

Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire

NICOLE K. M. VIEIRA,* WILLIAM H. CLEMENTS,* LYNETTE S. GUEVARA[†]
AND BRIAN F. JACOBS[‡]

*Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, U.S.A.

[†]Surface Water Quality Bureau, New Mexico Environment Department, Santa Fe, NM 87502, U.S.A.

[‡]Resources Management, Bandelier National Monument, National Park Service, Los Alamos, NM 87544, U.S.A.

SUMMARY

1. Wildfires are often followed by severe, sediment-laden floods in burned catchments. In this study, we documented resistance and resilience of stream insect communities to repeated postfire flash floods in a 'burned stream'. We employed a before-after-control-impact (BACI) design, where communities in comparable reaches of a burned stream and a reference stream were sampled from 2 years before, to 6 years after, a crown wildfire in north-central New Mexico.

2. The first 100-year flood following the 1996 Dome wildfire reduced total insect density and taxon richness to near zero in the burned stream. Despite showing low resistance, density returned rapidly to prefire levels because of colonisation by simuliids, chironomids and the mayfly *Baetis tricaudatus*. In general, taxa that were generalist feeders (collectors) with strong larval dispersal dominated communities in early postfire years with repeated, moderate flash floods.

3. Taxon richness and community composition were less resilient to postfire hydrologic disturbances. Taxon richness did not recover until floods dampened 4 years after the fire. Despite hydrologic recovery, composition in the burned stream still differed from prefire and reference stream compositions after 6 years postfire. A unique assemblage, dominated by taxa with strong larval or adult dispersal, was established after flash floods abated. Specialist feeders (shredders and grazers) that were common in prefire years were reduced or absent in the postfire assemblage.

4. Community succession in the burned stream was explained by the interaction between species traits, geographic barriers to colonisation and hydrologic conditions after the fire. Comparable changes in insect density, taxon richness, community composition and trait representation were not found in the reference stream, providing strong evidence that repeated postfire flash floods shaped community responses in the burned stream.

Keywords: community recovery, flash flood, species traits, succession, wildfire

Introduction

Physical disturbance, such as hydrologic events (Poff & Ward, 1989; Poff, 1992) and associated substratum movement (Death & Winterbourn, 1995; Townsend,

Scarsbrook & Doledec, 1997a), is an inherent property of lotic systems (Resh *et al.*, 1988). Wildfires, through alterations of the terrestrial environment, can initiate a suite of physical disturbances to streams (Gresswell, 1999). For instance, Scott & Van Wyk (1990) noted increased soil erodibility and reduced infiltration after a fire, which resulted in 100-fold increases in peakflow and fourfold increases in sediment load in streams draining burned catchments (hereafter referred to as

Correspondence: Nicole K. M. Vieira, Department of Biology, Colorado State University, Fort Collins, CO 80523, U.S.A.

E-mail: nicolem@cnr.colostate.edu

'burned streams'). Others have documented increases in annual runoff, and frequency or magnitude of flood events, associated with reduced evapotranspiration and interception from vegetation (Lavabre, Torres & Cernesson, 1993; Mackay & Band, 1997). In addition to postfire hydrologic disturbance, changes in sediment transport (Troendle & Bevenger, 1996), water chemistry (Spencer & Hauer, 1991) and inputs of organic matter (McIntyre & Minshall, 1996) may persist from days to decades in burned streams.

While the direct effects of wildfire on stream insects are typically negligible, communities are less resistant and resilient to sediment-laden floods after a fire (Rinne, 1996; Minshall, Robinson & Lawrence, 1997; Minshall, Royer & Robinson, 2001a). Community resistance (magnitude of change from the prefire state) to postfire flooding depends on whether insect populations can avoid mortality and displacement (*sensu* Sousa, 1984) during a flood event. Community resilience (recovery rate to the prefire state) reflects the recolonisation ability of insect populations (Gray & Fisher, 1981; Cushing & Gaines, 1989), and is reduced when floods after the fire continually reset recovery trajectories (Minshall, Brock & Varley, 1989). Repeated hydrologic disturbances after a wildfire may be 'ecologically surprising' events (*sensu* Paine, Tegner & Johnson, 1998) relative to the historical disturbance regime, and thus may overwhelm the ability of the community to recover (Poff & Ward, 1990). That is, some species in the original community may lack the traits (i.e. life-histories, morphology and behaviour) necessary to exist under the postfire hydrologic regime, as these traits were not essential under more benign, prefire conditions (Poff, 1997).

In this study, we documented community recovery after a series of moderate to severe postfire flash floods in a burned, first-order stream. Repeated 100-year flash floods following the 1996 Dome fire near Los Alamos, NM dramatically altered stream morphology and bed substratum in the burned stream (Cannon & Reneau, 2000; Veenhuis, 2002). Moderate (i.e. 2–10 year recurrence intervals) but progressively dampening floods continued for up to 3 years until hillslope vegetation was re-established (Veenhuis, 2002). We had the rare opportunity to employ a before-after-control-impact (BACI; *sensu* Stewart-Oaten, Murdoch & Parker, 1986) approach, where we compared peakflows and community responses between a burned stream and a reference stream from

2 years before, to 6 years after, the fire. To determine community resistance and resilience in the burned stream, we measured changes in total insect density and taxon richness after the fire and after specific postfire flood events. Unlike most studies measuring community responses to postfire hydrologic disturbance (see review in Gresswell, 1999), we were able to make necessary comparisons with prefire and reference communities to gauge recovery.

Catchment-scale disturbances can have long-term effects on community composition (Yount & Niemi, 1990), providing an opportunity to explore the theory of succession in lotic ecosystems (Fisher, 1983, 1990). In this study, we documented seasonal and annual changes in composition before and after the fire, and compared changes between burned and reference streams. Successional patterns in our burned stream were compared with patterns reported in the literature, and were interpreted in the light of how functional traits of taxa in the regional species pool may have interacted with postfire environmental conditions. Specifically, we investigated temporal trends in the proportion of insects in the community with different (i) functional feeding modes and (ii) larval and adult dispersal ability. We expected the proportion of shredders in the community to decrease, because of loss of riparian vegetation, and the proportion of generalist feeders (i.e. collectors) to increase in the burned stream (Minshall *et al.*, 1997). We also expected the proportion of grazers to increase in the burned stream because of an increased algal biomass associated with reduced shading (Minshall *et al.*, 1989). Finally, we predicted that insects with strong larval and adult dispersal would be dominant in postfire communities.

Methods

Study area

Our study streams were located in the Capulin and Rito de los Frijoles (herein referred to as Frijoles) canyons of the Pajarito Plateau, in Bandelier National Monument near Los Alamos, NM (Fig. 1). The Plateau ranges from 3109 to 1615 m altitude, sloping from the Jemez Mountains to the Rio Grande River in a series of canyons and mesas. First-order streams that drain these canyons are similar in geomorphology, drainage area (approximately 50 km²), flow permanence (i.e.

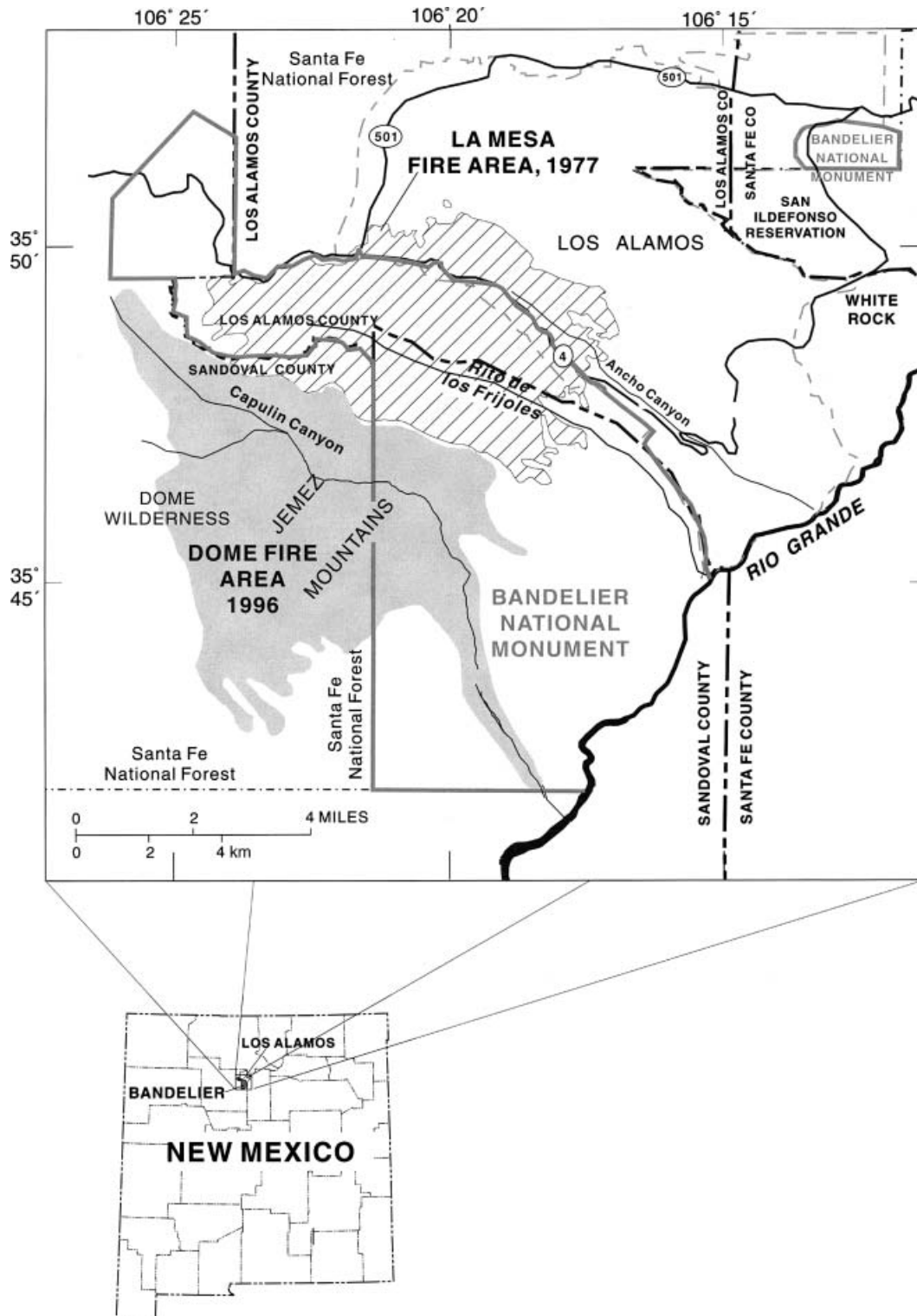


Fig. 1 Location of recently burned (Capulin) and reference (Frijoles) study streams relative to the 1977 La Mesa and 1996 Dome wildfires in Bandelier National Monument and Santa Fe National Forest, near Los Alamos, NM. Reprinted from Veenhuis (2002).

spring-fed ephemeral upper reaches, perennial mid-canyon segments, no perennial tributaries), gradient (changing from 3 to 7% with altitude), and baseflow ($0.04\text{--}0.06\text{ m}^3\text{ s}^{-1}$). Composition of the substratum in Plateau streams consists largely of fine sediments (i.e. >50% sand/silt), followed by moderately embedded, coarser sediments (cobble, gravel and pebble) and occasional boulders (Stevens, 1996; Vieira, 2003). Typical riparian vegetation includes western box elder (*Acer negundo* Linnaeus), narrowleaf cottonwood (*Populus angustifolia* James), alder (*Alnus oblongifolia* Torrey), and ponderosa pine (*Pinus ponderosa* Douglas ex Lawson and C. Lawson). Hydrologically, Plateau streams are snowmelt driven in mid-spring and show flashy responses to monsoon precipitation in summer. Localised and intense monsoon storms (July to September) generate flash flooding in one canyon while adjacent canyons remain at base flow. Annual base flow is driven by El Niño climatic events that bring increased spring and summer precipitation approximately every 4 years (Andrade & Sellers, 1988).

Frequent ground fires occurred historically on the semiarid Plateau, but have been replaced by infrequent high-intensity crown fires as a result of fire suppression and grazing (Touchan, Allen & Swetnam, 1996). In April 1996, the Dome Fire burned 66.8 km^2 of the western portion of the Plateau, including approximately 90% of the Capulin catchment (Fig. 1). The 1977 La Mesa Fire burned 65 km^2 of the eastern Plateau (including 58% of the Frijoles catchment). These wildfires reduced hillslope and riparian vegetation in burned catchments, resulting in increased runoff during monsoon storms. Annual peakflows in burned streams increased from $0.4\text{ m}^3\text{ s}^{-1}$ (prefire average) to over $80\text{ m}^3\text{ s}^{-1}$, and then dampened progressively over several years (Veenhuis, 2002). Flooding and debris flows in Capulin canyon dramatically altered stream geomorphology (Cannon & Reneau, 2000), and shifted the dominant bed substratum from fine sediments to a gravel/cobble mixture (Vieira, 2003). Postfire flood magnitude tracked the recovery of hillslope and riparian vegetation rather than total annual or summer rainfalls (Veenhuis, 2002). In this study, Capulin was our 'burned' stream and Frijoles served as our reference stream to take advantage of prefire hydrologic and community data in these streams (Stevens, 1996; Veenhuis, 2002). Stream insect communities in Frijoles canyon have been shown to be comparable to com-

munities in unburned canyons of the Pajarito Plateau (Vieira, 2003).

Insect communities were compared between the Frijoles and Capulin streams from 2 years before (1994–95) to 6 years after (1996–2001) the 1996 Dome fire. Three 50-m reaches, at least 100 m apart and at approximately 2000 m altitude, were sampled in each stream during 1994–95 as part of an earlier study (Stevens, 1996). These reaches were re-sampled in postfire years using the original sampling schedules, techniques and equipment. Pre- and postfire sampling for stream insects was conducted in spring (April to May) and summer (July to August), and also in autumn (October) when possible, to capture seasonal variation. Seasonal sampling also allowed comparison of communities before and after flash flood events. The timing and magnitude of peakflows in both streams were determined from publications (Veenhuis, 2002) and United States Geological Survey (USGS) data archives (USGS Frijoles stream gauge number 08313350; USGS Capulin stream gauge number 083133655). Because the Capulin gauge only recorded peakflows until the end of 1998, peakflows in 1999–2001 were estimated from (i) measurements of postflood debris lines and (ii) movement of marked substratum particles between sample periods (Vieira, 2003).

To document stream insect communities, we collected three standard-sized (0.093 m^2 area) 750- μm mesh Surber samples per reach ($n = 9$ per stream) on each sample date. This mesh size, while coarser than the 500- μm typically used to sample macroinvertebrates, was selected to maintain consistency with sample methods employed in 1994–95. Samples were collected in three randomly selected riffles (current velocity range: $0.4\text{--}1.0\text{ ms}^{-1}$) within each reach. Similar to prefire methods, riffle selection was restricted to sites without boulders or coarse woody debris but with substratum consisting of at least 25% cobbles. Hazardous fire conditions in Capulin restricted us to one sampling period in the summer of 1996 (after the first postfire flood), while flood hazards prevented us from collecting samples in the spring of 1997. Insects were preserved in 80% ethanol in the field and transported to the laboratory, where a dissection microscope was used to classify insects to taxonomic levels reported for prefire samples. We documented total insect density, taxon richness, taxon-specific density and taxon presence/absence.

We assigned taxa to functional feeding groups and dispersal ability groups using invertebrate keys and texts (Merritt & Cummins, 1996; Ward, Kondratieff & Zuellig, 2002), publications (Rader, 1997), and expert opinion (B. C. Kondratieff & N. L. Poff, Colorado State University). Adult dispersal ability was rated as weak, moderate or strong based equally on a consideration of adult flight strength, typical dispersal distance (<1 km or <10 km), and adult life span (days, weeks, or months). Juvenile dispersal strength was also rated as weak, moderate or strong based primarily on the propensity to drift and, to a lesser degree, on swimming ability and crawling rates. Drift propensity was determined from drift samples collected in the Frijoles and Capulin canyons (Vieira, 2003) and from published values (see Rader, 1997). Swimming ability and crawling rates were derived from expert opinion. The relative abundance (percent) of individuals within functional feeding groups, and within adult and larval dispersal ability groups, was compared between burned and reference streams before and after the wildfire.

Statistical analysis

To determine annual and seasonal responses to the fire and to postfire flood events, we compared means of total insect density and taxon richness between streams and across sample dates ($n = 9$ Surber samples on each date). We also compared the mean taxon-specific density and relative abundance of feeding and dispersal groups. Because the probability of capture of taxa differs substantially across seasons, taxon densities and trait abundances were compared on an annual basis ($n = 27$ Surber samples per year for most years; $n = 9$ in 1996 and $n = 18$ in 1994 and 1997 because of restricted access in Capulin canyon). A two-way analysis of variance (ANOVA) was employed to determine whether total insect density and taxon richness were significantly related to the main effects of canyon, time (i.e. sample period), or their interaction. Sample reaches were included in both models as a random effect nested within canyons. *A priori* linear contrasts were constructed for statistically significant ($P < 0.05$) 'canyon \times time' interactions to investigate community resistance and resilience to postfire floods (see further detail below). For all hypothesis testing, total insect density was natural log-transformed, taxon richness was square-root transformed, and Surber samples were

averaged across each reach ($n = 3$ per stream per sample period) to meet parametric assumptions (Ott, 1993). Statistical analyses were conducted with use of SAS/STAT statistical software (SAS Institute, 1996).

Linear contrasts tested whether changes in community response variables (insect density and taxon richness) in Capulin differed from changes observed in Frijoles between the same time periods. To contrast community resistance, the magnitude of change in response variables between sample dates before and after postfire floods was compared between streams. Differences in responses between July 1995 and the first postfire sample (July 1996) tested resistance to the Dome fire and also to the first 100-year flood event. To determine resistance to moderate floods, we also compared changes in both responses before and after the 5–10 year recurrence-interval floods in 1997 (July versus October 1997), and after the 2–5 year recurrence-interval floods in 1998 (July versus October 1998). For resilience contrasts, mean density and taxon richness in consecutive postfire years (1997–99) were compared with mean measures in 1995 (prefire) to determine rate of recovery to prefire levels. The year 1999 represented the first postfire year without a significant peakflow event. For all contrasts, a significantly greater change between time periods in Capulin compared with Frijoles indicated lower resistance or resilience of Capulin communities.

We employed canonical discriminant analysis (CDA) to investigate annual changes in community composition in both streams over the 8-year study period. This descriptive, dimension-reducing, multivariate technique constructs linear combinations of independent measurement variables (taxon presence) to maximise separation between pre-assigned groups (years 1994–2001) based on a set of observations (Surber samples). Rare taxa were aggregated to Family or Order as necessary to meet parametric assumptions. CDA for Capulin and Frijoles were conducted separately, but the same taxa (and taxonomic aggregations) were used to allow for comparison of results across analyses.

Results

Total insect density was similar between Capulin and Frijoles in the 2 years prior to the Dome Fire (Fig. 2a). However, following the fire and the first 100-year flood event in July 1996, only a few individuals were

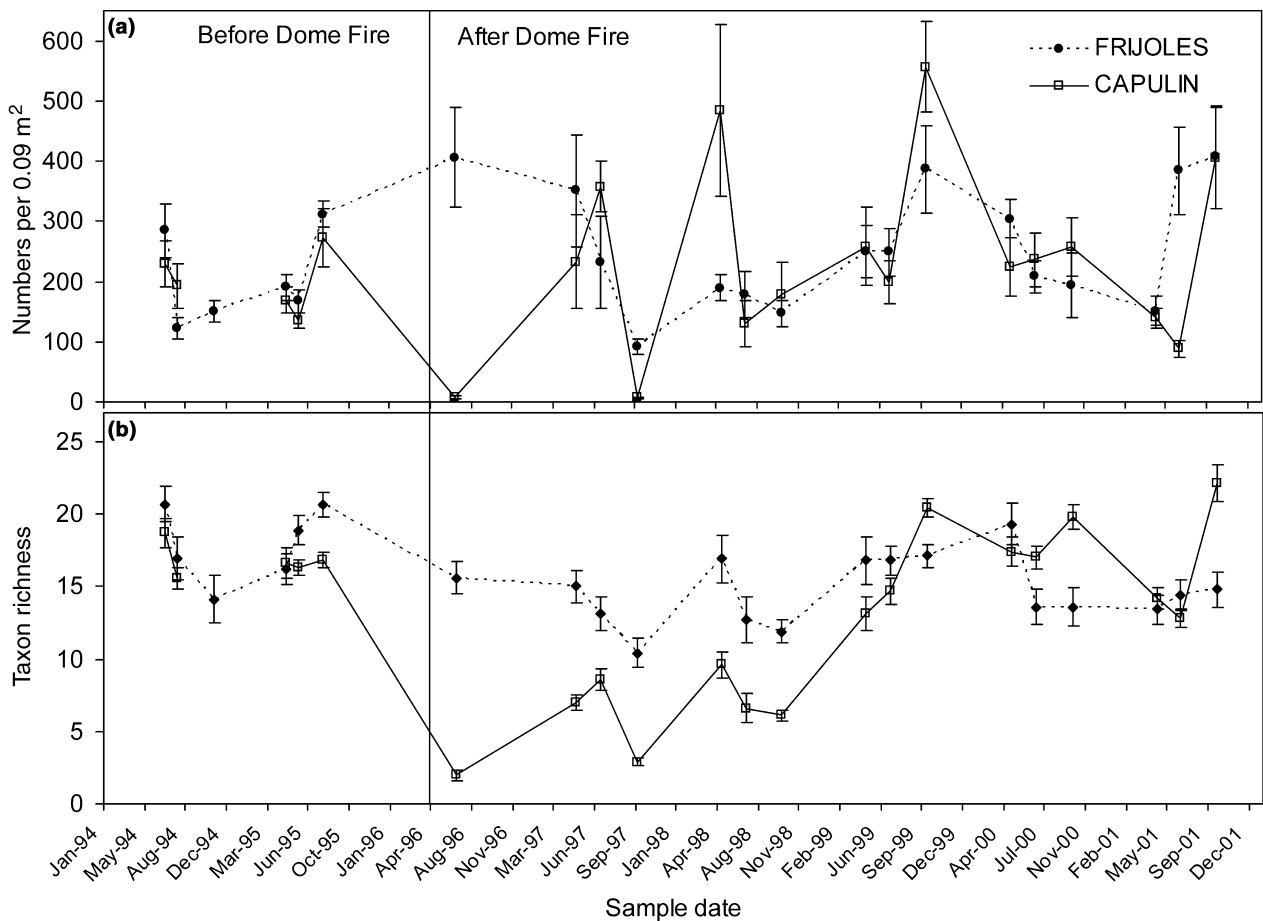


Fig. 2 Mean (± 1 SE) of (a) total density per 0.09 m² and (b) taxa richness for sample periods before and after the 1996 Dome fire in a burned stream (Capulin) and a reference stream (Frijoles) near Los Alamos, NM. Flash floods were recorded on the following dates in Capulin: 26 July, 25 August and 3 September in 1996 (100-year flood events); 6 August, 22 August, 3 September and 7 September in 1997 (5–10 year flood events); and 27 July and 13 August in 1998 (2–5 year flood events). A 2-year flood event also occurred in Frijoles on 13 August in 1998.

collected in Capulin samples, whereas densities in samples from Frijoles increased. Insect density in Capulin recovered to prefire values by May 1997 due largely to recolonisation by *Simulium* sp., Orthocladinae and *Baetis tricaudatus* Dodds (56, 22 and 17% of total density, respectively). These taxa were patchily distributed, resulting in high variability in total density among samples. Density in Capulin was severely reduced again in October 1997 following flash floods in late August and early September of 1997, but thereafter remained similar to (or higher than) prefire and Frijoles densities.

While taxon richness was similar between Capulin and Frijoles in prefire years, taxon richness in Capulin was reduced in July 1996 to a mean of only two taxa per sample (Fig. 2b). Most of the remaining organisms

were elm mid beetle larvae [Elmidae: *Optioservus* sp. and *Zaitzevia parvula* (Horn)], although first-instar hydropsychid caddisflies (*Ceratopsyche* sp.) were also found. Taxon richness in Capulin did not recover to values recorded before the fire or in Frijoles until October 1999. Thereafter, taxon richness remained similar to (or higher than) prefire and Frijoles values. By contrast, taxon richness in Frijoles changed little in 1996, and showed only modest seasonal fluctuations between 1997 and 2001 (Fig. 2b).

Canyon \times time interactions were significant, after adjustment for random effects of reaches nested within canyons, in two-way ANOVA models for insect density ($F = 10.89$, $P < 0.0001$) and taxon richness ($F = 11.55$, $P < 0.0001$). Linear contrasts revealed that total insect density and taxon richness showed similar

resistance to postfire flooding in Capulin. Differences in both response variables between July 1995 and July 1996 samples were significantly greater in Capulin compared with differences in Frijoles (Table 1). Similarly, density and taxon richness were reduced to a greater degree in Capulin as compared with Frijoles after moderate floods occurred in Capulin canyon in 1997. Temporal changes in insect density and taxon richness were similar between streams in 1998 after moderate (2–5 year) floods occurred in both streams. Linear contrasts also revealed that taxon richness was less resilient than insect density in Capulin (Table 1). Differences between prefire and postfire densities were similar between streams as early as 1997, whereas the reduction in taxon richness in Capulin was significantly greater than in Frijoles until 1999.

Canonical discriminant analysis showed that community composition in Capulin differed dramatically among years (Wilks' Lambda: $F = 18.27$; $P < 0.0001$). The first two canonical axes explained 73.9% of the variation in composition among years. Canonical axis 1 explained 54.9% of the variation ($F = 12.5$; $P < 0.0001$) and generally distinguished communities in postfire years with moderate to severe flash floods (1996–98) from those in prefire (1994–95) and late postfire (1999–2001) years (Fig. 3a). Canonical axis 2 explained 19.0% of the variation in composition among years ($F = 8.66$; $P < 0.0001$) and separated

communities in prefire years (1994–95) and in the year of the fire (1996) from those in subsequent postfire years (1997–2001) (Fig. 3a). Taxa (or taxonomic aggregations) that were important in defining canonical axes are highlighted in Fig. 3a (also see Table 2).

Annual changes in community composition were less dramatic in Frijoles, and temporal patterns differed from those in Capulin. Significant trends across years were found (Wilks' Lambda: $F = 3.33$; $P < 0.0001$), but the first two canonical variables only explained 54.7% of the variation in composition among years. Canonical axis 1 explained 33.4% of the variation ($F = 3.33$; $P < 0.0001$), and distinguished the community in 1999 from those in 1996–97 (Fig. 3b). Canonical axis 2 explained 21.3% of the variation ($F = 2.79$; $P < 0.0001$) and distinguished the community in 1998 from those in 2000–01 (Fig. 3b). Taxa (or taxonomic aggregations) correlated with canonical axes, and thus important in separating communities among years in Frijoles, were different from those that differentiated the same years in Capulin (Table 2; Fig. 3b).

Annual changes in the density of taxa contributing to CDA axes further distinguished compositional trends in Capulin, and differed from changes in Frijoles over the same years (Fig. 4). *Simulium* sp., Chironomidae, Baetidae (*B. tricaudatus* and *Fallceon quillieri*) and other Diptera (i.e. Empididae) recovered to, or exceeded, prefire density in the first year

Table 1 *A priori* linear contrasts testing differences in total insect density and taxon richness over specific time periods to reflect resistance (magnitude of change between time periods) and resilience (annual rate of recovery to prefire levels) to postfire floods. Temporal changes in a stream burned in the 1996 Dome fire, near Los Alamos, NM (Capulin) were compared with changes observed in a nearby reference stream (Frijoles). Student's *t*-test values and associated significance levels (*P*) are presented. A positive sign for *t*-statistics indicates a greater reduction, and thus lower resistance or resilience, in Capulin than in Frijoles.

Linear contrasts	Total insect density		Taxon richness	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Resistance				
Before versus after the first 100-year flood (July 1995 versus July 1996)	10.21	<0.0001	8.64	<0.0001
Before versus after 5–10 year floods in second postfire year (July 1997 versus October 1997)	6.68	<0.0001	2.46	<0.0157
Before versus after 2–5 year floods in third postfire year (July 1998 versus October 1998)	–0.55	0.5832	–0.07	0.9466
Resilience				
Prefire year versus second postfire year (1995 versus 1997)	1.31	0.1935	4.65	<0.0001
Prefire year versus third postfire year (1995 versus 1998)	–0.79	0.4341	3.83	0.0002
Prefire year versus fourth postfire year (first year without a moderate flood event) (1995 versus 1999)	–0.80	0.4275	–0.73	0.4672

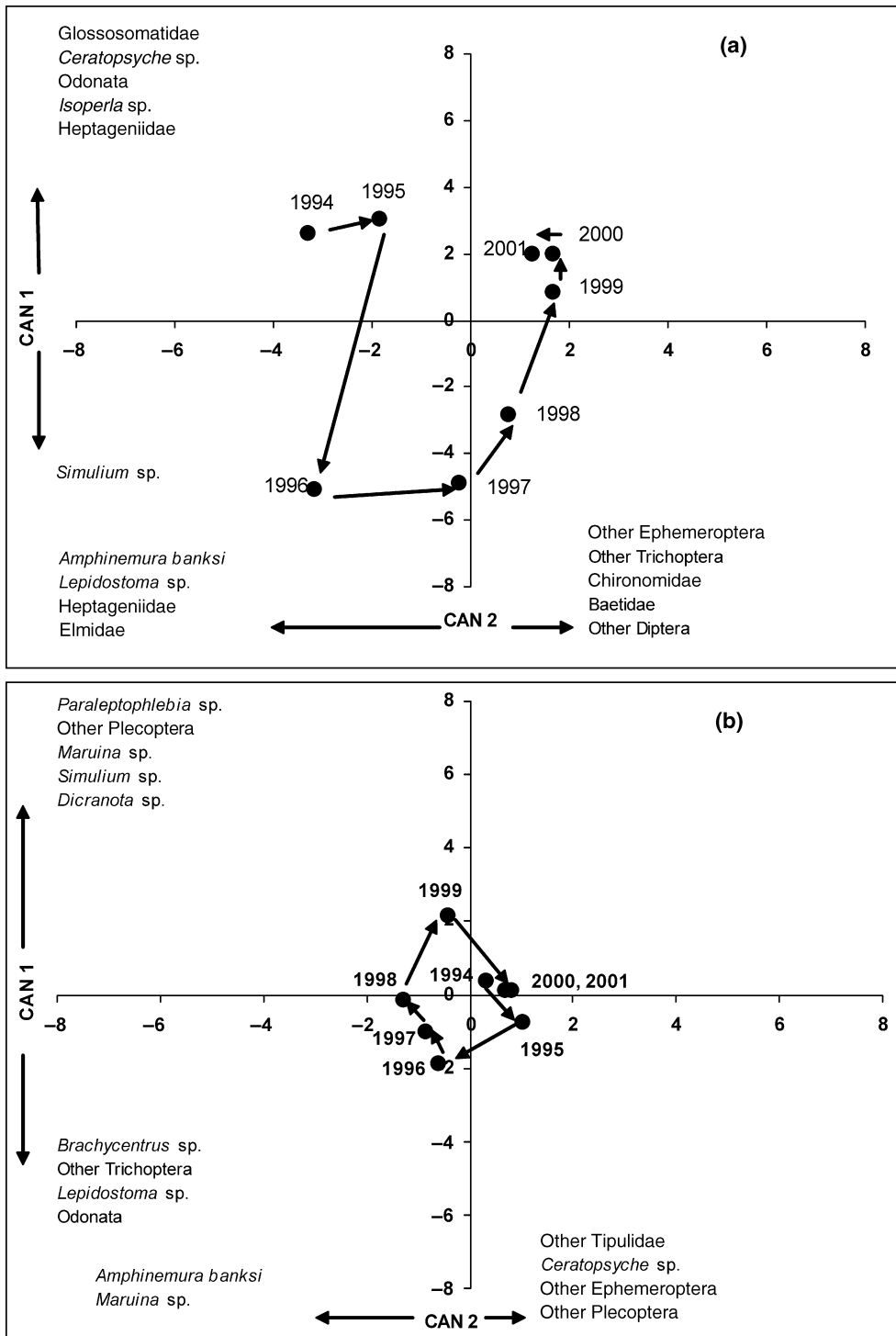


Fig. 3 Mean canonical discriminant analysis values for community composition along the first two canonical axes (CAN1 and CAN2) in (a) a stream burned in the 1996 Dome fire (Capulin) and (b) a reference stream (Frioles), near Los Alamos, NM. Presence of taxa (or taxa groups) was used to discriminate among the years 1994–2001. Samples sizes are reported in the text. Taxonomic groups most strongly correlated with the canonical axes are indicated (see Table 2 for correlation statistics and identification of dominant taxa in each group).

Table 2 Summary of canonical discriminant analysis for eight sample years in a stream burned in the 1996 Dome fire (Capulin) and a reference stream (Frijoles), near Los Alamos, NM. Pearson correlations between presence of each taxa and the first two canonical variables (CAN1 and CAN2), and significance levels (*P*-values from univariate ANOVA indicating whether presence of each taxa differed among years) are presented.

Taxonomic groups	Frijoles			Capulin		
	CAN1	CAN2	<i>P</i>	CAN1	CAN2	<i>P</i>
Baetidae [<i>B. tricaudatus</i> and <i>Fallceon quilleri</i> (Dodds)]	0.11	0.06	ns	0.39	0.36	***
<i>Ephemerella</i> sp.	0.23	-0.17	***	0.52	0.16	***
Heptageniidae (<i>Nixe</i> sp., <i>Cinygmula</i> sp., <i>Epeorus</i> sp.)	-0.07	0.12	**	0.64	-0.39	***
<i>Paraleptophlebia</i> sp.	0.40	0.28	***	0.38	0.26	***
Other Ephemeroptera (<i>Tricorythodes minutus</i> Traver, <i>Ameletus</i> sp.)	0.02	0.42	***	0.22	0.58	***
Nemouridae (<i>Amphinemura banksi</i> Baumann and Gaufin)	0.03	-0.34	***	0.53	-0.54	***
<i>Isoperla</i> sp.	0.12	0.15	***	0.65	0.12	***
<i>Pteronarcella badia</i> Hagen	0.00	0.01	ns	—	—	—
Other Plecoptera (Capniidae, Chloroperlidae, Perlidae)	0.39	0.30	***	0.30	-0.19	***
<i>Brachycentrus</i> sp.	-0.59	0.15	***	—	—	—
<i>Ceratopsyche</i> sp.	0.03	0.43	**	0.78	0.18	***
<i>Lepidostoma</i> sp.	-0.28	0.21	***	0.45	-0.49	***
Other Trichoptera (<i>Hesperophylax</i> sp., <i>Oecetis</i> sp., <i>Polycentropus</i> sp. Hydroptilidae, <i>Rhyacophila</i> sp.)	-0.30	0.22	***	0.39	0.40	***
Glossosomatidae (<i>Agapetus</i> sp. and <i>Glossosoma</i> sp.)	0.00	-0.05	***	0.81	0.34	***
Chironomidae (Tanypodinae, Orthoclaadiinae, Chironominae, Tanytarsini)	0.07	0.20	ns	0.39	0.37	***
<i>Dicranota</i> sp.	0.31	0.09	ns	0.19	0.10	***
Other Tipulidae (<i>Antocha</i> sp., <i>Hexatoma</i> sp., <i>Pedicia</i> sp., <i>Tipula</i> sp.)	0.13	0.48	***	0.34	0.31	***
<i>Maruina</i> sp.	0.33	-0.26	***	0.20	0.23	***
<i>Simulium</i> sp.	0.31	0.27	***	-0.08	0.25	***
Other Diptera (<i>Caloparyphus</i> sp., <i>Dixa</i> sp., Empididae, <i>Palpomyia</i> sp., <i>Pericoma</i> sp.)	0.21	0.00	ns	0.06	0.36	***
Elmidae [<i>Optioservus</i> sp., <i>Z. parvula</i> , <i>Narpus concolor</i> (LeConte)]	0.00	0.00	ns	0.57	-0.39	***
Odonata [<i>Oplonaeschna armata</i> (Hagen), <i>Argia</i> sp., <i>Cordulegaster dorsalis</i> Hagen]	-0.26	-0.16	*	0.76	0.09	***
Other Coleoptera and Hemiptera (<i>Agabus</i> sp., <i>Helichus striatus</i> LeConte, Hemiptera)	-0.11	0.10	ns	0.08	0.01	ns

P-values: ns >0.06; *0.002–0.05; **0.01–0.001; ***0.001

‘—’ does not occur in stream.

postfire with moderate flash floods (1997). By contrast, densities of elmids (*Optioservus* sp. and *Z. parvula*), *Amphinemura banksi*, *Lepidostoma* sp. and heptageniids were reduced to near zero between 1997 and 1999, and had not recovered by the end of the study (with the exception of a resurgence of heptageniids, largely *Cinygmula* sp., in 2000). Densities of *Tricorythodes minutus* and *Ceratopsyche* sp. had recovered by 1998, while densities of glossosomatids (*Agapetus* sp. and *Glossosoma* sp.), Odonata (*Oplonaeschna armata*, *Argia* sp., and *Cordulegaster dorsalis*), *Hesperophylax* sp. and *Isoperla* sp. recovered in the first postfire year without significant peak-flows (1999). Taxa that recovered in 1998 or 1999 in Capulin typically exceeded prefire densities in later postfire years (2000–01).

The relative abundance of functional feeding groups was similar between streams before the fire, but showed notable differences in postfire years (Fig. 5). After the fire, shredders (including *A. banksi*, *Lepidostoma* sp., *Hesperophylax* sp., Capniidae and *Tipula* sp.) decreased in proportion in Capulin and had not recovered by 2001. Grazers (Heptageniidae, *Ameletus* sp., Hydroptilidae, Glossosomatidae and *Helichus striatus*) also decreased in proportion in Capulin after the fire. By contrast, collectors (gatherers: Baetidae, Ephemerellidae, *T. minutus*, Chironominae, Orthoclaadiinae, several dipteran and elmid taxa; filterers: *Simulium* sp., *Ceratopsyche* sp. and Tanytarsini) increased in Capulin immediately after the fire. The relative proportion of shredders, collectors and grazers remained fairly similar across the 8-year

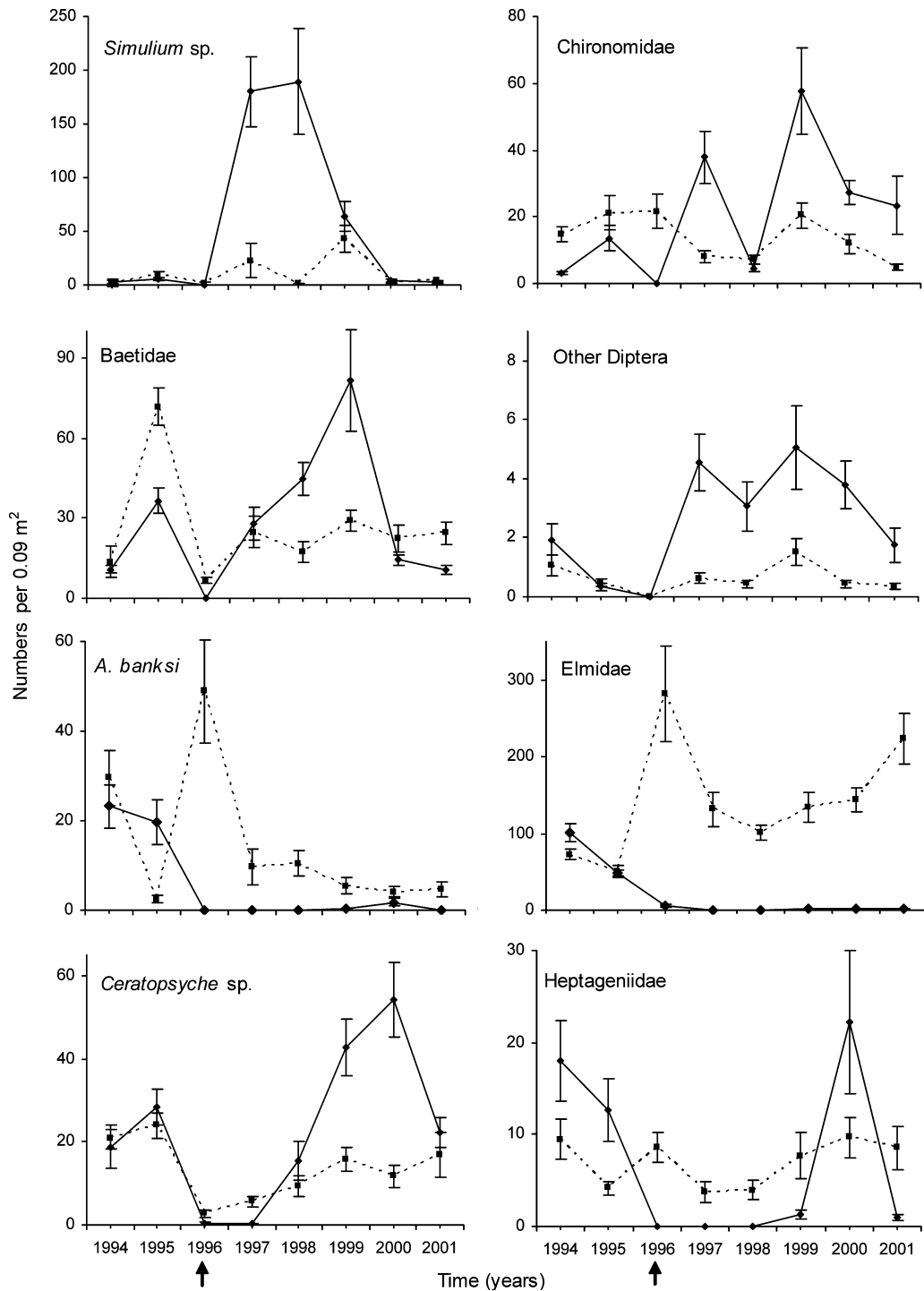


Fig. 4 Mean taxon-specific density (numbers per 0.09 m² ± 1 SE) in each year before and after the 1996 Dome fire, for a burned stream (Capulin; solid line) and a reference stream (Frijoles; broken line), near Los Alamos, NM. Sample sizes for each year are reported in the text. Arrow indicates the 1996 Dome fire.

period in Frijoles (Fig. 5). The proportion of predators (*Isoptera* sp., *Hexatoma* sp., *Dicranota* sp., Tanypodinae, odonates, empidids and *Agabus* sp.) remained similar

between streams until 1999, when the proportion increased dramatically in Capulin.

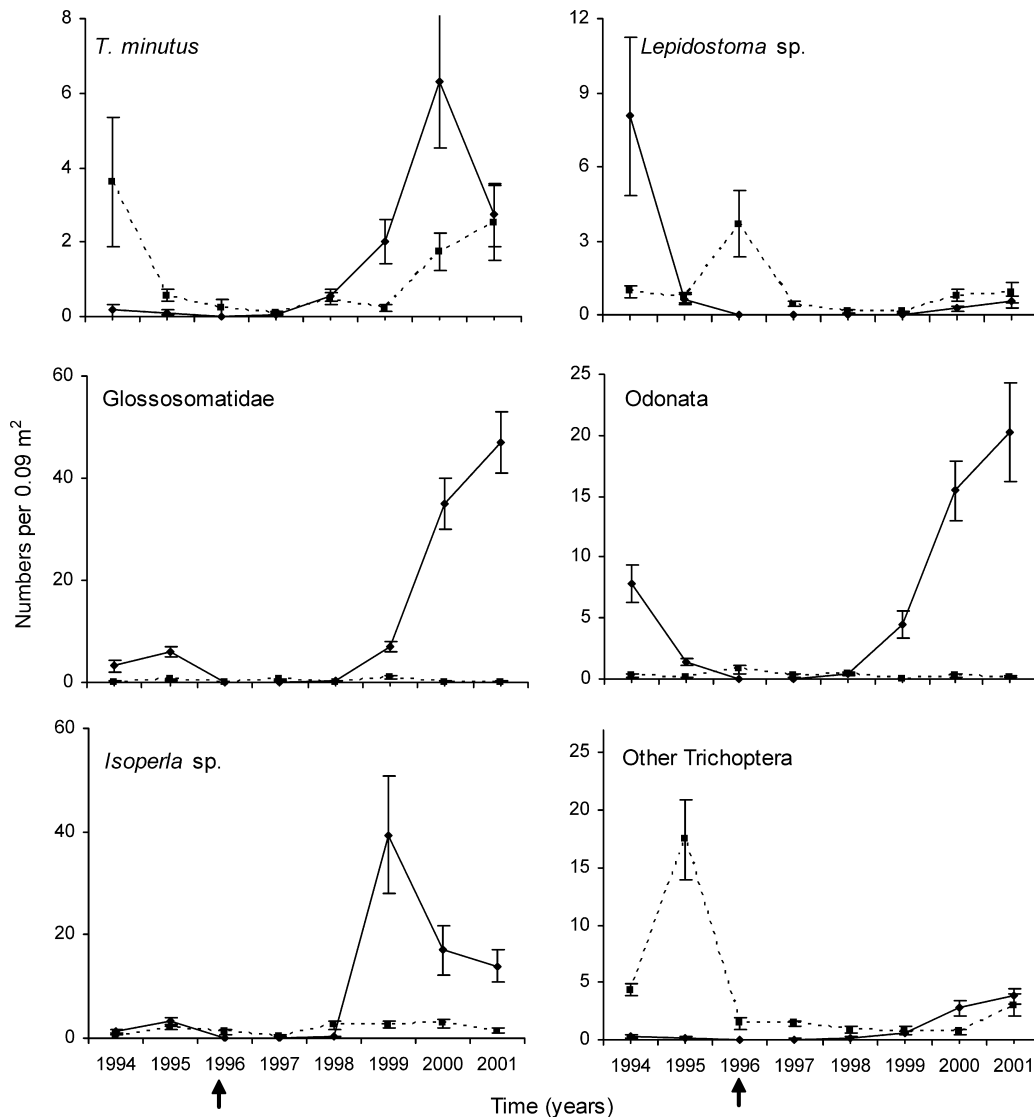


Fig. 4 (Continued)

The relative abundance of strong or weak larval and adult dispersers was similar between streams before the fire (Fig. 6). After the fire, taxa with weak adult dispersal ability (many mayfly taxa, some dipterans, elmids and *H. striatus*) decreased dramatically in Capulin and did not recover to prefire proportions. In contrast, the proportion of taxa with strong larval dispersal (Baetidae, Orthocladiinae, Tanyptodinae, *Simulium* sp. and *Siphonurus* sp.) increased between 1997 and 1999 in Capulin. Similarly, taxa with strong adult dispersal (*Ceratopsyche* sp., odonates, *Hesperophylax* sp. and *Agabus* sp.) returned to prefire proportions between 1998 and 1999, and exceeded both prefire and Frijoles proportions by 2000–01. Taxa with

weak larval dispersal ability (stonefly taxa other than *Isoperla* sp., caddisflies other than *Ceratopsyche* sp., Tipulidae and some dipterans) decreased in Capulin in 1997, but eventually exceeded prefire and Frijoles values by 2000. The relative abundance of weak or strong larval and adult dispersers in Frijoles communities showed less fluctuation across years, with the exception of 1996 (Fig. 6).

Discussion

Stream insect communities in the burned catchment showed low resistance and resilience to repeated hydrologic disturbances after the 1996 Dome wildfire.

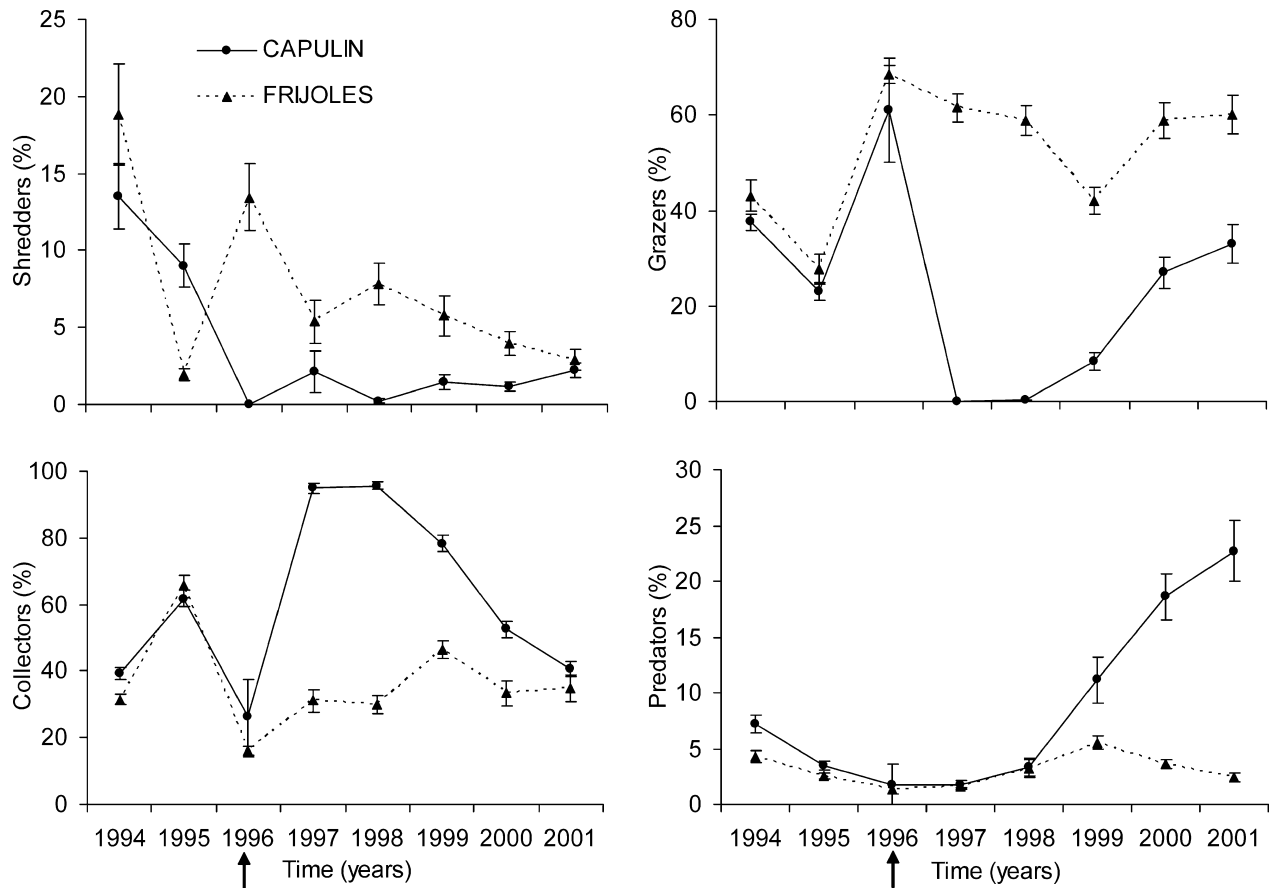


Fig. 5 Mean proportion (± 1 SE) of taxa with different functional feeding groups, for each year before and after the 1996 Dome fire, in insect communities of a burned stream (Capulin) and a reference stream (Frijoles), near Los Alamos, NM. Sample sizes for each year are reported in the text. Arrow indicates the 1996 Dome fire.

Several 100-year flash floods severely altered stream morphology and bed substratum in the year of the fire, and hydrologic and physical attributes of the stream did not stabilise until 4 years later (Cannon & Reneau, 2000; Veenhuis, 2002). Total insect density and taxon richness decreased dramatically following the first 100-year flood and after repeated, moderate floods in the second year postfire. Despite low resistance, insect density recovered quickly after postfire floods because of rapid colonisation by simuliid blackflies. Taxon richness showed less resilience than insect density, and did not recover until flash floods abated in the fourth postfire year. Community composition changed dramatically in the year of the fire and had still not recovered 6 years later, despite the fact that annual peakflow magnitudes had returned to prefire values. Over the same 8-year period, communities in a nearby reference stream

showed only minor fluctuations in total insect density, taxon richness and composition. Our BACI study strongly suggests that repeated floods after a wildfire were responsible for dramatic and long-lasting changes in the stream insect community.

Insect communities in other burned streams have shown low to moderate resistance and resilience to postfire hydrologic disturbances. For instance, Rinne (1996) found that sediment-laden floods severely reduced insect density and diversity in first-order, south-western streams after a wildfire. After both the 1979 Mortar Creek fire in Idaho and the 1988 Greater Yellowstone Area fires, the recovery of insect density and taxon richness was delayed in high-gradient burned streams that were physically altered by runoff events (Minshall *et al.*, 1997, 2001a,b). Community composition showed the lowest resilience in these studies, requiring up to a decade or more to recover.

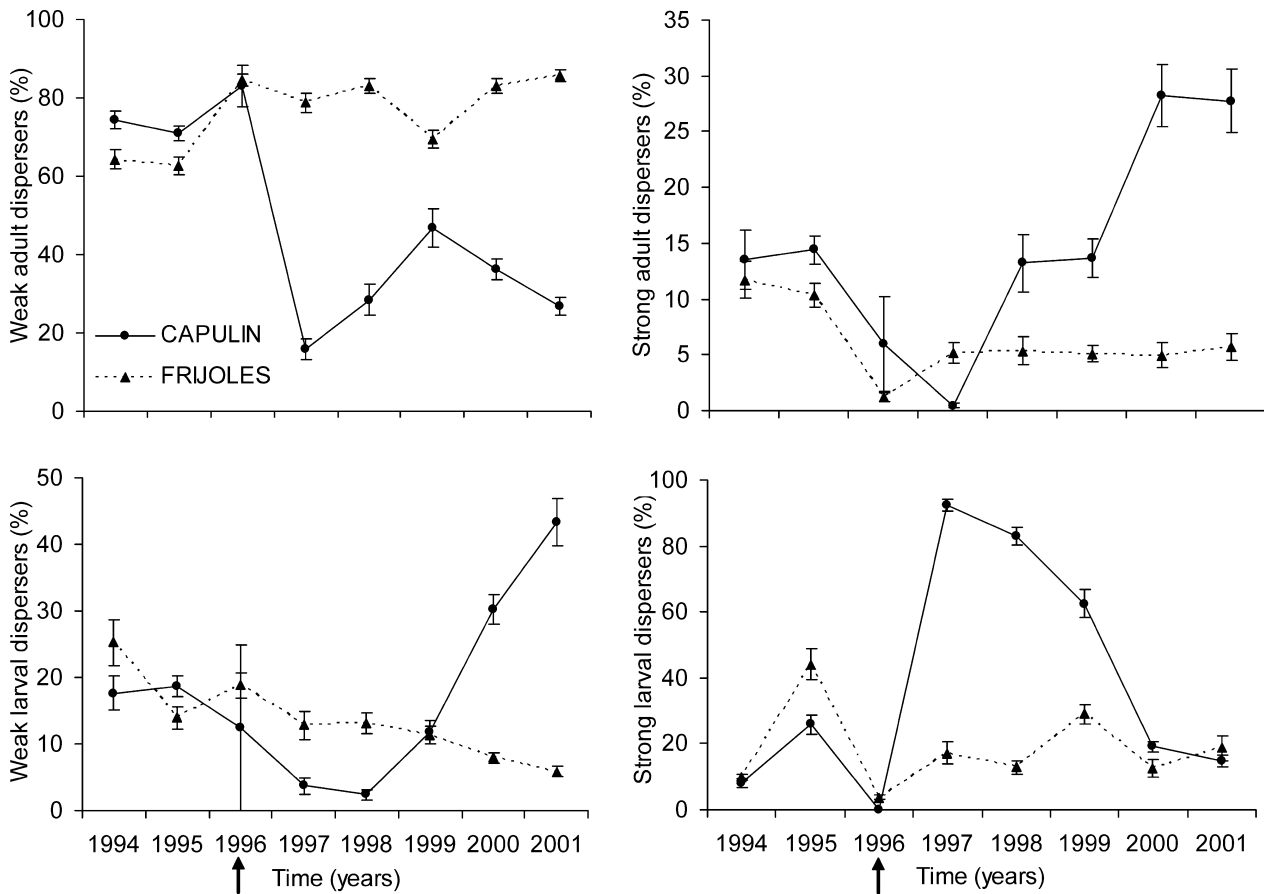


Fig. 6 Mean proportion (± 1 SE) of taxa with weak and strong larval and adult dispersal abilities, for each year before and after the 1996 Dome fire, in insect communities of a burned stream (Capulin) and a reference stream (Frijoles), near Los Alamos, NM. Sample sizes are reported in the text. Arrow indicates the 1996 Dome fire.

In contrast, taxon richness, total density and composition of stream insects have shown high resilience in burned catchments that experienced only minor postfire flooding (Gresswell, 1999). Differences in hydroclimatology may partially explain differences in community resilience among studies. Postfire spates in hydrologically stable, snowmelt-driven streams are typically less severe than floods in flashy, monsoon-driven streams, and thus cause less physical damage to the streambed. We found that postfire flash flooding dramatically altered the physical properties of our burned stream, which likely hindered the recovery of the insect community.

Community composition in our burned stream shifted with postfire changes in the hydrologic regime. *Simulium* sp., Chironomidae and *B. tricaudatus* recolonised rapidly and dominated communities during early postfire years with moderate to severe

floods. In contrast, common prefire taxa, such as heptageniid mayflies (especially *Epeorus* sp.), nemourid stoneflies and elmids were eliminated by severe flash floods and remained rare in postfire communities. Once floods abated, odonates, glosso-somatids, *Ceratopsyche* sp., *Isoperla* sp. and limnephilids recolonised to establish a unique postfire community. Compositional shifts in the burned stream differed from those in the reference stream, which cycled climatically with dry (i.e. 1995 and 2001) and wet (i.e. 1996, 1999) years (<http://www.ncdc.noaa.gov>). However, compositional changes in our burned stream were similar to those observed after the 1988 Greater Yellowstone Area fires (Mihuc, Minshall & Robinson, 1996; Minshall *et al.*, 1997, 2001a) and the 1979 Mortar Creek Fire (Minshall *et al.*, 2001b). In these studies, baetid mayflies and Chironomidae increased in early postfire

years, while elmids, heptageniids and ephemeropterid mayflies, glossosomatid caddisflies and *Isonychia* sp. stoneflies were reduced in postfire communities for up to 10 years.

Patterns of community succession in the burned stream corresponded to patterns observed in other burned streams of the western U.S. Comparable successional sequences have also been noted after other catchment-scale disturbances, including catastrophic flooding, logging, volcanic eruptions and mudslides (see reviews in Niemi *et al.*, 1990; Yount & Niemi, 1990). For example, Baetidae, *Simulium* sp., Orthocladiinae and Hydropsychidae recolonised early, while many stonefly taxa, heptageniids and *Lepidostoma* sp. were slow to recover, after a severe scouring event in a Rocky Mountain stream (Zuellig, Kondratieff & Rhodes, 2002). Primary succession in a newly formed glacier stream in Alaska was also similar to successional sequences observed in our study (Flory & Milner, 2000). These authors found that Orthocladiinae, Baetidae and Simuliidae were early colonists, followed by other dipterans (including empidids) and several limnephilid caddisflies. Many stonefly, caddisfly and mayfly taxa common in nearby, older glacier streams were slower to colonise or were absent.

Mechanisms behind community succession in the burned stream

Interpreting succession in terms of changes in representation of species traits in the community may explain the successional sequence of species. Traits are both ecologically and evolutionarily relevant because they interact with the environment to influence species recovery, and because traits ultimately reflect natural selection by the historical disturbance regime (Poff, 1997). If physicochemical effects of a disturbance act as 'filters' through which only a sub-set of traits may pass, species with these traits should recolonise earlier in the successional series. Specifically, species with traits conveying resistance (i.e. hydrodynamic body shape, small size, attachment to the substratum) and resilience (i.e. strong dispersal, multi-voltinism and generalist resource use) to hydrologic disturbance (Townsend, Doledec & Scarsbrook, 1997b) should have an advantage under postfire flood conditions. Investigating temporal trends in trait representation, and placing

these trends in context of the physical habitat template (*sensu* Southwood, 1977), should provide mechanisms behind community succession after postfire hydrologic disturbances.

The interaction between dispersal ability, feeding mode, postfire environmental conditions and geographic barriers in the Plateau ecosystem explained species succession in our burned stream. Organisms that survived the first 100-year flood after the fire (primarily elmids) probably arrived via catastrophic drift during flooding. The low density of beetle survivors (i.e. one to two individuals per sample), despite their numerical dominance in the prefire community, suggests that few in-stream refugia existed near study reaches. Severe postfire flooding moved even large substratum particles (i.e. boulders, woody debris) along the entire perennial segment of the burned stream and greatly reduced flow refugia at the microhabitat scale (*sensu* Lancaster & Hildrew, 1993). Scouring to the naturally shallow bedrock layer that underlies Plateau streams eliminated hyporheic refugia (*sensu* Palmer, Bely & Berg, 1992) during flash floods. Repeated severe floods in the year of the fire, lack of refugia and weak dispersal ability probably explain why elmids did not rebound to contribute to community succession in postfire years.

Other taxa with weak dispersal ability and specialised feeding requirements (i.e. heptageniid grazers and nemourid shredders) became rare after the fire. Poor dispersal capability, in combination with reduced inputs of organic matter and continual scouring of algae, were probably responsible for reduced shredder and grazer densities in the postfire community. These specialist feeders did not establish stable populations until riparian vegetation was re-established and flood magnitudes, substratum instability and suspended sediment loads were reduced. By contrast, generalist feeders (collectors) with strong larval dispersal (baetids, chironomids and simuliids) recolonised in postfire years despite moderate floods. These taxa dominated ephemeral upper reaches in the burned stream and probably recolonised via larval drift, as observed in other montane desert streams following flash floods (Molles, 1985). However, most taxa that recolonised in later postfire years were not found in headwater communities (Vieira, 2003), suggesting that they dispersed aerially from streams nearby. Recolonisation by aerial adults is often the primary mechanism for

community recovery after scouring flash floods in desert streams (Gray & Fisher, 1981; Fisher *et al.*, 1982). We were not surprised that taxa with strong adult flight (e.g. odonates and *Hesperophylax* sp.) contributed to succession in our burned stream, as the extreme topography of the Plateau (i.e. wide and arid mesas, deep canyons, no tributaries) presents numerous colonisation barriers. Aerial colonists that were specialist feeders were able to persist once the hydrologic regime and streambed habitat had stabilised, and detritus and algal food sources were no longer being flushed or scoured.

While we focused on traits describing dispersal and resource use, other traits such as voltinism, life history schedules, body size and the ability to leave the stream may have influenced community succession in our burned stream (Vieira, 2003). Insect populations in flashy, monsoon-driven desert (Lytle, 2002) and sub-tropical (Brewin, Buckton & Ormerod, 2000) streams typically have adaptations (i.e. development time, emergence schedules) allowing them to escape monsoon floods and recolonise rapidly. From the perspective of insect communities in Pajarito streams, flash floods are predictable, seasonal events in the historical disturbance regime (although typically at much lower magnitudes than postfire floods). Thus, insect species common to these streams are probably those that are adapted to a flashy flow regime. Even so, 100-year floods and a threefold increase in flood frequency in the burned stream (Veenhuis, 2002) probably lessened the benefit of such adaptations, requiring dispersal from outside the burned catchment. Our study adds to a growing body of literature (e.g. Charvet *et al.*, 2000; Gayraud *et al.*, 2003) demonstrating how monitoring changes in *relevant* species traits, and linking these changes with environmental drivers, can enhance our understanding of community recovery after disturbance.

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