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Spatiotemporal dynamics of intermittent stream fish metacommunities in response to prolonged drought and reconnectivity

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Abstract. Hydrological regimes are primary drivers of community structure and dynamics in streams with strong seasonal or annual flood and drought cycles. In the current study, we investigated the dynamics of fish metacommunities in two intermittent streams (Hickory Creek and Clear Creek) in north Texas, USA, by examining changes in diversity, abundance, assemblage structure and temporal stability associated with prolonged seasonal drought and reconnectivity. Diversity (α and γ), abundance and stability increased with initial isolation during summer drought but dramatically declined as drought or drying persisted through the winter (November–December). During post-drought reconnectivity in Hickory Creek, diversity and abundance increased and approached pre-drought levels. Abundance and body size varied greatly among species and indicated species-specific responses (i.e. mortality, recruitment, dispersal) to hydrologic fragmentation and connectivity. Ultimately, assemblage structures were significantly altered by drought in Hickory and Clear creeks, and despite a trend towards recovery in Hickory Creek, assemblages did not fully recover during the present study. Intermittent-stream fishes may be generally adapted to natural drought dynamics; however, climate change and human-mediated habitat alterations may result in prolonged and intensified drought conditions that exceed many species mechanisms of resistance or resilience having potentially large impacts on biodiversity across spatial and temporal scales.

Additional keywords: disturbance, fragmentation, isolation, refugia, resilience, species sorting.

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Introduction

Ecosystems worldwide are under increasing pressure from anthropogenic habitat alterations and climate changes, which have resulted in reduced, degraded, or fragmented ecological landscapes (Fahrig 2003; Bellard *et al.* 2012). Because many organisms must periodically move among habitats in order to fulfil various life-history requirements, temporal and spatial patterns of connectivity and fragmentation are increasingly recognised as critical factors that influence community dynamics and biodiversity at both local and regional scales (Leibold *et al.* 2004; Swan and Brown 2011). Not surprisingly, negative impacts of habitat loss and fragmentation have been widely reported for nearly all ecosystem types (Fahrig 2003; Fischer and Lindenmayer 2007). Fluvial ecosystems, in particular, have experienced dramatic changes in habitat connectivity as a result of modifications to flow regimes at multiple scales from impoundments, road crossings, water abstraction and diversion, and climate change (Poff *et al.* 1997; Bunn and Arthington 2002; Fagan 2002). Concomitantly, native freshwater biodiversity has experienced widespread declines over the past century (Ricciardi and Rasmussen 1999; Dudgeon *et al.* 2006).

Among lotic ecosystems, intermittent streams experience recurring fragmentation because of seasonal and aseasonal

fluctuations in precipitation and temperature, which often result in intense flood and drought disturbances (Larned *et al.* 2010; Lake 2011). The often extreme temporal variation in hydrology of intermittent streams imposes strong selective pressures on stream biota (Poff 1997), such that many species possess evolved traits, which provide a degree of resistance or resilience to natural hydrological disturbances (Dodds *et al.* 2004; Lytle and Poff 2004). Thus, the structure of intermittent-stream assemblages often fluctuates in response to hydrological variation and reoccurring fragmentation and reconnectivity (Matthews 1988). However, the magnitude of population or community change (e.g. abundance, richness, composition) and the time it takes for populations and communities to recover from changes in hydrology depend on the intensity, timing and duration of hydrological periods and disturbances. Under normal conditions (i.e. within some threshold of natural environmental variability), post-disturbance assemblages should theoretically recover to their pre-disturbance states (Grossman *et al.* 1998; Magalhães *et al.* 2007; Matthews *et al.* 2013).

Collectively, intermittent and small-order streams comprise a considerable portion of watershed stream length, discharge and the interaction between terrestrial and aquatic habitats, as well as harbor high proportions and unique components of

aquatic biodiversity (e.g. endemics or highly adapted species; Meyer *et al.* 2007; Larned *et al.* 2010; Acuña *et al.* 2014). Current and future changes in global climate, coupled with continued or intensified human habitat alteration and pressure on freshwater resources, will likely exacerbate hydrological extremes by increasing the frequency, intensity and spatial extent of drought conditions, fragmentation and intermittency (Dai 2011; Melillo *et al.* 2014). Intensified, widespread and novel hydrological regimes may exceed many species' mechanisms of resistance and resilience, having potentially large consequences for biodiversity (Matthews and Marsh-Matthews 2003; Dodds *et al.* 2004; Lake 2011).

The current study investigates the dynamics of intermittent-stream fish metacommunities in response to seasonal hydrological conditions and the impacts of and recovery from intense drought and fragmentation. Using a spatially structured sampling design and detailed field surveys over 16 months (including before, during and after seasonal drought), we tested the following hypotheses: (1) seasonal drought impacts fish assemblages by reducing species richness and abundances at local (α -diversity) and regional (γ -diversity) scales and increasing variation among local assemblages (increasing β -diversity), (2) assemblage structure (i.e. species richness, composition and abundance) during post-drought periods would recover (be similar) to pre-drought levels and (3) temporal stability of local assemblages would be lower during connected hydroperiods, as individuals would be able to move among patches, and higher during the drought owing to fragmentation (though this pattern is expected to break down as drought conditions intensify over time and sensitive species are lost).

Materials and methods

Study area

The present study was conducted in two intermittent streams in the southern Great Plains ecoregion of North America. Hickory Creek (watershed area 334 km²) and Clear Creek (764 km²) are tributaries of the Elm Fork River in the upper Trinity River Basin in north-central Texas, USA (Fig. 1a, b). Both streams intermittently flow south-east through agricultural, pastoral and sub-urban landscapes before emptying into a large municipal reservoir (Lake Lewisville) near Denton, Texas. The study sites on Hickory Creek (33°11'59"N, 97°12'50"W) are generally characterised by narrow channels (<10 m at bankfull), alternating riffle-pool habitats, predominantly gravel, cobble and detrital substrates, and mostly intact riparian vegetation and canopy. Clear Creek sites (33°20'1.82"N, -97°10'59"W) are characterised by slightly wider and shallower channels, sandy runs punctuated by gravel or bedrock riffles, and larger pool habitats. Despite these general differences, stream sites at Hickory Creek and Clear Creek were originally chosen and treated as replicates. Hydrologic conditions of small streams in the southern Great Plains are naturally dynamic owing to mid-continental weather patterns that result in seasonal drought or fragmentation and frequent yet unpredictable flooding (Dodds *et al.* 2004).

Fish sampling

Fishes and stream habitats were surveyed monthly from February 2012 to May 2013 on Hickory Creek and from

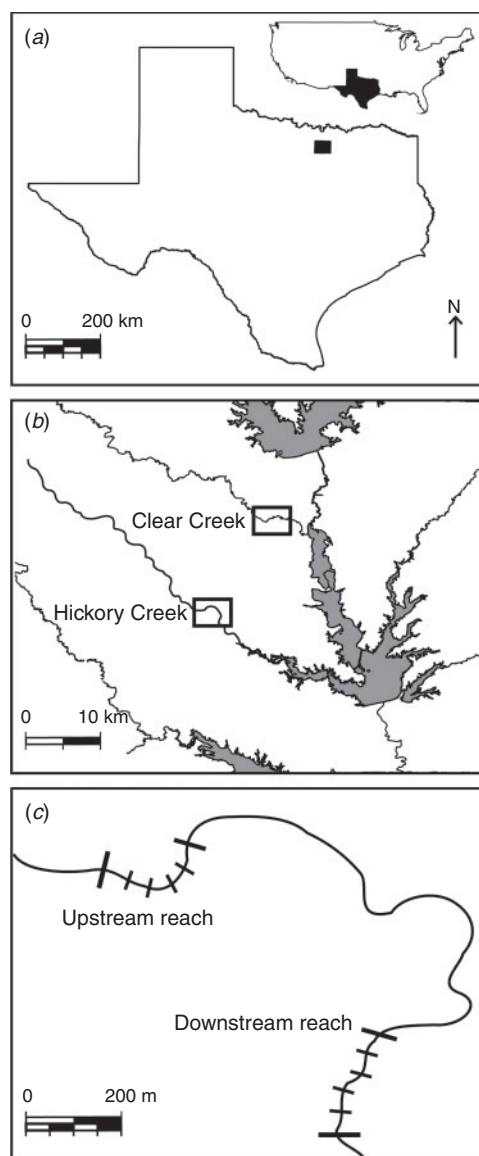


Fig. 1. Location of study streams in north-central Texas, USA (a), and configuration of study sites at the stream-scale, reach-scale and 50-m sections (b–c).

February 2012 to March 2013 on Clear Creek (sampling was terminated earlier on Clear Creek owing to near-complete desiccation and lack of return flows). Sampling locations at both Hickory and Clear creeks consisted of a hierarchical design with sample sections (local sites or patches) nested within reaches (upstream and downstream) and streams (Hickory and Clear creeks), allowing for evaluation of community structure at multiple scales. Sampling localities at each stream consisted of two disjunct reaches (designated by their upstream or downstream position), each 250 m in length, separated by a distance of ~1 km along the course of the river (Fig. 1c). Each reach was then subdivided into five adjacent 50-m sections, and each section included riffle-run-pool macrohabitat types. The hierarchical scale used in the current study was based on previous field surveys and reconnaissance, which indicated that isolated

pool refugia during drought in both Hickory and Clear creeks are generally small (<50 m) and the distance between refugia varies from a few to a few hundred metres. As such, the sampling design appropriately captures the natural scale of drought-induced fragmentation for these low-order intermittent streams.

Fish communities were sampled from all available macrohabitats from each 50-m section by two consecutive passes with a backpack electrofisher (Smith-Root LR-24, pulsed DC output; Smith-Root, Vancouver, WA, USA) and multiple seine hauls (4.6 m × 1.8 m × 4.8-mm seine). Electrofishing consisted of one operator and two netters moving from downstream to upstream. Seining techniques varied depending on stream conditions and targeted habitats, including seine hauls parallel and perpendicular to stream flow or stationary kick sets in riffles or around habitat structure. During periods of connectivity, mesh block nets were used to prevent fish from moving to adjacent sections while sampling.

For each stream section, fishes were quantified separately for electrofisher pass 1, pass 2 and as a cumulative seine sample. Fishes were identified to species (or to genus when species level identification in the field was confounded between similar species, e.g. *Fundulus olivaceus* v. *Fundulus notatus*, or young of year, e.g. *Lepomis*) and a random subset of individuals of each species was measured for total length in the field (cm TL; up to 30 individuals per species for each sample method). Once processed, all individuals were allowed to recover and then released alive within the stream section from which they were captured.

Habitat measurements

Habitat variables were measured at five permanent transects within each 50-m stream section, with transects set at 10-m intervals and 5 m from both the upstream and downstream section boundaries. Stream depth (m), dissolved oxygen (DO; mg L⁻¹), temperature (Temp; °C), flow (m s⁻¹) and substrate were measured at evenly spaced points along each transect (maximum of 5 points). Substrate composition was evaluated by the dominant substrate type at each point: mud or silt (MS; <0.06 mm); sand (S; 0.06–2 mm); gravel (G; >2–60 mm); cobble (C; 6–25 cm); boulder (B; >25 cm); bedrock (BR); compacted clay bedrock (CBR); or organic detritus (D; [Texas Commission on Environmental Quality 2007](#)). An index of substrate diversity (Sub.Div) was calculated from the relative proportions of each substrate type from each stream section using the inverse of Simpson's diversity. Specific conductivity (Cond.; µS) and pH were measured at the midpoint of each transect. Canopy cover was measured at four points at each transect (left bank facing left, midpoint facing left and right, and right bank facing right; [Texas Commission on Environmental Quality 2007](#)) with a convex densiometer (Forest Densiometers, Bartlesville, OK, USA). Macrophytes (Macro), algae, woody debris (Woody) and undercut bank (Undercut) were evaluated along a swath 3 m up- and downstream of each transect. The relative abundance of macrophytes and algae were categorically assessed as absent (0% coverage), rare (<25%), common (25–75%), or abundant (>75%) and assigned numeric dummy variables (0–3 respectively). Woody debris and undercut bank were evaluated as a percentage of cover along each transect

and on both banks. Additionally, we generated an index of site connectivity (0, 0.5, 1) for each section during each month by counting the proportion of connected adjacent sections. For example, (i) connectivity of sections connected to both adjacent upstream and downstream sections = 1; (ii) sections connected to only one adjacent section = 0.5; and (iii) completely isolated sections = 0. The relative proportions of pool, run, riffle and dry macrohabitats were assessed for each section. Transects and sections that were completely dry or without habitable surface water were recorded as 'dry' and no data were collected. For pools that were very small or were between permanent transects, additional or supplemental measurements were taken.

Prior to statistical analysis, the mean and coefficient of variation (CV) were calculated for each habitat variable, as well as minimum (Min) and maximum (Max) flow velocity and the presence or absence (PA) of flow, undercut bank and woody debris for each stream section.

Data analyses

Principal components analysis (PCA) was used to compare stream habitat variables among sample sites and over time. Habitat data from each stream were standardised using z-scores before analysis and broken-stick models were used to identify relevant axes for interpretation ([Peres-Neto et al. 2005](#)). To determine if environmental habitat variables differed significantly among defined hydro-periods (pre-drought, drought and post-drought), multivariate analysis of variance (MANOVA) was performed using site scores from the first two PCA axes as dependent variables and stream hydro-period as the categorical predictor variable. Hydro-periods were defined by sampling months that contained connected or flowing conditions versus isolated stream pools: (i) pre-drought = sample months occurring before isolation of pools in Hickory or Clear creeks; (ii) drought = sample months falling between first isolation of pools and return of connectivity; or (iii) post-drought = sample months following return of connectivity. Post-hoc analysis (Tukey HSD) tested for significant pairwise differences in environmental variables (PC scores) between each of the three hydro-periods for Hickory Creek (only two hydro-periods were present for Clear Creek because of the lack of return flows).

To test our hypotheses related to hydro-period and drought disturbance on fish diversity, we partitioned diversity among measures of α , γ and β -diversity. α -diversity is the mean local species richness calculated across local stream sections from each month. We used two different metrics of α -diversity: α_0 and α_x . α_0 was calculated using local species richness values from all stream sections from both upstream and downstream reaches (10 sections total), including dry sections with richness = 0. α_x was calculated using local species richness from only wetted stream sections where richness > 0. γ -diversity is the total number of species summed across all sampled sections from the same stream during the same month (i.e. regional diversity). The relationship between local and regional species richness was assessed using Whittaker's measure of β -diversity ($\beta = \gamma/\alpha$). β -diversity was calculated using both α_0 and α_x , and is represented as β_0 and β_x respectively. Diversity measures calculated with and without dry sites are complementary and represent landscape (including temporally unsuitable or

uninhabited patches) and metacommunity perspectives (Wine-miller *et al.* 2010).

Temporal change in total abundance and density was assessed using the summed abundance of all species sampled during each month. Species-specific change in mean abundance among hydro-periods was calculated using the summed abundance of each individual species during each month divided by the number of months within each hydro-period. Analysis of variance (ANOVA) and Tukey HSD were used to test for significant changes in abundance of each species among and between hydro-periods. Density (fish m^{-3}) was calculated using total and individual species abundance divided by total monthly stream volume. Mean body size (TL) of each species was calculated from all measured individuals from each hydro-period and ANOVA was used to test for temporal differences among hydro-periods.

Non-metric multidimensional scaling (NMDS) was used to compare general spatial patterns of fish assemblage structure between Hickory and Clear creeks, and to compare assemblage structure among hydro-periods within each creek. Permutational multivariate analysis of variance (PERMANOVA) was performed to test for differences in assemblage structure between streams, and among hydro-periods and reaches within each creek. Prior to analysis, species abundance matrices were $\log(x+1)$ transformed and then NMDS was performed using the Bray–Curtis index to ordinate assemblages from each stream section in two dimensions. To test for temporal assemblage stability we calculated the mean similarity of assemblages between each pair of adjacent sampling months (e.g. May+June, June+July) using both Bray–Curtis and Jaccard's similarity values. Bray–Curtis similarities were generated using $\log(x+1)$ transformed abundances and Jaccard's similarities were generated using species presence–absence. This analysis using Bray–Curtis is analogous to the mean pair-wise distances among monthly samples (i.e. centroids) in the NMDS ordination. Significance of statistical tests was assessed at $\alpha=0.05$, and from 999 permutations for PERMANOVA. PERMANOVA was performed using the PERMANOVA+ package in the software program PRIMER-E, version 6 (Primer-E Ltd, Lutton, UK; Anderson *et al.* 2008). All other statistical analyses were performed in R, version 3.0.1 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Seasonal climate patterns resulted in fluctuations in hydrological conditions for both Hickory and Clear creeks (Fig. 2a–e). In Hickory Creek, late winter and spring rains resulted in stream connectivity or periodically flowing conditions from February to May 2012 (pre-drought hydro-period) and again in January–May 2013 (Post-drought; Fig. 2a). Fragmentation or drought conditions occurred in Hickory Creek from June to December 2012 (Drought, ~203 days). Although connectivity was restored on Hickory Creek (post-drought hydro-period), flowing conditions (i.e. discharge) were present only 23% of the days during the post-drought hydro-period, compared with 78% flow days during the pre-drought hydro-period for Hickory Creek. In Clear Creek, connectivity and periodic flow occurred only during February–May 2012 (i.e. pre-drought), and fragmentation or

drought conditions persisted uninterrupted from June 2012 to May 2013 (~295 days; Fig. 2c).

Environmental variables in both creeks followed significant seasonal or temporal gradients among or between hydro-periods for each creek (Pillai's trace: $F_{2,98}=22.499$, $P<0.001$ and $F_{1,73}=155$, $P<0.001$ for Hickory and Clear creeks respectively; Fig. 2b; Table 1; see Fig. S1 of the Supplementary material). Pairwise comparisons for Hickory Creek were significant between each hydro-period for PC1 (PR \times DR: $P<0.001$; PR \times PO: $P<0.001$; DR \times PO: $P<0.001$), and pre-drought conditions were significantly different from drought (PR \times DR: $P=0.010$) and post-drought conditions (PR \times PO: $P=0.005$) on PC2 (Fig. 2b). For Clear Creek, pre-drought and drought hydro-periods were significantly different for both PC1 ($F_{1,73}=304$, $P<0.001$) and PC2 ($F_{1,73}=6.72$, $P<0.011$; Fig. 2d). For both Hickory and Clear creeks, pre-drought conditions were strongly associated with metrics of greater habitat size, connectivity and flow, as well as greater proportion of riffle and run habitats for Hickory Creek and greater substrate diversity and DO for Clear Creek, and were represented by negative values on PC1 for both ordinations. Drought conditions were characterised by increased proportion of dry habitats (98 and 99% reduction in total stream volumes for Hickory and Clear creeks respectively), and increased variability in temperature (range 3–35°C and 2–38°C) and DO (range <1–12 mg L^{-1} for both), and were represented by more positive values on PC1 for both ordinations. For both streams, post-drought conditions were represented by intermediate values on PC1 and variation among post-drought sites represents transitional environmental conditions, which occurred as connectivity was restored. PC2 distinguished environmental conditions at the transitions between hydro-periods and between early (summer) and late (autumn or winter) drought primarily associated with macro-habitat availability (i.e. deeper pool habitats with woody debris at positive values on PC2 and shallower macrohabitats with or without flow on negative values of PC2).

A total of 26 181 individuals was collected from both Hickory and Clear creeks across all sampling months, representing 31 taxa and 11 families (see Table S1 of the Supplementary material). The families Centrarchidae, Cyprinidae and Ictaluridae were the most common across both streams with nine, six and five taxa respectively. Clear Creek was more diverse (31 taxa) and had higher total abundance of fishes collected ($n=16\,445$) than Hickory Creek (26 taxa, $n=9736$). Taxa collected in Hickory Creek comprised a subset of those collected in Clear Creek, and the taxa only collected in Clear Creek represented rare or transient taxa (1% total abundance). Assemblages from both streams were characterised by several common species including western mosquitofish (*Gambusia affinis*), longear sunfish (*Lepomis megalotis*), green sunfish (*Lepomis cyanellus*), red shiner (*Cyprinella lutrensis*) and topminnow (*Fundulus* spp.), which accounted for 62 and 70% of total fish abundances in Hickory and Clear creeks respectively.

Patterns of α , β and γ -diversity varied over time and differed depending on the inclusion or exclusion of dry sections in the analyses, but temporal patterns were generally similar between creeks (Fig. 3). In Hickory Creek, α_0 and γ -diversity were both high and β_0 -diversity was low during pre-drought (Fig. 3a). With the onset of drought, α_0 -diversity declined steadily from

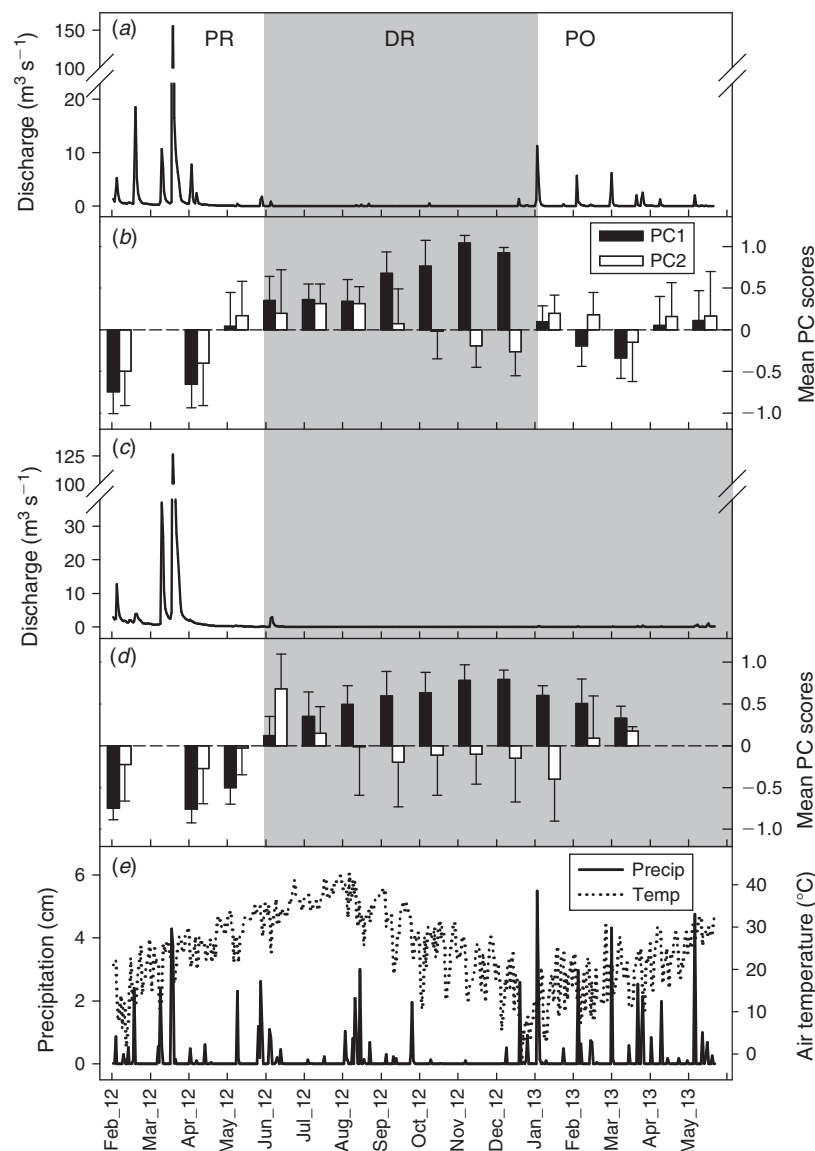


Fig. 2. Mean daily discharge and mean PC scores for Hickory Creek (a, b) and Clear Creek (c, d), and regional precipitation and air temperature (e). Discharge data are from USGS gage stations located at or near stream sites (Hickory Creek – 08 052 780; Clear Creek – 08 051 500); mean PC scores are the mean (± 1 s.d.) of all sample scores for each stream during each sampling period (see the full PCA in Fig. S2, Supplementary material); precipitation data are from the Denton Municipal Airport located near the study sites. Shaded areas signify boundaries between pre-drought (PR), drought (DR) and post-drought (PO) hydro-periods.

June to December, γ -diversity remained stable through October but declined sharply in November and December, whereas β_0 -diversity increased gradually through October and sharply in November and December. During the post-drought, α_0 and γ -diversity increased and β_0 -diversity decreased steadily through May 2013, with each approaching values observed during pre-drought. Conversely, α_x in Hickory Creek increased and remained stable through October before decreasing in November and remaining low through post-drought, whereas β_x remained low and relatively stable over time (Fig. 3b). In Clear Creek, α_0 and γ -diversity increased and β_0 -diversity

decreased during pre-drought. Similar to Hickory, with the onset of drought in Clear Creek, α_0 -diversity declined steadily, γ -diversity increased through September and then declined sharply beginning in November, whereas β_0 -diversity increased steadily through February (Fig. 3c). In contrast, during drought α_x remained fairly stable through October but declined markedly from November to January, whereas β_x was stable over time (Fig. 3d).

Total fish abundance and density (Fig. 4) differed among hydro-periods, with the magnitude of changes in abundance and body size varying among species (see Supplementary material

Table 1. PCA axis loadings of environmental parameters for Hickory Creek and Clear Creek

CV, coefficient of variation of the associated environmental variable; Sub. Div, substrate diversity index; DO, dissolved oxygen; PA, presence-absence of associated environmental variable; Cond, specific conductivity; Macro, macrophyte; Undercut, undercut bank; Woody, woody debris; Avg./Min./Max.Flow, mean, minimum and maximum flow velocities (see Material and methods). Environmental factor loadings correspond to Fig. S1

Environmental factor	Hickory Creek		Clear Creek	
	PC1 24.80%	PC2 13.60%	PC1 29.00%	PC2 12.50%
Pool	0.120	0.909	0.091	1.182
Run	-0.439	-0.771	-0.658	-0.542
Riffle	-0.692	-0.352	-0.605	-0.519
Dry	0.830	-0.112	0.935	-0.448
Connectivity	-0.865	-0.193	-0.998	-0.065
Length	-0.832	0.119	-0.963	0.479
Width	-0.780	0.220	-1.001	0.068
CV.Width	0.063	0.593	0.235	0.615
Depth	-0.713	0.565	-0.743	0.359
CV.Depth	-0.162	0.138	-0.302	0.592
Area	-0.929	0.171	-1.063	0.141
Volume	-0.906	0.348	-0.862	0.274
Sub.Div	-0.023	0.340	-0.397	-0.096
DO	-0.557	-0.390	-0.612	-0.265
CV.DO	0.701	0.340	0.603	0.419
Temp	0.173	0.219	-0.080	0.480
CV.Temp.	0.522	0.221	0.521	0.147
Avg.Flow	-0.636	-0.666	-0.796	-0.646
CV.Flow	-0.576	0.200	-0.735	-0.076
Max.Flow	-0.760	-0.511	-0.829	-0.609
Min.Flow	0.406	0.227	0.484	-0.001
Flow.PA	-0.879	-0.245	-1.022	-0.408
Cond	0.435	0.357	-0.006	-0.394
CV.Cond	0.564	-0.220	0.197	0.611
pH	-0.521	-0.468	-0.248	0.484
CV.pH	0.186	-0.162	0.231	0.375
Canopy	-0.120	0.736	-0.259	0.175
CV.Canopy	0.104	-0.667	0.255	-0.431
Algae	0.149	0.020	-0.097	-0.773
Macro	-0.227	0.506	-0.170	-0.695
Undercut	-0.451	0.615	-0.597	0.339
CV.Undercut	-0.497	0.516	-0.635	0.409
Undercut.PA	-0.529	0.647	-0.740	0.380
Woody	0.137	0.027	0.055	0.687
CV.Woody	-0.169	0.842	-0.389	0.552
Wood.PA	-0.241	0.824	-0.498	0.802

Tables S2–S5). In Hickory Creek, total fish abundance increased slightly during the early onset of drought, then declined by ~80% during the late autumn and winter drought months to less than 200 individuals remaining in December 2012 (Fig. 4a). However, total fish abundance recovered fairly quickly during the post-drought period, with a 700% increase (from <200 to >1600 individuals) from January to May 2013. Density increased with the onset of drought and increased dramatically in October before falling precipitously to pre-drought levels by January. In Clear Creek, total fish abundance increased during pre-drought and early summer drought, peaking in July 2012 at nearly 4000 individuals (Fig. 4b). However,

abundances declined by ~95% between August 2012 and March 2013 to just over 200 total individuals remaining. Similar to Hickory, total density in Clear Creek peaked in October and declined to near pre-drought levels in January, even without the return of flows. For both streams, despite higher densities during drought for many species (especially topminnow, mosquitofish and bass (*Micropterus* spp.) and all sunfish species (*Lepomis* spp.)), only topminnow, mosquitofish and bass actually increased in abundance during drought in Hickory Creek (and similarly for Clear Creek with the addition of a few transient species; see Supplementary material Tables S2, S3 and Fig. S2).

Assemblage structure (i.e. species composition and relative abundances) was significantly different between Hickory and Clear creeks (PERMANOVA: $F_{1,179} = 27.416$, $P < 0.001$; Fig. 5a). In Hickory Creek, fish assemblage structure varied significantly among hydrological periods (PERMANOVA: $F_{2,100} = 11.62$, $P < 0.001$, Fig. 4b) and between each pairwise comparison of (PR × DR: $t = 3.69$, $P = 0.002$; PR × PO: $t = 3.29$, $P = 0.002$; DR × PO: $t = 2.95$, $P = 0.002$; Fig. 5b). Similarly in Clear Creek, fish assemblages differed significantly between pre-drought and drought hydro-periods (PERMANOVA: $F_{1,74} = 7.37$, $P < 0.001$; Fig. 5c).

For both creeks, comparison of fish assemblage structure between adjacent sampling months showed generally lower temporal stability (i.e. low similarity, high turnover) among local assemblages during periods of connectivity (i.e. pre- or post-drought) compared with drought, although this pattern was stronger for Hickory Creek (Fig. 6a–b). During drought, temporal stability was fairly stable during the summer months (i.e. high similarity, low turnover), but decreased from October to November in Hickory Creek and from November to January in Clear Creek due to accumulating species loss, then increased again as fewer additional species were lost during the remaining drought months in each creek.

Discussion

Hydrological regimes are primary drivers of community structure and dynamics in fluvial systems, particularly in intermittent streams with strong seasonal or annual flood and drought cycles (Poff and Ward 1989; Larned *et al.* 2010). In the present study we detailed the spatiotemporal dynamics of fish metacommunities in two intermittent streams during pre-drought, drought and post-drought hydro-periods. Measures of fish diversity, abundance, density, body size, assemblage structure and assemblage stability in Hickory and Clear creeks responded strongly among and within hydrological periods, particularly as streams transitioned between connected and isolated periods (and vice versa). As expected, fish diversity and abundance were ultimately reduced during drought, but the effects of summer drought on fishes were fairly benign, whereas severe declines occurred as drought continued into autumn and winter in Hickory Creek and the following spring in Clear Creek. Within the general trend in abundance, the direction and magnitude of changes varied among species, with some common species (i.e. red shiner, redfin shiner) showing large negative impacts during drought coupled with slow or limited recovery during the post-drought hydro-period whereas others (i.e. mosquitofish, bass) increased in abundance during drought and into post-drought.

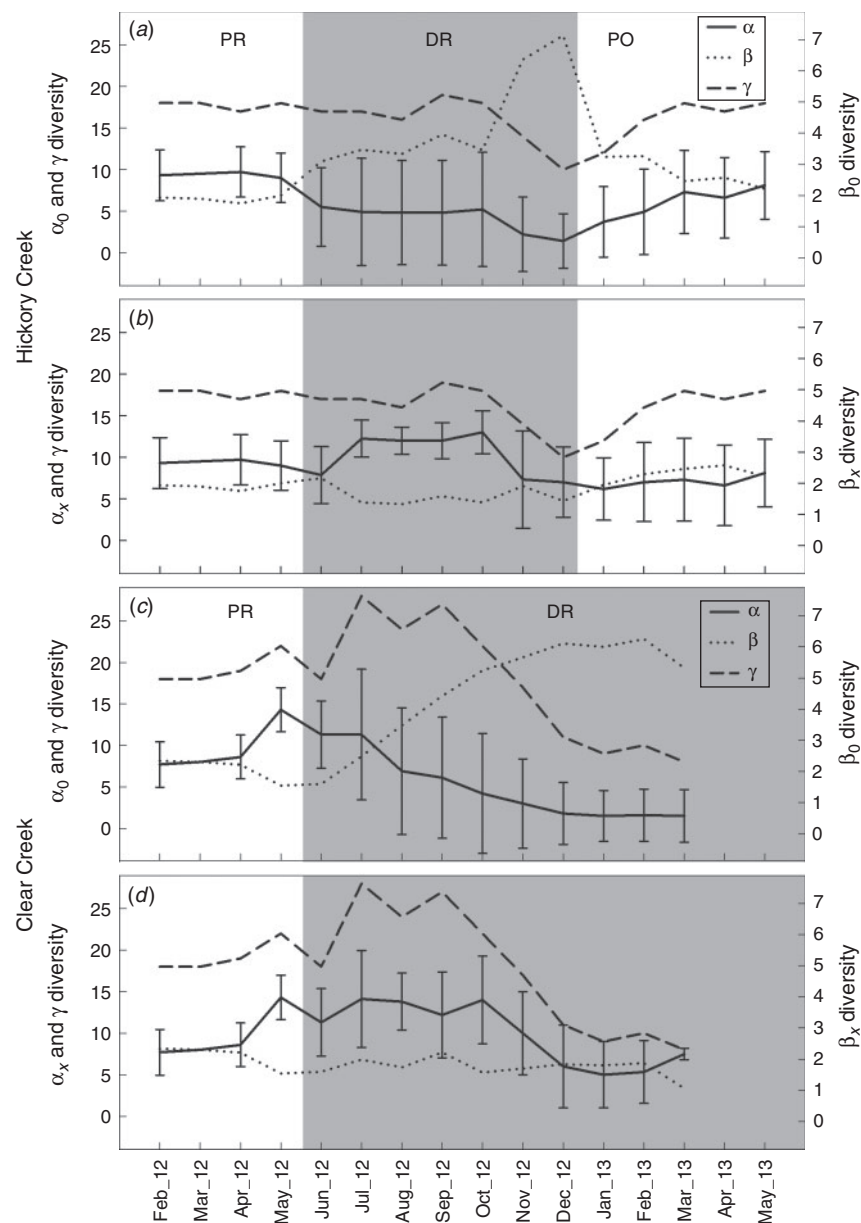


Fig. 3. Temporal patterns of α , β and γ -diversity for Hickory Creek (a, b) and Clear Creek (c, d) with dry sites included (α_0 , β_0) or excluded (α_x , β_x). Error bars indicate s.d. in mean species richness. Shaded areas signify boundaries between pre-drought (PR), drought (DR) and post-drought (PO) hydro-periods.

Fish assemblages showed generally increased stability during initial periods of habitat isolation (summer drought), whereas stability fluctuated with accelerated species losses during winter drought and was relatively low when habitats were connected. Although α , β and γ -diversity approached pre-drought levels during the post-drought period, the structure of post-drought fish assemblages did not fully recover to that observed during the pre-drought hydro-period.

Drought, isolated pools and dynamics of 'refugia'

Increases in air temperature coupled with decreased precipitation through the late spring and summer months resulted in

progressive reduction in stream size (habitat area and volume) and isolation of pool habitats in both Hickory and Clear creeks. During initial stream drying (May) and early isolation (June–July) we observed an increase in fish abundance, density and mean diversity (i.e. α_x). Similar to other studies, these initially positive drought or drying-related effects are likely due to movement (and concentration) of fish into pool refugia as shallower habitats (e.g. riffles and runs) dried (Ostrand and Wilde 2004; Dekar and Magoulick 2007; Hodges and Magoulick 2011). As pools became increasingly isolated over time, assemblage similarity increased (particularly in Hickory Creek) and remained reasonably stable through summer, indicating that

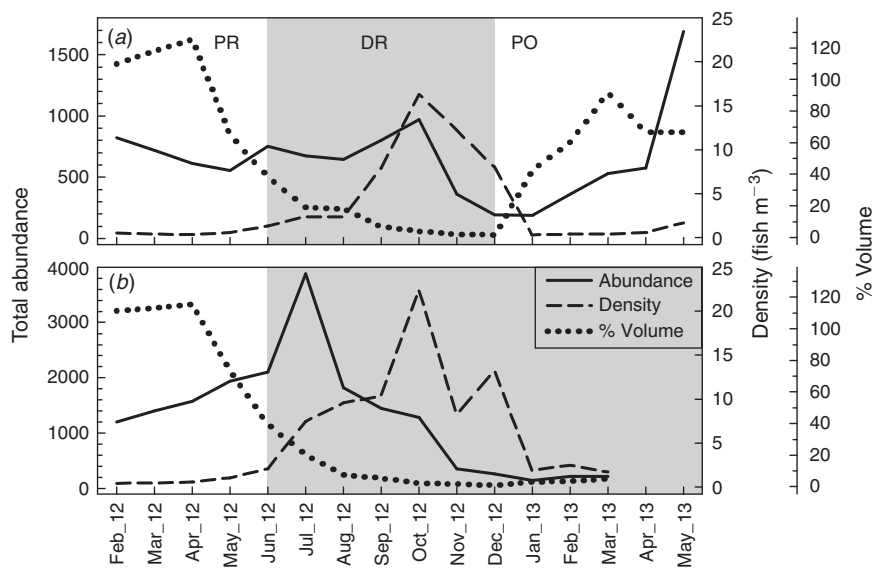


Fig. 4. Temporal patterns of fish total abundance, density (fish m^{-3}) and relative stream volume (%).

isolated pools functioned as important refugia during summer drought. Convergence and stability of isolated assemblages during summer drought is perhaps due to similar deterministic outcomes among environmentally similar pool refugia (i.e. predation, physiological stress; Chase *et al.* 2009; Beesley and Prince 2010) as well as lack of immigration (Medeiros and Maltchik 2001) and reduction of species sorting among pool, run and riffle macrohabitats as species that utilised riffles and runs during flowing conditions were forced into refugia. In contrast to our results, divergence among local assemblages during periods of isolation has been commonly reported and attributed to differential outcomes of colonisation or dispersal histories, species interactions and habitat heterogeneity among isolated pools (Capone and Kushlan 1991; Matthews and Marsh-Matthews 2006; Pires *et al.* 2010).

As drought conditions persisted through autumn and winter in Hickory Creek and into the following spring in Clear Creek, assemblages experienced dramatic declines in local and regional diversity (47 and 61% reduction in γ -diversity) and total abundance (80 and 95%) respectively. Despite generally high tolerances and adaptations of intermittent stream fishes to variable environments (e.g. Matthews and Styron 1981; Ostrand and Wilde 2001), the combined effects of decreased stream volume and extreme low diurnal water temperatures and dissolved oxygen levels (during which we observed fishes respiring or gulping air at pool surfaces) resulted in massive mortality of fishes including destruction of entire assemblages in drying pools. Variability in abundance and species loss among the few remaining pools in November corresponded with temporarily reduced stability, but assemblage similarity increased again between November and December, as assemblages were simplified and consisted largely of common and highly tolerant taxa (e.g. sunfishes, topminnow and mosquitofish). Differences in assemblage responses between summer drought and winter drought suggest that natural or anthropogenic effects on drought duration or timing may

have significant consequences for intermittent-stream fish assemblages.

On a species level, changes in mean abundances and body sizes from pre-drought to drought hydro-periods were highly variable. Considered alongside each species' life-history strategy (i.e. classifications for these species in Hoeinghaus *et al.* 2007), these data may help elucidate contrasting mechanisms of population dynamics that promote survival and persistence, such as local reproduction and recruitment *v.* colonisation by juveniles and adults (Mims and Olden 2013; Dexter *et al.* 2014; Pires *et al.* 2010). For example, increased mean abundance but decreased body size of topminnow and mosquitofish (tolerant, top-water invertivores with opportunistic life-history strategies) during drought suggests that abundances were primarily driven by reproduction in refugia. Bass (tolerant piscivores with equilibrium-periodic life-history strategies) also increased in mean abundance during drought, but significantly larger body size during drought indicate that reproduction occurred earlier during the pre-drought period with subsequent movement or concentration into pools during onset of drought and growth of both juveniles and adult individuals during isolation. In contrast, red shiner and redbfin shiner (in Clear and Hickory creeks respectively), with intermediate opportunistic-periodic life-history strategies, decreased in mean abundances and increased in body sizes during drought. These patterns indicate an increase in mortality and perhaps reduced or failed reproduction or recruitment during drought. Matthews and Marsh-Matthews (2007) speculated that decreased connectivity or dispersal and increased predation associated with fragmentation and reoccurring seasonal drought were responsible for the recent extirpation of red shiner from a similar stream in Oklahoma, USA.

Throughout the drought hydro-period, patterns of diversity differed substantially when dry habitats were included in the calculation of mean local diversity ($\bar{\alpha}_0$) and β diversity (β_0). Inclusion of zeroes in diversity measures revealed a higher

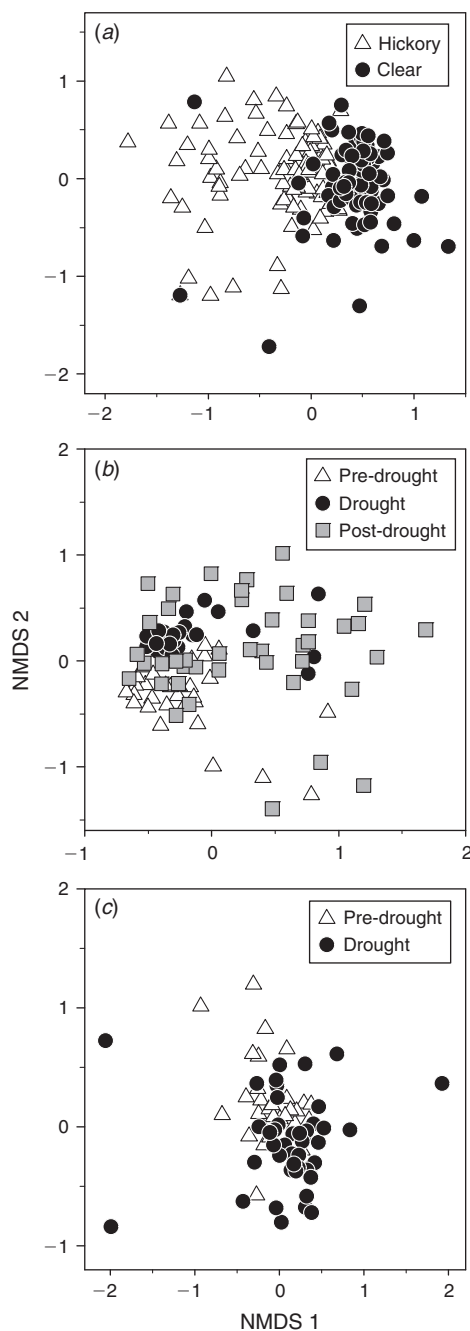


Fig. 5. Non-metric multidimensional scaling (NMDS) ordination comparing assemblage structure between Hickory and Clear creeks (a), and among or between hydro-periods for Hickory (b) and Clear (c) creeks.

degree of local extirpations, higher species turnover and the loss of whole assemblages during drought in both creeks. Patterns of $\bar{\alpha}_x$ represent assemblages surviving within refugia pools only, whereas $\bar{\alpha}_0$ provides a landscape perspective of the distribution of species among all patches (Winemiller *et al.* 2010), including those that are periodically unsuitable or simply unoccupied. Recognition of different diversity patterns in relation to occupied or unoccupied habitat patches is important because spatially or temporally unoccupied sites can be

ecologically informative, particularly in fragmented or disturbed systems (Fagan 2002; Brown and Swan 2010). Although recognised as fundamental components of island biogeography and metapopulation and metacommunity theory (MacArthur and Wilson 1967; Leibold *et al.* 2004), unoccupied sites or patches are often omitted from multivariate community analyses owing to the inability of some analyses to mathematically handle sample sites that contain only zeroes (e.g. similarity metrics, ordination, elements of metacommunity structure; Borcard *et al.* 2011; Leibold and Mikkelsen 2002). Distinction between ‘available-occupied’, ‘available-unoccupied’ v. ‘unavailable’ sites is a topic that is not sufficiently addressed in studies of community dynamics in response to fragmentation or disturbance.

Reconnectivity and community dynamics

Return of habitat connectivity and periodic stream flow to Hickory Creek beginning in January 2013 had immediate effects on diversity and abundance. Regional diversity recovered rapidly, returning to pre-drought levels by March 2013, and by May 2013 local diversity $\bar{\alpha}_0$ was only slightly lower than the previous year. However, when comparing pre- and post-drought species composition, black bullhead (*Ameiurus melas*), yellow bullhead (*A. natalis*) and crappie (*Pomoxis* spp.) were only present during pre-drought, whereas common carp (*Cyprinus carpio*), orangethroat darter (*Etheostoma spectabile*) and smallmouth buffalo (*Ictiobus bubalus*) were only present during post-drought. Similar to other studies (Sheldon and Meffe 1995; Lonzarich *et al.* 1998; Adams and Warren 2005), abundance was slower to recover than diversity and many species were unable to fully recover to pre-drought abundances during the time frame of the present study. Increased abundances during post-drought were associated with a combination of reproduction and immigration, and the relative importance appears to differ among species. The abundance of smaller-bodied (young-of-year) spotted sucker (*Minytrema melanops*), bass and several sunfishes provide evidence that recruitment was an important component of post-drought recovery for these species. In contrast, predominantly larger redbfin shiner during post-drought suggests immigration of adult individuals was important for increasing abundance of this species, although abundances were still lower than pre-drought. Matthews *et al.* (2013) reported similar increases of young-of-year suckers and bass following drought with decreased abundance of minnows, and speculated that increased reproduction or survivorship of some benthic spawning species may be associated with reduced predation on eggs and larvae by some minnow species.

Despite the recovery of species diversity, differences in species composition and relative abundance resulted in different assemblage structure in pre- and post-drought hydro-periods. Assemblage recovery and species-specific responses following drought often depend on variability in the timing and duration of connectivity with respect to species’ life histories, the spatial extent and severity of drought, the distance and spatial configuration of local source or sink habitats, as well as residual effects on individuals (e.g. decreased fitness; Lonzarich *et al.* 1998; Matthews and Marsh-Matthews 2003; Adams and Warren 2005). Despite recovery of regional diversity and increased

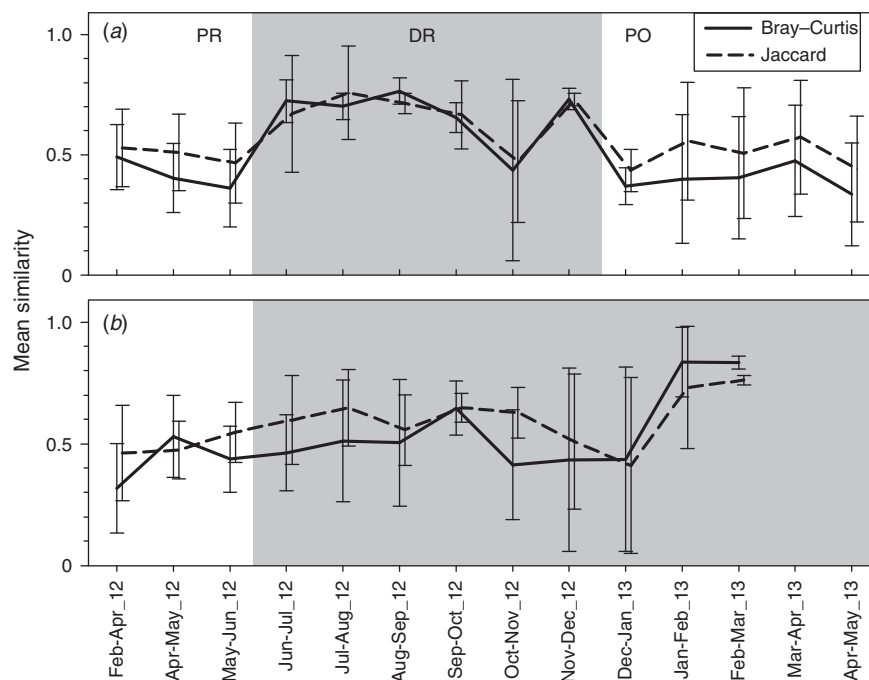


Fig. 6. Mean similarity of local assemblage structure (Bray-Curtis) and composition (Jaccard's) between pairs of consecutive monthly samples for Hickory Creek (a) and Clear Creek (b). Shaded areas signify boundaries between pre-drought (PR), drought (DR) and post-drought (PO) hydro-periods.

abundance of many species, it is likely that duration of habitat connectivity during the post-drought hydro-period had a strong influence on species-specific and assemblage-level patterns of recovery in Hickory Creek. Specifically, we expect that the duration of connectivity was not long enough to allow recovery (e.g. dispersal or reproduction) of several species. Further, it is possible the community dynamics observed in Hickory and Clear creeks are also an artefact of consecutive years of severe drought (e.g. record drought in 2011 followed by record high summer temperatures and extreme drought in 2012). Other studies from comparable stream systems have shown highly variable patterns of recovery from several months (Detenbeck *et al.* 1992; Bayley and Osborne 1993) to years or decades (Magalhães *et al.* 2007; Matthews *et al.* 2013). We cannot speculate as to longer-term influences of the observed supra-seasonal drought on the dynamics of our study system, but note that understanding the impacts of such events, as well as significant ramp disturbances such as climate change and water abstraction, generally requires long-term monitoring that is limited for intermittent-stream systems (Magalhães *et al.* 2007; Matthews *et al.* 2013).

Periodic connectivity and metacommunity dynamics

Theoretical and empirical metacommunity studies have shown that patterns of connectivity or dispersal, environmental heterogeneity and species interactions are important mechanisms that drive community structure at local and regional spatial scales, and that community patterns may be associated with one or several theoretical paradigms (e.g. species sorting, mass

effects, patch dynamics, neutral theory; Leibold *et al.* 2004; Cottenie 2005) or idealised spatial structures (e.g. Clementsian, Gleasonian, nested; Leibold and Mikkelsen 2002; Presley *et al.* 2010). Although we did not test or discriminate among theoretical and idealised metacommunity models in the present study, our results show that both environmental factors and connectivity and dispersal were important structuring components, and that the relative influence of these factors changed over time in relation to hydro-period and connectivity.

Mass effects (dispersal driven) and species sorting (niche driven) are the most commonly cited structuring mechanisms within heterogeneous ecosystems (Cottenie 2005). Mass effects arise when dispersal rates are high enough to allow taxa to colonise and persist in suitable and unsuitable habitats in which assemblages may become homogenised (Leibold *et al.* 2004). Species-sorting patterns arise when dispersal allows species or assemblages to sort themselves among preferred or optimal habitats. In our study, patterns of abundance and body size, increased spatial structuring of local assemblages and decreased temporal stability suggest that, during habitat connectivity, dispersal was not high enough to allow colonisation of all local habitat patches and that species distributions were more strongly influenced by the local environment and biotic interactions (i.e. species sorting). Falke and Fausch (2010) similarly suggest that species sorting is likely to occur with increased connectivity during spring months as fishes seek specific habitats (particularly spawning habitats). Urban (2004) found that heterogeneity in local habitat permanence (pool persistence) was more important than dispersal in explaining variation in invertebrate assemblages among ponds, suggesting

that the quality and distribution of refugia habitats in dynamic and frequently disturbed systems can result in species sorting (although mass effects also played a role).

Studies investigating spatial metacommunity structures have reported that fish assemblages were variably structured by dispersal or colonisation and environmental factors over short periods of time (i.e. months; Fernandes *et al.* 2013; Erős *et al.* 2014). Fernandes *et al.* (2013) found that fish assemblages had high turnover in relation to seasonal flood and drying hydro-periods in a tropical floodplain, in which connectivity and dispersal factors were important in shaping nested assemblages during the beginning of flood period, whereas heterogeneity in environmental factors were important in shaping Clementsian assemblages (i.e. species sorting) during the drying period. Preliminary analysis of temporal patterns of metacommunity structure from Hickory and Clear creeks (unpublished data) suggest that transition from connected to isolated (and vice versa) among hydro-periods may also result in similar spatial structures (Clementsian and nested).

Conclusions

Population and metacommunity-level responses in both creeks during drought showed that fish assemblages were only weakly affected by summer drought (June–September), but dramatically affected by prolonged drought during winter. Subsequent increases in diversity and abundance immediately following reconnectedness in Hickory Creek demonstrate the sensitivity and vagility of stream fishes to changes in hydrological conditions. However, lack of recovery of Hickory Creek fish assemblages during post-drought to those observed during pre-drought reinforce the importance of connectivity in maintaining populations, diversity and assemblage structure over time and suggest possible residual or multiyear impacts of drought on intermittent-stream fish assemblages. Intermittent-stream fish metacommunities may be generally adapted or resistant to summer drought conditions, but our results indicate that prolonged or intensified drought, which are predicted to increase in frequency due to continuing climate change, may have significant negative impacts across spatial and temporal scales.

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