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PRIMARY RESEARCH PAPER

Effects of experimental multi-season drought on abundance, richness, and beta diversity patterns in perennially flowing stream insect communities

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Abstract Freshwater systems are projected to experience increased hydrologic extremes under climate change. To determine how small streams may be impacted by shifts in flow regimes, we experimentally simulated flow loss over the span of three summers in nine 50 m naturally fed stream channels. The aquatic insect community of these streams was sampled before, during, and after experimental drought treatments as well as following one unforeseen flood event. Abundance, richness, and beta diversity were measured as indicators of biotic effects of altered flow regimes. Abundance declined in proportion to flow loss. In contrast, we observed a threshold response in richness where richness did not decrease except in channels where losses of surface flow occurred and disconnected pools remained. The flood reset this pattern, but communities continued their prior trajectories shortly thereafter. Beta diversity partitions suggested no strong compositional shifts, and that the effect of drought was largely experienced uniformly across taxa until flow cessation. Pools served as a refuge, maintaining stable abundance gradients and higher richness longer than riffles. Upon flow resumption, abundance and richness returned to pre-treatment levels within one year. Our results suggest that many taxa present were resistant to drought conditions until loss in surface flow occurred.

Keywords Aquatic insects · Climate change · Flooding · Beta diversity

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Introduction

Rapidly shifting climate patterns have resulted in greater hydrologic extremes in freshwater systems (Siam & Eltahir, 2017; Byun et al., 2019). Extreme flow events, such as catastrophic wintertime rain on snow events (floods) and uncharacteristically long periods with low precipitation (droughts), lead to changes in key abiotic variables. These extreme flow events are some of the strongest determinants of community persistence (Dahm et al., 2003; Herbst & Cooper, 2010). In mid- to high-altitude streams and rivers, altered timing of extreme snowmelt events has led to earlier peak flows (Maurer, 2007; Musselman et al., 2017), which result in unpredictable floods and a lack of sustained baseflow late in the season that manifest as remarkably strong droughts and increased flashiness (Dettinger et al., 2004; Herbst et al., 2019). In turn, studies of the effects of flow variability on aquatic organisms in natural systems have been hampered by the stochastic nature of floods and droughts and the difficulties in establishing appropriate historical reference conditions considered unaltered by humans (Boulton, 2003; Wright et al., 2004).

The effects of experimental flow disturbance on aquatic insect communities have been studied using experimental mesocosms in several regions of the world, albeit with varying results. Studies of streams in the lowlands of the Netherlands, southern Ireland, and in a temperate mixed-hardwood forest in northeastern USA showed no significant changes in community diversity following pronounced shifts in biomass or abundance due to experimental drought and floods, suggesting high resistance in diversity metrics even when biomass or abundance are less so (Walters & Post, 2011; Verdonschot et al., 2014; Woodward et al., 2015). Other experiments suggest less resistance through high species replacement following flow disturbance, with increased production of small, short-lived, rapid dispersing taxa following extreme drought events in English chalk streams and in streams in southwestern USA (Ledger et al., 2011; Bogan et al., 2015; Aspin et al., 2018a).

The lack of consistency between experimental flow perturbation studies may reflect evolutionary adaptation of stream-inhabiting taxa and variable drought conditions between studies. Bogan et al. (2015) found that strong dispersers replaced longer lived, weak dispersers after supraseasonal drought in streams. However, in perennial systems few taxa have drought resistance and resilience strategies compared with those in intermittent streams, leading to catastrophic reductions in total insect biomass as a result of water loss (Doretto et al. 2018). Hyporheic water availability may also strongly effect system responses, as it is an important refuge for the drought resistance of insects (Stubbington, 2012; Vander Vorste et al., 2016). Although the interaction of flow variability and aquatic community persistence has been documented (Stubbington et al., 2017), inherent system-specific differences remain. Thus, the ranges of flow variability that can be tolerated by taxa given unique environmental context, the aspects of the disturbances that drive divergent community responses, and the factors that lead to recovery require further investigation.

In addition to changes in biomass and abundance, previous studies show significant divergence of composition following a gradient of flow reductions (e.g., Doretto et al. 2018). Intermittent streams that are subjected to higher flow variability and drought stress show community dissimilarities that manifest as high nestedness, where the taxa present are a limited, resistant subset of those in sites with greater flow permanence (Arscott et al., 2010; Sarremejane et al., 2021). Conversely, Aspin et al. (2018a, b) found unique assemblages of specialists following drought treatments of historically perennial streams, indicating high turnover and replacement by functional variants, albeit without the adaptations to extreme droughts that are found in communities of arid land streams (Boersma et al., 2013). Beta diversity measures of community dissimilarity have recently been adapted from incidence-based approaches to partition abundance-based community measurements. The two partitions of abundance-based dissimilarity include balanced variation, where the individuals of species at a site are substituted by the same amount of individuals of different species at another site, analogous to turnover, and abundance gradients, where individuals are lost from one site to another, analogous to nestedness (Baselga, 2013, 2017). These recent methodological advances in abundance-based partitioning of beta diversity may reveal greater insight into mechanisms that drive community dissimilarity.

Although aquatic insect responses to flow disturbance have been studied in streams worldwide, the observations are context dependent and no experimental studies have been performed in North American high-altitude systems. In the eastern Sierra Nevada Mountain Range in California, USA, stream insect communities are adapted to a perennial stream hydrology that is driven mostly by accumulated snowmelt, but have been increasingly experiencing losses in surface flow, drought conditions, and flow erraticism. For example, one of the strongest droughts in the history of the Sierra Nevada took place between 2012 and 2015, decreasing flow significantly throughout most watersheds in the eastern Sierra Nevada (Herbst et al., 2019). At the same time, warmer winters have generated rain on snow events that triggered massive and unpredictable floods that shifted aquatic community composition in degraded streams (Herbst & Cooper, 2010). Some regions of the Sierra Nevada are expected to become increasingly dry with the onset of climate warming, and shifts in hydrograph are expected to produce occasional peak flows from snowmelt in the winter, instead of in the spring, with overall greater intermittency of flow (Maurer, 2007; Swain et al., 2018). Disturbance tolerant aquatic communities will likely become more prevalent in response to the above hydrological changes, yet these communities will still be subject to novel flow heterogeneity (Herbst et al., 2019). To determine the effects of these changes on freshwater communities—even those more typical of disturbed systems—hydrological resistance thresholds and resilience capacities need to be identified for responses of communities to changes in flow regimes (Boulton, 2003).

We examined the responses of a preconditioned drought stream community that had already experienced background regional drought conditions to further extreme flow loss. We established an experimental flow reduction gradient across a set of experimental channels and measured the abundance and richness of insect communities before, during, and after experimental drought conditions, compounded with a flood during drought conditions. The flood was unanticipated, but this event is typical of future flow erraticism and yielded a rare opportunity to determine how flooding affects communities during ongoing drought.

We examined community responses in terms of both resistance, defined as the ability of communities to withstand a disturbance in situ, and resilience, defined as a communities' capacity to recolonize a site and re-establish populations or communities similar to those that were present before disturbance (Holling, 1973; Bogan et al., 2015). First, we asked whether the abundance, richness, and beta diversity of aquatic insect communities show resistance to flow variability, and if there exists a resistance threshold in the hydrograph. Second, given the multi-year regional drought and experimentally imposed flow variation, we asked whether the abundance, richness, and beta diversity exhibit resilience by returning to their pre-experimental status a year after flow is experimentally restored. Although the flood event was not anticipated, we predict similar responses of abundance, richness, and beta diversity in terms of resistance and resilience as with drought in this study.

When considering question one, if the community was highly resistant, we predicted richness to not significantly change except in response to the most extreme flow perturbations. However, abundance could fluctuate even under a resistant community, as past studies have documented individuals concentrating in remnant habitat (Verdonschot et al., 2014). Additionally, in a scenario of high resistance, we predicted that beta diversity would show low compositional turnover in the balanced variation partition, indicating low replacement and resulting high resistance. In contrast, we expected a less-resistant community to exhibit greater responses across a broader range of flow reductions, with significant shifts in richness and abundance, and high compositional turnover with respect to balanced variation that would indicate losses of taxa from the community.

When considering question two, in a high resilience scenario, we expect for the aquatic insect community to recover from the effects of flow perturbation by establishing increased richness, abundance and beta diversity patterns comparable to before perturbation when flows are restored indicating rapid replacement of lost taxa (Sarremejane et al., 2019); however, if the effect of regional drought is still prevalent when flows are restored, the resilience of the community may be impeded by limiting drift colonization. In the latter case, lower resilience would lead to richness and abundances that continue to be altered relative to the pre-experimental conditions, with beta diversity partitions that are not significantly different from post flow perturbation values.

Methods

Study area

This study was performed at the Sierra Nevada Aquatic Research Laboratory (SNARL), a University of California Natural Reserve near Mammoth Lakes, CA (37° 37′ N, 118° 50′ W). SNARL has an average elevation of 2154 m ASL with summer and winter temperatures ranging from 0 to 28 °C and − 22 to 13 °C, respectively. SNARL straddles Convict Creek, which is a perennial oligotrophic stream that runs from the snowmelt-fed alpine lake Convict Lake. Typically, major peaks in the stream flow regime, measured at the inlet of Convict Creek to SNARL, occur in June (700–5700 l/s), and discharge decreases rapidly afterward, leveling to the base flow (100–300 l/s) from late October until April. On average, water temperatures are freezing in the winter, about 5 °C in March with frozen stream surfaces, and range between 12 and 17 °C in the summer (Jenkins et al., 1999). There was a long-term, unprecedented region-wide drought in the Sierra Nevada Mountains which took place from 2012 to 2015, which enveloped the duration of this study (Herbst et al., 2019).

Experiments were conducted in nine 50-m-long channels, which were constructed of concrete and sealed with epoxy resin (Fig. 1A). The channels simulate alternating pool-riffle habitats and have six pools and riffles each. The channels are 1 m wide at the riffles, while the pools average 1.5 m in diameter and contain fiberglass reinforced concrete sheets that simulate undercut banks. The substrate in the channels is approximately 30 cm deep and comprises silt, sand, gravel, and pebbles with the majority being pebble in riffles, and pebble/silt in pools. Six parallel channels are connected to a top inlet basin, and three more are connected in parallel to a lower inlet basin. Both inlet basins are naturally fed from Convict Creek and the channels are arranged in a flow-through setup. Water from the bottom of the stream channels falls into outlet basins from a height of 2 m. To emulate natural drift processes and water properties, no water was recycled. Because the flow is diverted directly from Convict Creek, insects can drift or oviposit naturally into the channels. Although no riparian vegetation is present immediately along the channels (Fig. 1A), previous studies demonstrated the presence of similar periphytic and aquatic insect communities to those in Convict Creek (Jenkins et al., 1999). However, due to the extended regional drought, flow from Convict

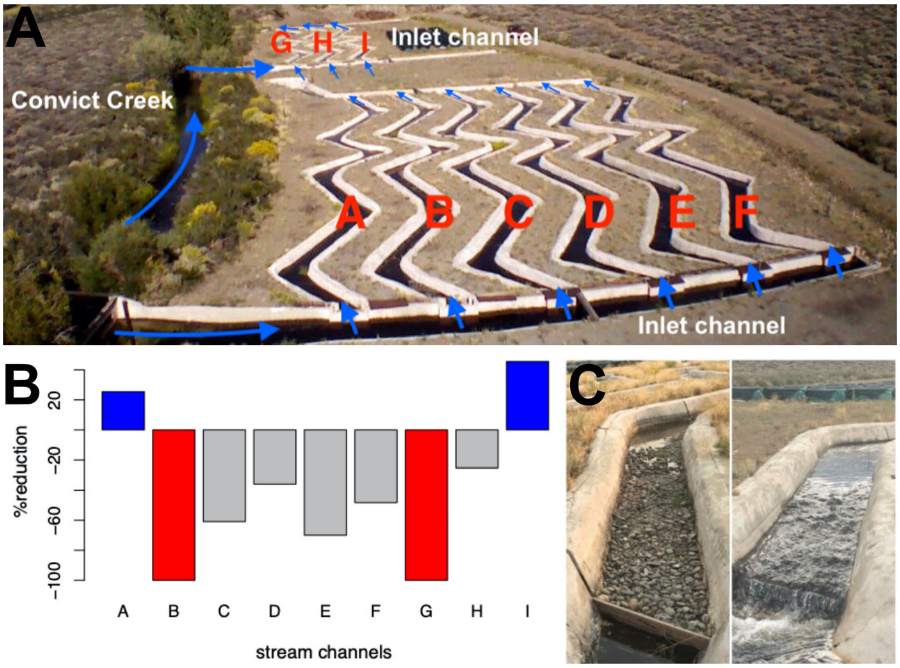

Fig. 1 Layout of Sierra Nevada Aquatic Research Laboratory (SNARL) channels used in the experimental drought manipulation (letters refer to treatments as described in the text and arrows denote the direction of flow) (**A**); percentage changes in discharge relative to pre-experimental levels, which were maintained throughout the two-year period at the flow gates, except for the July 2015 flood (blue bars indicate control channels, red bars indicate dry channels, and gray bars indicate moderately perturbed channels) (**B**); comparison of the 98% flow reduction channel (left, channel B) with a control channel (right, channel A) after drought treatments (**C**)

Creek to the experimental channels was greatly reduced throughout the duration of the experiment, and thus the richness of the communities inhabiting the channels was reduced in relation to historic observations (Table S2). Flow gates at the top of each channel were used to reduce or completely stop discharge into the channels.

For five years preceding the start of the project, the channels were naturally colonized by Convict Creek biota and experienced a similar stream flow regime to that of Convict Creek. A large population of naturalized brown trout (*Salmo trutta* Linnaeus, 1758) is present in the creek. These were reportedly introduced to the region by German freshwater enthusiasts in the 1890s (Jenkins et al., 1999). Due to their invasive nature and ability to radically alter aquatic communities, fish, including juveniles, were excluded from the channels by inserting double stacked, pre-cut 2 × 4 wood struts to the head of each channel.

Experimental design

To test for the effects of flow reduction on the resistance and resilience of aquatic insect communities, we measured the response of abundance, richness, and beta diversity to different levels of experimental flow loss. Resistance and resilience were inferred from the response of abundance, richness, and beta diversity to flow loss. As percentage flow losses, targeted flow reductions were 0% (control, free-flowing), 25%, 50%, 75%, and 100% (dry riffles with hyporheic flow and isolated pools; Fig. 1A). Some deviation from target flow levels was noted over the study period (Fig. 1B). Specific flow reduction increments were determined by averaging discharge during flow loss conditions (situations where discharge was rapidly lost within a week) in Convict Creek over the past 50 years. The channels were assigned to flow reduction (drought condition) treatments using a random number generator, although single random channels were selected as controls for the top six and bottom three channels. Flow into the channels was reduced by closing the inflow gates from the holding reservoir.

Flow was incrementally reduced over the course of seven days after calculating the number of flow regulator turns needed to reduce discharge by a certain percentage. After establishing drought treatments, discharge from each channel was monitored daily and the flow gates were adjusted to compensate for variations in discharge from Convict Creek. The channel flow reductions began on 19 July 2014 and were completed by 26 July 2014. On 12 July 2015, the experimental channels experienced an unanticipated flood event. A buildup of debris clogged the outlet of Convict Lake to Convict Creek and the US Forest Service cleared the dam which flooded some areas at SNARL, with water completely submerging and flowing over the experimental channels. The flow gates were thus opened to prevent damage to the concrete structures. After the flood passed through the channels, flow levels were restored to experimental drought conditions after four days and the field team arrived on-site. Although this flood event was unexpected, it represents realistic and expected future erratic flow patterns in the Sierra Nevada (Herbst & Cooper, 2010), and thus this event presented a rare opportunity to study the compounded influence of both droughts and floods in the region. The flow gates were opened on 23 August 2015 to end the experimental drought period. Flow was unimpeded thereafter.

Sampling regime

Benthic insect communities were sampled once before drought treatments to measure baseline conditions (18 July 2014), six times during the drought treatments to measure community resistance (three times per summer season; 26 July 2014, 19 August 2014, 25 August 2014, 18 July 2015, 25 July 2015, 22 August 2015), and once after flow restoration to measure resilience (26 July 2016). These sampling intervals and duration were chosen because this time period is when aquatic insect biomass is highest, after snowmelt runoff has subsided from the spring, and before streams start to experience surface freezing (Jenkins et al., 1999). Thus, the summer season at SNARL is when most aquatic insects are dependent on surface water, but when the lowest flows exist. Temperature, conductivity, and dissolved oxygen (DO) were measured using a YSI Professional Pro Plus (Xylem Inc., Yellow Springs, Ohio, USA), and discharge was calculated by measuring current velocity, depth, and stream wetted width with a Marsh-McBirney Flo-Mate 2000 Electromagnetic Flow Meter (Hach Company, Loveland, Colorado, USA). The aforementioned environmental variables were measured in the same places and on the same days as biotic samples using standard methods (Hauer & Hill, 2011).

Samples of benthic insects were taken upstream, in the middle, and downstream of riffle/pool pairs in each channel using a custom-made aluminum-frame Surber sampler with a 250-µm mesh (900-cm^2 areas were sampled). Benthic habitats were vigorously scrubbed by hand, allowing attached biota to flow into the Surber sampler and be collected into 200-ml containers attached to the end of the sampler's net for about 60 s. In channels with flow restrictions, water was hand-swept through the Surber net. We removed large organic matter and rocks from samples and followed an elutriation protocol to clear benthic invertebrates from most organic matter. Care was taken to separate cased caddisflies from the debris (as in Herbst et al., 2018). We then poured sample fractions through a 100-µm aquarium net into 250-ml containers containing 90% ethanol to be identified in the lab. We collected and combined two samples from riffles, and two separately for pools. To prevent re-sampling of habitats that were disturbed by Surber sampling, we collected samples from every other pool/riffle. We also divided each section of the riffles and pools into 8 and randomly assigned single sections to each sampling date so previously sampled habitat was not re-sampled. In the laboratory, aquatic insects were identified at the genus level, with the exception of non-biting midges (Chironomidae), which were identified to family. Insects were not present in dry riffles after 18 July 2014, and we checked to a depth of ~ 25 cm into the hyporheic zone, although it is uncertain if they made it deeper.

Since the SNARL channels are oligotrophic in nature, primary production is often a limiting factor in aquatic insect production, and flow reductions may exacerbate this limitation (Reimers et al., 1955; Kratz, 1996). To determine the influence of chlorophyll-a on the aquatic insect community during flow perturbations, benthic algae were sampled by scrubbing two pebbles that were randomly selected from the same upstream, middle, and downstream riffle/pool pairs as for the Surber samples. After scrubbing with a nylon bristle brush, cobbles were rinsed and the resulting algal solutions were homogenized in the sample tray. Solutions were filtered through 1-µm glass fiber filters (GF/E filter) using a 60-ml syringe attachment. We extracted chlorophyll-a with cold ethanol for 24 h and then determined chlorophyll-a concentrations of using established fluorometric methods (Sartory & Grobbelaar, 1984). Areas of the two pebble substrates were estimated from recorded measures of substrate length, width, height, and circumference and chlorophyll-a contents per unit area were calculated (Herbst & Cooper, 2010).

Data analysis

To test which set of measured predictors best explained variation in abundance and richness, we fitted a set of generalized linear models (GLM), with discharge being the key variable given drought and flood conditions. Date, DO, temperature, chlorophyll-a, discharge, and a date*discharge interaction term were included as explanatory variables. Conductivity was not used due to autocorrelation with other variables. We used GLM because assumptions of normality were rejected by Shapiro–Wilk tests of residuals. We employed Poisson and negative binomial distributions for richness and abundance models, respectively. Negative binomial was chosen for abundance to account for overdispersion. Changes in corrected AIC (ΔAICc) values were calculated to determine which combination of variables most parsimoniously explanation in abundance and richness in aquatic insect communities. An information-theoretic (ΔAICc) approach to model selection was chosen over stepwise regression to minimize potential issues with data overfitting and to place equal emphasis on model fit and complexity (Hegyi & Garamszegi, 2010). The top ten models for richness and abundance are presented since most of those models had a ΔAICc of less than 7, as models where the ΔAICc is between 2 and 7 have been shown to still have some support (Burnham et al., 2010).

Since the discharge and discharge * date factors in our models appeared to explain a high amount of variation in the data, we performed post-hoc analyses of the form of the relationships between richness and abundance and discharge to detect for resistance thresholds. These responses were also compared across time, with a particular emphasis on comparing responses from 2014 and 2015 to 2016 to assess resilience in abundance and richness once experimental channels were once again free-flowing. We examined these visual relationships between richness, abundance, and discharge using scatterplots with added trendlines calculated by polynomial regression and AIC to determine function type. Analyses were conducted using the lme4, MASS, and bbmle packages in R (R Core Team, version 3.5.1).

We calculated the Bray–Curtis dissimilarity on raw abundances to quantify the extent to which observed responses in community resistance and resilience to flow manipulations were due to shifts in composition versus changes in abundances. This index accounts for dissimilarity due to components of balanced variation with respect to abundance and unidirectional abundance gradients between pairs of sites in experimental channels (Baselga, 2017). We used summed dissimilarities because averaging pairwise dissimilarity measures over more than three pairs is reportedly problematic (Diserud & Odegaard, 2007; Baselga, 2013). To assess heterogeneity of genus compositions among all sites over time, we calculated overall multiple-site dissimilarity using the same two components of the Bray–Curtis dissimilarity in abundance (Baselga, 2017). Community data were also converted from abundances to presence-absence to test results with an incidence-based, Sorensen beta diversity index, but results were not qualitatively different, and in efforts to reduce data transformations, we retained an abundance-based approach.

To visualize overall site dissimilarity at each timepoint, we plotted multiple-site dissimilarity against sampling date regardless of channel treatments. Because 100% drought channels had zeros in abundance for all taxa, we inserted three dummy taxa with Bray–Curtis values of 1 into genus × site matrices (Slimani et al., 2019), as dissimilarities between rows of zeros cannot be calculated. After investigating transformations and calculating beta diversity with or without sites, with zeros, and with or without dummy variables, the dummy variables capture all variations in the data while accounting for sites with only zeros. Ordinations and traits information, such as non-metric multi-dimensional scaling and functional feeding groups were not used here due to low taxonomic diversity and resulting low trait diversity in the channels and a lack of significant compositional shifts upon inspection using Bray–Curtis dissimilarity.

To understand the relationship between flow alteration, beta diversity, and resulting resistance or resilience, pairwise differences in discharge between channels on each sampling date were used as measures of drought intensity. We adopted Aspin et al.'s (2018b) term "drought intensity", but did not ordinate our suite of environmental variables into one axis because our predictors did not collapse into similar axes as in their system. Resultantly, drought intensity was defined as difference in discharge between two timepoints and sampling sites. Discharge levels were different each year. After, we fit negative exponential models using the betapart package and the "decay.model" function, and examined decay in dissimilarity for balanced variations and abundance gradients relative to drought intensity (Rodríguez & Baselga, 2018). This function adjusts a GLM with dissimilarity as the response variable and drought intensity as the predictor. We selected negative exponential decay models over the optional power-law functions by comparing AIC values for both. Goodness of fit from the models was assessed on pseudo R^2 values calculated from the GLMs. Significant relationships between dissimilarity and drought were identified by randomizing drought intensity 9999 times and determining the proportion of models in which deviance was smaller than that of the randomized model (Rodríguez & Baselga, 2018).

Results

We successfully established a gradient of flow loss treatments (Fig. 1B and 1C) with water flow reductions ranging from almost complete flow loss (channels B and G) to intermediate flow reductions (channels C, D, E, F, and H) relative to ambient conditions. Control channels exhibited slightly increased flow because more discharge was available to those unregulated channels (channels A and I, see Fig. 1B). Outside of the flood event, riffles in channels B and G had zero surface flow and were reduced to hyporheic flows, allowing disconnected pools to remain wet. The hyporheic flows were confirmed visually by observing water flowing into the pools from the bottom portion of benthos in connecting riffles. Pools in treated channels had relatively stable environments through June and July, but conditions became more extreme in late August, with temperatures fluctuating between 8.7 and 28 °C in pools in most dry channels, compared with 14–19 °C in pools in control channels when temperature was measured hourly within a 24-h period. DO levels followed diel fluctuations in the pools of dry channels with levels as low as 0.6 mg/l in the evenings and

5.9 mg/l during the day. Channels with highest flow reduction were colonized with terrestrial plants after two years of drying conditions (pers. obs.).

The aquatic insect community present during the experiment in the channels consisted of six orders, with four genera in Ephemeroptera, one in Plecoptera, six in Trichoptera, one in Coleoptera, one in Megaloptera, and at least two in Diptera (non-biting midges were not identified past suborder, Table S2). The most dominant aquatic insect taxa across sampling dates were the genera *Baetis* (Ephemeroptera), *Micrasema, Wormaldia, Hydroptila* (Trichoptera), *Optioservus* (Coleoptera), and chironomid dipterans. Of these, *Hydroptila, Optioservus,* and chironomids were the most abundant in pools during drying periods. *Drunella* and *Epeorus* ephemeropterans and *Glossosoma* trichopterans were most rare or absent in drying pools.

Response of stream insect abundance to flow disturbance

Generalized linear models with discharge, chlorophyll-a, DO, date, and the date*discharge interaction as predictors had the lowest ΔAICc values when modeling abundance (Table 1). Date, discharge, and date*discharge were present in every model, and were within ΔAICc < 3.0 of the most highly ranked model. The model with only discharge, date, and date*discharge had a ΔAICc value of 3.0. Differences in support for the top-ranked models were generally small, and models with such low variation in AICc require *a priori* knowledge of the system in order to decide on a final model (Burnham et al., 2010). Thus, we accepted the discharge, date, and date*discharge model as the most parsimonious for further analyses, given that flow dictated many of the other processes in our system. When analyzing the relationship of insect abundance and richness with channel average

Table 1 GLM models used to explain variations in stream insect abundances (upper) and genus richness (lower) across flow loss treatments

Model	Model predictors	df	ΔAICc	AICc
Abundance	Discharge, ChlA, DO, date, date*discharge	7	0	976.5
	Discharge, DO, date, date*discharge	6	0.2	976.7
	Date, ChlA, discharge, date*discharge	6	0.3	976.8
	Discharge, ChlA, DO, temp, date, date*discharge	8	2.1	978.6
	Discharge, ChlA, conductance, DO, date, date*discharge	8	2.3	978.8
	Discharge, date, date*discharge	5	3.0	979.5
	Discharge, ChlA, conductance, DO, temp, date, date*discharge	9	4.2	980.7
	Discharge, conductance, DO, temp, date, date*discharge	8	4.5	981.0
	ChlA, conductance, temp, date, date*discharge	8	4.9	981.4
	Discharge, ChlA, conductance, DO, temp, date	8	16.3	992.8
Richness	Discharge, date	3	0	325.1
	Discharge, date, date*discharge	4	0.3	325.4
	Discharge, ChlA, date	4	2.2	327.3
	Discharge, ChlA, date, date*discharge	5	2.6	327.7
	Discharge, conductance, DO, temp, date	6	2.9	328.0
	Discharge, ChlA, DO, temp, date	6	4.0	329.1
	Discharge, conductance, DO, temp, date, date*discharge	7	4.4	329.5
	Discharge, ChlA, conductance, DO, date	6	4.4	329.5
	Chla, DO, date*discharge	6	4.8	329.9
	Discharge, ChlA, conductance, DO, date, date*discharge	8	6.5	331.9

Models are ranked according to corrected Akaikes Information Criterion (AICc) values discharge separately per year, a weak positive relationship was identified between aquatic insect abundance and discharge in riffles and a weak negative relationship was identified in pools before drought treatments. In post-drought conditions, aquatic insect abundance was greater in higher-flowing channels than in low-flow and dry channels, in which insect abundance generally decreased in riffles through time during 2014 (Fig. 2). In contrast, there was no strong model fit between aquatic insect abundance and discharge rates in pools until 25 August 2014.

No relationship was found between aquatic insects and discharge in pools or riffles during sampling shortly after the 2015 flood event. At the end of the sampling season in August 2015—well after the flood—a slight positive relationship between discharge and aquatic insect abundance appeared to emerge in riffles, although abundance was much lower across all treatments. In 2016, average channel discharges increased considerably (up to 15-fold) with the cessation of the experimental treatments and subsequent resumption of flow. At this point during

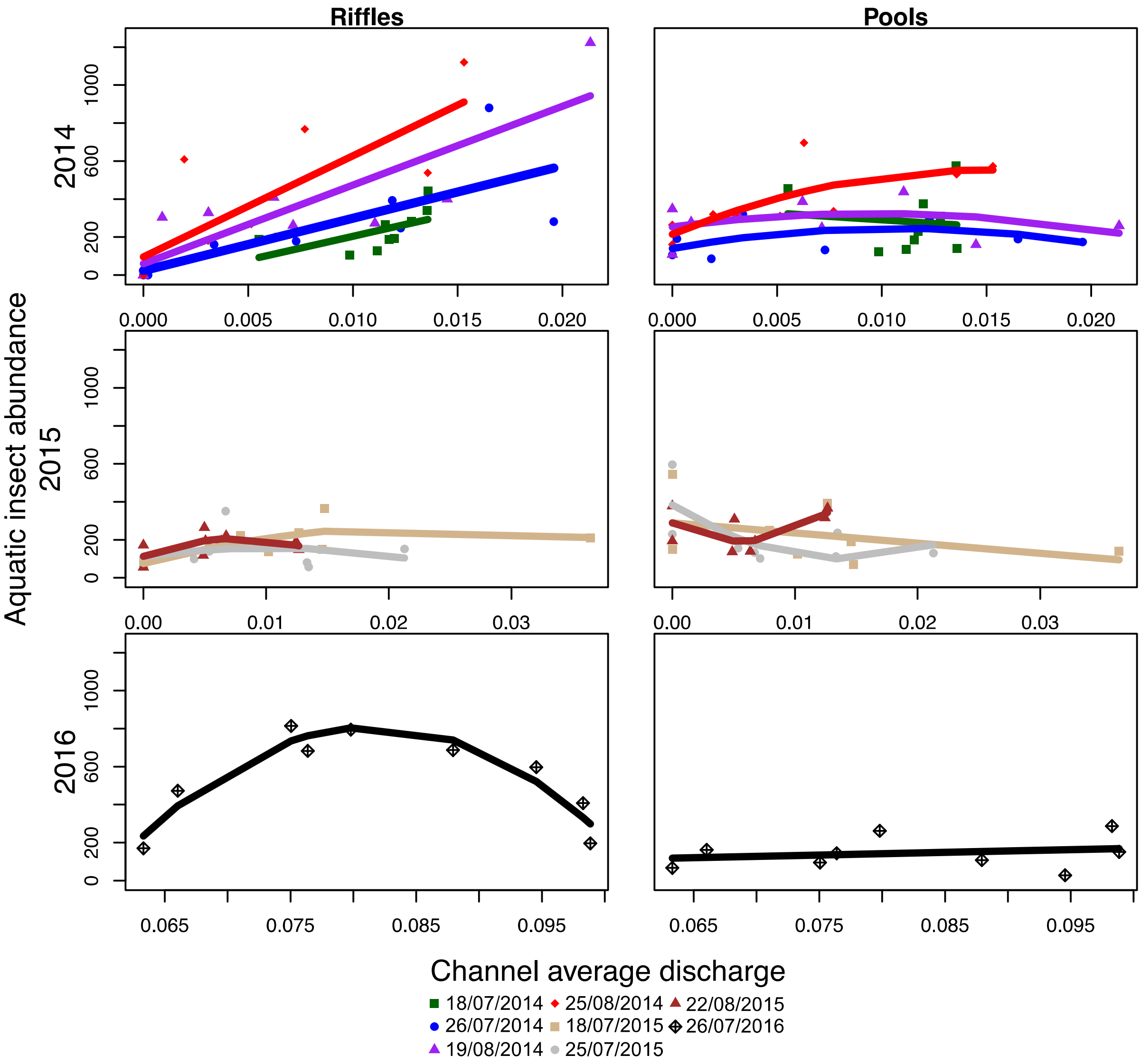

Fig. 2 Relationships between aquatic insect abundance and average discharge over time in differing habitats (pool or riffle); trends are illustrated using best-fit polynomial models

our 2016 sampling, a unimodal relationship between discharge and aquatic insect abundance was established in riffles. No relationship between discharge and aquatic insect abundance was apparent in pools (Fig. 2).

Responses of stream insect richness to flow disturbance

The model with discharge and date had the lowest ΔAICc value for taxonomic richness of aquatic insects (Table 1). Models with only date or only discharge factors resulted in a ΔAIC of over 7 and were not included in Table 1. In contrast with abundance, date was not a consistently strong factor for explaining variation in richness, although when taken without the date interaction, discharge was a strong factor. In general, models that included discharge were the most consistent in explaining variations in aquatic insect richness across the experimental channels.

No relationship was apparent between discharge and richness before flow disturbance, in neither pools or riffles. (Fig. 3, 2014, Pools pane). Immediately after implementation of the flow reduction manipulation, aquatic insect richness exhibited a positive, saturating relationship with discharge, with an asymptote at 13 ± 2 taxa in riffles (Fig. 3). This relationship became more pronounced by 25 August 2014 (Fig. 3, 2014, Riffles pane). Aquatic insect richness in pools only responded to variations in discharge after drought conditions (25 August 2014), with a slight positive linear relationship. The aquatic insect threshold effect continued into 2015 in riffles, but not in pools, where richness wasn't lost until the most extreme cases of flow loss occurred. In 2016, we found no relationship between aquatic insect richness and discharge in pools or riffles after the cessation of the experimental treatments and resumption of natural flow.

Community dissimilarity

The beta diversity among the channels was generally high throughout the experiment, ranging from 0.6 to 0.8. Total dissimilarity between all sites increased immediately in riffles after drought perturbations ($\beta = 0.73$–0.83), whereas dissimilarity in pools stabilized at original values after an immediate decrease (between $\beta = 0.70$–0.75; Fig. 4). Upon establishment of drought conditions, community dissimilarities were consistently higher across habitats and sites, except when the channels were flooded on 12 July 2015, at which point community dissimilarities returned to predrought levels. Dissimilarity in the riffle communities increased again briefly after the flood, and after a year of free flow, dissimilarities between all the sites markedly decreased to lower levels than before flow reductions in the channels ($\beta = 0.65$; Fig. 4). In pools, site-wide dissimilarity was relatively constant across drought periods, flood periods, and the flow resumption period ($\beta = 0.70$–0.72), but declined immediately after drought treatments ($\beta = 0.63$; Fig. 4).

After partitioning dissimilarity into balanced variation and abundance gradients in riffles, a significant relationship ($R^2 = 0.139$, $P = 0.001$) weakly explained the decay in abundance gradient similarity due to flow before any perturbation (Fig. 5). After drought treatments, the abundance gradient exhibited a saturating response across the drought intensity gradient. This relationship remained positive ($R^2 = 0.175$–0.330, $P = 0.001$) until natural flow was restored. In 2016, when all channels had natural flow, the abundance gradient had a relationship similar to that of before drought treatments were in place ($R^2 = 0.141$, $P = 0.001$). In contrast, the relationship between balanced variation and flow was never significant in riffles during all years.

In pools, balanced variation and abundance gradients showed weak, nonsignificant responses across the flow gradient before drought treatments (Fig. 5). These responses became significant immediately following flow disturbance ($R^2 = 0.075$, $P = 0.012$ for abundance gradient, $R^2 = 0.114$, $P = 0.004$ for balanced variation; Table S1). On 19 August 2014, responses between the two partitions started to diverge. The strength of the positive relationship with the abundance gradient increased ($R^2 = 0.362$, $P = 0.001$), whereas that with the balanced variation became negative and was not significant until 25 August 2014 (Table S1). These relationships were reset immediately after the 2015 flood, and pre-flood patterns were re-established after 1 month. In 2016, both partitions exhibited positive relationships with drought intensity, but only the balanced variation was explanatory in the distance-decay model ($R^2 = 0.130$, $P = 0.002$). These partitions suggest that there were no strong compositional shifts in the stream insect community over time, and that the main effect of the

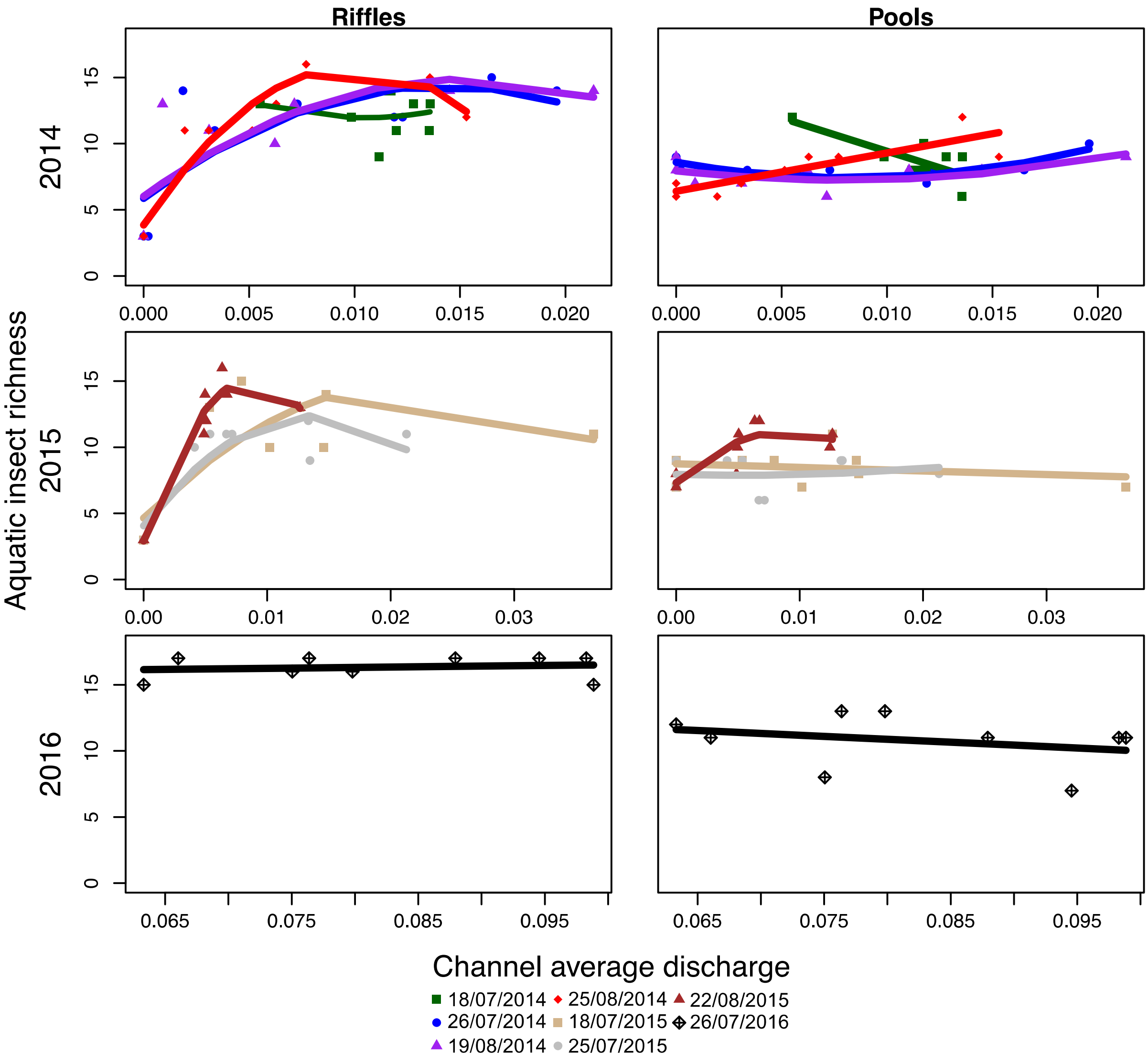

Fig. 3 Relationships between aquatic insect richness and average discharge over time in differing habitats (pool or riffle); trends were identified using best-fit polynomial models

drought was to reduce abundances uniformly across taxa.

Discussion

Novel flow regimes, whether from direct anthropogenic manipulation or from climate change, are substantially altering freshwater communities. These alterations include simplification of community structure and shifts in dominant traits (Ruhí et al., 2018; Tonkin et al., 2018; Aspin et al., 2018a). As flow regimes are increasingly altered, a continuing challenge is to understand patterns of biodiversity resistance and resilience across different freshwater ecosystems and flow alteration scenarios. In our study, experimental discharge reductions had a strong, direct effect on the aquatic insect community, where insect abundance declined consistently across reduction treatments, indicating only moderate drying resistance. In contrast, richness exhibited higher resistance, as significant losses in richness were only observed in the most severe cases of flow reduction when surface flow was lost in riffles later in sampling. This threshold

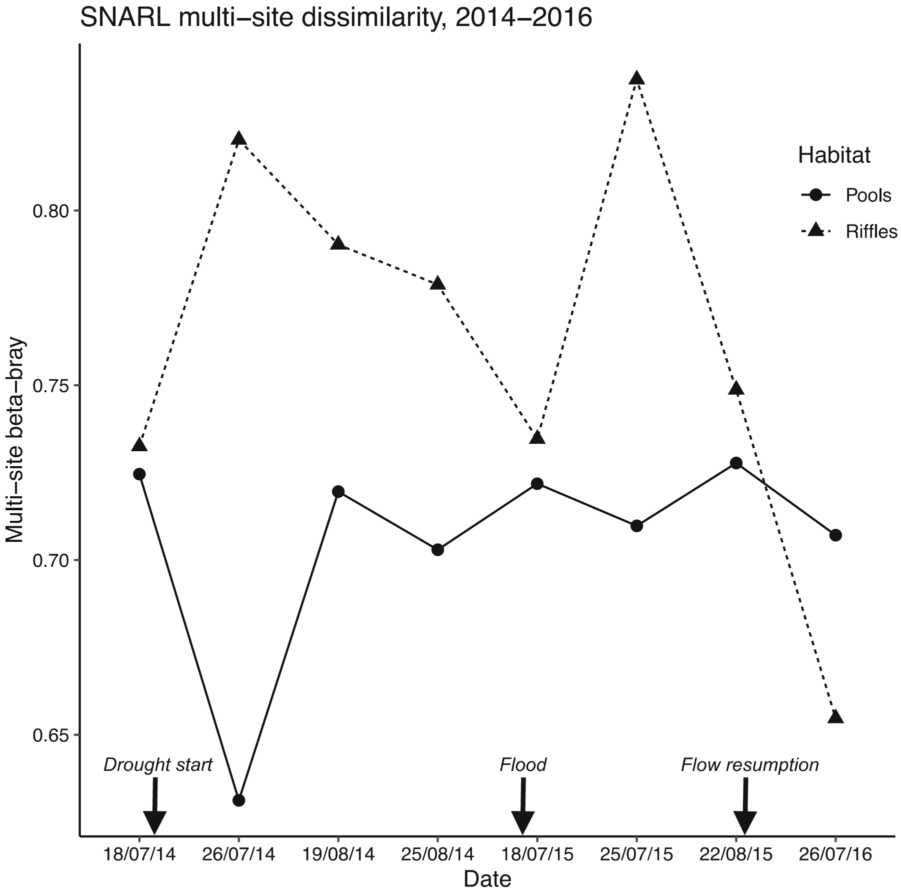

Fig. 4 Multi-site beta dissimilarity on each sampling date; major flow changes are indicated with arrows. Dotted and solid lines represent beta dissimilarities in riffles and pools, respectively

effect was evidenced by support for the discharge*-date interaction in richness models (Table 1). The flood event on 12 July 2015 reset these patterns, which slowly re-emerged toward the end of 2015. In support of our prediction of resistance, beta diversity among channels was largely driven by changes in abundance, as indicated by positive abundance gradients, especially in pools, but was not related to compositional turnover, as indicated by minimal shifts in balanced variation (Fig. 5). Increases in beta diversity among channels were related to the loss of individual taxa in the driest channels, resulting in nested subsets of the pre-disturbance communities, with no replacement of lost taxa by other taxa. Thus, most taxa were able to persist across most of the drought perturbation treatments, though many individuals were lost during the treatments. Our findings, particularly high resistance in species richness to all but most extreme flow loss, is consistent with a community already shaped by background regional drought conditions. Additionally, we found evidence for our prediction of high resilience, whereby taxa recovered in richness and abundance, and established similar pre-perturbation beta diversity values after flow was restored for one year.

Other studies of experimental flow reductions show that drought-affected communities shift toward more resilient smaller taxa with faster life cycles (Ledger et al., 2011; Aspin et al., 2018a), with strong dispersers replacing weak dispersers (Bogan et al., 2015), a higher proportion of lentic adapted taxa (Piano et al., 2020), and a shift in dominance toward generalists (Doretto et al., 2018). We did not find such pronounced shifts in taxonomic composition, and cursory examinations of traits yielded consistently low trait variation at all times of the study. Rather, declines were evident across all taxa up until when surface flow was lost, implying community resistance to flow loss, and the most affected communities became nested subsets of less affected communities. Therefore, insect

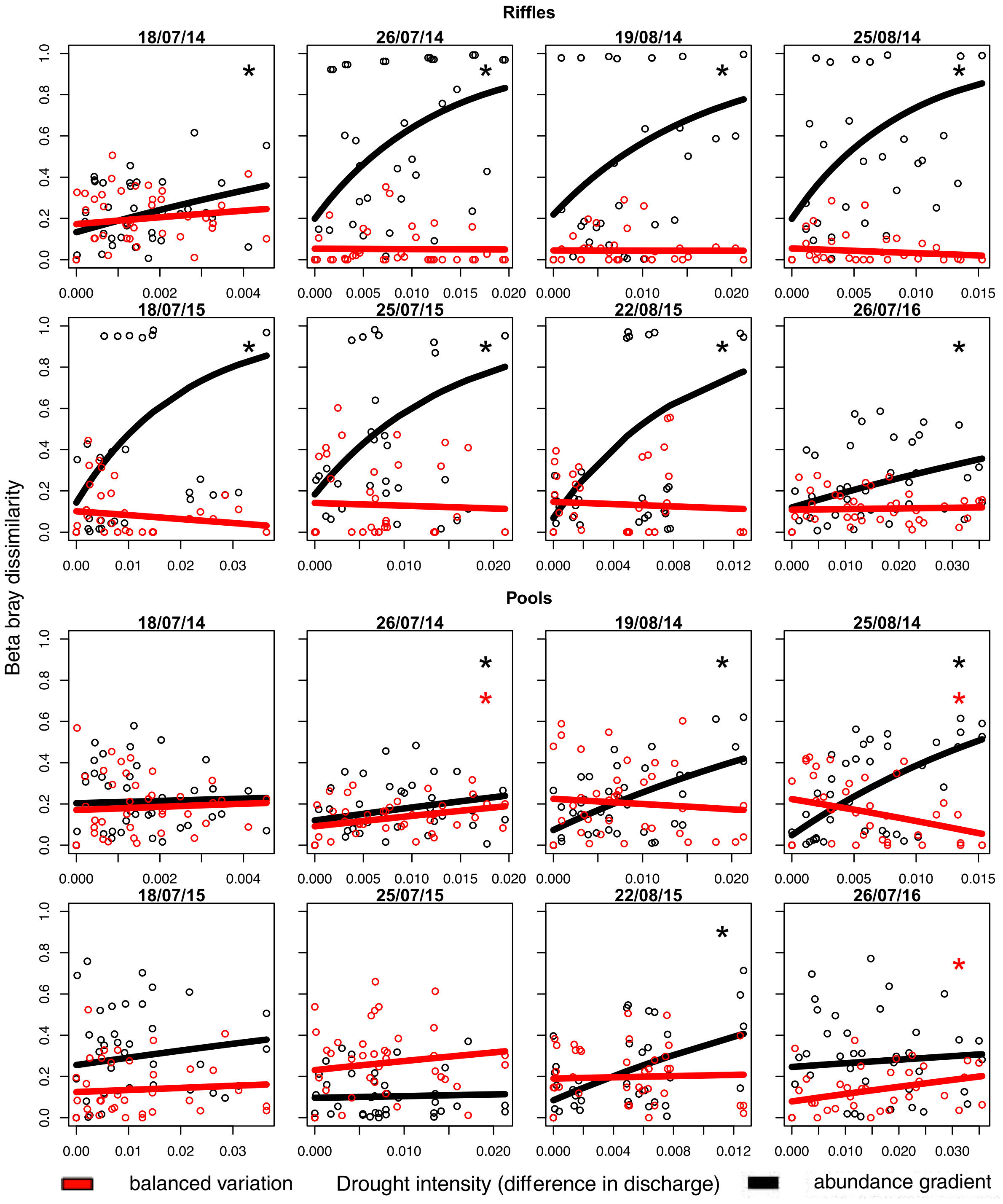

Fig. 5 Partitioned pairwise beta-bray dissimilarity values in riffles (upper panels) and pools (lower panels); data are plotted against drought intensity on sampling days. The lines were fitted using negative exponential distance-decay models. Black asterisks indicate significant relationships ($P < 0.05$) with abundance gradient, and red asterisks indicate significant relationships with balanced variation

community adaptations to the perennial flow regime may have led to particular vulnerability to the region-wide long-term drought taking place during our experiment, resulting in a drought-preconditioned community already shaped by drought before the onset of the experiment. This could have led to consistent declines in abundance among all taxa during our experiment (Lytle & Poff, 2004; Stubbington et al., 2009, 2019). In arid systems where low-flow events are typical, taxa like the flightless Belostomatidae have been shown to crawl long distances to find water (Bogan et al., 2015). These specific drying-tolerant traits appear to be lacking in the insects at SNARL during the study duration, for which constant densities were maintained in channels with sustained surface flows and rapidly declined in dry channels due to emigration or direct mortality. Thus, the community appeared to be resistant to flow loss up until surface flow was lost. Abundance gradients were less pronounced after the flood of 2015 than before it, yet they were re-established, indicating a bias of drifting colonization toward higher-flowing channels (Fig. 5).

The proximity of the experimental channels to the source community in Convict Creek (within 15 m) could have provided an efficient colonization route into the channels via drift or oviposition and promoted observed community resilience during the flood event and when flow was restored. Close proximity of source communities to perturbed sites has been shown to promote resilience (Boersma et al., 2013). In our study, after a year of higher flows in 2016, drifting insects successfully and rapidly recolonized the channels and exhibited a preference for riffles, as indicated by higher levels of richness and abundance. However, it is less likely that drift immigration influenced in-channel community responses during the experimental flow manipulations. Daily measurements using 250-μm nets that covered the widths of the channels at the inlets and recorded negligible amounts of immigrating invertebrates at the start of the experiment (personal observation, data not shown). We speculate that the lack of drift was due to growth of the lentic macrophyte *Elodea* near the flow gates in the channel heads at the start of drought treatments (Robach et al., 1997). The rampant growth of these plants may have closed off drift routes into the channels. Upstream crawling of insects into the channels was also unlikely because of the 2 m drop from the bottom of channels to the outlet basin. Drift immigration likely increased after the 2015 flood event also, with the increased discharge bringing in new individuals. In areas without drift immigration, such as headwater systems, drought scenarios could result in high community turnover similar to what has been found in drought studies with no immigration in recirculating mesocosms (Aspin et al., 2019; Leigh et al., 2019).

A prolonged drought was recorded from 2012 to 2015 in the Sierra Nevada, likely resulting in unique environmental conditions and a filtering of the regional species pool that was preconditioned to drought conditions (Herbst et al., 2019). Benthic samples were taken from Convict Creek in the summer of 2014 and had a genus richness of 35 taxa, compared with 15 in the channels. A long-term study during the prolonged drought found significant shifts in aquatic insect communities in the Sierra Nevada, where sensitive species were depleted and generalists became dominant (Herbst et al., 2019). In line with our results, hyporheic flows in pools from the aforementioned study contributed to community resistance, whereas extreme flow losses resulted in diel fluctuations in DO and temperature with significant decreases in richness (Herbst et al., 2019). However, the novelty of our experimental study was the ability to subject aquatic insect communities to extreme—yet potentially more frequent—flow conditions impossible to achieve in nearby streams. Even our drought-preconditioned subset of the local species pool containing species able to persist though the multi-season regional drought, showed sensitivity to extreme habitat loss.

In our experiments, pools emerged as a temporary refuge and conferred resistance by maintaining stable balanced variation and abundance gradients longer than riffles during drought conditions. The impact of drought on aquatic insect beta diversity was minimal for the first four weeks of the experiment because pools likely sustained hyporheic flows, with small amounts of water passing into dry flow-disconnected channels. Additionally, all channels had 30 cm of substrate to allow cooler water to flow underneath likely without evaporation, heating, or loss of oxygen. Later in the experiment, these conditions changed. The pools in the dry channels experienced diel temperatures that fluctuated between 8.7 and 28°C, leading to stronger abundance gradients emerging (Fig. 5).

Though pools appear to maintain abundance gradients longer than riffles during drought periods, environmental heterogeneity, such as substrate profile and canopy cover was not as pronounced in our system as in Convict Creek and other Sierra Nevada streams. Previous comparisons between pools and riffles in other small Sierra Nevada streams showed significant differences in environmental conditions and aquatic insect assemblages, suggesting that many taxa distributions respond to heterogeneity of pool / riffle environments (Herbst et al., 2018). We attribute this difference in response to the impact of the multi-year regional drought taking place during our study, as environmental conditions of pools influence their use as refuges during drought events (Doretto et al., 2018).

Additionally, given the regional drought during the duration of our experiment, relatively few riffle specialists were present in the channels. Thus, the pre-experimental drought community had a higher proportion of resistant lentic taxa enabling persistence in remnant pools for several weeks. This pool-tolerant taxonomic profile, preconditioned by the regional drought, may explain why no strong shifts in composition were recorded. In other studies, however, interactions between extreme temperature ranges, low-flow, lack of pool refugia, and loss of substrate moisture with the contraction of hyporheic zones were most detrimental to aquatic insect diversity in streams during drought events (Rader & Belish, 1999; Stubbington & Datry, 2013; Vander Vorste et al., 2016). Remnant disconnected pools following complete flow loss can become overcrowded and then experience mass mortality following drying events, and riffle preferring taxa are unable to persist in interspersed pools (Verdonschot et al., 2014; Herbst et al., 2019). Thus, even pool-tolerant, drought-preconditioned communities in the experimental channels were unable to persist through extreme low-flow conditions of over one month.

Drought and resulting low flows can result in lasting shifts in environmental conditions, such as decreased organic matter availability and quality, alterations to riparian vegetation, and changes to the channel geometry (Stromberg et al., 2005; Ylla et al., 2010). At SNARL, cattail, bulrush, and some perennial grasses colonized the exposed banks of stagnant pools in low-flow and dry channels. This riparian vegetation was not present in pools of high-flowing channels, but it persisted into 2016, a year after natural flows were restored. Changes in riparian habitats may have influenced components of instream biotic diversity that did not conform with our general findings of static community composition under most experimental flow conditions. For example, megaloptera of the genus *Sialis* established larval populations in low-flow pools, likely reflecting preference for burrowing behavior and stagnant habitats in which eggs can be laid on objects over the water (Woodrum & Tarter, 1973). Drought-stricken streams may therefore harbor some legacy effects when flow is lost for long enough. Future studies are required to consider experimental flow reductions in the context of structural habitat changes that may only manifest over longer timescales.

Aquatic insect populations recovered from drought treatments after flow resumption in 2016, suggesting that the channel-dwelling taxa can re-establish themselves in one year. With unperturbed flow from 25 July 2015 to 26 July 2016, genus abundance and richness were restored to similar levels as those before the drought treatments were started in 2014. Further, in this year of natural flows, beta diversity became homogenous among channels, with greater similarity than before the drought treatment. Although we were logistically challenged to sample at a higher frequency, our year-long timescale of recolonization is longer than the durations of weeks or months reported in previous studies, and other work has shown that 21 days of recolonization is insufficient to establish pre-drying communities, as some taxa can take many years to re-establish (Doretto et al., 2018; Sarremejane et al., 2019). In the present study, dispersal (drift, crawling, and oviposition by aerial adults) between the channel communities and Convict Creek was likely the largest contributor to the recolonization of drought-affected channels, with resistance traits (desiccation-tolerant eggs) being a lessor factor, although some *Paraleptophlebia* are drying specialists (Table S2). Accordingly, dispersal mechanisms are vital determinants of community structure when sites are flow connected (Datry et al., 2015). Dispersal was most influenced by the presence of surface flow and high flow events. For example, trajectories of beta diversity were reset by the 2015 flood and by flow resumption in 2016. These observations suggest that individuals drifted into the channels to recolonize immediately following channel re-wetting, and adult insects later repopulated the channels via oviposition.

Thus, an interaction between stream connectivity and the specific timescales of our flow disturbance may have facilitated recolonization.

Taking a metacommunity perspective can help to generalize responses of aquatic insects to flow disturbance, because it explicitly considers extinction and recolonization dynamics for different taxa (Leibold et al., 2004; Heino et al., 2015; Downes et al., 2017). During drought, local community structure may most reflect within-channel species sorting, favoring disturbance and stress adapted taxa. In our experimental channels, inhospitable local environmental conditions, especially in the dry channels, abolished normal dispersal pathways and resulted in strong depleted abundance gradients (Campbell et al., 2015; Aspin et al., 2018b; Leigh et al., 2019). Site-wide community dissimilarity was lower after flow was restored in the channels (Fig. 5), suggesting that in future drought scenarios, mass effects may be crucial to recovery when rivers regain flow connectivity. In agreement, flow connectivity facilitated high dispersal rates between channels in a previous study, and the communities became more homogeneous when drought conditions were eased (Tonkin et al., 2017). The lower site-wide dissimilarity at SNARL may also follow higher flow in 2016 than in the previous two years, allowing for higher rates of drift. Moreover, high rates of source (Convict Creek)—sink (SNARL channels) dynamics may have overwhelmed local environmental processes and facilitated immigration back into the channels.

When surface flow is lost due to drought conditions, pools are sustained by hyporheic flows but demand resistance of insect communities that are adapted to perennial flows (Herbst et al., 2019). When considering the management of potentially flow impaired streams, priority should be placed on the establishment of sustained surface flow in streams for the persistence of diverse and abundant insect communities. Additionally, management should focus on regions that lack the hydrogeology to sustain groundwater inflows, such as those from springs, since aquatic insects may be most imperiled by drought in these areas. In future studies, we recommend that routes of colonization before and after flow disturbances be controlled to determine the mechanisms through which taxa respond to disturbances and how they recolonize (Vander Vorste et al., 2016; Downes et al., 2017). Flow disturbance studies performed at larger spatial scales and during heterogeneous flow years may also indicate divergent persistence mechanisms of aquatic insects. Alternatively, spatial variations could be simulated in smaller experimental facilities by mimicking the unique dispersal and environmental conditions at different stream orders within the study system.

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Availability of data and material Available upon request and can be accessed on the corresponding author's Github page.

Code availability N/A see above.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

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