Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams

MICHAEL T. BOGAN*, KATE S. BOERSMA[†] AND DAVID A. LYTLE[†]

*Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, U.S.A.

[†]Department of Integrative Biology, Oregon State University, Corvallis, OR, U.S.A.

SUMMARY

1. Climate change is expected to intensify drought in many regions, but ecological impacts on stream communities are poorly understood. Many arid-land streams are characterised by predictable seasonal cycles of wetting and drying, to which species are adapted, but unpredictable supraseasonal droughts may constitute extreme events that challenge resident biota.

2. In this article, we synthesise research conducted in arid-land streams of the Madrean Sky Islands (MSI) in Arizona, U.S.A, to evaluate the resistance and resilience of invertebrate communities to drying disturbances caused by normal seasonal drying and severe supraseasonal drought. We also highlight how spatial context (e.g. distance to perennial refuges) influences recovery patterns.

3. Invertebrate community structure changes predictably as habitat contraction progresses from loss of lateral connectivity to complete drying of MSI streams. When drying events are predictable (e.g. seasonal drying), post-drought community recovery is often rapid, since most MSI taxa possess life history traits conferring high resistance and/or resilience to stream drying.

4. Extreme supraseasonal droughts, in contrast, cause unprecedented transitions from perennial to intermittent flow in some MSI streams. While species richness may recover quickly following this flow regime shift, marked turnover in community structure can occur and may delay or preclude recovery to pre-drought conditions. In such cases, short-lived (<1 year) strong dispersers replace relatively long-lived (≥1 year) weak dispersers. As habitat isolation increases, the potential for community recovery from extreme drought decreases.

5. Many MSI aquatic species are threatened by extreme drought. Extinctions of endemic aquatic species due to habitat drying have already been observed in nearby deserts. Further studies are urgently needed to identify drought-sensitive species and understand how the loss of such species may affect stream ecosystem functioning.

Keywords: community recovery, disturbance, extreme climatic events, flow regime, long-term study

Introduction

Arid-land streams are characterised by harsh, but often predictable, cycles of flooding and drying (Lake, 2003). However, climate change and water withdrawals are altering flow regimes in these systems and may disrupt the predictability of seasonal flow patterns, with uncertain impacts on resident biota (Barnett *et al.*, 2008; Seager & Vecchi, 2010; Grantham *et al.*, 2012; Ficklin, Stewart & Maurer, 2013). Climate models predict that the frequency, duration and severity of meteorological drought will increase across many arid and semi-arid regions (e.g. Seager *et al.*, 2007). Meteorological droughts generally lead to hydrological droughts (e.g. flow reduction or cessation: Boulton, 2003; Lake, 2003) that can have major impacts on river flows. Many stream basins in the western United States are expected to transition from a semi-arid to arid state by the 2080s, with summer flows

declining by >45% (Ficklin *et al.*, 2013). The intensification of drying disturbance associated with drought presents significant challenges for stream biota adapted to predictable hydrology (Lake, 2003; Bêche *et al.*, 2009). For instance, adaptations to seasonal drying may not confer stability to future events of unprecedented frequency, intensity or duration (Bogan & Lytle, 2011; Jaeger, Olden & Pelland, 2014).

Given the growing prevalence of drought in some regions, it is essential to understand how aquatic communities respond to stream drying and how they recover (or fail to recover) from these events. Boulton (2003) proposed a conceptual model of aquatic invertebrate community responses to drought in which periods of gradual biodiversity loss associated with declining water quantity and quality are punctuated by abrupt, significant losses of biodiversity caused by the loss of lateral, longitudinal and vertical connectivity (also see Boulton & Lake, 2008). However, aquatic invertebrate species that experience regular drying disturbances, such as those in arid-land streams, are more likely to have life history adaptations that confer resistance and/or resilience to drought (Lytle & Poff, 2004). Evaluating the extent to which arid-land stream biota conform to Boulton's (2003) model can reveal whether their response to drying disturbance is typical or not and may also provide insight into their sensitivity to more extreme drought regimes.

While Boulton's (2003) conceptual model describes biodiversity loss during stream contraction and drying, it does not address post-event community recovery. Biotic recovery from stream drying partly depends on event predictability and is often faster for annual seasonal drought than for unpredictable supraseasonal droughts (Gasith & Resh, 1999; Lake, 2003; Verkaik *et al.*, 2013). Stream biota generally exhibit low resistance and variable resilience to supraseasonal drought (Lake, 2003). While definitions vary, we use the term 'resistance' to describe the ability of individuals or communities to withstand a disturbance *in situ*, while the term 'resilience' describes individuals' or communities' capacity to recolonise a site and reestablish populations or communities similar to those that were present before the disturbance. Our ability to interpret resistance or resilience at any given site requires knowledge of the disturbance history of the system, including the frequency and severity of antecedent droughts (Lake, 2013). In addition to disturbance history, the spatial context in which drying disturbance occurs can shape post-disturbance recovery. Close proximity to drought refuges may facilitate recovery (Robson, Chester & Austin, 2011), while recovery in isolated habitats may take much longer (e.g. multiple years: Resh, 1992).

In this study, we synthesise research conducted in arid-land headwater streams of south-eastern Arizona, U.S.A, to evaluate ecological responses to seasonal versus supraseasonal drought. We report how aquatic invertebrate communities change as habitats contract and dry and describe the mechanisms of resistance and resilience that contribute to community recovery when habitats are rewetted. As seasonal drought in the study area often results in stream flow alteration that would be considered extreme in many regions (e.g. >95% habitat contraction and/or complete flow cessation: Bogan & Lytle, 2007), we first describe the impacts of these harsh, but predictable, seasonal droughts. We then consider the effects of unpredictable supraseasonal droughts which produce unusually intense drying events that extend into one or more wet seasons. We also discuss the spatial factors that constrain community recovery following these different types of droughts. We use these findings to adapt the conceptual model developed by Boulton (2003) and include potential post-drought recovery trajectories to explore whether extreme drought events alter even the most drought-adapted arid-land stream communities.

Study region and streams

The work we describe here was conducted in headwater streams of the Madrean Sky Islands (MSI). The MSI region encompasses a series of >30 semi-arid mountain ranges (2000–3300 m) isolated from one another by arid, lowland desert (800–1200 m). Stream networks in the region are not connected by continuous flow, but rather exist as a series of isolated perennial or intermittent headwater reaches, with long ephemeral reaches between perennial habitats (Bogan, Boersma & Lytle, 2013a; Stromberg *et al.*, 2013). While some aquatic invertebrates (e.g. Dytiscidae: Coleoptera) in the region readily disperse among these isolated aquatic habitats (Bogan & Boersma, 2012), genetic analyses of others (e.g. Hemiptera: Belostomatidae) indicate that dispersal across arid uplands is very limited (Finn, Blouin & Lytle, 2007; Phillipsen & Lytle, 2013).

The flow regimes of MSI streams are determined by a bimodal precipitation cycle that consists of intense, highly localised, summer monsoons (July–August) and less intense, more widespread, winter rains (November–March). Summer monsoons cause destructive flash floods in MSI streams (Lytle, 2000) but generally do not increase flow for more than a few days following storms

(Paulson *et al.*, 1991). Winter precipitation, in contrast, can raise groundwater levels across the region and result in widespread flow in intermittent reaches and increased base flow in perennial reaches (Bogan & Lytle, 2007; Bogan *et al.*, 2013a). While some MSI streams flow all year, most fragment to perennial pools or dry completely during dry seasons, especially in early summer (April–June) when wetted habitat area can contract by >95% (Fig. 1, arrows; Bogan & Lytle, 2007). Many MSI streams with intermittent flow will dry completely during early summer and may be dry for >9 months each year (Bogan *et al.*, 2013a). Ephemeral streams in the region generally flow for only a few hours or days following heavy precipitation (Jaeger & Olden, 2012) and were not sampled in the studies reviewed here. In addition to seasonal variation in precipitation and flow, interannual variation in these factors is also quite high.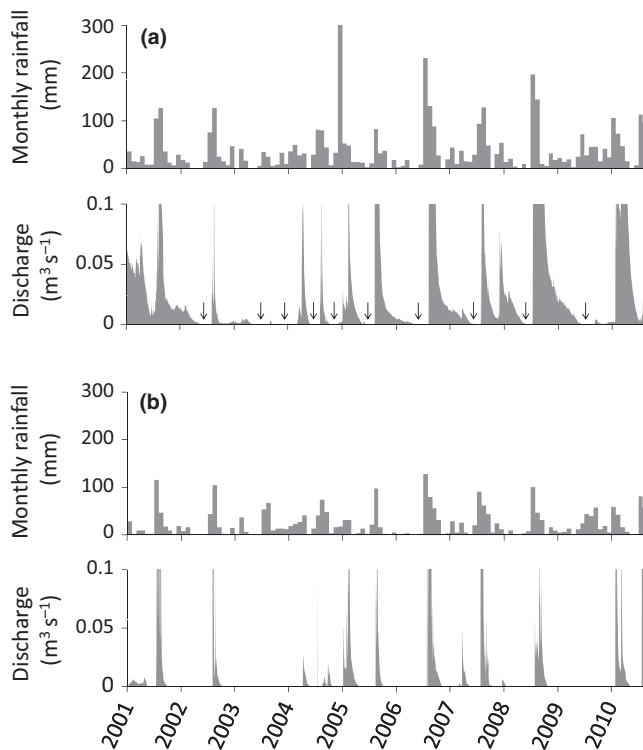 El Niño events (e.g. 2005, 2010, Fig. 1) bring abundant winter rains which result in higher flows in perennial reaches and widespread activation of intermittent reaches, while La Niña events (e.g. 2009, Fig. 1) may bring so little rain that no winter flow occurs.

Despite this high seasonal and interannual flow variability and the limited amount of aquatic habitat in this arid region, the MSI harbours a diverse aquatic invertebrate fauna. To date, we have recorded over 400 aquatic invertebrate taxa from the MSI (Bogan, 2012; Bogan *et al.*, 2013b,c). This high diversity is due in part to the overlapping biogeographic distribution of Nearctic and Neotropical faunas and the large number of regional endemics (Warshall, 1994; Bogan & Lytle, 2007; Bogan *et al.*, 2013b). MSI streams are ideal model systems to explore aquatic community responses to drought because they are highly diverse, tractable (i.e. small habitats simplify sampling and species detection) and can be replicated experimentally (i.e. via mesocosms which mimic dry season pools). Resident biota regularly experience harsh seasonal drought conditions and are generally regarded as being relatively resistant and/or resilient to predictable drying disturbances. However, it is less clear whether species with adaptations to regular drying events will persist through extreme droughts with no historical analogue (Leigh, 2013; Jaeger *et al.*, 2014).

Changes in species richness and community composition along a drying gradient

Loss of lateral connectivity

Loss of lateral connectivity of surface water occurs at the earliest stages of drought in streams, when formerly submerged, riparian, littoral areas dry (Fig. 2: threshold A). In many regions, this first transition represents an important loss of unique microhabitat, such as beds of aquatic plants or the submerged roots of riparian trees (Boulton, 2003). Arid-land streams, however, are rarely connected laterally to riparian corridors. Rather, many of these streams are in a state of either expansion or contraction (Stanley, Fisher & Grimm, 1997) and connection to lateral margins of the stream channel occurs only briefly. Thus, in most arid-land streams, it is unlikely that many species specialise in these ephemeral marginal habitats. However, a very small number of MSI streams are spring-fed and have nearly constant flow, including stream habitats known regionally as ciénegas (Hendrickson & Minckley, 1985) and desert oases (Felger, 1999). These spring-fed habitats support several species that are

Fig. 1 Examples of the high seasonal and interannual variability in monthly rainfall (mm) and daily mean stream discharge (m³ s⁻¹) in Madrean Sky Island streams, including (a) a perennial stream (Garden Canyon, AZ) where pools remain even when flow ceases during seasonal drought (indicated by arrows) and (b) an intermittent stream (Banning Creek, AZ) where flow occurs only during rainy seasons and the stream is completely dry for months (or years) between rainy seasons. Data are from United States Geological Survey flow gauges and peak discharges are truncated to facilitate display of dry season differences.
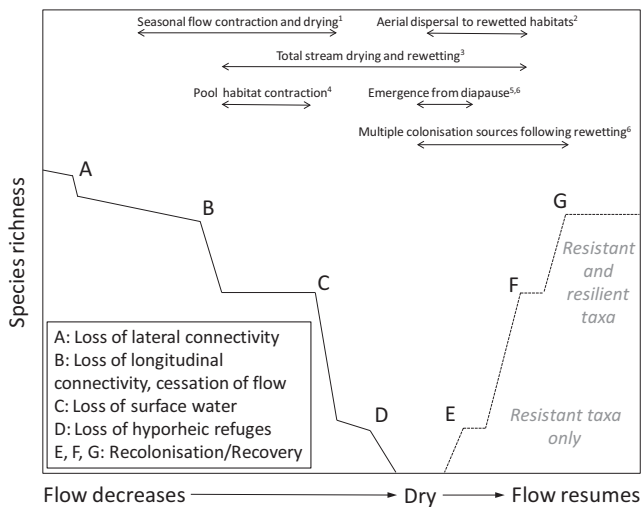
Fig. 2 Changes in aquatic invertebrate species richness in Madrean Sky Island streams as flow decreases due to drought conditions (solid line) and potential recovery trajectories (dashed line) following flow resumption [adapted from Boulton (2003)]. A–D: thresholds during drying when species richness declines rapidly due to macrohabitat loss. E: recovery by drought-resistant taxa only. F: recovery of species richness via aerial recolonisation of resilient taxa. G: full recovery of species richness via multiple resistance and resilience (instream and overland) pathways. Arrows at the top of the figure indicate processes contributing to species loss during drying and recovery and describe the time frames in which they are important. Superscripts reference studies quantifying the relationship between species richness and drying and rewetting events: [1]Bogan & Lytle, 2007; [2]Bogan & Boersma, 2012; [3]Bogan & Lytle, 2011; [4]Boersma *et al.*, 2014; [5]Bogan *et al.*, 2013a; [6]Bogan, 2012.

rare or absent in runoff-fed streams, including caddis flies that feed on aquatic vegetation (e.g. Hydroptilidae: *Oxyethira*) or freshwater sponges (Spongillidae) that encrust on submerged roots and support regionally rare populations of the spongillafly *Climacia chapini* (Bogan *et al.*, 2014). Thus, we would expect the loss of a small number of specialised species if drought or water withdrawals were to cause flow in these spring-fed habitats to decline and leave lateral stream margins dry (Fig. 2: threshold A).

Flow reduction and loss of longitudinal connectivity

Streams that maintain any year-round flow are uncommon in the MSI. Most streams in the region have only intermittent or ephemeral flow, although perennial pools may persist (Bogan & Lytle, 2007; Bogan *et al.*, 2013a). Streams with perennial flow support a number of taxa that are rare or absent in streams with temporary flow, including riffle beetles (Elmidae), water penny beetles (Psephenidae), crawling water bugs

(Naucoridae) and several families of stoneflies (Perlidae, Perlodidae and Chloroperlidae). A slight decline in the richness of assemblages is evident along a gradient of perennially flowing streams in the MSI (Fig 2: between thresholds A and B), from larger streams that maintain strong flow during seasonal drought to smaller streams that maintain only trickles of flow during the dry season (Bogan, 2012; M. T. Bogan, unpubl. data). Some taxa (e.g. Elmidae: *Macrelmis*; Psephenidae: *Psephenus*; Perlidae: *Anacroneuria*, *Hesperoperla*) are found only in larger streams that are less prone to seasonal flow declines, while others (e.g. Elmidae: *Zaitzevia*, *Microcylloepus*; Naucoridae: *Ambrysus*) are found across a range of flow types, including in streams where perennial riffles contract to small trickles (<4 L min^{-1}) during seasonal drought.

As drought conditions persist for several months, intermittently flowing streams in the MSI cease flowing entirely and only isolated perennial pools remain (Fig. 1). Boulton (2003) noted that this transition would likely be accompanied by a large loss of lotic species, with only lentic taxa remaining in stagnant water, a pattern observed in other arid-land stream systems (Stanley *et al.*, 1994; Leigh, 2013). In MSI streams, most lotic taxa disappear locally as longitudinal connectivity is lost, including stoneflies (e.g. Capniidae, Nemouridae), mayflies (e.g. Baetidae: *Baetis*) and caddis flies (e.g. Hydropsychidae), leaving only a tolerant subset of the year-round beetle (e.g. Dytiscidae: *Rhantus*, *Stictotarsus*), true bug (e.g. Belostomatidae: *Abedus*), caddis fly (e.g. Calamoceratidae: *Phylloicus*) and true fly taxa (e.g. Chironomidae, Stratiomyidae). The decline in species richness in these perennial pools due to flow cessation is only transient, however, as numerous species in several beetle and true bug families (e.g. Notonectidae, Corixidae, Hydrophilidae) soon colonise the pools. This seasonal drought-induced 'time-sharing' of stream habitats between the lotic Nearctic stonefly, mayfly and caddis fly taxa and lentic Neotropical beetle and true bug taxa occurs across the region (Bogan & Lytle, 2007; Bogan, 2012), provided that off-season refuges are available to serve as colonisation sources (see below). While the drying disturbance of seasonal drought does result in the local loss of many lotic species, these events actually increase the total number of species found at a site through time by opening up stream habitat to different taxa during the dry season (Bogan & Lytle, 2007). This predictable seasonal drying disturbance thus enables more aquatic invertebrate species to occupy a given MSI stream than would be found in the absence of seasonal drought.

Declining water levels in remnant pools

As water evaporates and groundwater inputs decline during seasonal drought, water levels in remnant pools decline and water temperature and conductivity increase while dissolved oxygen concentrations decrease (Lake, 2003). Whether such intensifying abiotic conditions reduce taxonomic diversity depends on the local history of drought and the extent to which aquatic organisms at a given site possess traits to withstand drying (Lake, 2003; Lytle & Poff, 2004). Where local taxa are adapted to predictable seasonal droughts, drying may not significantly reduce diversity until all surface water is lost. Pool drying is a complex process that can modify many biotic and abiotic processes (Boulton, 2003), and experimental manipulations are necessary to disentangle various potential mechanisms.

Boersma *et al.* (2014) conducted a mesocosm experiment to test the effect of declining pool volume on MSI aquatic invertebrate community structure during seasonal drought. They established mild, moderate and severe pool contraction treatments (water depths of 10, 7 and 1 cm, respectively) and restricted both emigration from and immigration to mesocosms to isolate community resistance to drying from resilience following drying. At the end of the 6-week experiment, severe drying increased conductivity and temperature above that in the other treatments, but community structure was not affected. Boersma *et al.* (2014) also calculated the functional diversity of traits associated with respiration, diapause, body size and functional feeding role and again found no treatment effect. This experiment revealed the high resistance of dry season taxa throughout the drying process and suggests that MSI stream pool taxa are well-adapted to harsh abiotic conditions, excepting complete drying.

Loss of vertical connectivity: complete stream drying

Complete stream drying occurs in temporary streams during typical drought seasons (Fig. 1; Bogan *et al.*, 2013a), but may also occur in normally perennial pools during unusually intense or prolonged droughts (Bogan & Lytle, 2011). This loss of vertical connectivity to ground water causes a drastic reduction in invertebrate richness, including the local extirpation of lentic fauna. Even highly resistant beetles, true bugs and true flies tolerant of marked reductions in water depth cannot withstand complete stream drying (Fig 2: threshold C), and many species use increasing water temperatures and conductivity as cues to aerially disperse from dry-

ing pools in search of perennial habitats (Velasco & Millan, 1998). Other taxa use positive rheotaxis to move towards perennial reaches during drying events (Lytle, McMullen & Olden, 2008). In the MSI, flightless species (e.g. Belostomatidae: *Abedus herberti*) may abandon dried pools and crawl along the dry stream channel in search of perennial water (Boersma & Lytle, in press). By contrast, many poor dispersers remain within the drying habitat and may seek refuge under damp substrata (e.g. *A. herberti*; Dytiscidae: *Agabus*; M. T. Bogan & D. A. Lytle, personal observ.). Refuge-seeking behaviour has also been reported in nearby Sonoran Desert streams (Stanley *et al.*, 1994; Shepard, 2011). These damp refuges are transient, however, and generally do not last longer than a week or two, after which time pool inhabitants have either dispersed aerially, sought refuge deeper in the hyporheic zone or perished (Stanley *et al.*, 1994).

Loss of wetted hyporheic habitats

There is some evidence that invertebrates can avoid dry surface conditions by migrating to wet hyporheic sediments (Stubbington, 2012), but during intense droughts, even these subsurface refuges can desiccate, impacting interstitial biota. Research on the hyporheos of MSI streams is lacking, but in nearby Sonoran Desert streams, mature biting midge larvae (Ceratopogonidae: *Probezzia*) appear almost immediately when surface flows resume, suggesting they use the hyporheic zone as a refuge from surface drying (Stanley *et al.*, 1994). Horsefly larvae (Tabanidae: *Tabanus*) can also diapause in these hyporheic habitats to avoid dry periods (Gray, 1981). Surface-dwelling invertebrates (e.g. *Probezzia*, *Tabanus*) are typically detected in the shallower sediments (<50 cm depth), suggesting they may be vulnerable to hyporheic drying as interstitial water levels decline (Fig. 2: between thresholds C and D). Surveys in Sonoran Desert streams found many obligate hyporheic invertebrates (10–50 taxa, mainly copepods, amphipods and mites) in deep sediments (up to 100 cm depth, Boulton, Valett & Fisher, 1992; Clinton, Grimm & Fisher, 1996). These taxa can migrate even further (>100 cm) to escape declining groundwater levels (Clinton *et al.*, 1996), but may be threatened where ground water recedes to great depth during extreme drought (Fig. 2: threshold D). Consistent with this, arid-land streams that dry to bedrock contain less diverse hyporheic communities than those that retain some water at depth, suggesting that many obligate hyporheic taxa lack desiccation-resistant stages (Cooling & Boulton, 1993; Boulton &

Stanley, 1995). In the case of complete hyporheic drying, only taxa with an anhydrobiotic resting stage (e.g. diapausing eggs or larvae) persist.

Resistance and resilience to seasonal and supraseasonal drought: recovery following rewetting

The wet/dry seasonal and interannual cycles that characterise the MSI region eventually return water to dry streams, even if only briefly (Fig. 1), providing an opportunity for aquatic community recovery (Fig. 2: thresholds E through G). Following drought, local species richness and community composition depend on two primary factors: (i) the severity of the drying disturbance (i.e. Was drought mild or extreme?) and (ii) the geographic context of the recovery process (i.e. Are colonist sources near or far?) (Robson *et al.*, 2011). The local history of drought frequency, duration and magnitude may also shape aquatic invertebrate responses to future disturbances. For example, a short-duration (e.g. 2 month) drying event is likely to be of little biological significance in an intermittent stream dominated by species with life history adaptations to drought, but may well represent an extreme disturbance in a perennial stream with no history of drying.

Recovery via resistance mechanisms

Few surface-dwelling aquatic invertebrates are truly resistant to complete drying of MSI streams, but there are a small number of specialised stoneflies (Capniidae), midges (Chironomidae), blackflies (Simuliidae) and dobsonflies (Corydalidae) that have egg or larval diapause stages that can withstand long dry periods (>9 months; Bogan & Lytle, 2007; Bogan, 2012; Bogan *et al.*, 2013a). These taxa are found almost exclusively in intermittent streams, including streams that are dry for a year or longer (Bogan *et al.*, 2013a). While taxonomic richness in these highly intermittent streams may only reach 10–20 species following rewetting (Fig. 2: threshold E), recovery occurs rapidly. Many resistant taxa reappear within 2–3 days of flow resumption (Bogan, 2012), and within 8–10 weeks, invertebrate densities in intermittent reaches are often equal to those in perennial reaches (Bogan *et al.*, 2013a). As most MSI intermittent streams are geographically isolated (>10 km) from perennial reaches and flow for only 10–12 weeks at a time, the stream fauna is typically of low diversity, with further community development curtailed by stream redrying.

Recovery via resilience mechanisms

Few MSI aquatic invertebrate species are resistant to drought, but many use aerial dispersal as a resilience mechanism. The predaceous diving beetle *Agabus* (Dytiscidae) is often one of the first predators to aerially colonise intermittent streams on rewetting (Bogan, 2012). The beetles use these habitats for breeding, and both larvae and adults consume the drought-resistant stoneflies, midges and blackflies that are abundant in the early stages of flow resumption (Bogan *et al.*, 2013a). *Agabus* was the first beetle colonist in a Sonoran Desert stream during the winter flow period, where they completed their life cycle in 4–8 weeks (Gray, 1981). Adult dytiscids are strong aerial dispersers (Bogan & Boersma, 2012) and can detect polarised light reflecting from the water surface (Schwind, 1991). However, many other aerially dispersing species fail to locate isolated intermittent sites during the short (10–12 week) winter hydroperiod (Fig. 1b) and are restricted to intermittent streams with more persistent flow. For example, aerial colonisation of an isolated (2 km to refuges) intermittent stream with a relatively long (20-week) hydroperiod took 16 weeks for some taxa (e.g. Lestidae: *Archilestes*; Hydroptilidae: *Hydroptila*; Psychodidae: *Maurina*) (M. T. Bogan, unpubl. data).

Monsoon rainfall during the summer triggers the aerial dispersal of aquatic invertebrates among MSI freshwater habitats, including from perennial refuges to newly rewetted streams (Bogan, 2012). In arid regions, the increased humidity associated with rainfall events may prolong survival of aquatic species as they disperse. In a colonisation experiment along two MSI streams, the quantity of monsoon rainfall explained 75% of the variation in aerial colonisation of mesocosms near streams (Bogan & Boersma, 2012). In the same experiments, 66 invertebrate taxa (one-third of the local species pool) colonised mesocosms in 6 weeks. A related recolonisation study of isolated (10 km from the nearest perennial stream) monsoon-refilled stream pools recorded 40 aerially colonising taxa over 3 months (Bogan & Lytle, 2011). In fact, the vast majority of the drought-tolerant taxa that dominate perennial stream pools in the pre-monsoon dry season are strong aerial dispersers (Boersma *et al.*, 2014) that can rapidly colonise rewetted sites (Fig. 2: threshold F).

The most complete recovery observed in MSI streams following seasonal or supraseasonal drought (Fig. 2: threshold G) occurs in sites that regain flow for at least 4–5 months and are near, and perhaps directly downstream of, perennial refuges. In high-elevation

(2800–3300 m) MSI mountain ranges, headwater seeps and springs constitute year-round cool water refuges from which Nearctic fauna disperse to repopulate downstream reaches in winter (Bogan & Lytle, 2007). This seasonal pattern of recovery of Nearctic-derived assemblages from refugia has been widely observed across the MSI (Bogan & Lytle, 2007; Bogan, 2012). Invertebrates recolonise rewatered habitats by several routes, notably drift from upstream sources, aerial dispersal (e.g. Dytiscidae: *Rhantus*, *Stictotarsus*), redistribution from instream refugia (e.g. Limnephilidae: *Hesperophylax*; Siphlonuridae: *Siphlonurus*) or diapause (e.g. Blephariceridae: *Agathon*; Capniidae: *Eucapnopsis*). Frequently, robust recovery from drought in MSI streams is underlain by a combination of resistance and resilience mechanisms (Fig. 2: threshold G).

Extreme supraseasonal drought and lack of recovery to pre-drought conditions

The recovery trajectories described thus far have all been observed in streams experiencing drought and drying disturbances that are within the normal range of historical disturbance events for those systems. For example, resistance-dominated recovery patterns occur in intermittent streams that dry predictably each year and are rewetted only for short time periods (e.g. 10 weeks). Resilience-dominated recovery of Nearctic-derived stonefly, mayfly and caddis fly assemblages in other MSI streams occurs when flow returns after predictable dry season contraction to isolated pools and other refuges (e.g. headwater springs). However, these observations may not adequately predict recovery patterns in streams that experience extreme supraseasonal droughts. Unprecedented drying disturbances, such as transitions from perennial to intermittent flow, may generate novel community trajectories (e.g. Bêche *et al.*, 2009; Sponseller *et al.*, 2010; Bogan & Lytle, 2011).

In the MSI, a recent 6-year supraseasonal drought (1999–05) was the most intense documented in the historical record (Seager, 2007) and resulted in the lowest stream flows ever recorded in the region (Phillips & Thomas, 2005). This extreme drought resulted in the loss of vertical connectivity and the complete drying of all surface habitats at one MSI stream, French Joe Canyon, as documented during an 8-year observational study (Bogan & Lytle, 2011). Prior to this, genetic, geomorphic and anecdotal evidence all suggest that flow at French Joe had been perennial for hundreds of years or longer. Nevertheless, following the supraseasonal drought, French Joe transitioned to intermittent flow (in 2005),

drying and rewetting a further two or three times over the next 4 years.

The unprecedented flow regime shift at French Joe had surprisingly little effect on aquatic invertebrate taxon richness, but significantly altered community composition (Bogan & Lytle, 2011). Within 3 months of flow resumption in 2005, richness equalled that of predrying conditions, although the identity of those taxa changed dramatically. Six species were extirpated by the initial drying event at French Joe, including the flightless top predator (Belostomatidae: *Abedus herberti*) and the largest shredder (Calmoceratidae: *Phylloicus mexicanus*). These dispersal-limited species failed to recolonise in the ensuing 4 years, likely because French Joe is nearly 10 km from the nearest perennial stream habitat. The pre-drying community was dominated by relatively large, long-lived and sedentary taxa, whereas the post-drying taxa were smaller, shorter-lived and highly vagile, including strong aerial dispersers that readily colonise newly wetted habitats (Bogan & Boersma, 2012). The composition of French Joe Canyon's aquatic invertebrate community has not returned to its pre-drying state, nearly 9 years after transitioning to intermittent flow (M. T. Bogan, unpubl. data). Since all evidence suggests that French Joe had not experienced complete drying prior to 2005, resident taxa did not possess resistance traits (e.g. drought-resistant diapause stages) such as those observed in MSI streams with a historical context of predictable intermittency (Bogan *et al.*, 2013a). Hence, the lack of post-drying recovery in community composition at French Joe resulted from a combination of historical context, drought severity and the site's geographic location.

Relating local species richness to drought severity and habitat isolation

Our research in the MSI region suggests aquatic invertebrate community responses to, and recovery from, drought varies with drought severity and stream geographic isolation (Fig. 3). Here, we use species richness as a descriptor of community recovery to illustrate our model because the metric responds fairly uniformly to drying disturbance across geographic regions (Datry *et al.*, 2014) and effects of isolation are well-documented (e.g. MacArthur & Wilson, 1967). Our observations suggest invertebrate species richness is highest in streams with mild and predictable seasonal drought (e.g. flow cessation for 4–6 month year^{-1}) where perennial refuges are nearby to serve as a source of colonists (Point A in Fig. 3). At such sites, 'time-sharing' occurs, with lotic

taxa exploiting running water habitats in the wet season and lentic taxa using pools in the dry season. Where seasonal drought does not occur, higher flows would exclude some lentic taxa, thus reducing species diversity from its peak (left of point A, Fig. 3). Where streams are most isolated, local species richness is relatively low, reflecting stochastic extirpations of fauna with weak dispersal abilities (Point B in Fig. 3). Intermediate drought severity and isolation also constrain local species richness as some weak dispersers and drought-sensitive taxa are absent (Point C in Fig. 3). Streams that experience severe drought are generally dominated by a few resistant taxa. However, where these streams are close to perennial refuges, some resilient taxa may also colonise, thereby increasing diversity over that of highly isolated

streams (Point D in Fig. 3). Sites with both high isolation and high drought severity often support very few, highly resistant, species (Point E in Fig. 3).

The future of MSI streams and research on the community-level effects of droughts

Over the past 15 years, south-western North America has experienced extreme droughts that equal or exceed any documented in the historical record (Seager, 2007). Although these recent droughts are slightly less intense than those of the medieval warm period from AD 900–1200, the record high temperatures of the 20th and 21st centuries may be amplifying their hydrological effects (Woodhouse *et al.*, 2010). In addition to these patterns of
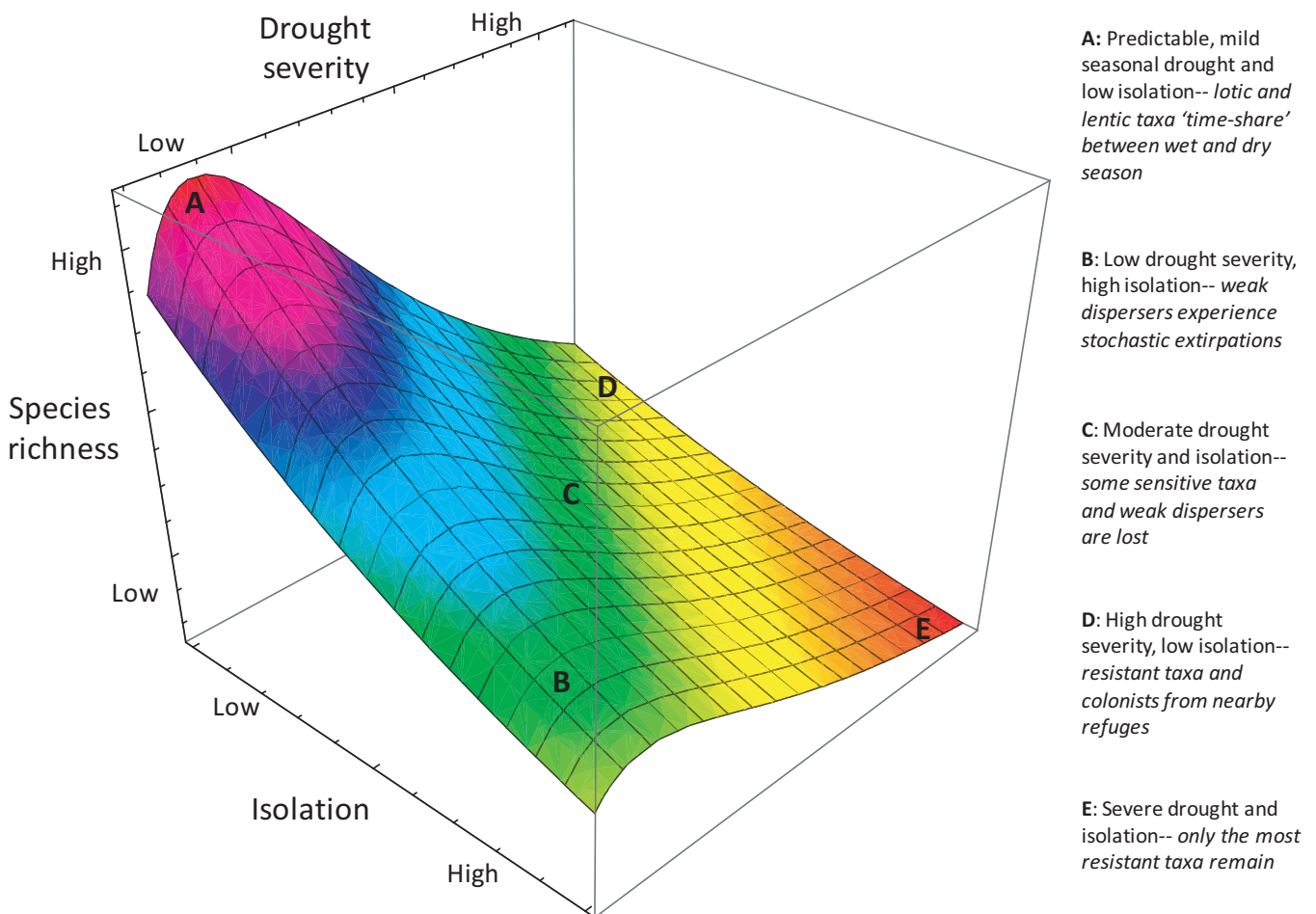

A: Predictable, mild seasonal drought and low isolation-- *lotic and lentic taxa 'time-share' between wet and dry season*

B: Low drought severity, high isolation-- *weak dispersers experience stochastic extirpations*

C: Moderate drought severity and isolation-- *some sensitive taxa and weak dispersers are lost*

D: High drought severity, low isolation-- *resistant taxa and colonists from nearby refuges*

E: Severe drought and isolation-- *only the most resistant taxa remain*

Fig. 3 A conceptual model illustrating potential interactive effects of drought severity (defined here as a combination of drying intensity and duration) and habitat isolation (distance to nearest perennial refuge) on aquatic invertebrate species richness in streams. This model was constructed with a combination of ecological theory (e.g. theory of island biogeography) and observations from the Madrean Sky Island stream studies reviewed here. A: moderate drought disturbance (e.g. brief seasonal drying) increases the overall richness of a given site by allowing lentic taxa to colonise the stream for part of the year. B–D: high drought severity or isolation, or a combination of moderate drought severity and isolation, acts as abiotic filters to reduce richness. E: only a few highly resistant or resilient taxa can persist in highly isolated sites that also experience high drought severity.

increasing temperature and drought severity, anthropogenic water withdrawal across south-western North America has further decreased stream flow in many basins (Deacon *et al.*, 2007; Barnett *et al.*, 2008; Grantham *et al.*, 2012). Many arid-land streams are characterised by seasonal and interannual periods of drought, but decreasing rainfall, rising temperatures and growing water withdrawals are intensifying these historical disturbance regimes. This combination of factors is causing some MSI streams to transition from perennial to intermittent flow. When these extreme drying events and flow regime transitions occur in isolated streams, resident taxa adapted to perennial flow exhibit very low resistance and variable resilience to these unprecedented disturbances. Numerically, species richness may recover in these streams, but long-lived taxa and weak dispersers are replaced by more vagile or short-lived taxa. These 'replacement' taxa may not be functionally equivalent to the extirpated taxa, especially since drought-sensitive taxa in the MSI include the largest predators and shredders in the region.

These observations highlight the need for more species-specific dispersal data, and a greater understanding of the spatial context in which a disturbance occurs, to adequately predict community responses to climate change (Travis *et al.*, 2013). If extreme supraseasonal droughts occur more frequently, as is predicted for south-western North America (Seager *et al.*, 2007), then widespread transitions from perennial to intermittent flow and increased isolation of remaining perennial habitats could eventually lead to species-level extinctions. Unprecedented stream drying may also have cascading effects on the biodiversity of riparian areas (McCluney & Sabo, 2012).

Madrean Sky Islands streams support numerous invertebrate species with limited distributions, including those only recently known to science (e.g. Ruiter, 2011) or endemic to a single mountain range or spring (e.g. Smith & Cook, 2006). Drought and water withdrawals have already caused the extinctions of regionally endemic springsnail species in the nearby Chihuahuan Desert (Hershler, Liu & Landye, 2011). In the MSI, invertebrate taxa with weak dispersal abilities (e.g. *Abedus herberti*) or those dependent upon the few remaining streams with strong, cool, year-round flow (e.g. *Hesperoperla*) may be useful as sentinel species of climate change, and their populations should be monitored.

While short-term studies can elucidate the impacts of and recovery from seasonal disturbances, only long-term studies can reveal the unique impacts of supraseasonal drought (cf. Jackson & Fureder, 2006). Recent long-term studies of streams in arid and semi-arid regions of North America (Bêche *et al.*, 2009; Sponseller *et al.*, 2010), the Mediterranean (Pace, Bonada & Prat, 2013) and Australia (Chessman, 2009) have advanced understanding of both general and system-specific responses of aquatic communities to supraseasonal drought. Additionally, well-designed mesocosm experiments can simulate the effects of unprecedented drying disturbances. Recent mesocosm studies along British streams showed that invertebrate communities were resilient to stream drying occurring at relatively low frequency (quarterly), but impoverished when these events occurred more often (monthly), despite the close proximity of potential colonists (Ledger *et al.*, 2013). Although logistically challenging, long-term mesocosm manipulations (e.g. Chase, 2007) may be a valuable way to examine the mechanisms underpinning responses to changing flow regimes.

We hope that our regional synthesis inspires further research on drought impacts in stream ecosystems. Specifically, we suggest that the following topics would be fruitful avenues of research: (i) measuring species-specific overland dispersal capabilities to predict how species will respond to increased habitat isolation in drought-affected streams; (ii) conducting long-term mesocosm studies that manipulate both drought intensity and colonisation potential; (iii) analysing the biological traits of species experiencing extreme drought to link changes in aquatic communities to ecosystem functioning (e.g. impacts of shredder extirpations); (iv) examining how the rate of stream drying and the manner of flow resumption affect biotic responses to drought and (v) quantifying the predictability and intensity of drought events across multiple regions to determine how these factors shape biodiversity and community composition. The latter suggestion would facilitate comparisons across biotic regions (mesic and xeric) and allow for quantitative global meta-analyses of drought impacts, as have been conducted for flood disturbance (e.g. McMullen & Lytle, 2012). Knowledge gained from a diversity of regions will be essential to understanding how stream ecosystems will respond to future extreme drought events.

Acknowledgments

(to KSB). We thank Dawn Wilson, Claire Zugmeyer and Heidi Fischer for logistical support over the course of many of the studies reviewed here. Thanks also to Stephanie Carlson, Mark Ledger, Dave Strayer and two anonymous reviewers for insightful comments on previous versions of this manuscript.

References

Barnett T.P., Pierce D.W., Hidalgo H.G., Bonfils C., Santer B.D., Das T. *et al.* (2008) Human-induced changes in the hydrology of the western United States. *Science*, **319**, 1080–1083.

Bêche L.A., Connors P.G., Resh V.H. & Merenlender A.M. (2009) Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography*, **32**, 778–788.

Boersma K.S., Bogan M.T., Henrichs B.A. & Lytle D.A. (2014) Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology*, **59**, 491–501.

Boersma K.S. & Lytle D.A. (in press) Overland dispersal and drought escape behavior in a flightless aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). *The Southwestern Naturalist*

Bogan M.T. (2012) *Drought, Dispersal, and Community Dynamics in Arid-Land Streams*. PhD dissertation, Oregon State University, Corvallis, OR.

Bogan M.T. & Boersma K.S. (2012) Aerial dispersal of aquatic invertebrates along and away from arid-land streams. *Freshwater Science*, **31**, 1131–1144.

Bogan M.T., Boersma K.S. & Lytle D.A. (2013a) Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshwater Biology*, **58**, 1016–1028.

Bogan M.T., Gutiérrez-Ruacho O., Alvarado-Castro A. & Lytle D.A. (2013b) Habitat type and permanence determine local aquatic invertebrate community structure in the Madrean Sky Islands. In: *Merging Science and Management in a Rapidly Changing World: Biodiversity and Management of the Madrean Archipelago III*. (Eds G.J. Gottfried, P.F. Folliott, B.S. Gebow, L.G. Eskew & L.C. Collins), pp. 277–282. Proceedings RMRS-P-67.USDA Forest Service, Fort Collins, CO.

Bogan M.T., Gutiérrez-Ruacho O., Alvarado-Castro A. & Lytle D.A. (2013c) New records of *Martarega*, *Graptocorixa*, and *Abedus* (Heteroptera: Notonectidae, Corixidae, Belostomatidae) from northwestern Mexico and Arizona, including the first record of *Graptocorixa emburyi* in the United States. *The Southwestern Naturalist*, **58**, 494–497.

Bogan M.T. & Lytle D.A. (2007) Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. *Freshwater Biology*, **52**, 290–304.

Bogan M.T. & Lytle D.A. (2011) Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology*, **56**, 2070–2081.

Bogan M.T., Noriega-Felix N., Vidal-Aguilar S.L., Findley L.T., Lytle D.A., Gutiérrez-Ruacho O.G. *et al.* (2014) Biogeography and conservation of aquatic fauna in spring-fed tropical canyons of the southern Sonoran Desert, Mexico. *Biodiversity and Conservation*, **23**, 2705–2748.

Boulton A.J. (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, **48**, 1173–1185.

Boulton A.J. & Lake P.S. (2008) Effects of drought on stream insects and its ecological consequences. In *Aquatic Insects: Challenges to Populations*. (Eds J. Lancaster & R.A. Briers), pp. 81–102. CABI, Oxfordshire.

Boulton A.J. & Stanley E.H. (1995) Hyporheic processes during flooding and drying in a Sonoran Desert stream. II. Faunal dynamics. *Archiv für Hydrobiologie*, **134**, 27–52.

Boulton A.J., Valett H.M. & Fisher S.G. (1992) Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. *Archiv für Hydrobiologie*, **125**, 37–61.

Chase J.M. (2007) Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 17430–17434.

Chessman B.C. (2009) Climatic changes and 13-year trends in stream macroinvertebrates in New South Wales, Australia. *Global Change Biology*, **15**, 2791–2802.

Clinton S.M., Grimm N.B. & Fisher S.G. (1996) Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society*, **15**, 700–712.

Cooling M.P. & Boulton A.J. (1993) Aspects of the hyporheic zone below the terminus of a South Australia arid-zone stream. *Australian Journal of Marine and Freshwater Research*, **44**, 411–426.

Datry T., Larned S.T., Fritz K.M., Bogan M.T., Wood P.J., Meyer E.I. *et al.* (2014) Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. *Ecography*, **37**, 94–104.

Deacon J.E., Williams A.E., Williams C.D. & Williams J.E. (2007) Fueling population growth in Las Vegas: how large-scale groundwater withdrawal could burn regional diversity. *BioScience*, **57**, 688–698.

Felger R.S. (1999) The flora of Cañón de Nacapule: a desert-bounded tropical canyon near Guaymas, Sonora, Mexico. *Proceedings of the San Diego Society of Natural History*, **35**, 1–42.

Ficklin D.L., Stewart I.T. & Maurer E.P. (2013) Climate change impacts on streamflow and subbasin-scale hydrology in the Upper Colorado River Basin. *PLoS One*, **8**, DOI: 10.1371/journal.pone.0071297.

Finn D.S., Blouin M.S. & Lytle D.A. (2007) Population genetic structure reveals terrestrial affinities for a

headwater stream insect. *Freshwater Biology*, **52**, 1881–1897.

Gasith A. & Resh V.H. (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, **30**, 51–81.

Grantham T.E., Newburn D.A., McCarthy M.A. & Merenlender A.M. (2012) The role of streamflow and land use in limiting oversummer survival of juvenile steelhead in California streams. *Transactions of the American Fisheries Society*, **141**, 585–598.

Gray L.J. (1981) Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *American Midland Naturalist*, **106**, 229–242.

Hendrickson D.A. & Minckley W.L. (1985) Cienegas – vanishing climax communities of the American Southwest. *Desert Plants (USA)*, **6**, 131–175.

Hershler R., Liu H.-P. & Landye J.J. (2011) New species and records of springsnails (Caenogastropoda: Cochliopidae: *Tryonia*) from the Chihuahuan Desert (Mexico and United States), an imperiled biodiversity hotspot. *Zootaxa*, **3001**, 1–32.

Jackson J.K. & Fureder L. (2006) Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. *Freshwater Biology*, **51**, 591–603.

Jaeger K.L. & Olden J.D. (2012) Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. *River Research and Applications*, **28**, 1843–1852.

Jaeger K.L., Olden J.D. & Pelland N.A. (2014) Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 13894–13899. DOI: 10.1073/pnas.1320890111.

Lake P.S. (2003) Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, **48**, 1161–1172.

Lake P.S. (2013) Resistance, resilience and restoration. *Ecological Management & Restoration*, **14**, 20–24.

Ledger M.E., Brown L.E., Edwards F.K., Milner A.M. & Woodward G. (2013) Drought alters the structure and functioning of complex food webs. *Nature Climate Change*, **3**, 223–227.

Leigh C. (2013) Dry-season changes in macroinvertebrate assemblages of highly seasonal rivers: responses of low flow, no flow and antecedent hydrology. *Hydrobiologia*, **703**, 95–112.

Lytle D.A. (2000) Biotic and abiotic effects of flash flooding in a montane desert stream. *Archiv für Hydrobiologie*, **150**, 85–100.

Lytle D.A., McMullen L.E. & Olden J.D. (2008) Drought-escape behaviors of aquatic insects may be adaptations to highly variable flow regimes characteristic of desert rivers. *The Southwestern Naturalist*, **53**, 399–402.

Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, **19**, 94–100.

MacArthur R.H. & Wilson E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

McCluney K.E. & Sabo J.L. (2012) River drying lowers the diversity and alters the composition of an assemblage of desert riparian arthropods. *Freshwater Biology*, **57**, 91–103.

McMullen L.E. & Lytle D.A. (2012) Quantifying invertebrate resistance to floods: a global-scale meta-analysis. *Ecological Applications*, **22**, 2164–2175.

Pace G., Bonada N. & Prat N. (2013) Long-term effects of climatic-hydrological drivers on macroinvertebrate richness and composition in two Mediterranean streams. *Freshwater Biology*, **58**, 1313–1328.

Paulson R.W., Chase E.B., Roberts R.S. & Moody D.W. (1991) National Water Summary 1988–89, Hydrologic events and floods and droughts. *United States Geological Survey Water-Supply Paper (USA)*, **2375**, 181–188.

Phillips J.V. & Thomas B.E. (2005) Hydrological conditions in Arizona during 1999–2004: a historical perspective. *US Department of Interior: US Geological Survey Fact Sheet*, **2005–3081**, 1–4.

Phillipsen I.C. & Lytle D.A. (2013) Aquatic insects in a sea of desert: population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. *Ecography*, **36**, 731–743.

Resh V.H. (1992) Year-to-year changes in the age structure of a caddisfly population following loss and recovery of a springbrook habitat. *Ecography*, **15**, 314–317.

Robson B.J., Chester E.T. & Austin C.M. (2011) Why life history information matters: drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. *Marine and Freshwater Research*, **62**, 801–810.

Ruiter D.E. (2011) Two new species of *Ochrotrichia* (Trichoptera: Hydroptilidae) from the southwestern United States. *Zoosymposia*, **5**, 420–424.

Schwind R. (1991) Polarization vision in water insects and insects living on a moist substrate. *Journal of Comparative Physiology A*, **169**, 531–540.

Seager R. (2007) The turn of the century North American drought: global context, dynamics, and past analogs. *Journal of Climate*, **20**, 5527–5552.

Seager R., Ting M., Held I., Kushnir Y., Lu J., Vecchi G. *et al.* (2007) Model projections of an imminent transition to a more arid climate in Southwestern North America. *Science*, **316**, 1181–1184.

Seager R. & Vecchi G.A. (2010) Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21277–21282.

Shepard W.D. (2011) Survival of stream dewatering by *Postelichus immsi* (Hinton) (Coleoptera Byrroidea: Dryopidae). *Pan-Pacific Entomologist*, **87**, 54–56.

Smith I.M. & Cook D.R. (2006) North American species of *Diamphidaxona* (Acari: Hydrachnida: Hygrobatidae). *Zootaxa*, **1279**, 1–44.

Sponseller R.A., Grimm N.B., Boulton A.J. & Sabo J.L. (2010) Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. *Global Change Biology*, **16**, 2891–2900.

Stanley E.H., Buschman D.L., Boulton A.J., Grimm N.B. & Fisher S.G. (1994) Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist*, **131**, 288–300.

Stanley E.H., Fisher S.G. & Grimm N.B. (1997) Ecosystem expansion and contraction in streams. *BioScience*, **47**, 427–435.

Stromberg J., McCluney K.E., Dixon M.D. & Meixner T. (2013) Dryland riparian ecosystems in the American Southwest: sensitivity and resilience to climatic extremes. *Ecosystems*, **16**, 411–415.

Stubbington R. (2012) The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research*, **63**, 293–311.

Travis J.M.J., Delgado M., Bocedi G., Baguette M., Barton K., Bonte D. *et al.* (2013) Dispersal and species' responses to climate change. *Oikos*, **122**, 1532–1540.

Velasco J. & Millan A. (1998) Insect dispersal in a drying desert stream: effects of temperature and water loss. *The Southwestern Naturalist*, **43**, 80–87.

Verkaik I., Vila-Escale M., Rieradevall M. & Prat N. (2013) Seasonal drought plays a stronger role than wildfire in shaping macroinvertebrate communities of Mediterranean streams. *International Review of Hydrobiology*, **98**, 1–13.

Warshall P. (1994) The Madrean Sky Island Archipelago: a planetary overview. In *Biodiversity and Management of the Madrean Archipelago*. (Eds L.F. Debano, G.J. Gottfried, R.H. Hamre, C.B. Edminster, P.F. Ffolliott & A. Ortega-Rubio), pp. 6–18. United States Department of Agriculture, Forest Service, Fort Collins, CO.

Woodhouse C.A., Meko D.M., Macdonald G.M., Stahle D.W. & Cook E.R. (2010) A 1,200-year perspective of 21st century drought in southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21283–21288.