

ORIGINAL ARTICLE

High and dry in days gone by: Life-history theory predicts Appalachian mountain stream fish assemblage transformation during historical drought

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Abstract

Understanding the ecological dimensions of drought is critical for predicting how humans and nature will be affected by the expected increased prevalence of drought in the future. We tested life-history-based predictions for fish assemblage responses to drought using retrospective analysis of long-term (1986–2003) fish surveys from two streams in the Appalachian Mountains of North America. We hypothesised that (1) fish assemblage composition would correlate with wet and dry hydrologic conditions as assemblages fluctuated within a loose equilibrium and (2) life-history traits of fishes would correlate with dry versus wet periods such that opportunistic life-history strategists would dominate during drought. Results showed fish assemblage changes in Little River and Cataloochee Creek correlated with drought severity measured one year prior to fish surveys. Fish assemblages at all three sampling sites in Little River and two sites in Cataloochee Creek fluctuated within a loose equilibrium, while the remaining two sites in Cataloochee Creek indicated directional change. Life-history traits for fishes in Cataloochee Creek correlated with one-year time lag fluctuations in drought caused by opportunistic species being dominant during drought and periodic/equilibrium species dominant during wet periods. Time series plots of fish abundances aggregated by life-history strategy revealed dominance of opportunistic species emerged at the onset of a multi-year drought spanning 1998–2004, particularly for the two sites undergoing directional change. Our work provides empirical evidence for theoretical linkages between life history and environmental fluctuations and can ultimately be used to predict stream fish community response to future drought regimes.

KEYWORDS

aquatic biodiversity, community ecology, fish assemblages, functional traits, hydrologic disturbance, life-history theory

1 | INTRODUCTION

Mounting evidence points to future droughts of greater frequency and duration for most portions of the world (Dai, 2013; Slette et al., 2019). Understanding the ecological dimensions of drought is critical for predicting how humans and nature will be affected by the expected increased prevalence of drought in the future (Crausbay et al., 2017). Drought has been formally studied by ecologists for nearly a century (Gorham & Kelly, 2018), and although we have learned much regarding how organisms respond to drought, further research is needed to understand species succession during drought as well as long-term assemblage-level effects of drought (Lennox et al., 2019). Progress towards addressing this challenge requires integration of conceptual frameworks and empirical research aimed at testing and influencing theory as it applies to the emerging prevalence of drought (Marquet et al., 2014; Trenberth et al., 2014). Two concepts in ecology are useful for developing predictions for the ecological consequences of drought: community ecology and life-history theory.

Community ecology theory is less of a unified theory than it is a collection of theoretical and conceptual models with a shared focus on co-occurring species (Mittelbach & McGill, 2019; Reiners et al., 2017). Community ecology theory posits that long-term species coexistence is mediated and maintained, in part, by spatial and temporal environmental variation (Chesson, 2000). From these environmental fluctuations, patterns in stable (i.e. equilibrium) versus unstable (i.e. nonequilibrium) community trajectories can emerge (DeAngelis & Waterhouse, 1987). A stable community trajectory involves the long-term persistence of species as a community oscillates around some long-term “average” structure, while an unstable community trajectory involves species loss and directional change. The “loose equilibrium concept” describes stable community structure through time despite environmental variation causing slight changes in species abundance or occurrence (DeAngelis et al., 1985). In theory, extreme disturbances or environmental fluctuations are capable of pushing a community from a stable to an unstable state (Fukami & Nakajima, 2011). Tests of community ecology theory in terrestrial plant, insect, mammal and bird communities (Collins, 2000) as well as freshwater fish communities (Matthews & Marsh-Matthews, 2016; Matthews et al., 2013) have revealed general support for theoretical expectations regarding disturbance and loose equilibrium versus directional change.

Species life history is a central concept in ecology (Reiners et al., 2017) and life-history theory ranks among the most widely embraced ecological theories (Marquet et al., 2014). Life-history theory posits that organisms must allocate energy to growth, survival or fecundity, but cannot simultaneously maximise each of these demographic parameters (Stearns, 1977). Furthermore, species with unique trait combinations along these demographic axes are expected to experience differential survival across environmental gradients through the process known as environmental filtering (Partridge & Harvey, 1988). For example, the tri-lateral continuum model of Winemiller and Rose (1992) for North American fishes describes three endpoint

life-history strategies defined by trade-offs along axes of age at maturation, fecundity and juvenile survivorship. “Opportunistic” strategists have young age at maturation, low fecundity and low juvenile survival; “Periodic” strategists mature at an older age, have high fecundity and experience low juvenile survival; and “Equilibrium” strategists mature at an older age, have low fecundity and experience high juvenile survival. In theory, opportunistic strategists experience maximum fitness under stochastic resource availability owing to their ability to quickly recolonise, periodic strategists experience maximum fitness under predictable but seasonal resource availability because of their delayed maturation and high fecundity, and equilibrium strategists experience maximum fitness under stable resource availability because of their high investment in juvenile survival (Winemiller & Rose, 1992). These theoretical expectations have been tested in the context of streamflow regimes filtering life-history traits of freshwater fishes over evolutionary time scales and a general pattern of support for the theory has emerged (Mims & Olden, 2012; Olden & Kennard, 2010; Tedesco et al., 2008).

Community ecology and life-history theory have potential for predicting freshwater fish responses to drought. Fishes are among the mostly commonly studied animals in ecology (Gorham & Kelly, 2018), yet there is still more to learn regarding their responses to drought (Lennox et al., 2019). For example, drought-induced declines and extirpations among fishes believed to be drying-tolerant highlights misconceptions regarding ecological aspects of drought (Meijer et al., 2019; Perkin et al., 2019). These misconceptions arise because of a general lack of knowledge regarding the mechanisms through which drought affects fishes (Matthews & Marsh-Matthews, 2003). However, insight into these mechanisms can be gained through research of communities and traits of constituent species related to fitness-based components of individual performance, including growth, reproduction and survival (Violle et al., 2007). Viewing fish communities and their traits through the lenses of community ecology and life-history theory might be expected to illuminate the ecological dimensions of drought for at least three reasons. First, streamflow is tightly coupled with drought cycles, and stochastic streamflow during drought is a global phenomenon (Chiew et al., 1998; Haslinger et al., 2014; Nigam et al., 1999). Long-term data sets that include drought cycles therefore represent the opportunity to test for directional change in communities as environmental fluctuations play out (Matthews et al., 2013; Perkin et al., 2015). Second, Chessman (2013) analysed relationships between drought conditions and freshwater fish traits (including life-history traits) in Australia and found traits were predictive of species responses to drought, though no formal test of theoretical expectations was conducted. Third, environmental filtering of freshwater fish life-history traits over ecological timescales and in response to streamflow fluctuations has been demonstrated multiple times. Examples include human alterations that transform flow regimes along gradients of stochastic (unaltered) to stable (altered by dams) flows resulting in greater abundance of equilibrium species and reduced abundance or extirpation of opportunistic species (Mims & Olden, 2013; Olden et al., 2006; Perkin et al., 2017). These previous works collectively

set the stage for advancing basic community ecology and life-history theories by testing their applicability to the emerging pattern of expected drier and increasingly drought-stricken conditions facing freshwater fishes in the future (Lennox et al., 2019).

Here, we test predictions from community ecology and life-history theory using retrospective analysis of long-term fish assemblage surveys (1986–2003) from two streams in Great Smoky Mountains National Park located in the Appalachian Mountains region of the eastern United States. We incorporate three measures of hydrologic condition (drought, precipitation and streamflow) and assess relationships between these variables and fish assemblages across time lags ranging 0–2 years. We hypothesised that (1) fish assemblage composition would correlate with hydrologic conditions such that wet-period and dry-period assemblages would exist but these fluctuations would be bound within a loose equilibrium and (2) life-history traits of fishes would correlate with dry-wet periods such that opportunistic life-history strategists would dominate during drought periods as flows became more stochastic and periodic/equilibrium strategists would dominant during wet periods when flows were more permanent.

2 | MATERIALS AND METHODS

2.1 | Overview

To test our hypotheses, we combined multiple measures of hydrology with time series fish community data in a set of retrospective analyses. We first obtained hydrology data in the form of drought intensity, precipitation and streamflow for two stream systems in the southern Appalachian Mountains in North America. We then reviewed historical fish community data from a total of seven sites distributed across the two stream systems. We compiled life-history

information for each of the fish species encountered during the historical sampling using a recent meta-analysis of fish life-history traits (Thorson et al., 2017). Using these data, we first tested for correlations between hydrologic variation and stream fish community structure and then tested for correlations among hydrology, fish abundances and life-history traits.

2.2 | Study area

We studied fish assemblage and hydrologic trends in Great Smoky Mountains National Park (GRSM) in the Appalachian Mountains region of the United States. This region has a temperate climate and receives 55–85 inches of rainfall between 98 and 127 days annually, thereby classifying the region as a temperate rainforest. Late summer to early fall (September–October) is typically the dry season when streams reach base flows, though precipitation events cause flow pulses. Average monthly air temperatures recorded from 1981 to 2010 by National Oceanic and Atmospheric Administration (NOAA) weather stations at Cataloochee, North Carolina (station GHCND:USC00311564), and Townsend, Tennessee (station GHCND:USC00409065), ranged 4.1–19.0°C and were warmest in the summer (maximum 27.6°C) and coolest in the winter (minimum –5.3°C) (NOAA, 2019a). The region is prone to droughts that follow approximately decadal cycles, and during these droughts, precipitation and streamflow levels are lowest (Kloepfel et al., 2003). Within GRSM, the dominant land cover is forest, and human alterations to landscapes are minimal outside of road construction (Kumar et al., 2015). We studied two streams with their headwaters in GRSM, Little River and Cataloochee Creek. Little River (LR) is an 5th order stream that drains west out of GRSM, and Cataloochee Creek (CC) is an 4th order stream that drains east out of GRSM (Figure 1). Three sampling sites (LR1–LR3) were distributed along the longitude of LR,

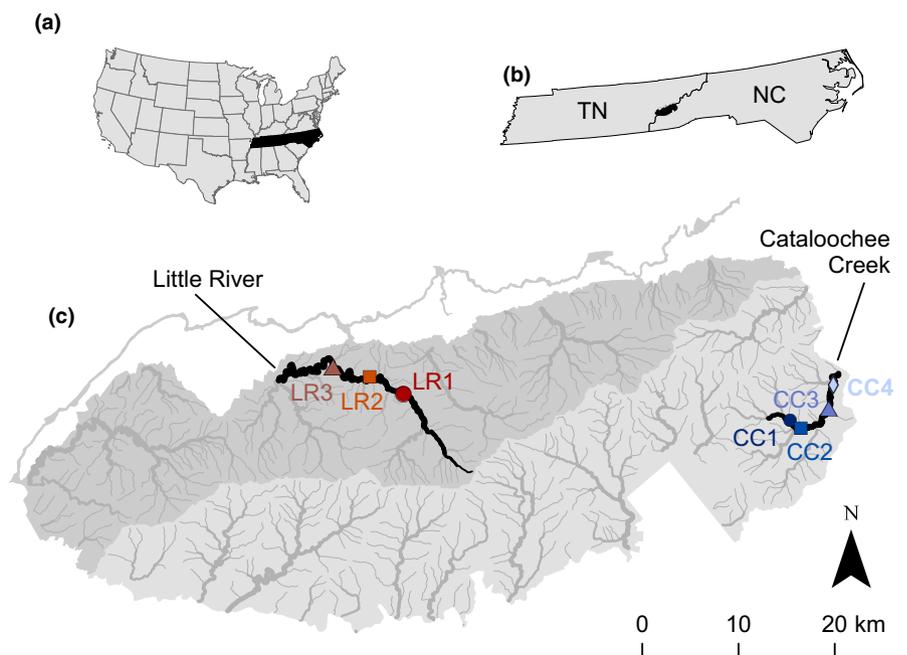


FIGURE 1 Map of study area showing (a) the southeastern United States and (b) the border between Tennessee (TN) and North Carolina (NC), where (c) Great Smoky Mountains National Park spans the ridgeline of the Appalachian Mountains. Three sampling sites (LR1–LR3) were located on the Little River draining into TN on the west side (darker grey) of the park and four sampling sites (CC1–CC4) were located on Cataloochee Creek draining into NC on the east side (lighter grey) of the park

and four sampling sites (CC1–CC4) were distributed along the longitude of CC. All of these sites are located at higher elevations relative to the surrounding region, including 550–750 m above sea level (MASL) for LR and 750–900 MASL for CC.

2.3 | Hydrologic conditions

We collected historical data for monthly Palmer Drought Severity Index (PDSI), precipitation and streamflow for each study stream. The PDSI integrates precipitation, temperature, latitude and available water content data and represents a long-term, broad-scale measure of wet versus dry conditions. The PDSI provides quantitative thresholds for drought severity, including extreme drought ($\text{PDSI} > -4$), severe drought ($-3.0 < \text{PDSI} > -3.9$), moderate drought ($-2.0 < \text{PDSI} > -2.9$), normal or near normal ($-1.9 < \text{PDSI} > 1.9$), unusually moist spell ($2.0 < \text{PDSI} > 2.9$), very moist spell ($3.0 < \text{PDSI} > 3.9$) and extremely moist spell ($\text{PDSI} > 4.0$). Drought measures based on PDSI have been linked to fluxes in fish assemblage composition elsewhere (Perkin et al., 2015) and represent a course scale measure of climatic influences on aquatic assemblages. We downloaded monthly PDSI from NOAA (2019b) for climatic divisions 40–01 (Tennessee–Eastern) for LR and 31–01 (North Carolina–Southern Mountains) for CC. Monthly precipitation provides an intermediate scale measure of wet versus dry conditions and is linked to fish populations dynamics in the Appalachian Mountains (Kanno et al., 2015). We downloaded historical monthly precipitation data for the same climatic divisions as PDSI data (NOAA, 2019b). Streamflow magnitude provides a fine-scale measure of wet versus dry conditions and is commonly linked to fish assemblage dynamics in streams (Poff & Zimmerman, 2010). We downloaded daily streamflow data from the U.S. Geological Survey (USGS, 2019) for LC above Townsend, TN (USGS gage # 03497300), and CC near Cataloochee, NC (USGS gage # 03460000).

We summarised temporal variation in hydrologic indices for each stream using hydrographs and graphical function maps (GFM). We first calculated monthly mean streamflow from daily data to match the temporal grain size used for PDSI and precipitation. We then plotted time series of PDSI as grey bars and overlaid precipitation (cm/month) to illustrate temporal correlation between these variables. We plotted change in streamflow (m^3/s) using a similar bar graph for PDSI and a line graph for mean monthly streamflow. Finally, we illustrated relationships between all three hydrologic variables using GFM. Graphical function maps are a useful tool for showing causal relationships among multiple quantitative functions (Evans, 2016). In our case, the level of drought (measured as PDSI) is predictive of precipitation because it is a broad measure of moisture availability and tightly linked to climatic fluctuations (Mika et al., 2005). Precipitation, in turn, influences streamflow because of runoff from land into streams as well as water that entered the stream channel upstream (Groisman et al., 2001). We used quantile regression (quantiles 0.10, 0.25, 0.50, 0.75, 0.90; Cade & Noon, 2003) to describe functional relationships between PDSI and precipitation

and then precipitation and streamflow using corresponding monthly values for each measure of hydrology. We fit quantile regression models using the “rq” function from the “quantreg” package in R (Koenker, 2018).

2.4 | Fish assemblage surveys

Fish community abundance data were collected as part of the GRSM long-term ecological monitoring programme (NPS, 2014). Surveys were conducted annually at each site during summer months between 1986 and 2003. Some sites were occasionally not sampled because of high flows, but generally effort was made to visit each site annually. Fish abundance was determined using the three-pass depletion technique with block nets set at the upper and lower site boundaries to meet the assumption of no immigration or emigration (Habera et al., 2010; Kanno et al., 2017; Trout Committee SDAFS, 1992). One backpack electrofishing unit was used for every 3–4 m of mean stream width for a given site (Trout Committee SDAFS, 1992). Fishes collected in each pass were held in holding cages outside of the sampling area until all sampling was completed. At least 30 minutes elapsed between passes to ensure that assumptions equal catchability were met (Trout Committee SDAFS, 1992). After each pass, fish were sorted by species and total length (mm) and mass (g) were measured. All fish were returned to the site after the third pass. Abundance was estimated using Microfish 3.0, a software that utilises the Burnham maximum-likelihood estimate model (van Deventer & Platts, 1989).

2.5 | Life-history traits

We assigned life-history traits to each fish species encountered during surveys using a meta-analysis of fish life-history data. We used the framework described by Thorson et al. (2017) in which eight variables (seven life history and temperature) were predicted for >32,000 fish species worldwide. The modelling approach includes taxonomic structure for residuals across taxonomic levels class, order, family, genus and species, meaning predictions are possible for species with few data based on the principle of phylogenetically constrained life-history evolution (Thorson, 2017). Life-history parameters included maximum size (L_{inf}), size at maturity (L_{mat}), Brody growth coefficient (K), maximum mass (W_{inf}), maximum age (A_{max}), age at maturity (A_{mat}), natural mortality (M) and mean water temperature (T). We assigned life-history parameter estimates to each fish species using the “FishLife” package in the R statistical environment (Thorson, 2017). For species with little available information, genus or family level data were used to estimate life-history parameters. Given this data limitation, we supplemented life-history estimates for least-studied nontrout fishes using maximum total length information obtained directly from specimens collected from GRSM (NPS, 2021). Specifically, for all fishes outside of the family Salmonidae, we replaced L_{inf} from Thorson (2017) with the maximum total length of

TABLE 1 Species, codes, life-history attributes and life-history classification (LH; O = opportunistic; P/E = Periodic/Equilibrium) for fishes collected from Great Smoky Mountains National Park (GRSM) during 1984–2003. Life-history attribute predictions are from Thorson (2017) except that parenthetical maximum size data are measurements of maximum total length from fishes collected from GRSM

Species	Code	Maximum size (cm; L_{inf})	Growth coefficient (K)	Maximum mass (g; W_{inf})	Maximum Age (y; A_{max})	Age at maturity (y; A_{mat})	Natural mortality (M)	Size at maturity (cm; L_{mat})	Temperature (°C)	LH
Central Stoneroller (<i>Campostoma anomalum</i>)	camano	23.21 (22.8)	0.36	182.09	5.92	1.61	0.68	12.73	14.59	O
Warpaint Shiner ^a (<i>Luxilus coccogenis</i>)	luxcoc	26.62 (11.8)	0.31	303.57	6.47	1.77	0.62	14.03	17.61	O
River Chub ^b (<i>Nocomis micropogon</i>)	nocmic	29.64 (23.6)	0.29	460.20	6.85	1.89	0.60	15.07	20.65	O
Tennessee Shiner ^a (<i>Notropis leuciodus</i>)	notleu	20.33 (9.5)	0.39	150.34	5.37	1.43	0.78	10.85	21.12	O
Saffron Shiner ^a (<i>Notropis rubricroceus</i>)	notrub	20.33 (8.4)	0.39	150.34	5.37	1.43	0.78	10.85	21.12	O
Blacknose Dace ^b (<i>Rhinichthys atratulus</i>)	rhiatr	29.64 (10.0)	0.29	460.20	6.85	1.89	0.60	15.07	20.65	O
Longnose Dace ^b (<i>Rhinichthys cataractae</i>)	rhiatc	29.64 (15.0)	0.29	460.20	6.85	1.89	0.60	15.07	20.65	O
White Sucker (<i>Catostomus commersonii</i>)	catcom	48.84 (33.2)	0.18	1354.35	14.87	4.10	0.31	26.93	14.72	P/E
Northern Hogsucker ^b (<i>Hypentelium nigricans</i>)	hypnig	36.94 (39.8)	0.25	606.63	11.04	3.00	0.43	20.76	17.37	P/E
Mottled Sculpin ^a (<i>Cottus bairdii</i>)	cotbai	12.22 (13.3)	0.30	22.92	6.58	2.04	0.59	7.07	10.45	O
Rainbow Trout (<i>Oncorhynchus mykiss</i>)	oncmyk	57.46	0.47	2148.77	7.29	3.02	0.96	38.42	14.51	P/E
Brown Trout (<i>Salmo trutta</i>)	saltru	53.03	0.25	1723.86	6.83	2.23	0.58	24.46	9.48	P/E
Brook Trout (<i>Salvelinus fontinalis</i>)	salfon	32.30	0.26	336.25	7.35	2.60	0.83	16.29	8.42	P/E

^aGenus level prediction.

^bFamily level prediction.

species recorded in the GRSM database. All variables except T were log-transformed for analysis in “FishLife,” and we back-transformed these variables for interpretation (Table 1).

2.6 | Statistical analyses

We tested our hypotheses regarding fish assemblage dynamics using multivariate community ordinations. All fish abundances were fourth-root transformed prior to analysis to down-weight the influence of abundant versus rare species on ordinations (Clarke, 1993). We used nonmetric multidimensional scaling (NMDS) models based on Bray–Curtis distances calculated based on the estimated abundances of fishes and specified two dimensions (Smith & Mather, 2012). We checked two-dimensional stress values to ensure they were <0.10 and therefore reliable representations of community patterns (Kruskal, 1964). We initially tested the influence of river basin (LR versus CC) on fish assemblage structure using a permuted multivariate analysis of variance (PMANOVA) to determine if basins should be analysed independently. The initial PMANOVA revealed a significant difference ($F_{1,109} = 328$, $p = 0.001$, $R^2 = 0.38$) in fish assemblage structure between LR and CC basins, so we proceeded with NMDS analyses for each basin separately. We did not model individual sites within basins independently because of the potential for fish movement among sites. We tested for correlations between NMDS scores and hydrologic variables across three time lags, including data from the year of surveys (lag = 0), the year prior to surveys (lag = 1) and two years prior to surveys (lag = 2). We used the “envfit” function from the “vegan” package in R to test which hydrology variables and time lags were correlated with assemblage structures. The “envfit” function computes R-square values and permuted tests of significance for relationships between the community matrix and each environmental variable included in the model (Oksanen et al., 2019). We retained variables with $p < 0.05$ for interpretation and overlaid vectors on NMDS plots to illustrate the direction and magnitude of correlations, where vector direction indicates axis correlation and longer vectors represent stronger correlations. Based on the nature and direction of environmental correlations with assemblage structure, we plotted temporal trajectories of NMDS axis scores and hydrologic variables to illustrate temporal patterns from multivariate analyses.

We tested our hypothesis regarding loose equilibrium versus directional change using NMDS results. Matthews et al., (2013) provided a conceptual framework for identifying six community trajectory types, including nondirectional, directional and directional-with-return, all of which can follow saltatory or gradual paces. This framework was later formalised by Matthews and Marsh-Matthews (2016), including a test for directional versus nondirectional change based on distances between temporally distributed samples and the centroid of all samples combined. We extracted NMDS scores for all samples at each site and calculated the site-specific centroid using the “betadisper” function from the “vegan” package in R. We then plotted a time series of absolute Euclidean distances from the

centroid, where 0 represented a sample near the middle of all sites in multivariate space and positive values indicate a greater Euclidean distance from the centroid. Following Matthews and Marsh-Matthews (2016), we then counted the number of return steps in which a movement away from the centroid (i.e. increase in distance from centroid) was followed by a return to the centroid (i.e. decrease in distance from centroid). Assemblages conforming to expectations under the loose equilibrium concept should show several returns towards the centroid for a majority of the possible steps. Because returns must follow a movement away from the centroid, this means the threshold for majority is equal to the total number of steps divided by two. In cases when the initial step is towards the centroid, the threshold value is equal to one plus the quotient of total steps divided by two (Matthews & Marsh-Matthews, 2016). We considered assemblage dynamics at a site to be consistent with predictions from loose equilibrium if return steps occurred in more than 50% of possible steps, otherwise we concluded the site was undergoing directional change.

We summarised life-history trait data using multivariate statistics and tested for correlations among traits, assemblage structure and hydrology as a means of testing if fish life histories were an underlying mechanism for community fluctuations. We first summarised predicted trait data for all species using principal component analysis (PCA; Poff & Allan, 1995). The PCA model was useful for identifying latent gradients in life-history traits that could be interpreted as strategies. For example, fishes with high natural mortality (M), fast growth rates (K), small size at maturity (L_{mat}), young age at maturity (A_{mat}) and small body size (L_{inf} , W_{inf}) can be classified as “fast” life-history strategists, whereas those with contrary traits can be classified as “slow” life-history strategists (Promislow & Harvey, 1990). These life-history strategies are consistent with Winemiller and Rose (1992) designations of opportunistic versus periodic/equilibrium respectively. We then conducted fourth-corner analysis (FCA) as described by Legendre et al., (1997) and Dray and Legendre (2008) to determine three-way interactions among life-history traits, species abundances and environmental variables related to drought. We included only PDSI values measured at the three time lags in the FCA because these variables were related to fish assemblage structure in both basins (see ordination results). We used the “fourthcorner” function from the package “ade4” and selected “modeltype = 6” to reduce type-1 error inflation as suggested by ter Braak et al., (2012). We illustrate significant correlations (i.e. $p < 0.1$) between life-history traits and PDSI using red (positive correlation) and blue (negative correlation) panel plots for each time lag, where nonsignificant correlations are shown as grey. We used the significance threshold of 0.1 rather than 0.05 because many correlations were on the border of the 0.05 threshold and these relationships, although weaker, are still of ecological interest (Gido et al., 2013). A positive correlation (red) here would indicate that wet periods (positive PDSI) correspond with a particular trait, while a negative correlation (blue) would indicate that dry periods (negative PDSI) correspond with a particular trait. Based on FCA correlation results, we then plotted temporal patterns in the abundance

of opportunistic versus periodic/equilibrium life-history strategists overlaid on temporal trends in the associated hydrologic variables.

3 | RESULTS

3.1 | Fish assemblage surveys

Thirteen fish species were encountered during long-term surveys in LR (1987–2003) and CC (1986–2003). Some sites occasionally did not have fish surveys, including LR1 (2000), LR2 (1990, 2000), LR3 (1990, 1995, 2000) and CC1–CC4 (1989), otherwise surveys were present for each year. All species (Table 1) except for Brook Trout (*Salvelinus fontinalis*) were present in surveys from LR, while only eight were present in CC. Fishes present in CC included Central Stoneroller (*Camptostoma anomalum*), Blacknose Dace (*Rhinichthys atratulus*), Longnose Dace (*Rhinichthys cataractae*), White Sucker (*Catostomus commersonii*), Northern Hogsucker (*Hypentelium nigricans*), Rainbow Trout (*Oncorhynchus mykiss*), Brown Trout (*Salmo trutta*) and Brook Trout. Two species encountered are non-native to the region, including Rainbow Trout and Brown Trout. The six

most abundant species across all surveys in LR accounted for 89% of occurrences and included Mottled Sculpin (*Cottus bairdii*), River Chub (*Nocomis micropogon*), Longnose Dace, Central Stoneroller, Rainbow Trout and Warpaint Shiner (*Luxilus coccogenis*). The five most abundant species across all surveys in CC accounted for 99% of occurrences and included Longnose Dace, Rainbow Trout, Central Stoneroller, Brown Trout and Northern Hogsucker.

3.2 | Hydrologic conditions

Drought conditions for LR ranged from extreme droughts (PDSI < -5) to extremely moist spells (PDSI > 4) during 1985–2003, with periods of little rainfall corresponding with drought periods (Figure 2a). Streamflow in LR showed distinct annual cycles, though maximum and minimum flows had smaller magnitudes during drought periods (Figure 2b). All quantiles tested for GFM were significant (Appendix S1 Table S1) and maps showed periods of constrained precipitation during drought (Figure 2c) that ultimately constrained streamflow (Figure 2d). Wet and dry conditions in CC were more constrained compared with LR, though extreme droughts (PDSI <

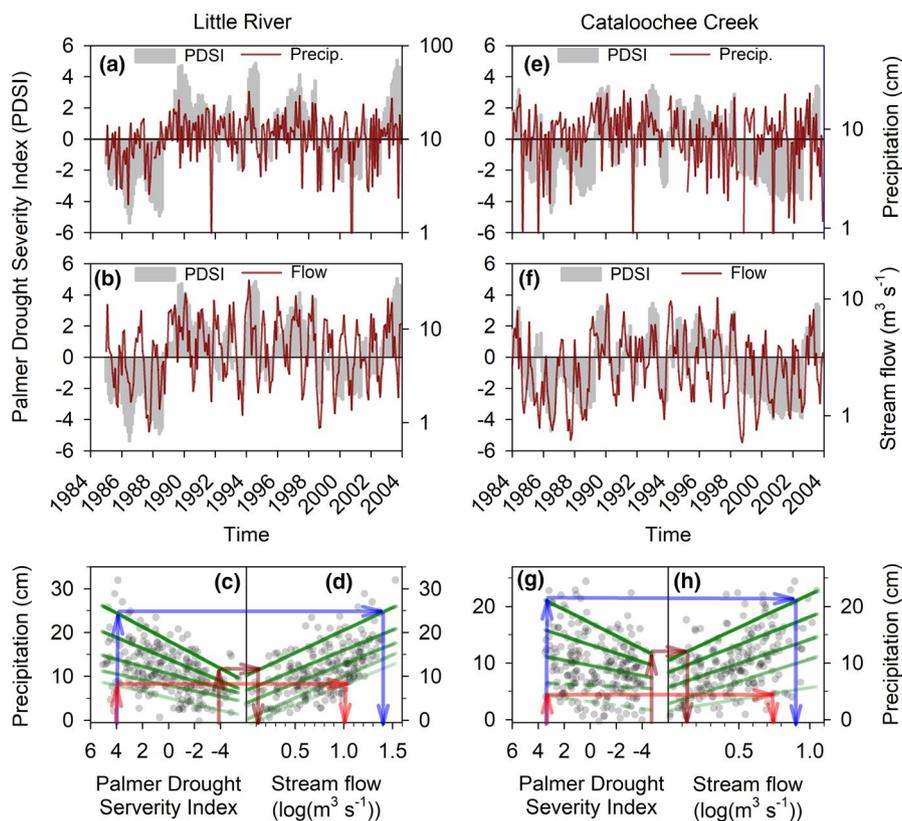


FIGURE 2 Change in monthly Palmer Drought Severity Index (PDSI), precipitation and streamflow in the Little River (a–d) and Cataloochee Creek (e–h) in Great Smoky Mountains National Park during 1984–2004. Time series for (a, e) PDSI and precipitation are based on data from NOAA (2019a, b) and time series for (b, f) streamflow based on data from USGS (2019). Graphical function maps illustrate relationships between PDSI, precipitation and streamflow for (c–d) Little River and (g–h) Cataloochee Creek. Quantile regression lines plotted for 0.10, 0.25, 0.50, 0.75 and 0.90 quantiles are shown as light (0.10) to dark (0.90) green; nonsignificant quantiles are shown as dashed lines. Graphical function maps illustrate drought-induced variation in streamflow as mediated by precipitation for (blue arrows) a rainy year outside of drought (light red arrows) a dry year outside of drought and (dark red arrows) a relatively rainy year during drought. Note y-axes for (a–b) and (e–f) are on a log scale and vary among panels and that (c–d) versus (g–h) y-axis scales differ

-4) and extremely moist spells (PDSI >4) did occur. Precipitation was less in CC compared to LR, including commonly <10 cm/y during drought periods (Figure 2e). Streamflow was also lower in CC compared with LR, including streamflow magnitudes that were reduced during drought (Figure 2f). The two lowest quantiles (0.1, 0.25) for the relationship between PDSI and precipitation were nonsignificant for CC, though all others were significant (Appendix S1 Table S1). The GFM for CC showed constrained precipitation during drought (Figure 2g) that ultimately constrained streamflow (Figure 2h), though slopes for lower quantiles were generally shallower compared with LR.

3.3 | Assemblage ordinations

The NMDS analysis for LR had a two-dimensional stress value of 0.03, indicating it was a representative two-dimensional illustration of assemblage structure (Figure 3a). The first NMDS axis illustrated an upstream (LR1, negative scores) to downstream (LR3, positive scores) gradient in fish assemblage structure. The second NMDS axis illustrated a temporal gradient in fish assemblage structure, and all temporally dynamic hydrology variables that were significantly related to assemblage structure were correlated with this axis (Table 2). Sites that experienced wet periods with large PDSI values one or two years prior and high flows one year prior to fish surveys were positive along the second NMDS axis, while sites that experienced higher precipitation during the survey year were negative along the second axis. Temporal trajectories of individual site scores along NMDS2 illustrated basin-wide fluctuations in fish assemblage structure as drought periods transitioned from wet (positive PDSI, positive NMDS2 scores) to dry (negative PDSI, negative NMDS2 scores) through time, though with a 1- or 2-year time lag (Figure 4a). All sites in LR were consistent with expectations from the loose equilibrium concept, including a majority of return steps for LR1 (71%), LR2 (71%) and LR3 (63%; Appendix S2; Figure S1).

The NMDS analysis for CC had a two-dimensional stress value of 0.09, indicating it was a representative two-dimensional illustration of assemblage structure (Figure 3b). The first NMDS axis illustrated an upstream (CC1, negative scores) to downstream (CC4, positive scores) gradient in fish assemblage structure. The second NMDS axis illustrated a temporal gradient in fish assemblage structure, and the only temporally dynamic hydrology variable significantly correlated with assemblage structure (drought at 1-year time lag) was correlated with this axis (Table 2). Sites that experienced wet periods with large PDSI values one year prior to fish surveys were positive along the second axis. Temporal trajectories of individual site scores along NMDS2 illustrated basin-wide fluctuations in fish assemblage structure as drought periods transitioned from wet to dry through time, though with a 1-year time lag (Figure 4b). Two of the four sites in CC were consistent with the loose equilibrium concept, including return steps the majority of the time in CC1 (67%) and CC4 (56%). The remaining two sites showed indications of directional change, with drought-period samples (1998–2003) distinctly negative along

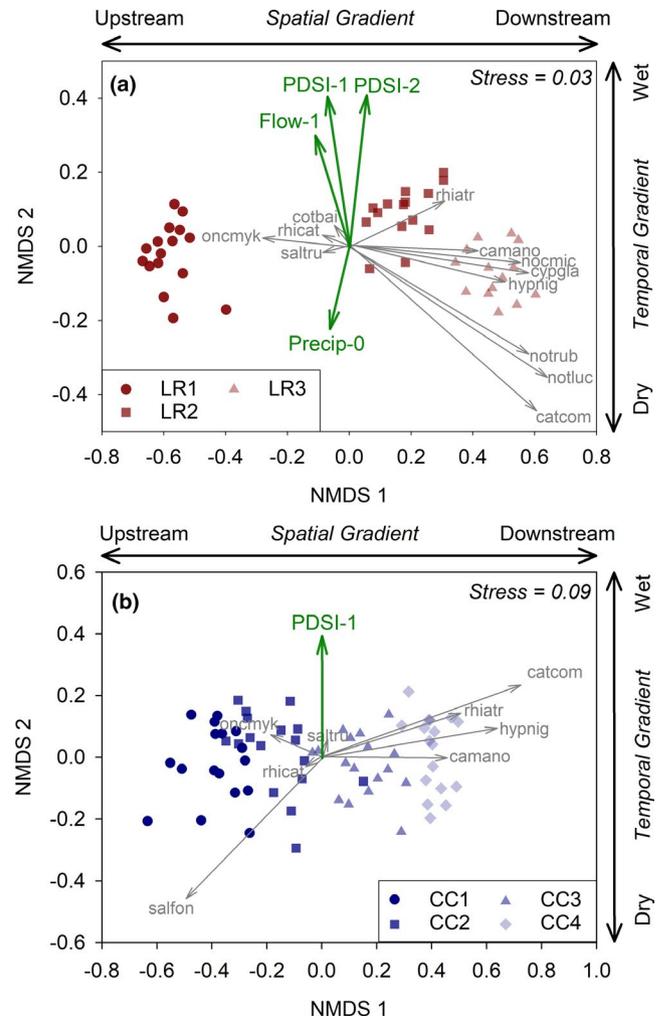


FIGURE 3 Fish assemblage ordinations based on nonmetric multidimensional scaling (NMDS) analyses for (a) Little River sampling sites (LR1-3) and (b) Cataloochee Creek sampling sites (CC1-CC4) in Great Smoky Mountains National Park (see Figure 1 for site locations). Points represent fish assemblage surveys from each site during 1984–2004, grey arrows are species scores (see Table 1 for species codes), and green arrows represent environmental correlates with assemblage structure (see Table 2). Axes represent spatial (NMDS1) and temporal (NMDS2) gradients in fish assemblage structure as labelled along the top and right of each panel

NMDS 2 and return steps a minority of the time for CC2 (44%) and CC3 (44%; Appendix S2 Figure S2).

3.4 | Life-history traits

Life-history traits of fishes collected from GRSM streams spanned gradients in L_{inf} from 12.22 to 57.46 cm, A_{mat} from 1.43 to 4.10 y, and M from 0.31 to 0.96 (Table 1). When ordinated with PCA (Table 3), separation in multivariate space was evident (Figure 5a). The first PC explained 62% of variation in life-history variables, and the second PC explained 20%. Directions of PCA vectors for

TABLE 2 Results of tests for correlations between fish assemblage structure and hydrologic variables representing annual drought (Palmer Drought Severity Index), precipitation (cm/year) and streamflow (m³/s) measurements across three time lags (0 = year of fish surveys, 1 = 1 year prior to fish surveys, 2 = 2 years prior to fish surveys). Variable scores along nonmetric multidimensional scaling (NMDS) axes 1 and 2, correlation with fish assemblage structure (R^2) and significance of correlations (p -value) are shown. Variables with significant correlations are shown in bold

Variable	Little River				Cataloochee Creek			
	NMDS1	NMDS2	R^2	p	NMDS1	NMDS2	R^2	p
Drought lag 0	-0.29	-0.96	0.01	0.78	-0.70	-0.71	0.02	0.58
Drought lag 1	-0.05	1.00	0.19	0.02	-0.11	-0.99	0.13	0.02
Drought lag 2	0.02	1.00	0.18	0.01	-0.05	-1.00	0.07	0.08
Precipitation lag 0	-0.10	-0.99	0.13	0.04	-0.08	-1.00	0.06	0.15
Precipitation lag 1	-0.21	0.98	0.02	0.59	-0.13	-0.99	0.02	0.58
Precipitation lag 2	-0.03	1.00	0.10	0.12	-0.20	-0.98	0.04	0.26
Streamflow lag 0	-0.07	-1.00	0.03	0.51	-0.20	0.98	0.05	0.19
Streamflow lag 1	-0.09	1.00	0.14	0.05	-0.23	0.97	0.01	0.65
Streamflow lag 2	0.01	1.00	0.13	0.06	-0.37	-0.93	0.00	0.98

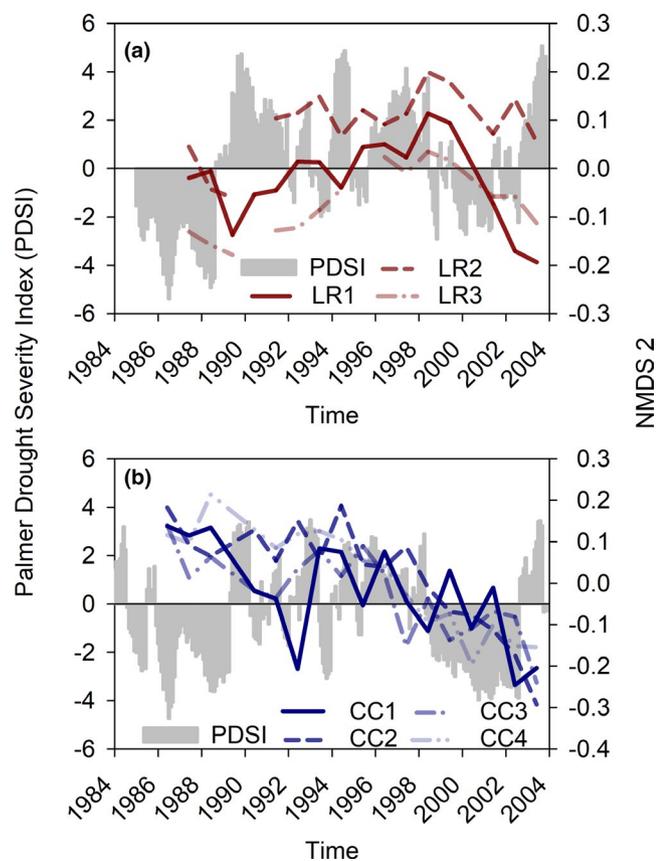


FIGURE 4 Co-plots of Palmer Drought Severity Index (PDSI) and fish assemblage structure measured along the second nonmetric multidimensional scaling (NMDS) axis (see Figure 3) for (a) Little River (LR) and (b) Cataloochee Creek (CC) in Great Smoky Mountains National Park. Grey bars illustrate monthly PDSI values (left y-axis), and lines represent sampling sites scores (right y-axis) through time during 1984–2004

A_{mat} , L_{inf} and M indicated the first PC was primarily a gradient in age at maturity with the “Opportunistic” strategy endpoint positioned negatively, and endpoints for “Periodic” and “Equilibrium”

TABLE 3 Life-history traits, codes and scores along the first two principal component axes (PC) for fish species collected from the Great Smoky Mountains National Park during 1985–2004. See Figure 5a for plot of principal components analysis

Life-history Trait	Code	PC1 Score	PC2 Score
Maximum size (cm)	L_{inf}	0.8482	0.6055
Growth coefficient	K	-0.8978	0.5384
Maximum mass (g)	W_{inf}	0.7892	0.5445
Maximum age (y)	A_{max}	1.0311	-0.3285
Age at maturity (y)	A_{mat}	1.046	-0.1932
Natural mortality	M	-0.8589	0.6723
Size at maturity (cm)	L_{mat}	0.8675	0.6299
Temperature (°C)	T	-0.5095	-0.2196

strategies positioned positively (Figure 5b). The second PC was primarily a gradient in survivorship (negative) versus maximum length (positive). In the broader context of life-history theory, PC1 represented a gradient in species expected to benefit from hydrologic stochasticity being positioned negatively and species expected to benefit from hydrologic predictability being positioned positively.

Fourth-corner analysis revealed correlations among fish assemblages, life-history traits and hydrology for CC but not LR. No significant correlations were detected for any life-history traits in LR (Figure 5c), but all life-history parameters for fishes in CC were correlated with PDSI from the year prior to fish surveys (Figure 5d). In CC, PDSI from the previous year showed significant positive correlations with L_{inf} ($r = 0.05$, $p = 0.02$), W_{inf} ($r = 0.05$, $p = 0.09$), A_{max} ($r = 0.05$, $p = 0.06$), A_{mat} ($r = 0.05$, $p = 0.05$) and L_{mat} ($r = 0.05$, $p = 0.05$), but significant negative correlations with K ($r = -0.05$, $p = 0.06$), M ($r = -0.05$, $p = 0.07$) and T ($r = 0.05$, $p = 0.03$). These correlations aligned with PC 1 in that all life-history parameters with negative correlations were negative along PC 1, and all life-history

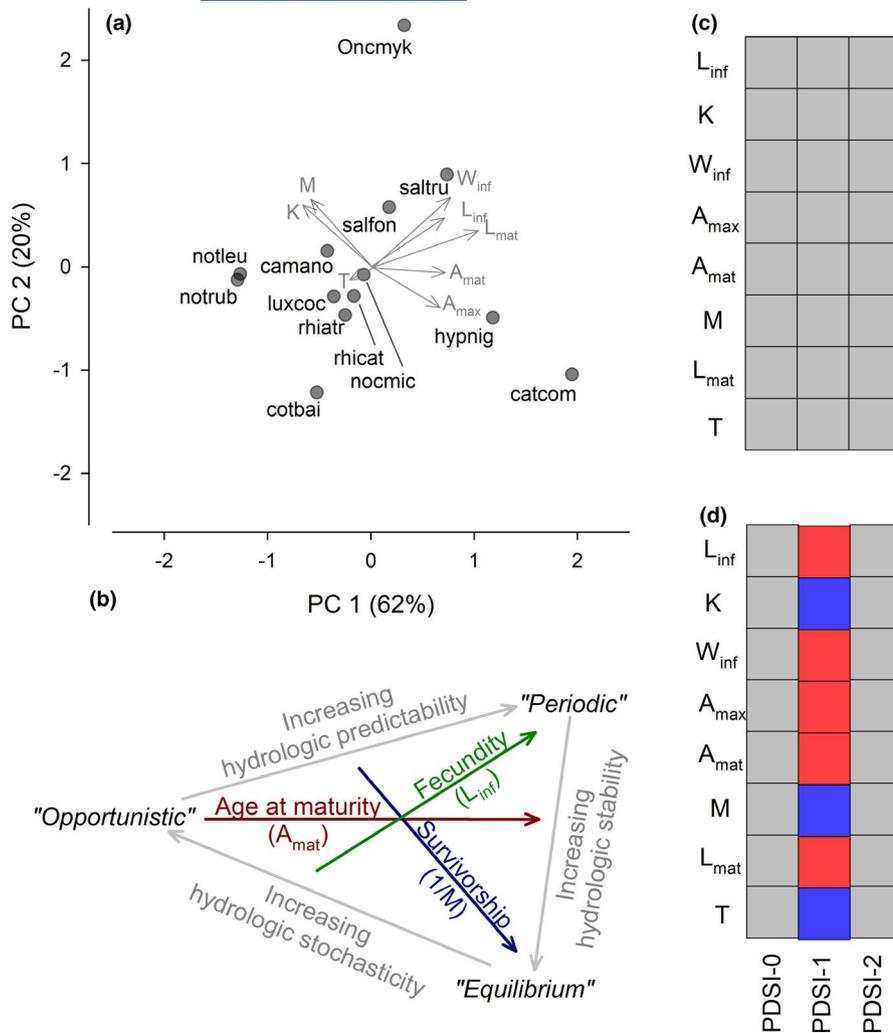


FIGURE 5 Life-history trait analysis for fish assemblages from two streams in Great Smoky Mountains National Park and correlations with drought. (a) Principal component (PC) analysis results illustrating species (six-letter codes defined in Table 1) along latent axes of life-history traits (see Table 1). (b) Patterns from panel (a) shown in the context of life-history strategies defined by Winemiller and Rose (1992). Results of fourth-corner analysis of relationships between fish assemblages, life-history traits and drought measured as Palmer Drought Severity Index (PDSI) measured across three time lags (0 = year of fish survey, 1 = 1 year prior to fish survey, 2 = 2 years prior to survey) for (c) Little River and (d) Cataloochee Creek. (c and d) Grey boxes represent no significant correlation, red boxes indicate significant positive correlations, and blue boxes indicate significant negative correlations between life-history traits and PDSI

parameters with positive correlations were positive along PC 1. Given this finding, we summed the abundances for all fishes with species scores that were negative along PC 1 (considered opportunistic strategists) as well as all fishes with species scores that were positive along PC 1 (considered periodic/equilibrium strategists). Temporal trends in strategist abundances for sites in CC showed dynamic trends with periodic/equilibrium strategists typically outnumbering opportunistic strategists at upstream sites or after periods of drought among the downstream sites (Figure 6). However, during 1997–1998 during the period leading up to a sustained, multi-year drought, opportunistic strategists rapidly increased while periodic/equilibrium strategists steadily decreased at CC1 (Figure 6a), CC2 (Figure 6b), CC3 (Figure 6c) and CC 4 (Figure 6d). Dominance by opportunistic strategists was maintained over the course of the sustained drought during 1998–2003.

4 | DISCUSSION

We retrospectively examined the effects of hydrologic variation on fish assemblages in two perennial riverine systems within a least-disturbed temperate rainforest. Hydrologic conditions measured as

drought severity, rainfall and streamflow all indicated generally wetter conditions in LR compared to CC, though both systems fluctuated between wet and dry periods. Based on the loose equilibrium theory, we hypothesised that fish community structure would fluctuate in association with hydrologic variation but would repeatedly return towards an “average” state through time. Results revealed support for this hypothesis at all three sampling sites in LR and at two of four sampling sites in CC. At the sites supporting the loose equilibrium concept, assemblage structures correlated with drought intensity from the year prior to fish surveys and this correlation manifested as coincidental oscillations in drought intensity and fish assemblage structure. We also hypothesised that fish life-history traits would correlate with drought intensity such that opportunistic strategist abundance would be greater during drought periods while periodic/equilibrium strategist abundance would be greater during wet periods. This hypothesis was supported only in CC, where fourth-corner analysis revealed correlations between life-history traits and drought intensity measured one year prior to fish surveys. Specifically, fishes with faster individual growth rates (K), higher natural mortality (M), younger age (A_{mat}) and smaller length (L_{mat}) at maturity, all characteristic of opportunistic strategists, were more abundant during periods of lower PDSI values (i.e. drought periods).

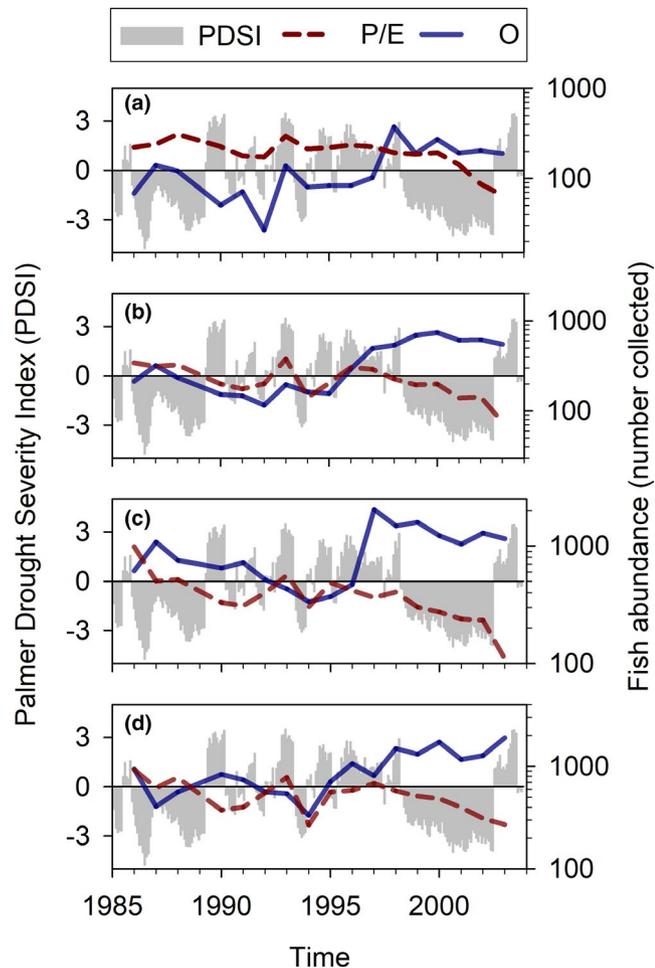


FIGURE 6 Co-plots showing temporal change in monthly Palmer Drought Severity Index (PDSI; grey bars; left y-axis) and annual abundances of fishes with opportunistic (O; solid blue lines; right y-axis) versus periodic or equilibrium (P/E; dashed red lines) life-history strategies at survey sites located on Cataloochee Creek in Great Smoky Mountains National Park. Panels represent sampling sites (a) CC1, (b) CC2, (c) CC3 and (d) CC4 (see Figure 1 for site locations)

Based on this evidence, we hypothesise that fish assemblages at most sites fluctuated within a loose equilibrium as hydrologic conditions oscillated between drought and wet periods; however, severe ($PDSI < -3$) and prolonged (>2 years) drought at some sites in CC filtered life-history traits in favour of opportunistic strategists and contributed to directional change in fish assemblage structure.

Spatiotemporal gradients in fish assemblage structure occurred in both river systems. The stronger spatial gradient in both streams was related to widely reported upstream-to-downstream changes in fish assemblage structure (reviewed in Roberts & Hitt, 2010) associated with the river continuum concept (Vannote et al., 1980). Although spatial variation was not a primary focus of our hypotheses, upstream-to-downstream fish assemblage variation along elevation gradients is reported on a global scale and can influence the abundance and distribution of species and functional traits (e.g. Askeyev et al., 2017; Carvajal-Quintero et al., 2015; Costa et al., 2018). In our study, species richness increased from upstream to

downstream in both systems and larger benthic species (e.g. Central Stoneroller and Northern Hogsucker) were common at downstream sites while salmonids (i.e. Rainbow Trout) were common at upstream sites. Despite these longitudinal differences in assemblage composition, we found temporal trajectories moved in parallel among sites within each stream. Furthermore, temporal changes in the abundances of opportunistic versus periodic/equilibrium strategists occurred consistently among the four sampling sites distributed along the longitudinal gradient of CC. This pattern points to influence by broad-scale or riverscape-scale factors that simultaneously affect all sampling sites and is consistent with previous studies documenting regional or basin-scale effects of hydrologic variation, particularly drought, on stream fish assemblages (Magalhaes et al., 2007; Matono et al., 2012). For example, Magalhaes et al., (2007) found that summer drought correlated with regional changes in fish assemblage structure among Mediterranean streams in Portugal, including concordant changes among stream reaches despite the lack of a consistent spatial pattern in assemblage structure. Another spatial pattern evident in our results was that the magnitude of divergence from the centroid was generally greater at upstream sites in both LR and CC, perhaps indicating headwater streams act as a precursor to directional change downstream if drought intensity and duration are sustained (Appendix S2, Figures 1 and 2). A similar pattern was uncovered by Buisson and Grenouillet (2009), who demonstrated differential responses by fish assemblages to climate change along the upstream-downstream gradient with upstream and midstream assemblages becoming more modified and downstream assemblages becoming more homogenised. In summary, although clear spatial differences in fish assemblage structure existed, synchronised temporal responses to drought occurred across the two riverscapes we studied.

We hypothesised that fish assemblage composition would correlate with hydrologic conditions and assemblage fluctuations would be bound within a loose equilibrium. Previous studies have documented hydrologically induced fish assemblage change over time with assemblages eventually returning to previous states (Matono et al., 2012; Matthews et al., 2013; Mota-Ferreira et al., 2020). As examples, Matono et al. (2012) found that Mediterranean stream fish assemblages showed high resilience to recurrent drought and maintained long-term stability, while Matthews et al. (2013) found that although stream fish assemblages in the Southern Great Plains changed more when a drought occurred between repeated surveys, assemblages still returned to their predrought structure. The results of our tests for loose equilibrium supported these findings for five of the seven sampling sites. Loose equilibrium might be expected because of long-term adaptations by fishes to naturally occurring hydrologic variability (Lytle & Poff, 2004), as previously demonstrated for Appalachian stream fishes (Grossman et al., 2006; Kanno et al., 2017). However, under conditions of nonstationarity (e.g. Poff, 2018) such as increasing drought intensity and frequency, assemblages might be pushed outside the bounds of their historical loose equilibria (Matthews & Marsh-Matthews, 2017; Perkin, 2018) and perhaps towards extinction (Grossman et al., 2016). Magalhaes

et al., (2007) alluded to this point when they suggested that although present-day droughts in Mediterranean streams contribute to subtle changes in fish community structure, future droughts of increased magnitude could result in species declines and altered fish assemblages. Recent studies have demonstrated directional assemblage change caused by failed recruitment and subsequent extirpation during drought (e.g. Perkin et al., 2019), but predicting such change is critical for understanding how future droughts will influence current species. Mounting evidence suggests trait-based approaches are the most promising avenue for generating predictions for ecological responses to future hydrologic scenarios (Wheeler et al., 2018) and our results point to life-history traits as useful for generating such predictions.

Our second hypothesis was that opportunistic species would be dominant during drought while periodic/equilibrium species would be dominant during wetter periods. We tested this hypothesis using a trait-based methodology as recommended by Frimpong and Angermeier (2010), who suggested trait-based research on freshwater fishes could benefit our understanding of how traits might be used to predict responses to environmental change. Trait-based analyses for freshwater fishes were historically limited by data availability (reviewed by Cooke et al., 2012), but meta-analyses and development of trait databases have improved availability of existing data (Frimpong & Angermeier, 2009; Froese, 1990; Pyron et al., 2011). In particular, FishLife (Thorson, 2017) traits were useful for recreating the tri-lateral continuum life-history model (Winemiller & Rose, 1992) for species collected from LR and CC. The tri-lateral continuum of fish life-history strategies is validated as a predictor of fish assemblage response to hydrologic and landscape alteration across multiple continents (Mims & Olden, 2012; Olden & Kennard, 2010; Tedesco et al., 2008), including fish assemblage transformations over ecological timescales ranging 1–4 decades (Mims & Olden, 2013; Perkin et al., 2017). Our work builds on these previous findings by directly correlating fish life-history attributes with drought intensity and demonstrating environmental filtering occurred on an ecological time scale and in the direction predicted by life-history theory. The major correlation with life-history traits in the fourth-corner analysis was along the opportunistic to periodic/equilibrium gradient, but only for CC at a 1-year time lag. Opportunistic fish responded rapidly, even before the PDSI transitioned to drought. This indicates favourable hydrologic conditions were present before PDSI values were classified as a drought, probably because proximal cues detectable by fishes occurred during the transition into drought conditions (e.g. increasing water temperature; Matthews & Berg, 1997). Based on our results, increases in drought intensity and frequency may push higher elevation (>500 masl) fish assemblages outside of their historical loose equilibrium by benefiting opportunistic life-history strategists over periodic/equilibrium strategists. However, this pattern is inconsistent with findings by Chessman (2013) because some fishes with opportunistic life-history traits (e.g. young age at maturity, small size) in the Murray–Darling Basin in Australian were most vulnerable to drought. This inconsistency suggests contexts surrounding the natural flow regime of focal systems and the nature

and intensity of drought are important considerations for predicting life-history-based responses to drought (Lennox et al., 2019).

Our work includes caveats and limitations that should be considered when interpreting the results. First, although our data spanned multiple decades, the temporal extent of the collections was still limited compared to the tempo of drought oscillations. Our study utilised data spanning two decades that captured several short-term hydrologic extremes, but long-term data sets are necessary to adequately predict fish assemblage response to persistent climate change (Paukert et al., 2017). Over a broader temporal extent, the “average condition” used to test for loose equilibrium will undoubtedly change and potentially affect conclusions regarding directional change (e.g. as pointed out by Perkin, 2018). Whether sites in CC have returned towards a loose equilibrium in the years since 2004 could be tested with additional data points in the future. We suggest continuation of long-term sampling is necessary to address this need as well as other data needs related to species distribution modelling (Feeley & Silman, 2011). Second, our data analysis focused on broad-scale measures of hydrologic variation, but fine-scale data on water temperature or water quality (e.g. pH) are needed to uncover the mechanism for fish response to drought (Lennox et al., 2019). For example, Harmon et al., (2020) showed that long-term changes in stream acidification can influence fish assemblage structure, and the effects of drought on water quality and biogeochemistry are still being uncovered (Gómez-Gener et al., 2020). Third, our analyses focused on relationships between abiotic variables and fish community structure and did not focus on species interactions that might have been altered simultaneously. Predator–prey interactions and inter- or intra-specific competition likely changed during periods of drought given potential for higher densities of fish during low flow periods. Also, if predatory periodic/equilibrium strategists declined early during the onset of drought, then it could have released opportunistic prey species from predatory suppression (e.g. Power et al., 2008). A fourth caveat is that traits for some species could only be predicted at the family or genus level in our analysis of life-history traits because of limited data (Thorson, 2017). Even among species for which life-history information is known, some species may exhibit life-history trait plasticity in response to drought and the extent to which this plasticity affects model predictions is unknown (Glarou et al., 2019). Finally, our models did not specifically consider the effects of changes in capture efficiency across high versus low flow conditions, though our use of triple-pass depletion is one method commonly used to guard against the effects of imperfect detection (Gwinn et al., 2016; Habera et al., 2010; Peoples & Frimpong, 2011).

Conservation and management of freshwater ecosystems requires consideration of ecological and societal water needs given competition for this limited resource is likely to become exacerbated under a changing climate (Cassardo & Jones, 2011). Although climate change is expected to decrease functional diversity and result in homogenisation of fish assemblages (Buisson et al., 2013), predicting where and when such alterations are likely to occur is critical for informing management actions aimed at maintaining freshwater ecosystem integrity (Segurado et al.,

2016). Though there is still much uncertainty about how climate change will affect hydrology and how hydrology in turn will influence the ecology of stream ecosystems (Buisson & Grenouillet, 2009), there is potential for hydrologic extremes to increase in frequency and magnitude in the future (Jackson et al., 2001; Wu et al., 2014). Our work provides evidence for how fish assemblages might respond to increased drought severity and if these predictions hold true, fish assemblages will be altered by a warmer and drier climate (Lennox et al., 2019). Although fish assemblages can be resilient and ultimately resist directional change by remaining within a loose equilibrium during short-term drought (Matthews & Marsh-Matthews, 2003), large-scale climate change will likely lead to reduced or novel assemblages through directional change (Matono et al., 2012).

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DATA AVAILABILITY STATEMENT

All data used in this manuscript are publically available at the links provided in data references, including the precipitation data (NOAA, 2019a), drought data (NOAA, 2019b), streamflow data (USGS, 2019) and fish data (NPS, 2021).

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