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Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment

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Abstract

1. Predicted trends towards more intense droughts are of particular significance for running water ecosystems, as the loss of critical stream habitat can provoke sudden changes in biodiversity and shifts in community structure. However, analysing ecological responses to the progressive loss of stream habitat requires a continuous disturbance gradient that can only be generated through large-scale manipulations of streamflow.
2. In the first experiment of its kind, we used large artificial stream channels (mesocosms) as analogues of spring-fed headwaters and simulated a gradient of drought intensity that encompassed flowing streams, disconnected pools, and dry streambeds. We used breakpoint analysis to analyse macroinvertebrate community responses to intensifying drought, and identify the taxa and compositional metrics sensitive to small changes in drought stress.
3. We detected breakpoints for >60% of taxa, signalling sudden population crashes or irruptions as drought intensified. Abrupt changes were most pronounced where riffle dewatering isolated pools. In the remnant wetted habitat, we observed a shift to larger body sizes across the community, primarily driven by irruptions of predatory midge larvae and coincident population collapses among prey species (worms and smaller midges).
4. Our results suggest that intense predation in confined, fragmented stream habitat can lead to unexpected changes in body sizes, challenging the conventional wisdom that droughts favour the small. Pool fragmentation might thus be the most critical stage of habitat loss during future droughts, as the point at which impacted rivers and streams begin to exhibit major shifts in fundamental food web properties.

KEYWORDS

disturbance gradient, drying, macroinvertebrates, predation, stream drought

1 | INTRODUCTION

Many regions of the world are expected to experience more intense and prolonged droughts over the coming century (Trenberth et al., 2014). In running waters, the ecological impacts of droughts have been less well studied than those of floods (Boulton & Lake, 2008; Reich & Lake, 2015) or changes in average conditions (Ledger & Milner, 2015), yet they can have more profound and immediate impacts on stream communities (Thornton, Ericksen, Herrero, & Challinor, 2014; Woodward et al., 2016). Much of our understanding of stream drought comes from studies of intermittent systems that experience predictable, seasonal drying events. Many biota in these systems possess adaptations (Lytle & Poff, 2004) that confer resistance to drying until surface water disappears (e.g. Boersma, Bogan, Henrichs, & Lytle, 2014; Bogan, Hwan, Ponce, & Carlson, 2017; Drummond, McIntosh, & Larned, 2015). By contrast, droughts in perennial systems are inherently rare and unpredictable (Lake, 2003), and can have pervasive impacts on community structure even in the absence of complete drying (Ledger, Harris, Armitage, & Milner, 2012).

Despite this context dependence of ecological responses to drying, prevailing theory, developed by Boulton (2003) and others (e.g. Bogan, Boersma, & Lytle, 2015; Boulton & Lake, 2008; Chadd et al., 2017), depicts drought as a stepped ramp disturbance. Here, gradual biotic response to steadily escalating environmental stress (the ramp) is punctuated by sudden changes in community structure as critical habitats are lost (the steps). For example, community composition may remain relatively stable until the loss of riffles fragments the channel into pools, eradicating lotic taxa and intensifying biotic interactions (Boulton, 2003; Boulton & Lake, 2008; Dewson, James, & Death, 2007; Lake, 2003). These pools then shrink until surface water disappears and the remaining obligate aquatic taxa are suddenly lost (Boulton, 2003; Boulton & Lake, 2008). The steps in this conceptual model are examples of ecological thresholds, which describe when a small change in the value of an environmental parameter (e.g. marginal decrease in water level) triggers a disproportionately large ecological response (e.g. dramatic fall in species richness; Capon et al., 2015). Thresholds can therefore be viewed as a defining characteristic of community structural responses to stream drying, but their existence has not been rigorously demonstrated, as few studies have analysed the continuous intensity gradient required for their detection, at least in the context of extreme drought (see McHugh, Thompson, Greig, Warburton, & McIntosh, 2015 for an example from intermittent streams).

Moreover, we know little about how body size—a critical attribute closely tied to trophic structure, species' interactions and a host of functional traits (Woodward et al., 2005)—changes as stream habitat is progressively lost. Larger, more *K*-selected invertebrate taxa, including crustaceans, leeches, and many Ephemeroptera, Plecoptera, and Trichoptera (EPT) species, are often the most vulnerable to drought. These taxa have relatively high individual metabolic demands and limited ability to access refugia and exploit the niche space available to smaller *r*-strategists (e.g. worms and midges) in stressful environments (Lake, 2011; Lancaster & Ledger, 2015; Ledger, Edwards, Brown, Milner, & Woodward, 2011; Ledger et al., 2012; Pianka, 1970; Woodward et al., 2016). However, predator: prey ratios can increase as channels fragment (McHugh et al., 2015; McIntosh et al., 2017), which would be expected to equate to an increase in body sizes, given that most freshwater food webs are strongly size-structured (Woodward et al., 2005). Despite these potential impacts, trends in invertebrate body sizes across multiple stages of stream habitat loss have rarely been explored (but see Aspin et al., 2019).

A lack of gradient-based approaches prevents robust empirical testing of even well-established theoretical models (e.g. Bogan et al., 2015; Boulton, 2003; Chadd et al., 2017), and constrains our ability to predict the impacts of future drought intensification. This research gap can be addressed using mesocosms, which can simulate broad stress gradients while supporting more complex and realistic ecosystems than smaller scale (e.g. laboratory microcosm) experiments (Stewart et al., 2013). By isolating a particular environmental driver (e.g. drought intensity), mesocosms can also remove confounding influences on ecological response variables common in field survey data (e.g. water quality; Durance & Ormerod, 2009; Floury, Usseglio-Polatera, Ferreol, Delattre, & Souchon, 2013). Furthermore, once-through stream mesocosms can recreate the key physicochemical characteristics and biocomplexity of natural lowland streams when located outdoors and fed by natural water sources (Brown, Edwards, Milner, Woodward, & Ledger, 2011; Ledger, Harris, Armitage, & Milner, 2009).

To test the ideas outlined above at relevant experimental scales, we used 21 large, replicate stream mesocosms as analogues of perennial, groundwater-fed headwaters to establish a gradient of drought intensity. This was manifested as a progressive decline in water level, loss of aquatic habitat and increase in temperature variability, mimicking the complex syndrome of primary stressors that dictate physicochemical (e.g. oxygen levels, conductivity) and biological responses during stream drought (Lake, 2011). The gradient incorporated extreme drying conditions (extensive habitat loss, supra-seasonal duration), allowing us to explore beyond the limits of current disturbance regimes and affording insights into possible impacts of future droughts (Kayler et al., 2015). We analysed macroinvertebrate community responses to intensifying drought using a threshold detection approach (Toms & Lesperance, 2003), to pinpoint the most important stages of habitat loss and identify the most sensitive taxa. We tested three hypotheses: (1) thresholds in community- and population-level responses to drought would be detected in advance of complete drying; (2) taxa exhibiting negative thresholds (i.e. signalling abrupt population collapse) would be large *K*-strategists (crustaceans, leeches, and/or EPT species). We predicted that these population collapses would outweigh the effects of increasing predator: prey ratios, and therefore that (3) drought would drive a shift to smaller body sizes across the community.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The experiment was carried out from February 2013 to August 2014 at an outdoor stream mesocosm facility on the banks of the Candover Brook, a mesotrophic chalk stream and tributary of the River Itchen, Hampshire, UK (51°10′21″N, 1°18′70″W; see Supporting Information Figure S1). We used 21 stainless steel channels (each 15 m length × 0.5 m width × 0.5 m height), fed by borehole water pumped through feeder pipes and drained by outlet weirs. Each channel was designed to mimic a typical (i.e. groundwater-dominated; Sear, Armitage, & Dawson, 1999) spring-fed headwater chalk stream, and consisted of uniformly alternating sections of riffle and pool habitat (three riffles and four pools), created by adding clean gravel to 15 cm depth in the pools and 25 cm in the riffles. Each channel was seeded with macrophytes (*Ranunculus penicillatus* subsp. *pseudofluitans* (Syme) S.D. Webster, seven rooted plants) and macroinvertebrates (10 × 5 min kick samples), collected from nearby streams and left to establish and stabilise for 6 months before drought treatments were applied.

In August 2013, drought treatments were implemented by adjusting the sluice valves on the inlet pipes (with random distribution of treatments among channels) to generate prescribed inflows that would establish and maintain a gradient of declining water volume (i.e. volume of water above stream bed; 1.9–0.001 m^3), wetted area (6.5–0.3 m^2) and flow (2.2–0.001 L/s; Supporting Information Figure S2). These trends were accompanied by increasing temperature variability, with the maximum annual water temperature range in each channel varying from 6 to 40°C. Groundwater-dominated systems, such as many chalk stream reaches across southern England, typically maintain moderate to high flows throughout the year (Garner, Van Loon, Prudhomme, & Hannah, 2015; Sear et al., 1999), but protracted dry weather and groundwater abstraction can give rise to supra-seasonal droughts, during which prolonged but patchy fragmentation and drying of the streambed can occur (Folland et al., 2015; Kendon, Marsh, & Parry, 2013; Westwood, Teeuw, Wade, & Holmes, 2006).

2.2 | Data collection and processing

Four benthic macroinvertebrate samples were collected using a Surber sampler (0.0225 m^2, mesh size 300 μm) from each channel (one per pool) after 1 year of drought (August 2014). Each sample equated to the entire surface area of the Surber frame to a bed depth of 3 cm, enabling direct comparison of flowing and non-flowing habitats. Samples were sorted to separate macroinvertebrates from detritus, and animals were identified to the lowest practicable taxonomic level (species or genus, excepting Oligochaeta) and counted. Abundance data from each of the four pools were then combined to provide a single measure of density (individuals per m^2) per channel. Water temperature was logged at 15-min intervals in the terminal pool of each mesocosm using Tinytag loggers (Gemini Data Loggers Ltd, Chichester, UK). As oxygen depletion can be an important stressor in drying pools (Lake, 2011), we measured dissolved oxygen (DO) concentrations every 5 min over one 24-hr period each month using MiniDOT loggers (PME Inc., Vista, CA, USA) suspended in each channel.

2.3 | Data analysis

2.3.1 | Abiotic data

Each mesocosm exhibited a different combination of flow (discharge), water volume, wetted area, and temperature variability. During stream drought these natural covariates act closely in concert, rather than individually, to determine secondary stressors (e.g. oxygen availability) and biological responses (Lake, 2011), and thus we created a compound index of drought intensity (DI) using the scores from the first axis of a principal component analysis (PCA) of these four primary drivers (explained variance = 94%). The PCA axis 1 scores were then rescaled to range from 0 (lowest drought stress) to 1 (most stress). Water temperature variability was calculated as the maximum recorded temperature range, on the basis that temperature extremes are likely to hold greater ecological relevance than means (Thompson, Beardall, Beringer, Grace, & Sardina, 2013; Vasseur et al., 2014). Six channels experienced only slight loss of water depth, volume, and flow and remained longitudinally connected (low DI, <0.2); 12 were fragmented into isolated pools of varying depths (moderate DI, 0.2–0.7), three of which (DI 0.2–0.3) retained some remnant connectivity between pools due to the cross-sectional asymmetry of the streambeds (cf. Walters & Post, 2011). The remaining three channels were largely dewatered, experiencing >95% loss of wetted area (high DI, >0.7). The drought gradient thus encompassed the stages of pool fragmentation and streambed drying outlined by Boulton (2003).

These critical stages were apparent in the trends of the component variables of the DI index (Supporting Information Table S3; Supporting Information Figure S3). Increasing drought intensity was associated with initial steep declines in flow and water volume, which both levelled off as channels fragmented (Supporting Information Figure S3a,b). There were stepped decreases in wetted area, with steps corresponding to the drying of riffles and the loss of remaining surface water in pools (Supporting Information Figure S3c). Temperature variability increased gradually under low intensity drought then more rapidly once channels fragmented (Supporting Information Figure S3d), while mean daily minimum DO concentration declined linearly across the gradient (Supporting Information Figure S4). Our DI gradient thus captured the typical syndrome of environmental and habitat drivers that unavoidably co-occur during natural stream droughts, analogous to the multifaceted nature of other compound stressors such as organic pollution and acidification.

2.3.2 | Community structure

The impact of drought on macroinvertebrate community composition was analysed using non-metric multidimensional scaling based

on Bray–Curtis dissimilarity. Non-metric multidimensional scaling was preferred to an eigenvector approach due to the potential for drought to drive nonlinear changes in community structure (Boulton, 2003). To test for thresholds in community-level responses, we examined the impact of drought on taxon richness (mean number of taxa per sample) and total invertebrate abundance (numbers per m^2). Given that we expected large, relatively *K*-selected species to be particularly sensitive to drought, we also separately analysed the responses of total EPT richness and abundance.

As habitat fragmentation and shrinkage can increase predator: prey ratios and thus intensify predator–prey interactions during drought (Boulton, 2003; Boulton & Lake, 2008; Dewson et al., 2007; Lake, 2003; McIntosh et al., 2017), we derived a trait that described vulnerability to predation. Predator–prey feeding linkages between taxa were inferred from published trophic interactions among UK freshwater species, including records from chalk streams with taxonomically similar communities to our study system (Gray et al., 2015). Of the 59 invertebrate taxa recorded, 58% were present in the reference dataset as an exact match and/or at the species or genus level; 92% were present when generalising to family level; and 100% of taxa had order-level matches. When exact matches could not be found, we inferred feeding links by generalising taxa to the next highest taxonomic resolution (e.g. subfamily for chironomids; following Gray et al., 2015). We assumed that a predator–prey interaction reported in the literature would be realised in the mesocosms where both taxa co-occurred (following Thompson et al., 2018).

Calculation of trophic vulnerability involved several steps (see Supporting Information), namely: (1) establishing a list of potential predators for each prey species; (2) dividing the abundance of each predator by the total number of individual prey items that predator could potentially exploit; (3) summing the values obtained from step (2) across all the predators of a given prey species, thus obtaining the per capita risk of predation for that prey species; and (4) calculating community-averaged trophic vulnerability as the geometric mean of per capita predation risk across all prey taxa (values from step (3) were $\log_{10}$-transformed to reduce the influence of interactions involving rare prey). Our method thus accounted for the dietary breadth of each predator, ensuring that increases in the relative dominance of generalists over specialists would not artificially inflate our estimate of predation risk.

Chironomidae midge larvae were the most diverse family in our study, and contained some of the most common predators (Tanypodinae) and primary consumers (Orthocladiinae and Chironominae; Supporting Information Table S1; Moog, 2002). We therefore also analysed changes in Tanypodinae abundance as a percentage of total Chironomidae abundance (hereafter relative tanypod abundance). To test for thresholds at the population level (second hypothesis), we examined responses to drought of 13 core taxa, which dominated across all or part of the gradient (densities >100 individuals per m^2 in >30% of samples).

To test our third hypothesis (drought causes a shift from large to small species), we obtained body mass data from our samples. An ocular graticule was used to measure the body lengths of a representative number of random individuals per species per sample (minimum 30 for abundant taxa), to an accuracy of 0.1 mm (total number of body length measurements = 11,730; total number of individuals recorded = 19,800). These measurements were then converted to body mass estimates (mg dry mass) using length–mass regressions derived from the literature (Supporting Information Table S2) and extrapolated to the rest of the community. Body mass data were pooled for all taxa, and the impact of drought on the median body mass of the community was examined. This was preferable to a mass–abundance scaling approach (i.e. comparison of allometric slopes) as it is less sensitive to small changes in abundance at very large size classes.

2.3.3 | Threshold analysis

To test for ecological thresholds, we compared the fit of linear and segmented regression models relating the response variables to drought intensity. Segmented regression offers a statistically robust approach to threshold detection, differing from other nonlinear methods (e.g. polynomial regression) in two key respects: (1) it incorporates an objective procedure to identify a threshold (significance test of break in slope); and (2) it produces associated confidence intervals (Toms & Lesperance, 2003). In segmented regression models, thresholds are displayed as breakpoints that connect best-fit lines of significantly different slopes, thereby giving an estimate of the threshold value and the overall shape of the relationship (Toms & Lesperance, 2003). Both linear and segmented regression were used to analyse the relationships between drought intensity and (1) each community metric; (2) abundance of each core taxon; and (3) median body size. Two criteria needed to be satisfied to select the segmented model over the linear model, specifically: (1) a Davies test (Davies, 1987) detected a significant breakpoint in the relationship; and (2) the segmented model had a lower Akaike information criterion and an ANOVA test confirmed a significant improvement in model fit. If these criteria were not satisfied, the linear model was selected where it was a significant fit. For each segmented model, we obtained an estimate of the single most significant breakpoint (expressed as a DI value) with a 95% confidence interval.

Influential outliers ($n = 3$) that exceeded the relevant Cook's distance cut-off value (Cook & Weisberg, 1982) were excluded from the analyses (following Paillex, Dolédec, Castella, Mérigoux, & Aldridge, 2013). We did not adjust *p* values for multiple comparisons due to the overly conservative nature of the sequential Bonferroni correction (Nakagawa, 2004) and instead considered effect sizes (Nakagawa & Cuthill, 2007) by (1) calculating confidence intervals on R^2 values, following the procedure outlined by Smithson (2001), and (2) standardising regression slopes (Schielzeth, 2010). Ordination was carried out on *ln*(x + 1)-transformed abundance data in R (version 3.2.4) using the package *vegan* (Oksanen et al., 2016) and regression on untransformed data using the R package *segmented* (Muggeo, 2015).

3 | RESULTS

3.1 | Invertebrate community composition

Drought intensification led to major changes in community composition across the drought gradient. Axis 1 of a non-metric multidimensional scaling ordination (stress = 0.13) accounted for almost all (87%) of the variability in the invertebrate compositional data (Axis 2 = 0.05%) and was significantly positively correlated with temperature variability (Pearson $r = 0.84$) and negatively correlated with water volume (−0.60), wetted area (−0.82) and flow (−0.53), as well as minimum DO (−0.73, $p < 0.05$ in all cases). Axis 1 thus broadly mirrored the drought gradient as an integrated syndrome of these covariates (Figure 1a). There were clear shifts in the relative abundance of different taxa as drought intensified: abundances of EPT species, orthoclad chironomids, and beetles peaked under low intensity drought; as channels fragmented, flatworms, mosquitoes, and other (non-orthoclad) chironomids became more dominant; and semi-aquatic Diptera (e.g. biting midges and soldierflies) and arachnids were associated with high intensity drought (Figure 1b). We nonetheless observed some overlap between these three groupings: partially fragmented channels (DI 0.2–0.3) supported mixed assemblages of both rheophilic (e.g. *Clinocera stagnalis*) and lentic (e.g. *Anopheles claviger*) species, while some obligate aquatic taxa survived in low numbers in dry streambed refugia (DI >0.7).

3.2 | Threshold analysis

Community-level responses to drought were either broadly linear or crossed thresholds at moderate drought intensity, corroborating our first hypothesis. Species richness, total invertebrate abundance and EPT richness and abundance were better described by linear than segmented regression models, and declined monotonically as drought intensified (Figure 2a,b; Supporting Information Figure S5). Breakpoints were, however, detected in trophic vulnerability and relative tanypod abundance: both abruptly increased as drought

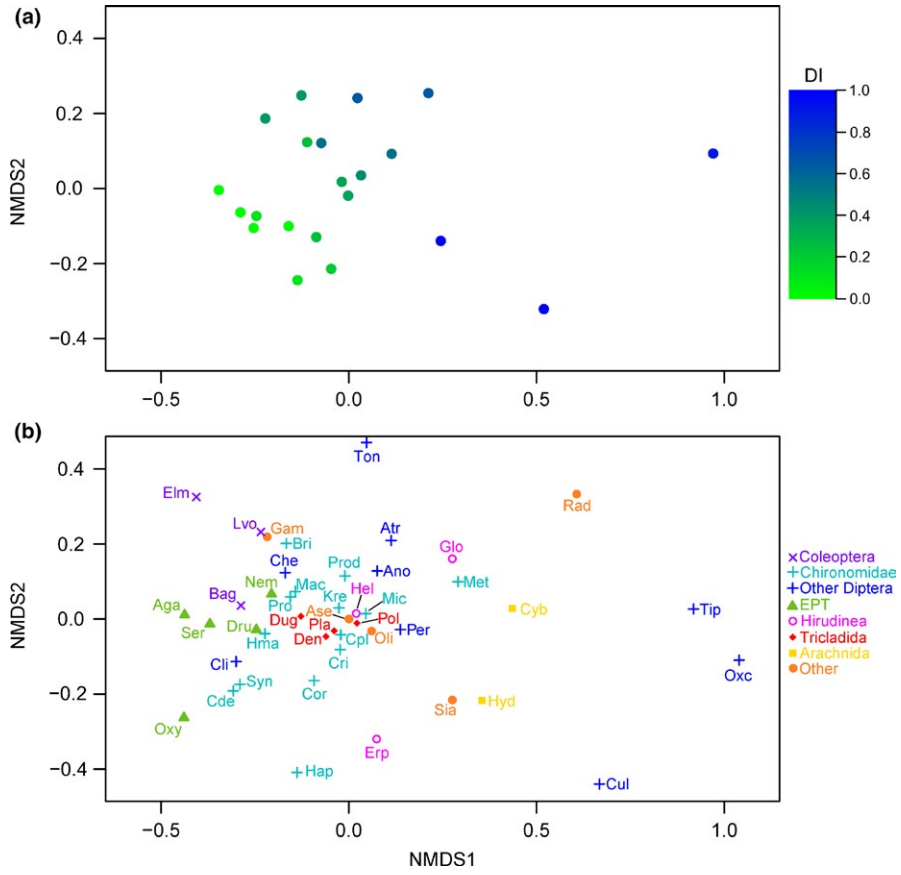

FIGURE 1 Non-metric multidimensional scaling (NMDS) biplots of (a) mesocosms (filled circles) in species space and (b) taxa. Taxa abbreviations in (b) are as follows: Aga = *Agapetus fuscipes*; Ano = *Anopheles claviger*; Ase = *Asellus aquaticus*; Atr = *Atrichopogon*; Bag = *Bagous*; Bri = *Brillia*; Cde = *Chaetocladius dentiforceps*; Che = *Chelifera precatoria*; Cli = *Clinocera stagnalis*; Cor = *Corynoneura*; Cpl = *Chironomus plumosus*; Cri = *Cricotopus fuscus*; Cul = *Culicoides*; Cyb = Cybaeidae; Den = *Dendrocoelum lacteum*; Dru = *Drusus annulatus*; Dug = *Dugesia*; Elm = *Elmis aenea*; Erp = *Erpobdella octoculata*; Gam = *Gammarus pulex*; Glo = *Glossiphonia complanata*; Hap = *Heterotanytarsus apicalis*; Hel = *Helobdella stagnalis*; Hma = *Heterotrissocladius marcidus*; Hyd = Hydrachnidae; Kre = *Krenopelopia*; Lvo = *Limnius volckmari*; Mac = *Macropelopia*; Met = *Metriocnemus eurynotus*; Mic = *Micropsectra*; Nem = *Nemurella pictetii*; Oli = Oligochaeta; Oxc = *Oxycera*; Oxy = *Oxyethira*; Per = *Pericoma*; Pla = *Planaria*; Pol = *Polycelis*; Pro = *Procladius*; Prod = *Prodiamesa*; Rad = *Radix balthica*; Ser = *Sericostoma personatum*; Sia = *Sialis lutaria*; Syn = *Synorthocladius semivirens*; Tip = *Tipula*; Ton = *Tonnoiriella*. Only common taxa (found in at least three samples) are shown

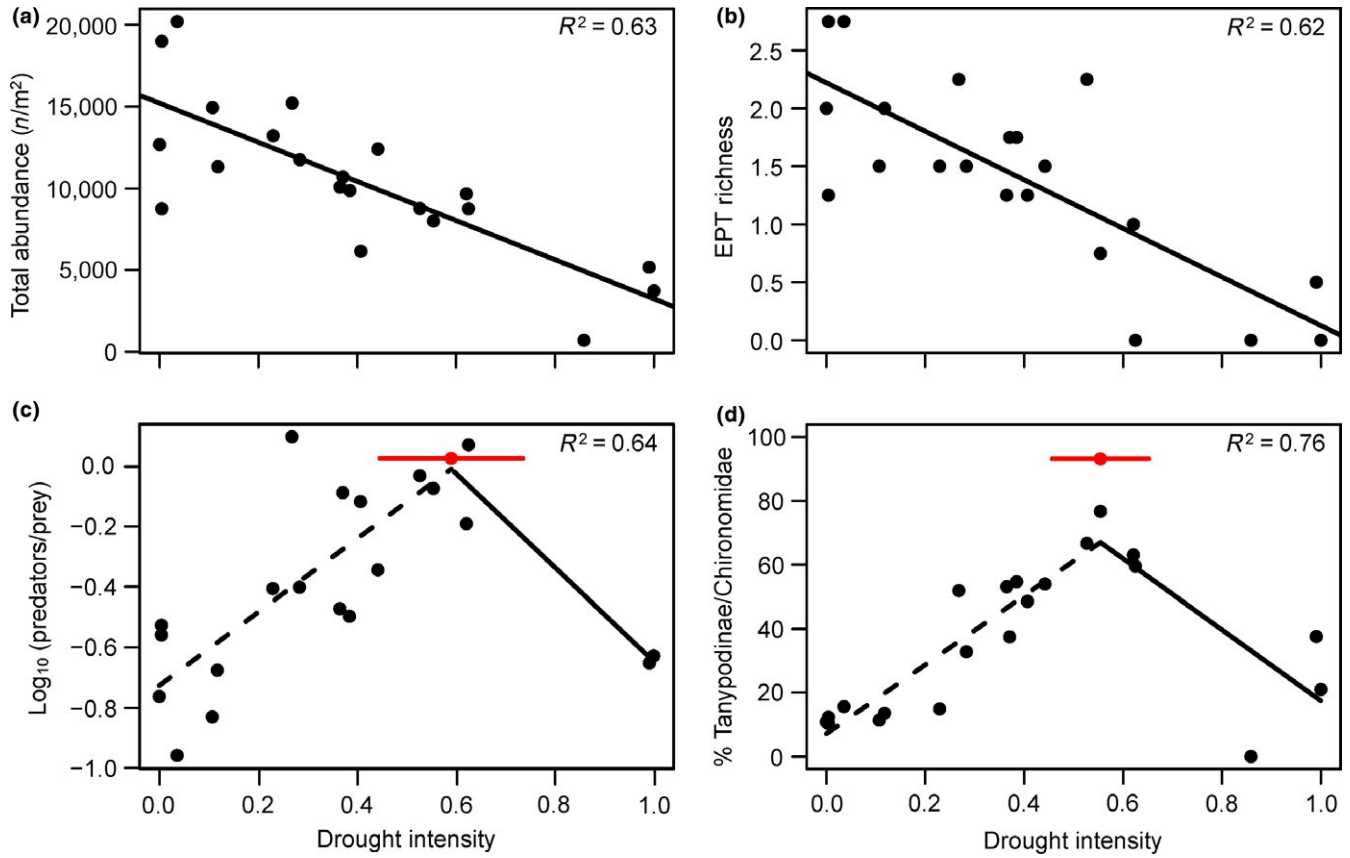

FIGURE 2 The impact of drought intensification on selected community metrics: (a) total invertebrate abundance; (b) Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness; (c) trophic vulnerability; and (d) abundance of Tanypodinae as a percentage of total Chironomidae abundance. Richness data in (b) are mean values per sample. Trophic vulnerability was calculated as the geometric mean of potential predator abundance per prey individual across all taxa, based on feeding links recorded in the literature. Relationships were fitted with either linear (a, b) or segmented (c, d) regression models, depending on the detection of a breakpoint by a Davies test. For each segmented model, the line of best fit is dashed until the breakpoint is reached and solid thereafter; the red circle marks the position of the breakpoint and the horizontal bar the 95% confidence interval

initially intensified and channels fragmented, before declining under more intense drought (Figure 2c,d; Table 1).

Comparisons of regression models identified four distinct response classes among the core taxa. Group A taxa showed no significant response along the gradient, and consisted of predatory flatworms (*Polycelis*), leeches (*Helobdella stagnalis*), and chironomids (*Macropelopia*; Figure 3a; Supporting Information Table S4; Supporting Information Figure S6). Group B taxa were characterised by threshold responses, with irruptions as channels fragmented followed by abrupt declines as channels dried (Figure 3b). This group comprised other predatory chironomids (*Procladius*, *Krenopelopia*) and flatworms (*Dendrocoelum lacteum*), together with isopods (*Asellus aquaticus*) and mosquitoes (*A. claviger*; Supporting Information Figure S6). Group C taxa exhibited threshold responses that contrasted with those of Group B, with population collapses as channels fragmented and no subsequent recovery (Figure 3c). These taxa were small primary consumers, namely oligochaete worms and orthoclads (*Cricotopus fuscus*, *Chaetocladius dentiforceps*), contrary to our prediction (hypothesis 2) that large *K*-strategists would be disproportionately sensitive to drought. Group D contained trichopteran (*Drusus annulatus*) and chironomid (*Micropsectra*) taxa that declined linearly in abundance as drought intensified (Table 1; Figure 3d; Supporting Information Table S4; Supporting Information Figure S6).

Median body mass increased abruptly as channels fragmented, contradicting our third hypothesis (Figure 4). This unexpected shift corresponded to the collapses in the populations of small primary consumers (Group C), as prey exposure to predation increased upon pool disconnection (Figure 2c). As drought further intensified median body size declined, with the breakpoints of Group B taxa marking population collapses, and eventual replacement by smaller drought specialists (e.g. biting midges), as channels dried.

4 | DISCUSSION

In running waters, habitat loss has long been suspected to drive abrupt, nonlinear changes in stream community structure (Bogan et al., 2015; Boulton, 2003), but ours is the first study to test for statistical thresholds and to demonstrate causality. We show that drought can lead to profound shifts in macroinvertebrate communities long before surface water is completely lost, when the most dramatic biological changes are assumed to occur (Boersma et al., 2014;

TABLE 1 Summary of fitted linear and segmented regression models

Response variable	Selected model	Breakpoint (95% CI)	R^2	Standardised slope
Community metrics				
Richness	Linear (\)	ns	0.30*	−0.54
Abundance	Linear (\)	ns	0.63***	−0.79
EPT richness	Linear (\)	ns	0.62***	−0.79
EPT abundance	Linear (\)	ns	0.40**	−0.63
Trophic vulnerability	Segmented (/\)	0.59 (0.45, 0.74)	0.64***	1.21, −2.76
% Tanypodinae	Segmented (/\)	0.55 (0.46, 0.65)	0.76***	1.44, −1.48
Median body mass	Segmented (/\)	0.34 (0.20, 0.49)	0.59**	1.92, −0.89
Core taxa				
Procladius	Segmented (/\)	0.53 (0.39, 0.67)	0.57**	0.96, −1.71
Krenopelopia	Segmented (/\)	0.52 (0.37, 0.66)	0.58**	1.28, −1.37
Anopheles	Segmented (/\)	0.46 (0.27, 0.65)	0.47**	1.35, −0.88
Asellus	Segmented (/\)	0.26 (0.03, 0.49)	0.48^{ns}	1.04, −1.08
Dendrocoelum	Segmented (/\)	0.11 (0, 0.23)	0.38^{ns}	4.69, −0.67
Oligochaeta	Segmented (_)	0.28 (0.14, 0.43)	0.69***	−2.31, 0.03
Cricotopus	Segmented (_)	0.40 (0.25, 0.54)	0.79***	−1.89, −0.03
Chaetocladius	Segmented (_)	0.39 (0.30, 0.49)	0.89***	−2.05, 0.04
Drusus	Linear (\)	ns	0.34**	−0.58
Micropsectra	Linear (\)	ns	0.25*	−0.50

The symbol in brackets in the second column denotes the general shape of response. The breakpoint and associated 95% confidence intervals are given as drought intensity (DI) values. Significance values are as follows: ns = non-significant ($p > 0.05$); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. See Supporting Information Table S4 for full results. EPT = Ephemeroptera, Plecoptera, and Trichoptera

Bogan et al., 2017; James & Suren, 2009). Drought also produced sudden and unexpected shifts in body size: although larger (particularly EPT) species were negatively affected by drought, small worms and orthoclad midges were among the most sensitive invertebrates, ostensibly due to elevated predation pressure in fragmented pools. These taxa are typically resistant to stagnation and deteriorating water quality (Boulton & Lake, 2008; Lake, 2011), being generally tolerant of oxygen minima lower than those we recorded in disconnected channels (Supporting Information Figure S4; Moog, 2002), suggesting that prolonged drought can trigger population collapses before abiotic tolerance limits are exceeded.

Shifts in community composition as drought intensified appeared to reflect differences in habitat preference and abiotic resistance, as dominance progressively changed from flow-dependent EPT species to a variety of habitat generalists (chironomids, flatworms) to drought-resistant specialists and/or air-breathers, such as arachnids, soldierflies, and biting midges (Boulton & Lake, 2008; Lake, 2011). However, the abundance trends of several core taxa were not well explained by physicochemical stress, as we observed contrasting responses of different chironomids with similar tolerances of flow cessation and oxygen depletion (Chadd et al., 2017; Moog, 2002). Indeed, channel fragmentation coincided with irruptions of certain taxa typically associated with well-oxygenated conditions (e.g. *Krenopelopia*; Moog, 2002), implying that DO levels were not widely limiting until severe dewatering occurred. This is consistent with the results of a traits-based analysis of the mesocosm communities, which revealed abrupt shifts in respiration mode as streams dried (see Aspin et al., 2019). In that companion study, which was based on samples collected after 18 months of simulated drought, we did, however, find that non-aerial dispersers (e.g. crustaceans, leeches, flatworms) were more sensitive to pool fragmentation than in the present study. This discrepancy is consistent with the importance of disturbance duration relative to species' generation times (Iwasaki & Noda, 2018), with longer droughts having disproportionately severe impacts on weak dispersers with limited capacity for recolonisation of disconnected habitats.

Here, most individual breakpoints, at both the community- and population-level, formed part of a consistent pattern, whereby the irruption of predators (notably tanypods) as channels fragmented was accompanied by collapses in core prey populations (worms and orthoclads). An increase in predator densities as habitat area contracts has previously been reported during drought (Acuña et al., 2005; Bogan & Lytle, 2007; Boulton, 2003; Walters & Post, 2011), but impacts on prey have been more equivocal (Dewson et al., 2007). Nonetheless, tanypods are voracious predators of worms (Baker & MacLachan, 1979) and orthoclads (Armitage, Cranston, & Pinder, 1995) and can suppress populations of both taxa (Brinkhurst & Kennedy, 1965; Hershey, 1986; Vodopich & Cowell, 1984). Under low intensity drought tanypods comprised 10–16% of total chironomid abundance, consistent with values from natural lowland rivers (Lindegaard, 1997), but rose to 51 ± 5% in fragmented channels (Figure 2d), signifying a dramatic reversal of predator: prey ratios.

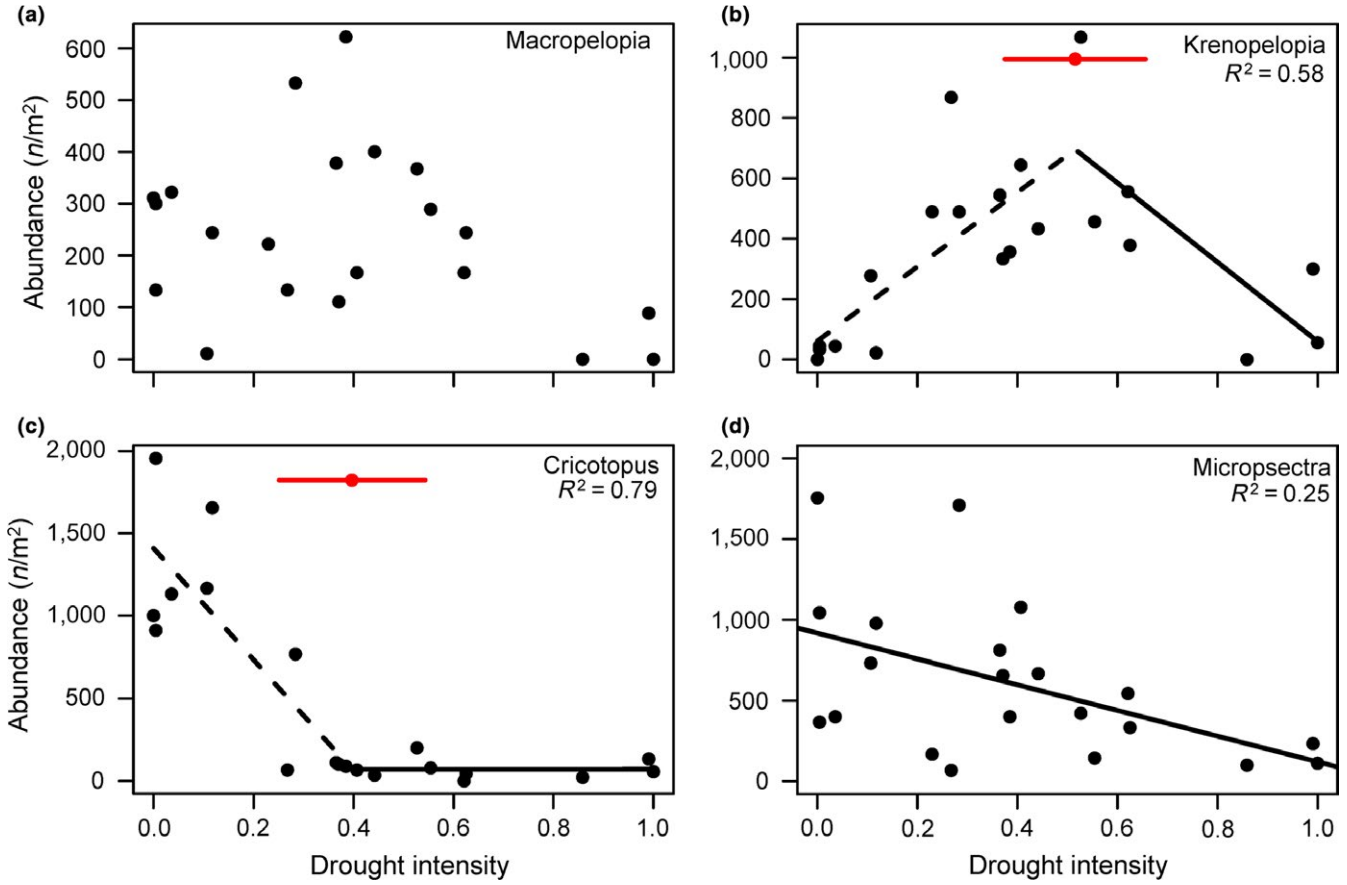

FIGURE 3 The impact of drought intensification on the abundance of four Chironomidae, representing the four types of response exhibited by core taxa (i.e. taxa with densities >100 individuals per m^2 in at least 30% of samples): (a) no significant response; (b) irruption; (c) collapse; (d) linear decline. For interpretation of segmented models see Figure 2. Responses of all core taxa are shown in Supporting Information Figure S6

Shifts in the relative dominance of different chironomids as drought intensified thus appeared to be a response to habitat, rather than strictly environmental, filters (sensu Kraft et al., 2015), whereby changes in relative species' abundances were amplified by intense predation. Prevailing theory primarily attributes thresholds in biological response to drought to an intolerance of the abiotic environment (Bogan et al., 2015; Boulton, 2003); our results suggest that biotic stress may also trigger catastrophic change at the mesohabitat scale, consistent with the concept of stream drought as a compound disturbance comprising inextricable biotic and abiotic drivers (Boulton & Lake, 2008).

The abrupt increase in trophic vulnerability in fragmented pools implies strengthening predator–prey interactions, which can potentially undermine food web stability (Ledger et al., 2013; McIntosh et al., 2017; Thompson et al., 2012). Drought therefore appeared to alter fundamental food web properties even at moderate disturbance intensities (i.e. when >50% of wetted habitat remained). However, our results only provide a snapshot of community properties in time, with the caveat that intense trophic interactions in fragmented pools are likely to be transient before predators exhaust their preferred food sources (Ledger et al., 2013). Nonetheless, rewiring of predator–prey linkages following prey loss can be strongly destabilising in

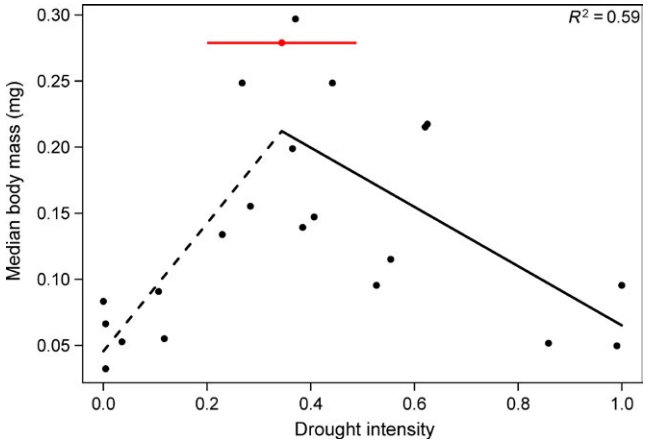

FIGURE 4 The impact of drought intensification on median body mass across all individuals of all taxa. For interpretation of segmented models see Figure 2

freshwater food webs, potentially leading to the extinction of secondary prey species (Gilljam, Curtsdotter, & Ebenman, 2015). Given that the dominant predators in our mesocosms were generalists (tanypods), and hence likely to be able to exploit alternative prey,

the population crashes of prey species we observed may thus have negative implications for network resistance over the longer term.

Prey population collapses as channels fragmented led to unexpected changes in body size. We predicted a trend to smaller body sizes as drought intensified (cf. Ledger et al., 2011), but instead observed an abrupt increase in median body mass under moderate drought intensity, as worm and orthoclad populations crashed. This body size response thus appeared to be a product of transient predator–prey interactions, and could therefore be similarly short-lived. Indeed, such a marked change in body sizes in response to pool fragmentation was not observed after 18 months of drought, when the primary impact was an irruption of small taxa as streams dried (Aspin et al., 2019). This suggests that, as drought duration increases (and/or as remnant pools dry), the principal driver of body size in stream invertebrate communities is likely to shift from predator–prey interactions to the competitive advantage afforded by *r*-selection. Our findings nonetheless challenge the consensus that drought disproportionately affects high trophic levels (Ledger et al., 2013) and contribute to a growing body of evidence (e.g. Gibb et al., 2017; Nelson et al., 2017; O'Gorman et al., 2017) documenting exceptions to the general principle that climate change and environmental disturbance discriminate against large body size (Daufresne, Lengfellner, & Sommer, 2009; Ledger et al., 2013; Woodward et al., 2005).

Our finding of abrupt shifts in community structure under relatively low intensity disturbance implies that stream ecosystems may be more vulnerable to future droughts than the received wisdom suggests, given that much of our knowledge comes from seasonal drying events in historically intermittent systems (Datry, Fritz, & Leigh, 2016). Gauging ecological resistance to truly extreme drought (i.e. in the absence of any evolutionary adaptation) will thus rest on more manipulative experiments exposing communities to alien hydrological conditions across broad disturbance gradients (Kayler et al., 2015). We have shown this last detail to be crucial, as a gradient-based approach can capture the potentially destabilising effects of progressively intensifying trophic interactions in increasingly confined or fragmented habitats. The population collapses of prey taxa that may result are unlikely to be detected by common biomonitoring indices, as these are typically formulated on the basis of abiotic tolerance profiles and presence–absence data (e.g. Chadd et al., 2017). We therefore propose adapting monitoring programmes and management strategies for drought- and abstraction-impacted streams, to incorporate greater recognition of the impacts of biotic stress.

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SUPPORTING INFORMATION

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

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