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Research article

The only lasting truth is change: multiple dimensions of biodiversity show historical legacy effects in community assembly processes of freshwater fish

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How communities are structured is a fundamental ecological question. Community structure, while constrained by the regional species pool, may be altered by changes in climate and other environmental stressors. Changes in patterns of functional and phylogenetic dispersion over time can illuminate the temporal dynamics of the processes structuring communities. We quantified temporal changes in taxonomic, functional and phylogenetic diversity of stream fish assemblages in the southern plains of the U.S. across four decades to assess how climatic change has influenced community patterns. We also explored how the use of three different functional trait categories (life history, environmental tolerance and trophic level) and all traits combined affected the response of functional diversity to environmental drivers. We found, for all diversity indices, that assemblages with low historical richness had high contemporary diversity, while assemblages with high historical richness had low contemporary diversity. Functional richness based on life history traits, trophic traits, and all traits combined decreased in diversity over time, while functional richness based on environmental tolerance traits showed the opposite pattern. Phylogenetic dispersion of both over- and under-dispersed communities shifted toward randomness. Changes in fish diversity patterns were influenced by changes in temperature over time, though impacts were metric dependent. Overall, we found that while community structure has changed, specific changes were more strongly predicted by the historical richness of the community than by regional climate change.

Keywords: climate change, freshwater fish, functional traits, niche dimensions, phylogenetic diversity, temporal trends

Introduction

Linking diversity patterns to community structure is central to understanding how communities are assembled (Weiher and Keddy 1995). Several mechanisms can shape

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the phylogenetic and functional diversity of communities, including historical priority effects (Fukami 2015), interspecific interactions, and environmental constraints (Weiher and Keddy 1995). While phylogenetic and functional diversity have been shown to vary across spatial scales and environmental gradients (Giam and Olden 2018, Li et al. 2019, Jia et al. 2021), changes to the same communities over time can offer new insights into how climate change may influence diversity patterns. As changing climates impact species' environments, altering ranges (Moritz and Agudo 2013) and likely increasing the stress many species experience (Kuczynski and Grenouillet 2018), the processes by which communities assemble may also change.

The stress dominance hypothesis relates community structure with environmental conditions, where increased environmental harshness results in low diversity (Weiher and Keddy 1995). Under environmental filtering, only species able to tolerate specific abiotic conditions persist, resulting in communities in which species exhibit greater trait similarity or are more closely related than expected by random chance (resulting in patterns of under-dispersion; Webb et al. 2002, Swenson and Enquist 2007). Conversely, in benign habitats many species can co-exist, resulting in higher diversity than expected by chance (resulting in patterns of over-dispersion). As species are limited by the niches available, competitive exclusion results in a single species occupying each niche (i.e. limiting similarity; Webb et al. 2002). Under climate change, as environments become more stressful (van Vliet et al. 2013), communities may lose diversity through time. Although other processes, such as mutualism and facilitation can also influence community structure, they typically act at smaller spatial and temporal scales, making their impacts difficult to distinguish at larger-scales (Ågren and Fagerström 1984, Valiente-Banuet and Verdú 2007, Mayfield and Levine 2010, McIntire and Fajardo 2014, Kunstler et al. 2016, Münkemüller et al. 2020).

Functional and phylogenetic diversity patterns are expected to reflect the processes that have shaped community assembly (Monnet et al. 2014, Kuczynski and Grenouillet 2018, Li et al. 2019). Functional traits capture ecological differences between organisms and relate communities to ecosystem processes (Naeem and Wright 2003, Petchey and Gaston 2006, Violle et al. 2007, Monnet et al. 2014, Jarzyna and Jetz 2017). However, despite the increasing use of functional diversity across ecology, the link between community diversity and underlying processes may be influenced by which traits are chosen (Weiher and Keddy 1995) as different traits are related to different ecological processes (Bernard-Verdier et al. 2012, Spasojevic et al. 2014, Münkemüller et al. 2020). Therefore, analyzing trait groups separately can result in signals that are hidden when analyzing all traits altogether (Saito et al. 2016, Côte et al. 2019, Münkemüller et al. 2020). Phylogenetic diversity, in contrast, captures total evolutionary relatedness between species (Gerhold et al. 2013). While some studies suggest that phylogenetic diversity is linked to ecosystem functioning (Cadotte et al. 2012), these patterns do not always clearly indicate an assembly process (Mayfield and Levine 2010). Both functional and phylogenetic diversity offer more insights into community diversity patterns than taxonomic richness alone, although neither metric is completely independent of it (Jia et al. 2021). For example, if functional richness increases with species richness, one can assume that as new species are introduced, new traits are also being introduced. However, opposite patterns in functional and taxonomic diversity could indicate that communities have high functional redundancy, that dominant species traits contribute more to functional diversity than rare ones (Wang et al. 2021), or that there is a loss of functional specialization (Villéger et al. 2010). To overcome this limitation, diversity indices can be standardized using a null model approach, after which trait and phylogenetic dispersion can be inferred in reference to a randomly structured community (Gotelli and Graves 1996). While there are limitations of both functional trait and phylogenetic based approaches to community assembly (Gerhold et al. 2013, Sobral and Cianciaruso 2016, Münkemüller et al. 2020), using both can offer complementary and multifaceted insights into diversity patterns (Mayfield and Levine 2010, Cadotte et al. 2013).

The state of Oklahoma in the central United States spans steep gradients in temperature and precipitation. Under climate change, Oklahoma is projected to see increased average annual temperatures (Zhang and Nearing 2005, Garbrecht et al. 2014), reduced annual precipitation (Zhang and Nearing 2005) and more extreme hydrological conditions such as droughts and floods (Bertrand and McPherson 2018). Thus, Oklahoma rivers provide a critical opportunity to understand how changes in climate may affect the diversity and assembly of freshwater fish communities. We combined climatic information and river fish abundance across Oklahoma to detect changes in community dispersion patterns through time in response to climate change stressors. Fish are good study organisms as their movement is limited by the dendritic networks of rivers, which results in trait selection based on local environmental constraints (Dias et al. 2014, Bower and Winemiller 2019). In addition, fish are ectotherms whose distribution is largely reliant on behavioral control of body temperature (Beitinger and Fitzpatrick 1979). Thus, local climate is essential in the reproduction and survival of species (Bütikofer et al. 2020). In addition, the well-studied and clearly defined traits of river fishes make them a model system to understand responses to environmental changes (Frimpong and Angermeier 2009, Bower and Winemiller 2019).

We explored how fish community diversity patterns changed over a minimum of eight years under the influence of climate related stressors using taxonomic, functional and phylogenetic diversity. Specifically, we hypothesized that under the influence of climate change stressors, fish communities would experience loss in diversity (i.e. shift towards under-dispersion) as species experience increased environmental harshness. Secondly, in response to increased environmental stress, we hypothesized that historically diverse communities (i.e. over dispersed) would be more likely to experience diversity loss over time, as these communities are likely to host rare or specialist species. Finally, we hypothesized that traits related to the abiotic niche (such as thermal tolerance) would show a stronger response to climate change than traits related to interspecific interactions (such as trophic position).

Material and methods

Sites

To explore the temporal dynamics of taxonomic, functional and phylogenetic diversity in freshwater fish across Oklahoma, we compiled fish abundance data collected from 1972 to 2014 (Pigg 1987, Matthews and Marsh-Matthews 2017a, Supporting information). We restricted data to include observations from 69 locations that were sampled at least eight times over a minimum of eight years to document changes over a multi-year period while still retaining most sites. To understand how functional diversity within communities changed through time, we retained localities with at least four species, the minimum number necessary for estimating functional richness using a three-dimensional convex hull volume method. The final dataset included abundance observations of 159 species with sampling events occurring on average 11 times at each site over 13 years (Supporting information). As non-native species in our dataset represented on average 0.005% (SD = 0.02) of the total abundance of any given sample, and their relative abundance was steady over time based on a generalized least square models (GLS; estimate = 0.011, $p = 0.5$), we did not differentiate native from non-native species in our analyses (Miller and Robison 2004, Foster et al. 2008).

Functional and phylogenetic data

Analyzing trait groups separately may show signals that would be hidden when analyzing all traits together (Saito et al. 2016, Münkemüller et al. 2020). To identify which trait shifts are best predicted by climate change stressors, we used three functional trait categories: trophic ecology, life history and environmental tolerance based on those presented by Frimpong and Angermeier (2009) and previous studies (Supporting information). Trait information was extracted from Fish Traits, the most complete trait database for freshwater fish that covers multiple dimensions of the functional niche (Frimpong and Angermeier 2009). We performed a principal coordinates analysis (PCoA) on trophic and environmental functional distance matrices, using Gower distance (Gower 1971) with equally weighted traits. For trophic traits (100% completeness), we used those that describe fish species diet (Supporting information) and kept the first two PCoA axes (Supporting information). Environmental tolerance traits (100% completeness) were based on reproductive habitat, habitat preferences (Frimpong and Angermeier 2009) and temperature tolerance (Supporting information) and the two first PCoA axes were retained (Supporting information). For life history traits (97% completeness on average), we used age at maturity, body length and fecundity (Frimpong and Angermeier 2009; Supporting information) and kept the three axes (Supporting information). Finally, we ran a global PCoA based on all individual traits, weighing individual traits so categories were equally represented in the global PCoA (Supporting information), and kept the first three axes (Supporting information).

To quantify phylogenetic diversity, we used the most comprehensive time-calibrated phylogeny for fish available (Rabosky et al. 2013) and extracted the subset of species observed in our samples (100% completeness; Supporting information).

Interpretation of functional diversity patterns relies on all traits either being phylogenetically conserved or convergent (Webb et al. 2002). To interpret our results of functional diversity, we tested whether species' positions in functional space (i.e. PCoAs species' scores) were phylogenetically conserved using Blomberg's K, an estimate of the phylogenetic signal in traits (Blomberg et al. 2003) with the R package motmot (Puttick 2019). Species' scores across all axes showed a significant phylogenetic conservatism (all $p < 0.05$; Supporting information), indicating that closely related species exhibit similar values across all PCoA axes (i.e. position within the functional space). These values were thus used in subsequent analyses as the species-specific functional traits (Supporting information).

Diversity indices

We measured taxonomic diversity using species richness and estimated four diversity indices to quantify dispersion: functional richness, phylogenetic richness and functional and phylogenetic Rao's quadratic entropy (Table 1). We calculated functional richness (FR) using the convex hull volume, the multi-dimensional trait space defined by PCoA axes and occupied by species present in each sample (Cornwell et al. 2006, Villéger et al. 2008) with the 'geometry' package (Roussel et al. 2019). A maximum of three axes were used to define the functional space based on which the convex hull volume is defined (Supporting information). We calculated phylogenetic diversity (PD) as the sum of branch lengths that link all species co-occurring in each sample (Faith 1992) with the picante package (Kembel et al. 2020). Rao's quadratic entropy offers a complementary understanding on diversity changes as it combines both dispersion (abundance) and richness (De Bello et al. 2010) and is less sensitive to outliers than either functional richness or Faith's PD (Laliberté and Legendre 2010). Functional Rao's quadratic entropy (Rao) was computed using the Gower distance matrix based on raw functional traits (Supporting information). We also used Rao's quadratic entropy (Rao) to calculate phylogenetic diversity using phylogenetic distance between species using the ade4 package (Villéger et al. 2008, Dray et al. 2021).

Table 1. Summary of diversity indices used, including what the index measures, how it is calculated and expected results to the addition of a new species.

Diversity index	Measures	Expected results
Functional richness (FRic)	Measure the volume occupied by a community within trait space based on most extreme trait values, not weighted by abundance	Richness – increases as new species are added to a community only if species has extreme traits
Phylogenetic diversity (PD)	Sum of branch lengths within a community, not weighted by abundance	Richness – increases as new species are added to the community
Rao's quadratic entropy (Rao)	Measures variation among multiple traits/branch lengths, weighted by abundance	Richness and divergence – increases as new species are added to a community and/or as the abundances of current species increases

Community dispersion patterns: over- versus under-dispersion

Functional and phylogenetic diversity indices tend to be broadly correlated with species richness. Therefore, we used a null model approach can be used to standardize diversity indices (i.e. removing the numerical artefact due to species richness; Gotelli and Graves 1996). The species pool for each assemblage was composed of all the species in the focal assemblage and all the species with which they co-occur anywhere in the study region at any point in time (i.e. pools were not time-series specific; Fig. 1: Step 1). This assumes that if two species co-occur at some point within space and time, the two species can coexist (e.g. because of similar biogeographic origins and historic contingencies), indirectly incorporating dispersal into the models (i.e. the full dispersion field, Lessard et al. 2012b). From this assemblage-specific pool, the number of species equal to the species richness of the focal sample was randomly drawn. Moreover, we kept the abundance distributions fixed as in the focal assemblage (Fig. 1: Step 2). From the dispersion field for each assemblage, we drew 999 random assemblages. The dispersion field approach allows for communities to vary in the size and composition of the species pool (Graves and Rahbek 2005), which is likely more realistic than using the same pool for assemblages distributed over large spatial scales or across environmental gradients (Lessard et al. 2012b).

For each null assemblage, we computed all 10 diversity indices (functional richness: FR_{global}, $FR_{trophic}$, FR_{env}, FR_{LHT}; functional Rao's quadratic entropy: Rao_{global}, $Rao_{trophic}$, Rao_{env}, Rao_{LHT}; phylogenetic diversity: PD; and phylogenetic Rao's: Rao_{phylo}) and calculated the average and standard deviation (X_{mean} and X_{std}, respectively) for each index (X) for each random assemblage (Fig. 1: Step 2). We computed the standardized effect size of each index as $(X_{obs} - X_{mean})/X_{std}$ where X_{obs} is the observed value for the index X. Positive values indicate over-dispersion (more diversity than expected in a randomly assembled community) while negative values represent under-dispersion (less diversity than expected in a randomly assembled community; Fig. 1: Step 3).

For each site, a time series of standardized effect sizes was generated based on the samples taken at each time point and

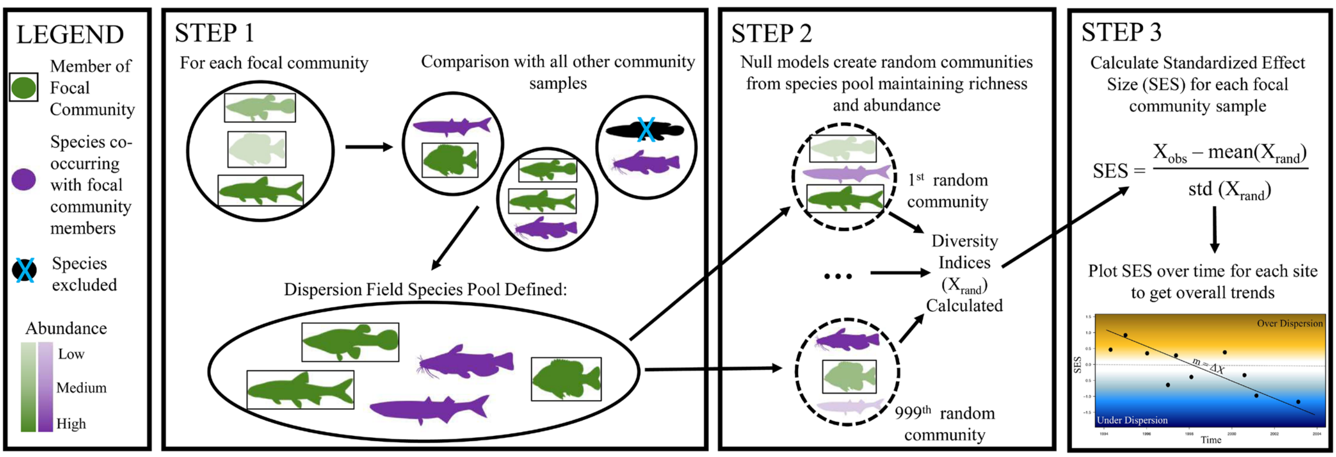

Figure 1. Conceptual figure of the methods for these analyses, outlining the steps done for each individual focal community. Different fish outlines represent unique species. In Step 1, a focal community is selected, and focal species are identified. The species found in the focal community are highlighted in green and are inside a box. Shades of color represent different abundance levels, with darker shades indicating higher abundances. The focal community is then compared to all other community samples in the data set. Any fish that co-occurs with a species from the focal community at any point in time or space (purple fish) is included in the dispersion field species pool. In Step 2, 999 null models are created using species only from the dispersion field species pool. In addition, we ensured that the abundance distributions from the focal community sample are consistent in each null model, as shown by the shading of the fishes. Diversity indices are calculated for each random community to calculate the standardized effect size as shown in Step 3. Overall trends for each site were calculated using the slope of the timeseries ($m = \Delta X$). Fish silhouettes from PhyloPic.org.

the null models created from each sample. From each time series, overall trends were computed (see Temporal trends and relationship with climatic changes section; Fig. 1: Step 3). To quantify the relationship between historical processes and changes over time, we calculated Pearson correlations between the historical standardized effect size (i.e. the standardized effect size calculated at the first sample point) and the slope of the standardized effect size time series for each diversity index. This comparison allowed us to view the overall changes in community diversity structure in relation to historical community structure. We ran a Kolmogorov–Smirnov test to compare differences between the distributions of historical and current values with the stats R-package (www.r-project.org) to test for changes in over- and under-dispersion over time.

Environmental data

We compiled environmental data for each site to identify the drivers of temporal changes in diversity patterns using the R package Stream Network Tools (Kopp 2019). We extracted nine physical and geological variables from each river that contained one of our 69 sites: the Strahler order for root node, number of headwater reaches, maximum and minimum elevation of the reach, slope of the reach, number of tributary junctions, the drainage area of the basin, the total length of network flowlines and drainage density. We kept two PCA axis (49.01 and 26.38% of explained variance) to represent the upstream–downstream gradient (UP–DOWN1 and UP–DOWN2) or the natural, spatially driven longitudinal changes in rivers (Vannote et al. 1980, Supporting information).

We quantified the climatic change experienced by fish communities using yearly climate data (precipitation and temperature) from the CHELSA database from 1969 to 2016 (Karger et al. 2017). From these data, we calculated the change in yearly maximum temperature (ΔTMAX), change in total annual precipitation (ΔPREC) and change in temperature range (the difference between the yearly maximum and yearly minimum; ΔTRANGE) over time. For each site, trends were estimated as the slope of the regression between a given climatic variable and time using GLS. The GLS incorporated temporal autocorrelation (autocorrelation structure of order 1 – corAR1), which take data from the previous year into account when calculating the regression. Using the slope allowed us to reduce the influence of extreme years as well as year-to-year fluctuations across the 42-year period.

Temporal trends and relationship with climatic changes

To quantify temporal trends in standardized diversity, we fit a GLS on each standardized effect size time series, using the standardized effect size as the response variable and the year as the explanatory variable. We extracted the slope of the model as a measure of the change in standardized effect size over time (hereafter Δ; Fig. 1: Step 3). A positive slope value indicates that communities are becoming more over-dispersed over time, while a negative slope indicates communities are becoming more under-dispersed. ΔPD and $\Delta FR_{trophic}$ were minimally spatially autocorrelated (Moran's $I = 0.08, -0.08$, respectively), while the other eight indices were randomly distributed. We therefore did not consider spatial autocorrelation in our models. To better understand the mechanisms behind diversity trends, we tested Pearson correlations between changes in functional and phylogenetic diversity and changes in species richness.

To quantify climatic changes, we used environmental variables as response variables (ΔTMAX, ΔTRANGE, ΔPREC, UP–DOWN1 and UP–DOWN2). To investigate the relationship between temporal changes in diversity and environmental conditions, we used linear models with diversity changes as the response variable and environmental changes as explanatory variables with the lme4 package (Bates et al. 2015). We found no evidence of multicollinearity between the changes in environmental factors in the linear models (Supporting information). All analyses were done in R (www.r-project.org).

Results

Our results showed that few sites exhibited a significant decline in species richness (SR), global functional richness (FR_{global}, Rao_{global}) or phylogenetic diversity (PD, Rao_{pylo}) over time (5 sites or fewer across 69 sites total). For each index, changes in diversity were significantly correlated with historical diversity (ΔSR: $r = -0.37$, $p = 0.002$; ΔFR_{global}: $r = -0.49$, $p < 0.001$; ΔRao_{global} $r = -0.63$, $p < 0.001$; ΔPD: $r = -0.45$, $p < 0.001$; and ΔRao_{phylo}: $r = -0.57$, $p < 0.001$; Fig. 2). These changes were consistent across all diversity indices, where sites with low historical diversity became more over-dispersed and sites with high historical diversity became more under-dispersed over time.

We found increased under-dispersion for measures of global functional diversity (FR_{global} and Rao_{global}) by comparing Pearson correlations between historical and contemporary standardized effect sizes. Conversely, measures of phylogenetic diversity displayed different patterns: for PD, most sites showed a decrease in over-dispersion while Rao_{phylo} showed an overall decrease in under-dispersion (Fig. 3). Despite these overall patterns, a Kolmogorov–Smirnov test showed that historical and current standardized effect size distributions were not significantly different ($p > 0.05$ for all indices).

Similar to global functional richness and phylogenetic diversity patterns, categorical functional richness indices showed that high historical richness was correlated with negative change in standardized effect size (increasing under-dispersion), and low historical richness was associated with positive change in standardized effect size (increasing over-dispersion; Fig. 4). This pattern persisted for trophic richness ($\Delta FR_{trophic}$: $r = -0.37$, $p = 0.002$; $\Delta Rao_{trophic}$: $r = -0.39$, $p = 0.001$), life history richness (ΔFR_{LHT}: $r = -0.62$, $p < 0.001$; ΔRao_{LHT}: $r = -0.63$, $p < 0.001$) and environmental tolerance richness (ΔFR_{env}: $r = -0.30$, $p = 0.001$; ΔRao_{env}:

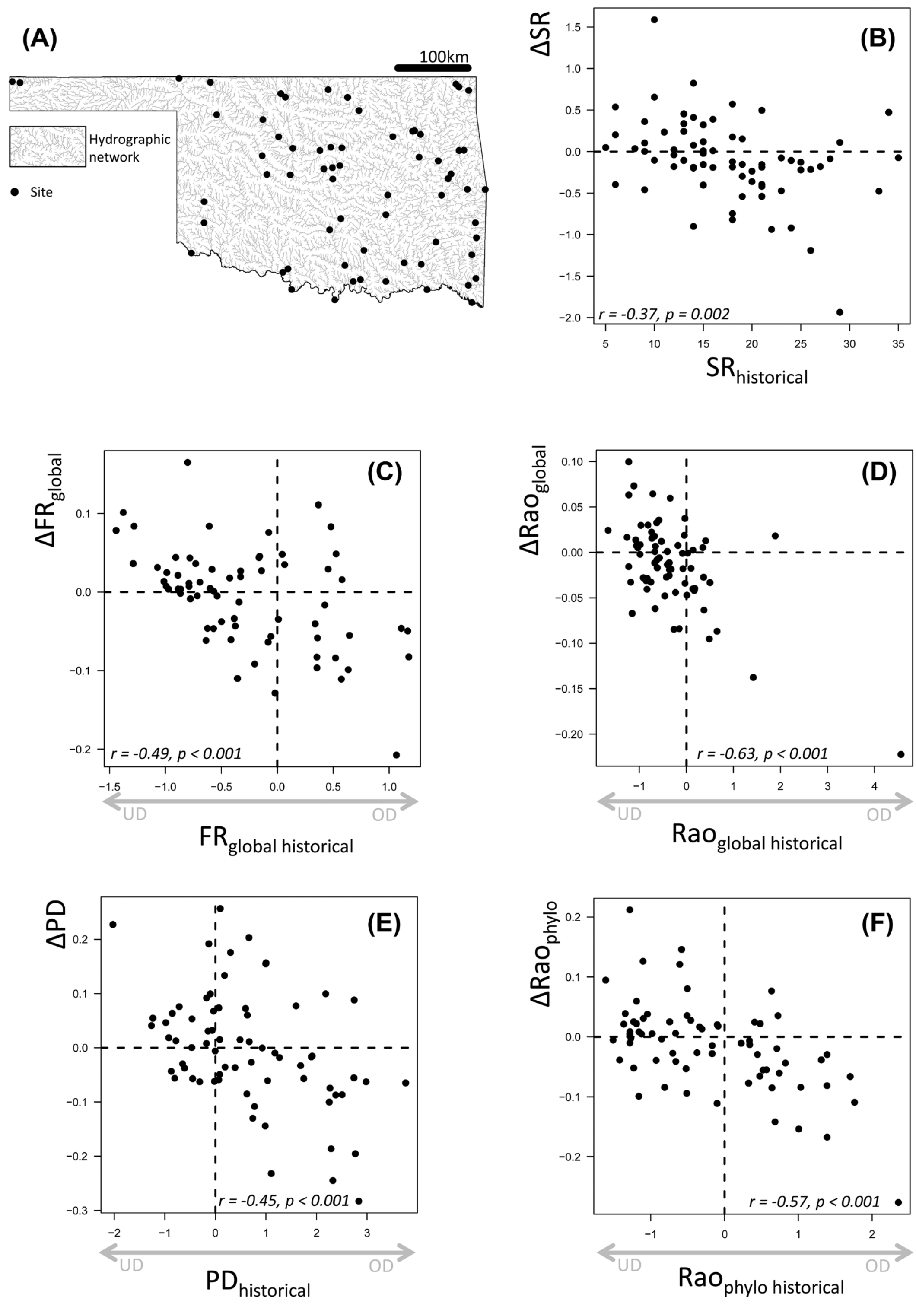

Figure 2. Map of sites across Oklahoma (A) and correlations between the indices calculated for the first community sample (historical) and index changes as measured by the slope of a GLS regression of standardized effect size values over time for: species richness (SR; B), functional richness for all traits (FR_{global}; C), Rao's quadratic entropy (Rao_{global}; D), phylogenetic richness (PD; E) and Rao's quadratic entropy (Rao_{pylo}; F). Stream networks are displayed on the map as hydrographic networks (A) and sites are denoted with black circles. Historical refers to the standardized effect size (SES) calculated at the first sample point for each site (C, D, E and F) or the species richness (B) at the first sampling point. SES calculations were not made for SR; thus, axes represent the first SR value at each site compared to the slope of SR values over time. Each black circle represents a site, with positive values demonstrating over-dispersion (OD) and those with negative values indicating under-dispersion (UD). The results of the Pearson correlation test are reported as r values along with p values.

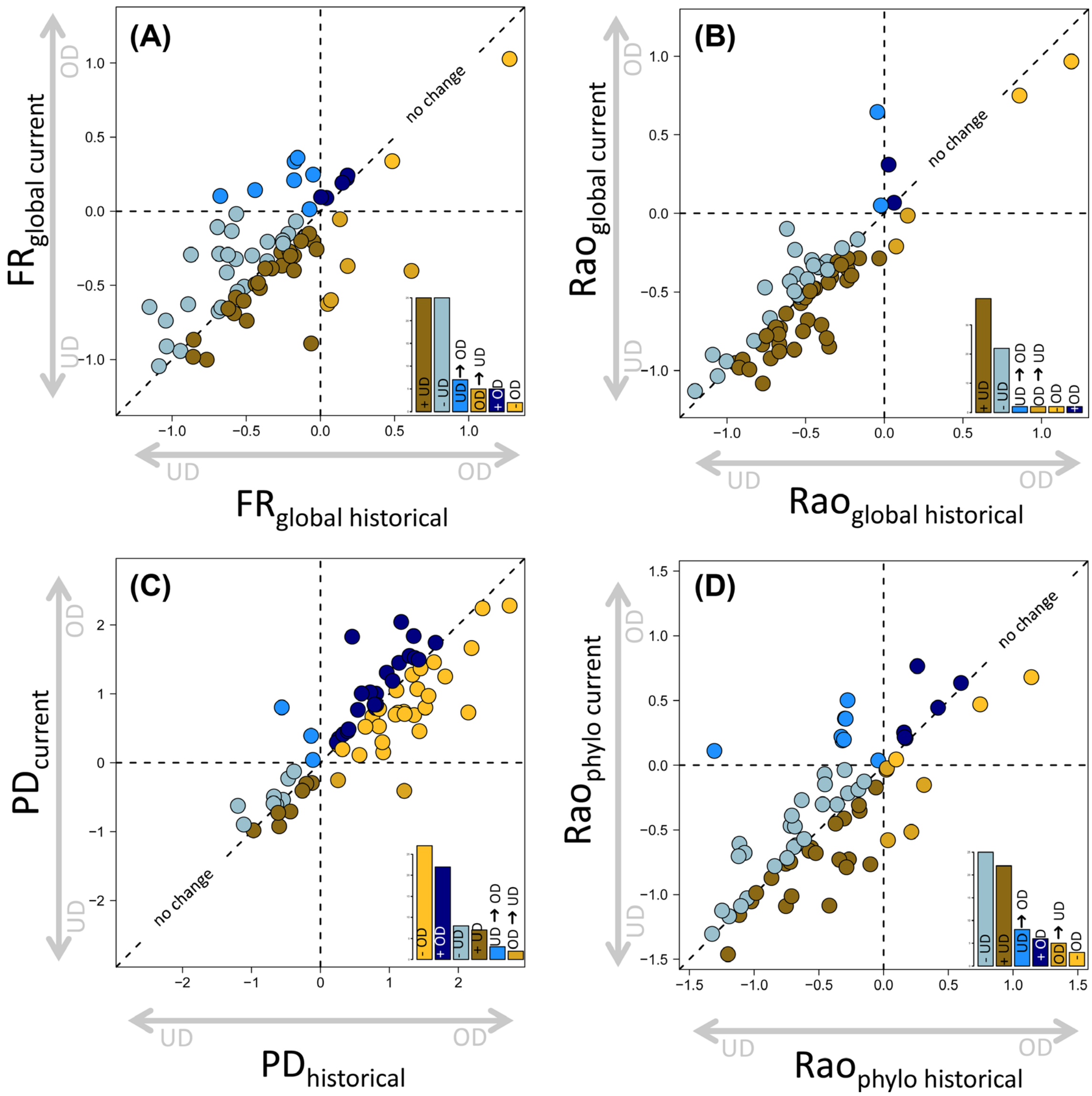

Figure 3. Correlations between historical and contemporary standardized effect size (SES) values for (A) global functional richness (FR_{global}), (B) functional Rao's quadratic entropy (Rao_{global}), (C) phylogenetic diversity (PD) and (D) phylogenetic Rao's quadratic entropy (Rao_{phylo}) across each site over time. Historical and contemporary values demonstrate the SES at the first and last time point for each site, with an average of 13 years between them. Interpretations of changes in standardized effect size are indicated by site position on the plot and matched in box plots: broadly, blue colors indicate an increase in over-dispersion (OD) while yellow colors indicate an increase in under-dispersion (UD). Sites in the upper left quadrant (blue) shift from UD to OD; possibly demonstrating a shift from environmental filtering to limiting similarity; UD –> OD), whereas sites in the bottom right quadrant (gold) show the opposite shift from OD to UD (OD –> UD). In the upper right and bottom left quadrants, sites either increase in or decrease in UD or OD relative to their position against the 1:1 line (dashed line): light blue, decrease in UD (– UD); dark gold, increase in UD (+ UD); dark blue, increase in OD (+ OD); yellow, decrease in OD (– OD). Bar graphs indicate the number of sites which can be found in each subsection of the plot.

$r = -0.34$, $p = 0.004$). There appeared to be an outlier for ΔFR_{LHT}, $\Delta Rao_{trophic}$ and ΔR_{LHT} (Fig. 4B, D and E, respectively). We tested correlations without this point and found little change in our results (ΔFR_{LHT}: -0.31, $p = 0.01$; $\Delta Rao_{trophic}$: -0.34, $p = 0.005$; and ΔRao_{LHT}: -0.23, $p = 0.06$).

All trait categories demonstrated changes in under-dispersion over time. $\Delta FR_{trophic}$ and ΔFR_{env} both demonstrated decreasing under-dispersion over time (39 and 23% of sites, respectively). For all other indices, however, most sites demonstrated increasing under-dispersion over time (ΔFR_{LHT} 32%; $\Delta Rao_{trophic}$ 42%; ΔRao_{LHT} 49%; ΔRao_{env} 33%; Supporting information).

We found that ΔSR was positively correlated with two functional indices (ΔFR_{LHT}: 0.29, $p < 0.05$; and ΔFR_{env}: 0.38, $p < 0.01$) and one phylogenetic metric (ΔPD: 0.59, $p < 0.001$; Fig. 5) using a Pearson test.

Over time, we found maximum temperature (TMAX) increased by 0.17°C, temperature range (TRANGE) increased

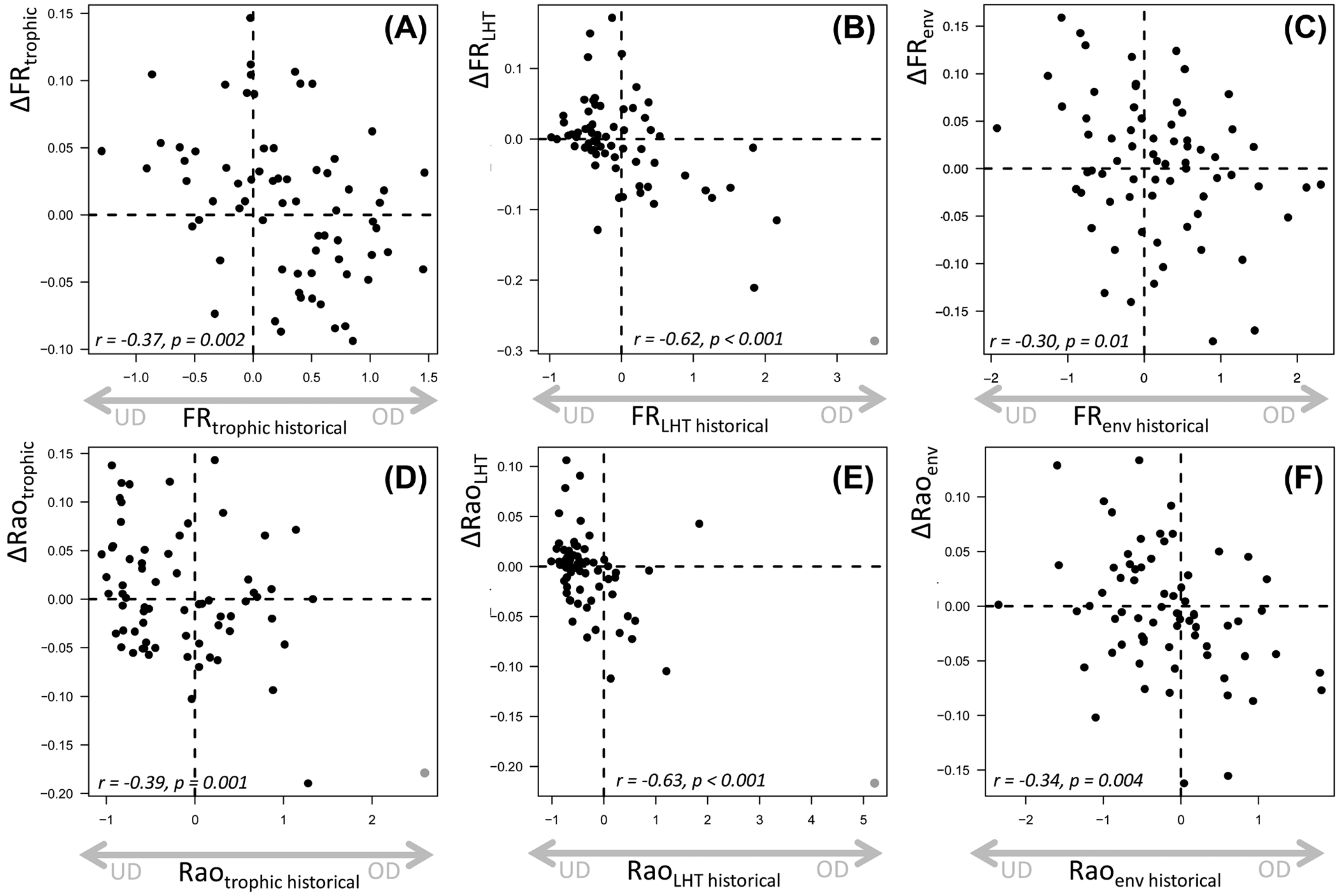

Figure 4. Correlations between the change in standardized effect size (ΔSES) over time and the value of the first index calculated for a site (historical) for functional richness trait categories: $FR_{trophic}$, trophic ecology traits (A), FR_{LHT}, life history traits (B), FR_{env}, environmental niche traits (C), $Rao_{trophic}$, trophic ecology traits (D), Rao_{LHT}, life history traits (E) and Rao_{env}, environmental niche traits (F). ΔSES was measured by the slope of a GLS regression of richness changes over time. Historical refers to the SES calculated at the first sample point for each site. Each black circle represents a site, with positive values demonstrating a more important role of limiting similarity and negative values indicating a more important role of environmental filtering. In panels B, D and E the outlier is highlighted in gray. Correlations were performed including and excluding this point, and our results show that its inclusion did little effect on the strength or significance of the relationship (FR_{LHT} $r=-0.31$, $p=0.01$ (B); $Rao_{trophic}$ $r=-0.34$, $p=0.005$ (D), Rao_{LHT} $r=-0.23$, $p=0.06$). The results of the Pearson correlation test are reported as r values along with p values.

by 0.19°C, and annual precipitation (PREC) increased by 14.86 mm on average per year. We found significant coefficients between models that compared $\Delta FR_{trophic}$ and ΔRao_{phylo} to ΔTMAX (−0.62, $p < 0.01$ and −0.30, $p=0.04$, respectively) and ΔSR to the second UP–DOWN axis (−0.36, $p=0.03$; Table 2). The other diversity indices were not significantly correlated with any environmental driver.

Discussion

We found that changes in the functional and phylogenetic diversity of fish assemblages in Oklahoma were better predicted by historical patterns than climate change. We hypothesized that fish communities would experience functional and phylogenetic diversity loss (i.e. shift towards under-dispersion), that historically diverse communities (i.e. over dispersed) would be more likely to experience diversity loss, and that environmental tolerance traits would be increasingly more important in structuring communities as they respond to climate change. Supporting our first hypothesis, both global functional richness indices indicated a loss of diversity (i.e. increase in under-dispersion). Phylogenetic diversity, however, demonstrated an approach towards randomness, as PD and Rao_{phylo} shifted in opposite ways. Additionally, we found that historical context had a stronger influence over how communities changed than environmental harshness, in contrast to our second hypothesis. Finally, our third hypothesis was not supported; trophic traits, rather than environmental traits, were correlated with environmental changes over time.

While our results show overall changes in diversity, functional richness and phylogenetic diversity demonstrated conflicting patterns. Indices for functional richness showed an increase of under-dispersion, following the stress dominance

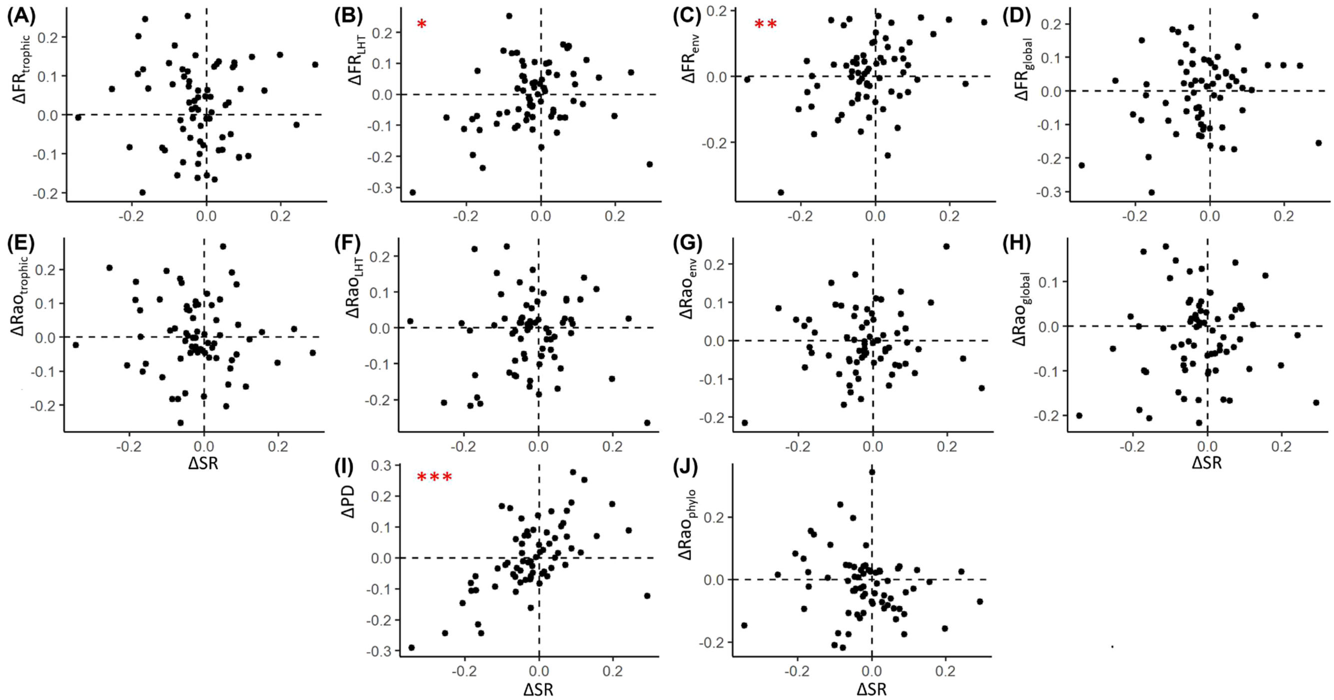

Figure 5. Correlations between changes in species richness (ΔSR) and changes in functional (trophic traits: (A) $\Delta FR_{trophic}$ and (E) $\Delta Rao_{trophic}$; life history traits: (B) ΔFR_{LHT} and (F) ΔRao_{LHT}; environmental tolerance traits: (C) ΔFR_{env} and (G) ΔRao_{env}; all traits combined: (D) ΔFR_{global} and (H) ΔRao_{global}) and phylogenetic diversity indices ((I) ΔPD and (J) ΔRao_{phylo}). *'s indicate the significance of the correlation, with * indicating $p < 0.05$, ** indicating $p < 0.01$ and *** indicating $p < 0.001$.

hypothesis. This suggests that as temperature and precipitation patterns change, communities adapted to previous conditions will face more environmental stress, limiting what species can be present at a given location. Contrary to this evidence, phylogenetic indices shifted towards randomness, contradicting our expectations under the stress dominance hypothesis. While diversity patterns often conflict (Gómez et al. 2010, Pavoine and Bonsall 2011, Cianciaruso et al. 2012, Sobral and Cianciaruso 2016), reasons behind these disconnects are not clear. In our study, causes for these conflicting patterns may be due to the limited spatial scale, which may not have provided a large enough species pool to detect climate change impacts on phylogenetic dispersion. Our spatial scale also limited the environmental gradient in our study, which could have constrained functional diversity, limiting the range of variation between our sites (Srivastava et al. 2012). However, we found that functional patterns were more sensitive than phylogenetic ones, suggesting that functional diversity may be more sensitive over limited spatial scales. In addition, human induced disturbances may act as an additional environmental filter, which tends to decrease phylogenetic diversity (Helmus et al. 2010). Regardless, our results indicate that fish assemblages are becoming more functionally similar while becoming less phylogenetically related. This could suggest that phylogenetic diversity is more reflective of changes in trait space of traits we did not measure, such as those

Table 2. Outcomes of GLS regression analyses relating environmental variables (ΔTMAX: change in maximum temperature; ΔTRANGE: change in temperature range; ΔPRECIP: change in precipitation; UP–DOWN: stable upstream–downstream gradient) to diversity indices. Coefficient of regression and p-values are listed. Significant relationships are highlighted in bold.

	ΔTMAX	ΔTRANGE	ΔPRECIP	UP–DOWN1	UP–DOWN2
ΔSR	−0.07, p = 0.69	−0.02, p = 0.89	−0.07, p = 0.72	0.10, p = 0.50	**−0.36, p = 0.03**
ΔFR_{env}	0.09, p = 0.58	−0.06, p = 0.73	0.09, p = 0.61	0.12, p = 0.41	−0.05, p = 0.73
ΔFR_{LHT}	−0.10, p = 0.53	−0.25, p = 0.12	−0.14, p = 0.46	0.14, p = 0.34	−0.21, p = 0.18
$\Delta FR_{trophic}$	**−0.62, p < 0.01**	0.11, p = 0.44	−0.01, p = 0.92	0.01, p = 0.96	−0.10, p = 0.46
ΔFR_{global}	−0.13, p = 0.41	−0.13, p = 0.41	−0.12, p = 0.52	0.15, p = 0.33	−0.21, p = 0.18
ΔRao_{env}	−0.07, p = 0.63	0.13, p = 0.41	0.03, p = 0.88	−0.01, p = 0.95	−0.29, p = 0.06
ΔRao_{LHT}	0.25, p = 0.13	−0.23, p = 0.16	−0.08, p = 0.68	0.04, p = 0.80	0.21, p = 0.19
$\Delta Rao_{trophic}$	0.06, p = 0.75	0.09, p = 0.59	−0.05, p = 0.78	0.14, p = 0.39	0.02, p = 0.89
ΔRao_{global}	0.14, p = 0.41	−0.13, p = 0.43	−0.09, p = 0.63	0.04, p = 0.81	−0.01, p = 0.94
ΔPD	0.25, p = 0.13	−0.12, p = 0.46	−0.06, p = 0.73	0.08, p = 0.61	−0.15, p = 0.35
ΔRao_{phylo}	**−0.30, p = 0.04**	0.10, p = 0.47	0.14, p = 0.38	0.05, p = 0.71	−0.17, p = 0.24

related to phenology (Flynn et al. 2011, Galland et al. 2019). Thus, using phylogenetic diversity and functional richness can provide a more complete picture of community variation through space and time, despite not being proxies for one another (Pavoine and Bonsall 2011, Sobral and Cianciaruso 2016, Jia et al. 2021).

While functional and phylogenetic diversity indices provide more information on community diversity than taxonomic diversity alone, they are not independent (Jia et al. 2021). Our results suggest that variations in FR and PD are due to gains and losses of unique species, particularly with respect to life history and abiotic niche strategies. Trophic traits, however, were not related to species richness. This could be due to the smaller number of traits we used to define this category. However, the lack of co-variation between species richness and trophic traits in comparison to other trait categories suggests the trophic niche space was not a useful axis of variation for community comparison in our study. In contrast to FR, Rao's quadratic entropy indices were not significantly correlated with species richness, suggesting this index is independent of species richness and therefore potentially more useful in understanding diversity patterns through time.

Trophic traits were the only category to be significantly related to environmental change, refuting our hypothesis that environmental tolerance traits would be the most related to environmental change. One possible reason for a lack of relationship may be that our communities were not sampled from the margins of individual fish distributions, where species are more likely to be closer to the limits of their niche (Holt and Gaines 1992) and environmental changes may play a bigger role in community reassembly. Therefore, considering traits related to both the biotic and abiotic environment gives a fuller picture of community diversity than trait subsets, in part due to their interaction with environmental gradients across space. We argue that looking for patterns in functional richness across all traits, particularly when exploring larger spatial scales, is most useful for conservation and management to identify, for instance, hotspots of functional diversity.

We also found that changes in temperature had the strongest effect on diversity changes for two (out of eleven) indices, which parallels the findings of other studies relating fish communities and environmental stressors (Daufresne and Boët 2007, Whitney et al. 2016). Increases in maximum temperature led to loss of trophic diversity ($FR_{trophic}$) and phylogenetic diversity (Rao_{phylo}). As average and maximum temperatures continue to increase, more species are likely to experience temperatures outside their historical range, leading to extirpation and extinction in these vulnerable river systems (Matthews and Zimmerman 1990, Dodds et al. 2004). Additionally, community composition appears to change at a faster rate when communities approach thermal thresholds for multiple species (Comte et al. 2021). The relatively weak responses of Oklahoma fish communities to changes in temperature suggest that the largest impacts of temperature are yet to be observed.

While our results suggest that temperature is the most important driver of community reorganization where it occurred, most changes in diversity were not explained by any of the tested drivers. However, we found the upstream–downstream gradient drove changes in species richness, suggesting that species richness trends are changing along elevation gradients or across stream orders. Other diversity indices had no relationship to the upstream–downstream gradient, indicating that headwaters and lowland rivers are experiencing changes in diversity at similar rates or that species replacement is taking place with functionally and phylogenetically redundant species. While the longitudinal gradient of rivers is recognized as a driver of diversity (Vannote et al. 1980), as shown by its significant impact on species richness, the upstream–downstream gradient is likely to not be altered by climate change stressors. In addition, changing precipitation had no effect on changes in community structure despite the direct impact that precipitation can have on discharge (Power 1981, Favier et al. 2009). Discharge influences fish spawning behavior (Lytle and Poff 2004) and impacts food webs by altering nutrients (Reist et al. 2006) and therefore stream productivity (Power 1981). We also may have failed to detect stronger relationships with environmental changes because contemporary community diversity is also related to historical habitat conditions (Harding et al. 1998, Burcher et al. 2008), and land use change can increase environmental stress at a particular site. As land use changes can interact with climate change to alter communities (Mantyka-Pringle et al. 2014, Comte et al. 2021), further studies should investigate the role of change in land use and climate on assembly rules.

While our study detected changes in fish diversity patterns, we found that community changes were linked to historical processes. Across richness indices, we found that historically rich communities lost functional and phylogenetic diversity and shifted from over- to under-dispersion, supporting the stress dominance hypothesis. With more extreme climatic conditions expected over time (Daufresne and Boët 2007), sensitive or specialist species will likely be lost due to threshold responses (Brejão et al. 2018). On the other hand, sites that historically exhibited low diversity showed an increase in diversity over time, shifting from under- to over-dispersion. This pattern suggests that historically vacant niches have provided space and opportunity for new species to establish. This could indicate the spread of non-native species (Vitousek et al. 1997, Gavioli et al. 2019) which can compete with or predate upon natives within a river system, creating new species interactions (Lynch et al. 2016). The lingering impact of historical processes on contemporary community diversity in our results may dampen the effects of recent environmental change, which may be why we did not detect stronger support for the stress dominance hypothesis or more relationships between environmental drivers and diversity indices.

While null models are intended to standardize diversity changes across different assemblages, they also introduce biases. For example, our null models used a regional species pool spanning 40 years; had our null assemblages been specific to smaller sampling periods (i.e. 1–3 years), the species pool for each focal community may have been smaller, decreasing the standard deviation of the random communities and ultimately leading to larger standardized effect sizes. In addition, the dispersion field species pool definition accounts for dispersal barriers in addition to large scale habitat preferences (Graves and Rahbek 2005), thereby accounting for species dispersal ability. However, this species pool is dependent on the species in the focal sample, and may include species that never actually overlap with species in the focal community (Lessard et al. 2012a), which could lead to biases against over dispersion (i.e. limiting similarity; Carstensen et al. 2013). Finally, we assumed that no species invaded or became extirpated from the region during this sampling period, and that functional traits remained constant despite the known plasticity of fish traits (Crozier and Hutchings 2014). Future studies with more individual fish trait measurements would better illustrate the influences of changing climates on fish assemblages.

Our results demonstrate the importance of considering multiple indices of diversity, historical context and environmental drivers when testing community diversity patterns. Unlike in other studies, we did not find consistent patterns across our diversity indices (Jarzyna and Jetz 2017, Kuczynski and Grenouillet 2018), highlighting the need for careful consideration of indices and methods used to study various aspects of diversity. The Great Plains are a transition zone in the continental United States, encompassing a variety of biomes and a range of environmental gradients. The lack of consistent changes in diversity patterns highlights the need for further studies to better clarify the pressures acting on fish and other assemblages in transitional zones. Our study also demonstrates the importance of historical conditions on assemblages, highlighting the need for data consolidation and long-term studies. Understanding where historical conditions impact assemblage responses to environmental changes could allow managers better identify conservation needs under climate and environmental changes.

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Author contributions

Michelle H. Busch: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Daniel C. Allen**: Conceptualization (equal); Funding acquisition (lead); Project administration (equal); Supervision (supporting); Writing – review and editing (equal). **Katharine A. Marske**: Conceptualization (equal); Funding acquisition (lead); Project administration (equal); Supervision (supporting); Writing – review and editing (equal). **Lucie Kuczynski**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (lead); Software (equal); Supervision (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2435k (Matthews and Marsh-Matthews 2017b). The Jimmie Pigg data set: http://www.oknaturalheritage.ou.edu/index.php.

Supporting information

The Supporting information associated with this article is available with the online version.

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