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Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying

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SUMMARY

1. Seasonal droughts are predictable components of arid-land stream hydrology, and many arid-land aquatic taxa have adapted to their extreme environment. However, climate change is altering this predictable hydrology, producing longer and more severe droughts and creating novel disturbance regimes for resident organisms.

2. The hydrologic transitions from flowing stream to fragmented pools to dry stream bed are frequently associated with steep decreases in taxonomic and functional diversity, referred to as thresholds of biodiversity loss. Less is known about how taxa respond between these thresholds, as fragmented pools gradually dry and abiotic conditions intensify. While an increasingly extreme environment may be expected to reduce taxonomic and trait richness, species adapted to predictable seasonal fragmentation may be resistant to declining water levels until all surface water is lost. We used aquatic mesocosms to test two competing hypotheses of the relationship between richness and pool drying for arid-land stream invertebrates: (i) the drought vulnerability hypothesis (richness gradually decreases with drying) and (ii) the drought resistance hypothesis (richness remains constant until complete drying occurs).

3. We inoculated replicate mesocosms with aquatic invertebrates from arid-land streams in Arizona, U.S.A., and applied three drying treatments representing a continuum of drying stress commonly observed in local streams during the summer dry season (water depths: 10, 7 and 1 cm). Mesocosms were covered to restrict dispersal and colonisation processes and to isolate resistance (*in situ* survival of species) from resilience (community recovery following disturbance). After 45 days, we destructively sampled all invertebrates in the mesocosms and calculated various taxonomic and functional trait metrics.

4. Taxonomic richness and composition did not differ between drying treatments, providing strong support for the drought resistance hypothesis. Severe drying was associated with lower invertebrate abundances and higher densities than the moderate and control treatments. This finding suggests that density-dependent processes generated by decreased available habitat may be more important determinants of community composition during droughts than abiotic stress in this system.

5. We observed a near-complete overlap of trophic traits (body size and functional feeding group) and resistance traits (respiration mode and diapause) among the three treatments. This high functional redundancy may provide a buffer against changes to ecosystem functioning, even in cases of severe-drying-induced habitat contraction and fragmentation.

Keywords: aquatic community, climate change, drought, drying disturbance, functional redundancy

Introduction

Droughts are predicted to increase in frequency and severity in many arid regions (Hoerling & Eischeid, 2007; Seager *et al*., 2007; Balling & Goodrich, 2010), and it is imperative that we understand how aquatic communities will respond to these events. Arid-land streams are characterised by predictable cycles of severe floods

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and droughts (Lake, 2003), and most of the resident taxa have developed adaptations to this extreme environment (Lytle & Poff, 2004). However, drought-induced changes in seasonal hydrology may present aquatic taxa with novel disturbance regimes to which they are not adapted (Lake, 2003; Lytle & Poff, 2004), making it difficult to predict the responses of biological communities to these altered flow regimes.

Boulton (2003) proposed a useful framework to describe the relationship between aquatic biodiversity and stream drying through time (Fig. 1). He envisioned a stepped response, with gradual species losses punctuated by thresholds of high diversity loss as streams pass through important hydrologic transitions. These thresholds mark (i) the loss of lateral connectivity, when a flowing stream recedes away from the riparian zone (Fig. 1A), (ii) the cessation of flow, when a stream contracts into stagnant pools (Fig. 1B), (iii) the loss of surface water (Fig. 1C) and (iv) eventual loss of hyporheic refuges (Fig. 1D). Since the publication of Boulton's framework, multiple studies have provided empirical evidence of the existence of thresholds of biodiversity loss during drying of aquatic habitats (Acuña *et al.*, 2005; Dewson, James & Death, 2007; Walters & Post, 2010). However, the relationship between drying and biological diversity during the periods between these thresholds has received much less attention, despite its importance in understanding the overall community response to drying.

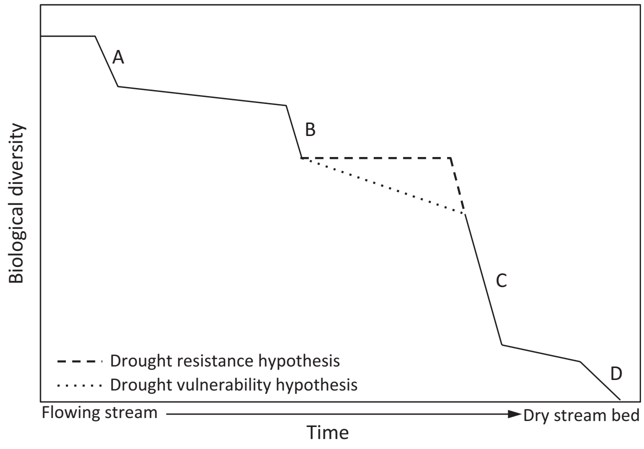

Fig. 1 Changes in biological diversity associated with major hydrologic transitions during stream drying, modified from Boulton, 2003 Figure 1. (A) Loss of lateral connectivity to the riparian zone, (A) loss of longitudinal connectivity and cessation of flow, (C) loss of surface water and (D) loss of hyporheic refuges. The period of this study is between thresholds B and C. The drought resistance hypothesis and drought vulnerability hypothesis are represented by dashed and dotted lines, respectively.

The period between flow cessation (Fig. 1B) and complete water loss (Fig. 1C) represents gradual drying of fragmented pools and is accompanied by concurrent changes in abiotic conditions. As stagnant pools dry, temperature and conductivity increase and dissolved oxygen decreases (Everard, 1996; Lake, 2000). Evaporation of water causes total habitat area to shrink, and the remaining aquatic fauna may reach high densities (Lake, 2003), increasing both the intensity of interactions among species (Power, Matthews & Stewart, 1985) and the likelihood that species could be eliminated via predation or competitive exclusion. These harsh abiotic conditions may act as a habitat filter that limits surviving species to those with traits conferring resistance to extreme environmental conditions (Chase, 2007). Under this premise, we may expect gradual losses in taxonomic and trait diversity as abiotic conditions in pools worsen and the slope of the line between thresholds B and C to be negative (Fig. 1, dotted line).

However, antecedent flow conditions and the natural periodicity of drought will affect species-specific responses to drying, potentially minimising the decline in diversity between drying thresholds. The local history of drought severity, frequency and duration probably determines whether aquatic organisms at a given site possess traits that allow them to withstand drought disturbances (Lake, 2003; Lytle & Poff, 2004). If local taxa are highly adapted to droughts and the biotic and abiotic changes that accompany them, then drying may not trigger a decrease in taxonomic or trait diversity until all surface water is lost, and the interthreshold slope may be zero (Fig. 1, dashed line). Predictable background cycles of severe floods and droughts in arid regions may mean that some droughts do not function as disturbances at all (Resh *et al.*, 1988).

In this study, we examined the relationships between severe pool drying and taxonomic and trait diversity in an arid-land stream system with a history of extreme yet predictable seasonal droughts. We tested two alternate hypotheses regarding the relationship between drying and diversity, which we have called the drought vulnerability hypothesis (negative interthreshold slope; Fig. 1, dotted line) and the drought resistance hypothesis (flat interthreshold slope; Fig. 1, dashed line). We expected taxonomic and trait diversity to respond similarly to drying since survival of any given species under harsh conditions should be determined by its biological traits. We inoculated aquatic mesocosms with arid-land stream invertebrates, applied three drying treatments representing a continuum of drying stress and then calculated taxonomic and trait diversity of the resulting communities. An observation of decreasing diversity with increasing severity of drying would support the vulnerability hypothesis, whereas the lack of a treatment effect would support the resistance hypothesis. We believe that understanding how arid-land stream biodiversity responds during this interthreshold period will inform our ability to manage these vulnerable ecosystems as drying regimes intensify in future.

Methods

System

This study was conducted in the Chiricahua Mountains of south-eastern Arizona, U.S.A., an arid-land mountain range that receives an average of 46 cm of rainfall annually (range: 18–65 cm, based on 1995–2011 records). Streams in this range generally contain reaches with perennial water between 1500 and 2200 m and become intermittent or ephemeral downstream. The extent and duration of flow are determined by bimodal annual precipitation patterns that consist of intense, localised monsoon rains during late summer (July to September), moderate but more widespread winter rains (November to March) and a late spring and early summer dry season (April to June). On average, only 6% (2.8 cm) of the annual rainfall occurs during this 3-month dry season. During the dry season, many streams naturally fragment to a series of small bedrock pools, often separated from one another by dry reaches (Bogan & Lytle, 2007).

Mesocosms

We simulated replicate fragmented pools with 40-L plastic tanks (hereafter 'mesocosms') filled with well water. We sampled aquatic invertebrates from three streams in the Chiricahua Mountains: Cave Creek, East Turkey Creek and North Fork Cave Creek, using a 500-μm-mesh D-frame net, taking care to sample representative microhabitats (see Bogan & Lytle, 2007 for full sampling description) and collect sediment and detritus in each stream. We combined these samples in a 200-L tank to create a diverse inoculum with which to seed the mesocosm communities (Boersma, 2013). The inoculum was distributed across 24 containers – 21 were added to the mesocosms and 3 were preserved in 70% ethanol as initial samples. Mesocosms were arranged in a grid, 25 cm apart and *c*.500 m from the nearest intermittent stream, and each contained a single cinder block as habitat structure. We added well water to mesocosms twice weekly to maintain three drying treatments: control – constant water level at 10 cm depth; moderate drying – water level was allowed to decrease to 7 cm; and severe drying – water level was allowed to decrease to 1 cm. Moderate and severe treatment mesocosms reached target water levels after weeks 1 and 3 of the 6-week experiment, respectively. We randomly applied treatments to 21 mesocosms, producing 7 mesocosms per treatment. Wildlife consumed the water in one mesocosm, reducing the sample size to six for the moderate treatment.

Several studies have documented the importance of aerial colonisation in driving community structure in streams in this region (Velasco & Millan, 1998; Bogan & Boersma, 2012; Boersma, 2013). In this study, however, we were interested in the *in situ* community responses to drying and subsequent loss of taxa, not the recovery of extirpated populations (e.g. resistance, not resilience, sensu Lake, 2013), so we restricted aerial colonisation by installing a shade cloth over each mesocosm. We compared taxa present in our three initial samples with those at the end of the experiment and found that the cover effectively prohibited most aerially dispersing taxa from colonising the mesocosms. Because of the small number of initial samples, we consider our inference of limited colonisation to be conservative. Despite the shade cloth, water temperature and conductivity in mesocosms equalled or exceeded typical in-stream measurements during the summer dry season (Bogan *et al.*, 2013b).

The experiment was conducted during the peak of the summer dry season, from 19 May to 3 July 2011. At the conclusion of the experiment, the contents of each mesocosm were preserved in 70% ethanol and identified to the lowest practical taxonomic level given available keys (Merritt, Cummins & Berg, 2008). We measured temperature, dissolved oxygen, conductivity and pH in each mesocosm at the end of the experiment. We installed six iButton temperature loggers (Maxim Integrated, San Jose, CA, U.S.A.) to record temperature every 6 h in the mesocosms. Only two loggers survived the harsh mesocosm conditions, in control and moderate treatments. These loggers reported a mean diurnal temperature fluctuation of 13.3 °C and an overall mean of 27.5 °C and will not be discussed further. All references to temperature are from measurements taken by hand.

Statistical analysis

Abiotic variables. After examining statistical distributions for each variable and verifying that parametric assumptions were met, we compared environmental variables between treatments at the end of the experiment using analysis of variance (ANOVA).

Community turnover. The small number of initial samples (three) prohibited direct multivariate comparisons between initial and final samples; however, we did examine the identities and abundances of taxa that were exclusive to either initial or final samples. We considered a taxon to have been eliminated by the drying treatments if initial samples contained >5 individuals and it was absent from final samples. We considered a taxon to have colonised despite the shade cloth if it was absent from initial samples and final samples contained >5 individuals.

Taxonomic and functional diversity. We calculated species richness, Shannon diversity and abundance for each mesocosm and compared them between treatments using analysis of variance (ANOVA), as richness values were large enough to meet parametric assumptions. To account for habitat loss during drying, we also calculated densities of individuals per unit volume of water and compared them using the Kruskal–Wallis test (unequal variance among treatments prohibited the use of parametric tests). We used permutation-based ANOVA (PERMANOVA) to test for treatment differences in community composition. We calculated community dispersion with a Sørensen distance measure (Sørensen, 1948) and compared dispersions between treatments using a permutation test with 999 permutations (Anderson, 2006).

According to the habitat filter framework (Townsend & Hildrew, 1994; Poff, 1997), an extreme environment may eliminate species with maladaptive trait combinations and permit those with favourable trait combinations to survive. We used *a priori* knowledge from other studies conducted in the region (Bogan & Lytle, 2011; Bogan, Boersma & Lytle, 2013a; Boersma, 2013) to select four traits that we believed would be associated with organismal responses to drying disturbance: two resistance traits (respiration mode and diapause capacity) and two trophic traits (body size and functional feeding group). Trait values for each taxon were treated as exclusive categories, producing a total of 17 modalities, 15 of which were represented in species collected in our experiment. Reliable trait information was not available for four taxa of non-insects (copepods, ostracods, aquatic mites and oligochaetes). These taxa were rare in mesocosm samples and were eliminated from our calculations. Trait modalities, values and references are provided in Appendices S1 and S2 in Supporting Information.

We calculated two functional diversity metrics to quantify differences in trait composition between treatments: functional richness and Rao's quadratic entropy. Functional richness is the volume of trait space occupied by a set of species and is determined by the presence or absence of individual trait combinations (Villéger, Mason & Mouillot, 2008). Rao's quadratic entropy (Q) is an abundance-weighted metric that measures the mean pairwise distances of randomly selected individuals in the community (Rao, 1982; Botta-Dukát, 2005). Both metrics require *a priori* identification of traits that can be measured or specified from the literature for every species. Combined, these two metrics provide information on the overall range of trait combinations and how these combinations are distributed across species. We compared functional richness between treatments using a Kruskal–Wallis test and Rao's quadratic entropy with ANOVA.

We used non-metric multidimensional scaling (NMDS) ordination with a Sørensen distance measure to visualise compositional patterns in species traits for species with >5 individuals in the final samples. After considering NMDS stress and interpretability, we present two-dimensional ordinations of the untransformed trait matrix here. In addition to quantitatively comparing the functional diversity metrics between treatments, we visually examined patterns in functional redundancy by plotting resistance and trophic traits by treatment.

Previous research has documented a high proportion of invertebrate predators in drying streams (Stanley *et al.*, 1994; Acuña *et al.*, 2005; Bogan & Lytle, 2007, 2011). To examine differences in predator proportions across a drying intensity gradient, we compared the prevalence of predators between treatments using predator/prey ratios, defined as the abundance of predatory taxa >10 mm divided by the abundance of all remaining taxa. We tested for differences in predator/prey ratios using ANOVA.

All analyses were conducted in R, version 2.14.1 (R Development Core Team) with the vegan (Oksanen *et al.*, 2012) and FD (Laliberté & Legendre, 2010; Laliberté & Shipley, 2011) packages.

Results

Abiotic variables

Mean water levels were 10.7, 7 and 1.1 cm for control, moderate and severe treatments, respectively (Table 1). Steep mesocosm walls caused the surface area of benthic habitat to vary little among treatments, although the

Table 1 Abiotic measurements taken at the end of the *c*.45-day experiment

	Treatment	Maximum	Mean	Minimum	Standard deviation	Significant pairwise comparisons
Depth (cm)	Control	11	10.7	10	0.49	All***
	Moderate	8	7	6	0.89	
	Severe	2	1.1	0	0.69	
Conductivity (μS cm^{-1})	Control	1211	1064	998	83.5	
	Moderate	1352	1269	1160	87.8	Control versus Moderate***
	Severe	3270	2907	2180	385.4	Control versus Severe***
Dissolved oxygen (ppm)	Control	12	8.2	5	2.8	None
	Moderate	11	8.2	6	2.2	
	Severe	12	10	7	2	
Temperature (°C)	Control	29.9	29.0	28.3	0.53	
	Moderate	30.6	29.7	29	0.59	Control versus Severe*
	Severe	31.9	30.5	28.7	1.21	
pH	Control	8	7.3	7	0.45	None
	Moderate	7.5	7.2	7	0.27	
	Severe	8	7.6	7	0.42	

Statistical significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

level of inundation above the substratum was more variable within severe treatment mesocosms than in the other treatments. Substratum in control and moderate treatment mesocosms was inundated by a minimum of 9 and 5 cm of water, respectively. The severe treatment mesocosms were characterised by *c*.20% wet, exposed substratum and *c*.80% shallow puddles of 2 cm depth or less (Table 1). On average, conductivity was nearly three times higher in the severe treatment than in the control (means: control = 1064 μS cm^{-1}, moderate = 1269 μS cm^{-1} and severe = 2907 μS cm^{-1}, Table 1), and temperature was higher in the severe treatment for both control/severe and moderate/severe comparisons (means: control = 29.0 °C, moderate = 29.7 °C and severe = 30.5 °C, Table 1). We observed no differences between treatments in pH or dissolved oxygen (Table 1) at the end of the experiment.

Community turnover

Sixty-three taxa were present in our three initial samples. Twenty taxa were eliminated during the course of the experiment (provided in Appendix S3), including 14 true fly taxa (10 midges and 4 other Diptera taxa) and two taxa each of caddisflies, mayflies and true bugs. Most of these 20 drying-eliminated taxa are normally found in cooler, flowing water (Merritt *et al.*, 2008) rather than in warm, still pools like those simulated by our mesocosms. An examination of coarse trait patterns for surviving and eliminated taxa revealed no apparent patterns in body size, diapause or respiration. We found that taxa classified as collector-gatherers showed a higher rate of extirpation than other functional feeding groups (40% of disappearing taxa versus 24% of surviving taxa) although formal statistical analyses were not applied, so we cannot draw inferences from this pattern.

Sixteen insect taxa in the final samples were not present in the initial samples (provided in Appendix S4), representing either rare taxa that were not detected due to the small number of initial samples or taxa that colonised despite the colonisation barrier. Of these, 12 had abundances ≤5 individuals and were probably not detected in the initial samples due to sampling effects. The remaining three taxa were the mosquito *Anopheles*, the beetle *Berosus punctatissimus* and the true bug *Ambrysus woodburyi*, with 30, 23 and 7 individuals in final samples, respectively. All of the *Anopheles* and nearly all of the *Berosus* were larvae found in a single mesocosm, suggesting that these individuals developed from a single egg mass during the course of the study. *A. woodburyi* are capable of dispersing over land as adults and colonising isolated mesocosms (Bogan & Boersma, 2012), and the most parsimonious explanation for their presence in final mesocosm samples is that they landed on shade cloths and entered through small gaps at the edges of the mesocosms.

Taxonomic diversity

Fifty-two taxa were identified in our final mesocosm samples. We found no significant differences between treatments in species richness (ANOVA, $F_{2,17} = 2.111$, $P = 0.152$; Fig. 2a) or Shannon diversity (ANOVA, $F_{2,17} = 0.4923$, $P = 0.620$; Fig. 2b). Total mesocosm abundance was significantly higher in control and moderate treatments than in the severe treatment (ANOVA, $F_{2,17} = 11.367$, $P = 0.0007$;

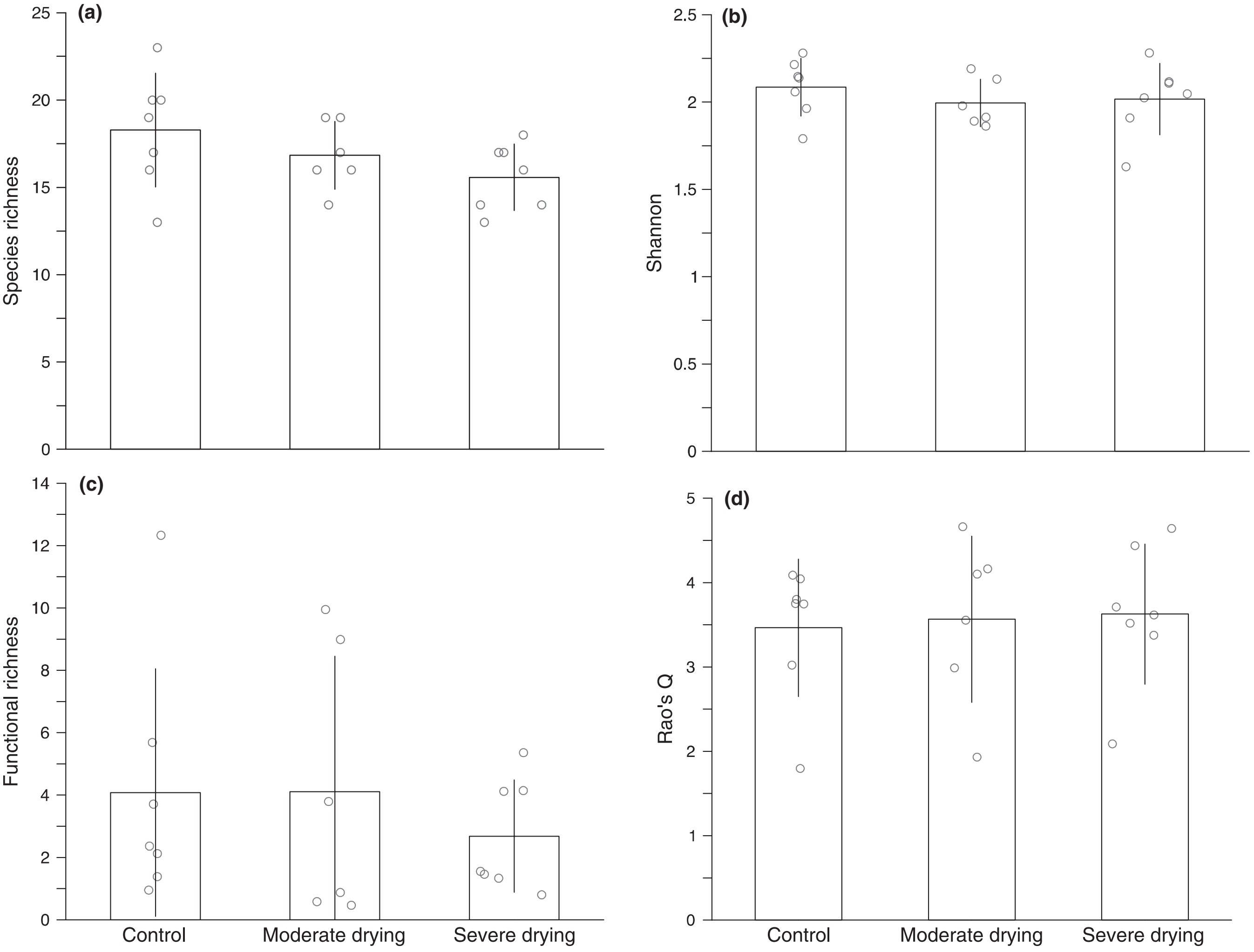

Fig. 2 Taxonomic and functional diversity metrics by drying treatment. (a) Species richness, (b) Shannon diversity, (c) functional richness and (d) Rao's quadratic entropy. Points are jittered along the *x*-axis to facilitate interpretation of variability in the response. There are no significant differences between any treatment combinations for any panel.

Bonferroni-corrected multiple comparisons: control/moderate, $P = 0.580$; control/severe, $P = 0.0007$; moderate/severe = 0.0186, Appendix Figure S5a), although density increased with drying severity (Kruskal–Wallis, $\chi^2_2 = 13.895$, $P = 0.001$; multiple comparisons: control/moderate, $P > 0.580$; control/severe, $P < 0.001$; moderate/severe, $P < 0.05$, Appendix Figure S5b).

We found significant differences in community composition between the treatment groups based on species abundances (PERM ANOVA, $F_{2,17} = 2.070$, $P = 0.018$) and species densities (PERMANOVA, $F_{2,17} = 6.382$, $P = 0.001$). However, this pattern disappeared when we analysed the presence/absence (species richness) matrix (PERMANOVA: $F_{2,17} = 0.818$, $P = 0.695$), suggesting high overlap of species composition among treatments. Multivariate dispersion did not differ between treatments for abundance, density or presence/absence matrices (permutation test: species abundances, $P = 0.735$; species densities, $P = 0.391$, presence/absence, $P = 0.18$).

Functional diversity

We found no treatment effects on either functional richness (Kruskal–Wallis, $\chi^2_2 = 0.4918$, $P = 0.782$; Fig. 2c) or Rao's quadratic entropy (ANOVA, $F_{2,17} = 0.062$, $P = 0.940$; Fig. 2d), although the range of functional richness decreased along a gradient of increasing drought severity (range: control = 11.380, moderate = 9.485 and severe = 4.559). Also, we did not detect differences in predator/prey ratios between treatments (ANOVA, $F_{2,17} = 0.052$, $P = 0.950$). NMDS ordinations of species in trait space reflect the relationship between traits of taxa that were present in both control and moderate treatment mesocosms but not in severe treatment mesocosms

(NMDS, $k = 2$, stress = 0.0683, $R^2 = 0.979$, Fig. 3). These 'filtered-out' trait combinations were distributed across all trait modalities, demonstrating that there were no apparent patterns in the traits of species eliminated by the severe drying treatment. Separate plots of trophic and resistance traits highlight the complete redundancy of trophic traits (Fig. 4) and near-complete redundancy of resistance traits (not shown).

Discussion

We experimentally manipulated drying severity in mesocosms containing arid-land aquatic invertebrate taxa to test two competing hypotheses about how aquatic organisms respond to pool drying during the summer dry season. We found that taxonomic and functional richness of invertebrate communities did not differ between drying treatments despite dramatic differences in water quality and habitat availability. This lack of treatment effect supports the drought resistance hypothesis, under which taxonomic and trait diversity remains constant as water levels decline in fragmented pools. We did observe significant differences between drying treatments in the density of individuals, suggesting that decreasing water volume is an important factor in aquatic community responses to drought.

Resistance of taxonomic diversity

Our results corroborate other research documenting high tolerance of aquatic invertebrates to short-term drying stress, even in temperate streams without a history of severe drying. Dewson *et al.* (2007)conducted experimental water diversions in small streams in New Zealand and observed little change in species richness, which they credited to the presence of aquatic refuges during drying. As in our experiment, they saw a marked increase in the density of invertebrates in remaining

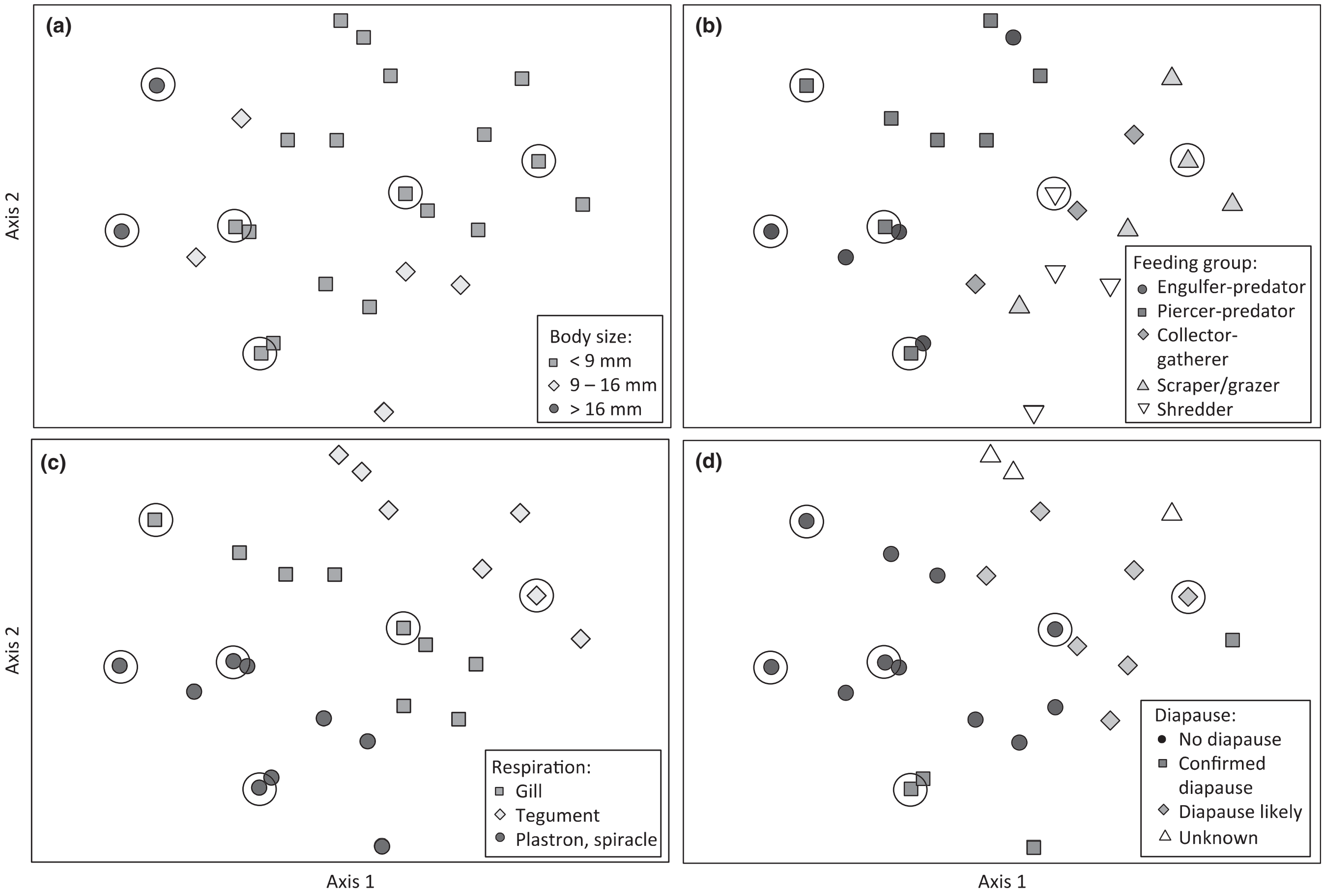

Fig. 3 Non-metric multidimensional scaling ordinations of species in trait space (NMDS, $k = 2$, stress = 0.0683, $R^2 = 0.979$). Each point is a species with abundance >5. Points are shaded to indicate different trait modalities within each trait category: (a) body size, (b) functional feeding group, (c) respiration and (d) diapause. Species that were present in the control and moderate drying treatments but absent from the severe drying treatment are indicated by grey circles. Note: species with overlapping trait combinations appear as a single point on each plot.

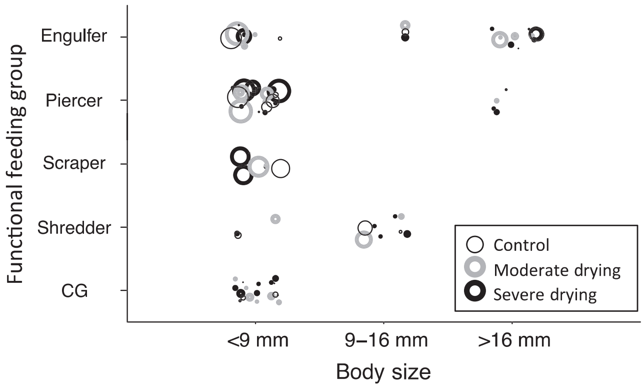

Fig. 4 Functional redundancy in trophic traits. Each circle represents a species, where circle size reflects its relative abundance and circle shading/weight reflects treatment: thin black = control; thick grey = moderate drying; and thick black = severe drying. Circles within each trait combination are jittered so the overlap among treatments is visible; blank spaces mark trait combinations that were not represented in our samples. All represented trait combinations contain circles of all three colours, indicating complete functional redundancy.

aquatic habitat. Walters & Post (2010) similarly found no effect of water diversion on species richness in small streams in the north-eastern U.S.A. and saw significant increases in invertebrate density and decreases in biomass as water receded. Habitat contraction and loss have been identified as drivers of aquatic community responses to drought in many other stream studies (Stanley, Fisher & Grimm, 1997; Bunn & Arthington, 2002; Acuña *et al.*, 2005), and the most commonly observed result is an increased density of invertebrates (e.g. Walters & Post, 2010).

While habitat contraction and decreasing water volume are likely drivers of invertebrate density, factors determining invertebrate abundances may be more complex. Intuitively, an increasingly extreme abiotic environment can decrease invertebrate abundances (Chase, 2007). However, the lack of a significant treatment effect on species richness suggests that biotic drivers may be more important in this experiment and that the abundance response may involve density-dependent processes occurring at individual, population and species levels. High densities of invertebrates are known to limit resource availability and increase the intensity of biotic interactions (Power *et al.*, 1985; Malmqvist & Sackmann, 1996). Further experiments manipulating both invertebrate density and environmental variables are necessary to disentangle the biotic and abiotic drivers of our observed abundance patterns.

While similar results have been obtained in other systems, our study is unique in that it isolated the *in situ* tolerance of organisms to deteriorating conditions from the movement of organisms between aquatic habitats (community resistance from resilience). Environmental stress, such as drying, heat and flooding, can trigger dispersal in many stream systems (Smith, 1973; Velasco & Millan, 1998; Lytle, Olden & Mcmullen, 2008), and Bogan & Boersma (2012) demonstrated that aerial dispersal occurs frequently in fragmented arid-land streams during the dry season. It is plausible that the drying–diversity relationship observed in many other studies could be due to the movement of individuals into and out of drying habitats instead of the survival or mortality of local individuals, as is frequently assumed. We minimised the confounding influences of dispersal and colonisation with a shade cloth installed just above the water's surface in each mesocosm. Thus, we can say with confidence that many arid-land stream pool taxa have high resistance to drying – with few exceptions, the only organisms in our mesocosms were ones that we inoculated or larvae that developed during the experiment.

Our dispersal/restriction canopy allowed us to isolate *in situ* resistance from dispersal/colonisation processes; however, it came with the cost of some ecological realism. The canopy limited light penetration, probably impacting primary productivity and diel temperature fluctuations. It prevented allochthonous inputs and the arrival of additional prey taxa, thereby restricting the availability of resources to resident taxa. All organic material in mesocosms arrived during the initial inoculations. The canopy also prevented insects from emerging from the mesocosms. We found few carcasses in our samples, suggesting that insects that were unable to emerge were consumed. The only dead or decaying organisms present in our samples belonged to three genera of caddisfly larvae that build protective cases out of small rocks and twigs (*Helicopsyche*, *Hesperophylax* and *Oecetis*) and were probably inedible to most predators (Nislow, Molles & Manuel, 1993).

Resistance of functional diversity

High resistance of taxonomic diversity is one way that arid-land stream communities are buffered against environmental extremes; a redundancy of functional traits is another. Functional redundancy is the degree to which taxonomically distinct species fulfil similar ecological roles in an ecosystem or possess similar traits (Rosenfeld, 2002), and it may provide ecosystems with a level of insurance against the loss of ecosystem functioning that accompanies species extinctions (Petchey *et al.*, 2007; Philpott, Pardee & Gonthier, 2012). We observed complete redundancy of trophic traits (Fig. 4) and near-complete redundancy of resistance traits (not shown) among treatments. High functional redundancy may explain the lack of a treatment effect on our two functional diversity metrics.

As many recent trait studies have demonstrated, our ability to observe patterns in functional diversity depends upon trait choice (e.g. Petchey & Gaston, 2006). With only four traits, we are more likely to observe redundancy and less likely to observe treatment effects than with a larger trait set. However, we selected these traits using extensive knowledge from studies on species responses to drought both from this and from other arid-land aquatic systems, and we believe that our trait analysis is robust. It is well documented that aquatic invertebrate trophic structure is vulnerable to drying stress in our system (Bogan & Lytle, 2007, 2011), and both body size (Daufresne, Lengfellner & Sommer, 2009; Walters & Post, 2010) and trophic level (Woodward *et al*., 2012; Ledger *et al*., 2013) are strongly affected by drying. Additionally, taxa that are adapted to intermittency are more likely to possess traits conferring desiccation resistance (Bonada, Rieradevall & Prat, 2007; Bogan *et al*., 2013a).

Conservation implications

While we found no effect of drying severity on taxonomic or functional diversity, our severe drying treatment maintained water depth at 1–2 cm so that sediment and detritus remained wet and small aquatic refuges were present. We did not apply a complete drying treatment in this study and therefore do not have direct evidence of the existence of a complete drying threshold (Fig. 1c). However, ample evidence for this threshold and the resulting biological responses comes from field observations of catastrophic drying events (e.g. Boulton & Lake, 1992; Acuña *et al*., 2005; Bêche *et al*., 2009; Bogan & Lytle, 2011). These field studies suggest that taxonomic richness is resilient to moderate and severe drying, but community composition and food web structure can change dramatically following complete drying events, when all aquatic refuges are lost. Bêche *et al*. (2009)found that recovery from supraseasonal drought was taxon specific and that large, dispersal-limited taxa never recolonised following drying disturbance. Bogan & Lytle (2011) observed no change in species richness post-drying but found similar selective recolonisation capacity, which led to the elimination of the top predator and a sharp increase in the abundance of mesopredators.

Understanding how aquatic communities respond to drying disturbances may allow us to manage aquatic resources to minimise catastrophic biodiversity loss during severe drought. Our research demonstrates that our dry season arid-land aquatic communities have high resistance and thus high buffering capacity against drought. For streams subject to both seasonal droughts and anthropogenic water use, water resource managers may be able to avoid catastrophic biodiversity losses during droughts by maintaining small aquatic refuges along the stream channel until water demands subside or drought ends (Magoulick & Kobza, 2003; Chester & Robson, 2011). Studies on resistance and resilience to drought are useful concepts to guide this research (Lake, 2013); however, it is important to understand how local background disturbance rates affect community responses to current and future disturbances (Lake, 2003; Lytle & Poff, 2004). Predictable seasonal droughts should be associated with pre-adapted communities that demonstrate high resistance and resilience to seasonal drying, whereas supraseasonal droughts are unpredictable and may act as catastrophic disturbances. The situation becomes grave when droughts are supraseasonal and water demands are not likely to subside. Given that arid lands are considered especially vulnerable to increased supraseasonal warming and drying in a changing climate, research on both biological and societal drivers of arid-land stream community structure will become increasingly important.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Trait modalities.

Appendix S2 Trait values for invertebrate taxa.

Appendix S3 Taxa eliminated by the drying treatments.

Appendix S4 Taxa absent from initial samples and present in final samples.

Appendix S5 Abundance and density of invertebrates by treatment.

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