Trait-space disparity in fish communities spanning 380 million years from the Late Devonian to present

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Abstract

The diversity and distribution of traits in an ecological community determine how it functions. Modern fish communities conserve trait space across similar habitats. However, little is known about trait-space variation through deep time. We examined two Devonian fish communities — a tropical reef (Gogo, Australia) and a tropical estuary (Miguasha, Canada) — and compares them with six modern communities from diverse habitats. Trait-space metrics reflecting the amount of diversity found in each community (functional richness) and the similarity among species in each community (nearest neighbour) indicated Devonian communities had similar scores to modern communities, but were consistently less functionally rich than their closest modern analogues. Metrics describing location in trait space (specialisation, centroid distances, hypervolume overlap) also showed distinctions between Devonian and modern communities. Indeed, location in trait space of Devonian and modern communities differed on several axes associated with a range of traits largely confined to modern communities. Thus, modern fish communities are more functionally diverse in the traits we considered, potentially due to greater evolutionary lability. These results highlight the importance of evolutionary constraints in shaping community trait space and raise questions regarding whether differences between Devonian and modern communities indicate differences in community structure and function.

Key words: functional diversity; palaeoecology; community assembly; evolutionary constraints; trait diversity; fish communities.

Introduction

The combination of a species' traits mediate its interactions with its environment [1,2], so the range and distribution of traits among interacting species is important in determining function and resilience of ecological communities [3–5]. Further, the diversity and distribution of traits in a community — also known as community 'trait space' — can provide insights into the rules of community assembly, including what roles evolution, species filtering, and niche differentiation play in controlling how specific communities form [6–8]. Indeed, recent research on the trait space of contemporary communities has addressed how communities develop and adjust to their ever-shifting environments [9,10]. However, it is still unclear whether patterns observed within and among modern communities also apply to ecological communities over deep time. Consistent spatial and temporal patterns in community trait space would suggest that community assembly rules are constant, whereas variation could indicate phylogenetic constraints [11], stochasticity in evolutionary pathways [12,13], and/or shifts in the environmental parameters that determine community composition [14].

A range of metrics are commonly used to describe and investigate community trait space [15]. Such trait-diversity metrics often indicate variation among communities in different habitats and climates [16,17]. For example, trait diversity in fish (non-tetrapod vertebrate) communities differs depending on substratum (e.g., reef *versus* seagrass *versus* sand) [18–20] and habitat complexity [21,22]. Despite this variation, there is also evidence for the conservation of trait space across similar habitats, even when there are substantial phylogenetic and taxonomic differences among the resident communities [23]. That evolutionarily distinct communities occupying similar habitats have similar trait spaces suggests convergence (through evolution and/or niche filtering) and highlights the importance of deterministic processes in shaping community trait space (i.e., environment determining trait space) [24,25].

Although trait space varies among habitats and is conserved within habitat types across locations in contemporary communities, it remains unclear how it varies through deep time. Few studies have examined changes in functional diversity and trait space over millions of years (but see [26] for impacts of extinction events on ecospace). By testing for patterns across time as well as across contemporaneous habitats, it is possible to test whether similar habitats select for similar community trait space irrespective of phylogeny and evolutionary history.

The Devonian Period (419.2 to 358.9 million years ago [Ma]) is popularly termed the "Age of Fishes". During that time, diverse fish communities established and radiated across the planet and gave rise to the first tetrapods (four-legged vertebrates). Four mass extinctions have since occurred (not including the current one) [27], which along with the passing of time and millions of 'background' extinction and speciation events, have caused massive phylogenetic turnover [28,29]. In addition, Devonian and modern fish communities differ in terms of the non-fish species and nutrient inputs that make up the wider ecological community [30,31]. For example, Devonian reefs were primarily built of stromatoporoid sponges, calcareous algae, and microbial communities rather than hexacorallian corals (but also included some rugose and tabulate corals) [32,33], and ancient estuaries generally had low invertebrate and algal diversity compared to modern estuaries [34,35]. Thus, although the environments Devonian fish communities experienced were physically similar to their modern counterparts, their vertebrate and non-vertebrate biota differed greatly. By comparing these ancient assemblages to modern communities, it is therefore possible to test if physical environment is the primary determinant of fish community trait diversity across space and time, or whether biological, phylogenetic, and evolutionary differences associated with the passing of hundreds of millions of years have a dominant effect on trait space. Such knowledge will improve our understanding of how communities have responded to change in the past, and how they could change in response to anthropogenic and non-anthropogenic disturbances in the future.

We compared the trait space of two of the best-described Devonian fish communities — a tropical reef (Gogo Formation, northern Australia) and a tropical estuary (Miguasha, eastern Canada) — to that of six modern fish communities from different habitats and climate zones, to identify how trait diversity varies through space and time and thereby shedding light on the processes of community assembly. We compared these communities in terms of two trait-space metrics that reflect diversity and distribution of traits within each community (functional richness and nearest neighbour) and three that quantify each community's position in trait space relative to other communities (specialisation, distance between hypervolume centroids, overlap of hypervolumes) [36]. We hypothesise that (*i*) if community trait space is primarily determined by habitat, there will be larger differences between communities from different habitats (i.e., reef *versus* estuary *versus* freshwater) than between Devonian and modern communities from the same habitat (e.g., Devonian reef community similar to modern reef community) or between tropical and temperate/subtropical communities from the same habitat (e.g., tropical reef similar to temperate reef). (*ii*) If

community trait space is primarily determined by climate, there will be larger differences between tropical *versus* temperate/subtropical communities than between communities from different periods of time or different habitat types within the same climate zone. (*iii*) If community trait space is primarily determined by evolutionary history and the phylogenetic makeup of its constituent species, there will be larger differences between Devonian and modern communities compared to between communities from different habitat types or different climate zones within the same period. (*iv*) If time, habitat, and climate all substantially affect community trait space, there will be consistent groupings/patterns across all these variables (e.g., community metric scores will group together based on time, habitat, and climate); and (*v*) If community trait space is independent of time, habitat, and climate, trait space metrics will not be grouped by period (Devonian *versus* modern), habitat or climate zone. By identifying which of these five patterns are observed in trait space metrics, we provide insight into the factors shaping community trait space (i.e., community assembly) in the past, present and future.

Methods

Sites and species lists

We compared two Late Devonian (Frasnian) and six modern fish communities. The Late Devonian communities of Miguasha (Escuminac Formation) in north-eastern Canada and the Gogo Formation in north-western Australia are two of only six recognised fish Lagerstätten from this period [37]. We selected these communities based on (1) their fossil records capturing most of the *in situ* fish diversity, and (2) the availability of trait data for a range of traits and species that make up these communities (see electronic supplementary material Table S1). Miguasha (modern: 48° 48′ N, 66° 16′ W) was a tropical estuary in Laurussia 385 to 374 million years ago [38–40]. Thousands of fish specimens have been preserved and recovered from Miguasha, representing at least 19 species [39]. The Gogo Formation (modern: 18° 26′ S, 125° 55′ E) represents the basinal and channel facies adjacent to a tropical, stromatoporoid sponge-dominated reef that was on the edge of the Gondwanan landmass 384 to 382 million years ago; the fish preserved in the Gogo Formation were deposited under anoxic marine conditions and came from the adjacent reef [33]. Fifty-three fish species have been identified from Gogo (including 47 described and 6 undescribed species; Electronic supplementary material Tables S1 and S2) [33,41]. Discovery curves suggest all (fossilised) fish species from Miguasha have been described [34] and that most (>

95%) fish species from Gogo have been identified (see electronic supplementary material Fig. S1; Table S2).

We selected six modern fish communities for comparison to capture fish assemblages from a diversity of environments (different habitat types and climate zones). Our selection was further guided by the availability of species lists for the communities and the presence of detailed information on trophic interactions (allowing for later development of trophic-network models of those communities). We included reef, estuarine, and freshwater communities, with tropical and temperate or subtropical representatives of each (i.e., we included each habitat-type/climate-zone combination). The modern communities were: Caribbean reefs (tropical; 18° 3′ N, 65° 28′ W) [42]; Chilean reefs (temperate/subtropical; 31° 30′ S, 71° 35′ W) [43]; Santa Cruz Channel, north-eastern Brazil (tropical estuary; 7° 46′ S, 34° 53′ W) [44,45]; Ythan Estuary, Scotland (temperate estuary; 57° 19′ N, 1° 59′ W) [46–48]; Braço Morto Acima and Abaixo, central Brazil (tropical freshwater oxbow lakes; 19° 41′ S, 56° 59′ W) [49–58]; and the Nepean River, New South Wales, Australia (temperate/subtropical freshwater river section; 33° 47′ S, 150° 38′ E; ala.org.au; see electronic supplementary material Table S3) [59].

Traits

We collected information on 13 traits from the 488 species in our study (416 extant species and 72 Devonian species; see electronic supplementary material Table S4). We chose traits based on their ecological relevance and their availability for both living and extinct species. The traits were: sagittal body shape, transverse body shape, maximum total body length (tip of snout to tip of caudal fin), standard body length, head length, eye diameter, pre-orbital length, body depth, position of mouth, position of eyes, presence of mandible, presence of spiracle, and caudal fin shape (Fig. 1; see electronic supplementary material Table S4). We expressed all morphometric variables (except maximum total body length) as a proportion of maximum total body length as a size standardisation and to reduce correlations among these traits. Due to inconsistencies in how standard body length is measured across different body shapes and taxonomic groups, we later removed that measure from our analyses. We also removed ‘presence of mandible’ because these data were highly uneven (4 without mandibles *versus* 483 with), which causes problems when calculating distances in multidimensional space. Thus, our final database included 11 traits for 488 species.

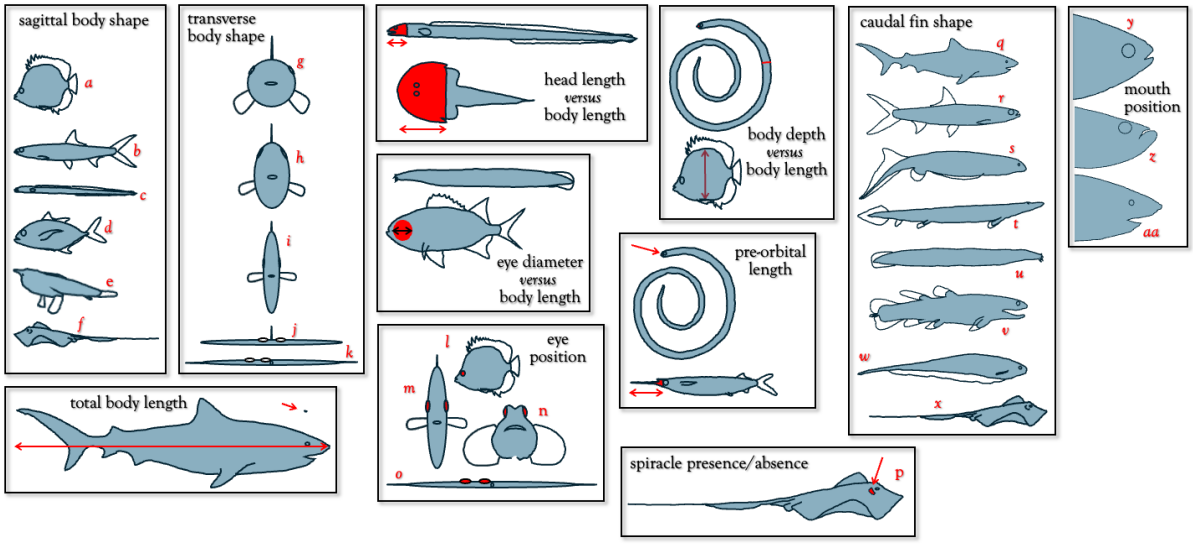

Figure 1. Fish traits used in the trait space analysis. An example from each category is shown for the categorical traits, whereas trait extremes are shown for continuous traits. Sagittal body shapes include (a) short and deep, (b) elongated, (c) eel-like, (d) fusiform, and (e & f) other. Transverse body shapes include (g) circular, (h) oval, (i) compressed, (j) flattened, and (k) compressed and lies on side. Eye positions included (l & m) lateral, (n) raised/top of head, and (o) migrated to one side and raised. Large spiracles could be present (p) or absent. Caudal fin shapes included (q) heterocercal, (r) homocercal, (s) hypocercal, (t) isocercal, (u) protocercal, (v) leptocercal, (w) reduced or absent, and (x) whip-like. Mouth positions included (y) terminal, (z) superior, and (aa) subterminal/inferior.

We collected trait data for Devonian species from the literature, specimens, and photographs of specimens. However, it was not possible to collect all traits for the species from the Gogo Formation because some of them are only known from incomplete or disarticulated body parts (due to the preservational environment) [60]. We addressed these gaps by estimating traits using: (1) expert opinion in cases where traits could be confidently inferred (inferences made by J. Long, A. Clement, B. Choo, and K. Trinajstic) or (2) multiple imputation using species' traits, coarse taxonomy, and the `missForest` R package [61,62]. Evaluating multiple imputation performance indicated out-of-bag error estimates of 0.30 (normalised root-mean-square error) and 0.11(proportion of falsely classified) for continuous and categorical variables, respectively. For modern species, we extracted trait data from *Fishbase* (using the `rFishbase` package) [63], photographs, and scientific literature [62]. We visually inspected the distribution of continuous traits, identifying two as right-skewed (total length and pre-orbital length); we $\log_e$-transformed these traits to normalise them.

Analyses

We built a Gower dissimilarity matrix [64] to quantify trait differences among species using the `gawdis` package in R [65]. Gower dissimilarity can handle mixed data types (our trait data included continuous and categorical variables) and can normalise the contribution of variables [6,64]. Including all traits resulted in an unbalanced distribution, so we also calculated Gower distances with the maximum number of traits that did not result in uneven distributions (there were three such combinations of nine traits). Observed patterns in functional diversity metrics were consistent across these trait sets (see electronic supplementary material Fig. S2 and S3). We therefore only present results from the 'all traits' Gower distance trait set in the main text.

We applied principal coordinate analysis (PCoA) to the Gower distances to ordinate species within a lower-dimensional space and calculate functional diversity metrics using the `mFD` R package [66]. The first eight principal coordinate axes explained 73% of the total variation [62]; we identified that eight was the optimal number of axes based on scaled mean absolute deviation and scaled root of mean square error (minimising the deviation between trait-based distances and functional space distances) [62]. We therefore used these eight axes to calculate each community's functional richness (proportion of functional space filled by the community), nearest neighbour (average distance in trait space to the nearest functional neighbour in the same community), and specialisation (average distance to the global centroid). These metrics calculated from PCoA coordinates are unitless 'scores' that can be used to compare communities.

Species diversity varied substantially among the included communities, ranging from 17 species in Ythan Estuary to 208 species in Caribbean reefs (Electronic supplementary material Tables S1 and S3). Functional diversity metrics can be correlated with species diversity [15,67], so we recalculated the three functional diversity metrics (functional richness, nearest neighbour, and specialisation) controlling for species diversity to test which, if any, patterns in these metrics persisted after removing species diversity-linked associations. To control for species diversity, we sub-sampled 10 species from each community and calculated the functional diversity metrics based on these sub-samples, replicating the process 100 times and taking the mean score for each metric for each community across the replicates. We plotted both the 'raw' and species-diversity controlled metrics, allowing us to evaluate visually whether period, habitat type, or climate zone grouped communities in any of these metrics.

We also used the principal coordinates to build trait hypervolumes for each community using Gaussian kernel density estimation and the `hypervolume` package in R [68]. We set the requested quantile to 0.95 and estimated the bandwidth for each axis in each community separately. We then used the mean estimated bandwidth for each axis across the eight communities as fixed bandwidths to recalculate hypervolumes (i.e., ensuring the same bandwidths for each community). The resulting hypervolumes were used to quantify distances between community centroids (geometric centre) and overlap in multidimensional trait space (Jaccard index). We made these comparisons between all pairwise community combinations to test if communities were grouped/clustered according to their period, habitat, or climate zone (see hypotheses listed in the introduction). We did not apply the sub-sampling technique as for the functional diversity metrics to these hypervolumes because (a) the average centroid from replicated sub-samples of a community is approximately the same as the centroid when including all species in the community (i.e., no change in distances between centroids), (b) when comparing overlap in trait space between communities (Jaccard index) to assess their similarity, it is more intuitive to use all species instead of sub-sampling species, and (c) the Jaccard index is a proportionate measure. Because distances between centroids suggested the fish community trait spaces were segregated, we identified the specific traits responsible by determining along which hypervolume axes the centroids differed, and which traits were correlated with these axes. We then investigated how these traits were distributed among the fish communities.

Results

Functional richness of the Devonian communities fell within the range observed in modern communities, irrespective of whether we controlled for species richness (Fig. 2a,b; not controlling for species richness: Gogo = 2.4×10^{-3}, Miguasha = 4.7×10^{-4}, modern assemblages = 2.6×10^{-5} to 0.29; controlling for species richness: Gogo = 3.6×10^{-7}, Miguasha = 4.1×10^{-6}, modern assemblages = 2.2×10^{-7} to 4.6×10^{-6}). However, the Devonian communities had lower functional richness than their closest modern counterparts (Gogo *versus* Caribbean: 2.4×10^{-3} *vs.* 0.29 [not controlling for species richness] and 5.6×10^{-7} *vs.* 3.8×10^{-6} [controlling for species richness]; Miguasha *versus* Santa Cruz Estuary 4.7×10^{-4} *vs.* 4.5×10^{-2} [not controlling for species richness] and 4.1×10^{-6} *vs.* 4.6×10^{-6} [controlling for species richness]). There was habitat-linked variation in functional richness, but the pattern differed depending on whether we controlled for species diversity (Fig. 2a,b).

Reef communities had the highest score followed by estuarine communities when all species were used to calculate functional richness (Fig. 2a), whereas estuarine communities had the highest scores followed by reefs after controlling for species diversity (Fig. 2b). This habitat-functional richness pattern, including the switching between reefs and estuaries as the most functionally rich communities when controlling for species diversity, emerged in both modern and Devonian communities (Fig. 2a,b). Among the modern assemblages, tropical communities consistently had higher functional richness than their temperate/subtropical counterparts (mean richness tropical *versus* temperate/subtropical: 0.11 vs. 0.0006 and 3.0×10^{-6} vs. 2.3×10^{-6} for richness calculated without controlling for species diversity and controlling for species diversity, respectively; Fig. 2a,b).

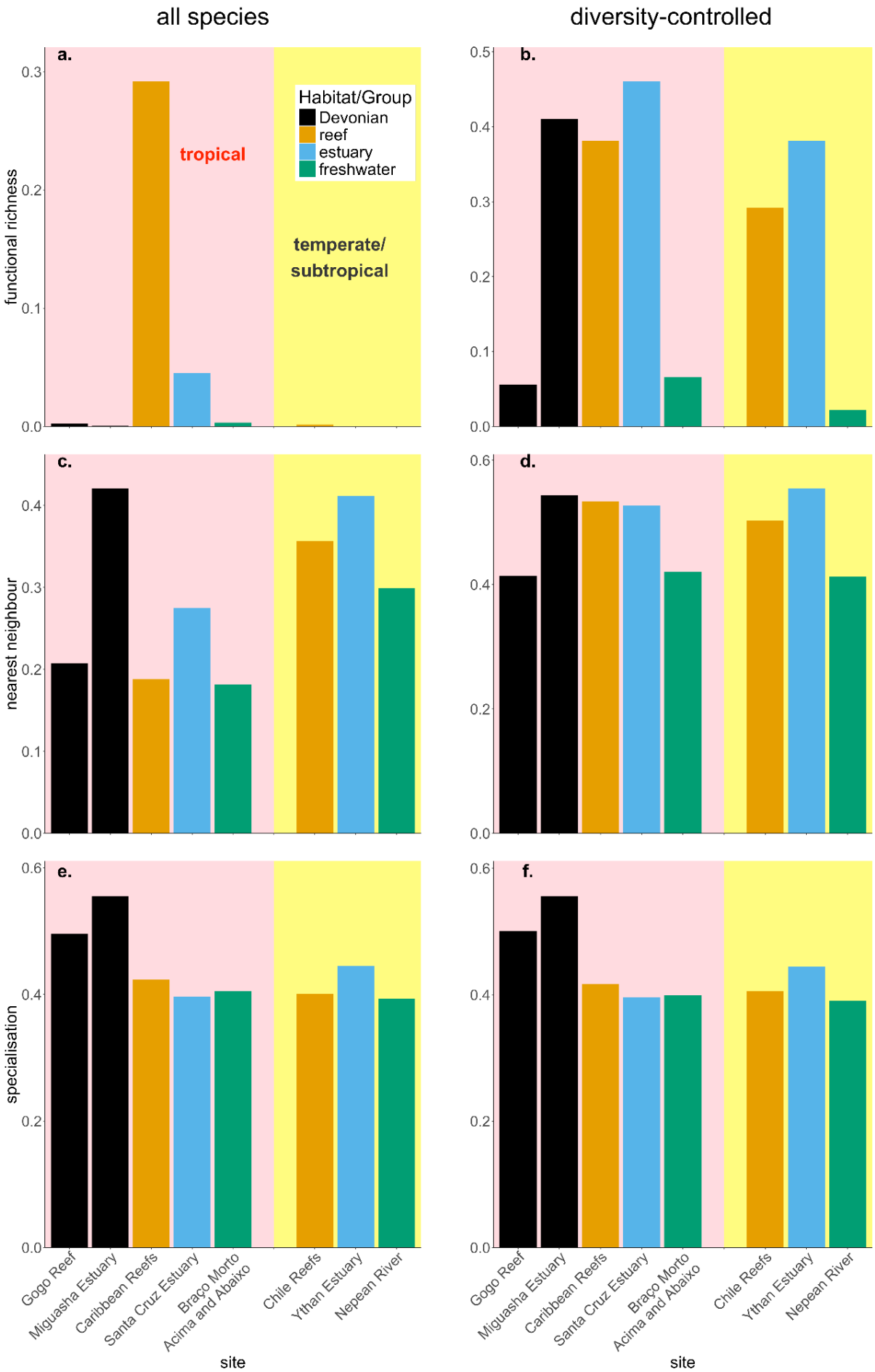
all species
diversity-controlled
a.
b.
c.
d.
e.
f.
functional richness
nearest neighbour
specialisation
Habitat/Group
Devonian
reef
estuary
freshwater
tropical
temperate/
subtropical
Gogo Reef
Miguasha Estuary
Caribbean Reefs
Santa Cruz Estuary
Braço Morto
Acima and Abaixo
Chile Reefs
Ythan Estuary
Nepean River
site

Figure 2. Functional diversity metrics for two Devonian and six modern fish communities. Three functional diversity metrics are shown, including: functional richness (a. and b.; volume of functional trait space filled by species in a community); nearest neighbour (c. and d.; mean distance in trait space to nearest neighbour in the same community); and functional specialisation (e. and f.; mean distance of species in a community to the mean position of species from the global pool). Panels in the left column show results when all species in each community are included to calculate these metrics (i.e., not controlling for species diversity), whereas panels in the right column show results controlling for species diversity using resampling. Pink background indicates the five tropical communities (ancient and modern), yellow background indicates the three temperate/subtropical communities (modern only). For display purposes, we scaled functional richness values in the controlled-diversity plot by multiplying by 100,000 (functional metrics calculated from principal coordinates are unitless and indicate relative differences).

Nearest-neighbour scores, reflecting the distance in functional space of each species to the nearest species in its community, were similar for Devonian and modern communities (Fig. 2c,d). Miguasha had a slightly higher score than the other communities when not controlling for species diversity (Fig. 2c; Miguasha = 0.421, Gogo = 0.207; modern assemblages = 0.181 to 0.411). After accounting for species diversity, nearest-neighbour scores for Gogo and Miguasha fell within the range observed in the modern communities (Fig. 2d; Gogo = 0.414, Miguasha = 0.544; modern assemblages = 0.413 to 0.554).

There were differences among habitats in nearest-neighbour scores within periods and climate zones. Freshwater communities consistently had the lowest nearest-neighbour scores (Fig. 2c,d). Estuarine communities consistently had the highest scores followed by reef communities, except in the tropical, species diversity-controlled comparison where these communities had similar scores (Fig. 2 c,d). Further, there was a latitudinal pattern among modern communities when not controlling for species diversity — species in temperate and subtropical communities were farther from their nearest neighbour than were species in tropical communities (Fig. 2c) — but this latitudinal pattern disappeared after controlling for species diversity (Fig. 2d).

The Devonian communities had the highest functional specialisation, irrespective of whether or not we controlled for species diversity (Fig. 2e,f; not controlling for species diversity: Miguasha = 0.555, Gogo = 0.496, modern communities = 0.393 to 0.445; controlling for species diversity: Miguasha = 0.556, Gogo = 0.500, modern communities = 0.391 to 0.444). High specialisation indicates species in these communities are farther from the global (combined communities) mean position/centroid. Similarly, the distances between hypervolume centroids of Devonian *versus* modern communities were greater than the distances between centroids of communities from the same period (Fig. 3a,b; distance between Devonian and modern: 0.16 ± 0.01, distance between communities from the same period: 0.07 ± 0.02; all values are means ± SD). Centroids of communities from the same

habitat type or the same climate zone were not closer together than centroids from different habitats or climate zones (Fig. 3c,d).

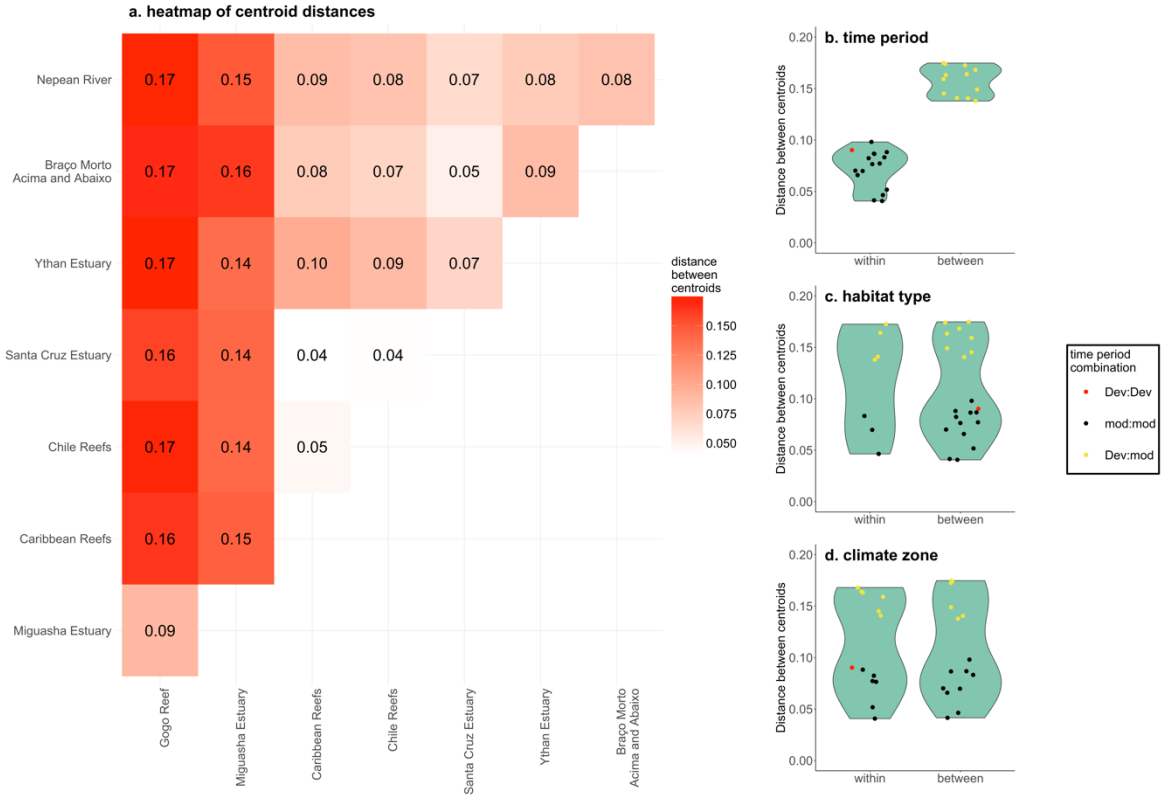

Figure 3. Distances between centroids of functional trait space hypervolumes for fish communities. Two Devonian (Gogo and Miguasha) and six modern fish communities from different habitats and climates are compared. On the left, plot a. is a heatmap showing distances between the centroids of each community. On the right are three violin plots showing distances between communities from either the same (within) or different (between): b. periods, c. habitat types, and d. climate zones. Hypervolumes were built using species coordinates on the first 8 axes from a principal coordinate analysis applied to a Gower dissimilarity matrix of the species' traits. Plot points in the violin plots represent individual comparisons between communities, jittered on the *x* axis for clarity.

The hypervolume Jaccard index measuring trait-space overlap also indicated less similarity between Devonian and modern communities compared to between communities from the same period (Fig. 4a,b; overlap between Devonian and modern: 0.05 ± 0.02, overlap between communities from the same period: 0.18 ± 0.07; all values are means ± SD). The overlap index between Devonian communities was within the range observed among modern communities (Devonian overlap = 0.16, modern community overlap = 0.09-0.37; Fig. 4a). There was no evidence of greater overlap between hypervolumes of communities from the same *versus* different habitat types or climate zones (Fig. 4c,d).

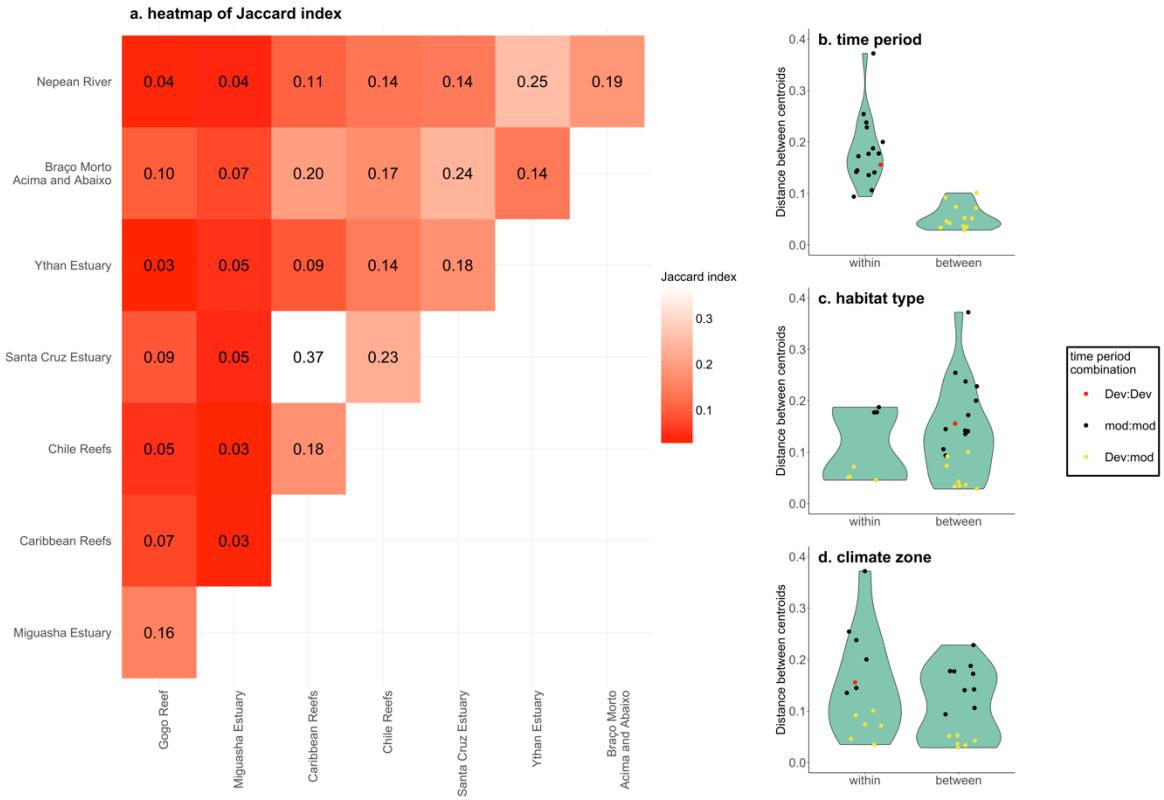

Figure 4. Jaccard Index comparing overlap in functional trait space hypervolumes for fish communities. Two Devonian (Gogo and Miguasha) and six modern fish communities from different habitats and climates are compared. On the left, plot a. is a heatmap showing Jaccard indices for all community comparisons. On the right is a series of violin plots showing Jaccard indices between communities from either the same (within) or different (between): b. periods, c. habitat types, and d. climate zones. Hypervolumes were built using species coordinates on the first 8 axes from a principal coordinate analysis applied to a Gower dissimilarity matrix of the species' traits. Plot points in the violin plots represent individual comparisons between communities, jittered on the *x* axis for clarity.

The centroids for both Devonian communities were outside the range observed in modern communities on axis 1 (Devonian ≤ -0.089, modern ≥ -0.045), axis 2 (Devonian ≥ 0.061, modern ≤ 0.009), and axis 7 (Devonian ≥ 0.026, modern ≤ -0.003; see electronic supplementary material Table S5).

Although directly linking the principal coordinate axes to traits is not possible because the axes are based on Gower distances between species, correlations between species coordinates along these axes and traits suggest they mostly reflect eye diameter, body depth, and caudal fin shape on axis 1; position of mouth and eye position on axis 2; and transverse body shape and presence of spiracles on axis 7 (Table 1). Accordingly, Devonian communities were distinct from modern communities in these traits. Devonian fishes tended to have smaller eye diameters and their bodies were not as deep relative to their length (axis 1; Fig. 5c,e). None of the fish in these Devonian communities had superior mouth position whereas all the

modern communities had some fish with this mouth position (axis 2; Fig. 6e). None of the Devonian fish had eyes migrated to one side of the body (as in flatfish; axis 2; Fig. 6f), spiracles and heterocercal tails were more prevalent in the Devonian than modern communities (axis 1 and 7, respectively; Fig. 6b,d), and the proportion of fish with a compressed transverse body shape is lower in the Devonian fishes (axis1; Fig. 6c).

Gogo's centroid was also extreme on axes 5 and 6 (with values of 0.056 and 0.019, respectively, compared to values ≤ 0.002 and ≤ 0.017 for the other communities on the same axes; see electronic supplementary material Table S5), while Miguasha's centroid was extreme on axis 4 (Miguasha = -0.049, other communities ≥ -0.026; see electronic supplementary material Table S5). Sagittal (not transverse) body shape was the most strongly correlated trait with these axes, showing a slightly stronger correlation with axis 5 (Table 1) than with axes 4 and 6 (sagittal body shape-axis correlation: $\eta^2 = 0.311$, $p < 0.000$ and $\eta^2 = 0.252$, $p < 0.000$ for axes 4 and 6, respectively; see electronic supplementary material Table S6). These correlations suggest that the extreme positions of Gogo and Miguasha could be attributed to Gogo's lack of eel-shaped and elongate (e.g., anguilliform) fish and to Miguasha's higher occurrence of fish with unconventional ('other') body shapes (Fig. 6a), which included the tadpole-shaped *Escuminaspis laticeps* and *Levesquaspis patteni*.

Table 1. Correlation between traits *versus* species coordinates on principal coordinate analysis axes, showing each trait and the axes with which it had its highest correlation (for all trait/axis correlations, see electronic supplementary material Table S6). We applied Kruskal-Wallis tests to categorical traits and linear models (regressions) to continuous traits. r^2 and η^2 describe the proportion of variance explained by the Kruskal-Wallis and linear models, respectively. Type I error rates (p-values) were < 0.0001 in all cases. See Fig. 1 for trait details.

Trait	axis	test	statistic	value
body depth	PC1	linear model	r^2	0.537
sagittal body shape	PC5	Kruskal-Wallis	η^2	0.397
transverse body shape	PC7	Kruskal-Wallis	η^2	0.378
caudal fin shape	PC1	Kruskal-Wallis	η^2	0.339
eye diameter	PC1	linear model	r^2	0.623
eye position	PC2	Kruskal-Wallis	η^2	0.371
head length	PC3	linear model	r^2	0.335
$\log_e$(pre-orbital length)	PC3	linear model	r^2	0.493
$\log_e$(total body length)	PC3	linear model	r^2	0.431
mouth position	PC2	Kruskal-Wallis	η^2	0.415
spiracle	PC7	Kruskal-Wallis	η^2	0.221

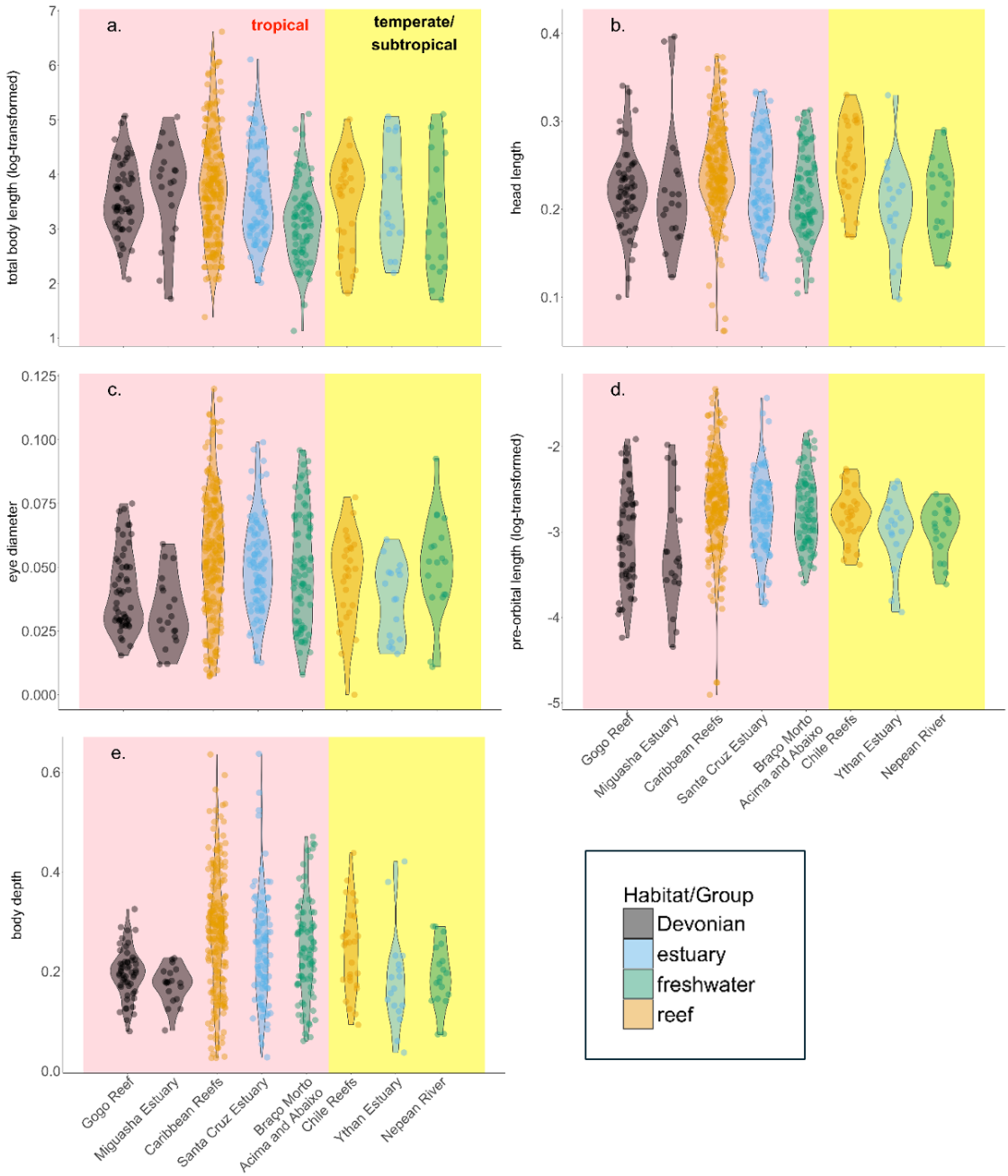

Figure 5. Violin plots of five continuous fish traits from two Devonian and six modern communities. Total body length is in centimetres and transformed using the natural logarithm ($\log_e$) to normalise. All other traits are expressed as a proportion of total body length ($\log_e$-transformed for pre-orbital length). Pink background indicates the five tropical communities (ancient and modern), yellow background indicates the three temperate/subtropical communities (modern only).

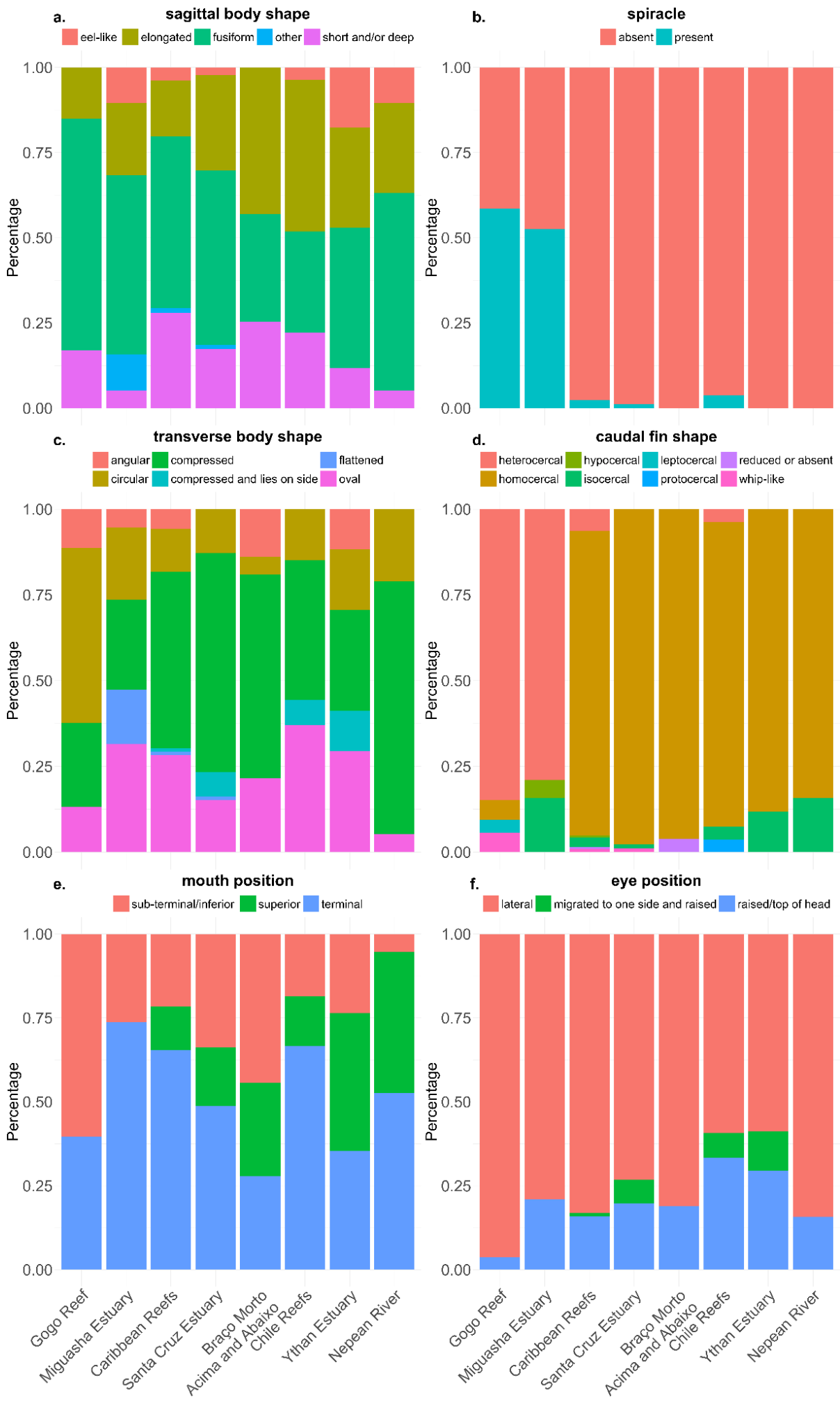
a.
sagittal body shape
eel-like
elongated
fusiform
other
short and/or deep
b.
spiracle
absent
present
c.
transverse body shape
angular
compressed
flattened
circular
compressed and lies on side
oval
d.
caudal fin shape
heterocercal
hypocercal
leptocercal
reduced or absent
homocercal
isocercal
protocercal
whip-like
e.
mouth position
sub-terminal/inferior
superior
terminal
f.
eye position
lateral
migrated to one side and raised
raised/top of head
Percentage
1.00
0.75
0.50
0.25
0.00
Gogo Reef
Miguasha Estuary
Caribbean Reefs
Santa Cruz Estuary
Braço Morto
Acima and Abaixo
Chile Reefs
Ythan Estuary
Nepean River

Figure 6. Stacked bar charts of six categorical fish traits from two Devonian and six modern communities: a. sagittal body shape, b. presence/absence of spiracles, c. transverse body shape, d. caudal fin shape, e. mouth position, and f. eye position. The *y* axis indicates the percentage of species in each community with each category of the trait.

Discussion

Our analysis of modern and ancient fish communities revealed patterns in community trait space associated with period, habitat type, and climate zone. The importance of these variables differed among trait-space metrics, indicating that different factors are important for different trait-space attributes. The two metrics that reflect diversity and distribution of traits within a community (functional richness and nearest neighbour) suggest: (1) broad similarity between Devonian and modern assemblages, but with Devonian communities having consistently lower functional richness than their closest modern counterparts, (2) an association with habitat type, and (3) an association with climate zone (Fig. 2; consistent with hypothesis *iv*). In contrast, period was the only variable that clearly differentiated fish assemblages in the three metrics that reflect a community's position in trait space relative to other communities (functional specialisation, distance between hypervolume centroids, and Jaccard index); we observed no associations between these metrics and habitat type or climate zone (Fig. 3e,f, 4, 5; consistent with hypothesis *iii*). The trait-space positions of Devonian communities were distinct from modern communities on several axes (see electronic supplementary material Table S5) associated with seven of the eleven traits we included in our analyses (Table 1); such trait differences could indicate disparity between Devonian and modern communities in terms of their structure and function. Further, that communities from the same period have similar trait spaces, while those from different periods are dissimilar (consistent with hypothesis *iii*), suggests evolutionary constraints and stochasticity in evolutionary pathways are potentially important in determining community trait space and community assembly.

Period

If the fish community trait space has changed through time, we would expect to see communities from different periods segregated in terms of their trait-space metrics (i.e., modern communities similar to each other and different to Devonian communities). This pattern is clear in four of the five metrics we calculated: Devonian communities consistently differed from modern communities in terms of functional richness, specialisation, centroid location, and hypervolume overlap (Fig. 2, 3, 4).

Although functional richness of Devonian communities was within the range spanned by all modern communities, the scores of Devonian communities in this metric were consistently lower than those observed in modern communities from the same habitat type and climate zone (i.e., Gogo Reef *versus* Caribbean Reef, Miguasha *versus* Santa Cruz Estuary; Fig. 2a,b). Despite the Devonian period being popularly named the 'Age of Fishes', Devonian fish communities tended to have lower species diversity compared to modern fish communities; our results suggest they also had lower trait diversity compared to their modern counterparts (Fig. 2a,b). Discovery curves confirm that most species in the Devonian communities we examined have been described (see electronic supplementary material Table S2, Fig. S1 and [34]), and, therefore, the relatively low functional and species richness in Devonian communities compared to their modern analogues are probably real features instead of preservational artefacts. Indeed, functional richness was lower for Devonian communities even after controlling for species diversity (Fig. 2b), providing further support for lower functional richness in those communities. However, it is not clear whether the entire 'missing' trait space in these Devonian fish assemblages was vacant. It is possible that non-fish taxa filled some of that space. For example, conodonts (early, non-fish, but fish-like, jawless vertebrates) might have occupied the trait space of modern lampreys, hagfish, and small eels [69,70], while invertebrates such as Eurypterids (sea scorpions) might have filled trait and trophic spaced occupied by predatory fishes in modern communities [71]. Similarly, non-fish taxa, such as sea snakes, turtles, and marine mammals, make unique contributions to the trait space in modern aquatic communities [72].

Functional specialisation, centroid distances, and the Jaccard index (trait-space overlap) are metrics that reflect the location of a community's trait space relative to other communities. The fact that Devonian and modern communities are separated by these metrics indicates variation in trait values (continuous traits), trait status (categorical traits), and/or trait combinations. By examining which hypervolume axes separated modern and Devonian communities, and which traits were correlated with these axes, we were able to identify the traits involved in differentiating the trait spaces of these communities. Seven of the eleven traits we included in our analysis appear to contribute to this differentiation, including: eye diameter (Fig. 5c); body depth (Fig. 5e); presence of large spiracles (Fig. 6b); transverse body shape (Fig. 6c); caudal fin shape (Fig. 6d); mouth position (Fig. 6e); and eye position (Fig. 6f). Of these traits, eye diameter, body depth, mouth position and eye position had lower diversity in Devonian compared to modern communities (Fig. 5,6). Thus, differences between modern and Devonian communities as indicated by specialisation, centroid

distances, and the Jaccard index reflect, at least in part, trait space that is absent in the Devonian fish, consistent with the observed differences in functional richness between communities from these periods (Fig. 2a,b).

Community trait space is linked to community structure and function [73,74]. Our trait space results therefore suggest substantial ecological differences between Devonian and modern fish communities. For example, the dearth of Devonian fish with a superior mouth position — an adaptation to feeding from above [75,76] — indicates differences in trophic interactions. While superior mouth position has been documented in Devonian species [77,78], the rarity of this trait in the Devonian contrasts with its widespread occurrence in modern communities (Fig. 6e). Greater diversity of mouth position does not only indicate a greater variety of feeding strategies used today, but also suggests that species in modern communities experience different predation pressures to those present in the Devonian (e.g., in terms of predator archetypes) [79], which could lead to the evolution of distinct antipredator strategies. Similarly, the lack of fish with deep, laterally compressed bodies in the Devonian communities (indicated by the body depth and transverse body shape traits; Fig. 5e and 6c) likely indicates ecological differences associated with microhabitat use and how a species interacts with conspecifics and other species [80,81]. Deep-bodied, laterally compressed jawless fish have been documented in older communities (Late Silurian and Early Devonian) [82], but they were less widespread compared to deep-bodied fish in modern communities, and they appear to have gone extinct before the Late Devonian (i.e., the epoch we examined). Thus, the relatively low variation of traits in Late Devonian communities suggests they were less ecologically/functionally diverse overall than modern fish communities.

The greater trait variation we observed in modern *versus* Devonian fish communities could result from (*i*) increased habitat/environmental complexity through time [83], (*ii*) the longer time modern fish assemblages have had to evolve/diversify [84], and/or (*iii*) the morphological flexibility of teleost fish, a group that did not evolve until the Triassic Period (> 100 million years after the Devonian; although greater variation in actinopterygian traits started to emerge immediately following the Hangenberg extinction event at the end of the Devonian) [85]. In modern fish communities, there is a positive correlation between habitat complexity and functional richness [22,86]. Thus, given that Devonian habitats appear to have been less complex than modern habitats (e.g., even the most complex Devonian reefs tended to be less structurally complex than modern coral reefs [87] and diversity of benthic/habitat-forming organisms was lower [88]), this factor might contribute to the lower

trait diversity in Devonian fish. Conversely, teleosts have several traits that foster morphological flexibility. For example, the prehensile mouth parts of teleosts give great flexibility in mouth-linked traits, leading to the evolution of different mouth positions and head shapes [89]. Other attributes that promote morphological flexibility in teleosts and other osteichthyans — fish that are more prevalent in modern communities compared to Devonian ones — include the presence of a swim bladder for buoyancy control and bony endoskeletons, facilitating diversification in movement patterns and body shape [90,91]. While our results suggest higher trait diversity in modern fish communities, we acknowledge that the choice of traits and the groupings used for categorical variables could influence conclusions regarding which taxa or communities are most diverse [6]. For example, if we had focused on bony armour plates and lobe-paired fin structure, Devonian communities would be classified as more trait-diverse than modern communities [92]. Regardless, our main conclusion — that trait space of modern and Devonian communities differ — should hold true for any broad sample of traits across the entire phenotype.

Habitat

Functional nearest-neighbour scores did not show consistent differences between periods, but did display variation with habitat type: freshwater communities consistently had the lowest scores (their constituent species were the most similar to each other), while estuarine communities had the highest nearest-neighbour scores in most cases (Fig. 2c,d). The low functional richness and low nearest-neighbour scores in the freshwater communities we examined (i.e., indicating low trait diversity and high similarity among species; Fig. 2a,b,c,d) is likely the result of strong niche filtering, corroborating previous conclusions that habitat filters determine species (and therefore trait) composition in freshwater communities [93,94]. Reef communities in both periods have high functional richness and low-to-intermediate nearest-neighbour scores when not controlling for species diversity (Fig. 2a, c), suggesting that many, densely concentrated niches are facilitated by complex reef habitats (corroborating research on modern communities) [95]. Estuarine communities have the highest nearest-neighbour scores in most cases (Fig. 2c,d), indicating that their species are distinct from each other in trait space. The trait variation among fish in estuarine communities might reflect that these assemblages are an admixture of species from different origins — they include marine, freshwater, and diadromous fish, as well as species that complete their life cycle in estuaries — and therefore include species that have experienced different niche/environmental filters [96,97]. The association between nearest-neighbour scores and habitat type, and the lack of a

consistent difference between communities from different periods, suggests that environmental factors are the primary determinants of how similar species within a community can be to each other. Furthermore, the high nearest-neighbour scores in Devonian and modern estuarine communities (Fig. 2c,d) suggest low trait and functional redundancy [98,99]. Communities with low redundancy might be particularly sensitive to the loss of species [100], depending on the network of species' interdependencies supporting the community [101,102]. Indeed, previous studies have reported low function redundancy in reef-fish communities [5,18]; our results suggest even lower redundancy in estuarine communities.

We also found that functional richness varied with habitat type, but the functional richness-habitat pattern depended on whether we controlled for species diversity (Fig. 2a,b). Across climate zones, reef communities had the highest functional richness followed by estuarine communities when all species were included, whereas estuarine communities had the highest richness followed by reef communities when controlling for species diversity (Fig. 2a,b). We observed this switching between which habitat type had the highest functional richness in modern and Devonian communities (Fig. 2a,b). High habitat complexity could explain the elevated species and functional richness in reef communities by allowing greater niche differentiation among resident fish [95]. Indeed, that species richness was higher for reef *versus* estuarine communities (e.g., 208 *versus* 86 species for tropical communities, and 27 *versus* 17 species for temperate/subtropical communities) also potentially explains why controlling for species diversity switches which habitat type had the highest functional richness. The difference might result from saturation of trait space in species-rich reef communities (i.e., the expansion of a community's trait space associated with the addition of a species diminishes as more species are added to the community) [6,103–106], a hypothesis supported by the low nearest-neighbour scores for the reef compared to estuarine communities when ignoring species diversity (Fig. 2c).

Climate

Functional richness of modern tropical communities was higher than that of modern temperate and subtropical communities, consistent with the previously reported pattern of increasing functional richness with decreasing latitude in fish, other vertebrates, and invertebrates [106–111]. Our results also revealed a latitudinal/climate pattern among modern communities in terms of their nearest-neighbour scores, with tropical communities having lower scores than their temperate/subtropical counterparts when ignoring species diversity

(Fig. 2c). Together, functional richness and nearest-neighbour scores indicate that fish communities in the tropics have greater variation in traits and their constituent species are packed more closely together in trait space than observed in temperate and subtropical communities (where species richness also tends to be lower) [107,112]. We were unable to assess whether latitudinal patterns occurred among the Devonian fish communities because both Devonian communities in our study were tropical at deposition. Thus, future research could test whether latitude (climate) has been important in determining community trait space through time, or whether this pattern developed recently.

Conclusion

The differences we detected between modern and Devonian fish communities indicate that the trait space has changed through time. Although the Devonian period is known for its diverse and abundant fish fauna, our results suggest that modern fish communities are in fact more trait-diverse than their Devonian counterparts, and that their trait spaces are centred in different locations in trait space. These differences could indicate several phenomena, including the longer time modern communities have had to develop and diversify [84], greater variation in habitats today [88,113], phylogenetic constraints of different fish lineages [114], and/or stochasticity in evolutionary pathways [115,116]. Irrespective of the root cause(s), the observed differences in trait space suggests Devonian communities were structured and functioned differently to modern communities. In other words, fish in these Devonian communities likely interacted with each other and their environment in different ways to that observed in modern communities. Further research on how community structure and function has changed through time, combining information from ancient and modern communities [117], could provide important insights into community-assembly rules and the ecological and evolutionary responses of communities to environmental disturbances in the past and the future.

Acknowledgements

We thank S. Libralato, R. Angelini, A. Pérez-Matus , S. Villéger, C. Brauer for help accessing species lists and trait data for modern fish communities. We thank T. Llewelyn for providing helpful feedback. We also acknowledge the traditional owners of the lands on which this research was done, including the Gooniyandi, Kaurna, and Mi'kmaq peoples. This work was supported by the Australian Research Council [DP220100825].

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