 phylogenetic trees.

that different species rely on the same food source, but each differs in their daily use of it. The strong correlation between the number of species and FEs indicates that the similarity in the level of trophic diversity is compensated by a high functional dissimilarity. Damselfish species differ along various functional axes of their niches that relate to biological, ecological and environmental factors or even in ecosystem functions they provide.

Despite the decoupling between species/FE richness and trophic space, we found that a higher number of species and FEs is mirrored by an increase in the size of functional space in each assemblage. This is especially striking for the damselfish assemblage in Dongsha (Figure 2), for which non-mutually exclusive factors can generate such pattern. First, Dongsha is located close to the “Coral Triangle,” which houses the greatest richness of marine species world-wide (Hoeksema, 2007). Moreover, its benthic coverage is heterogeneous with a mix of scleractinian hard corals and alcyonacean soft corals (DeCarlo et al., 2017); and habitats with high structural complexity are typically suggested to support more species than nearby less complex ones (Bell, McCoy, & Mushinsky, 1991). In addition, the protective status of Dongsha in conjunction with an intermittent and small human population may also help to maintain its species-rich damselfish assemblage. Although species richness is not monotonically related to disturbance intensity (Mouillot et al., 2013), we observed a smaller functional space in the two other studied reefs that are likely more affected by anthropogenic activities. These differences among reefs may explain the absence of species with extreme functional trait values (Mouillot et al., 2013), e.g. habitat specialists. Indeed, the reefs of Madagascar and Moorea shelter 2–3.3 times less coral-dwelling damselfish specialists than Dongsha (Tables S1 and S2 in Appendix S1).

The two other facets of trophic and functional diversity reinforce our finding of eco-functional differentiation of species within each assemblage. Although reefs displayed different morphological features (i.e., basins and microatolls on the inner side of the barrier reef in Madagascar vs. reefs including a lagoon and an outer reef for Dongsha and Moorea), we found consistently high values of divergence and evenness (i.e., values of IDiv, FDiv, IEve and FEve were >0.70). These results indicate that damselfish assemblages are composed of species whose eco-functional niches are highly differentiated because of a more even distribution of resources among them. Although we cannot firmly identify specific mechanisms underlying these patterns, competition (or limiting similarity) seems to have the strongest influence on the damselfish assemblage composition as similar species in terms of eco-functional trait values appear to be less favoured within each assemblage. Nevertheless, the low degree of functional dissimilarity among species’ assemblages rather emphasizes the influence of habitat filtering. As suggested for sunfish communities (Helmus, Savage, Diebel, Maxted, & Ives, 2007), these different mechanisms had probably confounded effects on the structure of the studied damselfish assemblages, which in turn may have been blurred by other external factors (e.g. human activities).

Our study includes damselfish assemblages from various reefs differing in taxonomic richness, morphology and degree of anthropogenic disturbance. Despite these variations, the eco-functional diversity of Pomacentridae behaves similarly among reefs, with an overall relatively high trophic and functional differentiation within each assemblage. In addition, FEs are also speciose and thus, the loss of a species from a particular reef represents (almost) the loss of a unique FE. This urges the need for effective conservation management plan in human-impacted coral reefs (e.g. the GRT in Madagascar; Andréfouët et al., 2013).

4.2 | Inconsistent patterns of phylogenetic structure and the absence of evolutionary conservatism in regionally distinct damselfish assemblages

The analysis of phylogenetic signals revealed that closely related damselfish species are no more ecologically similar than expected by random divergence and thus, phylogenetic relatedness is not necessarily a precondition to an eco-functional similarity. Despite the lack of evidence to support evolutionary conservatism, we found that phylogenetic signals of eco-functional traits varied among the three lagoonal assemblages (Table 1). This variation might be due to the prevalence of certain subfamilies in a given assemblage. Indeed, Chrominae and Stegastinae subfamilies mainly contain species that display one trophic strategy (pelagic feeders or benthic feeders, respectively), whereas Abudefdufinae and Pomacentrinae include the three trophic strategies (i.e. pelagic feeders, benthic feeders and intermediate group) (Frédérich et al., 2013). Species from Chrominae have also the tendency to exhibit similar habitat-behavioural requirements as well as those from Stegastinae and this could increase the detection of phylogenetic structure and conservatism (e.g. Gajdzik et al., 2016). In contrast to the assemblages of Madagascar and Moorea having a large number of species from Chrominae (Figures S1 and S2 in Appendix S1), the Dongsha assemblage comprises the highest proportion of

Pomacentrinae (68% of species' assemblage) and depicts a situation wherein closely related species exhibit different trophic strategies (Figure S3 in Appendix S1). There, the weaker link between phylogenetic relatedness and eco-functional similarity was likely the cause of a non-significant phylogenetic signal and an absence of phylogenetic structure. Despite differences in their prevalence, each damselfish assemblage systematically contained members of the four main subfamilies. This observation illustrates one outcome of the phylogenetic limiting hypothesis: competitive exclusion of closely related species results in the frequent coexistence of distantly related species in ecological communities (MacArthur & Levins, 1967). Taken as a whole, our results suggest that the Pomacentridae appears similar to *Anolis* lizards, which also repeatedly diversified across recurrent similar ecomorphs and for which evolutionary divergence overcomes niche conservatism (Losos et al., 1998, 2003). Nevertheless, we acknowledge that the interpretation of conservatism from phylogenetic signals has to be taken with caution. Phylogenetic signal is context- and scale-dependent (e.g. family vs. regional level) as phylogenetic conservatism may be more easily detected in only localized regions of the phylogenetic tree (Litsios et al., 2012). Similar phylogenetic signals may also be attributed to various evolutionary processes, which some increasing the signal (e.g. high differential niche rate, random drift) or others decreasing it (e.g. strong stabilizing selection, constant functional constraint) (Losos, 2008; Revell et al., 2008).

Based on our results of similar levels of trophic diversity in each assemblage of Pomacentridae (especially the size of trophic spaces) and on the iterative nature of their ecological diversification (Frédérich et al., 2016), we further suggest that such repeated convergences have likely driven the type of relationships between the damselfish consumers and the resources they utilized. For example, processes shaping plant–pollinator and herbivorous fishes–benthos dynamics (Brandl, Robbins, & Bellwood, 2015) or even planktivorous fishes–pelagic compartment relationships may be more alike than expected. These processes are precursors of niche specialization as nectar, algae and zooplankton are replenished at high rates in the environment and form an extremely diverse network of abundant resources with varying accessibility (Brandl et al., 2015), but they may also restrict the choice of dietary association either as a consumer–producer (damselfishes–algae) or a consumer–consumer (damselfishes–zooplankton) relationship. Intrinsic damselfish features (e.g. body plan and peculiar morphological traits) may also limit their diversification by impeding the colonization of new adaptive zones (e.g. Frédérich, Olivier, Litsios, Alfaro, & Parmentier, 2014) and this probably contributed to the overall similarity in the facets of eco-functional diversity among assemblages.

5 | CONCLUSION

This study reveals similar eco-functional diversity in damselfish assemblages across Indo-Pacific coral reefs that differ not only in their taxonomic diversity and reef morphology, but also in their degree of human impacts. Counter to our simple predictions, assemblages of Pomacentridae are consistently characterized by a high degree of differentiation in eco-functional niches that are evenly distributed in eco-functional spaces of similar sizes, although the size of functional space is affected by the species/FE richness. Niche-related processes mainly drive the assemblage structure of damselfishes in coral reef ecosystems. Nevertheless, phylogeny still plays a role as niche complementarity occurred not only at an ecological scale, but also during evolution. The inconsistent patterns of phylogenetic structure suggest that a lability of eco-functional traits seems to better describe our empirical dataset. Overall, our results offer a glimpse of which mechanisms maintain coral reef fish biodiversity, although large-scale studies across different faunas and ecosystems are required to broaden our findings. We anticipate that applying our approach more broadly may help to better understand how communities from impacted environments will recover and re-assemble along various trajectories of degradation.

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DATA ACCESSIBILITY

The topographic map generated for this study is available as grids from ETOPO5 database: http://www.ngdc.noaa.gov/mgg/global/etopo5.html. The satellite images of Madagascar, Moorea and Dongsha are available here: https://www.arcgis.com/home/index.html and http://www.nspo.narl.org.tw/en2016/. The functional dataset of damselfishes is provided in the supporting information of this paper (Table S1 in Appendix S1). The isotopic dataset was archived in the Dryad Digital Repository https://doi.org/10.5061/dryad.pj784 (Gajdzik et al., 2018). The time-calibrated phylogeny is described in Frédérich et al. (2013). R scripts are made available by Sébastien Villéger: http://villeger.sebastien.free.fr/Rscripts.html.

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