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

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Abstract

Aim: 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 (or across vastly different habitats). In this paper, we sought to identify how trait diversity varies through space and time.

Location: Global Devonian and modern fish communities.

Methods: We examined two Devonian fish communities — a tropical reef (Gogo, Australia) and a tropical estuary (Miguasha, Canada) — and compared their trait space with that of six modern communities from diverse habitats.

Results: Trait-space metrics reflecting the amount of diversity found in each community (functional richness: FRic) and the similarity among species in each community (functional nearest-neighbour distance: FNND) indicated Devonian communities had similar scores to modern communities, but were less functionally rich than their closest modern analogues. Metrics describing location in trait space (centroid distances and 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. Functional richness and nearest-neighbour distance also varied with habitat type and climate zone: estuarine communities had the highest nearest-neighbour distances followed by reef communities; reefs were the most functionally rich communities followed by estuaries; and functional richness was highest in tropical communities.

Main Conclusions: Fish community trait space varies with time, habitat and climate, suggesting (*i*) lability in fish trait space and (*ii*) evolutionary history, environmental filtering, and stochasticity influence community assembly. Furthermore, the large changes in community trait space that have occurred over deep time indicate changes in community structure and function.

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

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 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). 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, giving rise to the first tetrapods. 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 [FRic] and functional nearest-neighbour distance [FNND]) and two that

quantify each community's position in trait space relative to other communities (distance between hypervolume centroids and 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 (Table S1.1, see Appendix S1 in Supporting Information). 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; see Appendix S1, Tables S1.1 and S1.2) [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 Appendix S1, Fig. S1.1 and Table S1.2).

We selected six modern fish communities from a diversity of environments (different habitat types and climate zones) for comparison to the Devonian communities. Our selection of modern communities was further guided by the availability of species lists for the assemblage and the presence of 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; 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 Appendix S1, Table S1.3) [59].

Traits

We collected information on 11 traits from the 488 species in our study (416 extant species and 72 Devonian species; see Appendix S1, Table S1.4). 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), head length, eye diameter, pre-orbital length, body depth, position of mouth, position of eyes, presence of spiracle, and caudal fin shape (see Appendix S1, Fig. S1.2 and Table S1.4). All morphometric variables (except maximum total body length) were expressed as a proportion of maximum total body length as a size standardisation and to reduce correlations among these traits.

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] (GitHub folder). 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) [62], photographs, and scientific literature; GitHub folder). 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 [63] to quantify trait differences among species using the `'gawdis'` package in R [64]. Gower dissimilarity can handle mixed data types (our trait data included continuous and categorical variables) and can normalise the contribution of variables [6,63]. 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 Appendix S1, Fig. S1.3 and S1.4). 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 [65]. The first eight principal coordinate axes explained 73% of the total variation (GitHub folder); 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; GitHub folder). We therefore used these eight axes to calculate each community's functional richness (FRic) [66] and functional nearest neighbour (FNND) [67] scores. Functional richness, defined as the

205 proportion of functional space filled by a community, quantifies the functional diversity of a
206 community. In contrast, functional nearest neighbour is the average distance in trait space to
207 each species' nearest neighbour within the community, quantifying functional similarity
208 (redundancy) among species in a community. These metrics, calculated from PCoA
209 coordinates, are unitless 'scores' that can be used to compare communities. We also
210 calculated functional evenness, functional divergence, and functional specialisation
211 (indicating how regularly species are distributed in trait space, how distinct species are from
212 the centroid of the community's trait space, and how distinct species in a community are
213 from the global centroid, respectively) (see Appendix S1, Fig. S1.5).
214 Species diversity varied substantially among the included communities, ranging from 17
215 species in Ythan Estuary to 208 species in Caribbean reefs (see Appendix S1, Tables S1.1
216 and S1.3). Functional diversity metrics can be correlated with species diversity [15,68]. We
217 therefore also calculated standardized effect sizes — a method that controls for species
218 richness — for both metrics (functional richness and nearest-neighbour scores) [69]. To do
219 this, we generated 1000 null models by randomly shuffling species among the communities
220 while maintaining the species richness of each community. We then calculated the mean and
221 standard deviation of the functional diversity metrics for each community in the null models.
222 We subtracted null mean values from observed functional diversity metrics to calculate the
223 effect sizes, which we divided by the null standard deviations to standardize across scales.
224 Controlling for species diversity in this way allowed us to (*i*) separate patterns due to species
225 diversity from those due to functional diversity, (*ii*) detect patterns in functional diversity that
226 were masked by species diversity, and (*iii*) limit the effects of species with extreme traits. We
227 plotted both the 'observed' and standardized effect size (species-diversity controlled) metrics,
228 allowing us to evaluate visually whether period, habitat type, or climate zone grouped
229 communities in either of these metrics.
230 We also used the principal coordinates to build trait-space hypervolumes for each
231 community using Gaussian kernel density estimation and the `'hypervolume'` package in
232 R [70]. We set the requested quantile to 0.95 and estimated the bandwidth for each axis in
233 each community separately. We then used the mean estimated bandwidth for each axis across
234 the eight communities as fixed bandwidths to recalculate hypervolumes (i.e., ensuring the
235 same bandwidths for each community). The resulting hypervolumes were used to quantify
236 distances between community centroids (geometric centre) and overlap in multidimensional
237 trait space. We measured overlap using the Jaccard index, and we further decomposed non-
238 overlap into its turnover and nestedness components [71]. 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). 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. 1a,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 = -2.4, Miguasha = -1.0, modern assemblages = -0.8 to -2.9). However, the Devonian communities had lower functional richness than their closest modern counterparts when not controlling for species richness (Fig. 1a; Gogo *versus* Caribbean: 2.4×10^{-3} *vs.* 0.29; Miguasha *versus* Santa Cruz Estuary 4.7×10^{-4} *vs.* 4.5×10^{-2}). Standardized effect sizes controlling for species diversity indicated that Devonian communities had similar functional richness to their modern counterparts (Fig. 1b; Gogo *versus* Caribbean: -2.4 *vs.* -2.0; Miguasha *versus* Santa Cruz Estuary -1.0 *vs.*-1.8). There was habitat-linked variation in functional richness, but the pattern differed depending on whether we controlled for species diversity (Fig. 1a,b). Reef communities had the highest score followed by estuarine communities in observed/raw functional richness (Fig. 1a), whereas estuarine communities had the highest scores followed by reefs after controlling for species diversity (Fig. 1b). 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. 1a,b). Among the modern assemblages, tropical communities had higher observed functional richness than their temperate/subtropical counterparts (Fig. 1a; mean richness tropical *versus* temperate/subtropical: 0.11 vs. 0.0006), whereas temperate and subtropical communities had higher functional richness when controlling for species diversity (Fig. 1b; mean richness tropical *versus* temperate/subtropical: -2.2 vs. -1.0).

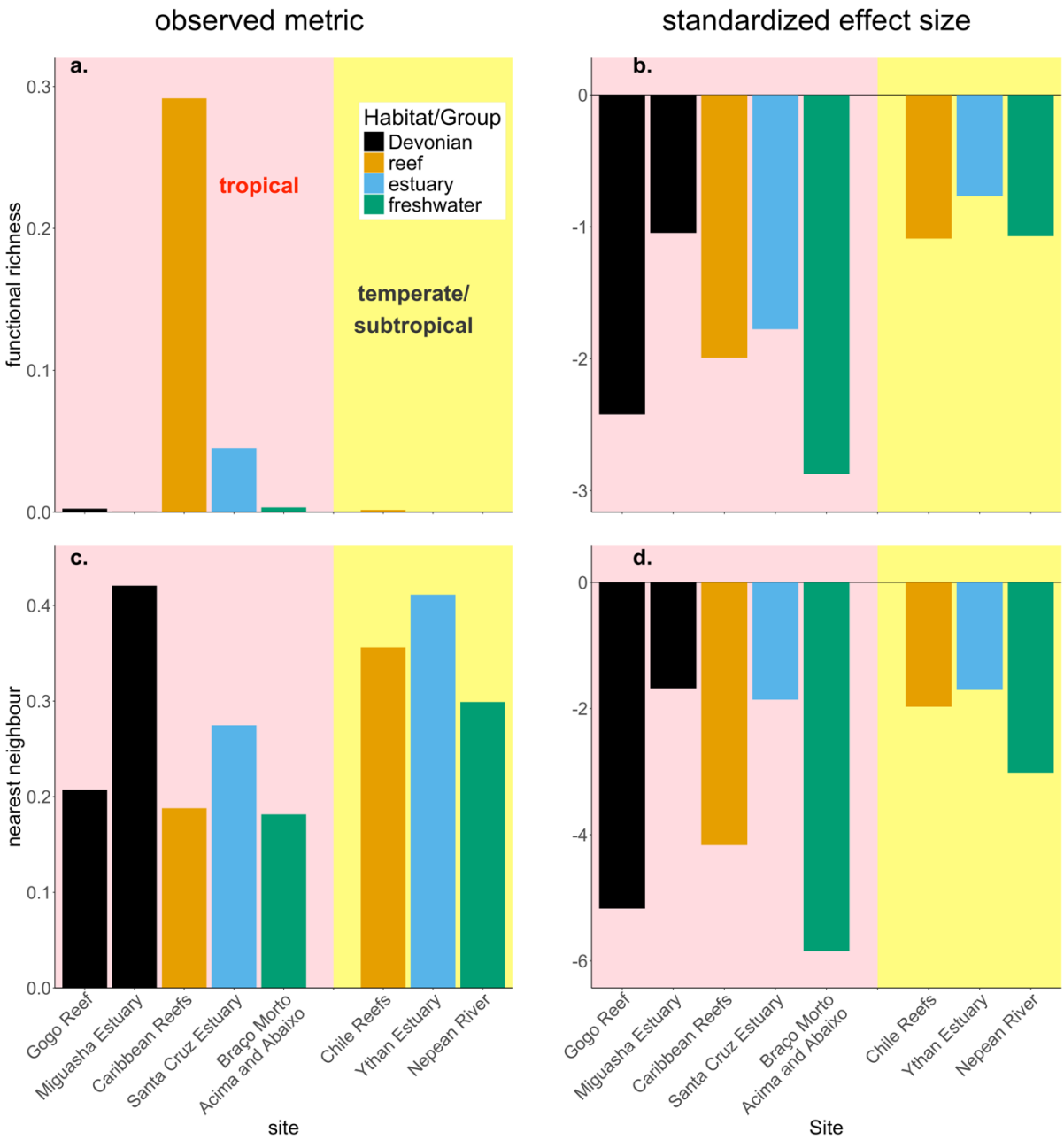

Figure 1. Functional diversity metrics for two Devonian and six modern fish communities. Two functional diversity metrics are shown: functional richness (a. and b.) and nearest neighbour (c. and d.). Panels in the left column show the observed metrics (not controlling for species diversity), whereas panels in the right column show standardized effect sizes (controlling for species diversity). Pink background indicates the five tropical communities (ancient and modern), yellow background indicates the three temperate/subtropical communities (modern only).

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. 1c,d). Miguasha had a slightly higher score than the other communities when not controlling for species diversity (Fig. 1c; 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. 1d; Gogo = -5.2, Miguasha = -1.7; modern assemblages = -1.6 to -5.8).

There were differences among habitats in nearest-neighbour scores within periods and climate zones. Freshwater communities consistently had the lowest nearest-neighbour scores followed by reef communities (Fig. 1c,d). Further, there was a consistent latitudinal pattern among modern communities — species in temperate and subtropical communities were farther from their nearest neighbour than were species in tropical communities (Fig. 1c,d; mean nearest neighbour tropical *versus* temperate/subtropical: 0.21 vs. 0.36 [not controlling for species diversity] and -4 vs. -2.2 [controlling for species diversity]).

The distances between hypervolume centroids of Devonian *versus* modern communities were greater than those between centroids of communities from the same period (Fig. 2a,b; distance between Devonian and modern: 0.16 ± 0.01, distance between communities from the same period: 0.07 ± 0.02; reported values are means ± SD unless otherwise stated), indicating that community trait spaces were centred in different locations depending on their time period. 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. 2c,d).

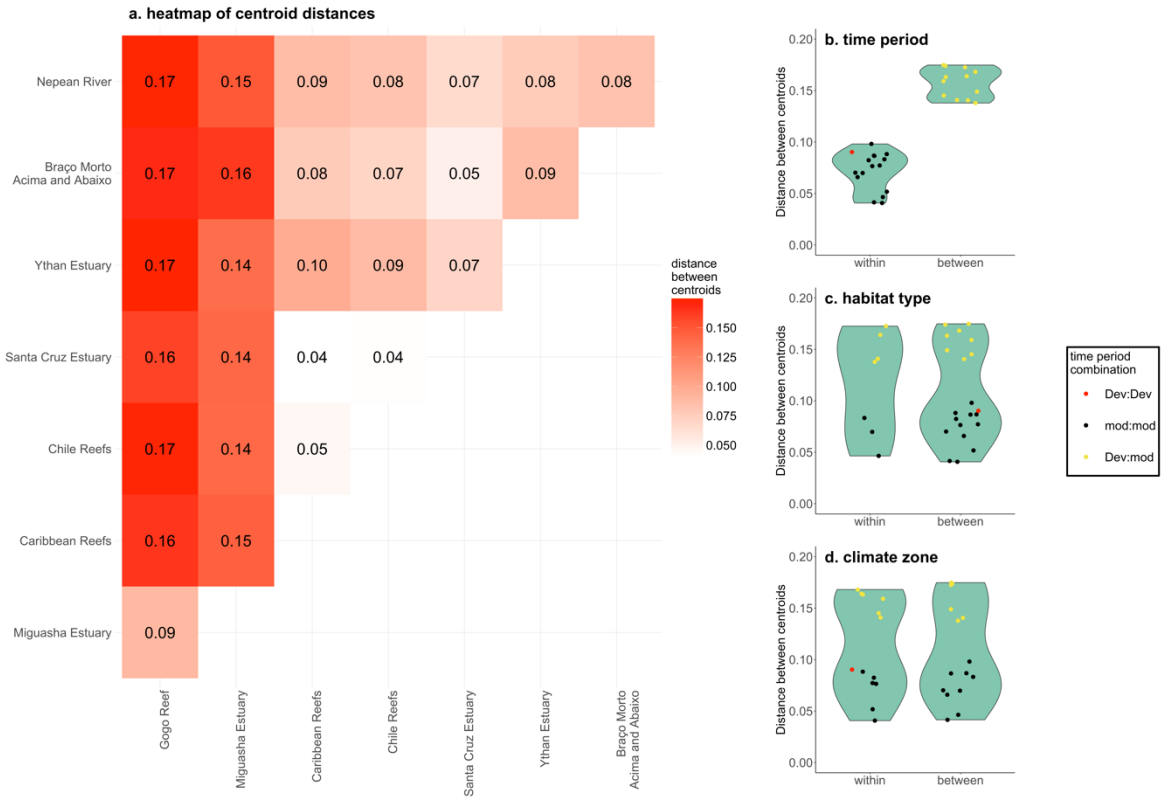

Figure 2. Distances between centroids of functional trait space hypervolumes for fish communities. Two Devonian (Gogo and Miguasha) and six modern fish communities from different habitats and climates are compared. On the left, plot a. is a heatmap showing distances between the centroids of each community. 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. 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. 3a,b; overlap between Devonian and modern: 0.05 ± 0.02, overlap between communities from the same period: 0.18 ± 0.07). 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. 3a). There was no evidence of greater overlap between hypervolumes of communities from the same *versus* different habitat types or climate zones (Fig. 3c,d). Partitioning the Jaccard index into components of dissimilarity due to turnover *versus* nestedness indicated that turnover largely explained differences among trait spaces i.e., communities occupied different trait spaces rather than subsets of each other's trait spaces (dissimilarity due to turnover: 0.52 to 0.96; dissimilarity due to nestedness: 0 to 0.3; see Appendix S1, Fig. S1.6 and S1.7).

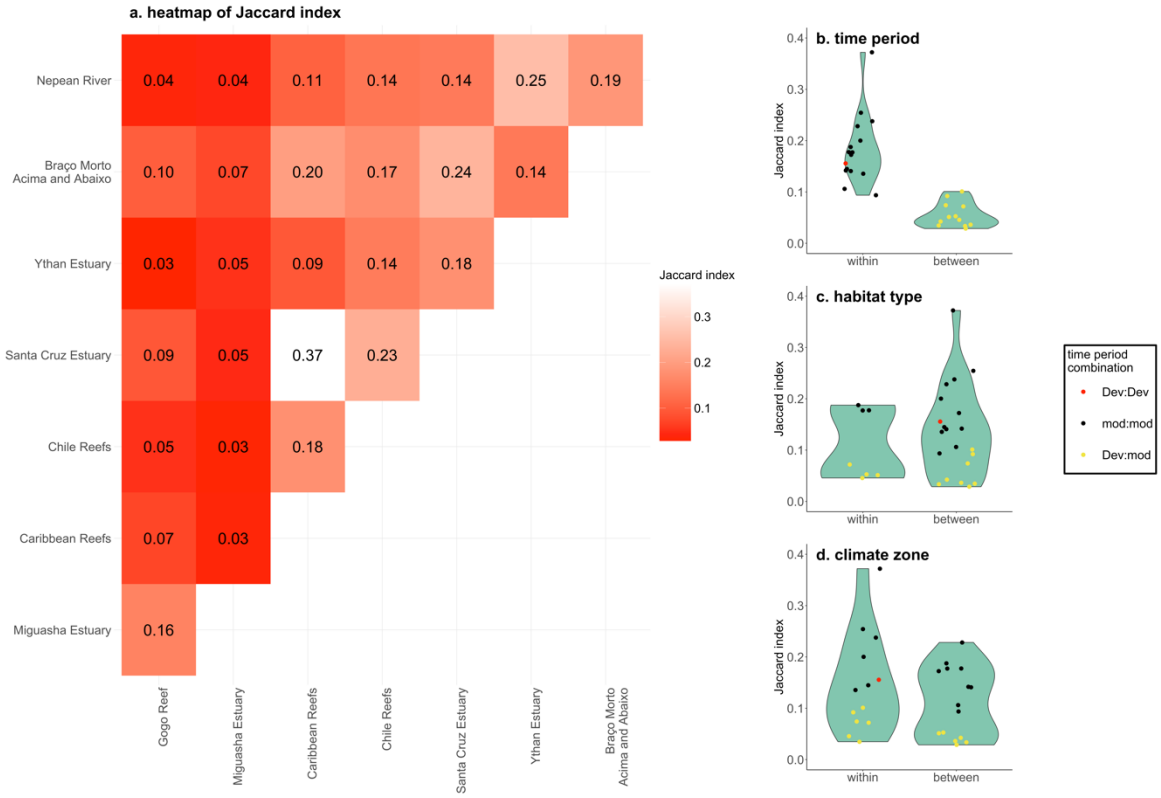

Figure 3. Jaccard Index comparing overlap in functional trait space hypervolumes for fish communities. Two Devonian (Gogo and Miguasha) and six modern fish communities from different habitats and climates are compared. On the left, plot a. is a heatmap showing Jaccard indices for all community comparisons. 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. 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 Appendix S1, Table S1.5 and Fig. S1.8).

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 (correlation: $\eta^2 = 0.623$, $p < 0.000$), body depth ($\eta^2 = 0.537$, $p < 0.000$), and caudal fin shape ($\eta^2 = 0.339$, $p < 0.000$) on axis 1; position of mouth ($\eta^2 = 0.415$, $p < 0.000$) and eye position ($\eta^2 = 0.371$, $p < 0.000$) on axis 2; and transverse body shape ($\eta^2 = 0.378$, $p < 0.000$), and presence of spiracles ($\eta^2 = 0.221$, $p < 0.000$) on axis 7 (see Appendix S1, Table S1.6). Accordingly, Devonian communities were distinct from modern communities in these traits. Fish in the Devonian communities tended to have smaller eye diameters, their bodies were not as deep, and they displayed less variation in these traits compared to fish in the modern communities (eye diameter relative to total body length: 0.039 ± 0.015 *versus* 0.052 ± 0.023, body depth relative to total body length: 0.190 ± 0.048 *versus* 0.257 ± 0.113, for Devonian and modern communities, respectively; see Appendix S1, Fig. S1.9c,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 (see Appendix S1, Fig. S1.10). None of the Devonian fish had eyes migrated to one side of the body (as in flatfish; see Appendix S1, Fig. S1.10), none of the modern fish had hypocercal tails (see Appendix S1, Fig. S1.10), spiracles and heterocercal tails were more prevalent in the Devonian than modern communities (large spiracles: 56% *versus* < 2%; heterocercal tails: 83% *versus* < 3% for Devonian *versus* modern communities, respectively; see Appendix S1, Fig. S1.10), and the proportion of fish with a compressed transverse body shape is lower in the Devonian fishes (25% *versus* > 55% in Devonian *versus* modern communities, respectively; see Appendix S1, Fig. S1.10c).

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 Appendix S1, Table S1.5), while Miguasha's centroid was extreme on axis 4 (Miguasha = -0.049, other communities ≥ -0.026; see Appendix S1, Table S1.5). Sagittal (not transverse) body shape was the most strongly correlated trait with these axes, showing a

slightly stronger correlation with axis 5 ($\eta^2 = 0.397$, $p < 0.000$) than with axes 4 and 6 ($\eta^2 = 0.311$, $p < 0.000$ and $\eta^2 = 0.252$, $p < 0.000$ for axes 4 and 6, respectively; see Appendix S1, Table S1.6). 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 (see Appendix S1, Fig. S1.10a), which included the tadpole-shaped *Escuminaspis laticeps* and *Levesquaspis patteni*.

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 lower functional richness than their closest modern counterparts when not accounting for species diversity, (2) an association with habitat type, and (3) an association with climate zone (Fig. 1; consistent with hypothesis *iv*). In contrast, period was the only variable that clearly differentiated fish assemblages in the two metrics that reflect a community's position in trait space relative to other communities (distance between hypervolume centroids and Jaccard index); we observed no associations between these metrics and habitat type or climate zone (Fig. 2, 3; consistent with hypothesis *iii*). The trait-space positions of Devonian communities were distinct from modern communities on several axes associated with seven of the eleven traits we included in our analyses (see Appendix S1, Table S1.5 and S1.6); 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 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 three of the four metrics we calculated: Devonian communities differed from modern communities in terms of functional richness, centroid location, and hypervolume overlap (Fig. 1a, 2, 3).

Functional richness of Devonian communities was within the range spanned by all modern communities, but the scores of Devonian communities in this metric were substantially lower than those observed in modern communities from the same habitat type and climate zone when not controlling for species diversity (i.e., Gogo Reef *versus* Caribbean Reef, Miguasha *versus* Santa Cruz Estuary; Fig. 1a). 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. 1a,b). Discovery curves confirm that most species in the Devonian communities we examined have been described (see Appendix S1, Table S1.2, Fig. S1.1 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. When we controlled for the effect of species diversity on functional richness using standardized effect sizes, Devonian communities were comparable to their modern counterparts (Fig 1b). This result emphasizes that changes in trait diversity between time periods are associated with changes in species diversity, although it remains unclear whether higher trait diversity is a cause or effect (or both) of higher species diversity.

Lower functional richness in Devonian fish assemblages does not necessarily mean that more trait space was vacant in these communities. It is possible that non-fish taxa filled some of the space occupied by fish in modern communities. For example, conodonts (early, non-fish, but fish-like, jawless vertebrates) might have occupied the trait space of modern lampreys, hagfish, and small eels [72,73], while invertebrates such as Eurypterids (sea scorpions) might have filled trait and trophic spaced occupied by predatory fishes in modern communities [74]. Similarly, non-fish taxa, such as sea snakes, turtles, and marine mammals, make unique contributions to the trait space in modern aquatic communities [75].

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, body depth, presence of large spiracles, transverse body shape, caudal fin shape, mouth position, and eye position (see Appendix S1, Fig. S1.6 and S1.7). Of these traits, eye diameter, body depth, mouth position and eye position had lower diversity in Devonian compared to modern communities (see Appendix S1, Fig. S1.6 and S1.7). Thus, differences between modern and Devonian communities as indicated by 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. 1a,b). However, decomposition of the Jaccard index dissimilarity suggested differences between Devonian and modern fish community trait spaces were primarily due to turnover rather than nestedness (see Appendix S1, Fig. S1.6 and S1.7). In other words, Devonian communities occupied different trait space to modern communities rather than a subset of that trait space. This result is counterintuitive because the modern communities largely encompass the trait variation found in the Devonian communities when traits are considered individually (see Appendix S1, Fig. S1.9 and S1.10). Thus, the dominance of turnover in explaining trait space dissimilarity is likely due to unique combinations of traits rather than unique trait values among Devonian fish.

Community trait space is linked to community structure and function [76,77]. 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 [78,79] — indicates differences in trophic interactions. While superior mouth position has been documented in Devonian species [80,81], the rarity of this trait in the Devonian contrasts with its widespread occurrence in modern communities (see Appendix S1, Fig. S1.7e). 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) [82], which could lead to the evolution of distinct antipredator strategies. Similarly, the lack of fish with deep, laterally compressed bodies in the Devonian communities (i.e., fish from these communities had body depths relative to their total length < 33%, and only 25% were laterally compressed; see Appendix S1, Fig. S1.6 and S1.7) likely indicates ecological differences associated with microhabitat use and how a species interacts with conspecifics and other species [83,84]. Deep-bodied, laterally compressed jawless fish have been documented in older communities (Late Silurian

and Early Devonian) [85], 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*) greater species diversity (which could be a cause or effect of trait diversity), (*ii*) increased habitat/environmental complexity through time [86], (*iii*) the longer time modern fish assemblages have had to evolve and diversify [87], and/or (*iv*) 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) [88]. In modern fish communities, there is a positive correlation between habitat complexity and functional richness [22,89]. 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 [90] and diversity of benthic/habitat-forming organisms was lower [91]), 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 [92]. 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 [93,94]. 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 [95]. 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 (Fig. 1c,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. 1a,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 [96,97]. Reef communities in both periods have high functional richness when species diversity was not controlled (Fig. 1a), and low-to-intermediate nearest-neighbour scores (Fig. 1c,d). This combination suggests that many, densely concentrated and diverse niches are facilitated by complex and productive reef habitats (corroborating research on modern communities) [98]. Estuarine communities have the highest nearest-neighbour scores in their climate zone and time period (Fig. 1c,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 [99,100]. 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.

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. 1a,b). Across climate zones, reef communities had the highest observed functional richness followed by estuarine communities, whereas estuarine communities had the highest richness followed by reef communities when controlling for species diversity (Fig. 1a,b). We observed this switching between which habitat type had the highest functional richness in modern and Devonian communities (Fig. 1a,b). High habitat complexity could explain the elevated species and functional richness in reef communities by allowing greater niche differentiation among resident fish [98]. 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) [6,101–104], a hypothesis supported by the low nearest-neighbour scores for the reef compared to estuarine communities (Fig. 1c,d).

Climate

Functional richness of modern tropical communities was higher than that of modern temperate and subtropical communities when not controlling for species diversity, consistent with the previously reported pattern of increasing functional richness with decreasing latitude in fish, other vertebrates, and invertebrates [104–109]. This pattern was reversed when we controlled for species diversity (Fig. 1b), indicating that high trait diversity in tropical fish communities is associated with high species richness.

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 (Fig. 1c,d). 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) [105,110]. This suggests stronger niche differentiation and reduced functional redundancy at higher latitudes, potentially indicating that competition is more limiting in temperate than tropical zones [111]. 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 community 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 (and species-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 [87], greater variation in habitats today [91, 112], phylogenetic constraints of different fish lineages [113], and/or stochasticity in evolutionary pathways [114]. Irrespective

of the root cause(s), the observed differences in trait space suggests Devonian communities were structured and functioned differently to modern communities. Further research on how community structure and function has changed through time, combining information from ancient and modern communities [115], 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].

Data availability statement

All data and code is available on Github (github.com/JohnLlewelyn/Trait-space-disparity). De-identified data and code will be made available to reviewers in a zip file.

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