VIMS Articles   Virginia Institute of Marine Science

2022

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ORIGINAL ARTICLE

Freshwater Biology WILEY

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Abstract

1. When investigating metacommunity dynamics, functional differences among species are often assumed to be as important as environmental differences between sites in determining β-diversity. However, few studies have examined the influence of functional diversity on β-diversity. We examine the relative importance of regional functional diversity partitioned by niche dimensions and environmental variation in structuring taxonomic β-diversity of stream fishes using a large dataset of stream fish assemblages (hereafter, simply β-diversity). We predicted that both functional diversity and environmental variation play a role in determining β-diversity.

2. We tested this prediction by modelling the patterns of stream fish β-diversity as a function of environmental variation, functional diversity and γ-richness across 10,220 sites for 329 fish species using a series of conceptual path models.

3. Environmental variation consistently affected β-diversity across all models, whereas functional diversity and γ-richness influenced β-diversity only in some models. We show that including relevant trait differences among species in path models can improve their ability to explain β-diversity, suggesting that functional traits influence β-diversity.

4. The ability of path models to explain β-diversity varied depending on the trait grouping included in the model, demonstrating that specific path models representing different niche dimensions can improve the ability of a model to explain β-diversity. In addition, parsing traits into different niche dimensions revealed alternative patterns of functional diversity–β-diversity relationships that otherwise would have been missed.

5. The selection of relevant traits and linked niche dimensions is critical for detecting relationships between functional diversity and β-diversity. Using traits associated with different niche dimensions allows for the identification of niche dimensions most strongly associated with species sorting and the detection of patterns missed by focusing on a single niche dimension. Determining the niche

dimensions that influence β-diversity could provide insights into the processes driving biodiversity and metacommunity dynamics, improving our ability to conserve or restore aquatic communities.

1 | INTRODUCTION

Exploring community assembly using metrics other than taxonomic diversity has become a valuable approach for ecologists to identify different mechanisms structuring communities from a variety of systems and taxa (Benone et al., 2020; Cadotte et al., 2013; García-Girón et al., 2019; Weinstein et al., 2014). Biodiversity can be characterised over local and regional scales, where α-diversity represents diversity at a local scale and γ-diversity characterises regional scale diversity. β-diversity characterises variation in species composition and represents an important measure of biodiversity by contextualising the relationship between α- and γ-diversity (β = γ/α), providing insight into how diversity is distributed across the landscape (Whittaker, 1972). Quantifying patterns of β-diversity can inform landscape-scale community analyses and provide functional targets for system-level conservation and reserve design (Anderson et al., 2011; Krynak et al., 2019). For example, examining β-diversity patterns and metacommunity dynamics across sites connected by dispersal can help identify communities that are important in source–sink dynamics and serve as keystone communities (Ruhí et al., 2017). Moreover, determining the drivers of β-diversity across the landscape can provide a mechanistic understanding of the factors influencing spatial and temporal change of communities within a regional species pool (Heino et al., 2019; Stoczynski et al., 2021). Therefore, trying to understand the factors that affect β-diversity has become a major research focus in the last decade (Dala-Corte et al., 2019; Heino et al., 2017; Rocha et al., 2018; Soininen et al., 2007).

Environmental variation generally is thought to be the primary driver of β-diversity on the assumption that species are able to disperse to a given site from a source location (Dala-Corte et al., 2019; Heino, Melo, Bini, et al., 2015; Peláez & Pavanelli, 2019). These findings support the niche-based hypothesis of environmental filtering in which local environmental conditions act as hierarchical filters that limit the establishment of species to those with certain sets of traits (Chase & Myers, 2011; MacArthur & Levins, 1967; Patrick & Swan, 2011; Poff, 1997). In this paradigm, landscape-level environmental variation positively affects species sorting at the local scale, producing assemblages with different taxonomic and trait compositions among regional units, and thus higher taxonomic β-diversity (Zbinden & Matthews, 2017). However, this outcome may not always be the case, and some studies find no relationship between β-diversity and environmental variation for streams and rivers (Heino, Melo, Bini, et al., 2015),

suggesting that factors other than environmental variation, such as biotic interactions, dispersal or spatial scale, may be playing a role in determining β-diversity.

In addition to environmental variation, taxonomic β-diversity patterns also may be linked to functional diversity (FD): the value and range of functional traits within species assemblages (Heino & Grönroos, 2017; Mason et al., 2013; Patrick & Brown, 2018; Spasojevic et al., 2018). Functional traits mediate the interaction between species and their environment, governing individual performance and providing a mechanistic link between species and environmental gradients (McGill et al., 2006; Verberk et al., 2013). Therefore, species occurrences are often determined by functional trait sorting––the selection of traits best suited to a given environment (de Bello et al., 2012; Thuiller et al., 2015). Functional trait sorting assumes that functional differences among species interact with environmental variation between sites to determine species compositional differences between assemblages (de Bello et al., 2012; Thuiller et al., 2015). Under a sorting paradigm, the magnitude of functional differences should positively relate to the degree of environmental variation and the variation in β-diversity assuming that dispersal is not a limiting factor (Kang et al., 2018). By contrast, species without functionally relevant differences, given a range of environmental conditions, would sort randomly into different habitats following neutral dynamics (Rosindell et al., 2011). Even in regions with a large range of environmental conditions, variation in β-diversity under a species-sorting paradigm is expected to be minimal if no meaningful functional differences exist (Patrick & Brown, 2018). Few studies have investigated the relationship between FD and β-diversity. In addition, these relationships varied across studies and functional feeding guilds (see Patrick & Brown, 2018; Spasojevic et al., 2018), limiting our ability to generalise how FD influences β-diversity in other systems and taxonomic groups.

One of the challenges with interpreting prior work on questions involving FD is the difficulty in distinguishing the mechanistic underpinnings of observed relationships between species pool FD and β-diversity. These observed relationships are the summation of interactions among component parts that can only be discerned when viewed in isolation. Because species interact with their environment via a combination of traits characterising different niche dimensions, no single trait can accurately capture species' response to environmental gradients (Laughlin, 2014; McGill et al., 2006; Pilière et al., 2016; Winemiller et al., 2015). However, individual traits associated with single niche dimensions can elucidate patterns and species responses that may be hidden in a multi-trait approach and fail

to contribute equally to observed patterns. Accordingly, analysing traits within single niche dimensions can provide information and mechanistic links not gained by using a combined niche dimension approach only (Trisos et al., 2014; Troia & Gido, 2015). For example, Troia and Gido (2015) found that overall reproductive life history trait dispersion of stream fishes was negatively related to stream size, yet morphological feeding traits showed the opposite pattern. Partitioning FD by trait groupings representing differing niche dimensions may help to parse out the key mechanisms by which FD influences β-diversity.

Stream fishes comprise an excellent system in which to apply these concepts in order to enhance our understanding of the mechanistic roles of environmental variation and species pool FD on β-diversity. The linear dendritic nature of streams restricts dispersal of obligate aquatic organisms to within the river network. This topology can cause fish assemblages that are close in Euclidean space but highly disconnected along the river network, to have distinct assemblage compositions (Tonkin et al., 2017). Unlike some aquatic organisms, temperate freshwater fishes are not capable of active overland dispersal, which allows catchments to form natural spatial units for comparing β-diversity (Jelinski & Wu, 1996). In addition to spatial separation among large catchments, the degree of connectivity among water bodies can vary within a catchment, resulting in additional complexity in stream β-diversity studies (Heino et al., 2017; Hitt & Angermeier, 2011). Further complicating β-diversity studies, assemblages in separate biogeographical areas can differ in taxonomic composition yet these assemblages may be functionally redundant, resulting in random sorting of species. Stream organisms also occupy a wide range of environmental niches to cope with highly heterogeneous environmental characteristics of stream ecosystems (Heino, 2005). This variation in environmental niches can lead to differentiation in community composition and trait structure along environmental gradients (Brown & Swan, 2010; Cunha et al., 2019; Gianuca et al., 2018; Peláez & Pavanelli, 2019; Wang et al., 2019).

We apply path analysis to a large dataset of stream fish assemblages to quantify the relative importance of regional FD at the catchment scale and environmental variation in determining taxonomic β-diversity (hereafter, simply 'β-diversity'). Firstly, our Hypothesis 1 is that environmental variation is positively related to β-diversity. Greater environmental variation can increase differences in the selective pressures driving species sorting among streams, increasing β-diversity in a landscape dominated by species sorting assembly mechanisms (Leibold & Chase, 2017). Secondly, Hypothesis 2 is that regional FD is positively related to β-diversity. Functional traits mediate the interaction between species and the environment so that species with disparate traits respond differently to environmental variation, producing different species compositions across heterogeneous habitats (Townsend & Hildrew, 1994). Thirdly, our Hypothesis 3 is that the relationship between regional FD and β-diversity will differ among niche dimensions.

2 | METHODS

2.1 | Data acquisition and preparation

We used a contemporary (mid 1990s to 2019) stream fish occurrence dataset compiled by previous studies from state conservation/regulation agency surveys of local species assemblages (Midway et al., 2015; Peoples et al., 2020; Peoples & Midway, 2018; Stoczynski et al., 2021; Wagner & Midway, 2014). The dataset spans 12 states in the eastern United States from Georgia to Maine and contains over 13,000 sites on 11,600 stream segments (Figure 1); 342 species are represented (Table S1). Site inclusion depended on on several stringent quality control parameters, including (1) researchers sampled at least 20–30 times mean stream width, a minimum distance to characterise richness (Barbour et al., 1999), (2) sampling and species identification were completed by professional biologists, and (3) sampling was carried out to quantify whole assemblages instead of being directed at a single species or only game species.

For fish, catchments are appropriate spatial units for exploring mechanisms of metacommunity assembly because movement among local communities occurs within catchments, and long-distance movement among catchments is less likely (Heino, Melo, Siqueira, et al., 2015; Hitt & Angermeier, 2011). Each catchment is uniquely identified by a hydrologic unit code (HUC) as given by the United States Geological Survey (USGS), with increasing HUC length indicating smaller catchments and resulting in a hierarchical classification of catchments (Seaber et al., 1987). We used the HUC8 scale to define a catchment following other large-scale aquatic studies that used this dataset (Guo & Olden, 2014; Muneepeerakul et al., 2008; Peoples & Midway, 2018). We averaged all metrics within each catchment, testing all hypotheses at the catchment scale. All sites with fewer than three species were removed because some FD metrics require at least three species. Only catchments with more than 15 sites were included to account for sampling density differences, leaving 168 catchments for analysis. β-diversity measurements across regions are contingent on sampling effort because measurements of γ-diversity will vary as a result of species–area relationships. Calculations and comparisons of β-diversity across regions can be contingent on γ-diversity and sampling effort (Bennett & Gilbert, 2016; Kraft et al., 2011). In an attempt to account for this contingency, null-model approaches calculate the deviation between β-diversity and random expectation. However, the null model approach can fail to remove the dependence of β-diversity on γ-diversity, making this approach poorly suited for comparisons across regions (Bennett & Gilbert, 2016). Instead, we used a novel approach to account for differences in sampling effort among regions. To account for sampling density differences among HUC8s, all metric calculations were taken from 10 randomly chosen sites in each HUC8, which was repeated 20 times and an average was taken from those 20 iterations (Patrick & Yuan, 2017). We used a minimum sampling density cut-off of 15 sites to ensure that a catchment had at
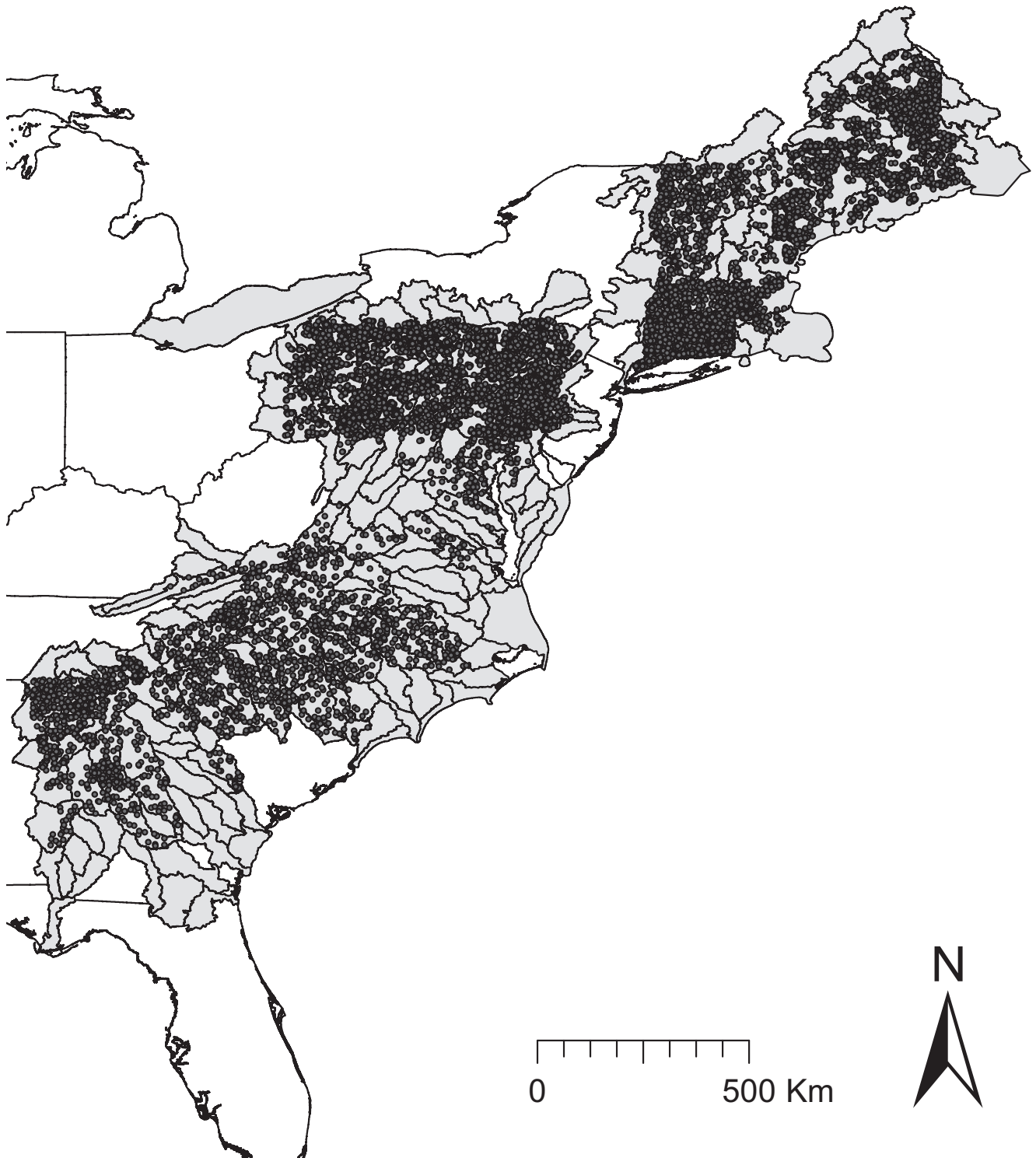
FIGURE 1 A map of the eastern United States from Georgia to Maine showing stream segments used in this study indicated by black points and associated HUC8s delineated by grey polygons.

least 50% more sampling events than the sample size ($n = 10$) used in our bootstrapped estimates of β-diversity, FD and γ-diversity (Patrick & Yuan, 2017).

We acquired 31 traits representing habitat preference, diet preference and life history for each species from the FishTraits Database (Table 1; Frimpong & Angermeier, 2009). Trait data were separated into

four datasets: an "all-traits" containing all 31 traits, a "habitat-traits" dataset containing habitat preference traits, a "diet-traits" dataset containing only diet preference traits, and a "life history traits" dataset of reproductive life history traits (Winemiller & Rose, 1992). For species with inadequate trait data, we assigned the missing data by first searching the literature, and if unavailable, we used the trait data of the

TABLE 1 Habitat preference, diet preference and life history trait for each species acquired from the FishTraits database

Trait code	Description	Trait grouping	Type
BENTHIC	Benthic feeder	Diet	Categorical
SURWCOL	Surface or water column feeder	Diet	Categorical
NONFEED	Adults do not feed	Diet	Categorical
ALGPHYTO	Algae or phytoplankton, including filamentous algae	Diet	Categorical
MACVASCU	Any part of macrophytes and vascular plants	Diet	Categorical
DETRITUS	Detritus or unidentifiable vegetative matter	Diet	Categorical
INVLVFSH	Aquatic and terrestrial invertebrates including zooplankton, insects, microcrustaceans, annelids, molluscs, etc. This group also includes larval fishes	Diet	Categorical
FSHCRCRB	Larger fishes, crayfishes, crabs, frogs, etc.	Diet	Categorical
EGGS	Eggs of fishes, frogs, etc.	Diet	Categorical
OTHER	Other diet components distinct from the preceding classes	Diet	Categorical
MAXTL	Maximum total length in centimetres	Life History	Continuous
MATUAGE	Mean, median or modal age at maturity in years for females	Life History	Continuous
LONGEVITY	Longevity in years based on life in the wild	Life History	Continuous
FECUNDITY	Maximum reported fecundity	Life History	Continuous
EURYHALINE	Species with wide salinity tolerance	Habitat	Categorical
MUCK	Muck substrate	Habitat	Categorical
CLAYSILT	Clay or silt substrate	Habitat	Categorical
SAND	Sand substrate	Habitat	Categorical
GRAVEL	Gravel substrate	Habitat	Categorical
COBBLE	Cobble or pebble substrate	Habitat	Categorical
BOULDER	Boulder substrate	Habitat	Categorical
BEDROCK	Bedrock substrate	Habitat	Categorical
VEGETAT	Aquatic vegetation	Habitat	Categorical
DEBRDETR	Organic debris or detrital substrate	Habitat	Categorical
LWD	Large woody debris	Habitat	Categorical
PELAGIC	Open water	Habitat	Categorical
PREFLOT	Lotic and lentic systems but more often in lotic	Habitat	Categorical
PREFLEN	Lotic and lentic systems but more often in lentic	Habitat	Categorical
POTANADR	Potamodromous or anadromous	Habitat	Categorical
SLOWCURR	Slow current	Habitat	Categorical
MODCURR	Moderate current	Habitat	Categorical
FASTCURR	Fast current	Habitat	Categorical

closest relative (Near et al., 2011). When trait data could not be acquired from the literature, we used the *missForest* function in the *missForest* package to impute the missing life history trait data for 14 of the 912 life history trait values (Stekhoven & Bühlmann, 2012). This package uses random forest models to predict and impute missing data based on relationships among all variables in the trait dataset. Imputations relied on 1,000 iterations and 100 trees to fill in the few missing traits. To represent environmental variation within each catchment, we obtained 18 environmental variables representing catchment-scale landcover, stream size, stream gradient and discharge for each sample site from the U.S. Geological Survey National Hydrography Dataset (Viger et al., 2016) and 2016 National Land Cover Database (Homer et al., 2012), Table 2.

2.2 | Data analyses

In order to calculate environmental variation, we first ran a principal components analysis (PCA) on all environmental variables (Table 2) based on correlations for each bootstrapped sample within a HUC8 and retained axes with eigenvalues greater than 1 using the *vegan* package (Oksanen et al., 2019; R Core Team, 2022) in R version 4.2.1. Environmental variation was measured as multivariate dispersion within this PCA space represented by the average Euclidean distance in PCA space of all points within a group to the centroid (Anderson et al., 2006). We used Rao's quadratic entropy (RaoQ) to quantify regional FD (Botta-Dukát, 2005). RaoQ is a widely used measure of FD because it is not as sensitive to changes in species

TABLE 2 Environmental variables from the U.S. Geological Survey National Hydrography Dataset and 2016 National Land Cover Database

Code	Definition	Mean (*SD*)
Q0001E	Mean monthly flow estimate with gage adjustments	198 cfs (1164)
StreamOrde	Stream order	NA
TotDASqKM	Total upstream cumulative drainage area	409 km (2447)
SLOPE	Stream slope	−12 (351)
MAXELEVSMO	Maximum elevation	25,351 cm (18641)
Latitude	Latitude	NA
NLCD21PC	Area-weighted percentage of open land developed	6.2% (6.4)
NLCD22PC	Area-weighted percentage of low intensity developed	2.6% (5.3)
NLCD23PC	Area-weighted percentage of medium intensity developed	1.1% (3.2)
NLCD24PC	Area-weighted percentage of high intensity developed	0.3% (1.2)
NLCD31PC	Area-weighted percentage of barren land (rock, clay or sand)	0.3% (1.0)
NLCD41PC	Area-weighted percentage of deciduous forest	42% (24)
NLCD42PC	Area-weighted percentage of evergreen forest	9.5% (10.3)
NLCD43PC	Area-weighted percentage of mixed forest	11.1% (13.6)
NLCD52PC	Area-weighted percentage of shrub land	3.6% (5.1)
NLCD71PC	Area-weighted percentage of grassland	1.7% (3.2)
NLCD81PC	Area-weighted percentage of cultivated crops	9.3% (10.4)
NLCD82PC	Area-weighted percentage of pasture	5.3% (9.8)

richness as other metrics (Mouchet et al., 2010). Gower distance was used to calculate RaoQ for the all-traits dataset due to the mix of categorical and continuous traits. We used Euclidean distance to calculate RaoQ for the life history traits because all four traits were continuous. The R/*fd* package was used to calculate RaoQ (Laliberté et al., 2014).

Mean β-diversity, mean γ-richness, mean environmental variation and mean regional FD were calculated for each catchment. Total β-diversity was calculated using the Sorensen index with the beta. multi function in R/*betapart* (Baselga & Orme, 2012). Sorensen β-diversity is one of the most widely used β-diversity measures, (Koleff et al., 2003), which relativises the total number of unique species with respect to the local richness in both sites and gives greater weight to shared species (Baselga, 2010; Equation 1):

$$\beta_{Sor} = \frac{b+c}{2a+b+c} \tag{1}$$

where *a* represents the shared species between two sites, *b* represent species unique to site 1 and *c* represents species unique to site 2. We measured γ-richness as the total number of observed species within a catchment.

We built six conceptual path models to test the relative roles of environment variation and FD in determining β-diversity (Figure 2). In these models, we also hypothesised that environmental variation will be positively related to FD and total β-diversity because of the prevailing understanding that environmental variation creates greater niche space that can be occupied by more functionally diverse local communities that change across the landscape (Chesson, 2000; Kraft et al., 2015; Stark et al., 2017). Models 1 and 4 hypothesise that environmental variation directly effects β-diversity but not functional diversity. Models 2 and 5 hypothesise that environmental variation directly effects functional diversity but not β-diversity. Models 3 and 6 hypothesise that environmental variation directly effects both β-diversity and functional diversity. We also hypothesised a positive relationship between FD and β-diversity for the reasons described above (Patrick & Brown, 2018). However, we also included models representing the possibility that although FD may be affected by environmental variation and/or γ-richness, it may have no direct effect on β-diversity, at least in some niche dimensions. Models 1–3 represent the hypothesis where FD has a direct positive effect on β-diversity, with changes in the role of environmental variation. Models 4–6 test the hypothesis that FD does not influence β-diversity (Figure 2). When evaluating species pool FD, one potential issue is the confounding effect of variation in γ-richness among catchments (Botta-Dukát, 2005). In addition, β-diversity could be related to γ-richness, since the likelihood of forming local assemblages with different species and higher replacements is greater when the regional species pool is more diverse (Grman & Brudvig, 2014). We accounted for this issue by including γ-richness as a predictor in our models affecting β-diversity and FD directly, except for models 3 and 6 where γ-richness is the only predict affecting β-diversity.

Path models were constructed as a series of linear mixed models using the psem and lme functions in the R/*piecewiseSEM* and R/*nlme*, respectively(Lefcheck, 2016; Pinheiro et al., 2017). We used HUC4 catchments as random intercepts to control for nestedness of HUC8s within HUC4s (a form of spatial autocorrelation). To meet the assumptions of linear models, we log-transformed environmental
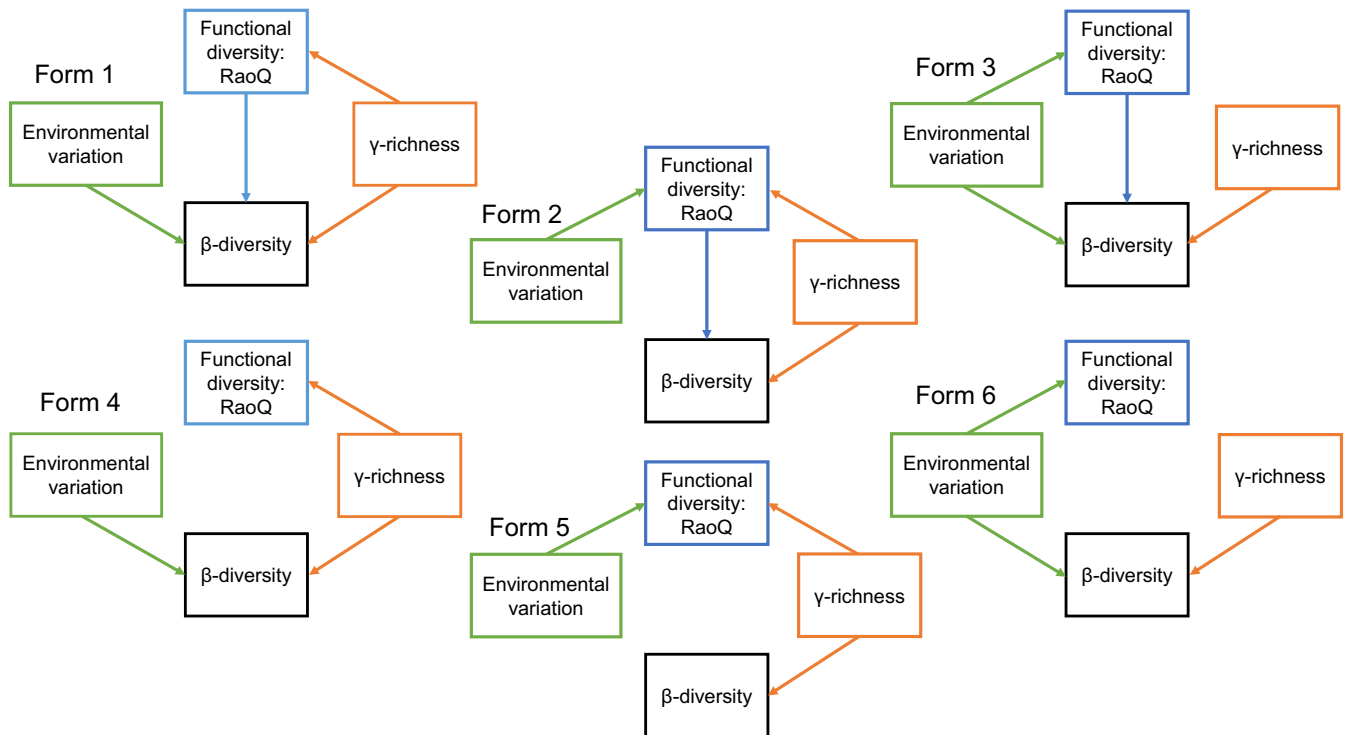
FIGURE 2 Alternate path models for the relationships among γ-richness (orange), functional diversity (blue), environmental variation (green) and total β-diversity (black). Models (forms) 1–4 represent hypotheses where functional diversity directly affects β-diversity, with varying roles of γ-richness and environment variation. Models 5–6 test the hypothesis that functional diversity does not directly affect β-diversity.

variation to achieve approximate normality. All variables were scaled and centred to a mean = 0 and $SD = 1$ before analysis. Model fit was evaluated using Fisher's C, a type of χ^2 test in which $p > 0.05$ indicates adequate model fit because the observed variance–covariance matrix does not differ significantly from the "expected" matrix as specified in the path model.

We used an information-theoretic approach (Anderson & Burnham, 2002) to compare path models representing the six hypotheses and determined the best model by comparing Akaike's information criterion (AIC) among models. Within each candidate set, the best model had the lowest AIC value; models within two AIC units of the best ($\Delta AIC \leq 2$) were considered as equally plausible as the top model. We calculated model weights (w_i) for each model; w_i values sum to 1.0 among the candidate model set and indicate relative weight of evidence among all models. Finally, we calculated evidence ratios by dividing model weights by one another. This selection process was done for each combination of functional trait grouping.

3 | RESULTS

A total of 329 species and 10,220 sites were analysed to determine the relative influence of FD and environmental variation on β-diversity (Table S1). Among the catchments, mean γ-richness ranged from 5.55 to 63.25 species ($\overline{x} = 30.81$), and β-diversity ranged from 0.72 to 0.91 ($\overline{x} = 0.84$).

The influence of regional FD on β-diversity differed depending on which trait set was investigated. For reproductive life history and diet traits, we detected a significant positive effect of FD on β-diversity (Table 3). For habitat preference-traits and all-traits datasets, we found no significant effect of FD on β-diversity (Table 3). For every trait dataset, we showed a significant positive influence of environmental variation on β-diversity (Table 3). γ-richness showed a significant positive relationship with β-diversity for models using the all-traits and habitat-traits datasets (Table 3). For the reproductive life history and diet-traits datasets, we showed a positive significant effect between γ-richness and β-diversity only for models that do not include a pathway between FD and β-diversity (models 4–6). None of the models showed an effect of environmental variation on FD (Table 3). All models, except those based on the habitat-traits dataset, showed a significant positive effect between γ-richness and FD (Table 3).

When considering reproductive life history traits, we found that Model 1 (where environmental variation, γ-richness and FD affect β-diversity, and γ-richness affects FD) was optimal, carrying 93% of the model weight (Table 3, Figure 3a). This model was 13.695-fold more likely than the next top model based on evidence ratios (Model 2, $\Delta AIC = 5.234$). The data fitted Model 1 well according to Fisher's C values ($p > 0.05$; Table 3).

We identified Model 1 as top for the diet preference-traits dataset (Table 3; Figure 3b). Model 1 showed that FD played a role in determining β-diversity. However, γ-richness had a non-significant

TABLE 3 Candidate path models (1–6) based on β-diversity (β), environmental variation (EV), γ-diversity (γ) and functional diversity (FD) for all trait datasets

Trait dataset	Fisher's C	AIC	ΔAIC	AIC weight	Evidence ratio	EV effect on FD	γ effect on FD	FD effect on β	EV effect on β	γ effect on β
Life history										
1	4.4	24.4	0	0.93	NA	NA	**0.53 (0.08)**	**0.29 (0.10)**	**0.18 (0.07)**	0.11 (0.11)
2	**9.7**	29.7	5.2	0.07	13.7	0.09 (0.05)	0.53 (0.08)	0.32 (0.10)	NA	0.11 (0.11)
3	39.6	59.6	35.2	<0.001	43,969,202.3	0.11 (0.05)	NA	0.29 (0.10)	0.18 (0.07)	0.11 (0.11)
4	**16.7**	34.7	10.2	0.006	167	NA	**0.53 (0.08)**	NA	0.20 (0.07)	**0.24 (0.10)**
5	**23.6**	41.6	17.2	<0.001	5,401.9	0.09 (0.05)	**0.53 (0.08)**	NA	NA	**0.26 (0.10)**
6	**51.9**	69.9	45.4	<0.001	7,346,574,595	0.11 (0.05)	NA	NA	**0.20 (0.07)**	**0.24 (0.10)**
Diet traits										
1	0.7	20.7	0	0.884	NA	NA	**0.56 (0.09)**	**0.19 (0.09)**	**0.20 (0.07)**	0.15 (0.11)
2	**11.5**	31.5	10.8	0.004	220.9	0.02	**0.56 (0.09)**	**0.19 (0.09)**	NA	0.16 (0.12)
3	**38.9**	58.9	38.3	<0.001	207,781,997.7	0.01	NA	**0.19 (0.09)**	0.20 (0.07)	0.15 (0.11)
4	6.8	24.8	4.1	0.111	7.9	NA	**0.56 (0.09)**	NA	0.20 (0.07)	**0.24 (0.10)**
5	**17.5**	35.5	14.9	0.001	1,692.6	0.02	**0.56 (0.09)**	NA	NA	**0.26 (0.10)**
6	**38.9**	63.1	42.5	<0.001	1,647,459,102	0.01	NA	NA	**0.20 (0.07)**	**0.24 (0.10)**
Habitat traits										
1	0.2	20.2	0	0.459	NA	NA	0.17 (0.11)	I−0.07 (0.08)	0.2 (0.07)	0.25
2	**11.4**	31.4	11.3	0.002	277.8	I−0.01 (0.07)	0.17 (0.11)	I−0.07 (0.08)	NA	0.27
3	4.4	24.4	4.2	0.056	8.2	0.01 (0.07)	NA	I−0.07 (0.08)	0.2 (0.07)	0.25
4	2.3	20.3	0.1	0.429	1.1	NA	0.17 (0.11)	NA	0.2 (0.07)	0.24
5	**13.5**	31.5	11.4	0.002	293.9	I−0.01 (0.07)	0.17 (0.11)	NA	NA	0.26
6	6.5	24.5	4.3	0.052	8.8	0.01 (0.07)	NA	NA	0.2 (0.07)	0.24
All traits										
1	0.2	20.3	0.6	0.434	1.3	NA	**0.49 (0.10)**	0.05 (0.8)	**0.20 (0.07)**	**0.23 (0.11)**
2	**11.3**	31.3	11.517	0.002	316.9	−0.01	**0.49 (0.10)**	0.06	NA	**0.24 (0.11)**
3	**25.7**	45.7	25.9	<0.001	422,312.1	0.03	NA	0.05 (0.8)	**0.20 (0.07)**	**0.23 (0.11)**
4	1.8	19.8	0	0.562	NA	NA	**0.49 (0.10)**	NA	**0.20 (0.07)**	**0.24 (0.11)**
5	**12.9**	30.9	11.1	0.002	260.7	−0.01	**0.49 (0.10)**	NA	NA	**0.26 (0.10)**
6	**27.1**	45.1	25.4	<0.001	326,276.4	0.03	NA	NA	**0.20 (0.07)**	**0.24 (0.11)**

Note: Bold text indicates statistical significance. NA indicates not applicable.

Abbreviations: EV, environmental variation; FD, functional diversity; β, β-diversity; γ, γ-diversity; γ, γ-richness.

positive effect on β-diversity in this model, whereas environmental variation and FD had significant positive effects on β-diversity (Figure 3b). In addition, γ-richness had a significant positive effect on FD in this model (Figure 3b). The Fisher's C values showed that the data fitted the model well ($p > 0.05$; Table 3).

Models 1 and 4 were equally likely when considering the habitat preference-traits and all-traits. No significant effect of FD on β-diversity was found for Model 1 in either dataset (Table 3), whereas Model 4 did not include FD as a predictor of β-diversity. Models 1 and 4 showed a significant positive effect of environmental variation and γ-richness on β-diversity (Table 3). However, a significant effect of environmental variation and γ-richness on FD was found for the all-traits and habitat preference-traits datasets. We identified Model 1 as the highest ranked model for the habitat-traits dataset and Model 4 for the all-traits dataset model, with evidence weights of 46% and 56%, respectively. Each of these models exhibited adequate model fit according to Fisher's C values ($p > 0.05$; Table 3).

4 | DISCUSSION

An underlying assumption of species sorting and environmental filtering is the existence of ecologically relevant functional variation which manifests through trait differences among species (McGill et al., 2006). Our study examined the relative importance of regional FD, γ-richness and environmental variation in structuring stream fish β-diversity across a large spatial extent. For two of the four trait datasets, the best models included the direct effect of FD on β-diversity, suggesting that the inclusion of FD increased the ability of these models to explain the β-diversity patterns found in eastern United States fish assemblages. However, we hypothesised that environmental variation, FD and γ-richness would all be positively related to β-diversity, yet none of our models fully supported these hypotheses. Supporting Hypothesis 1, environmental variation was consistently related to β-diversity suggesting that environmental variation among sites plays a significant role in determining metacommunity structure. We also found that β-diversity was positively influenced by FD for reproductive life history and diet preference-traits, supporting our Hypothesis 2 and suggesting trait differences among species interact with environmental variation to help structure assemblages across landscapes. However, none of the other trait datasets showed a significant positive effect of FD on β-diversity, indicating that not all traits play an equal role during

metacommunity assembly. This result suggests combining traits associated with multiple niche dimensions or the selection of traits associated with irrelevant niche dimensions may obscure detection of ecological processes.

Environmental variation was strongly associated with fish diversity at the catchment HUC8 scale. We found a positive relationship between environmental variation and β-diversity for all path models, suggesting that greater environmental variation among sites affects differences in community composition between sites at the catchment scale. Other studies also show that habitat heterogeneity influences β-diversity (Cunha et al., 2019; Specziár et al., 2018). For example, habitat heterogeneity based on vegetation complexity influenced β-diversity for stream fishes in Brazil (Cunha et al., 2019). The positive relationship found between β-diversity and environmental variation in previous studies and our study suggests that decreasing habitat heterogeneity would probably reduce fish β-diversity within catchments. For example, habitat homogenisation by deforestation has reduced stream fish β-diversity in the Amazon (Bojsen 2002). Owing to the isolated nature of headwater streams, dispersal of fishes among headwater communities can be all but nonexistent even though these communities may be close in overland distance, resulting in communities influenced more by environmental filtering with a positive effect on β-diversity (Heino, Melo, Siqueira, et al., 2015; Tonkin et al., 2017).

Supporting Hypothesis 2, we found a significant positive relationship between β-diversity and FD based on life history and diet traits. The top models included FD based on life history and diet traits as a predictor of β-diversity, implying this dimension of FD plays an important causal role in determining patterns of β-diversity. This pattern is likely to be caused by the strong tie between reproductive life history traits, such as age of maturity and maximum fecundity, and environmental variation. A species pool with greater variation in reproductive life history traits will respond more strongly to local sorting processes, such as differing flow or disturbance regimes, generating greater β-diversity among habitats (Mims & Olden, 2012; Winemiller & Rose, 1992). Life history characteristics are strongly influenced by habitat variables and habitat stability, and therefore help determine assemblage structure (Mims & Olden, 2012; Winemiller & Rose, 1992). For example, species exhibiting life history traits consistent with an opportunistic strategy will occupy areas with higher disturbance frequency or flow variability compared to other life history strategies (McManamay & Frimpong, 2015). Our findings are congruent with those of Patrick and Brown (2018), who found a

FIGURE 3 Top path models with a ΔAIC > 2 and the model estimates among γ-richness, functional diversity, environmental variation, and β-diversity (Table 3). (a) Top path models based on life history traits and β-diversity. (b) Top path models based on diet traits and β-diversity. The asterisks indicate significance ($p < 0.05$).
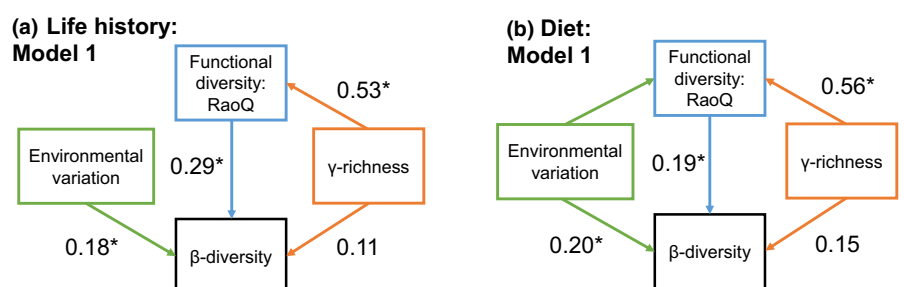
positive relationship between β-diversity and FD for stream macroinvertebrates at the sub-catchment (HUC10) scale when partitioning traits into different niche dimensions. This finding highlights the importance of selecting the appropriate traits in functional diversity studies.

In concordance with Hypothesis 3, we observed different results from path analyses considering different types of traits, leading to differing inferences regarding the relationship between FD, beta diversity and environmental variation. The use of traits associated with different niche dimensions can improve the capacity to detect ecological mechanisms and reveal greater ecological differentiation (Laughlin, 2014; Winemiller, 1991). Focusing on niche dimensions individually can help decompose effects within single dimensions and underlying mechanisms, whose effects may be hidden in a multidimensional approach (Trisos et al., 2014). For example, a positive relationship between FD based on life history traits and β-diversity suggests that removing or adding new species to an assemblage will lead to greater variation in life history characteristics within that assemblage. This pattern could be caused by many mechanisms, such as non-native introductions (Takács et al., 2021), increased disturbance (Winemiller & Rose, 1992), varying hydrological regimes (Mims & Olden, 2012) or stream size (Goldstein & Meador, 2004; Townsend & Hildrew, 1994), leading to a greater variation in species and traits present in the community.

We detected no relationship between β-diversity and FD in some of our models. There may be several reasons why we did not find a relationship between regional FD and β-diversity for some trait groupings. Firstly, the HUC8 scale may be spatially too broad to detect relationships between FD and β-diversity. The sorting processes may be acting on traits at finer scales within our delineation of metacommunities. For example, local factors, such as water velocity and habitat structure, can act as environmental filters, selecting for certain sets of traits (Bower & Winemiller, 2019; Burgazzi et al., 2021). However, the HUC8 scale is biologically meaningful because HUC8s represent major delineations among aggregations of wadeable streams contributing to mainstem rivers, a logical scale that is likely to delineate dispersal of most stream fish species over their lifetimes. Another reason for the disparity may be that the assemblages in our study were functionally redundant. In this case, the variation in FD among sites would not be sufficiently high to influence the models. Metacommunities with high functional redundancy can differ in species richness with relatively little change in FD, resulting in high β-diversity and little to no change in FD. This outcome could occur in small headwater streams where fish assemblages can differ taxonomically but contain relatively few and similar functional groups resulting in high β-diversity and low FD. Other studies also showed a negligible relationship between species traits and local contributions to β-diversity, yet did find that the contribution of individual species to overall β-diversity was related to species traits (Heino & Grönroos, 2017). In addition, sorting processes may be reduced by dispersal where metacommunity dynamics will likely be driven by mass effects or demographic stochasticity at very high or low dispersal, respectively (Patrick et al., 2021). Intermediate

levels of dispersal are thought to produce the greatest local sorting strength and increase the effectiveness of conservation and management efforts (Patrick et al., 2021).

Another potential explanation for our results is that the traits used in this study may be too coarse to adequately capture the variation among assemblages needed to detect a relationship between β-diversity and FD. For example, species with the same diet categorisation in this study such as *Semotilus atromaculatus* (Leuciscidae; Mitchill 1818) and *Lepomis macrochirus* (Centrarchidae; Rafinesque 1819) are likely to exploit trophic resources in different ways that are not captured in the coarse diet categorisation, to facilitate coexistence which is (Rohde et al., 2009). Likewise, including traits indexing dispersal capability may provide additional insights into relationships between functional and beta diversity as dispersal is a key mechanism structuring metacommunities (De Bie et al., 2012; Heino, Melo, Bini, et al., 2015; Heino, Melo, Siqueira, et al., 2015; Padial et al., 2014). Future work toward building more finely quantified, functional trait datasets that are strongly linked to the performance of species may be needed to further tease apart these relationships, but such a level of trait resolution does not currently exist for all species in our study. As we enter the era of big data and data sharing through open-access databases, trait data recorded at finer scales of resolution are increasingly likely to become available for large-scale studies.

We found positive relationships between γ-richness and β-diversity, suggesting that greater γ-richness and environmental variation increases differentiation of assemblage composition across sites. This result is unsurprising because the likelihood of forming local assemblages with disparate species compositions increases with the size of the regional species pool (Maloufi et al., 2016). Patrick and Brown (2018) also found a positive relationship between γ-richness and β-diversity for aquatic macroinvertebrates. For some of their species groupings, γ-richness had a stronger influence on β-diversity than environmental variation or FD. Our study encompassed a large spatial scale and a wide range of γ-richness, which is influenced by various biogeographical processes such as speciation, extinction, dispersal and environmental filtering (Mayden, 1988; Ricklefs, 2006; Vellend, 2010). These regional processes are likely to influence β-diversity directly or indirectly through changes in γ-diversity (Jackson et al., 2001). For example, dispersal limitation likely plays an increasingly important role in influencing the variation in species composition as distance between sites increases (Nekola & White, 1999). The role of dispersal may be particularly important for stream fishes whose movement is constrained to the linear river network. Unexpectedly, γ-richness showed no significant influence on β-diversity for some models. The relationship between γ-richness and β-diversity could be associated with the size of the local species pool (Koleff & Gaston, 2002). Besides the effect of the regional species pool size, another possibility may be that high and low rates of turnover occur simultaneously within a catchment, resulting in no detected pattern at this scale. The relationship between γ-richness and β-diversity may be more apparent at a finer spatial scale.

When trying to understand metacommunity processes, the relationship between environmental variation and β-diversity also depends on the spatial scale (Chin et al., 2018; Cunha et al., 2019; Hoeinghaus et al., 2007; Specziár et al., 2018). Spatial scale and species dispersal ability can greatly influence the drivers of β-diversity, changing the relationship between β-diversity and environmental variation (Heino et al., 2013). Evidence shows that increasing the size of spatial units causes a switch from environmental factors to spatial factors as the dominant influence on metacommunity assembly (Cai et al., 2017; Sály & Erős, 2016). Consequently, the processes influencing metacommunity dynamics and the results of metacommunity studies can change from local to regional spatial scales with each result contributing to our understanding the overarching mechanisms structuring stream fish communities. At the HUC8 scale, we showed that environmental variation played a role in determining β-diversity of stream fish assemblages, but this relationship may change as we increase or decrease the spatial scale. Cross-scale β-diversity analyses are a logical next step.

To the best of our knowledge, this study is the first to evaluate the relative importance of regional FD, γ-richness and environmental variation in shaping stream fish β-diversity. Although our dataset provides reasonable statistical power, it had several limitations. Data were collected by many agencies over several years, and slight differences in collection methods or environmental conditions at the time of sampling may have influenced our results. However, we addressed this issue by (a) coarsening abundance data to presence–absence and (b) only including data that were collected using standardised protocols focused on reliable and complete sampling of local stream fish communities. Ultimately, we expect the potential statistical uncertainty generated by these issues to be outweighed by the density and extent of sampling. Another limitation of working with this large dataset is the required use of segment-scale environmental data. Finer-scale processes may be more closely associated with relationships between functional and β-diversity. We found no significant relationship between FD and environmental variation which may be to the result of a lack of local-scale environmental data available for this large dataset. More detailed environmental and trait data may elucidate patterns that cannot be captured by coarse-scale data. In addition, the streams varied in channel size; effects of environmental filtering can vary with stream size, with stronger local filtering in smaller streams (Swan & Brown, 2014). Studies using finer-scale trait and environmental data across multiple taxonomic groups at the same scale are needed to further tease apart the relationship between FD and β-diversity.

Understanding the relationship between variation in traits associated with different niche dimensions and β-diversity will improve our understanding of the processes that drive biodiversity and metacommunity dynamics. We found that environmental variation was consistently associated with β-diversity, whereas only some of our models showed that β-diversity was associated with FD and γ-richness. In addition, including relevant trait differences among species in path models improved their ability to explain β-diversity, suggesting that functional traits associated with relevant niche dimensions can improve the capacity of models to detect biodiversity patterns and ecological mechanisms. Accordingly, the selection of traits associated with relevant niche dimensions is crucial when calculating FD and selecting non-relevant trait dimensions could lead to incorrect inferences drawn from any subsequent analyses using FD. We showed that functional traits positively influence β-diversity. However, the relationships between FD and β-diversity varied among the trait groupings, suggesting that selection of relevant traits and linked niche dimensions is critical when testing the relationship between FD and β-diversity. Parsing traits into different niche dimension groupings allowed us to identify the dimensions most strongly associated with species sorting, and such patterns would be missed by focusing solely on a single niche dimension. Conservation and management of species is enhanced by knowledge of how species sorting, dispersal and connectivity influence metacommunity structure and dynamics (Patrick et al., 2021). Identifying niche dimensions and trait groupings associated with species sorting or dispersal potential may provide a means to enhance indices of biotic integrity as well as refine how we model habitat and network connectivity in restoration efforts.

AUTHOR CONTRIBUTIONS

Conceptualisation: LMB, CJP, BLB. Developing methods: LMB, CJP, LS. Data analysis: LMB, LS. Preparation of figures and tables: LMB. Conducting the research: Data interpretation: LMB, CJP, BLB, LS, BKP. Writing: LMB, BKP, LS, CJP, BLB.

DATA AVAILABILITY STATEMENT

The data that supports the findings can be found in Data S1.

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SUPPORTING INFORMATION

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