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Rapid and repeated evolution of pigmentation patterns in reef fishes

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Abstract

Background Pigmentation patterns are central to animal biology—shaping camouflage, signaling, and mate selection—and uncovering the mechanisms driving their diversification is key to understanding the evolutionary principles that generate this fundamental dimension of biodiversity. Reef fishes exhibit an incredible variety of patterns, from simple spots to intricate designs. To date, the underlying evolutionary processes that govern their diversification remain unclear.

Results Here, we investigate the relationship between pigmentation pattern diversity, species richness, and geography across six iconic reef fish families. We provide evidence for a positive correlation between pattern diversity and species richness, with a high divergence of pigmentation patterns in every biogeographic region. Then, by using a suit of phylogenetically informed comparative analyses, we demonstrate that the evolution of pigmentation patterns is characterized by a combination of rapid and constrained phenotypic diversification.

Conclusions Overall, our findings illuminate factors that explain pigmentation pattern diversity in living reef fishes, revealing that speciation events have driven constant high levels of pigmentation pattern disparity within subclades and across globally variable reef fish assemblages.

Keywords Color evolution, Coral reef fishes, Convergence, Disparity, Diversification, Macroevolution

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Background

Color patterns are fundamental to the survival of organisms across the Tree of Life, often forming the basis for camouflage, mimicry, predator deterrence, and communication within and between species [1, 2]. The diversity of animal color patterns also plays an important role in the formation of reproductive barriers, facilitating speciation in lineages as disparate as butterflies and cichlids [3, 4]. The teleost fishes that comprise tropical coral reef fish communities exemplify pigmentation pattern diversity, exhibiting some of the most striking and diverse color patterns of all living vertebrates [5, 6]. However, the evolutionary processes that govern the diversification of these patterns are among the most persistent, unresolved questions in evolutionary biology. This knowledge gap limits our understanding of the relationship between

pigmentation patterns, ecological adaptation, and speciation. Resolution of this question hinges on whether the diversification of pigmentation patterns is primarily driven by local ecological pressures, leading to marked dissimilarity between regions, or if it is more strongly influenced by speciation processes—such as rapid diversification among closely related taxa—which could result in similar degrees of pigmentation pattern diversity across biogeographic regions despite differences in species compositions.

Tropical coral reefs across biogeographic regions, such as the Caribbean and Indo-Pacific, differ in notable key characteristics, including trophic structure, faunal composition, and species richness [7]. Accordingly, fish clades within these regions may also exhibit notable pigmentation pattern dissimilarities, attributed to ecological or sexual selective pressures. However, the pace at which fish pigmentation patterns have diversified in response to these forces remains an open question. Regional differences in fish assemblages largely reflect historical biogeography [8, 9]. Consequently, varying environmental conditions and competitive interactions may have driven steady divergence in pigmentation pattern over time, leading to a gradual accumulation of pigmentation pattern diversity within fish assemblages. Additionally, if pigmentation patterns function primarily for species recognition or communication, adaptive radiation theory predicts their diversification would lag early ecological divergence, emerging only after lineages differentiate habitat use and morphological specializations related to trophic resources [10]. With strong evidence for extensive speciation in reef fishes across most tropical oceans during the Pliocene [11–15], this scenario suggests that pigmentation pattern diversity would disproportionately evolve near the tips of phylogenies, driven by the reinforcement of reproductive barriers between closely related species. These hypotheses represent distinct views on the tempo and mode of pigmentation pattern diversification and determining which of these perspectives holds more explanatory power is crucial to understand the evolutionary dynamics shaping one of the most iconic traits in coral reef ecosystems.

Here we study the key factors shaping pigmentation pattern diversity in coral reef fishes by combining time-calibrated molecular phylogenies, biogeographic data, and comprehensive analyses of pigmentation patterns in six ecologically diverse and globally representative families: surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), snappers (Lutjanidae), goatfishes (Mullidae), angelfishes (Pomacanthidae), and damselfishes (Pomacentridae). We first test whether species richness explains pigmentation pattern diversity across biogeographic regions. Next, we investigate how pigmentation pattern disparity varies among reef fish clades across different global regions, providing an assessment of the degree to which ecological variance between regions explains standing patterns of trait disparity. Finally, we evaluate the pattern of evolutionary changes in pigmentation motifs through time and assess whether the diversity of pigmentation patterns has recent evolutionary origin. Collectively, our findings provide insight into the evolutionary mechanisms driving pigmentation pattern diversification and resolve critical aspects of this long-standing question in evolutionary biology.

Results

Pigmentation pattern diversity is correlated with species richness

Divergence in pigmentation patterns often plays a critical role in speciation [16, 17], and recent evidence has suggested an association between motif divergence and genetic divergence among some reef fish populations [18, 19]. This association raises the possibility that pattern diversity may be correlated with species richness within biogeographic regions. To test this hypothesis, we annotated 30 pigmentation motifs using images of 918 fish species from the six coral reef fish families, ensuring coverage of at least 75% of the species diversity within each family (Table 1 and Additional file 1: Data S1). These motifs included well-established categories such as stripe patterns (horizontal, diagonal, vertical, labyrinthine), spot patterns (spot and eyespot), and others (saddle-like, blotch, monotone). The head, trunk, and tail regions of each fish were binary coded to indicate the presence of each motif, distinguishing between single occurrences and repeated patterns. We then summarized the data using principal coordinate analysis (PCoA) for each family. Quality assessments confirmed that eight to ten principal coordinate axes were sufficient to capture the phenotypic diversity of each family without substantial loss of information (see Methods for details). Pigmentation data were integrated with geographic information from FishBase [20] and GBIF [21], and fish species were categorized into five major regions according to the classification by Kulbicki and colleagues [9]: Atlantic (including the Mediterranean Sea), Western Indian (including the Red Sea), Central Indo-Pacific, Central Pacific, and Tropical Eastern Pacific (Additional file 1: Data S1).

We quantified the diversity of pigmentation patterns present in each biogeographic region by measuring the *Richness* of motif diversity, defined by the hypervolume occupied by each family in the pigmentation pattern space [23, 24]. Using the *full dataset*—where widespread species were assigned to all regions where they occur—we initially find a strong and positive correlation between species richness and motif diversity per region for every fish family (Fig. 1). To account for the potential

Table 1 Overview of taxon sampling and number of images used to collect phenotypic data

	Number of studied species	Proportion of extant diversity (%)	Number of images	Number of species included in PCM
Acanthuridae	83	98	83	63
Chaetodontidae	133	97	288	97
Lutjanidae	128	96	128	109
Mullidae	80	79	80	62
Pomacanthidae	92	100	94	70
Pomacentridae	402	93	1126	335
Total	918		1799	736

Proportion of extant diversity is based on the total number of species given by Eschmeyer's Catalog of Fishes [22]. PCM (Phylogenetic Comparative Methods) refers to the analyses including phylogenetic information. Phylogenetic/genetic information was lacking for some species, preventing their inclusion in our analyses of the mode and the tempo of pigmentation pattern evolution

homogenizing effect of species that occur across multiple regions, we repeated the analysis using a re-sampling method (1000 iterations) in which any species present in more than one region was randomly assigned to a single region. The positive correlations persisted across families in these *re-sampled datasets* (Fig. 1).

We also assessed the distribution of species within each hypervolume using two additional metrics: *Divergence* and *Evenness*. *Divergence* measures the deviance from the mean distance to the centroid of the vertices shaping the convex hull of the studied assemblage, with high values indicating substantial differentiation from the average pigmentation pattern of the group. *Evenness* reflects the regularity of species distribution across the occupied hypervolume, with higher values indicating a more uniform spread in the pigmentation pattern space [23]. Across all geographical groups and families, both *Divergence* and *Evenness* were generally high, often approaching the maximum value of 1 while using the *full* and the *re-sampled datasets* (Additional file 2: Table S1). The lowest values of *Evenness* are observed in damselfishes (from 0.63 in the Atlantic Ocean to 0.70 in the Tropical Eastern Pacific and Central Pacific). Similarly, angelfishes had the lowest value of *Divergence* in the Tropical Eastern Pacific (0.65). However, unlike the relationship between motif diversity and species richness, divergence and evenness in pigmentation patterns were generally not correlated with species richness (all correlation tests: $p > 0.1$), except a significant negative relationship between *Divergence* and species richness in surgeonfishes ($0.01 < p < 0.04$; Additional file 2: Table S3).

We also investigated if the occurrence of some unique motifs is associated with species-rich regions. Accordingly, we computed species motif *Uniqueness* (i.e., species mean distance to the closest five neighbors) and *Specialization* (i.e., the distance between the species and the center of the trait space) across regions for each fish family. The region showing the highest levels of motifs *Uniqueness* and *Specialization* varied across families (Additional file 2: Table S2). *Uniqueness* and *Specialization* of pigmentation patterns were generally not associated with species richness (all correlation tests: $p > 0.08$, when considering *re-sampled datasets*; Additional file 2: Table S3). We only detected two significant correlations with opposite trends in two families when using the *full datasets*: a positive relationship between motif *Uniqueness* and species richness across regions in Mullidae ($R = 0.92$; $p = 0.027$), and a negative relationship between motif *Specialization* and species richness across regions in Acanthuridae ($R = -0.96$; $p = 0.009$).

Pigmentation patterns are evolutionarily labile but with limited spatial variation

Species richness and phylogenetic diversity can vary dramatically between biogeographic regions, suggesting that clade-specific biogeographic histories may have shaped variation in pigmentation diversity between regions. However, we found no significant variation in pigmentation pattern diversity among the biogeographic regions for any fish family when using the *full dataset* (np-MANOVA: $p > 0.05$; Additional file 2: Table S4). Significant variation among regions was only detected for angelfishes and damselfishes when using the *re-sampled dataset* (Additional file 2: Table S4). Visual exploration of the pigmentation pattern spaces (Additional file 2: Fig. S1) suggested the assemblages of the Atlantic and the Tropical Eastern Pacific mainly contributed to this variation in both families. Globally, our results indicated that divergence in pigmentation pattern diversity among regions was comparable for all studied fish families (Additional file 2: Fig. S1).

The consistency of pigmentation pattern diversity can be a consequence of lineages with distinct pigmentation patterns colonizing different biogeographic regions

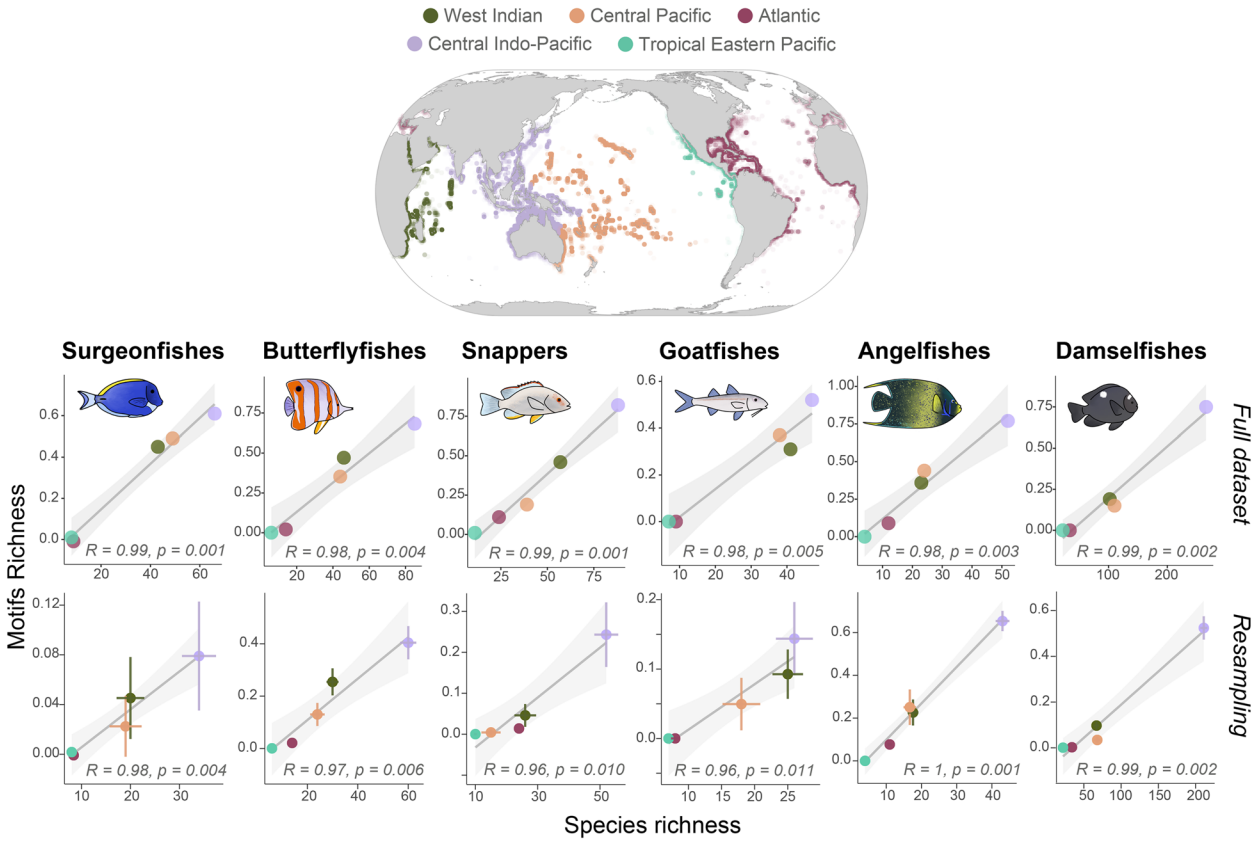

Fig. 1 Relationships between motif richness and species richness from the five main biogeographic regions. The richness of pigmentation patterns (i.e., motif richness) is directly proportional to the number of species present in each region. Tests of correlation are all significant and Pearson's *R* coefficients are close to a maximum value of 1, both when using the full (top row of plots) and the re-sampled (bottom row of plots) datasets. For results on the re-sampled dataset, points correspond to median values and error bars to standard deviations across 1000 re-sampling iterations

over time, or the repeated divergence of pattern motifs between close evolutionary relatives within the same biogeographic region, resulting in convergence between distantly related lineages. To differentiate between these scenarios, we leveraged time-calibrated molecular phylogenies to test the statistical dependence between pigmentation patterns and the phylogeny of each fish family (i.e., phylogenetic signal) using the multidimensional equivalent of Blomberg's *K* [25]. In all cases, values of *K* were close to 0 (Acanthuridae: $K_{mult} = 0.11$, $p < 0.01$; Chaetodontidae: $K_{mult} = 0.10$, $p < 0.01$; Lutjanidae: $K_{mult} = 0.22$, $p < 0.01$; Mullidae: $K_{mult} = 0.08$, $p < 0.01$; Pomacanthidae: $K_{mult} = 0.05$, $p < 0.01$; Pomacentridae: $K_{mult} = 0.06$, $p < 0.01$), indicating very low, but significant degrees of phylogenetic relatedness in pigmentation patterns. These low *K* values demonstrate that closely related species exhibit more divergent pigmentation patterns than would be expected under a null Brownian motion model, with significant *p* values in all cases revealing that diversification of pigmentation patterns is non-random with respect to phylogeny.

The diversification of pigmentation pattern is bounded and rapid

Variation in pigmentation patterns can influence the divergence and maintenance of reef-fish species boundaries [16, 26], suggesting that motif diversity may disproportionately diverge among closely related taxa and lead to accelerated diversification rates among tip-ward lineages. We tested this hypothesis through a comparison of five evolutionary models: (1) Brownian motion (BM) of stochastic diffusion (modeling gradual evolution); (2) the ψ (psi) model of mixed gradual and speciational evolution [27]; (3) the Ornstein–Uhlenbeck (OU) model that combines stochastic diffusion with a pull toward a central "optimum" value [28]; (4) the early burst (EB) model that describes an exponential decrease in evolution as is often expected in adaptive radiation; and (5) the accelerating (AC) model where evolutionary rates increase exponentially over time. Using sample-size corrected Akaike's information criterion (AICc) for model selection, we found strong support for the AC and OU models as the best fitting models for the majority of principal

coordinate (PC) axes, capturing 90% and 100% of the fitted PCs, respectively (Fig. 2, Additional file 2: Table S5 and Additional file 2: Fig. S2). The strong support for the AC model indicates that pigmentation pattern diversification has accelerated during the recent evolution of reef fish families.

It is possible that varying environmental conditions and competitive interactions could have promoted either early pulses or gradual accumulations of motif diversity within fish assemblages over time. However, our results suggest this to not be the case. The poor fit of the EB and BM models allowed us to reject hypotheses of decelerating evolutionary rates or constant diversification of pigmentation patterns. In contrast, we found strong support for the fit of the single-optimum OU model (OU1) to many PC scores (Fig. 2, Additional file 2: Table S5 and Additional file 2: Fig. S2). Strong support for the OU1 model indicates that while pigmentation patterns evolve rapidly, they do so around a constrained set of motifs. This result is concordant with our analyses of the occupation of pigmentation pattern spaces showing comparable motif diversity among regions (Additional file 2: Fig. S1) and aligns with the high level of homoplasy observed in animal coloration, where distantly related species often share similar pigmentation patterns [29]. These results support expectations of iterative evolution, where pigmentation motifs repeatedly emerge from a central set of patterns.

The bounded trait space supported by our analyses raises the possibility that pigmentation motifs may lose evolvability due to developmental constraints possibly limiting reversals or transitions between specific motifs. However, the accelerated evolutionary rates detected in our study suggest that pigmentation patterns remain highly labile. We estimated a very short phylogenetic half-life [i.e., the time to evolve half the distance between the root state and the selective optimum value ($t_{1/2}=\ln(2)/\alpha$)] for motifs, with a median value of 1.5 million years across fish families (Additional file 2: Table S5). This half-life is extremely short when contrasted with morphological traits in fishes (median half-life of 37.5 million years across 13 morphological traits [30]). Furthermore, the best-fit model for PC2 in butterflyfishes was the ψ model (Additional file 2: Fig. S2), illustrating that speciation and aspects of pigmentation pattern evolution are also closely linked for some clades. Collectively, these results underscore that pigmentation pattern diversification reflects highly rapid evolution within a

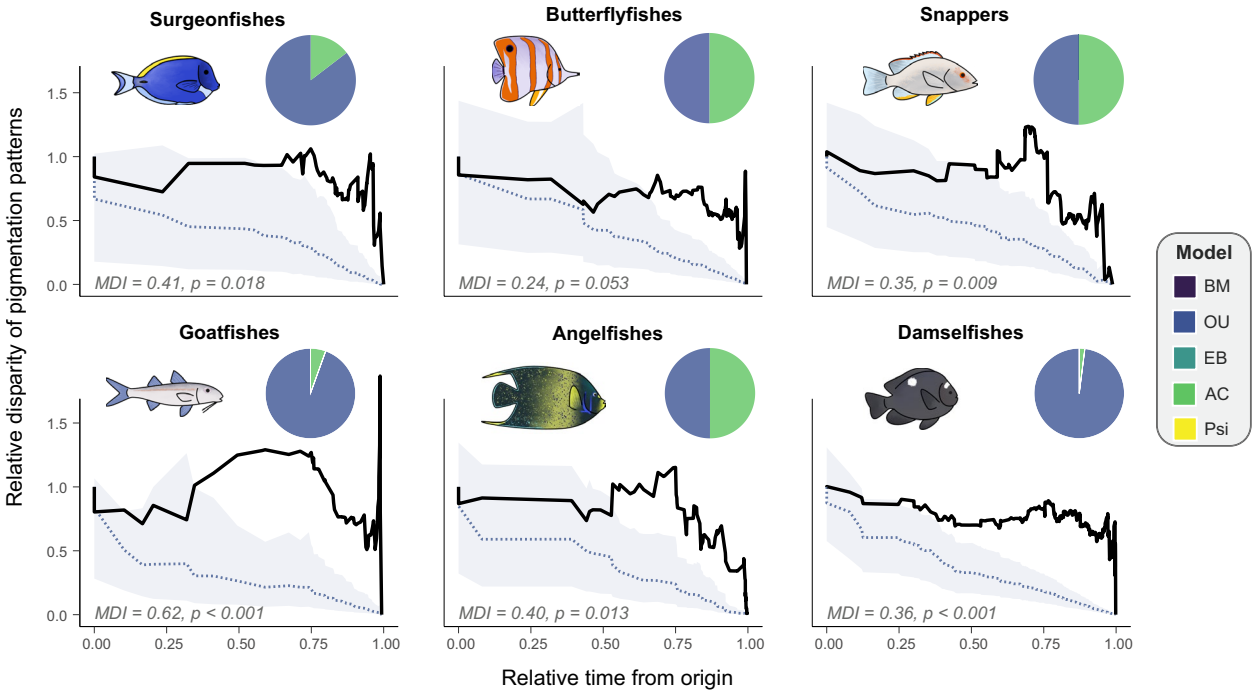

Fig. 2 Disparity through time (DTT) plots illustrating the evolution of subclade disparity across the phylogeny of each fish family. Higher relative disparity values (y-axis) correspond to a greater average volume of pigmentation pattern space occupied by subclades relative to the disparity of the entire family. The solid line represents the observed disparity calculated for each clade, while dashed line is median expected disparity under a null Brownian motion model based on simulations. Across all fish families, subclade disparity was significantly higher than expected under BM, with sharp increases of within subclade disparity toward the present, suggesting the potential for high motif convergence between subclades. Inset pie charts display the distribution of the Akaike information criterion weights (AICw) from trait evolutionary model (BM, OU, EB, AC, and psi) comparisons. Generally, support for BM, EB, and psi models was too low to be discernible on pie charts. Plots reflect model comparisons for PC1. Plots of PCs 2–3 are provided in Additional file 2: Fig. S2 and Additional file 2: Fig. S3

bounded space that is likely linked to rapidly shifting ecological or other selective pressures.

The observed pattern of rapid, yet bounded, evolution in pigmentation motifs may simply reflect a stochastic distribution of motif diversity across the phylogeny with no general phylogenetic structuring of trait disparity. We tested this possibility by assessing the partitioning of trait disparity among subclades over time through the quantification of morphological disparity index (MDI) values in an analysis of subclade disparity through time (DTT). In all cases, DTT plots of PC axes 1 to 3 demonstrated a sharp increase within subclade pigmentation pattern disparity in recent evolutionary history, with positive MDI values indicating a significant departure above median Brownian motion expectations (Fig. 2 and Additional file 2: Fig. S3). This pattern of recent subclade disparity being partitioned within versus between subclades provides strong support for the hypothesis that pigmentation pattern evolution has been characterized by consistent and repeated divergences between closely related taxa that culminate in convergences in pigmentation patterns among distantly related lineages.

To complement our analyses of the pigmentation pattern space, we leveraged the discrete scoring of individual motifs to examine the tempo of pigmentation pattern evolution. Using stochastic character mapping under the best fitting model of trait evolution for each motif based on AICc, we quantified the timing and frequency of motif transitions across the phylogeny. These analyses revealed that the vast majority of motif shifts occurred recently, within the last 5–10 million years (Fig. 3 and Additional file 2: Fig. S4), mirroring the temporal concentration of trait disparity observed in the DTT analyses. The congruence between results from discrete motif models (Fig. 3) and continuous trait models (Fig. 2 and Additional file 2: Table S5) supports the conclusion that pigmentation pattern diversity in extant coral reef fishes evolved recently and rapidly.

Discussion

We find that the divergence in pigmentation pattern diversity across biogeographic regions is relatively limited in coral reef fishes. This result challenges the hypothesis that pigmentation pattern disparity would be strongly partitioned between biogeographic regions as a consequence of regional differences in fish assemblages [8, 9]. Instead, our results indicate that pigmentation motifs, though evolutionarily labile, are structured more by lineage-level processes than by geography. We demonstrate a positive correlation between species richness and motif diversity per region (Fig. 1), suggesting that species differentiation is tightly associated with motif variation, regardless of regional patterns in species richness. This finding highlights the central role of pigmentation patterns in the speciation of coral reef fishes and aligns with the widespread taxonomic use of pigmentation traits in reef fish identification [16]. We hypothesize that strong interspecific competition and optimized signaling among congeners promotes maximized subdivision in the pigmentation pattern space. Based on results from our

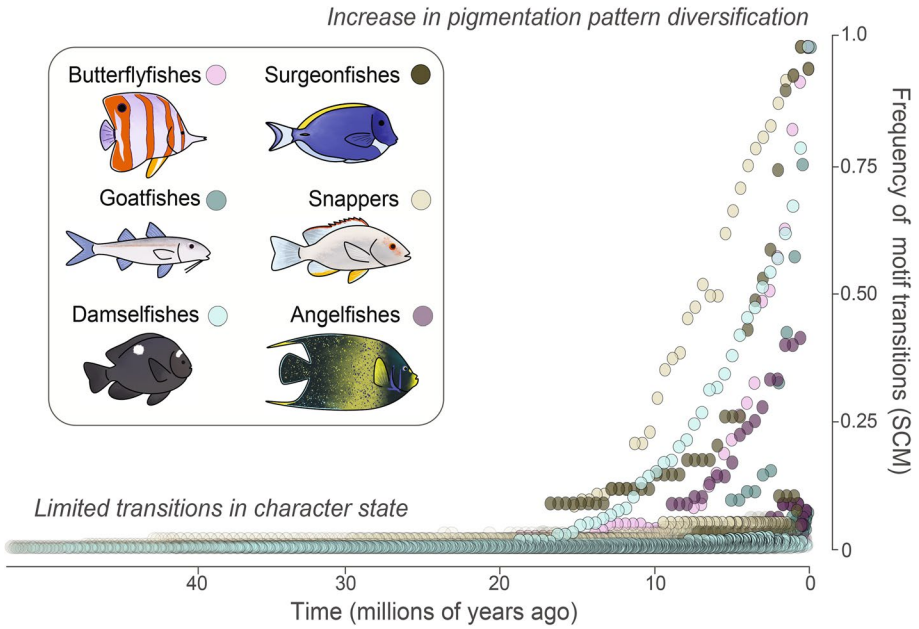

Fig. 3 Shifts in motifs over time across all studied fish families. The y-axis provides the frequency of all transitions between presence and absence of each motif across the stochastic character maps (SCM). Circles are the number of transitions across the SCM for every time point (node), which are standardized by the number of lineages present at that time. Circles are colored to correspond to each reef fish family

assessment of phylogenetic signals, we propose that convergences would not result from independent regional dynamics, but from repeated divergence among sister taxa that culminated in high diversity within clades and limited differences across regions.

Although the general pattern is one of regional conservatism, our analyses also reveal that some biogeographic structuring of pigmentation diversity does occur. In particular, the modest divergence observed in angelfishes and damselfishes (Additional file 2: Fig. S1) suggests that regional differences can emerge under certain phylogenetic and ecological configurations. These exceptions may stem less from independent regional dynamics and more from uneven phylogenetic representation. The species-rich damselfish subfamily Pomacentrinae (218 species [31]) is absent from the Atlantic Ocean and the Tropical Eastern Pacific. Consequently, regional differences in pigmentation motif diversity may arise not from region-specific evolutionary pressures, but from the spatial sorting of clades with distinct histories of motif innovation and do not contradict our finding of repeated within-clade diversification as a dominant driver of motif diversity.

Our results additionally resolve the seemingly paradoxical relationship between high trait lability and regional conservatism. Coral reef fishes possess the largest array of pigment cell types among vertebrates [5], yet the spatial distribution of pigmentation motifs remains strikingly conserved. Similarities in geographic patterning of *Divergence* and *Evenness* support common controls on motif diversity. It is possible that regional conservatism may reflect underlying molecular and cellular constraints on the generation of new motifs (e.g., pattern formation mechanisms, pigment cell diversity, physical pigment properties [6, 32, 33]). For example, labyrinthine motifs have been proposed to originate from interspecific hybridization between spotted species [29]. Likewise, new pigmentation patterns can be produced by a simple modification of developmental mechanisms [34, 35]. The absence of relationships between motifs *Uniqueness* and *Specialization*, and species richness across regions does not suggest that atypical pigmentation patterns appear only in highly species-rich regions. Conversely, it strengthens the hypothesis that unique pigmentation patterns would result from stochastic processes linked to developmental and molecular mechanisms. Our findings, alongside studies on the molecular basis of pigmentation [6, 29, 36], suggest that a limited set of developmental mechanisms and associated genes drive the evolution of pigmentation patterns, leading to recurrent phenotypic convergence under various selective pressures. This constrained evolutionary process may reflect a broader principle of phenotypic evolution, where natural selection operates on a limited set of developmental processes, resulting in recurrent patterns of convergence across diverse taxa.

When considering convergence of pigmentation patterns temporally, our findings reveal that recent speciation events have driven high levels of disparity within subclades. This recent and rapid diversification contrasts with the diversity dynamics of ecomorphological traits like head, fin, and body morphology, in which trait disparity is often partitioned between major subclades [37–40]. However, this does not imply that pigmentation pattern diversity did not exist in earlier geologic periods and did not follow bursts of diversification in deep time. On the contrary, motifs similar to those found today, such as spots and stripes, appear on fossilized fish from the Eocene [26], suggesting color pattern motifs to be both evolutionarily labile and ephemeral. These observations parallel findings in birds, where rapid plumage evolution also displays high evolutionary lability and homoplasy [41–43]. Moreover, our phylogenetic sampling is biased toward sampling all major lineages and missing primarily tip-ward lineages, suggesting that we are likely underestimating the rate of recent motifs diversification. As such, rapid and bounded diversification pattern may be a generalizable feature of pigmentation motif evolution.

Mechanistically, studies in model teleosts such as zebrafish have found pigment cell signaling and communication dynamics as key to generating diverse pigmentation patterns [6, 34, 44]. When considering the wide array of pigment cell types and color polymorphisms in coral reef fishes [5, 45, 46], these findings highlight the rich molecular and cellular substrate of pigmentation diversity upon which selection acts. Additionally, processes such as introgression [47, 48] and hybridization, especially in visually striking groups like butterflyfishes, angelfishes, and clownfishes [49, 50], possibly further fuel rapid and repetitive motif evolution. Future research investigating the role of hybridization and developmental pathways in pigmentation pattern formation will be crucial for understanding the evolutionary dynamics of these traits.

Our study relies on a comprehensive but simple quantification of pigmentation pattern diversity without information about colors. Future analyses should aim to add this color component in a similar comparative framework to fully explore the evolution of color patterns in coral reef fishes [51]. Moreover, considering how functionally robust these color-associated traits are to changes in species ranges, water turbidity, and habitat in response to environmental shifts over the next century remains an urgent priority.

Conclusions

The present work provides unprecedented insights into the tempo and mode of pigmentation pattern evolution in reef fishes. By integrating phylogenetic, biogeographic, and phenotypic data, we show that speciation events have continuously generated high levels of pigmentation pattern variation both within subclades and across reef fish assemblages worldwide. The accumulation of pigmentation pattern disparity in reef fishes appears bounded, leading to convergences. Future work, combining macroevolutionary analyses and EvoDevo approaches, will certainly help unravel the mechanistic facets driving the remarkable visual complexity that characterizes contemporary reef fish communities.

Methods

The present study focused on six conspicuous, coastal marine, teleost fish families, considered as strongly associated with coral reef ecosystems [52]: Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Lutjanidae (snappers), Mullidae (goatfishes), Pomacanthidae (angelfishes), and Pomacentridae (damselfishes). The great majority of species in these families are diurnal, and it is expected that pigmentation patterns play crucial roles in their ecology and behaviors. The choice of these families was mainly driven by (a) their extensive distribution in tropical and subtropical marine areas, (b) readily accessible photos that adequately represent their phylogenetic diversity, (c) availability of robust time-calibrated phylogenies with high taxon sampling, and (d) their ecological diversity, especially in terms of diet and habitat use.

Data collection

Fish images from illustrated scientific books [53–62] and public databases [20, 63–68] were used to categorize the presence or absence of pattern motifs. Our dataset includes a total of 918 species: 83 acanthurids, 133 chaetodontids, 128 lutjanids, 80 mullids, 92 pomacanthids, and 402 pomacentrids, representing a minimum of 75% of the extant diversity of each fish family (Table 1 and Additional file 1: Data S1). We aimed to use a minimum of three images per species. Pigmentation patterns were described at the adult stage only. If sexual dimorphism is present, we only quantified the pigmentation pattern observed in males. All 918 species were used in our investigation of the biogeographic distribution of pigmentation pattern diversity. Due to the lack of phylogenetic information for some species, a total of 736 species was used in phylogenetic comparative analyses and evolutionary model fitting.

Five regions aligned with major ocean basins were delineated, based on the methodology of Kulbicki et al. [9]. These regions are the Atlantic Ocean (including the Mediterranean Sea), the Western Indian Ocean (including the Red Sea), the Central Indo-Pacific (extending from the edge of India to the northern edge of New Zealand), the Central Pacific, and the Tropical East Pacific. According to Kulbicki et al. [9], the Atlantic Ocean should be split between Eastern and Western Atlantic. However, here, we grouped these two regions to make an Atlantic region to compensate for the small number of species in the Eastern Atlantic and to reach an adequate number of species. Geographical distribution patterns of each species were extracted from FishBase [20], which provides a validation of previously published assigned areas (i.e., miss-identification or changes in species taxonomy), and GBIF [69]. A species was considered to occupy a region when at least five observation points were displayed within it. Species having a widespread geographical distribution encompassing different regions were coded as occupying each of these corresponding regions (Additional file 1: Data S1).

Annotation of fish pigmentation patterns

Fish images were subjected to pattern annotation by the same three observers: L. Mittelheiser, J.R. Hodge, and L. Moulin. This task was triple checked independently by each observer. To describe the pigmentation pattern of each fish species, we targeted motifs commonly used in publications related to this topic [29]. Pigmentation patterns were initially annotated independently on the three main areas of the body (head, trunk, and tail) and then merged into a single "total" dataset. We formulated six classes of patterns: (1) the number of colors (one or more), (2) color separation (three possible types: H-sep—different background colors are separated following the body axis; V-sep—different background colors are separated perpendicularly to the body axis; O-sep—different background colors are separated with an orientation deviating from the body axis from around 20° to 70°), (3) stripe patterns (five possible types: H-stripes—horizontal stripe following the body axis; V-stripe—vertical stripe oriented perpendicularly to the body axis; O-stripes—oblique stripe deviating from the body axis from about 20° to 70°; Marbling: irregular, elongated, and connected patterns without a directional trend; and Beehive: juxtaposed hexagonal patterns), (4) blotch patterns (two types: Regular blotches—large and irregular markings; Saddle—blotch located on dorsally ahead of the caudal peduncle), (5) type of colored structures (two structures: Mouth—mouth has a different color than head's background color; Scalpel—scalpel has a different color from body's background color), and (6) other patterns (four possible types: Dots—small and rounded area of color; Reticulations—net-like pattern; Eyespot—large dot surrounded by a ring of a different color; Edging—structure is outlined with a color different from the structure's background color).

Each of these traits was coded as present (1) or absent (0) in studied taxa (Additional file 1: Data S1). Illustrations and detailed descriptions of each motif are provided in Additional file 3: Methods. The diversity of pigmentation patterns varied across the studied families. Following our objectives to best describe the diversity of phenotype within each taxon, the fish families were studied separately in the downstream analyses.

Quantitative analyses of pigmentation patterns

All analyses were conducted in R version 4.3.0 [70]. To summarize the diversity of motifs and to create a pigmentation pattern space, we calculated the distance between all pairs of species using Gower's metric. Then, we applied a principal coordinate analysis (PCoA, also called principal axes for simplicity) to this matrix [71]. Following the framework of Maire and colleagues [72], we identified the lowest number of dimensions that capture phenotypic diversity without losing information by performing a quality test using the function *quality.fspaces()* in the R-package *mFD* (version 1.0.7) [73]. Accordingly, we used species' coordinates on the first eight principal axes of the PCoA for Acanthuridae and Chaetodontidae; on the first seven principal axes for Pomacanthidae and Pomacentridae; and on the first six principal axes for Lutjanidae and Mullidae. Scatter plots illustrating the dispersion of species in the phenotypic space were produced using the function *ggplot()* (Additional file 1: Fig. S1).

Differences in the diversity of pigmentation patterns among fish assemblages from the five regions were tested by using a non-parametric MANOVA (np-MANOVA) [74], performed with the function *procD.lm()* using a randomized residual permutation procedure (RRPP) and 10,000 permutations from the R-package *geomorph* (version 4.0.8) [75]. We applied np-MANOVA analyses by using the number of principal axes suggested by quality tests.

To further explore the occupation of pigmentation pattern space, we used the multifaceted framework of functional ecologists [23, 76] to decompose the phenotypic diversity into three complementary components: *Richness*, *Divergence*, and *Evenness* [23]. *Richness* is the total extent of multidimensional space utilized by species (i.e., size of hypervolume). *Divergence* quantifies the distribution of species within the multidimensional space. *Divergence* approaches zero when species are close to the center of gravity of the space (or hypervolume) occupied by the group of species in the phenotypic space; it equals one when species are located on the edges of the space. The higher the value of this index, the more species are differentiated in the multidimensional space. *Evenness* characterizes regularity in the distribution of species along the shortest tree linking all of them. *Evenness* approaches zero when species are clustered within a small region of the multidimensional space, and it equals one for an even distribution of species in the space. High values of this index indicate a limitation in phenotypic similarity. The three indices were computed using the function *alpha.fd.multidim()* from the R-package *mFD*. Additionally, we quantified the *Uniqueness* (i.e., the mean distance of each species to its nearest five neighbors within the considered region) and the *Specialization* (i.e., the distance of each species to the centroid of the regional pigmentation pattern space) of motifs by using the *fuse*() function from the R-package *mFD*, and we then computed the median values of these two indices per region. The functions used to compute these indices require the number of variables (i.e., PC axes) to be lower than the number of observations (i.e., number of species in a given region). Given the low number of species in some regions for some families, the number of PC axes retained to compute the indices was reduced in three families: from eight to the seven in Acanthuridae, from eight to five in Chaetodontidae, and from seven to three in Pomacanthidae. The correlation between these indices and species richness was tested by using the function *cor.test()*.

One species can be present in multiple regions. Thus, we first calculated the five indices and performed np-MANOVA by assigning widespread species to all the regions where they are encountered. However, the presence of a single species in multiple regions could have a homogenizing effect on any differences among regions. Accordingly, the functional indices as well as np-MANOVAs were also computed using re-sampling techniques in which any species present in more than one region was randomly assigned to a single region. Out of the 918 species included in our dataset, 516 species were present in more than one region (Acanthuridae: 54 species in more than one region; Chaetodontidae: 46 species; Lutjanidae: 62 species; Mullidae: 38 species; Pomacanthidae: 18 species; Pomacentridae: 99 species). For the re-sampled analyses, all species in the dataset were assigned to a single region so that any species present in multiple regions was randomly assigned to one of the regions where it is present and labeled as absent in all other regions. However, to avoid further reducing the number of retained PC axes while maintaining the requirement of having more observations than variables, we allowed the duplication of a few species in multiple regions until the minimum sample size required by the function was reached. Re-sampling was performed 1000 times for each family. Functional indices and np-MANOVA were also computed for each iteration on the significant number of PC axes. Since np-MANOVAs do not require more

observations than variables, species were not duplicated for this test. The median value and standard deviations of each index and of the F values and p values of np-MANOVA tests were retained and are presented in the results.

Phylogenetic comparative analyses

Beyond exploring pigmentation pattern space occupation, we also studied the evolution of pigmentation patterns using a combination of comparative analyses that account for phylogenetic relatedness. We used published, strongly supported multi-gene, time-calibrated phylogenies. All details concerning the methods of phylogenetic reconstruction and time calibration are provided in these works: see Sorenson et al. [77] for Acanthuridae, Hodge et al. [78] for Chaetodontidae, Rincon-Sandoval et al. [79] for Lutjanidae, Nash et al. [40] for Mullidae, Baraf et al. [80] for Pomacanthidae, and McCord et al. [31] for Pomacentridae.

Phylogenetic signal is a measure of the statistical dependence among species' trait values on their phylogenetic relationships. It can be used to describe the conservatism or the evolutionary lability of traits across phylogenetic histories [81]. Here, we applied the multivariate version of the Blomberg's K (K_{mult}) available in the R-package *geomorph* (function *physignal*) to the number of principal axes of the pigmentation pattern space retained by the quality tests. Similar to the interpretation of the univariate Blomberg's K [25, 82], $K_{mult} = 1$ indicates strong phylogenetic signal that perfectly follows Brownian motion. A K_{mult} value > 1 means that closely related species trait values are more similar than expected under a Brownian motion model, whereas a value < 1 suggests a greater lability of trait values and a departure from a strong phylogenetic signal.

We tested the hypothesis that pigmentation patterns diversified recently in reef fish families by comparing the fit of five models of trait evolution. We fitted a single rate (σ^2) Brownian motion (BM) model, an Ornstein–Uhlenbeck model with a single optimum (θ) across the entire tree (OU1), a ψ (psi) model of mixed gradual and speciational evolution, an early burst (EB) model where the rate of evolution decreases exponentially through time, and an accelerating (AC) model where the rate of evolution increases exponentially through time. Modeling of continuous trait evolution was conducted using the function *transformPhylo.ML()* in the R-package *motmot* [83, 84] (version 2.1.3). For these comparative analyses, we fitted models separately on the first three principal axes to optimize convergence on reliable solutions. Models were compared using AICc (Akaike's information criterion, corrected for sample size) and Akaike weights, which balance goodness of fit with model complexity [85].

We further characterized the tempo of pigmentation pattern diversification using disparity-through-time analysis [86]. This approach computes the average subclade disparity for one trait at each node in the phylogeny and plots these as a function of node age. At the root of the tree, the average subclade disparity is simply the phenotypic disparity of the entire clade and is therefore high. At subsequent nodes, disparity is averaged over the total number of subclades in existence at that time. Under an early burst hypothesis, average subclade disparity is expected to decline rapidly in the early history of the clade as evolutionary rates slow and phenotypic variation becomes partitioned among subclades. Conversely, an average subclade disparity remaining high or even increasing through time signals high phenotypic variation within clades, potentially due to convergence. We also used the morphological disparity index (MDI) of Harmon et al. [86] to quantify the difference between average subclade disparity through time for our observed dataset and that expected under a null BM model. Negative MDI values indicate lower than expected subclade disparity relative to BM while positive MDI values indicate higher than expected subclade disparity. MDI statistics were computed for the first three principal axes over the first 90% of the time-tree using the R-package *Geiger* (version 2.0.11) [87]. We omitted the most recent 10% of the phylogeny in our analysis to avoid spurious MDI estimates due to incomplete sampling of tip species [86].

Finally, we quantified the dynamics of pigmentation pattern diversification by counting the number of motif shifts over evolutionary time. This was achieved by producing stochastic maps for every single motif using the function *make.simmap()* in the R-package *phytools* (version 2.1–1) [88]. Here, we sampled 10,000 character histories allowing the incorporation of the uncertainty associated with the timing of the transitions between presence and absence of the pattern motif, based on the best fitting model of trait evolution using AIC. For the parametrization of *make.simmap()*, we used the estimated ancestral state and the corresponding best-fit transition matrix between states for each model, allowing each motif to evolve independently. Data were then summarized by plotting the frequency of motif transitions over time, as well as the distribution of times spent in either character state for each trait across the phylogeny.

Abbreviations

PC	Principal coordinate
PCoA	Principal coordinate analysis
PCM	Phylogenetic Comparative Methods
BM	Brownian motion model
OU	Ornstein-Uhlenbeck model
OU1	Single-optimum Ornstein–Uhlenbeck model
EB	Early burst model

AC	Accelerating model
AIC	Akaike information criterion
AICc	Akaike information criterion corrected for sample size
MDI	Morphological disparity index
DTT	Disparity through time
np-MANOVA	Non-parametric Multivariate ANalysis Of Variance
SCM	Stochastic character maps

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12915-026-02544-4.

Additional file 1: Data S1. Data S1 List of the studied species (918) in surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), snappers (Lutjanidae), goatfishes (Mullidae), angelfishes (Pomacanthidae), and damselfishes (Pomacentridae). For clarity, families are distributed on different sheets. The coding of regions (biogeographic data) and motifs (raw data for the quantification of pigmentation patterns) are provided.

Additional file 2: Figures S1–S4 and Tables S1–S5. Fig. S1. Illustrations of the pigmentation pattern spaces for every fish family, within the first three axes of the principal coordinate analyses. Fig. S2. Comparisons of alternative models of trait evolution using the first three axes of the principal coordinate analyses summarizing the diversity of pigmentation patterns. Fig. S3. Disparity through timeplots illustrating the evolution of subclade disparity across the phylogeny. Fig. S4. Overview of the stochastic character mapsacross motif traits and fish families. Table S1. Motif *Richness*, *Divergence*, and *Evenness* in each region for the six fish families. Table S2. Motif *Uniqueness* and *Specialization* in each region for the six fish families. Table S3. Results from correlations between species richness and functional indicesacross regions for each family. Table S4. Results from the np-MANOVA. Table S5. Results from fitting models of pigmentation pattern evolution.

Additional file 3: Methods. Description of every motif used to quantify pigmentation patterns in the studied fish families.

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Authors' contributions
B.F., V.L. and A.D. conceptualized the study. B.F., L.M. and A.D. designed the study. B.F. supervised the study. B.F. and A.D. drafted the paper with inputs from L.M., A.G., J.H. and V.L. L.M. collected phenotypic and geographic data. J.H. contributed to phenotyping. B.F., L.M., A.G. and A.D. analyzed data. All authors contributed to interpretation and discussion of results. All authors read and approved the final manuscript.

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Data availability
The dataset generated and analysed as well as R-codes produced during the current study are available through figshare, https://doi.org/10.6084/m9.figshare.31169398 [89].

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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References

1. Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME, et al. The biology of color. Science. 2017;357:eaan0221.
2. Stevens M, Merilaita S. Animal camouflage: mechanisms and function. Cambridge: Cambridge University Press; 2011.
3. Fordyce JA, Nice CC, Forister ML, Shapiro AM. The significance of wing pattern diversity in the Lycaenidae: mate discrimination by two recently diverged species. J Evol Biol. 2002;15:871–9.
4. Seehausen O, van Alphen JJM. The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). Behav Ecol Sociobiol. 1998;42:1–8.
5. Salis P, Lorin T, Laudet V, Frédérich B. Magic traits in magic fish: understanding color pattern evolution using reef fish. Trends Genet. 2019;35:265–78.
6. Parichy DM. Evolution of pigment cells and patterns: recent insights from teleost fishes. Curr Opin Genet Dev. 2021;69:88–96.
7. Roff G, Mumby PJ. Global disparity in the resilience of coral reefs. Trends Ecol Evol. 2012;27:404–13.
8. Cowman PF, Parravicini V, Kulbicki M, Floeter SR. The biogeography of tropical reef fishes: endemism and provinciality through time. Biol Rev. 2017;92:2112–30.
9. Kulbicki M, Parravicini V, Bellwood DR, Arias-Gonzàlez E, Chabanet P, Floeter SR, et al. Global biogeography of reef fishes: a hierarchical quantitative delineation of regions. PLoS ONE. 2014;8:e81847.
10. Streelman JT, Danley PD. The stages of vertebrate evolutionary radiation. Trends Ecol Evol. 2003;18:126–31.
11. Cowman PF, Bellwood DR. Coral reefs as drivers of cladogenesis: expanding coral reefs, cryptic extinction events, and the development of biodiversity hotspots. J Evol Biol. 2011;24:2543–62.
12. Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, et al. Atlantic reef fish biogeography and evolution. J Biogeogr. 2008;35:22–47.
13. Hodge J, Bellwood DR. On the relationship between species age and geographical range in reef fishes: are widespread species older than they seem? Glob Ecol Biogeogr. 2015;24:495–505.
14. Frédérich B, Santini F. Macroevolutionary analysis of the tempo of diversification in snappers and fusiliers (Percomorpha: Lutjanidae). Belg J Zool. 2017;147:17–35.
15. Frédérich B, Sorenson L, Santini F, Slater GJ, Alfaro ME. Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). Am Nat. 2013;181:94–113.
16. Puebla O, Bermingham E, Guichard F, Whiteman E. Colour pattern as a single trait driving speciation in *Hypoplectrus* coral reef fishes? Proc Biol Sci. 2007;274:1265–71.
17. Hemingson CR, Cowman PF, Hodge JR, Bellwood DR. Colour pattern divergence in reef fish species is rapid and driven by both range overlap and symmetry. Ecol Lett. 2019;22:190–9.
18. Bernardi G, Holbrook SJ, Schmitt RJ, Crane NL, DeMartini E. Species boundaries, populations and colour morphs in the coral reef threespot damselfish (*Dascyllus trimaculatus*) species complex. Proc Biol Sci. 2002;269:599–605.
19. Borsa P, Sembiring A, Fauvelot C, Chen W-J. Resurrection of Indian Ocean humbug damselfish, *Dascyllus abudafur* (Forsskål) from synonymy with its Pacific Ocean sibling, *Dascyllus aruanus* (L.). CR Biol. 2014;337:709–16.
20. Froese R, Pauly D. FishBase (10/2024). Available from www.fishbase.org. 2024.
21. GBIF.org, GBIF home page (12/2024). Available from https://www.gbif.org. 2024.
22. Fricke R, Eschmeyer WN, Fong JD. Eschmeyer's catalog of fishes: species by family/subfamily. (http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp). Accessed 10 Oct 2024.

23. Villéger S, Mason NWH, Mouillot D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology. 2008;89:2290–301.
24. Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR. A functional approach reveals community responses to disturbances. Trends Ecol Evol. 2013;28:167–77.
25. Adams DC. A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. Syst Biol. 2014;63:685–97.
26. Bellwood DR, Goatley CHR, Bellwood O. The evolution of fishes and corals on reefs: form, function and interdependence. Biol Rev. 2017;92:878–901.
27. Ingram T. Speciation along a depth gradient in a marine adaptive radiation. Proc Biol Sci. 2011;278:613–8.
28. Butler MA, King AA. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. Am Nat. 2004;164:683–95.
29. Miyazawa S. Pattern blending enriches the diversity of animal colorations. Sci Adv. 2020;6:eabb9107.
30. Hodge J, Adams D, Williams K, Alencar L, Camper B, Larouche O, et al. Unravelling the effects of ecology and history in the phenotypic convergence of fishes. Syst Biol. 2025;74(6):881–96.
31. McCord CL, Nash CM, Cooper WJ, Westneat MW. Phylogeny of the damselfishes (Pomacentridae) and patterns of asymmetrical diversification in body size and feeding ecology. PLoS One. 2021;16:e0258889.
32. Owen J, Yates C, Kelsh RN. Pigment patterning in teleosts. In: Hashimoto H, Goda M, Futuhashi R, Kelsh RN, Akiyama T, editors. Pigments, pigment cells and pigmentation patterns. Springer; 2021. p. 247–92.
33. Kondo S, Miura T. Reaction-diffusion model as a framework for understanding biological pattern formation. Science. 2010;329:1616–20.
34. Patterson LB, Bain EJ, Parichy DM. Pigment cell interactions and differential xanthophore recruitment underlying zebrafish stripe reiteration and *Danio* pattern evolution. Nat Commun. 2014;5:5299.
35. Salis P, Roux N, Soulat O, Lecchini D, Laudet V, Frédérich B. Ontogenetic and phylogenetic simplification during white stripe evolution in clownfishes. BMC Biol. 2018;16:90.
36. Patterson LB, Parichy DM. Zebrafish pigment pattern formation: insights into the development and evolution of adult form. Annu Rev Genet. 2019;53:505–30.
37. Streelman JT, Alfaro M, Westneat MW, Bellwood DR, Karl SA. Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. Evolution. 2002;56:961–71.
38. Dornburg A, Sidlauskas B, Santini F, Sorenson L, Near TJ, Alfaro ME. The influence of an innovative locomotor strategy on the phenotypic diversification of triggerfish (family: *Balistidae*). Evolution. 2011;65:1912–26.
39. Frédérich B, Santini F, Konow N, Schnitzler J, Lecchini D, Alfaro ME. Body shape convergence driven by small size optimum in marine angelfishes. Biol Lett. 2017;13:20170154.
40. Nash CM, Lungstrom LL, Hughes LC, Westneat MW. Phylogenomics and body shape morphometrics reveal recent diversification in the goatfishes (Syngnatharia: Mullidae). Mol Phylogenet Evol. 2022;177:107616.
41. Omland KE, Lanyon SM. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. Evolution. 2000;54:2119–33.
42. Gluckman T-L, Mundy NI. Evolutionary pathways to convergence in plumage patterns. BMC Evol Biol. 2016;16:172.
43. Beltrán DF, Shultz AJ, Parra JL. Speciation rates are positively correlated with the rate of plumage color evolution in hummingbirds. Evolution. 2021;75:1665–80.
44. Eom DS, Bain EJ, Patterson LB, Grout ME, Parichy DM. Long-distance communication by specialized cellular projections during pigment pattern development and evolution. Elife. 2015;4:e12401.
45. Gaither MR, Coker DJ, Greaves S, Sarigol F, Payet SD, Chaidez V, et al. Does color matter? Molecular and ecological divergence in four sympatric color morphs of a coral reef fish. Ecol Evol. 2020;10:9663–81.
46. Messmer V, Jones GP, van Herwerden L, Munday PL. Genetic and ecological characterisation of colour dimorphism in a coral reef fish. Environ Biol Fishes. 2005;74:175–83.
47. He S, Robitzch V, Hobbs J-PA, Travers MJ, Lozano-Cortés D, Berumen ML, et al. An examination of introgression and incomplete lineage sorting among three closely related species of chocolate-dipped damselfish (genus: *Chromis*). Ecol Evol. 2019;9:5468–78.
48. Bernal MA, Gaither MR, Simison WB, Rocha LA. Introgression and selection shaped the evolutionary history of sympatric sister-species of coral reef fishes (genus: *Haemulon*). Mol Ecol. 2017;26:639–52.
49. Hobbs J-PA, Richards ZT, Popovic I, Lei C, Staeudle TM, Montanari SR, et al. Hybridisation and the evolution of coral reef biodiversity. Coral Reefs. 2022;41:535–49.
50. Litsios G, Salamin N. Hybridisation and diversification in the adaptive radiation of clownfishes. BMC Evol Biol. 2014;14:245.
51. Coulmance F, Akkaynak D, Le Poul Y, Höppner MP, McMillan WO, Puebla O. Phenotypic and genomic dissection of colour pattern variation in a reef fish radiation. Mol Ecol. 2023;33:e17047.
52. Siqueira AC, Muruga P, Bellwood DR. On the evolution of fish–coral interactions. Ecol Lett. 2023;26:1348–58.
53. Allen GR, Swainston R. Reef fishes of New Guinea: a field guide for divers, anglers, and naturalists. Madang, Papua New Guinea: Christensen Research Institute; 1993.
54. Allen GR, Erdmann M. Reef fishes of the East Indies: Andaman Sea, Myanmar, Thailand, Indonesia, Christmas Island, Singapore, Malaysia, Brunei, Philippines, Papua New Guinea, Solomon Islands. Perth, Australia: University of Hawai'i Press; 2012.
55. Bacchet P, Zysman T, Lefèvre Y. Guide des poissons de Tahiti et ses îles. Tahiti: Au Vent des Iles; 2016.
56. Taquet M, Diringer A. Poissons de l'Océan Indien et de la mer Rouge. Editions Quæ; 2012.
57. Randall JE. Surgeonfishes of the world. Honolulu: Mutual Pub; Bishop Museum Press; 2002.
58. Endoh K. Angelfishes of the world. Ricordea Pub; 2007.
59. Michael SW, Allen GR. Damselfishes & anemonefishes: the complete illustrated guide to their identification, behaviors, and captive care. T.F.H. Publications; Microcosm; 2008.
60. Allen GR. Damselfishes of the world. Melle, Germany: Mergus; 1991.
61. Allen GR. Butterfly and angelfishes of the world. Melle, Germany: Mergus; 1981.
62. Randall JE, Allen GR, Steene RG. Fishes of the Great Barrier Reef and Coral Sea. Honolulu: University of Hawaii Press; 1990.
63. Robertson DR, Allen GR. Shorefishes of the Tropical Eastern Pacific: online information system. Version 3.0 Smithsonian Tropical Research Institute, Balboa, Panamá. 2024.
64. Robertson DR, Van Tassel J. Shorefishes of the Greater Caribbean: online information system. Version 3.0 Smithsonian Tropical Research Institute, Balboa, Panamá. 2023.
65. Données d'Observations pour la Reconnaissance et l'Identification de la faune et la flore Subaquatiques (DORIS). https://doris.ffessm.fr. Accessed 10 Oct 2024.
66. Ahyong S, Boyko CB, Bernot J, Brandão SN, Daly M, De Grave S, et al. World Register of Marine Species (WoRMS). https://www.marinespecies.org. Accessed 10 Oct 2024.
67. iNaturalist. Available from https://www.inaturalist.org. Accessed 10 Oct 2024.
68. Edgar GJ, Cooper AT, Baker SC, Barker W, Barrett NS, Becerro MA, et al. Reef Life Survey: establishing the ecological basis for conservation of shallow marine life. Biol Conserv. 2020;252:108855.
69. GBIF.org (08 February 2024) Filtered export of GBIF occurrence data for Acanthuridae, Chaetodontidae, Lutjanidae, Mullidae, Pomacanthidae and Pomacentridae. https://doi.org/10.15468/dd.f6hzcs.
70. R Core Team, R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org. 2011.
71. Mouillot D, Villéger S, Parravicini V, Kulbicki M, Arias-González JE, Bender M, et al. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci USA. 2014;111:13757–62.
72. Maire E, Grenouillet G, Brosse S, Villéger S. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Glob Ecol Biogeogr. 2015;24:728–40.
73. Magneville C, Loiseau N, Albouy C, Casajus N, Claverie T, Escalas A, et al. MFD: an R package to compute and illustrate the multiple facets of functional diversity. Ecography. 2022;2022:e05904.
74. Collyer ML, Sekora DJ, Adams DC. A method for analysis of phenotypic change for phenotypes described by high-dimensional data. Heredity. 2015;115:357–65.

75. Adams DC, Otárola-Castillo E. Geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods Ecol Evol. 2013;4:393–9.
76. Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ. Functional ecology of fish: current approaches and future challenges. Aquat Sci. 2017;79:783–801.
77. Sorenson L, Santini F, Carnevale G, Alfaro ME. A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with revised family taxonomy. Mol Phylogenet Evol. 2013;68:150–60.
78. Hodge JR, van Herwerden L, Bellwood DR. Temporal evolution of coral reef fishes: global patterns and disparity in isolated locations. J Biogeogr. 2014;41:2115–27.
79. Rincon-Sandoval M, Duarte-Ribeiro E, Davis AM, Santaquiteria A, Hughes LC, Baldwin CC, et al. Evolutionary determinism and convergence associated with water-column transitions in marine fishes. Proc Natl Acad Sci U S A. 2020;117:33396–403.
80. Baraf LM, Pratchett MS, Cowman PF. Ancestral biogeography and ecology of marine angelfishes (F: Pomacanthidae). Mol Phylogenet Evol. 2019;140:106596.
81. Blomberg SP, Garland JT. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. J Evol Biol. 2002;15:899–910.
82. Blomberg SP, Garland JT, Ives AR. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution. 2003;57:717–45.
83. Thomas GH, Freckleton RP. MOTMOT: models of trait macroevolution on trees. Methods Ecol Evol. 2012;3:145–51.
84. Puttick MN, Ingram T, Clarke M, Thomas GH. MOTMOT: models of trait macroevolution on trees (an update). Methods Ecol Evol. 2020;11:464–71.
85. Anderson DR, Burnham KP, Thompson WL. Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manage. 2000;64:912–23.
86. Harmon LJ, Schulte JA, Larson A, Losos JB. Tempo and mode of evolutionary radiation in iguanian lizards. Science. 2003;301:961–4.
87. Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, Fitzjohn RG, et al. Geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. Bioinformatics. 2014;30:2216–8.
88. Revell LJ. Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol. 2012;3:217–23.
89. Frédérich B, Mittelheiser L, Gillet A, Hodge JR, Laudet V, Dornburg A. Data from: rapid and repeated evolution of the pigmentation patterns in reef fishes. figshare.

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