LETTER

Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient

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Abstract

The ecological and evolutionary consequences of extreme events are poorly understood. Here, we tested predictions about species persistence and population genomic change in aquatic insects in 14 Colorado mountain streams across a hydrological disturbance gradient caused by a one in 500-year rainfall event. Taxa persistence ranged from 39 to 77% across sites and declined with increasing disturbance in relation to species' resistance and resilience traits. For taxa with mobile larvae and terrestrial adult stages present at the time of the flood, average persistence was 84% compared to 25% for immobile taxa that lacked terrestrial adults. For two of six species analysed, genomic diversity (allelic richness) declined after the event. For one species it greatly expanded, suggesting resilience via re-colonisation from upstream populations. Thus, while resistance and resilience traits can explain species persistence to extreme disturbance, population genomic change varies among species, challenging generalisations about evolutionary responses to extreme events at landscape scales.

Keywords

Disturbance gradient, extreme event, genomic change, landscape vulnerability, population persistence, resilience traits, resistance traits, stream insects.

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INTRODUCTION

Ecological theory predicts that species surviving large disturbances will possess traits that confer high resistance to mortality and allow for recovery (resilience) after the perturbation (Connell 1978; Hodgson *et al.* 2015; Nimmo *et al.* 2015). Testing this theory in the context of extreme events is difficult due both to their unpredictable and rare occurrence (e.g. less than one-in-100 year probability, Milly *et al.* 2002) and to the general paucity of pre-event data that allow statistical analyses of population and species responses. Biologically, extreme events substantially exceed 'acclimatory capacities' of organisms and thus likely play a disproportionate role in shaping the ecology and evolution of organisms (Gutschick & BassiriRad 2003). The frequency of some extreme events is increasing (e.g. 1-day precipitation totals in the USA; NOAA 2017) and is projected to increase further as the Earth warms (Trenberth *et al.* 2003; Donat *et al.* 2016) with significant ecological and evolutionary implications. For example repeated population reductions or extirpations could cause persistent changes in community structure and ecosystem function. Extensive mortality could create population bottlenecks leading to a reduction in genetic variation and fitness in the face of future extremes, while simultaneously acting as a strong selection agent on organismal traits (Gutschick & BassiriRad 2003). A better understanding of mechanisms by which populations resist and recover from disturbance is needed to improve prediction of population and community responses to future extreme events (Nimmo *et al.* 2015).

Some examples of species responses to extreme events have been well documented. For example corals experience reduced growth and increased mortality under extreme warming (Smith *et al.* 2013), and subtropical aquatic and terrestrial species are physiologically susceptible to extreme cold spells (Boucek *et al.* 2016). Brushtail possums (*Trichosurus cunninghami*) exhibit resilience after wildfire through more flexible resource selection (Banks *et al.* 2011). Stream insects show resilience to wildfire-induced flooding via strong dispersal ability by flying adults (Vieira *et al.* 2014). Aside from magnitude, the timing of extremes may dictate the response of species, as suggested for stream fishes (Matthews *et al.* 2014). Prolonged extreme events may prevent near-term species recovery, as shown for floodplain birds following years-long drought (Selwood *et al.* 2015). Furthermore, the impact of an extreme event on species can vary according to landscape features that modulate the effective intensity of the event (Boucek *et al.* 2016).

At the population level, extreme events may alter genomic trajectories. Theory predicts populations can adapt to long-term regimes of environmental variability (Levins 1968; Slobodkin 1968), yet few studies have collected pre-disturbance data that allow for direct assessment of disturbance at the genetic level (e.g. Steinfartz *et al.* 2007; Plath *et al.* 2010;

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Suarez *et al.* 2012). Studies of population responses to fire (Dolan *et al.* 2008; Vicente *et al.* 2013; Shohami & Nathan 2014) and drought (Fauvelot *et al.* 2006a,b; Franks *et al.* 2016; Vandergast *et al.* 2016) have generally found evidence for rapid genetic change, including loss of genetic variation, changes in allele frequencies and increased gene flow. However, previous studies typically focused on a single species or populations, precluding comparisons of genetic consequences across species and across a disturbance gradient (but see Franks *et al.* 2016).

Several fundamental questions remain about how populations and species respond to extreme events. Can differences in species persistence during extremes be explained by interspecific variation in resistance and resilience traits? For persisting populations, do extremes induce bottlenecks that result in loss of genetic diversity, and does genomic change provide any insight into persistence mechanisms? Do population and species responses scale to extreme event size?

Here, we report on the response of communities of stream insects to an extreme flooding event that occurred during September 9–16, 2013, delivering up to 450 mm of rain over an extensive area of northern Colorado, USA (Fig. 1). Most of the deluge occurred in a 36-h period, caused extensive property damage and loss of life, and created runoff levels in montane streams across this region with estimated recurrence intervals of 1/50–1/500 years (Gochis *et al.* 2015). The role of anthropogenic climate change in generating this particular event is debated (Hoerling *et al.* 2014; Trenberth *et al.* 2015), but it provided an excellent opportunity to gain insights into biological responses to a rare rainfall extreme.

Fortuitously, we had collected pre-disturbance data on insect community composition (Harrington *et al.* 2016) and genomic data for several species (Polato *et al.* 2017). Those data afforded a unique opportunity to examine patterns of species persistence and population genomic response to extreme flooding. Streams are naturally disturbance driven (Resh *et al.* 1988; Poff & Ward 1989) and responses of stream insects to hydrological disturbance have been extensively reviewed (Stanley *et al.* 2010; McMullen & Lytle 2012). Few studies have, however, documented extreme hydrological events, and typically for one to a few sites (e.g. Matthews *et al.* 2014; Vieira *et al.* 2014; Robertson *et al.* 2015; Woodward *et al.* 2015). We tested 3 specific hypotheses. First, we predicted that persistence of taxa and community richness would decline as the intensity of extreme disturbance increased across stream sampling sites. Second, we predicted that differential persistence by taxa across the gradient would be explained by their having quantifiable resistance and resilience traits that reduce disturbance mortality. We expected the relative community-wide occurrence of these traits in persisting species would increase in response to disturbance intensity. Third, we predicted that, for persisting species, genetic variation at neutral loci would be reduced after the event and that the magnitude of genomic change would scale to disturbance intensity. More specifically, we expected a greater loss of allelic richness (A_r) than observed heterozygosity (H_o) due to the former's greater sensitivity to bottlenecks (Allendorf 1986). Ours is the first study to examine multiple species at multiple sites across an extreme event gradient to test theoretical predictions about mechanisms of species persistence and evolutionary change during extremes.

METHODS

We selected 14 sites along a gradient of rainfall intensity based on data obtained from a digital spatially interpolated map of the study region (Fig. 1). All streams were small and wadeable (2nd or 3rd order) with catchment areas of < 100 km^2 that occurred across a *c*. 1400 m elevation gradient (Table 1). We sampled these streams in June-July of 2014, within 2 weeks of the pre-disturbance sampling dates in 2011 (Harrington *et al.* 2016). Using 10-m digital elevation maps, we delineated the upstream catchment area for each sampling location to calculate rainfall totals (mm) in each stream catchment over the 8-day period and calculated runoff (mm km^{-2}), a measure of total area-adjusted flow volume passing through the sampling point over the September 9–16 period.

Quantifying disturbance

Benthic insect mortality during floods occurs when high flows export individuals downstream and when moving particles on the streambed crush individuals. None of our sampling sites had streamflow gauges, so we used two indirect methods to estimate streambed disturbance at each site. We first calculated a 'channel disturbance' index (CD) from a comparison of 24 pre- and post-flood photographs taken at six fixed locations in 100-m sampling reaches (facing upstream, downstream, left bank, right bank) in each of our 14 streams. At each stream we scored pre- vs. post-flood photographs in terms of channel erosion (conspicuous sediment scour and deposition laterally along the stream channel), from 1 = none to 5 = very high, for a possible maximum score of 120 per stream. All stream scores were divided by the maximum observed score to normalise the index to 0–1 (Supplementary Methods and Figure S3).

As a second disturbance index, we estimated forces acting vertically on the streambed during peak flows. At two or more locations at each stream, we located the peak water level during the flood, as marked by residual organic debris deposits along the shoreline. With a hand-held laser range finder we surveyed the cross section of the inundated valley bottom to extract maximum depth, width and water surface slope during peak flow. This information, combined with pre-flood streambed particle size data, allowed us to estimate shear stress acting on the bottom during peak flow. We adjusted estimated shear stress by the potential resistance provided by boulders and woody debris in the channel and floodway using our stream photographs to yield an index of hydraulic disturbance (HD). All 14 stream values of HD were normalised from 0 to 1 across all sites (Supplementary Methods).

Benthic insect community sampling and analysis

To quantify stream insect richness at a site, we used a standard D-frame net (500 micrometre mesh) to dislodge invertebrates from the streambed via kicking motions for a 5-min period distributed proportionately across all microhabitats
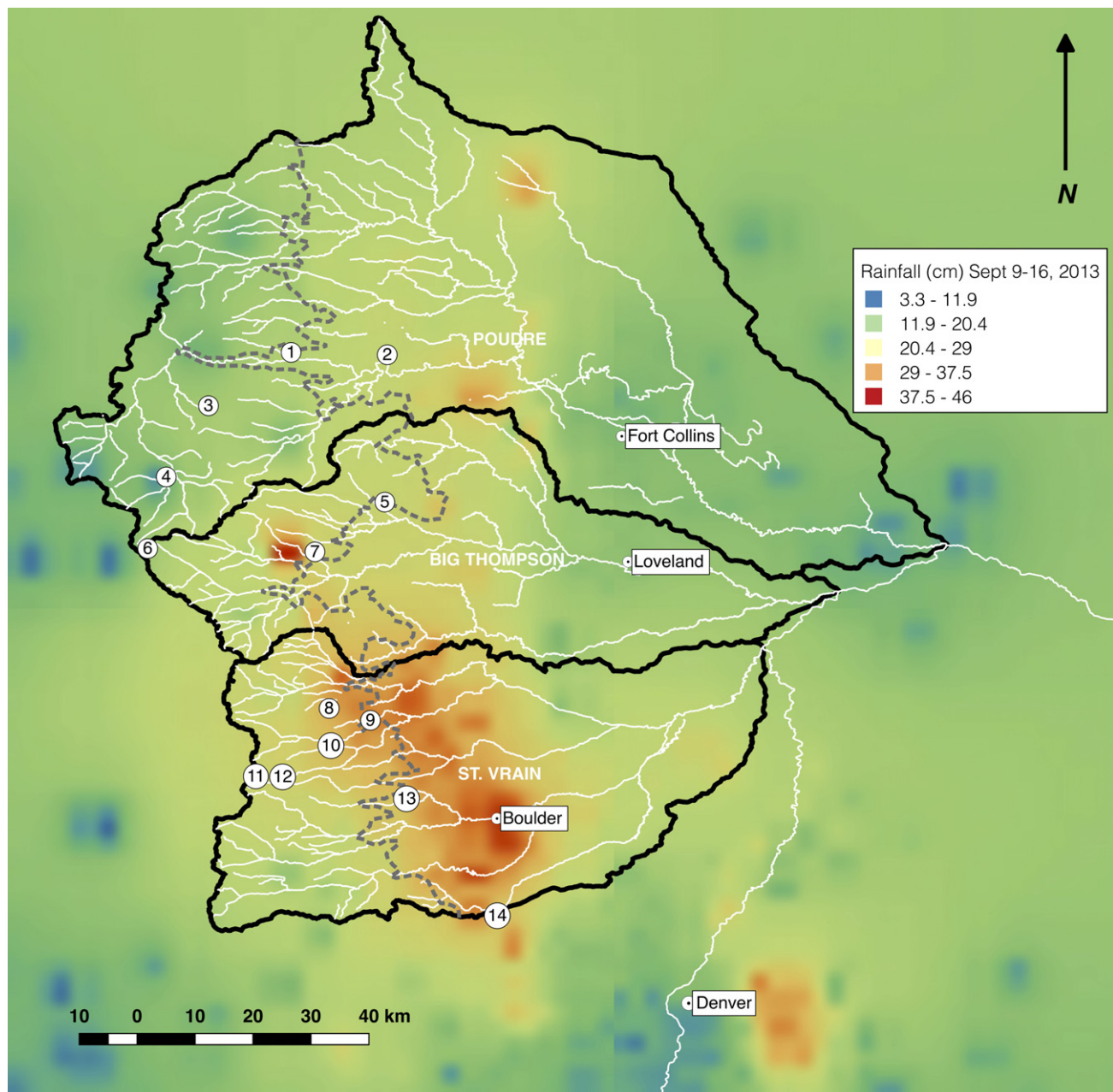
Figure 1 Map of 3 catchments in northern Colorado, USA, showing gradient of total rainfall falling September 9–16, 2013, based on interpolated NOAA data (http://criticalzone.org/national/news/story/weather-event-breaks-records/M60o93H7pQ09L8X1t49cHY01Z5j4TT91fGfr/). Study sites are numbered, corresponding to Table 1. Major drainages are delineated by grey dashed line, and the thick white line marks the 2500 m a.s.l. elevation band.

present (see Harrington *et al.* 2016). Samples were preserved in 100% ethyl alcohol and returned to the laboratory where insects were enumerated and identified to lowest practicable taxon under a dissecting microscope. Total individual insects collected were similar pre-flood (29 118 individuals) and post-flood (26 521 individuals) for the 14 sites.

Benthic insect trait assignment

We selected traits for benthic taxa in terms of whether they would enhance persistence to stream disturbance either through resistance to the event or resilience after the event (e.g. Grimm & Fisher 1989). In-stream mobility by larvae can provide resistance to mortality, and we used the database of Poff *et al.* (2006) to define mobility as a function of the ability to swim or drift to relocate to a more favourable habitat, or to crawl over the streambed. Taxa were assigned performance scores of 1 (low), 2 (medium) or 3 (high) for each trait (see Poff *et al.* 2006). We *a priori* defined mobile taxa as having a score of 2 or higher on two of the three traits, or a score of 3 on at least one trait, yielding summed scores across the three traits of 5 to 8. Immobile taxa were defined as those having a

Table 1 Information about sites used in analysis. Sites are ordered and numbered to correspond to Fig. 1

Site	Site #	Elevation (m, a.s.l.)	Ave. rain (mm)	Catchment runoff (mm km^{-2})	CD	HD	Taxa prop. pers.	# Taxa genom.
7 Mile	1	2212	149	7	0.50	0.48	0.80	2
Elkhorn	2	1992	187	2	0.64	0.32	0.43	1
East Fork Sheep	3	3166	145	45	0.20	0.19	0.64	2
Corral	4	3068	86	6	0.20	0.16	0.67	2
Miller	5	2252	234	9	0.46	0.38	0.65	6
Big Thompson	6	3364	113	161	0.20	0.71	0.53	2
Black Canyon	7	2411	288	18	1.00	1.00	0.50	3
Rock	8	2643	277	73	0.26	0.55	0.83	2
Cave	9	2388	319	22	0.50	0.27	0.53	4
Beaver	10	2830	269	20	0.40	0.25	0.68	2
Izzy	11	3348	230	135	0.20	0.37	0.75	2
Wigwam	12	3249	228	326	0.20	0.35	0.77	2
4 Mile	13	2189	227	7	0.74	0.45	0.71	2
Coal	14	2015	305	8	0.88	0.67	0.39	0

CD is normalised channel disturbance; HD is normalised hydraulic disturbance; Taxa prop. persist. is proportion of all taxa persisting; # taxa genom. is number of species used at each site in the genomics analysis.

maximum score of 2 on no more than one trait with summed scores of 3 or 4. Another trait that confers resistance to disturbance is resistance to crushing by moving sediment, through a hard exoskeleton or crush-resistant case or shell. Taxa with a score of 3 were rated as crush resistant.

We identified two traits that could contribute to post-flood recovery. Some aquatic species have larvae that can move thousands of metres downstream via drifting over periods of weeks (e.g. Hershey *et al.* 1993) and thus can quickly re-colonise disturbed habitats (Hammock & Bogan 2014). Species scored as 3 for drift ability were considered potentially resilient via instream re-colonisation. A second mechanism of post-disturbance recovery occurs when the aerial adults of aquatic insects oviposit back into the stream after disturbance. Adults are short-lived (days to weeks) and, if present at the time of the flood, could effectively act as a life history refuge for stream disturbance (Lytle 2001). Based on available literature and expert judgment from many years of entomological research in this region (B.C. Kondratieff, unpubl. data), we identified taxa expected to have terrestrial adults present during the September flooding. We coded them as either present (A+) or absent (A−). Although aerial adults can re-colonise from distant habitats, we reasoned the cool montane temperatures in late September minimised overland dispersal. We therefore considered species persisting in the following year's community as largely consisting of larvae that survived the flood in place or that re-colonised from upstream, and of local aerial adults that oviposited into the stream after the flood. A select group of taxa and their trait assignments are illustrated in Table 2. Trait assignments for all taxa are provided for all taxa in Table S1.

Community statistical analyses

Significance of the disturbance effect on response variables was set at α = 0.05 for all statistical tests, which were simple correlation, linear regression and t-tests. Our *a priori* expectation was that there would be declines across the disturbance gradient for percentage of taxa persisting (hypothesis 1) and

for proportion of taxa possessing low values for resistance and/or resilience traits (hypothesis 2); therefore, we used one-tailed tests for these predictions. Other tests were two-tailed. All analyses were done in R v. 3.3.3 (R Core Team 2016).

Genomic sample selection, library preparation and sequencing

We included six species in the genomic analysis with a minimum of 15 individuals per population (average = 28) for both pre- and post-flooding. We sequenced a total of 1530 specimens from six species and 14 localities, including mayflies *Baetis bicaudatus* Dodds, 1923 (9 populations), *B. tricaudatus* Dodds, 1923 (4), *Drunella coloradensis* Dodds, 1923 (6) and *Epeorus longimanus* Eaton, 1885 (6) and stoneflies *Hesperoperla pacifica* Banks, 1900 (3) and *Megarcys signata* Hagen, 1874 (3). All six species have high resistance and resilience scores (Tables 2, S1) and persisted during the flood. Species with low resistance and resilience scores were largely extirpated and were therefore unavailable for genomic analysis. We used previously collected sequences (Polato *et al.* 2017) from two of the species (*B. bicaudatus*, *B. tricaudatus*) to complete the pre-flood sampling. We used double digest restriction-site associated DNA (ddRAD) sequencing to genotype hundreds to thousands of presumably neutral, anonymous single-nucleotide polymorphisms (SNPs) for each species (see Supplementary Methods for details).

Genomic analyses

We calculated pre- and post-flood allelic richness (A_r), observed heterozygosity (H_o) and genetic differentiation (F_{ST}) for each site and species (Supplemental Methods). To compare changes in A_r and H_o among populations and species, we calculated the proportional change in these parameters, which we referred to as scaled ΔA_r and scaled ΔH_o. For example scaled $\Delta A_r = (A_{rPOST} - A_{rPRE})/A_{rPRE}$ such that a negative value indicates a loss of richness after the flood. We define *flood* F_{ST} as the pairwise F_{ST} value between pre- vs. post-flood samples for each site, making it a measure of

Table 2 Example insect taxa occurring in study streams, illustrating differences in the resistance and resilience traits

Mobility class	Taxon	Larval image	Resistance traits				Resilience traits	
			SWIM	DRFT	CRWL	CRSH	ADLT	DRFT
Mobile								
	Baetis tricaudatus		●	●	◉	○	+	●
	Baetis bicaudatus		●	●	◉	○	+	●
	Epeorus longimanus		◉	◉	◉	○	+	◉
	Zapada cinctipes		◉	◉	●	○	+	◉
	Megarcys signata		◉	○	●	○	+	○
	Simuliidae		○	●	○	○	+	●
Immobile	Tipulidae		○	○	○	○	-	○
	Clinocera sp.		○	○	○	○	-	○
	Glossosomatidae		○	○	◉	○	+	○
	Elmidae		○	○	◉	●	-	○

Mobile taxa are determined by cumulative numerical scores for ability to swim (SWIM), drift (DRFT) and crawl (CRWL) (● = score of 3, ◉ = score of 2, ○ = score of 1). See text for description. Resistance to crushing (CRSH) is also a resistance trait. Resilience traits include the possession of a terrestrial adult stage (ADLT) during the time of the flood and potential to re-colonise disturbed areas via larval drift. See text for further discussion. (Coding for all 56 taxa in the study are provided in Table S1). Insect images re-produced from Ward *et al.* (2002); re-printed with permission of the University of Colorado Press.

temporal changes in allele frequency within populations. We tested significance changes from 0 for *flood* F_{ST} values with F_{ST} in Arlequin v.3.5.2 (Excoffier & Lischer 2010), using the allele frequency method with $\alpha = 0.05$ and 1000 iterations. Global F_{ST} values were calculated for each taxon at each time point as a measure of genetic differentiation among sites where species occurred.

To test for an overall reduction in genetic variation among populations for each species, we tested whether mean scaled ΔA_r or mean scaled ΔH_o were significantly different from zero using one-sample t-tests. To test whether mean scaled ΔA_r or

mean scaled ΔH_o differed among species, we employed ANOVA and paired t-tests (two-tailed) with Bonferroni correction using R v. 3.3.3.

RESULTS

Disturbance and site characterisation

Average rainfall over the 8-day period for each stream catchment ranged from 86 to 319 mm (Table 1) and total catchment runoff from 21 to 326 mm/km². Rainfall was not
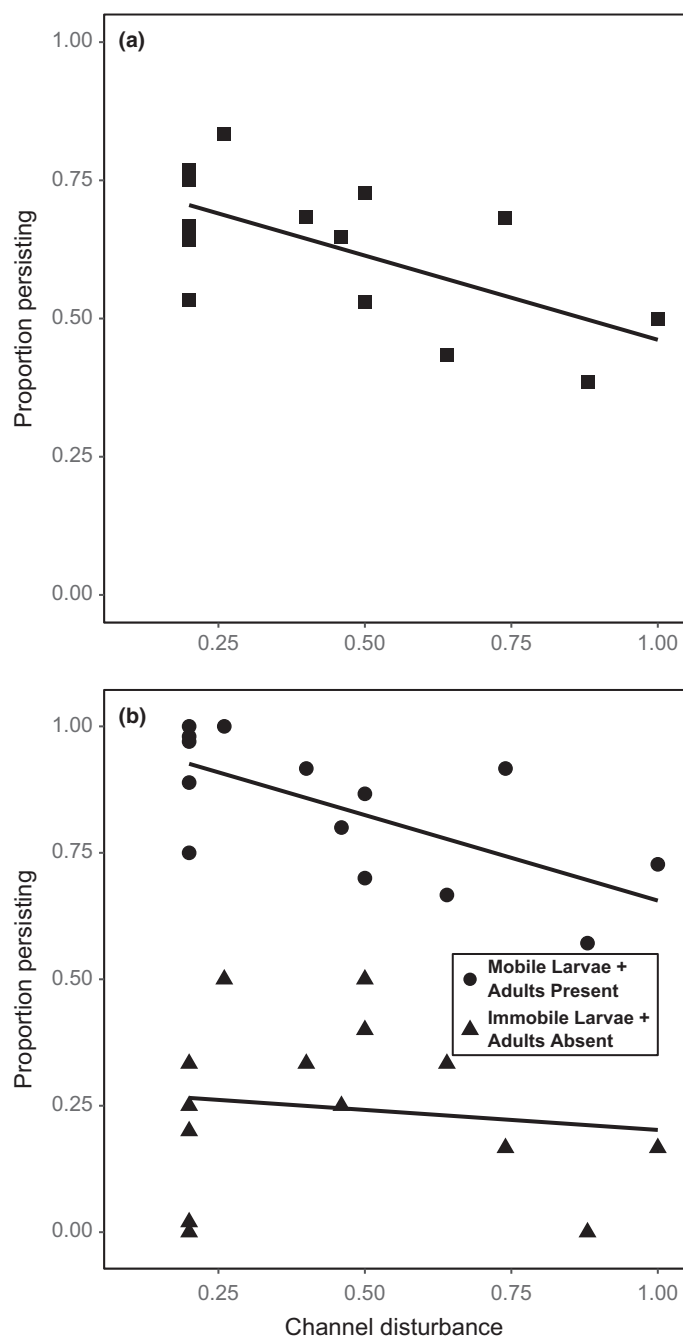
Figure 2 Proportion of taxa persisting following the September 2013 extreme floods in 14 streams that differed in disturbance intensity for all taxa combined (a) and for taxa divided into two groups defined by differences in resistance and resilience traits (b). Slopes of simple linear regressions are significant for all taxa ($P = 0.008$) and mobile taxa with adults ($P = 0.004$) but not for immobile taxa lacking adults ($P = 0.367$). See text and Table S2 for further details.

correlated with elevation ($r = -0.422$, $P = 0.132$), whereas runoff was strongly positively correlated with elevation ($r = 0.670$, $P = 0.009$), reflecting the relatively smaller catchment areas at higher elevation. Rainfall and runoff were only weakly correlated ($r = -0.083$, $P > 0.5$).

Normalised channel disturbance (CD) ranged from 0.2 to 1.0, and normalised instream hydraulic disturbance (HD)

from 0.16 to 1.0. CD was highly negatively correlated with elevation ($r = -0.805$, $P = 0.0005$), indicating lower elevation sites experienced higher disturbance intensities. In contrast, HD was not correlated with elevation ($r = -0.225$, $P > 0.4$), but the correlation between CD and HD was positive ($r = 0.579$, $P = 0.03$). CD was marginally correlated positively with rain ($r = 0.513$, $P = 0.061$) and negatively with runoff ($r = -0.527$, $P = 0.053$), whereas HD was not correlated with either rain ($r = 0.292$, $P > 0.3$) or runoff ($r = 0.016$, $P > 0.5$).

Species persistence along a disturbance gradient as a function of resistance and resilience traits

Across all 14 sites, 50 taxa were collected pre-flood and an additional 6 taxa were sampled post-flood (Table S1). Since pre- and post-flood samples were collected in the same season, we considered these 6 taxa to have been present prior to the flood but missed in our sampling, probably because they had emerged and were present as adults during the year of pre-flood sampling (e.g. *D. coloradensis* was collected as adults but not juveniles in the 2011 samples).

An average of 63% (range 39–77%) of taxa persisted across sites post-flood (Table S2). To test hypothesis 1, that species persistence declined across the disturbance gradient, we selected a metric of disturbance for analyses by determining the explanatory power of the normalised disturbance indices (CD and HD) individually and in combination. A simple linear regression using CD alone was the best fit model explaining the decline in proportion of taxa persisting with increasing disturbance intensity ($t_{13} = -2.791$, one-tailed $P = 0.008$) (Fig. 2a). A multiple regression model including both metrics was marginally significant ($F_{2,11} = 3.587$, $P = 0.063$) with CD being explanatory ($t_{12} = -2.259$; one-tailed $P = 0.022$) but not HD ($t_{12} = 0.141$, one-tailed $P = 0.445$). On the basis of these results, we used CD as our measure of disturbance in all analyses.

To test hypothesis 2, we examined how different combinations of traits changed across the disturbance gradient. Of the total 31 taxa classified as mobile, significantly more taxa (79%) persisted across sites compared to the 25 immobile taxa (21%; $t_{13} = 10.6$, one-tailed $P < 0.0001$). Persistence of mobile taxa declined across the disturbance gradient ($t_{13} = -2.166$, one-tailed $P = 0.015$). Of the 28 taxa with adults present (A+), 79% persisted across sites compared to the 28 taxa lacking adults (34%, $t_{13} = 7.7$, one-tailed $P < 0.0001$). Taxa with adults persisting also declined across the disturbance gradient ($t_{13} = -2.520$, one-tailed $P = 0.013$).

Because mobility and adult presence were strongly confounded, we classified taxa into four groups that combined larval mobility and adult stage presence for further analysis. Mobile taxa with adults present (Mob/A+) comprised 21 of 56 taxa, and immobile taxa without adults present (IMob/A-) comprised 17 taxa. The group Mob/A- had 10 taxa and IMob/A+ only 8 taxa, with many instances of 0 taxa per site (Table S2). Given these sample sizes, only Mob/A+ and IMob/A-groups were used to test hypothesis 2.

The proportion of Mob/A+ taxa persisting was high (mean = 84%) and showed a significant decline as disturbance increased (Fig. 2b: $t_{13} = -3.166$, one-tailed $P = 0.004$). Some
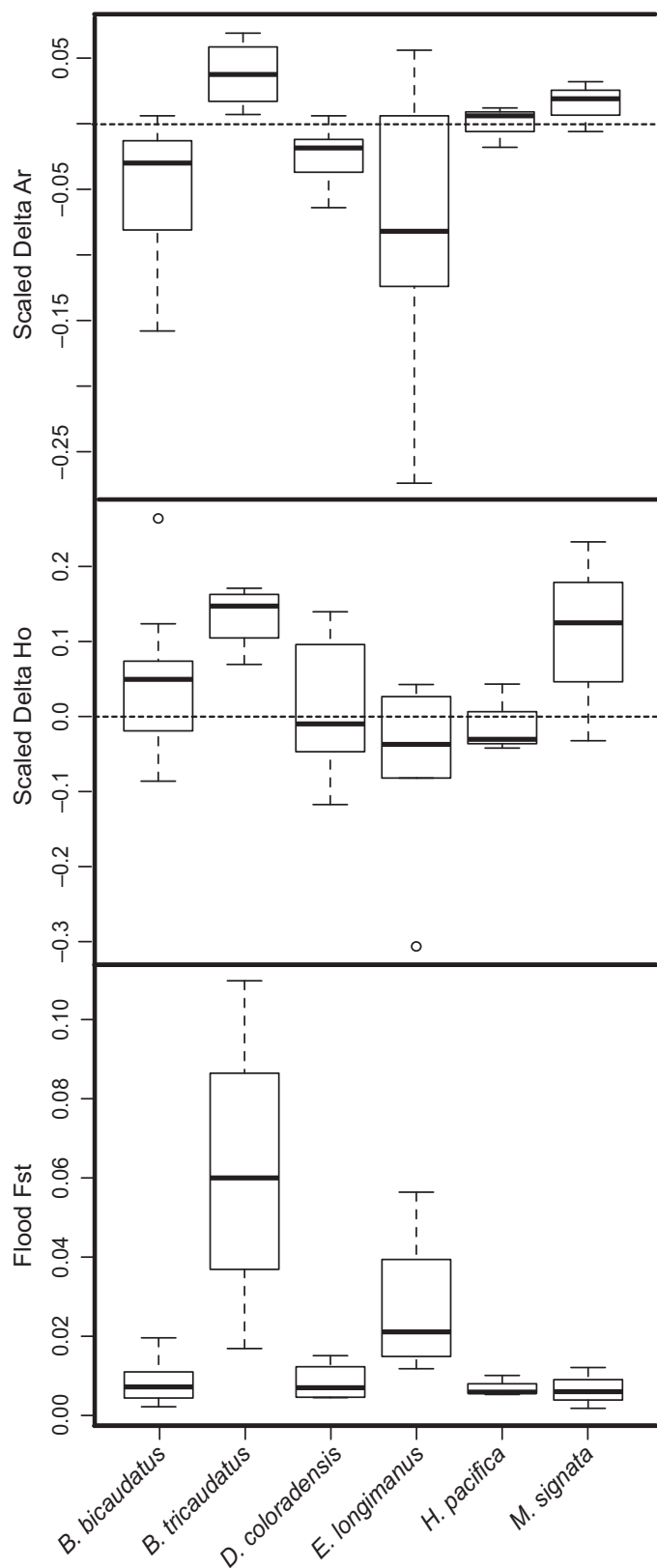
Figure 3 Boxplots showing the range of values for scaled ΔA_r (proportional change in allelic richness at site), scaled ΔH_o (proportional change in observed heterozygosity at a site) and flood F_{ST} (a measure of temporal change in allele frequency at a site) among sites for each species. Mean scaled ΔA_r was significantly different from zero for *B. bicaudatus*, *B. tricaudatus* and *D. coloradensis* and mean scaled ΔH_o was significantly different from zero for *B. tricaudatus* (see Table S3).

the simuliid blackflies (see Table 2). Mob/A+ taxa that were eliminated from higher disturbance sites were mostly crawlers and not swimmers or drifters, including the stoneflies *Zapada cinctipes* Banks, 1897 (lost from 4 of 13 sites that had highest disturbance) and *M. signata* (eliminated from 2 of 5 sites that had the greatest disturbance).

The proportion of IMob/A- taxa persisting was uniformly low (average = 25%) and did not change with increasing disturbance (Fig. 2b: $t_{13} = -0.445$, one-tailed $P > 0.3$). These taxa are mostly soft-bodied or wormlike (see Table 2), such as the empidid dipteran *Clinocera* (lost from 10 of 10 sites) and the crane fly dipteran *Tipula* (lost from 6 of 6 sites). The only exception to near-complete elimination of IMob/A- taxa was the crush-resistant elmid beetle. Interestingly, the 10 taxa that were Mob/A- persisted with an average of 54% across sites (Table S2), intermediate between Mob/A+ and IMob/A-.

We further examined our results by calculating the pre-post flood change in taxonomic β-diversity for each site, using the Sørenson similarity index calculated using pre- and post-flood communities at the same site. Higher changes in β-diversity were positively associated with higher CD (Fig. S2: $t_{13} = 3.181$, two-tailed $P = 0.008$).

Genomics

Species exhibited contrasting population genomic responses to the flood (Fig. 3). Allelic richness was, as predicted, more sensitive to the flood than heterozygosity. There was a significant change in mean scaled ΔA_r across all species and sites combined ($t_{30} = -2.148$, $P = 0.040$), and three species showed individually significant, but varying, responses (Fig. 3, Table S3). A_r declined for *B. bicaudatus* ($t_8 = -2.965$, $P = 0.04$; Fig. 3) and *D. coloradensis* ($t_5 = -2.422$, $P = 0.05$). In contrast, *B. tricaudatus* showed a gain in ΔA_r in four of four populations (Fig. 3, Table S3), and a *post hoc*, one-tailed test indicated this gain was significantly greater than 0 ($t_3 = 2.825$, $P = 0.033$). The remaining species had varied responses, with a reduction in A_r in *Epeorus longimanus* in 3 of 5, *Hesperoperla pacifica* in 1 of 3, and *Megarcys signata* in 1 of 3 populations.

Across all species and sites combined, loss in mean scaled ΔH_o did not differ from zero ($t_{30} = 1.390$, $P = 0.175$), and only *B. tricaudatus* showed a significant, and positive, change ($t_3 = 5.986$, $P = 0.009$) (Fig. 3, Table S3). The increase in genetic variation in *B. tricaudatus* was also apparent in a Principal Components Analysis that provides a visual representation changes in genetic variation across species and sites (Fig. S1). We did not find any consistent relationship between magnitude or direction of genomic change and intensity of site disturbance for any species.

In general, differentiation among sites as measured by global F_{ST} changed little after the flood (Table S4), with the

Mob/A+ taxa were lost from the more disturbed sites. At the most disturbed sites, persistent Mob/A+ taxa were the most highly mobile (based on swimming and/or drifting ability), such as the mayflies *Baetis bicaudatus* and *B. tricaudatus* and

exception of *B. tricaudatus* which increased *c.* 140% (Table S4). *Flood* F_{ST}, our measure of temporal change in allele frequency at a site, was significantly different than zero for populations of three species: *D. coloradensis* (two populations), *E. longimanus* (one population) and *H. pacifica* (two populations) (*P* < 0.05, 1000 iterations; Fig. 3).

DISCUSSION

Species traits and the genomics of persistence

Both resistance and resilience traits contribute to species persistence in the face of extreme flood disturbances and they therefore influence the potential for genetic change in local populations of these species. Previous work has shown that trait composition of benthic insects changes across a natural (non-extreme) disturbance gradient (Townsend *et al.* 1997), but our study demonstrates that under extreme disturbance, particular traits become important for persistence. Taxa that are highly mobile as larvae via swimming or drifting (*Baetis tricaudatus, B. bicaudatus,* simuliid blackflies) persisted even under the highest disturbance levels, whereas taxa that mostly crawl (e.g. *Zapada cinticpes, E. longimanus, M. signata*) did not (see Table 2). Only low mobility taxa that were crush-resistant (elmid beetles) were the exception, though they were lost from the most disturbed site.

The presence of an aerial adult at the time of the floods enhanced, but did not guarantee, persistence of mobile taxa, as seen by those few taxa having low mobility but an adult present (IMob/A+, Table S2), suggesting that a 'reservoir' of terrestrial adults alone is insufficient to ensure persistence under extreme disturbance that directly affects the aquatic larvae. Some previous work has shown that adults can sustain local populations by emerging prior to seasonally predictable stream disturbance (Gray & Fisher 1981; Lytle 2001) or by their happenstance presence at the time of an anthropogenic extreme event (Voelz *et al.* 1994). It would seem that under extreme disturbance a combination of larval mobility and presence of an adult would maximise persistence, perhaps conditioned on the fecundity of adult females.

Although unmeasured in this study, biotic interactions could possibly have contributed to differential species loss after the flood. Extreme flooding caused a reduction in algal resources through scouring compared to pre-flood levels (unpubl. data), which might increase competition among algivorous species. For example glossosomatid caddisflies had relatively low abundance at sites prior to the flood, and they failed to persist even though they had adults present during the flood. Abundant algivorous competitors (e.g. baetid mayflies, see Kohler 1992) could possibly have created a resource bottleneck for small populations of glossosomatids.

For the 6 Mob/A+ species we examined genomically, substantial species-level differences in response to the extreme event were observed (Fig. 3). Two species (mayflies *B. bicaudatus* and *D. coloradoensis*) showed subtle, but consistent-across-sites contraction in genomic diversity, suggesting population bottlenecks created by the extreme disturbance. Arguably, taxa that suffer such restriction or displacement of genomic diversity during extremes are more vulnerable to future genomic

bottlenecks as diversity is winnowed by repeated mortality events.

A different response was exhibited by the mayfly *B. tricaudatus*, in that it greatly expanded its genomic diversity after the extreme event, suggesting immigration of individuals from upstream refugia after the flood. Interestingly, the congeners *B. tricaudatus* and *B. bicaudatus* were assigned identical resilience and resistance traits (Table 2), reflecting their apparent ecological equivalence (Poff *et al.* 2006) and their similar physiological traits (Shah *et al.* 2017). Thus, the differential genomic response between these species was unexpected. However, our earlier studies show that *B. tricaudatus* has high levels of gene flow across stream networks in this region compared to *B. bicaudatus* (Polato *et al.* 2017), suggesting these species differ in fundamental dispersal strategy and hence in possible genomic response to repeated extreme events (see below). In an unrelated study, Vieira *et al.* (2014) reported that *B. tricaudaus* was among the first species to re-colonise severely disturbed and isolated stream habitats following fire-induced flash floods, suggesting this species is highly mobile at landscape scales.

We did not find genomic responses to be proportional to the level of disturbance at sites. This may be due to small numbers of sites for testing this relationship for most species. The small genetic changes, while perhaps unsurprising, were nonetheless strong enough to be measurable in three of the sampled species. These results provide evidence for species-specific genetic responses to extreme flooding rather than some generalised similarity in response across all taxa.

A role for landscape dynamics

An unexpected finding was that disturbance intensity (and associated species loss) was strongly negatively associated with elevation across our 14 sites ($r = -0.805$, Table 1). Previous work has documented faunal turnover along this Colorado elevation gradient, with low elevation sites (< *c.* 2500 m) having more taxa and more unique taxa than high elevation streams (> 3000 m) (Harrington *et al.* 2016). This elevation partition coincides with a hydro-climatological distinction, with streams originating at > 3100 m being dominated by a predictable, late-spring snowmelt pulse and streams heading at low elevations (< 2300 m) being controlled by precipitation from localised convective storms and larger scale monsoonal storms in summer (Kampf & Lefsky 2015). Thus, small streams at low elevation have much less predictable hydrological disturbance regimes, and they may not experience high flood flows for many years due to the stochastic nature and small spatial extent of late summer rains (Pitlick 1994). Ecological theory (e.g. Resh *et al.* 1988; Poff & Ward 1989) led us to expect that the timing of the rain event, relative to the historical disturbance regime, might cause differences in insect community response to the flood: taxa living in high elevation streams with predictable June-July snowmelt might respond more strongly to the non-seasonal (September) extreme flooding compared to low elevation fauna, which are likely to be more adjusted to late season, rainfall-driven disturbance. However, we observed just the opposite.

Interestingly, a second environmental factor appears to regulate the effective intensity of flood disturbance for a given runoff level across elevation. Below 2500 m elevation, rivers and streams in this region are influenced by an underlying geological instability that causes a strong headward downcutting of river channels draining onto the Great Plains (Anderson *et al.* 2012, 2015). Thus, streams at low elevation are in geomorphic disequilibrium, i.e. actively downcutting and dynamically transporting large quantities of sediment during high flow events (Anderson *et al.* 2012). Sites above 2500 m elevation lie above this geomorphic knickpoint and therefore have much more stable channels during high flows. These elevation differences are apparent from the photographs we used to calculate channel disturbance (see Fig. S3). Thus, despite the fact that high and low elevation sites experienced similar rainfall intensities, the *effective* disturbance (i.e. bed mobility) at the lower elevation sites was greater. High elevation sites experienced a non-seasonal flood pulse, but actual channel movement was minimal. This observation points to the importance of considering how broader geologic-landscape context regulates habitat stability and thus can modulate potential species responses to climatic extreme events (see also Boucek *et al.* 2016).

Implications of extremes for communities and genomic diversity

The loss of many taxa from these stream communities implies the possibility of shifts in community structure and function (unpubl. data). For those taxa not persisting (mostly immobile species), re-colonisation is probably a slow and stochastic process that is likely to result in modified genomic signatures for those populations that eventually establish. Indeed, repeated sampling in 2015 showed several immobile taxa were still absent the second year after the floods (unpubl. data). An increase in the frequency of extreme events could continue to decimate these species leading to long-term changes in community structure and function, with a shift to more mobile and resilient taxa.

The functional significance of genomic change at presumably neutral loci for mobile taxa that persisted the extreme event is unclear. Though taxon-specific, a small reduction in genomic diversity could eventually result in limitations to adaptive potential if additional winnowing of genomic diversity were to occur from future extreme floods, particularly for poorly dispersing taxa (e.g. *B. bicaudatus*). Although the proportion of A_r lost in most species and populations was fairly small, repeated extreme floods such as this, which will likely increase in frequency with climate change (Trenberth *et al.* 2003, 2015) have the potential to progressively erode A_r and negatively impact species' adaptive capacities (Robertson 1960; James 1970).

A key insight of this work is that the presence of a relatively invulnerable life stage during an extreme event is likely to promote persistence. Aquatic insects have complex life cycles, and terrestrial adults are common in riparian zones of montane Colorado streams in late summer (mid-September). Had the flood occurred a few weeks later (after onset of cooler autumnal weather), fewer adults would have been present (B.C. Kondratieff, pers. obs.), as would also be the case if a flood of similar magnitude occurred much earlier in the spring season prior to emergence of adults from the streams. The timing of disturbance relative to species' vulnerable life stages would seem to be an important contingency in predicting how communities of species will persist and evolve under future extreme events.

AUTHORSHIP

NLP and WCF conceived the project, along with input from BCK, ASF and KRZ. EIL and PES led the field and data collection (community and genomics respectively) and were assisted in laboratory and statistical analyses by SGM. NLP led in writing the manuscript, with significant inputs from WCF, PES and EIL, and contributions from KRZ, ASF, BCK and SGM.

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