

Numerical abundance and biomass reveal different temporal trends of functional diversity change in tropical fish assemblages

Ada Fontrodona-Eslava¹  | Amy E. Deacon²  | Indar W. Ramnarine² | Anne E. Magurran¹ 

¹Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, UK

²Department of Life Sciences, The University of the West Indies, St. Augustine, Trinidad and Tobago

Correspondence

Ada Fontrodona-Eslava, Centre for Biological Diversity, School of Biology, University of St Andrews, Sir Harold Mitchell Building, St Andrews KY16 9TH, Scotland, UK.
Email: afe1@st-andrews.ac.uk

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Abstract

Understanding how the biodiversity of freshwater fish assemblages changes over time is an important challenge. Until recently most emphasis has been on taxonomic diversity, but it is now clear that measures of functional diversity (FD) can shed new light on the mechanisms that underpin this temporal change. Fish biologists use different currencies, such as numerical abundance and biomass, to measure the abundance of fish species. Nonetheless, because they are not necessarily equivalent, these alternative currencies have the potential to reveal different insights into trends of FD in natural assemblages. In this study, the authors asked how conclusions about temporal trends in FD are influenced by the way in which the abundance of species has been quantified. To do this, the authors computed two informative metrics, for each currency, for 16 freshwater fish assemblages in Trinidad's Northern Range that had been surveyed repeatedly over 5 years. The authors found that numerical abundance and biomass uncover different directional trends in these assemblages for each facet of FD, and as such inform hypotheses about the ways in which these systems are being restructured. On the basis of these results, the authors concluded that a combined approach, in which both currencies are used, contributes to our understanding of the ecological processes that are involved in biodiversity change in freshwater fish assemblages.

KEYWORDS

biomass, freshwater fish, functional diversity, numerical abundance

1 | INTRODUCTION

Freshwater fishes are one of the most diverse vertebrate taxa (Magurran *et al.*, 2011), but also one of the most threatened because of multiple anthropogenic impacts including introductions of non-native invasive species, modification and destruction of habitats and overexploitation (Albert *et al.*, 2020; Dudgeon *et al.*, 2006; Reid

et al., 2019). As yet, there is only limited understanding of how the biological diversity of these fish assemblages is changing over time. Information on biodiversity change is particularly scant for tropical fresh waters, and for facets of biodiversity other than taxonomic diversity. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Conceptual Framework defines biodiversity as “variation in genetic, phenotypic, phylogenetic, and

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functional attributes, as well as changes in abundance and distribution over time and space, within and among species, biological communities and ecosystems" (Díaz *et al.*, 2015, p. 12). Filling this knowledge gap will be a substantial task involving many different teams, but it will also depend on fundamental insights into how the way in which diversity is measured influences the conclusions drawn. In particular, because fishes in a river or lake can vary substantially in body size, the method chosen to quantify abundance, such as number of individuals, biomass or catch per unit effort (CPUE), has the potential to generate different insights into biodiversity change. In this study, the authors focused on functional diversity (FD), a facet of biodiversity that is gaining increasing attention in the literature (Laureto *et al.*, 2015; Villéger *et al.*, 2017), and for this they used data from rivers in the Northern Range on the island of Trinidad in the Caribbean to ask how the choice of abundance currency influences the understanding of biodiversity change.

FD draws on the premise that biological traits explain the performance of organisms in ecological assemblages and communities (Violle *et al.*, 2007). Analyses of FD therefore use traits, rather than taxonomic species identity. There are a large number of FD metrics, some of which deal with the presence/absence of species, whereas others incorporate information on the abundance of species (Mouillot *et al.*, 2013). These abundance-based FD metrics evaluate functional roles described by the distinctive combination of biological traits and the commonness or rarity of the species within the system (Mouillot *et al.*, 2008), and therefore detect patterns that go beyond functional replacement (*i.e.*, the loss, gain or substitution of one functional role by another) (Mouillot *et al.*, 2013). The authors of this study used two widely used abundance-based FD metrics.

Ecologists recognise that two of the currencies that fish biologists use to quantify abundance (numerical abundance and biomass), while both ecologically meaningful, shed light on different processes (Dornelas *et al.*, 2011). Numerical abundance is particularly relevant in analyses of demography, intrinsic and extrinsic population growth, and biomass in investigations of resource allocation (Dornelas *et al.*, 2011). Nonetheless, the two currencies are not completely independent as they are related through their link with body size (Henderson & Magurran, 2010; Magurran & Henderson, 2012). In fish assemblages, numerical abundance is generally expected to decrease with body size, as the largest taxa in the assemblage are typically found in lower numbers (Cohen *et al.*, 2003; Cyr *et al.*, 1997). Biomass, on the contrary, tends to scale positively with body size, which results in an inverse relationship between currencies. If this relationship is not entirely symmetrical, then biomass and numerical abundance will reveal different patterns of abundance structure.

This asymmetry has consequences for the evaluations of the FD of fishes over temporal, spatial or other ecological gradients. Aquatic ecologists have tended to choose biomass over individual counts in the field (Arantes *et al.*, 2019; White *et al.*, 2007), but because of the scarcity of multi-currency data (Morlon *et al.*, 2009), the extent to which different abundance measures influence conclusions about temporal trends in FD is unknown.

In this study, the authors addressed this question using numerical abundance and biomass data from tropical freshwater fish assemblages surveyed repeatedly over 5 years (Magurran *et al.*, 2018). These assemblages are located on the island of Trinidad, which has a rich and well-studied ichthyofauna (Phillip *et al.*, 2013). In light of the different emphases the two currencies give to species relative abundances, the authors predicted that they would provide different conclusions about the temporal FD patterns observed in these rivers.

2 | MATERIALS AND METHODS

2.1 | Data collection

The Caribbean island of Trinidad is located 11 km from the Venezuelan coast (11°00 N, 61°00 W). The climate is tropical, with a dry season (January to May) and a rainy season (June to December) (Starr, 2009). The Northern Range mountain system extends across northern Trinidad and has a maximum height of around 900 m. It is drained by a system of small rivers that support fish species with both South American and Antillean origins (Phillip *et al.*, 2013).

Surveys were conducted with equivalent sampling effort for 5 years (2011–2015). Every year, the freshwater fish diversity of 16 sites (2 sites in each of eight Northern Range rivers) was monitored four times: at the beginning and end of both the dry and rainy seasons (Deacon *et al.*, 2015; Magurran *et al.*, 2018). This yielded a total of 20 sampling events per site. The first sampling event was excluded from analyses because of the differences in sampling effort (Magurran *et al.*, 2018). For each of the 16 sites, the same 50 m river stretches were revisited on every occasion. Fishes were sampled using consistent deployment of seining and electrofishing (see Deacon, Mahabir, *et al.*, 2017b) and identified to species in the field. During each sampling event, all fishes found were counted and weighed individually, and then returned unharmed to their habitat. Data collection met the ethical approval of the European Research Council during a review undertaken as part of the award of ERC AdG BioTIME 250189, and was conducted in compliance with the University of the West Indies Policy and Procedures on Research Ethics (FGP.P2C 2010/2011). Analysis of these data was approved by University of St Andrews Animal Welfare and Ethics Committee (24 April 2019).

A total of 19 descriptors were selected as proxies for biological traits to characterise the FD of the regional species pool in the Northern Range. These descriptors were selected from three main sources: FishBase (Froese & Pauly, 2020); Phillip *et al.* (2013) and Winemiller (1989). Four continuous, five ordinal and ten categorical variables were adopted (Supporting Information Table S2A). Categorical variables accommodated information available only in descriptive format and enhanced the scope of the study (Villéger *et al.*, 2017). The descriptors the authors used reflected key ecological aspects of species' performance in ecosystems such as their life history, feeding habits, environment/habitat association, locomotion/swimming ability and defence (Villéger *et al.*, 2017; Winemiller *et al.*, 2015) (Supporting Information Appendix S2).

2.2 | Statistical analysis

The authors used the compiled information on species trait descriptors to quantify the temporal change in FD in the 16 fish assemblages through the 5-year period covered by the survey. To assess FD in cases where there was limited trait information for a taxon, they inputted missing trait values. They used the missForest algorithm (Stekhoven, 2013), which is suitable for data containing a combination of continuous and categorical variables (Stekhoven & Bühlmann, 2012). The algorithm imputes values based on the known trait combinations among species. In this study, 5% of data gaps were filled this way. Because there are slightly different outcomes when an imputation is rerun (because of statistical resampling effects), the authors repeated the process 100 times and assessed the Pearson's r coefficient of all values of FD. This was always ≥ 0.9 .

To avoid correlation between traits when computing FD, the authors performed a principal coordinates analysis (PCoA) built on a Gower distance matrix (Gower, 1966) (Figure 2). A PCoA provides orthogonal axes that summarise the variation in the original variables, which can be a mix of continuous and categorical, in a multidimensional space. The authors selected the best number of synthetic axes in this multidimensional space – seven, in this case – following the framework proposed by Maire *et al.* (2015). The best number of axes defines a space where the initial distances between species are accurately represented, and can be determined by assessing the mean squared deviation (mSD) between the initial distances and the

distances in the coordinates of the multidimensional, functional space (*i.e.*, the lower the value of mSD, the more congruent are the initial and final distances) (Maire *et al.*, 2015). The authors used the function *quality_funct_space* deployed by Maire *et al.* (2015) to perform the PCoA and assess the quality of the functional space.

The authors selected two metrics that capture complementary facets of alpha FD (Mouillot *et al.*, 2013) (Figure 1). They chose metrics that were suitable for the analysis of species-poor assemblages (Colin *et al.*, 2018) given that the species richness of the rivers ranged from 2 to 15. The first metric they used is functional originality (FOri). This metric assesses the extent to which the rarest trait combinations in the entire region (*i.e.*, considering traits of all the fish species the authors recorded in the Northern Range) occur in any one local assemblage (Mouillot *et al.*, 2008, 2013). The second metric of this study was functional dispersion (FDis). FDis is the abundance-weighted mean of the distance of all species present in an assemblage to the abundance-weighted centroid of functional space of that assemblage (Laliberté & Legendre, 2010). The authors used the function *multidimFD* to compute both metrics (Mouillot *et al.*, 2013). The functions *quality_funct_space* and *multidimFD* are available online at <http://villegier.sebastien.free.fr/Rscripts.html>.

For each site and sampling event, the value of the FD metrics was computed twice, first using relative numerical abundance and then using biomass data. The authors performed a sensitivity analysis to evaluate if any given trait was driving the resulting values of FOri and FDis more than the others (Grenié *et al.*, 2018). To do so, they

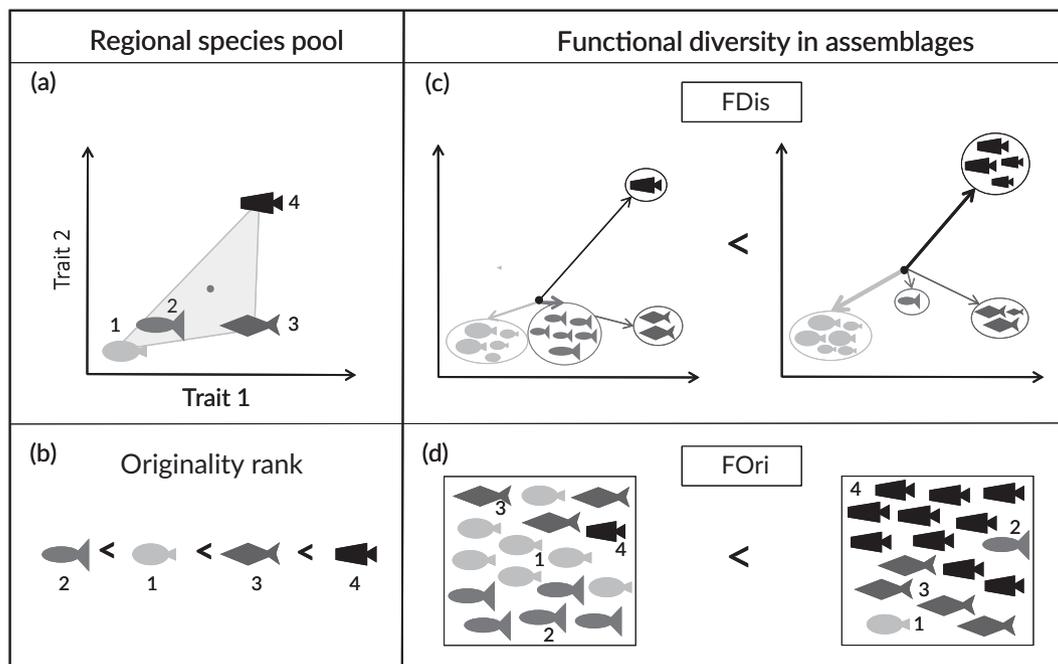


FIGURE 1 (a) Hypothetical 2D trait space occupied by a regional pool of four fish species. The position of each fish is defined by its values (coordinates) for trait 1 (x-axis) and trait 2 (y-axis). (b) Ranking of species in the region according to their nearest-neighbour distances (functional originality). (c) Representation of functional dispersion (FDis) in two fish assemblages that contain all the species in the region. In the right case-scenario dispersion is higher than in the left because species that are more functionally dissimilar to one another (1, 3 and 4) have higher relative abundances, causing the assemblage to be more dispersed in functions. (d) Representation of functional originality (FOri) in two assemblages that contain all the species in the region. In the right, the species that has the rarest combination of values for traits one and two (species 4) is the most relatively abundant. Therefore, this assemblage has higher originality than the one on the left

recomputed both metrics omitting one trait at a time ($n = 18$ traits) and assessed the correlation (Pearson's r) between the values of FD obtained from these analyses and those obtained using the complete set of 19 traits. After this process, the authors removed one trait from the final matrix – seasonal strategy – because it was over-influencing the results. After this trait was removed, correlations were very strong for all FD facets (Pearson's $r \geq 0.77$).

Next, the time-series of FDis and FOr values at each site, calculated with each currency, were individually regressed against chronological

sampling events ($n = 19$). An OLS linear regression was performed, and results yielded a total of 64 slopes and P -values. All analyses were conducted in R Statistical Software version 4.0.3 (R Core Team, 2020).

3 | RESULTS

Significant directional shifts were observed for both FD metrics even though the output from the analyses carried out with each currency was

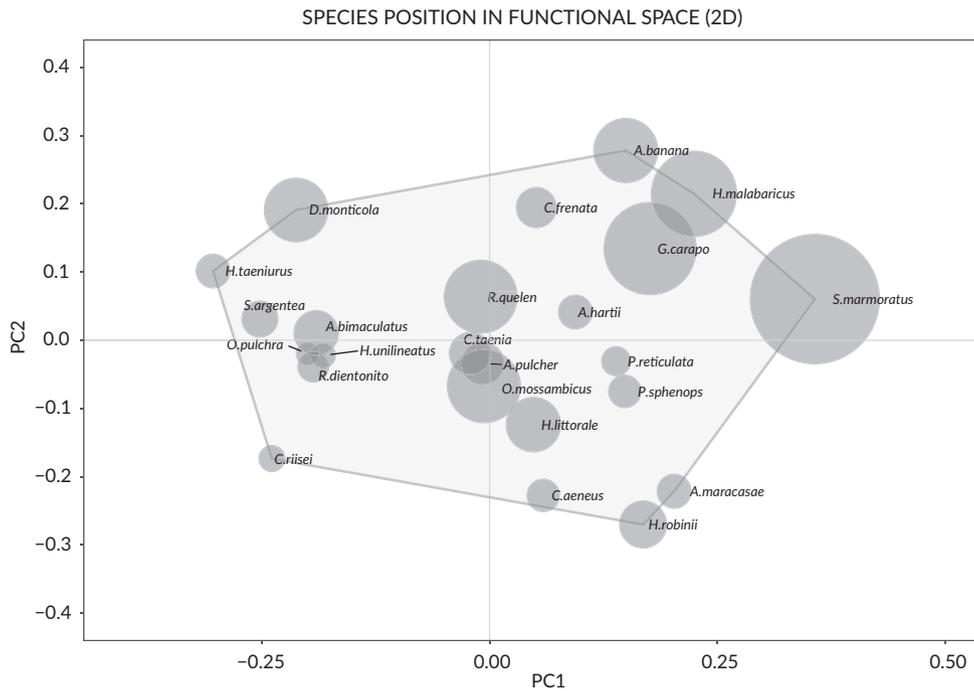


FIGURE 2 Position of the fish species present in the Northern Range assemblages in the first two summary axes of trait space. The area of the circles represents the maximum length of each fish species (first continuous trait, used as a proxy for body size) according to the information on FishBase (Froese & Pauly, 2020). Circle areas are scaled for visualisation using the function `scale_size_area()` in `ggplot2` (Wickham, 2016)

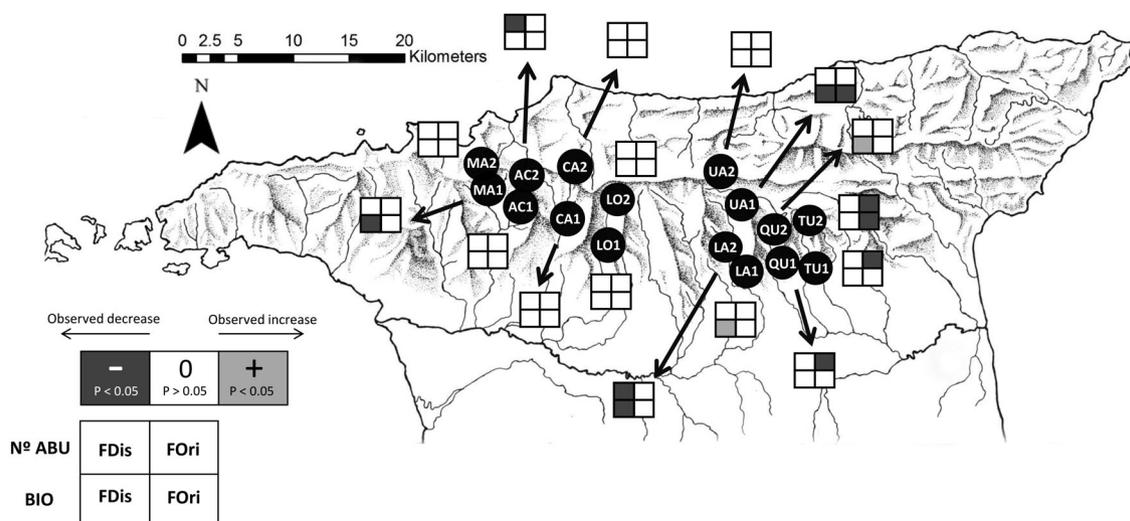


FIGURE 3 Map of the temporal trends (linear OLS regressions against time sessions) observed for FDis and FOr in the Northern Range rivers during the studied period (2011–2015). A four-cell grid is assigned to each site. The results for both metrics computed with numerical abundance are represented in the first row, and the results for the same metrics obtained with biomass data are represented in the second. The cells coloured with a darker shade of grey indicate a significant negative trend, whereas those coloured with a lighter shade indicate a significant positive trend. White cells indicate non-significant results for a given metric. Significance level is $\alpha = 0.05$

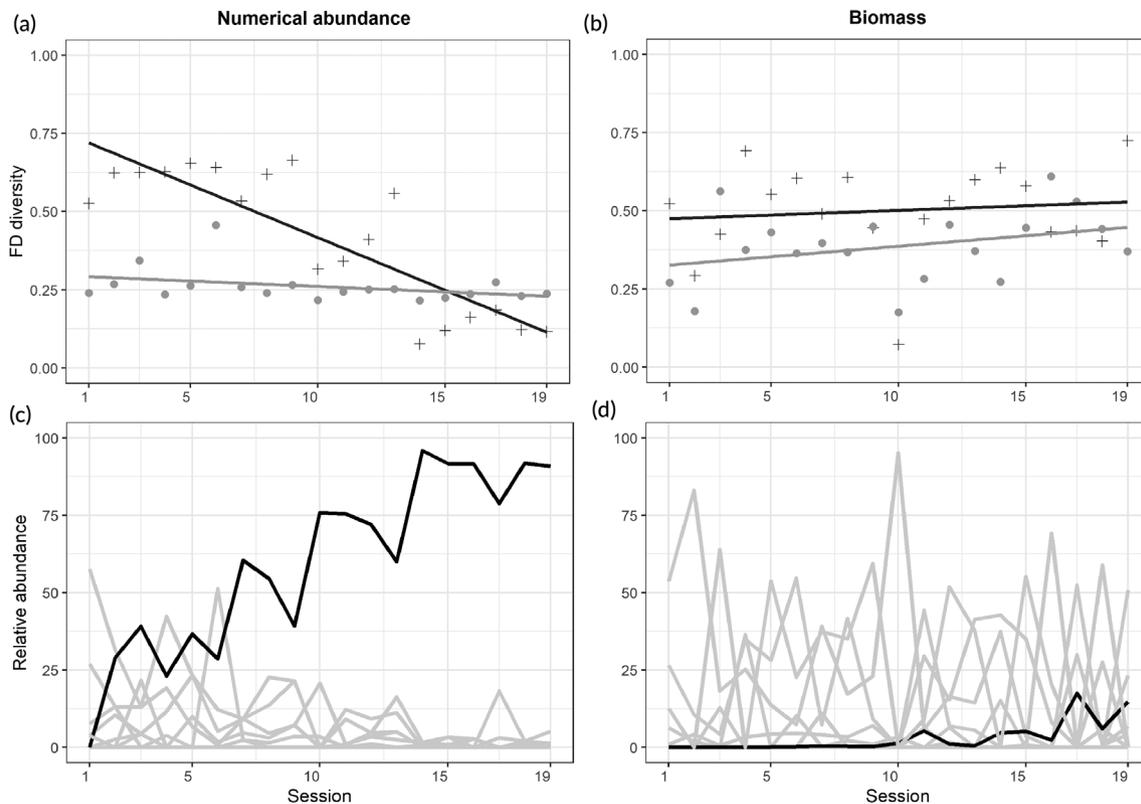


FIGURE 4 Temporal trends of FDIs and FOris computed with (a) numerical abundance (slope FDis = -0.034 , $P < 0.001$; slope FOr = -0.003 , $P = 0.139$) and (b) biomass data in the site AC2 (slope FDis = 0.003 , $P = 0.647$; slope FOr = 0.007 , $P = 0.178$). (c) Temporal change across sampling sessions ($n = 19$) of the relative numerical abundance (%) of the fish taxon *Poecilia reticulata* (black line) and other fish species present in AC2 (grey lines). (d) Temporal change across sampling sessions ($n = 19$) of the relative biomass (%) of *P. reticulata* (black line) and other species present in AC2 (grey lines). (—+) FDis; (—●) FOr. (—) *P. reticulata*; (—) other species

different (Figure 3). A total of nine assemblages experienced a directional shift ($P < 0.05$) over time in at least one of the two FD metrics measured with either numerical abundance or biomass data (Figure 3).

The analysis carried out using numerical abundance revealed that FOr decreased significantly in three assemblages over the 5 years of the study, including QU1, TU1 and TU2. Two negative directional trends were observed for FDis when it was computed using numerical abundance data, in LA2 and AC2 (Figures 3 and 4).

In contrast, the analysis using biomass data unveiled directional changes in the FDis of five sites (significant decrease in LA2, MA1 and UA1 and increase in LA1 and QU2, $P < 0.05$). In UA1 and TU2, the authors observed a significant decrease in FOr (Figures 3 and 5). Overall, only in two locations significant trends for the same FD facet were unveiled by both currencies (significant decrease in FDis in LA2 and in FOr in TU2) (Figure 3).

4 | DISCUSSION

This study investigated whether different currencies influenced our ecological understanding of the temporal change in FD experienced by tropical fish assemblages. The authors measured two facets of FD (Mouillot *et al.*, 2013) in assemblages from the Northern Range,

Trinidad, using numerical abundance and biomass data. They found that both currency-based analyses uncovered temporal directional patterns in FD, but often led to different conclusions about the nature of change in these assemblages. This confirmed the authors' predictions that these currencies cannot be assumed to be surrogates for one another when evaluating temporal change in assemblage structure (Morlon *et al.*, 2009; Saint-Germain *et al.*, 2007).

The analyses of this study using numerical abundance indicated a decline in functional originality in three sites and the analysis with biomass showed this trend in two locations. In contrast, when functional dispersion was assessed using biomass the authors concluded that almost one-third of the assemblages changed directionally over time, but found equivalent change in only two assemblages if the metric was computed with numerical abundance. The authors conclude that this is because, in many of these locations, these abundance currencies captured different shifts in the species' commonness-rarity gradient over the 5 years of study. Because this gradient is the structural backbone of an assemblage (Magurran & Henderson, 2011; Preston, 1948), these results suggest that using multiple currencies may be the key to developing a better understanding of the processes that underpin assemblage structure.

Ecologists quantify biodiversity not just to quantify patterns in time and space, but also to learn about the mechanisms by which

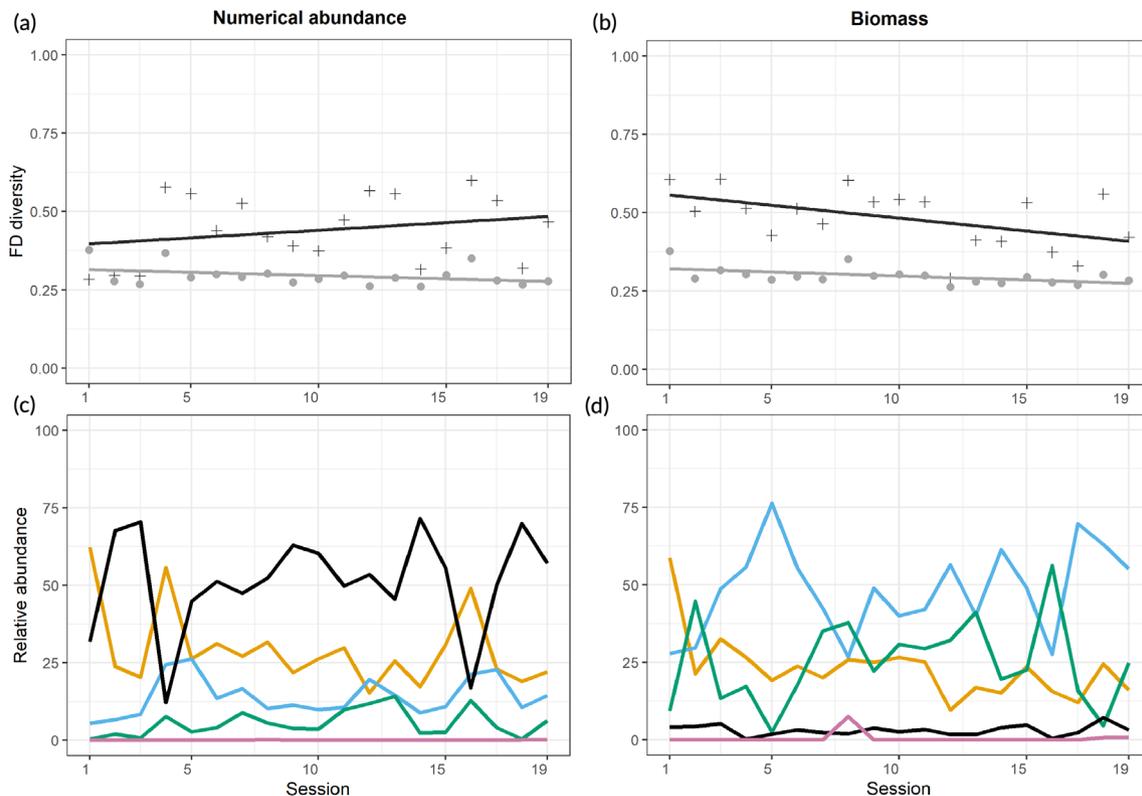


FIGURE 5 Temporal trends of FDis and FOr computed with (a) numerical abundance (slope FDis = 0.005, $P = 0.300$; slope FOr = -0.002 , $P = 0.147$) and (b) biomass data in the site UA1 (slope FDis = -0.008 , $P = 0.030$; slope FOr = -0.003 , $P = 0.019$). (c) Temporal change across sampling sessions ($n = 19$) of the relative numerical abundance (%) of the fish taxa present in UA1. (d) Temporal change across sampling sessions ($n = 19$) of the relative biomass (%) of the fish taxa present in UA1. (—+) FDis; (—●) FOr. (—) *P. reticulata*; (—) *A. hartii*; (—) *A. maracasae*; (—) *H. robinii*; (—) *S. marmoratus*

assemblages change. Specifically, the functional dimension of biodiversity can predict ecological processes that govern ecosystem functioning such as the flow of energy and nutrients along the trophic chain (e.g., Gagic *et al.*, 2015; Lefcheck & Duffy, 2015). In aquatic systems, these processes are heavily controlled by the effects of body size and metabolism on the performance of individuals (Brown *et al.*, 2004). Therefore, if alternative currencies lead to different conclusions about FD, it is because numerical abundance and biomass, through their distinctive link to body size (Henderson & Magurran, 2010), are weighting the performance of the individuals of each taxon in different ways. This study has shown that a multi-currency approach broadens our perception of temporal change in FD. The authors suggest that future work assessing FD through the lens of multi-currency analyses will elucidate the links that exist between functional roles and processes, and support a predictive framework of biodiversity change.

To illustrate how the different currencies lead to different insights into change in fish assemblage structure over time, it is useful to consider site AC2 in the Acono River as a case study. The Trinidadian guppy *Poecilia reticulata* Peters 1859 is a small poeciliid widely distributed in the Northern Range (Deacon *et al.*, 2015; Endler, 1978). *P. reticulata* was not present at AC2 in the first year of sampling, but became the dominant fish in numbers through time; this transition led

to significant decreases in functional dispersion. Simultaneously, the biomass of *P. reticulata*, though increasing, remained negligible compared to that of a few individuals of larger species such as the wolf fish *Hoplias malabaricus* (Bloch 1794), the river catfish *Rhamdia quelen* (Quoy & Gaimard 1824) or the coscorob *Andinoacara pulcher* (Gill, 1858). In other words, the marked change in the relative numerical abundance of *P. reticulata* did not impact the biomass structure of the assemblage, with the result that functional dispersion measured using biomass remained stable over the duration of the study.

The site UA1 in the Upper Aripo River represents another example of how currencies can provide different insights into temporal FD assemblage change. At this site, the authors observed how FD decreases significantly when computed using biomass but not when computed using numerical abundance. Three fish – the jumping guabine *Anablepsoides hartii* (Boulenger, 1890), the jumbie teta *Ancistrus maracasae* Fowler 1946 and the teta *Hypostomus robinii* Valenciennes 1840 – dominated in terms of relative biomass at this site. Further, their abundance dynamics across sessions had more influence on FD when biomass rather than numerical abundance was used, and when guppies were the dominant fish in almost all sessions. Indeed, the numerical abundance, but not the biomass, of guppies was almost always greater than that of any other fish taxon in the Northern Range assemblages investigated in this study.

Although focus of this study has been on temporal change in FD, any investigation that utilises information on the commonness and rarity of fish species needs to pay attention to the currency used to assess abundance. Assessments of the intensity of predation risk for *P. reticulata* along the longitudinal gradient of rivers in the Northern Range have been found to differ depending on whether numerical abundance or biomass was used to evaluate predator importance (Deacon, Jones, & Magurran, 2017a). Similar patterns of asymmetry in how currencies capture the relative abundance of species are likely to affect conclusions about temporal and spatial trends in the biodiversity of freshwater fish assemblages elsewhere. For instance, mismatches between the relative numbers and the biomass of fish species were observed in the Itá reservoir, upper Uruguay River, during a 10-year survey (Schork & Zaniboni-Filho, 2017) and in the Amapá Lake, Brazil, during a 1-year survey (da Silva *et al.*, 2013).

An additional issue that will require more attention in future work is the selection of traits, and their quantification. The Trinidadian freshwater fish assemblage provides textbook examples of intraspecific variation in life history, behaviour and morphology (Magurran & Seghers, 1991; Reznick & Endler, 1982; Walsh & Reznick, 2009). In line with the usual practice in work on FD, this study drew on information in the literature to delineate relevant traits and assign a value to them. It will nonetheless be interesting in follow on studies to explore how intraspecific variation in traits shapes patterns of FD over space and time.

The authors conclude that assessments of trends in FD based on different abundance currencies are needed to broaden our ecological understanding of the processes occurring in freshwater fish assemblages over temporal and other ecological gradients. Because FD draws on species' traits and these and abundances can be strongly associated through their links with body size (Brown *et al.*, 2004; White *et al.*, 2007; Woodward *et al.*, 2005), studies focused on this dimension of biodiversity should particularly benefit from multi-currency approaches. In this sense, the authors believe that the measurement of freshwater fish diversity using more than one currency in the field will be an important step towards the goal of achieving greater insights into the temporal change of the biodiversity of this group.

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AUTHOR CONTRIBUTIONS

Ada Fontrodona-Eslava and Anne E. Magurran conceived the study. Ada Fontrodona-Eslava analysed the data. Amy E. Deacon and Indar

W. Ramnarine led the field sampling. All authors participated in the manuscript preparation.

DATA AVAILABILITY STATEMENT

The trait values compiled for all fish species are available in the Supporting Information. The research data supporting this publication can be accessed at <https://doi.org/10.17630/fe0e350f-0f92-42e3-8d9c-1004a0e81d11> (Deacon *et al.*, 2021).

ORCID

Ada Fontrodona-Eslava  <https://orcid.org/0000-0001-7275-7174>

Amy E. Deacon  <https://orcid.org/0000-0002-7739-2925>

Anne E. Magurran  <https://orcid.org/0000-0002-0036-2795>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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